GENETIC STUDIES OF QUANTITATIVE AND QUALITY TRAITS IN RICE UNDER LOW AND HIGH SOIL NITROGEN AND PHOSPHOROUS CONDITIONS, AND A SURVEY OF FARMER PREFERENCES FOR VARIETIES

BY

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A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy (PhD) in Plant Breeding

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December 2010

Thesis Abstract

Rice is an important crop ranking third after maize and wheat in Kenya. Its demand is growing at 12% per annum, while production has stagnated for quite a number of years. This situation has lead to consumption outstripping production by about 84%. There is therefore an urgent need to step up domestic production.

To understand farmers' preferences, the first survey on rice production was carried out. To supplement on this survey information, focus group discussions and key informants were incorporated to further shed more information. The farmers demonstrated their preferences for varieties that were high yielding, hybrid rice and with high nutrient use efficiency and these constituted 53.7% of their wishes. Among the crops grown by the selected farmers, rice was the most important followed by maize, however, the hectarage of maize was higher followed by rice. The farmers also identified labour costs as a factor limiting production especially for irrigated rice and thus they preferred upland rice due to its ease of production. Farmers identified land preparation, inputs, planting, weeding and harvesting as the most expensive activities. The existing varieties were viewed as being highly dependent on inputs which they could not afford. The main fertilizers used were Diammonium Phosphate (DAP), Sulphate of Ammonia (SA), Calcium Ammonium Nitrate (CAN) and NPK (23:23:0), the amounts used were low even though the farmers were aware that soil fertility was low.

No studies or attempts had been carried out to determine performance of rice genotypes and their heritability parameters for adaptation to low soil nitrogen (N) and phosphorous (P) conditions identified by the farmers as a major constraint in Kenya. Since the existing genetic base was narrow, accessions were acquired to broaden the variability of the local cultivars. However, their adaptation to local conditions was important for them to be useful. Evaluation of 390 accessions showed that genotypes and soil environments were highly significant for all the ten traits studied. The degree of genetic determination (H^2) ranged from 8.0% for 1000 grain weight to 27% for top biomass. The phenotypic coefficient of variation of genotypes ranged from 12% for days to maturity to 149% for top biomass, while, that of days to maturity ranged from 14% to 160% for top biomass. The genetic advance (GA) had values ranging from, 0.2 for phosphorous tolerance to 1081 for grain yield, while the genetic advance expressed as percent of the mean was 6% for days to maturity and 88% for top biomass. The mean values for the ten characters studied had wide variability under the four soil environments with days to maturity ranging from 188 for genotype ARCCU1Fa1-L4P3-HB under both N and P application (N+P+) to 177 for genotype CT16333(1)-CA-1-M under none N and P application (N-P-) condition. The highest yielding genotype was CT16328-CA-18-M under none N and P application with 5916 kg ha^{-1}. The germplasm revealed usable variability under low soil N and P adaptation and thus warrant rice improvement for traits of interest to farmers.

In order to establish the genetic factors controlling upland rice adaptation to contrasting soil N and P a study was conducted to determine genotypes with better performance under the prevailing farmers' production environments. The GCA and SCA mean squares were significant and their interactions with environment were highly significant. The GCA:SCA ratios were mostly less than 1.0 for the majority of the traits under most of the soil N and P environments, indicating preponderance of nonadditive genetic effects. The maternal and nonmaternal mean squares were significantly different from zero ($P<0.05$) for most of the ten traits under study, indicating influence of cytoplasm effects

and cytoplasm by nuclear gene interactions, respectively. The GCA effects for the parents were significant under different experimental environments but they had both positive and negative signs indicating different directions of influencing the trait of interest. The genotypes had both specific and broad adaptation as exhibited by their diverse rankings under different environments.

The relationship between leaf and grain nitrogen (N) and phosphorous (P) with actual tolerance to low and high soil N and P conditions indicated significant genotypes, environments and genotypes by environment interactions. The analysis of genetic components gave highly significant GCA and SCA mean squares for the days to heading, anthesis and maturity, phosphorous and nitrogen tolerance, top biomass, plant height, number of panicles, 1000 seed weight and grain yield under the four soil experimental environments. The general combining ability (GCA) effects for parents were significant for both F_2 and F_3 segregants for the above ten traits and under the experimental conditions. The leaf and seed N and P contents gave significant genotype mean squares values for the three mega-environments. The GCA and SCA mean squares were significant for leaf and seed N and P for the three locations. The same case was observed for GCA effects for the parents, with all the nine parents showing significant values for leaf N and P for the three locations. The GCA:SCA mean square ratios were generally larger than 1.0 values for leaf N and grain P for the three locations. This clearly manifested the predominant role of additive gene action over the dominance effects and that improvement for tolerance to low soil N and P condition was practical.

The fragrance in rice is an important quality traits and an experiment was conducted to establish the association of organoleptic test and the variations in SSR marker (RM223) among the parents. Plant leaves of the parental genotypes were sampled for DNA analysis using SSR markers RM223 and RM284. The RM223 was polymorphic while, RM284 gave monomorphic results. Four alleles were detected as follows: 146, 155, 161, and 163. The GCA:SCA ratio was 1.48 indicating that the fixable additive effects were greater than the nonadditive effects in inheritance of fragrance. Test for independence using Chi-square indicated that there was no association between organoleptic and variations in SSR markers. The performance of the aromatic lines was generally lower than that of non-aromatic lines for the agronomic traits. There was negative relationship between fragrant score and other agronomic traits such as grain yield across the three soil N and P regimes. The NERICA1 was found to be a good donor for aroma based on sensory testing and can be exploited in a breeding programme.

Analysis on genetic components governing grain yield was investigated using Hayman's analysis to generate various components of variation and to elucidate their potential, utilization, and provide a thorough understanding of their role in grain yield development and improvement. The additive gene action was significant for all cases of soil N and P environments and the two mega-environments. They were also far above the dominant gene effects, indicating the need to use mass selection in the early generations of segregating populations. The narrow sense heritability (h^2_{ns}) for upland rice grain yield was 21.52% and 4.22% under soil P and N conditions, respectively.

Declaration

I, **Kimani John Munji**, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
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Signed……...……Date……..

Kimani John Munji

As the candidate's advisers, we agree to the submission of this thesis:

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Prof. Pangirayi Tongoona (Principal adviser)

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Dr. John Derera (Deputy-Adviser)

Signed……...……Date……..

Dr. Jedidah Danson (Deputy-Adviser)

Acknowledgements

Glory to God for with him, nothing is impossible! Special tribute to the Rockefeller Foundation, Bill & Melinda Gates Foundation (Alliance for a Green Revolution in Africa (AGRA) for sponsorship. I recognize Kenya Agricultural Research Institute (KARI) for granting me the study leave.

I will forever cherish and beholden to Prof. Pangirayi Tongoona, Dr. John Derera, Dr. Jedida Danson, Dr. Githiri Mwangi and Dr. Aggrey Nyende for whom a seed was sown, germinated, endured, flowered and set seeds. With joy, I heartily salute you all for building a solid and firm academic foundation in me. Your valuable advice, encouragement, positive critique was in no way a mean task, it greatly shaped my academic destiny.

Am greatly indebted to the entire African Centre for Crop Improvement (ACCI) and the University of KwaZulu-Natal, for making my life an easy stay and provision of a wonderful environment for my study. The able and visionary leadership of Prof. Mark Laing is profoundly appreciated for it was all system go. To Lesley, Felicity, Lindiwe, Amanda, Lourens Erasmus and all others, cheers for working tirelessly and timely to ensure the road was superb and marvellous.

I am grateful to KARI-Mwea Tebere Centre Director, Dr. Waweru Gitonga for his handy support that made my research possible. Am thankful to colleagues for they made sure I never looked back. I thank Kaboro, Micere, Michael, Wambui, Mwaura, Beatrice and all others for overseeing the natty gratis of the research trials. Am grateful to KARI Matuga (Mr Pole –CD and Mr Maingu), KARI Alupe (Mr Kisuya –OiC and Mr Mafura) and LBDA Alupe (Mr Rotich and Mr Egesa) for research plant care.
I sincerely thank CIAT Colombia (Dr. Martinez), Africa Rice Centre (Dr. Somado), Mali rice programme (Dr. Cisse) and IRRI (Dr. K. R. Singh and Dr. Arvind) for the lines used. I salute the 2006 Cohort; Rogerio Chiulele, Pascal Okwiri, Frank Kagoda, Sophia Killenga, Arnold Mushongi, Albert Chamango, Hilario Magaia; to you all guys, a 'hearty hello' for making my life easy at Pietermaritzburg. I thank International Foundation of Science for the grant that supported part of this thesis work.

This thesis could have been impossible, were it not for my dear and lovely wife, Lucy Wairimu Munji, sons; Collins, Lincoln and young one, Emmanuel. They inspired my life with joy and rekindled the flames of zeal to endure and keep going till the end. I cannot forget my parents, brothers and sisters, relatives and all other dear people who in one way or another acted in a manner that helped me achieve the dream of my life. To all, may almighty God shower his blessings upon you all.

Dedication

This thesis is special dedication to my dear parents; Peter Kimani Munji and Mary Njeri Kimani, who brought me into being, worked tirelessly to get me educated and give back to the human kind.

Table of Contents

Thesis abstract ii
Declaration iv
Acknowledgements vi
Dedication vii
Table of Contents viii
List of Tables xiii
List of Figures xv
List of Plates xvii
List of Appendices xviii
0.0 Introduction to Thesis 1
0.10 General rice production 1
0.11 Rice production in Kenya 1
0.12 Problem statement 5
0.13 Research justification 5
0.14 Overall goal and objectives 6
0.14.1 The research specific objectives were to: 6
0.15 Research hypotheses tested were: 7
0.16 Thesis structure 7
References 8
CHAPTER ONE 10
Literature Review 10
1.1 Introduction 10
1.2 The genus Oryza 10
1.3 General nitrogen dynamics in relation to rice 11
1.3.1 Function and mobility of nitrogen 11
1.3.2 Nitrogen deficiency symptoms 11
1.3.3 General method of nitrogen management 12
1.4 Rice breeding for low soil nitrogen (N) 12
1.4.1 Definitions of nutrient-use efficiency terminologies and their application 13
1.4.2 Classification of genotypes in relation to N-use efficiency 14
1.4.3 Mechanisms for genotypic differences in nutrient use efficiency 15
1.4.4 Rice yield potential 17
1.4.5 Breeding opportunities for low soil nitrogen environments 17
1.4.6 Utilization of remobilized internal N for breeding high yielding rice 21
1.5 Breeding rice for low soil phosphorus condition 21
1.5.1 Function and mobility of phosphorous (P) 22
1.5.2 P deficiency symptoms and effects on rice crop 22
1.5.3 Adaptation to low and high soil fertility nutrient resource conditions 24
1.6 Breeding for high quality grains 25
1.7 Farmers perceptions and preferences in rice varieties 30
1.8 Summary 32
References 33
CHAPTER TWO. 42
Farmers Participation in Identification of Upland Rice Variety Preferences, Production Constraints, Socio-Economic Information 42

Abstract.. 42
2.1 Introduction 43
2.2 Study objective 45
2.3 Materials and Methods 46
2.3.1 Trial layout 47
2.3.2 Data collection and analysis 49
2.4 Results 50
2.4.1 Parents selected and preferred traits 50
2.4.2 Participating farmers' distribution per village 51
2.4.3 Farmers preferred traits 51
2.4.4 Crops grown by the farmers and hectarage per village 52
2.4.5 Rice hectarage and number of participating farmers 54
2.4.6 Fertilizer usage and other farm inputs for production 55
2.4.7 Number of farmers and hectarage used for other crop apart from rice production 56
2.4.8 Respondents perceived farming challenges 57
2.4.9 Rice productivity 59
2.5 Discussion 60
2.5.1 Preferred variety traits by the farmers 60
2.5.2 Diversity of crops grown by the farmers 62
2.5.3 Perception of farmers on rice varieties 62
2.5.4 Farmers participation in breeding 64
2.6 Conclusion and Recommendation 65
References 65
CHAPTER THREE. 68
Characterization and Selection of Upland Rice Germplasm under Low and High Soil Phosphorous (P) and Nitrogen (N) Environments 68
Abstract. 68
3.1 Introduction 68
3.2 Study objectives 70
3.2.1 Hypothesis 70
3.3 Materials and Methods 71
3.3.1 Study location 71
3.3.2 Germplasm, experiment layout and trial management 71
3.3.3 Data collection 72
3.3.4 Data analysis 73
3.4 Results 74
3.4.1 Genetic components 74
3.4.2 Genotypic performance under the four experimental environments 75
3.4.3 Scatter plots and histograms for days to maturity and yield. 81
3.4.4 The distribution of the 390 rice lines for days to maturity under different soil N and P conditions 83
3.4.5 The distribution of the 390 rice genotypes for grain yield under different soil N and P conditions 85
3.4.6 The scattering of the 390 rice genotypes for grain yield against days to maturity under different soil N and P conditions 88

3.4.7 The scattering of the 25 best rice genotypes for grain yield against different soil N and P conditions 90
3.4.8 The correlation of grain yield against different soil N and P conditions 92
3.5 Discussion 94
3.5.1 The days to heading, anthesis and maturity 94
3.5.2 The plant height and above ground biomass production 96
3.5.3 The tolerance of genotypes under different soil P and N condition 97
3.5.4 Yield under varying soil N and P conditions 98
References 101
CHAPTER FOUR. 110
Combining Ability and Performance of Rice Genotypes Under Four Different Soil Fertility Environments 110
Abstract. 110
4.1 Introduction 111
4.1.1 Study objectives 113
4.1.2 Study hypothesis 113
4.2 Materials and Methods 113
4.2.1 Germplasm assemblage and parents selection 113
4.2.2 Diallel mating 114
4.2.3 Environmental locations for evaluation of the F_2 plants 115
4.2.4 The experimental design and management 116
4.2.5 Data analysis 118
4.3 Results 118
4.3.1 Genotype x environment interaction 118
4.3.2 The genetic component effects for the ten traits under different soil N and P experimental environments 119
4.3.3 General combining ability effects for the parents under the four soils N and P experimental environments 121
4.4 Discussion 128
4.4.1 The genetic effects, their interactions and its significance. 128
4.4.2 The genotypic and environment interactions and their significance 129
4.5 Conclusion 132
References 133
CHAPTER FIVE. 139
Genetic mechanisms controlling Soil Phosphorous and Nitrogen Tolerance Determined by Leaf and Seed Content in the F_2 and F_3 Rice Populations 139
Abstract. 139
5.1. Phosphorous (P) and nitrogen (N) concentration in rice leaves and grains 140
5.1.1 The objectives 141
5.1.2 The study hypothesis 142
5.2 Materials and Methods 142
5.2.1 Evaluation of F_2 and F_3 populations at three locations, KARI-Mwea, KARI-Matuga and LBDA Alupe 142
5.2.2 Data collection 143
5.3 Data analysis 144
5.4 Results 145

5.4.1 Gene action of the F_2s materials under contrasting soil N and P conditions 145
5.4.2 General combining ability effects for the nine rice parents. 149
5.4.3 The F_2 population means for the best ten rice lines for five traits under four soil N and P conditions 149
5.4.4 Leaf and seed tissue phosphorous and nitrogen genetic analysis for rice F_3 populations. 150
5.4.5 Mean squares of genetic components for the F_3 rice populations under the four soil N and P conditions 151
5.4.6 The mean values for five traits for the ten best F_3 rice populations under four soil N and P conditions 156
5.4.7 The physiological factors for low soil P and N tolerance for parents and F_3 generations 157
5.5 Discussion 160
5.5.1 Gene action for the F_2 and F_3 populations for the traits under four soil N and P environments 160
5.5.2 The general combining ability (GCA) for the ten traits for F_2 and F_3 populations under different soil N and P conditions 162
5.5.3. Mean values of ten traits for parents, F_2 and F_3 rice populations under different soil N and P conditions 162
5.5.4 F_2 genetics of leaves and seed nitrogen and phosphorous control 163
5.5.5 The physiological indices used for nutrient use efficiency for the ten traits 165
5.6 Conclusion 167
References 167
CHAPTER SIX. 171
Association of Phenotypic traits and Variations in SSR Markers for Fragrance and Metric Traits under different soil fertility regimes 171
Abstract. 171
6.1 Introduction 171
6.1.1 Study objectives 174
6.1.2 Study hypothesis: 174
6.2 Materials and Methods 174
6.2.1 Plant materials 174
6.2.2 Sensory fragrance evaluation 175
6.2.3 Leaf samples 175
6.2.4 Seed samples 176
6.2.5 DNA extraction 176
6.2.6. PCR - DNA markers analysis for fragrance rice gene 176
6.2.7 Phenotypic data collection 177
6.2.8 Analysis of data 177
6.3 Results 177
6.3.1 Association of variation in SSR marker (RM223) with fragrance 177
6.3.2 Gene action for fragrance 178
6.3.3 The mean performance values for the eight rice traits at KARI-Mwea 179
6.4 Discussion 184
6.4.1 Association of variation in SSR marker to fragrance 184
6.4.2 Fragrance genetics and phenotypic traits 185

6.4.3 Conclusion 186
References 187
CHAPTER SEVEN. 190
Genetic Analyses of Rice Grain Yield under Low Soil Phosphorous (P) and Nitrogen (N) Conditions for Two Mega-Environments 190
Abstract. 190
7.1 Introduction 190
7.1.1 Study objectives and hypothesis 191
7.2 Materials and Methods 192
7.2.1 F_2 populations evaluations under two contrasting phosphorous (P) and nitrogen (N) experimental environments at Mwea and Aupe 192
7.2.2 Evaluation experiment at KARI-Mwea and LBDA-Alupe 193
7.2.3 Data analysis 193
7.3 Results 195
7.3.1 The components of variation estimation 196
7.3.2 The variances and covariances estimates 196
7.3.3 The Covariance - Variance (W_r-V_r) graphs 198
7.3.4 The components of variation estimation. 201
7.3.5 Estimation of important genetic parameters 202
7.4 Discussion 203
7.4.1 The Covariance - Variance (W_r-V_r) graphs 204
7.5 Conclusion 205
References 206
CHAPTER EIGHT. 209
Thesis Overview 209
8.1 Introduction 209
8.2 Summary and implications 209
References 214

List of Tables

Table 0.1 Kenya Rice Production Statistics (Metric tonnes) 2001-2009 1
Table 1.1 Summary of soil and plant mechanisms plus other activities that influence genotypic variability in nutrient-use efficiency 16
Table 2.1 Rice lines selected by farmers as parents for the hybridization block 50
Table 2.2 Number of farmers per village 51
Table 2.3 Traits farmers wished to be improved in rice varieties they produce 52
Table 2.4 Types of crops grown and area of production (hectares) for surveyed farmers 53
Table 2.5 Farmers perceived production constraints and their rankings 58
Table 2.6 Farmers coping strategies for the perceived rice production constraints 59
Table 3.1 Soil properties at KARI Mwea-Tebere location, plus N and P ranges 72
Table 3.2 Mean squares and genetic parameters for ten rice traits across the four soil experimental environments 75
Table 3.3 The mean values of days to heading (DH), anthesis (DA), maturity (DM) and number of panicles for rice under four soil N and P conditions (highlighted were selected as parents) 76
Table 3.4 The mean values for P and N tolerance on 1000 seed wt and grain yield for the best and lowest ten rice lines under four soil N and P conditions 78
Table 3.5 Mean values of plant height and top biomass for ten best and worst rice lines under low and high soil N and P conditions 80
Table 3.6 Correlation of rice yield with four levels of soil nitrogen and phosphorous fertility tolerance levels 93
Table 4.1 Rice parents used in the diallel and their characteristics 113
Table 4.2 Soil analysis results for the Mwea, Alupe and Matuga regions 116
Table 4.3 Mean squares components for rice days to heading, anthesis, maturity; N and P tolerance and top biomass under four soil conditions 120
Table 4.4 The genetic mean square parameters for rice number of panicles, plant height, 1000 seed wt and grain yield under four soil conditions 122
Table 4.5 The GCA effects of rice parents for days to heading, anthesis, maturity; N and P tolerance, plant height, top biomass, number of panicles, 1000 seed wt and grain yield under four soil conditions 124
Table 4.6 Means of the best 15 F_2 segregants for days to heading, maturity; N and P tolerance, under four soil conditions (red are parents) 126
Table 4.7 Mean of the best 15 F_2 segregants for top biomass, 1000 seed wt and grain yield under four soil conditions (red are the parents) 127
Table 5.1 Source of variation and mean squares on 10 rice traits studied under four soil N and P conditions 146
Table 5.2 Source of variation and mean squares for genetic components of F_2 ten rice traits under four soil N and P conditions 147
Table 5.3 Mean squares of general combining ability effects for the nine rice parents under four soil N and P conditions 148
Table 5.4 The mean values for the best top ten F_2 rice lines under four soil N and P conditions 150
Table 5.5 Mean squares of genetic components for rice leaf and grain N and P for Mwea, Alupe and Matuga locations 152
Table 5.6 Mean squares for genetic components of ten rice traits under four soil N and P conditions 153

Table 5.7 Mean squares for genetic components of the F_3 rice populations 10 traits under four soil N and P conditions 154
Table 5.8 General combining ability effects for nine rice parents for ten traits under four soil N and P conditions 155
Table 5.9 Mean values for the ten best rice genotypes for five traits under four soil N and P conditions 156
Table 5.10 Physiological efficiency indices for the 72 rice F_3 and parents across two mega-environments 158
Table 6.1 Rice parents used in the diallel and their characteristics 175
Table 6.2 The crosses, marker, alleles and rice fragrance scores for the parents at KARI-Mwea 178
Table 6.3 Mean square values, rice parental GCA, SCA, Reciprocals, maternal and nonmaternal effects of the parents and F_2 rice lines 179
Table 6.4 The means of the rice parent lines for eight traits under the three soil N and P experimental environments 180
Table 6.5 The means for the phosphorous and nitrogen tolerance, plant height, top biomass, number of panicles, days to maturity, 1000 seed weight and grain yield for the F_2 rice populations under the three experimental environments 182
Table 7.1 The nine rice parents used in the diallel and their characteristics 192
Table 7.2 The mean square values of rice yield for components a, b_1, b_2, b_3, b, c and d for P and N effects at Alupe and Mwea. 195
Table 7.3 The analysis of variance of rice yield under P and N effects at Alupe and Mwea mega-environments 196
Table 7.4 The variances, covariance, mean array and rice parents for P condition at Alupe. 197
Table 7.5 The variances, covariance, mean array and rice parents for N condition at Alupe. 197
Table 7.6 The variances, covariance, mean array and rice parents for P condition at Mwea. 197
Table 7.7 The variances, covariance, mean array and rice parents for N condition at Mwea. 198
Table 7.8 The components *E, D, F, H_1, H_2, h^2 and their S.E. for rice yield under P and N conditions at Alupe and Mwea 202
Table 7.9 Important genetic parameters estimated for rice yield under P and N condition at Alupe and Mwea mega-environments 203

List of Figures

Figure 2.1 The number of respondents involved in rice production per village 53
Figure 2.2 The number of respondents involved in rice production 54
Figure 2.3 The hectarage and number of farmers involved in rice production village^{-1} 54
Figure 2.4 Respondents fertilizer use per village 55
Figure 2.5 The hectarage and number of farmers involved in non- rice crop production per village 57
Figure 2.6 The perception of farmers on agricultural land trend under crop production per village 57
Figure 2.7 The number of respondents and rice production figures per village 60
Figure 3.1 A leaf colour chart used to evaluate genotypes for nitrogen tolerance 72
Figure 3.2 Yield against days to maturity of the best rice genotypes under soil N-P- conditions. 81
Figure 3.3 Yield against days to maturity of the best rice genotypes under Soil N-P+ conditions. 82
Figure 3.4 Yield against days to maturity of the best rice genotypes under soil N+P- conditions. 82
Figure 3.5 Analysis of yield and days to maturity of the best rice genotypes under soil N+P+ conditions. 83
Figure 3.6 Histogram showing the distribution of the 390 rice lines according to maturity under soil N-P- condition. 84
Figure 3.7 Histogram showing the distribution of the 390 rice lines according to maturity under soil N-P+ condition. 84
Figure 3.8 Histogram showing the distribution of the 390 rice lines according to maturity under soil N+P- condition. 85
Figure 3.9 Histogram showing the distribution of the 390 rice lines according to maturity under soil N+P+ condition. 85
Figure 3.10 Histogram showing the distribution of the 390 rice lines for grain yield under soil N-P- conditions 86
Figure 3.11 Histogram showing the distribution of the 390 rice lines for grain yield under soil N-P+ conditions 86
Figure 3.12 Histogram showing the distribution of the 390 rice lines for grain yield under soil N+P- conditions 87
Figure 3.13 Histogram showing the distribution of the 390 rice lines for grain yield under soil N+P+ conditions 87
Figure 3.14 Scatter plot for rice yield versus days to maturity under N-P- 88
Figure 3.15 Scatter plot for rice yield versus days to maturity under N-P+ 89
Figure 3.16 Scatter plot for rice yield versus days to maturity under N+P- 89
Figure 3.17 Scatter plot for rice yield versus days to maturity under N+P+ 90
Figure 3.18 Head to head plot of the best 25 rice lines for yield versus soil N and P condition. 90
Figure 3.19 Head to head plot of the best 25 rice lines for yield versus soil N and P condition. 91

Figure 3.20 Head to head plot of the best 25 rice lines for yield versus soil N and P condition. 91
Figure 3.21 Head to head plot of the best 25 rice lines for yield versus soil N and P condition. 92
Figure 7.1 The $W_{r's}$ and V_r parabola and regression lines for rice grain yield under soil P condition at Mwea 199
Figure 7.2 The $W_{r's}$ and V_r parabola and regression lines for rice yield under soil N condition at Mwea 200
Figure 7.3 The $W_{r's}$ and V_r parabola and regression lines for rice yield under soil P condition at Alupe.....200
Figure 7.4 The $W_{r's}$ and V_r parabola and regression lines for rice yield under soil N condition at Alupe.....201

List of Plates

Plate 2.1 Farmers go through the 45 lines they selected earlier for further planting.....48
Plate 2.2 PPB farmers planting the 45 lines they selected.....48
Plate 2.3 PPB farmers observe the 45 lines they selected for hybridization.....48
Plate 2.4 PPB farmers discuss and select the best lines for hybridization block 48
Plate 2.5 Some of PPB Farmers engages the PI in discussion.....49
Plate 2.6 PPB farmer is impressed by the panicle 49
Plate 2.7 PPB farmers group discussion and training using visual aid message.....49
Plate 2.8 Discussion with some of the PPB farmers at the trial site 49
Plate 4.1 Crossing block with 2nd parent set 138
Plate 4.2 Emasculation for hybridization being effected.....138
Plate 4.3 A cross covered by straw and a tag.....138
Plate 4.4 A fertile cross between Dourado and NERICA1.....138

List of Appendices

Appendix 3.1 The 390 lines from WARDA and CIAT-Colombia evaluated for adaptability 107
Appendix 4.1 The pictorials of procedures used for pollinations 138

0.0 Introduction to Thesis

0.10 General rice production

Rice *(Oryza sativa* L.) is the world's most important staple food crop. More than three billion people in Asia, Africa and Latin America depend on rice (Ali et al., 2006). It supplies one third of the world's population with more than half their calories and nearly half their protein. In 2004 world rice production was 610 million metric tonnes (Mt) compared to 590 million Mt for wheat (IRRI, 2006).

Although Africa produces only 9% of the world total rice, it is nonetheless an important staple within individual countries (FAOSTAT, 2008). The three major rough (paddy) rice producers are Egypt (6 million Mt), Nigeria (5 million Mt) and Madagascar (2.8 million Mt) (FAO, 2005). According to Monem (2005), in East Africa, Tanzania (647,000 Mt) is the highest producer followed by Uganda (120,000 Mt) (FAO, 2005) and Kenya (35,775 Mt). However in Kenya and many other countries in Sub-Saharan Africa the demand exceeds supply.

0.11 Rice production in Kenya

In Kenya, rice is an important staple food crop after maize. Rice forms part of the larger diet for both urban and rural populations. It is a source of employment and income for the small-scale farmers and business people. The production and consumption figures for five years are as tabulated below.

Table 0.1 Kenya Rice Production Statistics (Metric tonnes) 2001-2009

	Years								
Crop	2001	2002	2003	2004	2005	2006	2007	2008	2009
Maize production	2,790,000	2,408,600	2,710,850	2,607,139	2,905,559	3,247,200	2,928,793	2,367,237	2,439,000
Ricecropped area	13,200	13,000	10,781	13,223	15,940	23,106	16,457	16,734	21,829
Rice production	45,000	45,000	40,502	49,295	62,677	64,840	47,256	63,248	37,198
Rice consumption	173,925	225,754	234,000	237,000	250,000	286,000	293,722	-	-

Source: FAOSTAT database and MoA (FAOSTAT, 2010; Rosemary *et al.*, 2010)

From Table 0.1, although rice production figures are low compared to maize, it is nonetheless an important staple crop. Rice production fluctuates from year to year but

the general trend is an overall slow increase from 2001 to 2009. While total production range within nine years was 64,840 to 37,198 Mt, the national consumption increased from 173,925 Mt to 293,722 Mt. In other words, while the total production decreased by 42.63%, consumption increased by 68.88%. Production for 2007 was 47,256 Mt against a consumption figure of 293,722 Mt (Rosemary *et al.*, 2010). The 83.91% rice deficit is made up by imports mainly from Pakistan, China, India and Vietnam (MoA, 2009; Monem, 2005).

Rice consumption in Kenya is continually increasing, exacerbating the need to import rice and the need to step up local production. Rice has a highly elastic demand due to urbanization and rising incomes coupled with changes in eating habits. It is also gaining popularity due to its easiness and flexibility during preparation of various recipes, it uses less fuel for cooking (FAO, 2006), especially for labour constrained households. Rice production needs to be increased by another 70% over the next 30 years in order to meet the growing food demand (GoK, 2002; MoA, 2009).

There are a number of reasons for inadequate growth of rice production in Kenya. These can be summed up as the inability of the irrigated rice systems to meet consumption demands, as the varieties grown are low yielding, susceptible to pests and diseases; and the limited production of rainfed rice which renders it unable to compensate for the deficiencies of the irrigated rice. A complex set of problems lies behind the limited production of irrigated rice, while upland rice production is marginally practiced despite its enormous potential in increasing national production figures.

Rice production is categorized into three classes depending on the source of water supply for the crop. Irrigated rice is currently the most important type of rice in Kenya. It is mainly produced under irrigation schemes managed by the Kenyan National Irrigation Board (NIB). About 40,000 hectares are under irrigation with an average national production of 4.5 tons ha^{-1} for the aromatic variety and 6 tons ha^{-1} for the non-aromatic varieties (FAO, 2006; NIB, 2008). The other two types, rainfed lowland rice and rainfed upland rice currently play a much less important role. There are 13,000 ha under rainfed rice production at Kwale, Kilifi, Tana River districts in the Coast Province, Bunyala and Teso districts in Western Kenya. The average yield for rainfed rice is below 2 tons ha^{-1} (GoK, 2003; Rosemary *et al.*, 2010).

Despite the importance of irrigated rice and its comparatively high yield, its production is limited by inadequate use of potential land and limited irrigation water. The potential for irrigated agriculture in Kenya is estimated to be 500,000 hectares or more but, only 40,000 hectares are actually under irrigation (NIB, 2008; Rudo and Jan, 1990). Kenya has the greatest potential for irrigation in the Lake Victoria basin but, the use of the basin is currently restricted by the Nile Treaty, signed in the 1920s between the British and Egyptian Governments. Under this treaty, this area cannot be engaged in any major irrigation activity. However, if properly utilized, the Lake Victoria basin has the potential to feed the East and Central African regions (Rudo and Jan, 1990).

The Kenya National Irrigation Board (NIB) was established in 1955 with the objectives of making Kenya self sufficient in rice production, cotton, sugarcane and provision of labour to the local communities around the schemes. The Board has seven large schemes, amounting to 10,000 hectares of irrigated land, in different parts of the country. Under these schemes rice, cotton, horticultural crops, and maize are mainly grown. Individual farmers were allocated plots of about 1.6 ha to cultivate scheduled crops only in the schemes. The schemes are centrally managed and the produce was centrally purchased. Tenants had thus limited freedom in organizing their production and were largely dependent on decisions and practices ordained by management. Tenants in these schemes were faced with opposing challenges, the need to commercialize and the need to produce collectively under parastatal management.

The NIB has over the years suffered various problems and setbacks, it has not therefore, managed to achieve its initial objectives. By 1985, only one scheme had managed to pay its way, whereas the others continued to receive government subsidies (Rudo and Jan, 1990). Production in these schemes has remained below projected levels. This is mainly due to technical problems such as expensive maintenance of infrastructure, lack of improved crop varieties, declining soil fertility while pests and diseases have further lowered the yields. Currently, except the Mwea irrigation scheme, all the other schemes are almost not operational as it is expensive to run them (Dave, 2009). This in effect has lead to reduced rice production causing serious rice deficit. The government's attempt to revive these schemes has been confronted by the problem of reduced water availability. This is due to various competing needs for water such as water for domestic and livestock production. The revival of these schemes is expensive

and population growth has put a lot of pressure on the available land (Oywa, 2006; Reporter, 2008). Although there is a glaring rice deficit to be made up, the above factors make it seem likely that this deficit will not be made up by the production of irrigated rice alone. Currently the area under irrigation has low capacity for expansion because of limitation of both land and available water for irrigation. Therefore, future increases in rice production will rely heavily on rainfed production. There is need therefore, to shift focus from irrigated rice to improving and expanding the production of relatively new rainfed rice.

The farmers' perception and preferences on upland rice production need to be established and documented. There is no study that has been conducted and information on farmers' constraints in terms of varieties and their traits and other socio-economic issues is scanty. It is well established elsewhere, that involvement of farmers' in varieties development lead to better adoption with consequent rise in productivity and their wellbeing in terms of socio-economic status (Walker, 2008; World Bank Group, 2007).

However, rainfed rice production also faces constraints that would have to be overcome to increase production and close the national production deficit. At present, only about 5% of potential upland rice area is under rainfed production. There is about 13,000 ha under production while the potential to produce rainfed rice is estimated to be about 1,000,000 ha to cater for the growing demand. Therefore, there is an urgent need to increase upland rice production and hectarage. Farmers should be allowed to grow the crop freely without much control as witnessed in the small tenant's plots in the irrigation schemes. There are numerous other production constraints facing the low input, aerobic rice crop. These include agro-economic constraints such as poor marketing systems, a lack of credit for small scale farmers, decreasing hectarage due to population growth. At the farm level the major constraints are acidic and prevalent infertile soils that are low in nitrogen (N) and phosphorus (P) due to N leaching and P fixation, poor rice crop husbandry practices, and inadequate use of farm inputs especially fertilizers. The major biotic constraints are insect pests such as white stem borers, African rice gall midge, bird damage; termites, rodents and diseases especially rice blast, rice yellow mottled virus, brown spot, sheath blight, leaf blight and weed competition. Other production constraints include drought, unimproved rice cultivars, tight grains, grain shattering, poor grain

quality, late maturity, lack of preferred grain aroma, shape and texture, low grain protein and micronutrients. Other problems are the high cost of rice production and post harvest losses.

0.12 Problem statement

Rice farming in Kenya offers immense potential for food security and incomes for the farmers and people involved in the rice value chain. However, rice production is low and has stagnated for the last couple of years due to constraints in its production and climate change related problems. The constraints are generally; inability of irrigated rice to give high yields due to expensive infrastructure maintenance and management, declining soil fertility, lack of improved and adapted varieties to replace the old cultivars, insect pests especially white stem borers and diseases especially the devastating rice blast , poor agronomic practices, expensive farm inputs, lack of credit facilities and drought. There is huge potential to boost especially upland rice by i) opening new land of the unexploited 1,000,000 ha suitable for rainfed rice (MoA, 2009; Rosemary *et al.*, 2010), ii) development and promotion of new high yielding varieties adapted to prevailing farmers' production environments to replace the cultivars, iii) promotion of better agronomic practices through the agricultural extension services and private partnerships, iv) formulation of sector based policies and provision of subsidies and sustainable provision of quality seeds.

The current varieties are low yielding at around 1 t ha^{-1} and poorly adapted to the prevailing low soil fertility production environments. They lack attributes highly valued by farmers and are prone to pests and diseases. Little research has been carried out and the genetics of low soil fertility adaptation and quality grain especially fragrance has not been investigated in an effort to bred superior varieties for Kenyan farmers.

0.13 Research justification

Currently, genetic improvement of rice for low soil fertility especially nitrogen (N) and phosphorous (P) on aerobic environment has received little attention in Kenya. As a result, very little information exists about rice improvement for higher grain yield and grain quality. This is despite the important role of rice as food security crop in the socio-economic lives of the people and the country as a whole.

In order to establish a sound rice breeding programme for development of varieties suited to the local environment and with the desirable end user traits, it is imperative that the necessary information be generated such as: i) the farmers and consumer preferences, ii) the amount of genetic variability that exists for the targeted traits, iii) the amount of genetic gain expected and heritability for the preferred traits, iv) the genetic control of fragrance and its association with variations in SSR markers. Studies have been conducted elsewhere to understand the genetic mechanisms conditioning low soil fertility tolerance especially P and N, grain yield components, relationship between leaf and grain N and P content to that available in the soil and fragrance (Bradbury, 2009; Fageria and Baligar, 2003; Kibria *et al.*, 2008; Nguyen and Buu, 2008; Wakil *et al.*, 2009; Zeigler and Adam, 2008).

However, there are limited studies in Kenya. Thus its necessary to undertake studies on genetics of the different traits for different environments in order to develop varieties with desirable characteristics and thus boost production. This study will generate information relating to upland rice in terms of genetic diversity, genetics of low soil N and P tolerance, fragrance, leaf and grain N and P dynamics and genetic control of grain yield components for establishment of a vibrant rice breeding programme and consequently high rice productivity to meet the consumption demand. This will bridge the rice deficit currently being experienced, contribute to food security and offer employment to participants in the rice value chain in Kenya.

0.14 Overall goal and objectives

The goal is to increase upland rice productivity by developing superior varieties with enhanced tolerance to low soil N and P and high grain yields of preferred quality.

0.14.1 The research specific objectives were to:

a) establish the production and culinary grain quality constraints by carrying out a survey and a participatory parent selection with farmers for hybridization,
b) evaluate and characterize at least 390 accessions under Kenyan conditions, and select the best early maturing, low soil N and P tolerant lines with good grain qualities and adaptation,
c) study the genetic mechanisms conferring low soil N and P tolerance,

d) determine the leaf and grain N and P content in relation to soil amounts and establish physiological indices for nutrient use efficiency,
e) determine the inheritance of fragrance both phenotypically and variations in SSR markers in parents,
f) establish the genetical components and their magnitudes for grain yield under low soil fertility, especially P and N conditions, and
g) estimate the heritability of grain yield under low soil P, N environments and two mega-environments.

0.15 Research hypotheses tested were:

i) Small-scale farmers identify low soil fertility, inputs, cultivars under use and insect pests and diseases as major rice production constraints.
ii) Wide and heritable genetic variation for low soil P and N tolerance exists in upland rice varieties.
iii) Low soil N and P tolerance is mainly under genetic rather than environmental control.
iv) There is appreciable genetic variability and heritability of grain yield in upland rice varieties under different soil N and P environments.
v) That additive gene action predominates over nonadditive effects and that fragrant genotypes have negative effects on metric traits.
vi) There are genetic variations between leaf and grain N and P contents under different soil N and P environments.

0.16 Thesis structure

The thesis is structured into eight discrete chapters as enumerated below:

Chapter	Title
0.1	Introduction to Thesis
1	Literature Review
2	Farmers Participation in Identification of Upland Rice Variety Preferences, Production Constraints, Socio-Economic Information
3	Adaptation Evaluation, Characterization and Selection of Upland Rice Germplasm under Low and High Soil Phosphorous (P) and Nitrogen (N) Environments

4 Combining Ability and Performance of rice genotypes Under Four Different Soil Fertility Environments

5 Genetic mechanism controlling Low and High Soil Phosphorous and Nitrogen Tolerance in Relation to Leaf and Seed Content in the F_2 and F_3 Rice Populations

6 Performance of fragrant rice genotypes under different soil fertility regimes

7 Genetics Analysis of rice grain yield under Low Soil Phosphorous (P) and Nitrogen (N) conditions for Two Mega-Environments

8 Thesis Overview

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CHAPTER ONE
Literature Review

1.1 Introduction

This chapter reviews the existing information available for meeting the objectives of this research which is to develop rice varieties well adapted to low soil fertility conditions especially nitrogen and phosphorous prevalent in potential upland production regions of Kenya. In the light of this objective, this chapter reviews various topics in the literature in order to provide the theoretical and practical framework for further research. The areas covered are: a) breeding rice for low soil nitrogen (N) and phosphorous (P) and high yields, b) critical genetic review and opportunities for upland rice development, c) breeding for high grain quality especially fragrance, and d) farmers perception and preferences for rice varieties and traits. The review also gives important definitions in the main topic areas. This chapter build up a reference base for the research study for now and in the future.

1.2 The genus Oryza

Rice belongs to the genus *Oryza* and family Poacae tribe oryzeae. It originated in Asia (*Oryza sativa* L.) and West Africa (*Oryza glaberrima* Steud). According to Vaughan et al. (2004) the genus *Oryza* is made up of 23 species, with two species being cultivated (*Oryza sativa* and O. *glaberrima*) while the other 21 are not domesticated. The *O. sativa* has further three subspecies; *indica* Kato, *japonica* Kato and *javanica* (Roschevicz, 1931). The subspecies *japonica* has two strains, namely *tropical* and *temperate* which are commonly sticky rice due to high amylopectin content. *Indica* are found in tropical and sub-tropical reegions, while *Javanica* are mainly grown in Indonesia and *Japonica* are found in temperate regions. In terms of grain characteristics; the *Indica* varieties have long grains. While, *Japonica* have short grains and *Javanica* have broad grains.

The breeding pattern in rice can be easy or complex depending on whether the hybridization is intra- or inter-specific. The crossing within the *O. sativa* has few hybridization incompatibilities likewise, within *O. glaberrima* group. However, any hybridization between *O. sativa* and *O. glaberrima* (Jones et al., 1997; Khush, 2000), and *O. sativa* and *O. officinalis* has to involve embryo rescue (Khush, 2000) in order to have successful crosses.

1.3 General nitrogen dynamics in relation to rice

There exists enormous potential for upland rice production in Kenya. However, various constraints namely low soil fertility especially nitrogen (N) and phosphorous (P), lack of adapted and high yielding varieties with desirable grain qualities, high input costs, high labour costs especially for irrigated paddy rice, drought, insect pests and diseases, poor agronomic practices and lack of simple implements to aid agronomic practices hamper its productivity. The low soil fertility, drought, high input costs and lack of certified seeds have been identified as the major constraints. Nitrogen constitutes one of the primary nutrients for effective rice crop growth and productivity as it is involved in many internal metabolisms (De-Datta and Broadbent, 1990).

1.3.1 Function and mobility of nitrogen

Dobermann and Fairhurst (2000) have observed that nitrogen is an essential constituent of amino acids, nucleic acids, nucleotides, and chlorophyll. It is responsible for rapid growth and increased leaf size, spikelet number per panicle, percentage filled spikelets in each panicle, and grain protein content. It therefore affects all components contributing to yield. They observed leaf N concentration to be closely related to the rate of leaf photosynthesis and crop biomass production; and that when sufficient N is applied to the rice crop, the demand for other macronutrients such as potassium (K) and phosphorous (P) is increased. The major forms of N available for uptake by plants are NO_3-N and NH_4-N, and most of absorbed NH_4-N is incorporated into organic compounds in the roots, whereas NO_3-N is more mobile in the xylem and is stored in the vacuoles of different plant parts (Dar *et al.*, 2006). The NO_3-N is involved in maintaining cation-anion balance and osmo-regulation, and its greatest requirement is during early to mid tillering and panicle initiation stages. Sufficient N supply during ripening is necessary to delay leaf senescence, maintain photosynthesis during grain filling, and increase the protein content in the grain. Nitrogen is one of the mobile nutrients within the plant being translocated from old senescent leaves and stems to younger leaves and grains, and thus deficiency symptoms tend to occur initially in older leaves (Shukla *et al.*, 2004).

1.3.2 Nitrogen deficiency symptoms

According to Dobermann and Fairhurst (2000) nitrogen deficiency is the most commonly detected nutrient deficiency symptom in rice characterized by old leaves and sometimes all leaves turning light green and chlorotic at the tip. Under severe deficiency leaves may die

except for young leaves, which are greener, narrow, short, erect, and lemon-yellowish green. The whole or affected field may appear yellowish, and N deficiency is known to often occur at critical growth stages such as tillering and panicle initiation when the demand for N is high. The overall effect of N deficiency is reduced tillering, small leaves, short plants and reduced grain number. They have indicated that plant tissue and crop based estimates provide the most reliable estimates of the indigenous N supply in intensive rice systems. However, in irrigated rice systems, most of the commonly used soil tests cannot be relied upon to predict soil N supply under field conditions. Therefore reliable general critical levels or ranges cannot be given, and soil organic carbon or total soil N content are not reliable indicators of soil N supply in irrigated rice systems, but are more important in upland rice systems.

1.3.3 General method of nitrogen management

The correction of N deficiency is not difficult because response to N fertilizer is rapid where farmers can afford N fertilizers and the crop is of high value. Once the N is applied response may be evident after five days by greening and improved vegetative growth, but this is highly dependent on the rice variety, soil type, weather conditions, N fertilizer used, amount applied, and time the method of application (Zhi-You *et al.*, 2006).

1.4 Rice breeding for low soil nitrogen (N)

Fageria and Baligar (2003) and Hou *et al.* (2007) reported that nitrogen is the most important nutrient for crop production, and its deficiency occurs in most rice growing regions of the world. They cited the main reasons for nitrogen (N) deficiency as (i) N leaching, volatilization, and denitrification; (ii) Lower rates of N application than rates of N removal in the harvested portion of the crop; (iii) Low N-use efficiency by the crops; (iv) Use of high yielding and N responsive cultivars; and (v) Soil degradation due to continued crop production. Roder *et al.* (1995), George *et al.* (2001) and Kimani (2002) have similarly noted that nitrogen and phosphate deficiencies are the most important nutrient disorders in the upland production environments. Delseny *et al.* (2001) as a result have estimated the resultant yield loss due to nutrient stress to be 2000 kg ha^{-1}. They argued that this loss can be mitigated by use of well adapted genotypes to various soil N conditions in order to increase farm yields. This can be done by exploiting genotypes that have traits for low soil N adaptation.

1.4.1 Definitions of nutrient-use efficiency terminologies and their application

Nutrient efficiency has been widely used as a measure of the capacity of a plant to acquire and utilize nutrient for biological and grain yield. Nitrogen-use efficiency (NUE) has been defined as the amount of biomass produced per unit of N applied. Fageria and Baligar (2003) and Singh *et al*. (1998) have further defined nutrients use efficiency as the maximum economic yield produced per unit of nutrient applied, absorbed or utilized by the plant to produce grain and straw. While plant genetic variability has been defined as the heritable character of a particular crop species or cultivar that exhibit varying responses in growth or production when compared to other species or cultivars of the same species under limiting and non-limiting growth conditions. However, Shaver and Melillo (1983) expanded nutrient-use efficiencies further and categorized them as agronomic, physiological efficiency (PE), agro-physical efficiency (APE), apparent recovery efficiency (ARE) and utilization efficiency. Nitrogen response efficiency (NRE) is defined as the production per unit N available. N-use efficiency is also defined as the ability of a genotype to produce superior grain yields under low soil N conditions in comparison with other genotypes.

The subject of NUE has been widely studied (Fageria and Baligar, 2003; Ishimaru *et al.*, 2001; Lawlor, 2002; Mae, 1997; Zhi-You *et al.*, 2006). High NUE is generally important under conditions of low soil N availability, as it entails high biomass production per unit of N uptake (Aerts and Chapin, 2000) and it is a useful index that combines both plant physiological and morphological responses along nutrient availability gradients. Vitousek (1982) has reviewed nitrogen dynamic terminologies as follows: Nitrogen response efficiency (NRE) as the net primary production (NPP) as a proportion of available N in the soil (Nav) and N-uptake efficiency (NupE) as the proportion of available soil N acquired by plants. As defined, NUE is the total net primary production per unit N absorbed or lost. Thus nutrient response efficiency can be defined as the product of nutrient uptake and use efficiency. A reduction in cultivar productivity with decreasing soil N can thus be mitigated if NRE (NPP/Nav) is increased through higher NupE (N_{ac} is the N taken up by the plant (N_{ac}/N_{av} (N_{av} is the N available in soil)), N-use (NPP/N_{ac}) or both. Pastor and Bridgham (1999) observed that the application of nutrient response efficiency, nutrient-uptake efficiency, and nutrient-use efficiency may give important information about the competitive abilities of different genotypes under different N available gradients. Use of NupE may be particularly important, as it has been found that N concentration in plant tissue and indices of soil nutrient availability do not show a clear relationship.

1.4.2 Classification of genotypes in relation to N-use efficiency

Genotypes response to different levels of soil N conditions is widely varied. Genotypes that do not respond to increasing rates of N due to either poor adaptation to high N supply environment or inherently low-yield potential are identified as inferior. Under low soil N supply, certain genotypes have been observed to respond well and give high grain yield, but they do not respond to additional N application. Singh *et al*. (1998) and Shrestha and Ladha (1996) observed that the higher N uptake observed in the long-duration genotypes may be attributed to the longer period of N accumulation at the vegetative and the higher associative nitrogen fixation, as opposed to the short duration ones. Inefficient genotypes in their study were observed to require higher N supply to achieve similar grain yields. They therefore, concluded that genotypic differences were either due to poor adaptation at high N or poor N-use and or uptake efficiency at low soil N supply. By using nitrogen productivity index (NPI), which integrates both grain yield (GY) and nitrogen physiological use efficiency (PNUE) as an effective parameter, they were able to rank genotypes into efficient, inefficient, and inferior ones in both duration groups. They reported the relationship between N-uptake and tiller number, and N-uptake and spikelets number, explained 73% and 86% of total variation in genotypes. They observed that 75% of the variation in grain yield was explained by N-uptake, genotypic differences remained, with the N-efficient genotypes having a consistently higher physiological N-use efficiency (PNUE). These are identified as N-efficient genotypes as they consistently produce high grain yield at all soil N levels. Cooper (1999) reported that such differences have important implications in both plant performance, high yield being achieved by lines with high nutrient uptake, high nutrient-use efficiency, high harvest index, and high nutrient harvest index.

Based on N-use efficiency and grain yield at a low soil N level, rice genotypes have been classified into four groups. Fageria and Baligar (2003) have suggested such classification to categorize crop genotypes for their nutrient use efficiency. The first genotype group is the efficient and responsive (ER), genotypes that produced above the average yield compared to all the genotypes tested in the experiment at low N level and had higher N-use efficiency than the average of all the genotypes. The second classification is genotypes that are efficient and non-responsive (ENR). These genotypes produce more than the average yield of genotypes tested at low N level, but N-use efficiency is lower than the average of all genotypes classified in this group. The third type is referred to as non-efficient and responsive (NER) genotypes. These genotypes produce less than average grain yield at low N level. The fourth group of genotypes are those that produced less than the average yield of genotypes tested at low N level and response to applied N (N-use efficiency) is also less

than the average of those genotypes. These types are classified as non-efficient and non-responsive (NENR) genotypes.

Fageria and Baligar (2003) argued that the genotypes which fall into ER group are the most desirable, because they can produce high yield at low soil N levels and also respond well to applied N. Thus, this group can be utilized with low as well as high input technology with reasonably good yield. The second most desirable group is efficient and non-responsive (ENR) genotypes. These can be planted under low soil N level and still produce more than average yield. The NER sometimes can be used in breeding programmes for their N-responsive characteristics (higher N use-efficiency). They concluded that the most undesirable genotypes were the non-efficient and non-responsive (NENR).

Nitrogen productivity index (NPI) ranking of genotypes is consistent with N-efficient genotypes exhibiting high NPI. Cooper (1999) concluded that PNUE, ANUE, and AR were biased either toward soil N or fertilizer N supply. Because of significant genotype, N supply, and genotype by N-supply interactions; germplasm evaluation for N partitioning, recovery, and efficiency; requires that N-supply to be at least at a low and a high level. He also observed that use of NPI for evaluating genotypic differences in N-use also requires field evaluation of genotypes at low N (or zero N fertilizer) and a high N level. Edmeades *et al*. (1997) also observed that the use of NPI is the most promising parameter for quantifying and ranking genotypes for soil N fertility situations.

1.4.3 Mechanisms for genotypic differences in nutrient use efficiency

Fageria and Baligar (2003) have observed that large differences occur among cultivars of the same species in absorption, translocation, and utilization of mineral nutrients. They have given the soil, plant mechanisms and processes including other factors that have great influence on differences of genotypes in their nutrient-use efficiency as indicated in Table 1.1. The main mechanisms cited were nutrient acquisition, nutrient movement in root, nutrient accumulation and remobilization in shoot among other factors. Nitrogen has also been described as the most difficult to manage due to its volatile nature and mobility. Nitrogen harvest index is a measure of N partitioning in rice, which provides an indication of how efficiently the plant utilizes the acquired N for grain production.

Table 1.1 Summary of soil and plant mechanisms plus other activities that influence genotypic variability in nutrient-use efficiency.

A. Nutrient acquisition
1. Diffusion and mass flow (buffer capacity, ionic concentration, ionic properties, tortuosity, soil moisture, bulk density, and temperature).
2. Root morphological factors (number, length, root hair density, root extension, root density).
3. Physiological (root:shoot ratio, root micro-organisms such as mycorrhizal fungi, nutrient status, water uptake, nutrient influx and efflux, rate of nutrient transport in roots and shoots, affinity to uptake (Km), threshold concentration (Cmin).
4. Biochemical (enzyme secretion as phosphate, chelating compounds, phytosiderophore), proton exudate, organic acid production such as citric, transaconitic, malic acid exudates.
B. Nutrient movement in root
1. Transfer across endodermis and transport within root.
2. Compartmentation = binding within roots.
3. Rate of nutrient release to xylem.
C. Nutrient accumulation and remobilization in shoot
1. Demand at cellular level and storage in vacuoles.
2. Re-transport from older to younger leaves and from vegetative to reproductive parts.
3. Rate of chelates in xylem transport.
D. Nutrient utilization and growth
1. Metabolism at reduced tissue concentration of nutrient.
2. Lower element concentration in supporting structure, particularly the stem.
3. Elemental substitution, e.g., Na for K function.
4. Biochemical nitrate reductase for N-use efficiency, glutamate dehydrogenase for N metabolism, peroxidase for Fe efficiency, pyruvate kinase for K deficiency, metallothionein for metal toxicities.
E. Other factors
1. Soil factors.
a. Soil solution (ionic equilibria, solubility precipitation, competing ions, organic ions, pH, phytotoxic ions).
b. Physico-chemical properties of soil (organic matter, pH, aeration, structure, texture, compaction, soil moisture).
2. Environmental effects.
a. Intensity and quality of light (solar radiation).
b. Temperature.
c. Moisture supply.
3. Plant diseases, insects, and allelopathy.

Source: Compiled by Baligar and Fageria (2001)

Genetic variability for N harvest index exists within the small grain genotypes and a high N harvest index in the genotypes is associated with efficient utilization of N. Variation in the N harvest index is a characteristic of genotype and such trait may be useful for selecting rice genotypes for higher grain yield. Importance of this trait is also indicated by a highly significant correlation between N harvest index and grain yield (Britto and Kronzucker, 2004).

1.4.4 Rice yield potential

Among all the important cereals, rice has the highest yield expressed in food and energy (Juliano and Villareal, 1993). However, there appears to be a barrier preventing yield increases above approximately 10 t ha^{-1}, as this ceiling-yield has remained unchanged in the tropics for more than 20 years (Khush, 2005). Amano *et al.* (1996) by contrast, have reported that grain yields of 13-15 t ha^{-1} have been observed for the temperate environments of Yanco, Australia and Yunnan China, and that this yield required an uptake of 250 kg N ha^{-1}. They observed that there is need to identify and quantify component parts of the tropical ceiling-yield barrier for rice, and develop ways to overcome that barrier. The imbalances between demand and supply of plant nutrients, in particular N, are the main common causes for yield limitations. The issue of how the plant can control the rate of deployment of its N resources for the construction of metabolic, structural and storage components has been cited as crucial in improving yields (Sheehy *et al*., 1996). Akita (1989) and Sheehy *et al*. (1996) estimated that maximum grain yield for the dry season at IRRI would be 15 t ha^{-1} at 14% moisture content. Scobie *et al*. (1993) estimated that at least 30% of the projected 70% increase in the global rice demand by the year 2030 must come from yields realized from increased rainfed rice productivity.

1.4.5 Breeding opportunities for low soil nitrogen environments

Nitrogen fertilization is expensive to the ordinary rice farmers. Furthermore, it has been observed that even for those who apply them they are not efficiently utilized by the rice plants thus need for breeding efficient varieties (Saito *et al*., 2006). One reason attributed for this is that rice is grown in environments that are conducive to N loss through nitrification-denitrification, ammonia volatilization, runoff, and leaching. It has also been observed that imbalanced use of fertilizers and occurrence of other macronutrient deficiencies combine to give rise to low N-use efficiency.

There are however, opportunities in rice improvement for low soil N conditions through development of varieties with enhanced N-use traits for grain yield. Zhi-You *et al*. (2006) reported that the net primary productivity (NPP) increased with N and water availability in their study on rice. The efficiency of whole plant N use, uptake, and response was observed to increase with decreasing soil N and water, and was higher on infertile than fertile habitat. It has been suggested that NUE theory rests on the premise that plants on poor soil N are less productive than those on N rich soils. High NUE is therefore, considered to be indicator of good adaptation to low soil N, because it shows high biomass production per unit of

N-uptake. Ishimaru *et al.* (2001) and Mae (1997) have observed that the ratio of Rubisco to total leaf N is a factor determining N-use efficiency in rice yields and that this is one of the main targets in development of N-use efficient varieties. They have indicated that by controlling N-use efficiency this can be a valuable tool for maintaining high yields under low input agricultural systems. This is the principle objective of large yield production of high quality with minimal agricultural inputs especially N.

Genotypes have been observed to vary in their ability to utilize N efficiently and partition N between various rice plant components. Zhi-You *et al*. (2006) and Singh *et al.* (1998) have observed great variability in rice for grain yield, N-uptake efficiency and partitioning parameters such as; physiological N-use efficiency (PNUE), agronomic N-use efficiency (ANUE), apparent recovery (AR), partial factor productivity of applied N (PFPN), N productivity index (NPI), and N harvest index (NHI). They reported the existence of significant differences among genotypes and N-levels for rice total biomass, total N-uptake, tillering ability, panicle numbers and total number of spikelets (m^{-2}). Straw and grain N concentration was also variable within rice genotypes. Singh *et al*. (1998) on the other hand, observed that differences in physiological efficiency may occur because of differences in critical concentrations (internal N requirement) for expansion, growth, mass accumulation, organ formation and differences in the ability to translocate, distribute and redistribute the absorbed N in various organs, and the efficiency of N-use in photosynthesis. N-use efficiency though largely dependent on interactions between nutrient balance, water availability, light intensity, disease pressures, and genotypes; can be improved through appropriate genetic manipulation. Selection and plant breeding techniques can be utilized to develop rice varieties that are resistant to pests, diseases, and adverse environmental conditions such as drought, nutrient deficiencies, toxicities, and salinity (Nguyen and Byun-Woo, 2006; Singh et al., 1998). However, selection to improve the rice crop's N-use efficiency remains viable and one to be exploited because it is sustainable and environmentally friendly.

The wide genotypic variability for low soil environment offers great opportunity for rice improvement. In this regard, Saito *et al.* (2006) observed that traditional cultivars were less responsive to N application, and grain yield of the traditional cultivars were increased by only 16% with N application (a 0.1–0.4 t ha^{-1} increase in grain yield), while grain yields of improved cultivars were increased by 37% with N application (a 0.9–1.2 t ha^{-1} increase in grain yield) in their study. Inthapanya *et al*. (2000a) observed that breeders often select their plant materials under high productive environments assuming strong genetic correlations with low productivity environments. If this is so, lines selected in high productive

environments are likely to perform well in low productive environments (Atlin and Frey, 1989). Ceccarelli (1994), Holland *et al.* (2003) and Kimani *et al.* (2007) have however, argued that breeding for target environment is the best approach as genotype performance under different fertility conditions are controlled by different gene systems. Several authors have reported that the potential exists for exploiting genotypic differences in rice for low N responsiveness (Broadbent *et al.*, 1987; De-Datta and Broadbent, 1993) during rice improvement for low soil N conditions.

Genotypes have been shown to differ in their nitrogen use-efficiency thus breeding for low soil N adaptation is of great advantage. Socolow (1999) reported that although N application increases yields, its use is known to have negative impacts resulting from N-compounds on the atmosphere, the ground water, and other segments of the ecosystems. One way to alleviate this problem has been cited as the use of low soil N-efficient cultivars, restriction on use of nitrogen fertilizers and rising the areas under organic farming (Presterl *et al*., 2003). Ohnishi *et al.* (1999) by combining the breeding objectives of yield improvement for both conditions of high and low N input were able to make progress in developing genotypes adapted to both low and high soil N conditions. A similar approach was advocated by Atlin *et al.* (2006b) who cited the following two breeding strategies; (i) indirect improvement where selection is done at only one N level, and the performance at the other N condition being obtained by correlated response; or (ii) combined evaluation where selection is based on an index of the weighted cultivar performance means at both high and low N levels as useful strategies for varietal improvement. They concluded that if combination of the two breeding objectives is not effective, then it would be important to breed for the high and low N conditions independently. In order to make a decision on to which of the two strategies would be the most effective, understanding of the quantitative genetic variances such as coefficients of genotypic correlation, genotypic variance components, heritabilities, and economic weights for yield under high and low soil N conditions is crucial.

Lawlor (2002) has strongly argued that there is need to increase production of food without expansion of agricultural land and with less fertilizer in order to feed the growing population and save fossil fuel energy used in its production. Use of less N fertilizer will decrease the cost of production, pollution and environmental problems resulting from methods of synthesis, inefficient use and uptake by crops and attainment of this objective is urgently needed (Kimani, 2002). The production per unit area with less fertilizer is to be pursued as this will give more yields at a lesser cost. Sheehy *et al.* (2000) as reported by (Lawlor, 2002) observed that it is desirable to improve the genetic potential of rice yields which have been stagnant for decades through breeding and achieving better yields with less N and other

resources. Lawlor (2002) reported that increasing the effective live of the leaves through breeding is a proven method for increasing yields. Productive rice varieties have greater root size, length and root surface area per volume of soil. These traits are genetically controlled and are important in N-uptake from low soil nitrates (NO^-_3) concentrations. Nitrogen content per unit biomass is used as the indicator of how adequate N supply is for crop growth. The shortcoming of this value is that it changes with crop age and environment. Nitrogen deficiency reduces the %N as leaf:shoot ratio decreases with crops development. In rice, yield production depends on the number of plants per unit area, tillers plant^{-1}, number of spikelets tiller^{-1}, grains panicle^{-1} and 1000 grains weight. However some of these traits have negative correlation with one another and hence their breeding is not straight forward. Baligar *et al*. (2001) argued that when N-supply is limiting to achieve genetic potential, then it is N-uptake that must be enhanced to obtain greater biomass. This can be done by breeding for roots traits that enhance N-uptake coupled with more efficient metabolic utilization of available N into useful products. This can be realized by expanding the period for light absorption for its effective use by breeding for rice with enhanced stay green-traits.

De-Datta (1981) observed that rice plants when grown at low N level (20 kg ha^{-1}) use fertilizer most efficiently for grain production during maximum tillering stage and flowering stage (between flowering and milk stages). High N supply reduces number of filled spikelets and 1000 kernel weight. The author argued that N application should be split with one dose at transplanting and another at panicle initiation especially for medium and long duration rice. Nitrogen absorbed from tillering to panicle initiation tends to increase the number of tillers and panicles, while that absorbed during panicle development (panicle initiation to flowering) increases the number of filled spikelets per panicle, while N absorbed after flowering tends to increase 1000-grain weight.

It has generally been observed that late maturing rice varieties accumulate a large amount of N in the plants due to increased N mineralization, and they produce higher grain yields. This is in contrast to early maturing lines that tended to have higher N concentration in the grains and stems thus are less efficient in N-use. Fukai *et al.* (1999a) have suggested that NUE for grain production may be a more useful trait in developing new low soil fertility conditions adapted cultivars. Seedling tests for screening genotypes adapted to low soil fertility suffer from inability to pick genotypic variation in reproductive traits such as HI, nutrient HI and grain nutrient concentration. It has been argued that small genotypic and fertilizer interaction justifies the use of moderately high levels of fertilizer rate in breeding programmes.

1.4.6 Utilization of remobilized internal N for breeding high yielding rice

The mobilization of N from areas of less active growth to regions of active development of the absorbed N within the plant can play a key role in breeding N-efficient rice plants. Mae *et al.* (1983) observed that major source of N for developing leaves of mature rice plants was the N mobilized from older, senescing leaves. Studies with ^{15}N revealed that mobilized N accounted for 64% of the total N in the youngest leaf blades of rice. Ladha *et al.* (1998) similarly concluded that efficiency in N mobilization from old leaves affected physiological efficiency (PE) in the process of grain production. The concept that tropical rice suffers high-light stress during grain filling in the dry season may help to explain why the maximum yields of inbred cultivars are higher under temperate conditions (12 to 13 t ha^{-1}) than they are under dry-season tropical conditions (9 to 10 t ha^{-l}). They reasoned that lower straw N concentration may be an indication of higher PE-biomass. Grain N concentration may have also an effect on physiological efficiency, although most lines they studied, 93% of them had grain N concentration of 0.95 to 1.2%. On average, grain N concentration decreased by only 0.1% when PE-grain increased by ten. Therefore, they concluded that human nutritional value of rice was not really changed with the improvement of nitrogen-use efficiency.

Harvest index (HI) is defined as the ratio of grain yield to the total biomass. This index is not constant but varies between sites and years due to differences in environment and N-supply among the genotypes (Lawlor, 2002). The genetic potential is defined as the total capacity of the plant, to form yield when environmental stresses are removed. Both inter- and intra-specific genetic potential variations in N nutrition have been recognized among cereal species and genotypes. This therefore, offers great potential to develop cultivars that are efficient at low nutrient levels or are capable of using N more efficiently when applied as fertilizer.

Genetic variability for N harvest index exists within the small grain genotypes and a high N harvest index in the genotypes is associated with efficient utilization of nitrogen. Variation in the N harvest index is a characteristic of genotype and such a trait may be a useful variable for selecting rice genotypes for higher grain yield. Importance of this variable is also indicated by a highly significant correlation between N harvest index and grain yield.

1.5 Breeding rice for low soil phosphorus condition

Phosphorous is an important nutrient in many crop species for development and growth, as it is involved in many metabolic functions.

1.5.1 Function and mobility of phosphorous (P)

Phosphorous is an essential major element in many plants among them rice crop and it is involved in various metabolic reactions. It is an important constituent of adenosine triphosphate (ATP), nucleotides, nucleic acids, and phospholipids. Its major functions are in energy storage and transfer and the maintenance of cell membrane wall integrity. Phosphorous is mobile within the plant and promotes tillering, root development, early flowering, and ripening especially where temperatures are low. It is particularly important in early growth stages (Dobermann and Fairhurst, 2000). The addition of mineral P fertilizer is required when the rice plant's root system is not yet fully developed and the native soil P supply is low. Phosphorous is remobilized within the plant during later growth stages if sufficient P has been absorbed during early growth.

1.5.2 P deficiency symptoms and effects on rice crop

Deficiency may be acute, occurring when a nutrient is suddenly no longer available to a rapidly growing plant or chronic deficiency that occurs when there is a limited but continuous supply of a nutrient, at a rate that is insufficient to meet the growth demands of the plant. Most of the classic deficiency symptoms described in textbooks are characteristic of acute deficiencies. The most common symptoms of low-grade, chronic deficiencies have been reported to be tendency towards development of darker green leaves and stunted or slow growth. According to Dobermann and Fairhurst (2000) the P-deficient plants are generally stunted with greatly reduced tillering. The leaves are in most cases narrow, short, very erect, and have a 'dirty' dark green. Stems are thin and spindly and plant development is retarded. The number of leaves, panicles, and grains per panicle is also reduced. Young leaves appear to be healthy but older leaves turn brown and often die. Lincoln and Zeiger (2010) have reported P deficiency in rice is associated with red and purple colors development in leaves if the variety has a tendency to produce anthocyanin. The leaves appear pale green when P and N deficiencies occur simultaneously. Other effects of P deficiency were reported to be delayed maturity beyond one week and that when P deficiency is severe, plants may not flower at all. Large proportion of empty grains may result. When P deficiency is very severe, grain formation may not occur at all and low 1,000 grain weight and poor grain quality result. Normally there is reduced response to mineral N fertilizer application. Varieties have low tolerance to cold water and there is absence of algae in floodwater. Poor growth results in small leaves and slow establishment of green manure crops.

It has been observed during vegetative growth before flowering that P supply may be sufficient and a response to P is usually very low when P leaf concentration is 0.2-0.4%. Yields greater than 7 t ha^{-1} require more than 0.06% P in the straw at harvest and greater than 0.18% P in the flag leaf at flowering. General measures to prevent P deficiency and improve P use efficiency are best based on varieties. This should start with selection of rice cultivars that use P efficiently, particularly on acid upland soils (Li et al., 2005). The P-efficient rice cultivars have either greater P acquisition, increased external efficiency because of better root morphology or increased excretion of organic acids or O_2 or higher internal efficiency of P use such as larger grain yield when P uptake is low. Examples of P efficient varieties are IR20, IR26, IR64, and IR74 (Dobermann and Fairhurst, 2000).

Phosphorus (P) supply is a prerequisite for realization of higher yield potential of modern rice varieties, as it plays a crucial role in energy storage and transfer within cells, speed up root development, facilitates greater N uptake and results in higher grain protein yield. Gill *et al.* (2004) have observed that the problem of limited phosphorus resource can be mitigated to some extent by reducing phosphorus loss and through better cycling in agricultural production systems and development of P-use efficient crop varieties. The differences in P uptake and use among varieties will help reduce costs of phosphorus fertilization and enhance productivity if more P-efficient varieties are used.

In Sub-Sahara Africa the estimated net per hectare loss during the last 30 years is 700 kg N, 100 kg P, and 450 kg K in about 100 million hectares of cultivated land (Breth, 1996). The figures are the balance of nutrient inputs that include fertilizers, minus nutrient outputs, which are harvested by crop removals. This is in total contrast to commercial farms in North America and Europe which have recorded net positive nutrient balance of 2,000 kg N, 700 kg P, and 1,000 kg K ha^{-1}, during the last 30 years is four times the cultivated land resulting sometime in ground water and stream pollution (Frissel, 1978).

Cultivars tolerant to low soil P support sustainable farming systems and reduce production cost and farmers dependence on fertilizers. Fukai *et al*. (1999a) and Hou *et al*. (2007) have reported that both N and P and their utilization efficiency (grains yield/unit nutrient uptake) to produce grain yield are important for low soil N and P environments. Genotypic variation in utilization efficiency was observed to be consistent across environments and that efficiency can be improved by development of cultivars that require low nutrient concentration in the plant and a higher concentration in the grain. Grain yield is reduced by both drought and low soil N and P in rice production regions (Shu *et al*., 2005). The genotypic variation in traits conferring low soil P adaptation must be present and can be incorporated into suitable

genetic background (Kimani *et al.*, 2007). The main gene action responsible for low soil phosphorus was observed to be mainly additive in common beans (Kimani and Kimani, 2001). Grain yield increase of 49% and 50% have been reported from application of 6.25 t ha^{-1} and 60 kg ha^{-1} of farmyard manure and N fertilizers, respectively (Fukai *et al.*, 1999a). These results illustrate the magnitude of low soil fertility; however, if drought occurs the use of fertilizer may not result in grain yield increase.

Healthy genotypes are known to better tolerate moderate water stress under low soil nutrient availability. Low soil N and P conditions affects canopy photosynthesis and hence dry matter production and grain yield. Large genotype by environment interaction has been shown to be due to differences in phenology (late maturing cultivars being affected by late season drought), response to drought and low soil P and N. With rising cost of fertilizers and reduced profit in rice production, development of cultivars adapted to low soil fertility is desirable. Ladha *et al*. (1998) have observed that the ideal cultivars are those that perform well under low soil fertility and respond well to applied N and P fertilizers. Significant interaction between genotype and fertilizer has been observed for grain yield and also significant correlation between grain yield and genotypes.

1.5.3 Adaptation to low and high soil fertility nutrient resource conditions

The adaptation systems for adverse soil fertility conditions can be diagnosed by examining resources that limit yield. Grain yield can be established with regard to acquisition and utilization efficiency of the particular resource. The nutrients that limit yield need to be established and genotypic variation in nutrient uptake and its utilization efficiency for grain production identified. The adaptation traits once identified can be used as selection criteria in plant breeding programme provided a proper screening procedure is developed. Grain yield (Y - kg ha^{-1}) is obtained as total dry matter (TDM) production at harvest in kg ha^{-1}, multiplied by proportion of TDM partitioned to grain (HI) (where HI is harvest index). Y=TDM*HI. This equation is a powerful one in assessing nutrient resource utilization by genotypes. The content of each nutrient in the grain (Y multiplied by the nutrient concentration of the grain) may be considered as a proportion of the total content of that nutrient in the plant biomass. This is obtained as the product of TDM by nutrient concentration of the plant biomass at harvest. Shoot weight has been reported to the plant parameter most sensitive to P deficiency and can hence be used as an indicator of P-use (Fageria *et al.*, 1988).

Plant species and cultivars within species have been reported to differ in their efficiency of nutrient uptake and translocation into grains. This together with differences in dry matter

accumulation per unit time and growth duration leads to differences in nutrient content. Fukai *et al.* (1999b) also reported that some genotypes are good in use of nutrients for total dry matter production and in the proportion and quantity of nutrients translocated into the grains. Low grain P is a desirable trait as it reduces P-removal from the soil thus contributing to sustainable land use. However, a minimum amount of P in the grain is required for nutritional reasons and for good seed germination (Gill *et al.*, 2004). High grain yield can be realized without reducing grain P concentration by improved translocation of P into grains and increased P uptake.

1.6 Breeding for high quality grains

Grain quality traits such as; grain size, aroma, shape, and milling percentages; are important in a rice improvement programme as they determine the market acceptability of milled rice. The most popular varieties in Kenya are the aromatic ones such as “pishori” and “basmati”. These have traits preferred by consumers such as long and slender fine grains, whiteness, translucency, and strongly scented grains.

Rice is grown in different ecologies with ecological and physio-chemical adaptations and properties. Sanni *et al*. (2005) identified about five physico-chemical properties that are used in rice quality assessment. These were given as amylase content, protein content, gel consistency, alkaline spreading value, swelling capacity and water absorption. The major attribute for rice consumption acceptability and hence its adoption is its grain quality traits. Aluko et al. (2004) have reported substantial information for physio-chemical and cooking traits for rice grown in Asia and U.S.A. In Kenya this information is scanty despite the major influence rice quality has on its consumption and marketing.

Some important parameters for eating and cooking quality, such as amylose content, gelatinization temperature (GT), gel consistency and starch paste viscosity (Bao et al., 2002) have been studied genetically, while other important starch properties, such as gel texture and swelling volume, have received little attention to date. Shi et al. (2000) have identified length and width of rice grain as the two most important quantitative traits closely related to the exterior quality of rice. Rice grain shape has become one of the main goals in rice breeding, because consumers usually prefer milled rice with spindly shape and greater transparency. For rice breeding programmes, understanding the inheritance, specifically gene action, for rice grain shape traits is desirable. Chen et al. (1998) in their genetic analyses of length and width of rice grain reported that rice grain shape is quantitatively inherited. It has recently been shown that rice grain shape is simultaneously controlled by

triploid endosperm genes, cytoplasmic genes and maternal plant genes (Shi and Zhu, 1996), and these have a large genotype-environment interaction(GEI) effects, but the genetic effects on the embryo have not previously been demonstrated.

Aromatic rice varieties are economically important as they fetch a premium price in agricultural markets worldwide. The most prominent examples are jasmine and basmati rice. Basmati rice is well known for its exquisite aroma and grain quality. Grain size, aroma, shape and milling percentages are important in a rice improvement programme as they determine the market acceptability of milled rice. However, their inheritance behaviour is not known among the Kenyan cultivars. Graham et al. (1999) reported that appearance and taste seem to be the factors that mostly determine quality. In rice, these preferences can be translated into measurable milling and physico-chemical properties. Yajima *et al.* (1979) identified a total of 114 different volatile compounds that are responsible for rice fragrance. Among them, 2-acetyl-1-pyrroline (2AP) stands out as the main fragrance compound in both jasmine- and basmati-style rice varieties, and the 2AP concentration in fragrant rice is high up to 0.09 mg kg^{-1}, 10 times more than that in nonfragrant rice (<0.006–0.008 mg kg^{-1}) (Chen *et al.*, 2006).

Two or three recessive or dominant genes have been reported to be responsible for the fragrance trait (Reddy and Reddy, 1987; Tripathi and Rao, 1979). However, most researchers believed that rice fragrance is controlled by one single recessive gene (Huang *et al.*, 1994; Jin *et al.*, 2003; Sood and Siddiq, 1978) with small gene modifiers. Unlike other traits controlled by major genes, rice fragrance which is a recessive trait is easily influenced by many elements, such as genetic background, environmental conditions and storage time among other factors (Chen *et al.*, 2006). Wongpornchai *et al*. (2004) noted that jasmine rice has gained an increasing popularity throughout the world food market because of its famous reputation in appearance, cooking quality and high aroma level. Rabiei *et al*. (2004b) has given rice grain quality traits as including milling, appearance, cooking and nutritional qualities which have great influence on rice consumers in most countries. Rice grain characteristics such as length, breadth and shape have a direct effect on the marketability, and therefore, the commercial success of modern rice cultivars. These characteristics affect the appearance of the rice grain and are quantitatively inherited. Since the economic value of a plant depends on its different traits, plant breeders should consider simultaneous selection for two or more traits to maximize the economic value of a plant along its production value chain.

Aromatic rice emits a definite odour in fields, during harvesting, storage, milling, cooking and eating (Efferson, 1985) and it is best developed in cooler temperatures during maturity. Inheritance of aroma has been reported to vary depending with materials used in the research, but it's inherited. Phosphorous has been reported to favourably influence rice grain quality, aroma, softness, fluffiness, whiteness, and glossiness as these are related to P content in paddy grain and not content in the plant (Suwanarit *et al*., 1997), and that organic fertilizers have no effect on rice cooking qualities (Jeong *et al.*, 1996). Several components contribute to rice grain quality, and among these, fragrance and taste qualities are the most important to consumers (Myint *et al.*, 2009).

Myint *et al*. (2009) have noted that rice grain quality affects the nutritional and commercial value of grains, and that it is of great importance to those involved in producing, processing and consuming rice. Rice grain quality includes factors such as processing quality, appearance, nutrition, cooking and taste qualities. However, rice cooking and taste qualities are the most important qualities to consumers. Although preferences vary from one group of consumers to another, rice grains with a pleasant fragrance and a soft texture usually achieve higher prices in national and international markets. Fragrant or scented rice that obtains a premium price in international markets is characterised by its natural fragrance or pleasant aroma and good taste quality. Nagaraju *et al*. (2002) have observed that in general, traditional fragrant rice varieties are of tall stature, prone to lodging, have low tiller number, high sterility, are sensitive to photoperiods and have poor response to fertilizer application thus leading to low yield potentials. This compound has been isolated from all parts of the rice plant except from the roots (Yoshihashi, 2002). Various techniques have been developed to assist breeders in the selection of individuals with distinctive fragrances. Sensory methods such as chewing seed samples and smelling leaf tissues from individual plants were reported by (Wongpornchai *et al.*, 2004), as well as heating seeds or leaf tissue with water or reacting with 1.7% KOH solution (Sood and Siddiq, 1978). However, these methods are limiting when processing a large number of samples. Chemical methods are possible for the identification and quantification of volatile compounds in the cooking water by using gas chromatography (Lorieux et al., 1996; Mahatheeranont et al., 2001). For example, quantification of 2AP by stable isotope dilution methods (Yoshihashi, 2002) and histochemical localisation of 2AP in thin sections of seeds by reacting with 2,4 dinitrophenol hydrazine (Nadaf et al., 2006). However these methods are not practical during the breeding process that generate many samples.

A major nuclear recessive gene has been reported to control the formation of fragrance in rice. The molecular marker for grain fragrance was first discovered by Ahn *et al*. (1992). The

RFLP analysis has shown that the fragrance locus is linked to a single copy DNA clone, RG28, on chromosome 8 of rice, at a distance of 4.5 cM fragrance gene. A number of PCR-based markers have been developed to detect fragrance and assist breeders in their selection of this trait through Marker assisted selection breeding programs (Bradbury et al., 2005). Conventional breeding methods combined with marker assisted selection can be more successful in the development of high quality new cultivars. This is because of the quantitative nature of grain quality traits and environmental variations that make it difficult to identify genetically superior lines due to their interferences. Molecular markers facilitate the selection of complex traits during the breeding process because they are reliable and they are unaffected by environmental conditions and thus consistent in their results.

Michael *et al*. (2009) have reported fragrance in the grain to be one of the most highly valued grain quality traits in rice, yet the origin and evolution of the betaine aldehyde dehydrogenase gene (*BADH2*) underlying this trait remains unclear. Despite multiple origins of the fragrance trait, a single allele, *badh2.1*, has been reported to be the predominant allele in virtually all fragrant rice varieties today, including the widely recognized Basmati and Jasmine types. Fragrance is reported to be produced in all parts of the rice plant except the roots, and it has a very low odour threshold, allowing humans to detect it at minute concentrations in field grown plants, macerated leaf tissue, as well as in the grain before, during, and after cooking. Fragrant accessions have been identified within at least three of the distinct genetic subpopulations of rice, including Group V that include Basmati and Sadri varieties, *indica* that include Jasmine varieties and tropical japonica.

Shu Xia et al. (2008) have observed that rice to be a primary food crop and has an important role both economically and in terms of food security. Aromatic rice varieties constitute a small but special group of rice and have gained greater importance with the worldwide increase in the demand for super rice. Not only is aroma one of the most important traits for determining good quality rice, but fragrant varieties have comparable or superior nutritional values and better amino acid profiles. For example, Basmati-370 rice has higher lysine, phenylalanine, leucine and methionine content than non-aromatic varieties (Sekhar and Reddy, 1982). Consumers are willing to pay higher prices for fine-grained aromatic rice, and therefore, sensory evaluation of grain quality has become an important consideration in rice breeding. There are different flavours or aromas occurring in diverse aromatic genotypes that arise from varied origins and hence there is no consensus yet on the nature of rice aroma (Dhulappanavar, 1976).

At least six chromosomes have been reported to be involved in the mapping process for aroma. Lorieux *et al*. (1996) have confirmed the close linkage between RG28 and *fgr* (5.8 cM) on chromosome 8 and identified two quantitative trait loci for fragrance, one on chromosome 4 and the other on chromosome 12. Li *et al*. (2006) and Bradbury *et al*. (2005) have reported significant polymorphisms between aromatic rice genotypes and non-aromatic genotypes with regard to the coding region of a gene with homology to the betaine aldehyde dehydrogenase 2 gene *BAD2*. However, *BAD2* appears not to be responsible for aroma in all aromatic rice varieties, since this gene is not responsible for a dominant aroma trait of an aroma mutant SA0420, a view also observed by Kuo *et al*. (2005). Even so, it has been established that in most rice varieties aroma is controlled by a single recessive gene mapped to chromosome 8 of *O. sativa* (Li *et al*., 2006). Molecular fine mapping for aroma and the subsequent use of this information in the selection process would greatly accelerate the efficiency of aromatic rice breeding programmes. In addition, physical mapping of aroma could be useful for understanding rearrangement in the rice genome and exploring candidate genes for aroma. The identified markers linked with aroma provide a useful avenue for molecular marker-assisted selection of genotypes arising from hybridization in future breeding programmes.

Nguyen and Bui (2002) have identified the two markers RG28, RM223 to be closely linked to extremely aromatic phenotypes. The aroma or fine flavor of cooked rice has been shown to be composed mainly of formaldehydes, ammonia and hydrogen sulfide. Some researchers reported that an increase of propanol, pentanol, and hexanol during storage seemed to be responsible for the stale flavor of cooked rice. As many as 100 volatile flavor components such as hydrocarbons, alcohols, aldehydes, ketones, acids, esters, phenols, pyridines, pyrazines, and other compounds have been identified in cooked rice. A molecular marker that is closely linked to the aroma gene can be used to facilitate early selection for the presence or absence of scent, and to identify the nature of the locus (homozygous or heterozygous condition), it may also be useful for the rapid incorporation of the scent character into breeding lines. Ahn *et al*. (1992) have reported a DNA marker closely linked to a gene for aroma in rice. It is generally agreed that gene marker and not flanking markers are more accurate in indentifying fragrance locus in breeding lines.

Xiangli *et al*. (2008) have conducted genetic studies and physical fine mapping to reveal that a candidate gene (*fgr*/*OsBADH2*) homologous to betaine aldehyde dehydrogenase is responsible for aroma metabolism in fragrant rice varieties, but the direct evidence demonstrating the functions of *OsBADH2* is lacking. A number of genetic analyses using reciprocal crosses repetitively showed that the fragrant characteristic trait is under recessive

monogenic inheritance without impact from cytoplasmic genes. In a recent study involving eight aromatic hybrid rice maintainer lines, a single recessive locus spanning SSR markers RM210 and RM515 on chromosome 8 was identified to be tightly linked to the fragrant trait (Ren *et al*., 2004). Physical mapping revealed that several candidate genes including a rice betaine aldehyde dehydrogenase (OsBADH2) homolog on chromosome 8 co-segregated with aroma production (Wanchana *et al*., 2005). Meanwhile, a study has demonstrated that the aroma production in fragrant genotypes was well correlated with the multiple mutations in the fragrance rice (*fgr*) locus that is identical to betaine aldehyde dehydrogenase (*OsBADH2*) on chromosome 8. The linkage of fragrant cultivars to undesirable agronomic performance and the molecular mechanism of this major weakness occurring in the aromatic rice cultivars is largely unknown. By using RNA interference (RNAi) technique combined with *Agrobacterium tumefaciens*-mediated T-DNA transfer, it has been shown that the directed degradation of *OsBADH2* transcripts resulted in a significantly elevated fragrance emission and 2-acetyl-1-pyrroline accumulation, unambiguously suggesting that *OsBADH2* locus is responsible for aroma production in fragrant rice varieties (Xiangli *et al*., 2008). In addition, disrupting of *OsBADH2* led to a detectable reduction of crop productivity, implying its multiple functions in secondary metabolism and agronomic performance. The results showed also reduction in plant height as well as 1000 grain weight in the *OsBADH2*-deficient plants when compared to the wild-type plants segregated out from the transgenic progenies.

1.7 Farmers perceptions and preferences in rice varieties

Various methods have been advanced that incorporate farmers participation, such as participatory rural appraisal (PRA), participatory variety selection (PVS) and participatory plant breeding (PPB) (Ceccarelli and Stefania, 2007; Walker, 2008; Witcombe, 2000). In Kenya, none of these methods has been employed and even literature on the same is rare. But elsewhere, various merits and demerits of the three methods have been practiced and widely discussed. Atlin et al. (2006a), Witcombe and Joshi (2003) argued for and against each of the methods. They observed that PRA is mainly used to gather information and share the results with the local people and Chambers (1994) has elaborately looked at its various forms. PRA actually is used to identify farmers' preferences in a variety with the aim of seeking to have wider adoption of a given variety that meets their desires. The PVS involves merely supplying the farmers with finished product to evaluate in their farms, while PPB involves farmers in selecting genotypes from a population that may involve accessions, advanced lines, segregating materials or cultivars; that can be used as parents in a breeding programme. In the later case because of actively involving the farmers in the breeding continuum, the adoption rate has been observed to be high and thus result into early release

of the varieties and ensures crop diversity (Ceccarelli and Stefania, 2007; Virk et al., 2003). Sperling et al. (1993), Witcombe et al. (1996) and Thakur (1995) have actually used PPB where farmers were visiting the research station to select suitable genotypes to be used as parents, and best ones from segregating population to develop varieties that were widely adopted within a short period. They have thus observed that PPB as opposed to PRA and PVS is the strongest tool for variety development and it ensures high adoption within a reasonable time frame (Almekinders and Elings, 2001; Walker, 2008). The case for PPB has specifically been advocated for and used by many authors to develop varieties suited to low input environments and for poor resource farmers (Ceccarelli and Stefania, 2007; Kimani and Derera, 2009; Morris and Bellon, 2004).

Since PPB is suitable especially when breeding for low input system as is the case here, where farmers can barely afford inputs like inorganic and organic fertilizers; it was found appropriate as opposed to the conventional plant breeding that favours farmers under high input environments (Ceccarelli and Stefania, 2007; Kimani et al., 2007). It is difficult for farmers' to modify the production environments and alter the poor soil health condition and also they may fear to replace their cultivars with modern high input dependent cultivars. This situation calls for ecosystem breeding (specific adaptability) where varieties suited to particular environments are developed by exploiting the skills of farmers in order to maximize gains in the target environment. This approach can efficiently cater for the various niche based farmers and thus optimise rice productivity by utilizing responsive genotype to different low soil N and P conditions. This way potential gains can be exploited through this decentralized and site specific adaptations and genotype by environment interaction is fully exploited. The situations where progress from crop improvement has been dismal and slow in marginal environments can be reversed as is the case in Kenya. Conventional and formal plant breeding programme practiced by national programmes have ignored indigenous germplasm as well as failed to breed directly for conditions faced by resource poor farmers, instead emphasizing selection for broad versus local adaptation. Further, Witcombe and Virk (2001) have argued that PPB is most likely to develop cultivars that may perform better than the products of convectional breeding when it is used in low-input systems, because in these situations the genetic gain between high-yield breeding nurseries and low-yield target environments is likely to be low or negative. Overall the low performance situation can be changed and that for this to happen an urgent reversal is required if food self sufficiency and improved livelihood is to be realized now than later.

Although studies on famers preferences have been conducted elsewhere, in Kenya documented information on rice is scanty. For example, a study conducted in Malawi, found

out that unsuitable varieties, high cost of inputs and lack of mechanical implements were the major constraints (Mzengeza, 2010), while in Uganda (Lamo, 2010) reported that farmers preferred high grain quality with high yields, however in West Africa farmers preferred tall and early maturing rice varieties (Efisue *et al*., 2008). Farmers' perception and preference can be used by breeders to develop varieties that might have higher adoption rate and thus higher productivity. This information is not documented in Kenya and farmers' varieties preferences, to guide rice breeding programme objectives, are not well known.

1.8 Summary

From the review, it is evident that little information exists on rice research work conducted in Kenya in particular and Africa in general. The information gathered may not apply directly because environments, varieties adaptation and general farming systems are quite different. This call for more research based solution to develop varieties that are suited to the unique production niches both existing and new ones.

Research is still required to develop genotypes that can yield highly under existing constraints in order to bridge the existing wide yield gap. This gap between potential and actual yield is a clear indication of the possibility for further shifts in yield character improvement. Yield improvement can be realized by breeding for adaptation and nutrient use efficiency for the prevailing production environments.

Most of agricultural environments have low soil nitrogen (N) and phosphorus (P), and this situation is further complicated by the fact that few farmers can afford the chemical fertilizers to apply for rice production. The cost of fertilizers has been rising steadily due to escalating oil prices, thus resulting in less use of fertilizers. This has lead to dwindling yields as rice continues to be produced on the same fields without soil replenishment despite massive soil depletion and degradation. However, the wide genetic variability that exists in rice varieties can be exploited to develop low soil N and P efficient varieties capable of producing economic yields. Although few studies were reported, improved low soil N and P efficient genotypes had consistently higher yield than unimproved genotypes.

Grain quality in rice is very important as it dictates cultivar acceptance by farmers, marketing and consumption and a variety of other uses. The appearance and taste has been documented as the main determinants of grain quality. The information on grain quality inheritance especially fragrance in general is lacking in Kenya, but the information gathered indicated that few genes are involved in control of traits such as aroma. Grain size and

shape are quantitatively inherited meaning breeding strategy could be to concentrate genes responsible for their control. Gel consistency has also been shown to be a trait greatly influencing the use of rice and therefore, its marketing.

Briefly, the various selected inheritance study methods have been discussed and their use is dependent on the kind of genetic information is being sought and their ease of application both in design, analysis and interpretation.

In conclusion rainfed rice varieties for the future should be more responsive to mineral fertilizer but should retain the stress tolerance and grain quality built into traditional varieties. Farmers would then be motivated to invest in more productive land preparation and fertility management practices that result in higher yields.

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CHAPTER TWO.
Farmers Participation in Identification of Upland Rice Variety Preferences, Production Constraints, Socio-Economic Information

Abstract

Farmers' participation in variety selection promotes adoption of the released cultivars. An Open Semi Structured Household Level Questionnaires (OSSHLQ) was administered in randomly to selected sixty seven households in the major rice production areas in Kenya, to obtain information on varietal preferences and production constraints. To supplement on this survey information, focus group discussions and key informants were incorporated. To ensure farmers desired traits were firmly anchored in the breeding programme, an on station research managed parent selection trial was established where farmers were involved in assisting the selection of varieties to be used as parents based on their own selection criteria. The farmers preferences were high yielding and good grain quality, hybrid rice and high nutrient use efficient varieties. These accounted for about 54% of their wishes. Rice was the most important crop among the selected farmers followed by maize, but the hectarage of maize was the highest followed by rice; probably this is due to the different spacing of these crops. Labour cost was identified as a factor limiting production, especially for irrigated rice and thus they preferred upland rice which is easy to produce. They identified land preparation, inputs, planting, weeding and harvesting as the most expensive activities. The majority of the respondents (66%) grew irrigated rice, while 25% grew upland rice. This disparity was attributed to the fact that upland rice was new, the varieties having been officially released in March 2009. This is in contrast to the irrigated varieties that they have been growing since 1951 when the irrigation scheme was established as a pilot scheme. However, the majority of the farmers expressed their desire to grow upland rice but lack of seeds, appropriate varieties and production knowledge was a major setback. The existing varieties were viewed as high input based and farmers could not afford the inputs. The main fertilizers used were Diammonium Phosphate (DAP), Sulphate of Ammonia (SA), Calcium Ammonium Nitrate (CAN) and NPK (23:23:0), though the amounts used were very low and contributed little to any consequential yields. This was the case even though the farmers were aware and indicated that soil fertility was poor due to continuous cropping under irrigation. Fourteen varieties were selected by farmers including Nerica1, Duorado, IR79913-B-176-B-4, CT16333(1)-CA-20-M, CT16333(1)-CA-22-M, CT16333(2)-CA-18-M, CT16313-CA-19-M, WAB964-B-3A 1.2, CT16317-CA-4-M, CT16307-CA-14-M, CT16337-CA-12-M, CT16345-CA-3-M, WAB 905-B-4A 1.1 and WAB 450-B-136-HB - NERICA9; but only nine of them were successfully used due to hybridization incompatibility.

2.1 Introduction

Involvement of farmers in variety development has been viewed by many authors as very important if the variety is to gain wide acceptability (Atlin *et al.*, 2006a; Joshi and Witcombe, 1995; Poussin *et al.*, 2006; Sperling *et al.*, 1993; Witcombe and Joshi, 2003). In rice farmers' preferences are varied and range from plant type, ability to perform under their growing environments, panicle size and shape, plant height, grain characteristics with regard to taste, grain shape and cooking qualities, their digestibility and maturity period. Other issues of interest to farmers include availability of market and credit facilities, yielding ability under different soil fertility conditions, availability of clean seeds, easiness of threshing, percent head rice, availability of labour, cost of production inputs, mechanization, top biomass, utilization of rice products, and resistance to insect pests and diseases (Rosemary *et al*., 2010; Witcombe, 2000). The information on farmers' participation in rice variety development in Kenya is scanty and even "grey" literature is not available on this. There has been no rice breeding work until very recently (2007), and the practice has been the evaluation of accessions from International Rice Research Institute (IRRI), International Institute of Tropical Agriculture (IITA) and recently Africa Rice Centre (AfricaRice) for upland rice. Farmers were involved during on-farm verification trials and later, the recommended or promising varieties were supplied to them for commercialization by the National Irrigation Board (MoA, 2009; NIB, 2008). Farmers adopted some of these varieties for production, while others became obsolete. The participation of farmers at the beginning of varieties development such that farmers' preferences are incorporated in the breeding programme is very vital (Nanda, 2001; Poussin *et al*., 2006; World Bank Group, 2007). It has been found that, participatory plant breeding (PPB) that involves farmers in selecting genotypes for use as parents or from segregating populations is very effective for wide adoption of varieties as opposed to participatory rural appraisal (PRA), and participatory variety selection (PVS) that provides merely polished breeding products to farmers for evaluation in their farms (Atlin *et al.*, 2006a; Witcombe, 2000; Witcombe *et al.*, 2003).

Rice is an important staple crop in Kenya, ranking 3rd after maize and wheat and most of its production is by small-scale farmers as a food and a commercial crop. Its production has stagnated at around 45-80,000 metric tons (MT), while consumption is above 300,000 MT (Jiddah, 2009; MoA, 2009; Muchiri, 2009). This stagnation can partly be explained by the following factors: lack of newly released irrigated varieties tolerant to diseases, insect pests, low soil fertility and low yielding under existing production environments. However, there is ample

opportunity to unlock this stagnation by exploiting the enormous potential of rainfed rice that exists. The current production is in favour of irrigated rice (95%) established by the government, while rainfed agriculture contributes a paltry 5% despite its huge potential. Kenya has a land area of 580,367 km^2 of which only 20% is suitable for agriculture, the rest being arid and semi-arid land. The potential production area for irrigated rice is about 540,000 hectares (ha), while rainfed potential area is 1.0 million ha (MoA, 2009; Rosemary *et al*., 2010). This rainfed production ecology needs to be explored as it offers immense potential of meeting the gap between production and consumption. This gap currently is being met by imports that cost the country about USD 87.5 million, thus straining other sectors of the economy (MoA, 2009). The productivity of irrigated rice is about 4-6 tons (t) ha^{-1}, while that of rainfed production is about 1 ton ha^{-1}. This is far below the optimum of about 10 t ha^{-1} and 7 t ha^{-1} for irrigated and rainfed rice, respectively (MoA, 2009). This can generally be attributed to lack of newly improved varieties, and certified seeds, high input costs, low soil fertility, insect pests and diseases, poor agronomic practices, limited water availability and lack of credit facilities. To reverse this condition, there is need to actively involve farmers' at various stages of variety development in order to meet the end-users' desirable traits and qualities, thus enhancing wide variety adoption.

Upland rice genotypes were introduced in Kenya in the 1980s in the western part of the country where on station evaluations were conducted. However, the information on their progress is scarce and it was not until 2003 when New Rice for Africa (NERICA) upland testing kits were introduced from AfricaRice by the Kenya Agricultural Research Institute (KARI) and other regional bodies (Jiddah, 2009). These helped the revival of upland rice production again. The kits comprised of 18 genotypes and were tested mainly in Nyanza, Western, Rift Valley, Central and Coast regions. In March 2009, four varieties; NERICA1, NERICA4, NERICA10, NERICA11 and a local variety *Dourado precoce* were released for commercialization. These varieties are being increased through seed certification for the farmers in the country. These varieties are being slowly adopted and produced by both farmers under the NIB and out growers (jua kali) who have taken up the advantage of rice sector liberalization to produce rice outside the scheme. Due to shortage of irrigation water many farmers are opting out for upland rice production as its less labourious and less expensive to produce. Also knowledge of its agronomic production practices is slowing diffusing out through various avenues both public and private, such as from national research system (KARI), NIB, extension services (MoA), farmer to farmer, collaborators and other stakeholders in the sector. This is a clear indication that despite the enormous potential these varieties have for meeting food self-sufficiency, they are yet to be

produced in large quantities by the farmers. Farmers have been producing *Dourado precoce* mainly in western part of the country, while coastal region have been growing lowland varieties of which some have been lost. Farmers in central part of the country have been growing irrigated rice, mainly aromatic BW370, BW217 and non-aromatic BW196 (MoA, 2009; Rosemary *et al*., 2010). These varieties are poorly adapted to low soil fertility, and famers have less choice on the varieties to grow.

The introduction of NERICA and other upland varieties offer immense potential to promote upland rice production through farmers' early participation, in variety development, and therefore, develop products with traits they prefer. These varieties have an advantage over irrigated rice, because it is possible to intercrop with other crops such as beans, bananas, coffee, maize and many others, thus less competition on available land. However without farmers broader active participation and training in the whole rice value chain the intended impact may not be realized. No systematic documentation of farmers' preferences, production constraints and participation in breeding to incorporate their traits of interest in new varieties has been carried out before. The current varieties in production are low yielding, old and un-adapted to conditions of low soil fertility in which they are produced. They have low grain quality, are susceptible to insect pests and diseases, information on upland rice production preferences and constraints is lacking; despite the enormous potential that exists; and rice imports to meet consumption needs are thus huge. It is with this in mind and the fact that upland rice production is hardly exploited despite the colossal potential that exists of producing enough and even surplus for export market, that this work was conceived. Already the policy makers have realised the enormous potential of the rice sector and a comprehensive national rice development strategy (NRDS) master plan has been developed for implementation (MoA, 2009).

2.2 Study objective

The broad objective was to document farmers problems, preferences, social-economic data, and involve them in a PPB for parental genotypes selection for the establishment of a breeding programme.

The specific objectives were to:

1. identify farmers upland rice preferences, production constraints, and gather other socio-economic information, and
2. indentify the best lines from the germplasm accessions together with farmers for use as parents in hybridization block.

2.3 Materials and Methods

The study was conducted in the central region of Kenya that produces 80% of the national rice (MoA, 2009). With the help of the Ministry of Agriculture (MoA) extension staff, four locations were selected based on their potential of producing upland rice. Out of these, six villages within the locations were selected based on their potential to grow upland rice, and farmers' from each village were randomly selected from the list of farmers' kept by the agricultural office, to which 67 Open Semi Structured Household Level Questionnaires (OSSHLQ) were administered. These were meant to capture and collate the perceptions on production constraints and preferred genotype traits. One important factor that was also considered was the ability for the willing members in these villages to visit the research trials for parents' selection. Those farmers that were coming from far off places were reimbursed their bus fare ticket as a way of defraying their cost and as a way of encouraging them to participate and aid in parental genotype selection from the adaptation trial.

Further, because the farmers had not been growing upland rice for a long period, many of them had heard about dry land rice but they did not understand how the new upland varieties were to be produced. They had been searching for information from fellow farmers, research station and NIB, and during the survey they requested that they be trained on its production. A Participatory Plant Breeding (PPB) approach was therefore, adopted to aid in selection of parents for the crossing block. The twin purpose of this approach was to demystify and expose farmers to practical upland rice production and ensure parents selected for the crossing block had farmers' preferences in a variety. This essentially meant that a hybrid participatory system had to be devised to benefit from Participatory Rural Appraisal (PRA), Participatory Variety Selection (PVS) and PPB.

The breeding programme being new and that only one cultivar was being used, materials had to be assembled from diverse origins, (314 lines from CIAT-Columbia, 75 lines from AfricaRice, 31 lines from the International Rice Research Institute (IRRI) and 30 lines from Mali rice breeding

program. This gave a total of 450 advanced genotype lines. To put the new breeding programme from the beginning on the right footing, and being aware that farmers were not fully conversant with upland rice production, though some knew of its existence and production. Farmers participation therefore, started from the adaptation trial of these materials on Kenyan conditions. Three casual workers and extension staff were requested to search for about 15 potential farmers to participate in the planting of the trial together with the principal investigator (PI), the Technical Assistants (TA) and casuals who had gained experience during earlier NERICA trials at the research station.

2.3.1 Trial layout

The materials were planted under four environments; no phosphorus (P) and nitrogen (N) application (N-P-), P application only (N-P+), N application only (N+P-) and finally both P and N applied (N+P+) blocks on 27th-30th November, 2007. The fertilizer used to supply these elements was Triple super phosphate (TSP) 60 kg P ha^{-1} and Calcium ammonium nitrate (CAN) 90 kg N ha^{-1}. Because of limited seeds, the plots were single rows of 4 metre length at hill spacing of 15 cm intra- and inter-plant (row) and replicated twice for each fertility experimental environment. Farmers were encouraged to freely visit the station for observation and learning of the agronomic practices being undertaken up to crop maturity. Their visits were recorded on a register kept by the two casuals who were manning the trials and details of dates visited and their comments or observations were recorded, plus any other issue they may have raised or observed.

At about 80% general crop maturity, fifteen farmers visited the trial for selection of the lines they preferred based on their own set criteria. The major aspects that they used were, panicle general appearance, grains type (slender were preferred), stature, maturity period, plant general aspect and yielding potential. This also helped the breeder to discard those materials that were extremely medium-late and late genotypes. Out of the 390 advanced breeding lines in the field trial (60 lines arrived late from IRRI and Mali and were evaluated separately in the screen house, where IR79913-B-176-B-4 was selected), they selected fourty five, providing a selection pressure of 11.5%. Farmers observed and discussed various lines that met their preferences where they tagged five best plants in a line being evaluated by using brightly coloured netting strings. These were harvested as bulk for further research work. Since these lines were still too many (and seed had been increased) for the PPB programme to be used as parents; these lines were immediately planted out again in a smaller area as an offseason trial where sprinkler

irrigation was used to supplement moisture. After 45 days the same lines were planted in the crossing block as potted plants and thereafter at every 24 day to end up with three sets in the hybridization block. This was to synchronize the flowering and thus ensure complete success of the complete diallel mating design. When the PPB farmers' materials approached 85% maturity, a group of twenty farmers who were to train other farmers, further selected the final 14 lines from the 45 as indicated in Table 2.1, this time a selection pressure of 31% was applied.

The PI discarded the 31 lines the farmers rejected and the remaining 14 genotypes were planted as parents in the hybridization programme in the crossing block. Following are pictorials of some of the activities of PPB (Fig 2.1-2.8).

Plate 2.1 Farmers go through the 45 lines they selected earlier for further planting

Plate 2.2 PPB farmers planting the 45 lines they selected

Plate 2.3 PPB farmers observe the 45 lines they selected for hybridization

Plate 2.4 PPB farmers discuss and select the best lines for hybridization block

Plate 2.5 Some of PPB Farmers engages the PI in discussion

Plate 2.6 PPB farmer is impressed by the panicle

Plate 2.7 PPB farmers group discussion and training using visual aid message

Plate 2.8 Discussion with some of the PPB farmers at the trial site

2.3.2 Data collection and analysis

The Open Structured Household Level Questionnaires (OSHLQ) were pre-tested before actual administration by a team made up of the principal investigator (PI), two enumerators and the extension staff in charge of the village. Data on farmers' preferences in varieties, production constraints, hectarage, fertilizer use, perceived solutions, crops grown, and other socio-economic data was collected. The data collected was analyzed using Statistical Package for the Social Sciences (SPSS) version 15 computer package. Focus group discussions and key informants were used to supplement the data collected by questionnaire method and also to gain more insight of farmers' perceptions and desires. The farmers' preferences, production constraints and possible solutions were listed and ranked. None structured general information was gathered from the PPB farmers by jotting down salient issues raised or observed during the discussions, field trial visits and evaluations. The parents with preferred traits were selected by the PPB participants and were used in development of new segregating germplasm in the hybridization block.

2.4 Results

2.4.1 Parents selected and preferred traits

The fourteen parents selected by farmers and their characteristics and needs for improvement are indicated in Table 2.1. The materials selected were from CIAT, Africa Rice Centre and IRRI (the IRRI lines were evaluated under screen house as they arrived late and farmers selected IR79913-B-176-B-4 line). The main selection criteria were nutrient use efficiency, earliness, grain quality and insect pests and disease resistance among others. They also selected the cultivar they grow as a parent due to its grain quality.

Table 2.1 Rice lines selected by farmers as parents for the hybridization block.

Diallel No.	Final selected line	Line	Source of lines	Traits	Improvement required
1	36	Nerica 1	WARDA	High grain quality, early, blast resistant	Yield, height
2	35	Duorado	Cultivar	Local cultivar, high grain quality	Yield, height, low fertility tolerance
3	34	IR79913-B-176-B-4	IRRI	Early, low soil N & P Tolerant	yield, panicle aspect
4	25	CT16333(1)-CA-20-M	CIAT-Columbia	Medium maturity, high yielding	Low soil N & P tolerance
5	22	CT16333(1)-CA-22-M	CIAT-Columbia	Tall, Low soil N and P tolerant, good panicles	Yield, earliness
6	13	CT16333(2)-CA-18-M	CIAT-Columbia	Low soil P tolerant, narrow long grains	Yield, tallness
7	9	CT16313-CA-19-M	CIAT-Columbia	Early, blast tolerant, good plant aspect	Yield, threshability
8	11	WAB964-B-3A 1.2	WARDA	Early, high yielding, good plant aspect	Low soil N & P tolerance
9	20	CT16317-CA-4-M	CIAT-Columbia	Low soil N tolerant, high tillering, tall	Yield, grain shape
10	2	CT16307-CA-14-M	CIAT-Columbia	Narrow slender long grains, tall	Yield, low soil N & P tolerance
11	3	CT16337-CA-12-M	CIAT-Columbia	Long panicles, medium maturity, tall	Yield, low soil N & P tolerance
12	6	CT16345-CA-3-M	CIAT-Columbia	High tillering, early, low N and P tolerance	Yield, pest & disease resistance
13	7	WAB 905-B-4A 1.1	WARDA	Tall, Low soil N and P tolerant, good plant aspect	Yield, pest & disease resistance
14	21	WAB 450-B-136-HB - Nerica9	WARDA	Earley, medium yield, disease resistance	Tallness, low soil N & P tolerance

2.4.2 Participating farmers' distribution per village

Seventy three per cent of the farmers engaged in OSHLQ were males. The number of participating farmers is shown in Table 2.2, of which Kirimara village had the largest number. This village is far from the main irrigated rice farming region and probably when they got information about upland rice that can grow in their aerobic conditions, they were highly interested and wanted to learn more thus the large number. In fact, during the PPB trial, they were always requesting for seeds to go and try in their farms. This indicates how eager the farmers were, such that they could not wait for new varieties to be developed. Luckily, their were some little quantities of the released four NERICAs' which were given out to them in small quantities. The numbers in the other villages were as selected by the agricultural office.

Table 2.2 Number of farmers per village

Village	No. of farmers	Per cent
Red soil	10	14.9
Kiorugari	15	22.4
Kirimara	21	31.3
Kathiriku	5	7.5
Mugumoini	7	10.4
Mathangauta	9	13.4
Total	67	100.0

2.4.3 Farmers preferred traits

The farmers disclosed a number of characteristics they wished to be improved. The top three preferences were high yield, hybrid (heterotic vigour), and input efficiency (Table 2.3). Some farmers felt that tall plants with long slender white grains and drought tolerant were important. More than half of the farmers (53.7%) considered yield and nutrient use-efficient varieties to be very important. Surprisingly, rice hybrids were preferred as they thought that these could yield more as it is the case with hybrid maize and tomatoes. They compared hybrid maize to open pollinated maize varieties (OPVs), and they were convinced that, although no hybrid rice is grown, it could be high yielding. Almost 15% of the farmers considered pests and disease tolerance as an important factor in varieties they would wish to grow (Table 2.3). Some farmers felt that varieties combining pests and diseases resistance, early maturity, high yielding and easy to thresh to be important. Others indicated drought tolerant varieties as being important for areas without irrigation water. The upland NERICA 4 variety is difficult to thresh and farmers have complained of this issue and probably this was one reason of desiring varieties with intermediate shattering for easy threshing. The weeds were also indentified as a problem,

where farmers believed that some varieties have capacity to suppress the weeds, thus leading to few weeding rounds and thus making savings on labour and herbicide costs. This results in fewer sprayings of both pre- and post-emergent herbicides that can be adverse to the environmental health and sanitation, especially where aqua-culture is being practiced.

Table 2.3 Traits farmers wished to be improved in rice varieties they produce

Trait	No. of farmers	Percent
Hybrids rice	12	17.9
Pest and disease resistance	10	14.9
Drought tolerance	8	10.4
Varieties with less fertilizers use	11	16.4
High yielding and easy to thresh varieties	13	19.4
Varieties with better grain quality	7	11.9
Early maturing varieties	3	4.5
Taller varieties with weed suppression traits	3	4.4
Total	67	100.0

2.4.4 Crops grown by the farmers and hectarage per village

Farmers grew a variety of crops, among which rice was the most widely grown followed by maize. The majority of the farmers who grew the widest range of crops were those of Kirimara village. As Table 2.4 shows, they had maize followed by rice as the main crops grown in terms of hectarage. At Red Soil village, the lowest crop diversity was observed with rice being second after Kiorugari village.

The number of respondents growing rice were 44 (65.7%), those not growing 18 (26.9%) while, 5 (7.5%) did not respond (Fig. 2.1). Mathangauta and Kirimara villages had farmers who did not grow rice, possibly because they are rainfed areas away from the scheme and they did not have upland rice seeds. There were 65.7% of respondents growing irrigated rice, while 17 grew upland rice. The irrigated varieties grown were aromatic Basmati 370, Basmati 217 and other non-aromatic; Basmati 196, IR and Sindano. The main variety grown was Basmati 370 (34%) followed by Basmati 196. The latter is mainly used for domestic consumption, while, the Basmati 370 is a cash crop thus the popular term ‘white gold’ due to its white grain colour and it fetches premium price on the market. The upland rice varieties grown were NERICA 10 (29%), NERICA 4 (3%) and NERICA 1 (1%). The low number of farmers growing NERICA 4 and NERICA 1 was that, NERICA 4 is hard to thresh, while NERICA 1 despite being aromatic had very low yields. It also emerged that these varieties require high inputs, which were not affordable by the respondents. Other reasons were that seed was not available unlike for

irrigated rice; production procedures for upland rice were not well known since they were new, and no advice or information of their production was available to the farmers.

Table 2.4 Types of crops grown and area of production (hectares) for surveyed farmers

Crop	**Village**						
	Red soil	Kiorugari	Kirimara	Kathiriku	Mugumoini	Mathangauta	Total hectarage
				hectares			
Rice	20	33.00	9.80	0.00	9.50	9.00	81.30
Beans	10	10.50	7.20	1.30	2.00	5.30	36.20
Maize	5	10.50	10.50	2.50	10.25	16.5	55.30
Water melons			6.30				6.30
Sukuma wiki			0.60				0.60
Irish potatoes			2.10				2.07
Sorghum			4.50				4.50
Cowpeas			4.50				4.50
Tomatoes				1.30	3.80		5.00
Bananas				1.30	2.00		3.30

The reasons given for growing upland rice was that, it was less tasking to grow, requires less water, less spraying, availability of land was not a problem, it's easy to weed and move around, and it can be intercropped. The respondents who preferred growing irrigated rice were 14.9%, 38.8% preferred upland and 46.3% had a preference for both production ecologies (Fig. 2.2).

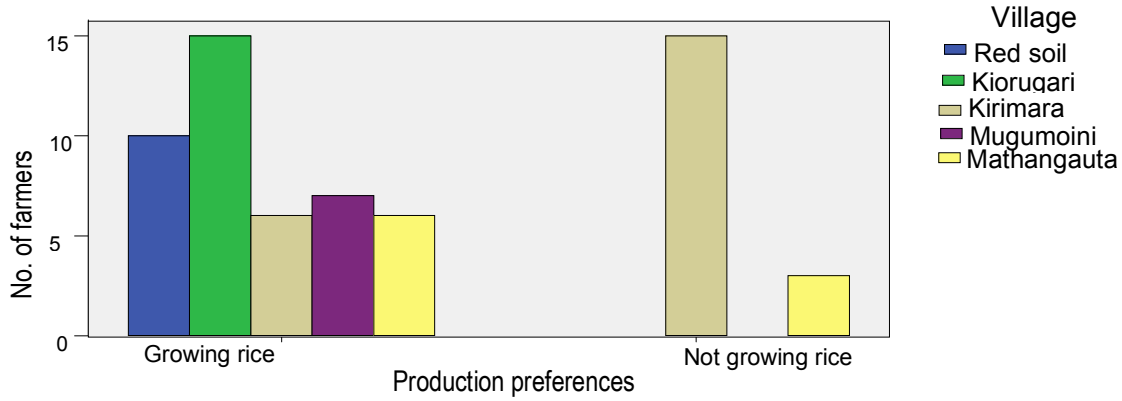

Figure 2.1 The number of respondents involved in rice production per village

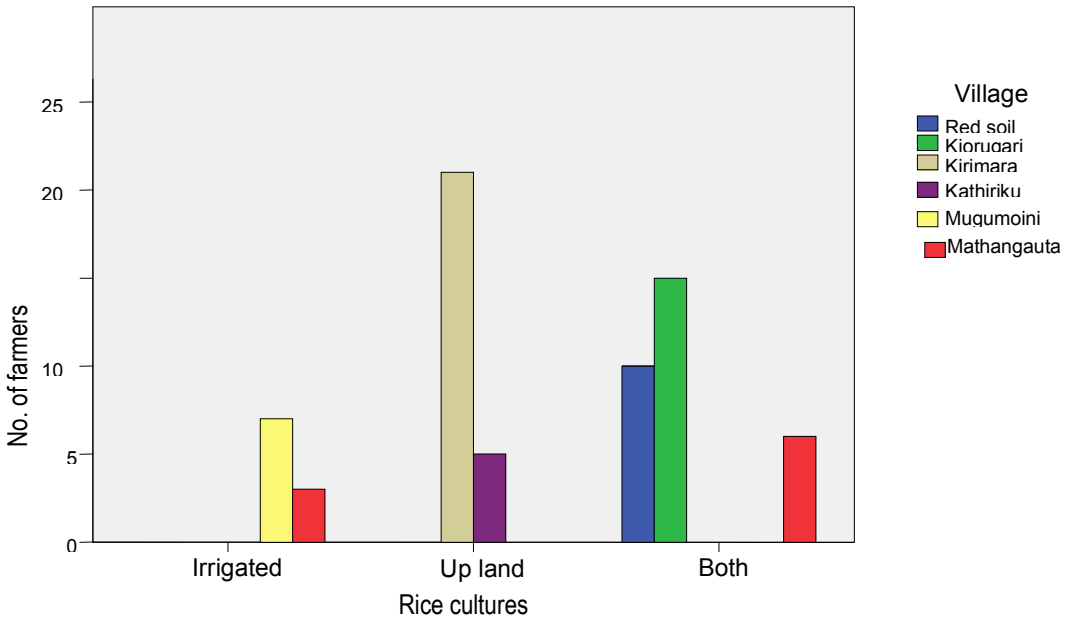

Figure 2.2 The number of respondents involved in rice production

2.4.5 Rice hectarage and number of participating farmers

The hectarage for rice ranged from 0.00 to 4.00 hectares among villages, with majority of the farmers (25.4% of respondents) each owning 0.00 and 2.00 hectares (Fig. 2.3). This was followed by 12 respondents (17.9%) who each produced rice on a 1.00 hectare. The figure of 0.00 hectares indicate farmers who rent land for rice production because they are landless. Overall, land ownership is shown in Fig. 2.3.

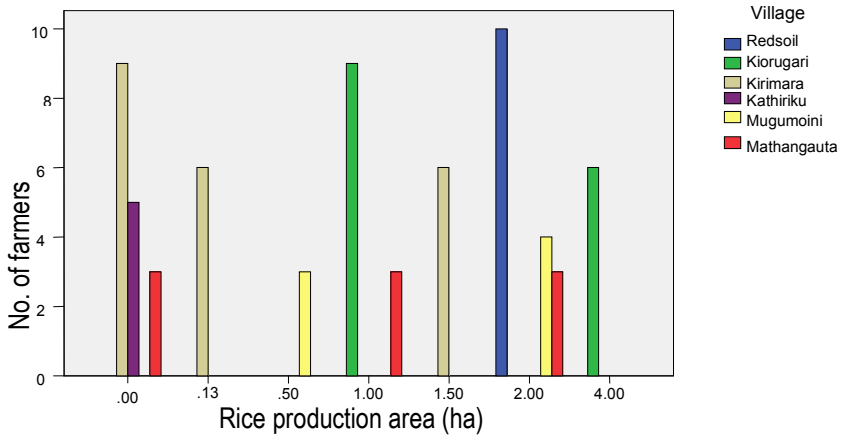

Figure 2.3 The hectarage and number of farmers involved in rice production village^{-1}

2.4.6 Fertilizer usage and other farm inputs for production

The majority of respondents 77.6% used inorganic fertilizers with only 9 indicating non-use, while 6 did not answer (Fig. 2.4). These were from Kirimara village. On rice production in particular, 70.1% of the respondents used fertilizer while 29.1% did not. The main fertilizers used were Diammonium super phosphate (DAP) followed by Calcium ammonium nitrate (CAN) and 23:23:0. These fertilizers were used in different combinations or singly depending on the crop and resource availability. The amounts used were in the region of 17 to 35 kg hectare^{-1} which is low (representing 19 to 40% of the recommended rates) for any meaningful crop productivity. The price of fertilizers has sharply gone up in the last three years and policy intervention by the government has not helped much. This has made many farmers to become desperate, in fact, many opting to scale down agricultural activities, while others resorting to use of more manure.

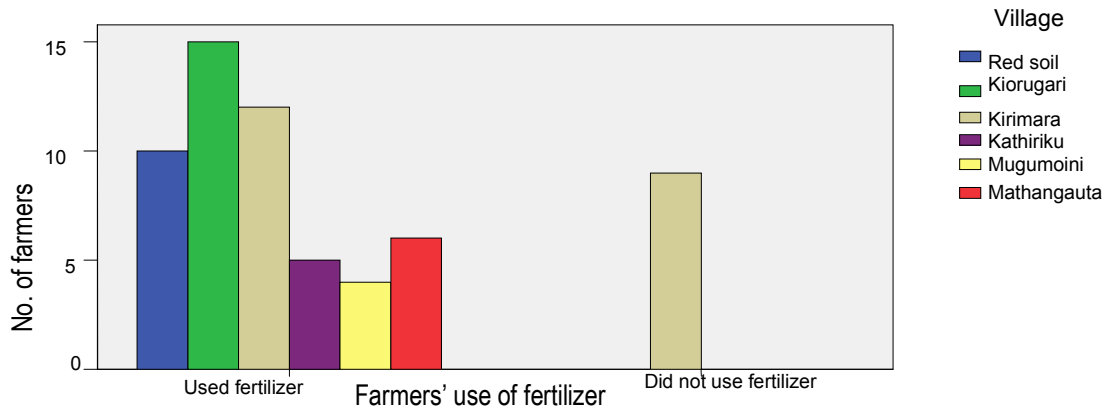

Figure 2.4 Respondents fertilizer use per village

The majority of farmers also used various forms of manure, though the quantities used were very small. There were three main types of manure used. Most of the farmers (52.2%) used farm yard manure (FYM), 37.3% farmers used animal manure and 28.4% of the farmers used compost manure, but these were used in varied amounts according to availability. It emerged that more fertilizer and manure were used on rice production though the amounts used were below the recommended rates, with irrigated rice being top dressed with sulphate of ammonia (SA), while with upland rice CAN was the one used. In terms of usage, Diammonium Phosphate (DAP), CAN and SA were the most applied fertilizers in that order.

The manure usage has resulted in other unforeseen problems like bringing new weeds and diseases, more so because it's normally not well prepared or decomposed to kill any weed seeds, pests and pathogens. The farmers have consequently been forced to use more labour, pesticides and fungicides.

2.4.7 Number of farmers and hectarage used for other crop apart from rice production

In the rice production region, land is very competitive as it is near Nairobi city. This area is predominantly used to grow horticultural crops. The land holdings are small and hence, farmers have to make important decisions on what to grow based on returns and seasons. However, rice is very important as indicated by area of its production (Fig. 2.3). The hectarage devoted to rice production ranged from 0.13 to 4.00 ha, with the latter being found at Kiorugari village. The lowest hectarage was found at Kirimara followed by Mugomoini and Mathangauta villages. Farmers from Kirimara, Kathiriku and Mathangauta used mainly rented land to produce rice. This was in contrast to other crop production, as the lowest hectarage was 0.75 ha (Fig. 2.5).
A good number of the respondents felt that the area under crop production was decreasing. Respondents from three villages; Kiorugari, Kathiriku and Mathangauta felt that it was diminishing, while those of Red soil village felt that it was increasing. However, two villages; Kirimara and Mugumoini had divided opinion but in favour of increasing crop land (Fig. 2.6). In total, 65.7% and 34.3% of the respondents indicated decreasing and increasing crop land area, respectively. The main reasons advanced for decreasing land area were growing population, infrastructure, high cost of inputs, poor soil health, crop diseases, lack of rain, decreasing returns from rented land, lack of markets for farm produce and high labour cost. The increase was due to opening of new land and farmers opting for rice production after scaling down production of other crops.

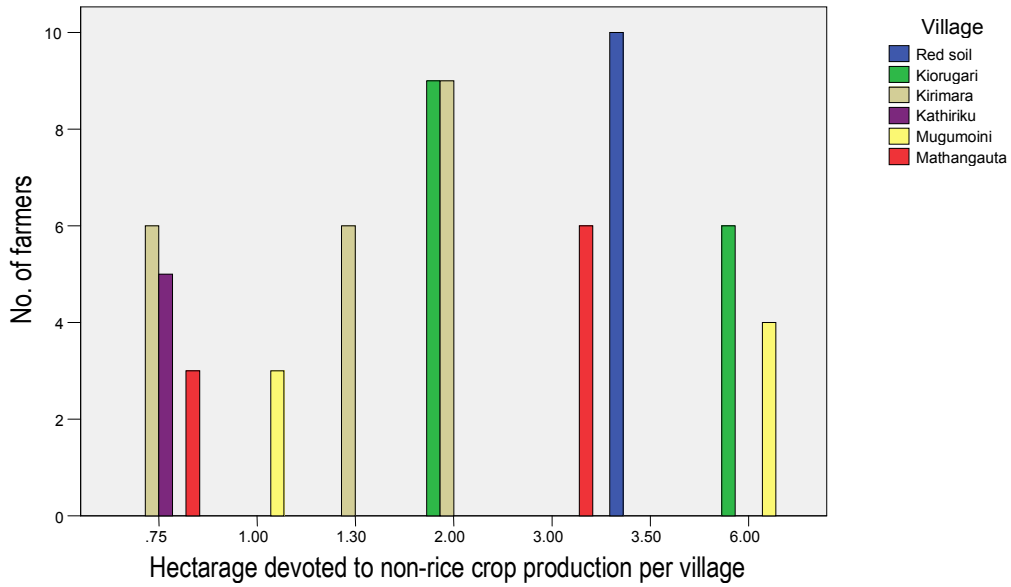

Figure 2.5 The hectarage and number of farmers involved in non- rice crop production per village

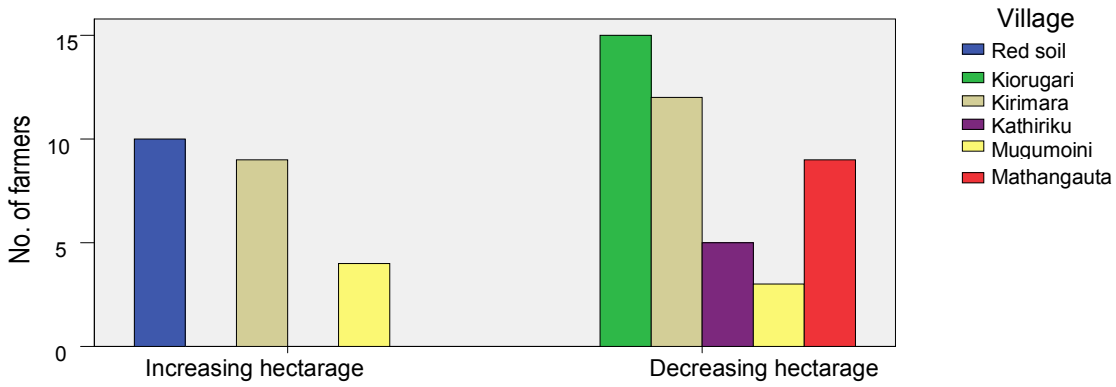

Figure 2.6 The perception of farmers on agricultural land trend under crop production per village

2.4.8 Respondents perceived farming challenges

There were many problems enumerated by the farmers during the focus group discussion, and key informants as listed in Table 2.5.

Table 2.5 Farmers perceived production constraints and their rankings

Problem	% of respondents (n=67)	Rank
Lack of production knowledge	19.4	13
Lack of certified seeds	28.4	9
High input costs	52.2	1
Pest and diseases	20.9	12
Lack of appropriate varieties	29.9	8
Lack of affordable machinery and implements	32.8	7
Lack of market for the produce	22.4	11
Low prices for the produce	34.3	6
High labour costs	37.3	5
Lack of water	38.8	4
Lack of resources (capital)	44.8	2
Low and unpredictable rainfall	41.8	3
High cost of rented land	25.4	10

The most limiting problems emerged to be high input costs, lack of funds, low and unpredictable rain. Even though the region has irrigation water, the farmers still considered water as a problem, mainly because the open earth canal water levels were low most of the times, especially when they needed it most. The low water levels were cited as the cause of most of their land remaining idle as water was rationed and directed to only one part of the irrigation scheme. They also felt that the water conveyance system had a lot of wastage through direct evaporation, transpiration from the luxuriant vegetation growing along the canal and seepage during its transmission.

When respondents were asked how they tried to solve the above problems, their coping strategies were varied and their success to differed in addressing some of the problems as indicated in Table 2.6. The problem of poor soil fertility was widely known to the majority of them. They indicated that due to continued cultivation and lack of or expensive manure, the land had greatly degenerated in fertility and soil structure. They indicated that they sought help and advice from the research station, extension services and from fellow farmers. The lack of certified rice seeds was a serious one and farmers had to resort to using their own farm saved seed or form groups and buy from research stations or national irrigation board (NIB) and in the worst cases they just bought from the market.

Table 2.6 Farmers coping strategies for the perceived rice production constraints

Problem	Coping strategy
Lack of production knowledge	Visit KARI, extension services and fellow farmers
Lack of certified seeds	Use farm saved seed, buy as a group, and from market
High input costs	Use manure and botanicals pesticides and fungicides
Pest and diseases	Spraying, field rotation and sanitation, use of resistant varieties
Lack of appropriate varieties	Seek from KARI, NIB, & seed companies for improved varieties
Lack of affordable machinery & implements	Switch to less demanding crops
Lack of market access for the produce	Store crop for better prices, direct sales without brokers
Low prices for the produce	Process, are helpless and desperate
High labour costs	Self hand till, rent out land
Lack of water	Switch to crops with less water requirement
Lack of resources (capital)	Borrow from friends, banks, merchants, rent out land
Low and unpredictable rain	Do water conservation farming
High cost of rented land	Rent land during low crop season

2.4.9 Rice productivity

The rice yields were reported to be generally low, unlike in the 1970-80's when they were high and the country was self sufficient. According to focussed group discussions and key informants, the yields were perceived to have dropped by more than half generally, while the cost of production had more than tripled. This was attributed to lack of rice research (rice has been an orphan crop, until around 2003 when it was recognized to have immense potential and thus research mandate was transferred from NIB to KARI), use of old varieties that have deteriorated over time and decline in soil fertility. They were in agreement that new varieties were long overdue and that these should be able to cope and be productive under the prevailing farmers' production environments. The majority of the respondents did not produce more than 2500 kg paddy ha^{-1} (Fig 2.7). However, Red soil and Kiorugari villages were able to surpass this as these are the so called "jua kali" farmers, meaning they are opening new fertile land for rice production outside the traditional NIB scheme.

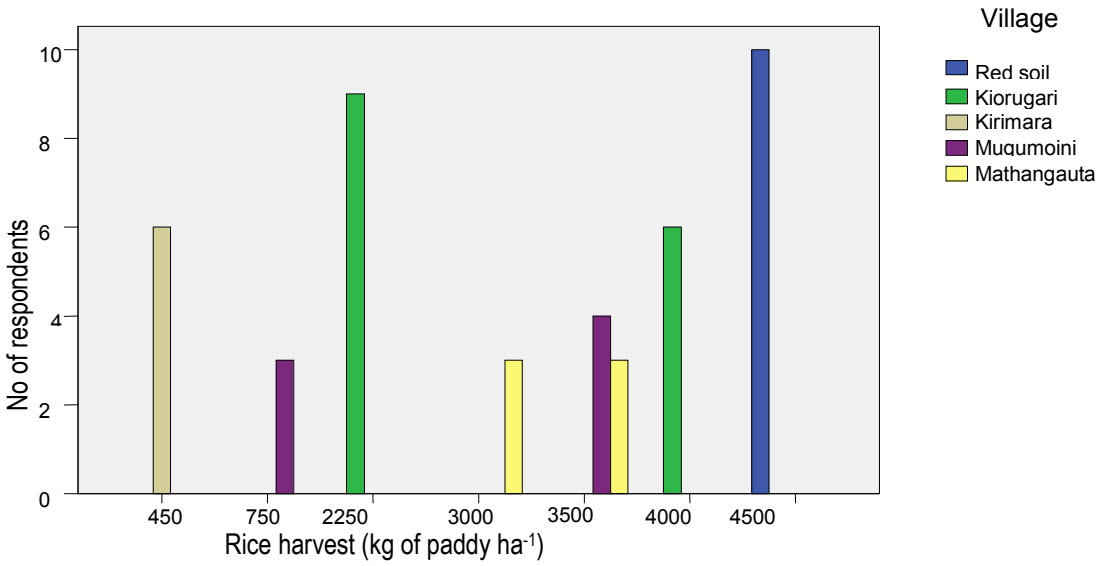

Figure 2.7 The number of respondents and rice production figures per village

2.5 Discussion

2.5.1 Preferred variety traits by the farmers

Farmers ranked the top three among others traits of rice varieties of their interest as high yields (19.4%), hybrids varieties (17.9%) and nutrient use efficiency (16.4%) (Table 2.2). The preference for hybrid rice varieties was a surprise, and probably they were influenced in making that choice because of performance of other hybrids like maize, pepper and tomatoes. It may have again occurred as a result of low yields despite fertilizer use that was now common in their fields and they may have heard about hybrid rice. Hybrid rice was successfully introduced in Asia and it's a success case in china where over 50% of the rice area is under hybrid rice (Virmani et al., 2003). Today over 20 countries worldwide are producing hybrid rice with yields of up to 10.5 t ha^{-1} from two line hybrids, by use of either photoperiod sensitive or thermosensitive genetic male sterility. Thus there is no doubt hybrid rice has superior yields but these are high input dependent currently (Virmani et al., 2003). The solution for low yield was thought to come from use of hybrid varieties, use of nutrient use efficient varieties and growing pests and disease resistant varieties. Varieties that are easy to thresh and taller were also preferred. Even though farmers preferred hybrid and taller rice, there are implication and

challenges such as hybrid seed production and yield penalty due to lodging in case of high N use and reduced harvest index (HI). This could mean searching for parents and breed for higher yield and non-lodging taller plants for easy harvesting and use of culms for feeds and other by products like making hats and thatching. The hybrid rice could imply use of male sterile lines as it is the case in China.

The top biomass is a trait valued by farmers for animal feed, and in recent years in Kenya, it has gained popularity as it is baled for animal feed. The cost of a bale is USD 3.3 serving as an extra income to the farmers. Thus the more the biomass, the better the price. Otherwise, the farmers used to burn the culms and thus control pests and diseases as well as enhancing soil fertility. This situation has changed and due to mining of soil nutrients through culm export for animal feed, and farm inputs being expensive, the soils are bound to deteriorate even further in terms of fertility and resurgence of diseases and pests may occur. The lack of organic matter and carbon, the important soil traits like soil texture and structure, C:N, C:K, N:K and other ratios may be disturbed negatively. This could further have an effect on soil microbial activities, and may reduce the rate of organic matter decomposition and nutrients availability. This behaviour of removing culms probably has led to silicon mining, an important element for cell wall membrane integrity and thus reduced defence mechanism against certain diseases. The recent highly devastating outbreaks of rice blast may have been influenced by culm removal (Newspaper, 2008). It is now a concern that transport of culms to other part of the country may introduce new pests and diseases, or elevate them to cause economic damage.

The respondents argued that some yield loss was associated with difficult threshing varieties like NERICA 4 as some grains remained behind and that it was also expensive because more labour was needed (Jiddah, 2009). They felt that easy to thresh varieties were cost effective as many bags would be threshed within a short period, especially given that labour is expensive, let alone the low head rice (% of milled grain compared to dehulled grains) and broken grains that results from sticky varieties due to use of excessive force for dislodging the firmly held grain. They further observed that, the resulting milled grains were of low quality and thus fetched low market prices, leading to lowering of profits.

2.5.2 Diversity of crops grown by the farmers

Among the crops grown by farmers, rice was ranked top followed by maize and in third place beans. The widest range of crops grown was found in Kirimara village, while lowest crop diversity was at Red soil village (Table 2.4). The number of respondents growing rice was 65.7% and this indicates how rice as an economic activity is very important. Mathangauta, Kathiriku and Kirimara had farmers who did not grow rice, probably because of lack of upland rice seeds and lack of irrigation water. This is despite their desire to have rice crop as an economic activity, given that rice is one of the most profitable enterprises and storage of dry grains does not require elaborate means like for the fresh vegetables such as French beans, tomatoes and baby corn among others. In terms of hectarage, farmers with about two hectares were 47.8%, while those with more than 2.5 ha were 52.3% (Fig. 2.3). Kiorugari village had the highest proportion of farmers growing rice on bigger hectarage when compared to the other villages. It was revealed that this village produced the best quality rice, a belief that had been held but not confirmed, it has been argued that this is because of the moderately warmer water in the Thiba River in that area and generally the environmental temperatures were a bit cooler than in the other areas during rice maturing stage (Bhattacharjee et al., 2002).

2.5.3 Perception of farmers on rice varieties

Among the varieties grown by farmers were the recently released NERICA varieties and farmers were of the opinion that these were high input dependent varieties and since the inputs were expensive, the farmers were only growing them on small plots. The farmers also cited lack of information on their production and lack of seed as the other reason for low adoption. It emerged that if farmers had less capacity to buy inputs they were more interested in producing an old variety BW196 that is used for domestic consumption due to poor grain quality, although its yields were higher on average; because they felt that it was a nutrient use efficient variety that gave economic yield even with minimum inputs. Although farmers (77.6%) used fertilizers (Fig. 2.4) the amounts used were low (17-35 kg ha^{-1}) for any significant economic gain. The recent rise in fertilizer prices has forced farmers to reduce further, the quantities used and even some farmers abandoning crops perceived to be highly dependent on high inputs. They argued that producing these high input dependent crops and even rice is uneconomical because yield realized could not meet the cost of production, especially given that labour is also expensive. This has forced farmers to scale down on magnitude of hectarage of such crops like rice, maize

and beans, and some farmers have resorted to upland rice production. The upland rice seemed popular due to its flexibility in its production practices that resulted into lower labour costs, especially for land preparation, planting, weeding and even spraying, unlike the paddy rice grown under difficult paddy conditions. It emerged that while the majority of males preferred growing both upland and irrigated rice, majority of the women preferred upland rice. Kirimara and Kiorugari village had the highest respondents opting for upland and both rice cultures, respectively (Fig.2.2).

It emerged that the input cost was a major inhibitory factor to rice production among other factors like lack of new varieties adapted to the production environments and unavailability of certified seeds. It is imperative then that ways of addressing these constraints be devised, and such solutions should be sustainable if consistent high yields are to be realized. Development of such new genotypes that meet the farmers' preferences is one way and this can be achieved by actively involving the farmers in the whole development process (Walker, 2008; World Bank Group, 2007). Of course not all farmers' problems can be addressed as some are more of policy issues, but some key ones like variety development can be accomplished. It was clear from the study that local farmers as is the case elsewhere, generally preferred high yielding varieties with high nutrient and water use efficiency and that some farmers favoured tall rice plants (Atlin *et al.*, 2006a; Efisue *et al.*, 2008; Morris and Bellon, 2004). The reasons for farmers preference of tall varieties was due to biomass that provide an extra income generated from sale of the by-product (culms) as animal feed and that it is easy to work and harvest the crop a notion expressed also in West Africa (Efisue et al., 2008). The drought that occurred in the year 2008 was severe such that the demand for rice culms was high and this pushed its price up. However, harvest index is negatively associated with taller plants due to factors like lodging, photosynthetic partitioning. The other reason farmers gave for preference of tall plants is that short varieties are near the ground and thus rodents, flooding and splash water, ground walking birds and termites tend to destroy the grains. They also argued that birds find it easy to perch on them because they are relatively stronger than the taller varieties that are easily swayed by slight wind movement.

The development of dual purpose varieties is an option that should be explored. The varied farmers' preferences or tastes can widely be incorporated through a breeding programme because most of the traits are heritable. The challenge is how should the farmers' best participate in the breeding process so that their aspirations are met and incorporated in the end

product. This is one way of ensuring that farmers know the products and can therefore easily adopt them leading to high and sustainable productivity.

2.5.4 Farmers participation in breeding

The outcome of the survey and PPB in the aspect of parent selection for hybridization was that farmers knew what traits were important (Table 2.3). The farmers were able to express their preferences and for a broader participation, given that upland rice production was relatively new to them, a PPB approach was adopted. The more resource based PPB was chosen, instead of the rapid and cost effective PVS, because there were no choices of cultivars (Witcombe et al., 2003; Witcombe and Joshi, 2003). The other reason was that this approach would help expose them to a wide array of agronomic practices and thus build their confidence in production of the newly released upland varieties. The farmers were involved in the actual planting of the accessions plus the cultivar and were free to visit the site located in the research station. When the crop was mature, they were invited to select the best materials based on their preferred traits of which 45 genotypes were selected, and later narrowed them to 14 from 390. The major selection criteria was high yield, large and well filled panicles, narrow long grains, healthy and tall plants that were fairly early maturing (Table 2.3). The farmers selection and preference criteria differed with that of breeders in that their quest was for hybrid varieties and taller plants. However breeders go for shorter varieties that do not lodge under heavy N use and have high HI. They also go for pure lines or other varieties because mass production of hybrid seed and its sustainability is not easy for rice which is self pollinated crop.

One major issue that respondents highlighted was lack of certified seeds and this was obvious as they desperately wanted the little seeds that were harvested for further hybridization and even selections from segregating materials. These genotypes are now in the fourth filial generation and soon they will be put into national performance trials for release by the regulatory authority. Sthapit et al. (1995), Joshi and Witcombe (1995) have used PPB to develop chilling tolerant rice and broadly based maize composite in Nepal and India, respectively. Salazar (1992) used PPB in rice breeding in Philippines where farmers selected promising materials from progenies of crosses involving traditional and modern varieties, but the method used is not explained.

2.6 Conclusion and Recommendation

It has been revealed that farmers are faced with many problems and limitations and that farmers are very particular on the varieties they desire to cultivate based on various attributes and for what purpose; such as for domestic consumption, local market or far market for income generation. The main production constraints were high input costs, drought, high labour costs, lack of certified seeds and lack of production knowledge. The farmers had preferences such as high yields (as indicated by farmers wishing to even grow hybrid rice), nutrient use efficiency, easy to thresh varieties, high grain quality especially fragrance and tall varieties that provide biomass for animal feed. It became evident that there was no variety that meet majority of farmers preferences probably because the existing varieties were developed without farmers involvement and thus their desires in a variety were not met. It was also disclosed that farmers are more eager to participate and adopt new varieties that will meet their perceived set criteria such as high yields, less input requirements, easy to thresh and tolerant to pests and diseases.

From this, it is highly recommended that farmers' participation be part and parcel of the breeding programmes and that farmers' preferences be incorporated in the programmes so that the end products are complete package of farmers' aspiration and wants. It is also important to adopt the PPB approach where farmers input and preferences will be captured in the variety development in the rice value chain and this may spur wider varietal adoption and thus higher rice productivity and an economical venture.

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CHAPTER THREE.

Characterization and Selection of Upland Rice Germplasm under Low and High Soil Phosphorous (P) and Nitrogen (N) Environments

Abstract

No studies have been carried out to determine performance of rice genotypes at low or high soil fertility in Kenya and elsewhere in developing countries where rice is grown under low fertilizer inputs. The 389 accessions and the local cultivar *Duorado precoce* were evaluated in a simple 30 x 13 alpha lattice design with two replications under four experimental environments (N-P-, N-P+, N+P- and N+P+) at the rate of 60 kg P and 90 kg N ha^{-1}. Data on Days to heading (days), anthesis and maturity, P and N tolerance, plant height (cm), above ground biomass (g), number of panicles (absolute numbers per ten plants), days to maturity (days), 1000 grain weight (g), and grain yield (kg ha^{-1}). The genotypes and environments were highly significant for all the traits studied. The degree of genetic determination (H^2) ranged from 8.0% for 1000-grain weight to 26.7% for above ground biomass. Thus inheritance of these traits is low thus limiting mass selection. The phenotypic coefficient of variation of genotypes ranged from 12.3% for days to maturity to 148.5% for above ground biomass, while that of days to maturity ranged from 14.3% to 159.7% for top biomass. The genetic advance (GA) had values ranging from, 0.2 for phosphorous tolerance to 1080.5 for grain yield, while the genetic advance expressed as percent of the mean was 5.7% for days to maturity and 87.9% for top biomass. The top biomass seems to be highly heritable trait and simple phenotypic selection is possible. The ten characters studied had wide variability under the four environments with days to maturity ranging from 188 for genotype ARCCU1Fa1-L4P3-HB under N+P+ to 177 for genotype CT16333(1)-CA-1-M under N-P- condition. The highest yielding genotype was CT16328-CA-18-M under N-P- with 5916 kg ha^{-1}. The germplasm showed usable variability for low soil N and P adaptation, and hence improvement was possible to take advantage of the vast unexploited upland environments for increased rice productivity. There was high variability in the genotypes to warrant rice improvement for yield.

3.1 Introduction

In Kenya, rice is an important staple food crop after maize and wheat, but it is grown under low fertility conditions resulting in low yields. Rice forms part of the diet and source of employment and income for both urban and rural populations. The domestic production oscillates between 45-

80,000 MT, while total national consumption is well above 300,000MT (Rosemary et al., 2010). This creates a deficit of more than 250,000 MT that has to be met through imports. The over 80% deficit cost the country about USD 90 million in imports from Pakistan, China, India and Vietnam (Monem, 2005). The current state of low productivity of the rice sector is worrisome, the rate of consumption is growing at 12% when the domestic production has stagnated for the last couple of years (MoA, 2009).

The development of upland rice varieties that have the end user traits can greatly contribute to higher adoption rate (Poussin et al., 2006). This, coupled by the fact that upland rice is unexploited despite the gigantic potential it has in terms of land availability and ease of cultivation, can unlock the current status of deficit rice production (MoA, 2009). However, the cultivars lack low soil N and P tolerance. The breeding methodologies must be embraced that encompass the full participation of end users of the technology being developed, use of the appropriate germplasm with the desirable genes that carry the traits of interest. Further, use of breeding methodologies in terms of mating designs and evaluation or environmental designs together with the use of proper data analytical software and interpretation of the results is vital if the desired result are to be realized (Atlin *et al.*, 2006a; Christiansen and Lewis, 1982; De-Datta *et al.*, 2002; Fasoula and Fasoula, 1997; Fasoula and Fasoula, 2000; Fukai *et al.*, 1999a). The genetics and variances contributing to the traits of interest should be determined and to make correct decisions regarding the varieties being used as parents and the progenies (Allard, 1960; Borojevi'c, 1990; Falconer, 1989; Simmonds and Smartt, 1999). If the genes conferring a sought trait are not present in the breeding materials used in a programme, even if all the other steps are correct; this is a total waste of time as no positive results can be realized (Ceccarelli, 1994; Presterl et al., 2003). It is therefore, of paramount importance that the germplasm being used for breeding purposes must contain the genes that confer the traits of interest (Chahal and Gosal, 2002; Falconer and Mackay, 1996; Hallauer and Miranda, 1989). Every effort should be made to ensure evaluation stress is present and that the 'cooking pot' has all the desirable ingredients for the sought end product technology to be of any value to the users (Banziger et al., 2006; Edmeades et al., 1997). It is for these reasons that germplasm was acquired and characterization carried out for the breeding program in Kenya.

In Kenya, rice breeding work has been lacking and no home grown varieties have therefore, been developed. The current varieties are from accessions from other parts of the world, of which the production condition are different to the local production environments. No attempts have been

made to breed for local genotypes tailored to perform under the prevailing poor soil fertility conditions that are rampant. The existing materials were acquired years ago, and their acquisition criteria have since changed and thus these materials are less relevant now. There is a strong need to acquire new accessions with the desirable qualities and traits, and evaluate them for adaptability under local production environments before selecting some to supplement the few existing one for breeding work. The need for genetic base broadening germplasm lead to acquisition of 390 lines that were requested on their tolerance to low soil N and P, good grain quality and drought tolerant. These were acquired in order to introduce gene systems missing in the local cultivars and hence their adaptation and characterization was necessary in order to determine their suitability and performance under Kenyan conditions. This also allowed selection of those adapted lines with the sought traits for use in hybridization programme to improve the local cultivars. The early maturing, well adapted lines to low soil N and P and with desirable grain qualities were the main traits sought.

3.2 Study objectives

The rationale of the study was to evaluate and select adapted promising genotypes with desirable genes for low soil P and N from the broad germplasm accession for hybridization with the local cultivars.

The specific objectives were to:

i. characterize the accessions for various agronomic traits under local conditions and different soil P and N conditions,
ii. determine variation and some genetic parameters responsible for performance under low and high soil P and N conditions, and
iii. identify adapted lines from the accessions to be used as parents in the breeding programme.

3.2.1 Hypothesis

There is large genetic variation for tolerance to low soil N and P conditions in rice genotypes that can be exploited in breeding new varieties.

3.3 Materials and Methods

3.3.1 Study location

KARI- Mwea Tebere (National Rice and Fiber Research Centre (NRFRC)) is located in Mwea Division, Kirinyaga South District, Central Province, Kenya. The Centre is 21 km South West of Embu town and about 112 km North East of Nairobi. It lies on Latitude 00^{o} 37' S and Longitude 37^{o} 20' E at an elevation of 1159 m above sea level (MASL). The average rainfall is about 850 mm with a range of 500 - 1250 mm divided into long rains (March – June with an average of 450 mm) and short rains (Mid-October to December with an average of 350 mm). The rainfall is characterized by uneven distribution in total amounts, time and space. The temperature ranges from 15.6º C to 28.6º C with a mean of about 22ºC. The soil is a nitosol, which is deep, well drained dusky-red to dark reddish-brown, friable clay with low fertility (Jaetzold and Schmidt, 1983).

3.3.2 Germplasm, experiment layout and trial management

Germplasm was sourced from different regions and it consisted of 314 lines from CIAT Columbia, 75 lines from Africa Rice Centre and the local check *Dourado precoce* (Appendix 3.1). The four experimental environments were blocks that had no P and N applied (N-P-), P applied only (N-P+), N applied only (N+P-) and both N and P applied (N+P+). The source of N and P were inorganic fertilizers calcium ammonium nitrate (CAN) and triple super phosphate (TSP-($CaHPO_4$)-32.5%), respectively. The P and N was applied as basal applications in the designated block at the rate of 60kg P ha^{-1} and 90 kg N ha^{-1}. The P was applied as basal during planting, while N was applied in two splits each 45 kg N ha^{-1} at planting and at panicle initiation stage. The soil was sampled in the 0-30 cm top soil layer over the experimental blocks. It was sampled in both diagonals at the four corners of the block, at the middle, between the corners, and between the middle of diagonals and corners making a total of 17 samples. These samples were analyzed separately and since they had almost the same values, these were composited and averaged. The soil analysis was carried out at JomoKenyatta University of Agriculture and Technology (JKCUAT) and had the properties indicated in Table 3.1.

The three hundred and ninety (390) accessions were planted out in an alpha lattice design arrangement as 30x13 replicated twice on 29th November, 2007. Fertilizer level was applied to the block, while genotypes were planted in the block. The experimental plot was 0.75 m^2 consisting of 34 plants. The inter- and intra-row spacing was 15cm. Three seeds were sown per hill and later

thinned to one. Normal cultural practices like weeding, spraying and harvesting were carried out manually. Supplementary sprinkler irrigation was only undertaken when necessary.

Table 3.1 Soil properties at KARI Mwea-Tebere location, plus N and P ranges

Parameter	Values	high	medium	low	Very low
$pH_{1:1}$	5.53				
ECe (Electrical conductivity)	0.11				
% N	0.16	>0.25	0.12-0.25	0.05-0.12	<0.05
Available P (ppm)	1.35	>18	10-17	5-9	<5
Extractable-Zn (ppm)	1.65				
Extractable-Cu (ppm)	8.52				
Extractable-Mn (ppm)	360				
Extractable-Fe (ppm)	379				

3.3.3 Data collection

Data on adaptation to local production environment was collected following the established standards for rice (IRRI, 2002) on the following traits; days to heading (days), days to anthesis (days), P tolerance (scale, 1-5), N tolerance (scale, 1-5), plant height (cm), top biomass (g), number of panicles for 10 plants (absolute numbers), days to maturity (days), 1000 grain wt (g), and grain weight ha^{-1} (kg). The nitrogen tolerance scale of 1-5 was used to measure leaf colour intensity which is related to leaf N status (Shukla et al., 2004) as follows; the leaf colour chart (LCC) developed at the International Rice Research Institute (IRRI, 2003) (Fig. 3.1) was used at booting stage. Ten disease free plants were selected randomly and the middle part of the top most leaf from each plant was placed on the LCC to compare the leaf colour. The value on LCC that matched the leaf colour was recorded and if the leaf colour fell between two LCC shades, the mean value was taken. This is a non-destructive method and readings were taken under the shade of the body to shield the sunlight as this would affect the colour reading. Plants that were N tolerant were given a score of one (but in LCC its 5) and those that were least tolerant were given a score of five (but in LCC its 5).

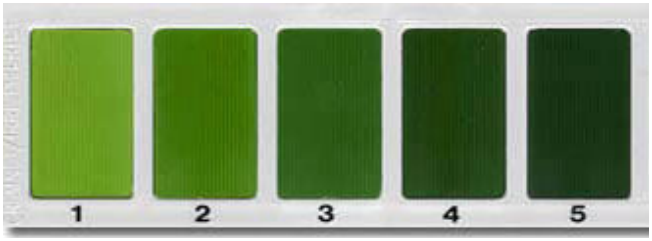

Figure 3.1 A leaf colour chart used to evaluate genotypes for nitrogen tolerance

The P tolerant scale was developed based on the following visual parameters of P deficiency that include; stunted growth, dull-green or blue-green colour, possible purple coloration on some part of the plant, reduced flowering, delayed maturity, leaf tips look burnt, followed by older leaves turning a dark green, and reddish-purple colour. The most P tolerant plants were rated one and these had normal vigorous growth without deficiency symptoms, while the least tolerant ones were rated five and these had high deficiency symptoms.

For the agronomic traits, ten plants were randomly selected for data collection and the early maturing lines were tagged with a different colour code of netting string, one colour per week for three weeks. The top biomass was taken from an area of 0.75 m^2 in grams (g) by cutting the culms at the ground level with a sickle. The harvested culms without panicles were dried to constant moisture and then weighed and data recorded. Plant height was measured as whole numbers (cm) from soil surface to the tip of the tallest panicle (awns excluded) (IRRI, 2002). Days to maturity were counted as number of days from seeding to grain ripening. One thousand seeds weight was measured at 14% moisture content using a precision balance. The yield was taken as the weight of unhulled grains harvested from an area of 0.75 m^2 and then converted to kg ha^{-1} at 14% moisture content.

3.3.4 Data analysis

The analysis of variance (ANOVA) was performed according to Gomez and Gomez (1984) using GenStat statistical package version 12 (Payne et al., 2009). The statistical model was $Y_{ijk} = \mu + \alpha_i + \beta_j + \varepsilon_k + \alpha\varepsilon_{ik} + \epsilon_{ijk}$,

where the term Y_{ijk} is the observed value of i^{th} genotype(i=1 to 390) in j^{th} replicate (j=1 to 2) for the k^{th} experimental environment, μ is the grand mean of the variable; α_i is the treatment effect for the i^{th} genotype, β_j is the block effect for j^{th} block; ε_k is the experimental effect for the k^{th} experimental environment, $\alpha\varepsilon_{ik}$ is the interaction term of i^{th} genotype in k^{th} experimental environment and ϵ_{ijk} is the random error associated with the Y_{ijk} experimental unit.

The genetic variances for the various traits were calculated following the method of Johnson et al. (1955) and Karim et al. (2007). Genetic parameters were calculated as follows:

i. Genetic variance (Vg) = (genotypic mean squares – error mean squares)/number of replicates.
ii. Phenotypic variance (Vp) = genotypic mean squares + error mean squares.
iii. The genotypic coefficient of variation (CVG) =(√vg/grand mean)*100
iv. Phenotype coefficient of variation (CVP) =(√vp/grand mean)*100

v. Heritability in the broad sense (H^2) was estimated following the method of (Allard, 1960; Falconer and Mackay, 1996; Holland et al., 2003; Johnson et al., 1955; Nyquist, 1991; Verma and Srivastava, 2004) as $H^2 = (Vg/Vp)*100$

vi. Genetic advance (GA) estimates $=(\sqrt{Vp}*H^2)*k$; where k=2.06 and it is the selection differential expressed in standard deviations (Karim et al., 2007), that assumed that 5% of the individual plants were selected from the population (Kearsey and Pooni., 1996).

vii. The percent genetic advance of the mean (GAM) = (GA/grand mean)*100

3.4 Results

3.4.1 Genetic components

The results of analysis of variance components showed that genotypic differences were very highly significant ($p<0.001$) for all the traits studied. This was also the case with experimental environments (Table 3.2). However, the interaction of genotypes by experimental environments was not significant ($p>0.05$) except for days to heading (DH), days to anthesis (DA), top biomass (TB) and days to maturity (DM).

The results of genetic components are shown in Table 3.2. The lowest Vg was for phosphorous tolerance (PT) and the highest for yield and this was also the case for Vp, except that nitrogen tolerance (NT) had the same Vp. The CVG was lowest for days to maturity and highest for top biomass (TB), this was the same case for CVP. The ranges for CVG and CVP were 12.3% - 148.5% and 14.3% to 159.7%, respectively. Broad sense heritability (H^2) estimates were highest for TB (36.5%) and lowest for PT (6.8%). The days to heading, days to anthesis, days to maturity and NT had a H^2 value of 23.9%. The genetic advance (GA) had the lowest value for phosphorous tolerance (PT) of 0.2 but the value was large for yield at 1080.5. The genetic advance as a percent of mean (GAM) was lowest for days to maturity (DM) but highest for top biomass (TB). The values for H^2, GA and GAM were generally low except for top biomass and yield.

Table 3.2 Mean squares and genetic parameters for ten rice traits across the four soil experimental environments

Table 3.2 Mean squares for various traits across the four experimental environments

Traits	DF	Days to heading (days)	Days to anthesis (days)	Phosphorous tolerance (scale 1-5)	Nitrogen tolerance (scale 1-5)	Plant height (cm)	Top biomass (g)	Number of panicles	Days to maturity (day)	1000 grain weight (g)	Yield (kg ha^{-1})
Source	DF										
Replication	1	752.6	435	4.313	86.0013	5215.5	169945	37773	435	183.51	9483000.0
Genotype	389	507***	494.1***	1.469***	1.959***	454.6***	1002130***	3989***	494.1***	57.25***	4346000***
Experimental environment	3	20595.9***	18058.2***	138.066***	74.7436***	3481.9***	1674391***	39612***	18058.2***	5022.78***	17000000***
Genotype.experimental environment	1167	216.1***	214.6***	1.028ns	0.702ns	133.4ns	181403***	960	214.6***	31.21ns	1305000ns
Residual	1559	178.4	174.7	1.119	0.6902	133.7	157061	1051	174.7	40.24	1173000.0
Mean		132.4	137.5	2.0	3.1	81.5	674.1	54.5	180.5	16.4	3639.0
Genotypic variance (Vg)		164.3	159.7	0.2	0.6	160.5	422534.5	1469.0	159.7	8.5	1586500.0
Phenotypic variance (Vp)		685.4	668.8	2.6	2.6	588.3	1159191.0	5040.0	668.8	97.5	5519000.0
Coeficient of variation of genotypes (CVG)		17.0	16.2	60.6	45.5	26.2	148.5	115.9	12.3	46.1	57.3
Coeficient of variation of phenotypes (CVP)		19.8	18.8	80.5	52.9	29.8	159.7	130.3	14.3	60.2	64.6
Broad sense heritability (H^2)		23.9	23.9	6.8	23.9	27.3	36.5	29.1	23.9	8.7	28.7
Genetic advance (GA)		10.4	10.3	0.2	0.6	10.7	592.5	33.0	10.3	1.6	1080.5
Genetic advance as % of mean (GAM)		7.9	7.5	10.5	21.1	13.1	87.9	60.6	5.7	10.0	29.7

*** Significant at P < 0.001

ns Non significant at P < 0.05

3.4.2 Genotypic performance under the four experimental environments

Different genotypes performed differently and their ranks varied under the four experimental environments. The earliest line to head was 39 (Caiapo) under N-P+ fertility condition (Table 3.3). It was the earliest in the other soil N and P fertility conditions except under N-P-. Some genotypes however, were poorly adapted like 272 (CT16345-CA-12-M) and 303 (CT16350-CA-27-M) which headed in 167 and 160 days, respectively.

Table 3.3 The mean values of days to heading (DH), anthesis (DA), maturity (DM) and number of panicles for rice under four soil N and P conditions (highlighted were selected as parents)

	Days to heading (days)							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	368	92.5	39	68.5	39	88.0	39	76.5
	378	92.5	362	83.0	356	90.0	355	90.0
	43	96.0	356	93.5	96	100.0	374	95.5
	381	96.5	285	94.0	362	101.5	356	98.0
	45	99.5	382	96.0	212	109.0	68	104.5
	49	101.0	328	98.0	355	109.5	388	104.5
	356	102.0	291	98.5	371	110.0	362	109.0
	212	103.5	160	99.5	242	111.5	314	111.5
	58	105.0	371	99.5	388	112.0	16	112.0
	277	105.0	376	99.5	2	112.5	15	114.5
	33	148.5	37	151.5	83	154.0	104	162.0
	68	148.5	62	151.5	7	154.5	185	162.0
	138	148.5	133	152.0	243	155.0	253	162.0
	297	148.5	24	156.0	342	155.5	259	162.0
	307	149.3	82	159.0	58	156.5	329	162.0
	12	149.5	196	159.0	169	157.0	86	162.5
	24	149.5	253	159.0	82	159.0	89	162.5
	32	150.0	294	159.0	192	159.0	186	162.5
	301	151.5	387	159.0	260	159.0	255	163.0
	10	153.0	303	159.5	271	159.0	272	166.5
Mean		128.2		139.0		128.5		133.9
	s.e.d.	l.s.d.						
Genotype	6.68	13.1						
Experimental environment	0.68	1.3						
Genotype*exprimental environment	13.36	26.2						
CV%	10.10							

	Days to maturity (days)							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	378	139.5	39	116.0	39	135.5	39	126.0
	368	142.0	362	129.5	356	137.5	355	136.5
	381	144.0	285	142.0	96	149.5	374	144.5
	43	145.0	356	142.5	362	150.0	356	148.5
	45	151.0	382	142.5	212	156.0	388	152.5
	212	151.0	328	144.5	355	156.0	68	153.5
	44	151.5	371	146.5	371	157.5	362	155.5
	92	151.5	41	148.5	388	159.0	16	159.0
	49	153.0	376	148.5	2	159.5	314	159.5
	194	153.5	291	149.0	54	160.0	385	161.5
	68	195.5	309	199.5	83	202.0	89	210.0
	24	196.0	37	200.0	155	202.0	124	210.0
	33	196.0	133	200.0	7	202.5	155	210.0
	297	196.5	24	204.0	58	204.0	253	210.0
	32	197.5	253	206.5	342	204.0	255	210.0
	307	197.5	82	207.0	169	205.0	259	210.0
	12	198.5	332	207.0	82	206.0	329	210.0
	298	199.0	303	207.0	192	206.5	104	210.5
	301	199.0	196	207.5	260	206.5	186	210.5
	10	201.5	387	207.5	271	207.5	272	215.0
		176.9		176.8		181.4		187.0
	s.e.d.	l.s.d.						
	6.61	13.0						
	0.67	1.3						
	13.22	25.9						
	7.30							

	Days to anthesis (days)							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	378	96.5	39	73.0	39	92.5	39	83.0
	368	99.0	362	86.5	356	94.5	355	93.5
	381	101.0	285	99.0	96	106.5	374	101.5
	43	102.0	356	99.5	362	107.0	356	105.5
	45	108.0	382	99.5	212	113.0	388	109.5
	212	108.0	328	101.5	355	113.0	68	110.5
	44	108.5	371	103.5	371	114.5	362	112.5
	92	108.5	41	105.5	388	116.0	16	116.0
	49	110.0	376	105.5	2	116.5	314	116.5
	194	110.5	291	106.0	54	117.0	385	118.5
	68	152.5	309	156.5	83	159.0	89	167.0
	24	153.0	15	157.0	155	159.0	124	167.0
	33	153.0	133	157.0	7	159.5	155	167.0
	294	153.5	24	161.0	58	161.0	253	167.0
	32	154.5	253	163.5	342	161.0	255	167.0
	307	154.5	82	164.0	169	162.0	259	167.0
	12	155.5	294	164.0	82	163.0	329	167.0
	298	156.0	303	164.0	192	163.5	104	167.5
	301	156.0	196	164.5	260	163.5	186	167.5
	10	158.5	387	164.5	271	164.5	272	172.0
Mean		133.9		133.8		138.4		144.0
	s.e.d.	l.s.d.						
Genotype	6.61	13.0						
Experimental environment	0.67	1.3						
Genotype*exprimental environment	13.22	25.9						
CV%	9.60							

	Number of panicles (numbers)							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	242	133.0	225	263.0	159	149.5	159	177.5
	69	121.5	157	215.5	341	142.5	54	155.0
	212	119.0	106	175.0	328	142.0	357	145.0
	223	118.5	54	172.0	96	141.5	74	126.0
	214	114.0	352	172.0	50	136.5	136	124.0
	54	113.5	281	164.0	212	128.5	79	121.0
	278	112.5	328	158.0	254	127.5	78	120.5
	185	110.5	336	146.0	54	126.5	354	120.0
	211	108.5	212	144.5	205	117.5	222	119.5
	292	107.0	239	139.0	140	116.0	96	119.0
	28	7.0	14	23.5	129	11.5	19	11.0
	33	7.0	167	27.0	180	11.5	32	10.0
	18	6.5	180	16.5	275	11.5	4	9.5
	20	6.5	338	16.0	11	11.0	26	9.0
	24	6.5	307	25.0	344	10.5	37	9.0
	5	6.0	310	12.5	20	9.5	1	6.0
	11	6.0	13	13.0	24	9.0	8	6.0
	17	6.0	18	6.5	38	8.5	17	6.0
	12	5.0	12	5.0	25	4.5	18	6.0
	32	4.0	177	15.5	17	3.5	28	4.5
		51.8		65.1		51.3		49.8
	s.e.d.	l.s.d.						
	16.21	31.8						
	1.64	3.2						
	32.42	63.6						
	59.50							

Two lines 362 (WAB 450-I-B-P-38-HB – NERICA1) and 96 (CT16317-CA-4-M) were selected as parents for crossing block appeared among the top ten in days to heading, anthesis and maturity. The genotypes for the codes are in Appendix 3.1.

Caiapo (39) still was the earliest in days to anthesis at 73 days under the N-P+ condition (Table 3.3). The genotypes ranked differently for days to heading, anthesis and maturity. Two parents (362 and 96) appeared among the top ten best genotypes. Line 272 (CT16345-CA-12-M) had its anthesis period being the latest at 172 days under N+P+.

The earliest line 39 (Caiapo) matured in 116 days under N-P+ experimental condition, but under N+P- it flowered in 136 days but still the earliest under this condition. The top ten lines in maturity displayed change of ranks under the four fertility conditions. Line 272 matured latest in 215 days under N+P+ condition.

Line 159 (CT16329-CA-10-M) was ranked top for number of panicles for 10 plants with 150 and 178 panicles under N+P- and N+P+ fertility conditions, respectively. However, it did not appear among top ten under N-P- and N-P+ conditions where line 242 (CT16340-CA-13-M) and 225 (CT16337-CA-7-M) was ranked at the top, respectively. Line 17 (ARCCU3Fa12-L 11 P82-HB) had the lowest number of panicles (4).

Line 6 (ARCCU1 Fa5-L4P1-HB) was ranked among the top 3 under N-P- and N-P+ fertility condition, while two lines, 96 (CT16317-CA-4-M) and 195 (CT16333(2)-CA-18-M) were among the top ten in phosphorous tolerance under N+P- and N+P+ fertility conditions (Table 3.4). Line 168 (CT16330(1)-CA-2-M) was the worst in terms of phosphorous tolerance under N-P- fertility condition.

Line 170 (CT16330(1)-CA-4-M) had consistent nitrogen tolerance except under N-P+ where it was not among the top ten. Lines 6 (ARCCU1 Fa5-L4P1-HB) and 167 (CT16330(1)-CA-15-M) showed consistent performance by appearing top ten under N-P+ and N+P- fertility conditions. Line 27 (ARCCU3Fa3-L7P1-HB) consistently displayed superior nitrogen tolerance ranking top under N+P+ and top three under N-P+ and N+P- experimental conditions. However, there was great variability in nitrogen tolerance as indicated by varied genotypes appearance or rankings for both top 10 best and worst cases. Lines 39 (Caiapo) and 267 (CT16344-CA-3-M) had the worst nitrogen tolerance under N-P+ fertility condition. The 1000 seed weight had extreme variability in that no single line appeared to be consistent in performance across the four fertility experimental conditions (Table 3.4). Only one parent 76 (CT16313-CA-19-M) appeared among the top ten lines for best performers under N+P- condition. Line 362 (WAB 450-I-B-P-38-HB-NERICA1) appeared among the worst performers under soil N+P+ environmental condition.

Table 3.4 The mean values for P and N tolerance on 1000 seed wt and grain yield for the best and lowest ten rice lines under four soil N and P conditions

Phosphorous tolerance (scale 1-5)								
lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
3	1.0	2	1.0	14	1.0	21	1.0
4	1.0	5	1.0	91	1.0	27	1.0
6	1.0	6	1.0	96	1.0	40	1.0
7	1.0	8	1.0	98	1.0	47	1.0
8	1.0	9	1.0	99	1.0	118	1.0
9	1.0	14	1.0	100	1.0	121	1.0
15	1.0	17	1.0	113	1.0	187	1.0
16	1.0	18	1.0	116	1.0	195	1.0
22	1.0	19	1.0	117	1.0	245	1.0
29	1.0	20	1.0	122	1.0	315	1.0
247	4.0	339	3.5	189	3.0	10	4.5
288	4.0	348	3.5	196	3.0	39	4.5
299	4.0	352	3.5	259	3.0	77	4.5
345	4.0	357	3.5	268	3.0	79	4.5
362	4.0	362	3.5	298	3.0	216	4.5
374	4.0	15	4.0	312	3.0	268	4.5
270	4.5	75	4.0	314	3.0	270	4.5
300	4.5	249	4.0	28	3.5	332	4.5
375	4.5	263	4.0	34	3.5	375	4.5
168	5.0	346	4.0	352	3.5	379	4.5
Mean		1.9		1.8		1.7		2.6
	s.e.d.	l.s.d.						
Genotype	0.529	1.0						
Experimental environment	0.054	0.1						
Genotype*exprimental environment	1.058	2.1						
CV%	52.900							

Nitrogen tolerance (scale 1-5)							
lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
12	1.0	6	1	3	1	27	1
32	1.0	20	1	6	1	303	1
68	1.0	27	1	27	1	21	1
170	1.0	30	1	167	1	316	1
177	1.0	167	1	170	1	170	1.5
180	1.0	307	1	247	1	247	1.5
352	1.0	13	1.5	250	1	282	1.5
1	1.5	272	1.5	256	1	300	1.5
3	1.5	280	1.5	282	1	332	1.5
4	1.5	294	1.5	294	1	338	1.5
381	3.5	380	4	316	4	13	4.5
383	3.5	384	4	322	4	16	4.5
388	3.5	386	4	327	4	60	4.5
213	4.0	107	4.5	333	4	197	4.5
238	4.0	150	4.5	335	4	355	4.5
240	4.0	263	4.5	340	4	75	4.5
283	4.0	301	4.5	344	4	270	4.5
291	4.0	358	4.5	343	4.5	281	4.5
342	4.0	267	5	240	5	42	5
382	4.0	39	5	39	4.5	39	4.5
	2.7		3.391		3.058		3.199
s.e.d.	l.s.d.						
0.42	0.8						
0.04	0.1						
0.83	1.6						
27.00							

1000 seed weight (g)							
lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
163	27.9	55	25.8	325	28.9	140	29.2
238	26.8	330	25.7	76	28.1	370	29.0
171	26.4	16	24.8	138	27.3	23	27.8
165	26.2	165	24.5	54	27.1	29	27.7
126	25.9	38	24.3	279	26.6	384	27.5
385	25.7	153	23.6	249	26.4	119	27.5
372	25.2	186	22.9	175	26.1	259	27.4
9	25.0	289	22.9	380	25.9	163	27.4
383	24.3	385	22.8	351	25.9	236	27.3
307	24.3	191	22.4	388	25.8	151	27.2
344	6.3	363	5.5	39	7.1	347	12.9
218	6.0	291	5.5	87	7.0	362	12.9
243	6.0	314	5.4	134	6.9	101	12.8
390	5.9	105	5.4	209	6.8	125	12.6
346	5.7	274	5.2	83	6.6	43	12.5
61	5.6	124	4.8	269	6.5	176	12.4
168	5.3	344	4.6	198	6.5	246	12.2
92	5.3	229	4.2	45	6.1	320	11.8
177	4.9	292	4.1	141	5.5	187	11.5
263	3.8	100	4.0	246	5.0	261	10.2
Mean		14.7		14.2		17.1		19.7
	s.e.d.	l.s.d.						
Genotype	3.17	6.2						
Experimental environment	0.32	0.6						
Genotype*exprimental environment	6.34	12.4						
CV%	38.70							

Yield (kgha^{-1})							
lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
151	5916.0	245	4948.0	222	4967.0	370	4970.0
370	5911.0	277	4939.0	19	4964.0	251	4954.0
259	5904.0	360	4916.0	29	4944.0	360	4940.0
253	5884.0	364	4912.0	54	4944.0	378	4937.0
163	5877.0	55	4902.0	378	4943.0	387	4936.0
354	5875.0	76	4892.0	181	4936.0	212	4933.0
74	5871.0	134	4867.0	353	4934.0	222	4927.0
182	5869.0	293	4852.0	273	4930.0	186	4925.0
77	5864.0	63	4848.0	104	4922.0	353	4925.0
54	5862.0	127	4847.0	117	4918.0	141	4921.0
125	990.0	363	1480.0	129	1757.0	179	1560.0
270	984.0	180	1471.0	339	1753.0	247	1517.0
152	949.0	257	1457.0	313	1750.0	324	1500.0
363	948.0	216	1410.0	85	1725.0	124	1450.0
263	914.0	264	1407.0	267	1725.0	203	1413.0
168	912.0	291	1350.0	270	1700.0	10	1400.0
225	848.0	270	1300.0	216	1635.0	320	1234.0
344	715.0	310	1200.0	363	1471.0	75	1114.0
345	549.0	249	1020.0	218	1150.0	263	1065.0
314	509.0	301	850.0	269	800.0	39	567.0
	3828.0		3676.0		3491.0		3559.0
s.e.d.	l.s.d.						
541.40	1062.0						
54.80	107.6						
1082.80	2124.0						
29.80							

Lines 182 (CT16333(1)-CA-20-M) and 76 (CT16313-CA-19-M) selected as parents appeared among the best ten yielders under N-P- and N-P+ fertility condition. Line 222 (CT16337-CA-3-M) was ranked top under N+P- and also appeared among the best ten under N+P+ fertility environments. Line 360 (WAB 450-I-B-P-20-HB) ranked number 3 under N-P+ and N+P+ fertility conditions thus displaying some consistency. This was also the case for line 378 (WAB 905-B-4A 1.1). Line 370 had superior performance under N-P- and N+P+ experimental fertility environments thus displayed adaptability and responsiveness to fertility environments. Line 39 (Caiapo) and 314 (CT16350-CA-7-M) had poor performance, especially for Caiapo that was early maturing and thus used as parent for earliness.

The plant height had varied performance under the four fertility conditions with many of the lines failing to show consistency (Table 3.5). The line 76 (CT16313-CA-19-M) that was selected as parent appeared among the top ten lines under N+P- condition.
Line 221 (CT16337-CA-3-M) had consistency in its performance under N+P- and N+P+ fertility condition, a case displayed by line 175 (CT16331-CA-8-M) under N-P+ and N+P- condition. Line 195 (CT16333(2)-CA-18-M) selected as parent appeared among the worst ten in height under N+P+ condition.

Genotypes performance for biomass were also widely varied with one line 96 (CT16317-CA-4-M) appearing among the best top ten under N+P- condition. Genotype 175 (CT16331-CA-8-M) has consistent performance under three experimental fertility conditions, ranking top under N-P+ and N+P+ conditions. The highest biomass (3888.5g) was associated with line 272 (CT16345-CA-12-M) under N-P- fertility condition, which also appeared under N-P+ condition. The worst line was 345 (CT16356(1)-CA-7-M) having 12.5g under N-P- fertility condition.

Table 3.5 Mean values of plant height and top biomass for ten best and worst rice lines under low and high soil N and P conditions

	Plant height (cm)								Top biomass (g)							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	77	107.5	272	110.9	175	114.7	221	115.2	272	3888.5	175	3088.5	254	2690.0	175	2495.0
	34	103.4	175	106.8	254	112.1	259	112.9	259	2406.5	272	2882.0	341	2616.0	159	2378.0
	74	101.3	289	105.9	337	110	176	112.8	254	2271.5	54	2810.5	175	2582.0	149	2154.5
	171	99.4	269	105.5	119	109.1	116	110.2	131	2249.0	159	2121.0	159	2490.5	221	1867.0
	319	97.8	94	103.5	272	108.7	78	109.4	341	2170.0	176	2093.0	96	2349.5	167	1842.8
	88	96.7	254	103.0	76	108.6	226	108.2	54	2075.0	212	2024.5	94	2346.4	142	1842.0
	134	96.7	335	102.6	221	106.9	285	107.9	74	2031.0	277	1999.5	372	2106.5	255	1823.5
	89	96.2	22	102.5	342	105.4	80	107.7	242	2031.0	341	1965.0	50	2049.5	170	1815.5
	272	95.6	91	102.5	183	103.7	142	107.1	212	1810.5	148	1916.0	54	2004.5	254	1617.0
	155	95.2	63	101.6	336	102.6	62	107.0	305	1750.5	254	1901.5	63	1973.0	166	1598.0
	362	62.4	185	86.0	321	62	173	58.2	31	50.5	3	124.5	297	146.5	32	94.5
	33	62.0	297	71.5	216	61.6	232	58.0	310	50.5	332	124.0	130	144.5	31	88.5
	36	61.8	249	60.9	320	57.5	228	57.8	330	45.0	344	112.5	352	142.5	234	85.5
	190	61.6	343	66.6	345	57	195	57.5	247	38.0	180	112.0	8	125.5	97	72.5
	275	61.5	225	93.3	340	56.8	216	57.5	250	37.0	34	110.0	36	124.0	19	59.5
	350	61.2	339	65.7	386	56.2	287	56.5	17	33.0	14	103.5	269	123.5	28	53.0
	28	61.1	224	78.5	75	55.32	344	56.5	32	31.0	12	87.5	20	107.0	10	48.0
	249	60.9	301	72.3	343	52	306	55.8	36	28.0	338	84.5	4	105.5	18	48.0
	73	60.3	263	68.9	39	46.5	39	55.2	16	23.5	39	51.0	32	101.0	17	35.5
	173	58.2	273	79.0	344	46	320	55.2	345	12.5	13	45.0	25	25.0	8	23.0
Mean		78.4		82.7		82.98		81.9		674.9		719.5		691.8		610.4
	s.e.d.	l.s.d.							s.e.d.	l.s.d.						
Genotype	5.78	11.3							198.15	388.7						
Experimental environment	0.59	1.1							20.07	39.4						
Genotype*exprimental environment	11.56	22.7							396.31	777.4						
CV%	14.20								58.80							

3.4.3 Scatter plots and histograms for days to maturity and yield.

From the display of scatter plot for yield versus days to maturity, Figure 3.2, the line 378 (WAB 905-B-4A 1.1) was the best in terms of yield and earliness among the 25 earliest lines under N-P- conditions. It was followed by 368 (WAB 880-1-38-20-15-P2-HB) and 381 (WAB 919-72-4-1-HB). Line 291 (CT16346-CA-8-M) was the most undesirable as it had low yields and was very late in maturity. The genotypes of the codes are in appendix 3.1.

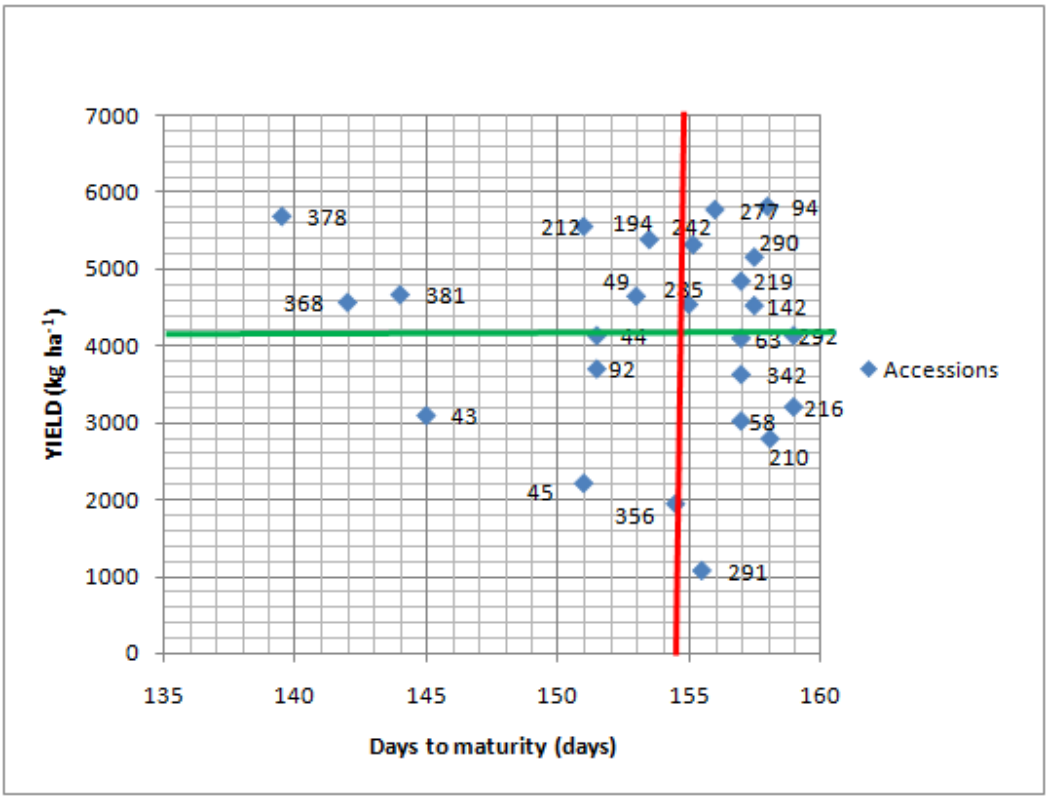

Figure 3.2 Yield against days to maturity of the best rice genotypes under soil N-P- conditions.

The scatter plot under soil N-P+ had genotypes 245, 277 and 364 being early and high yielding (Fig. 3.3). Genotype 74 was the latest among the best twenty five genotypes and its yield was around the mean. Genotype 361 although was around the mean in maturity, it had the lowest yield. Line 340 although it was the earliest it yield potential was around the mean.

Figure 3.4 displays the scattering of the best twenty five genotypes of which line 222 was the highest yielding and also it's maturity was below the mean. However line 353 although high yielding, it was late second to line 81 which was the second lowest in terms of yield. The earliest line was 96 which was within the early and high yielding quadrant. Line 102 was the lowest yielder but it was early hence not a desirable genotype. The majority of the genotypes were skewed toward lateness but high yielding.

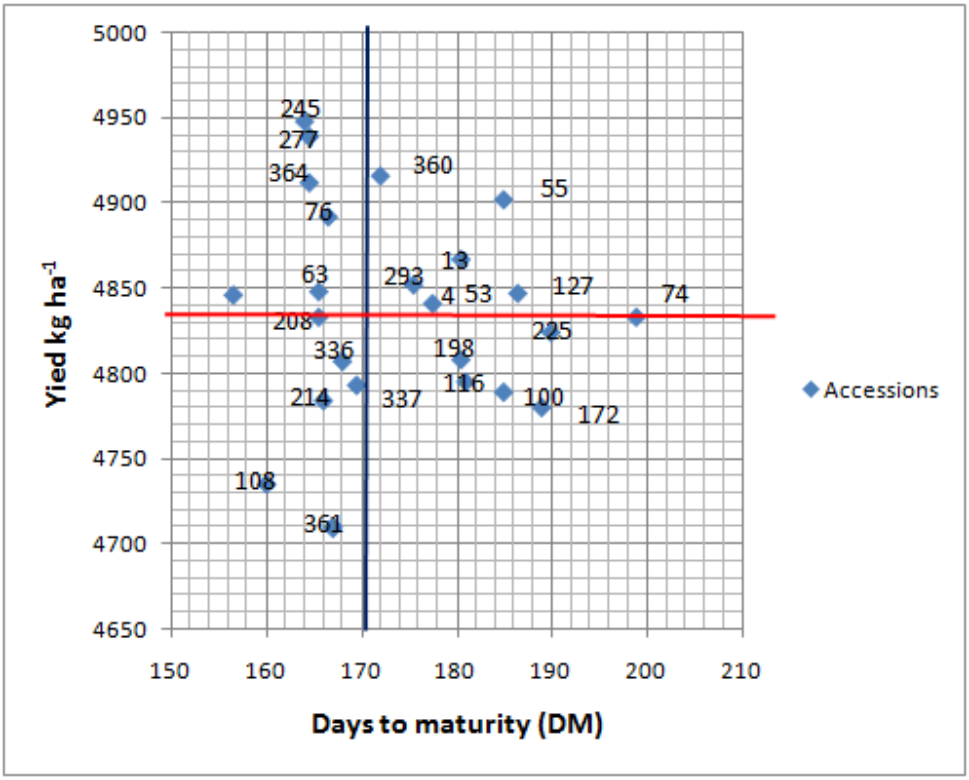

Figure 3.3 Yield against days to maturity of the best rice genotypes under Soil N-P+ conditions.

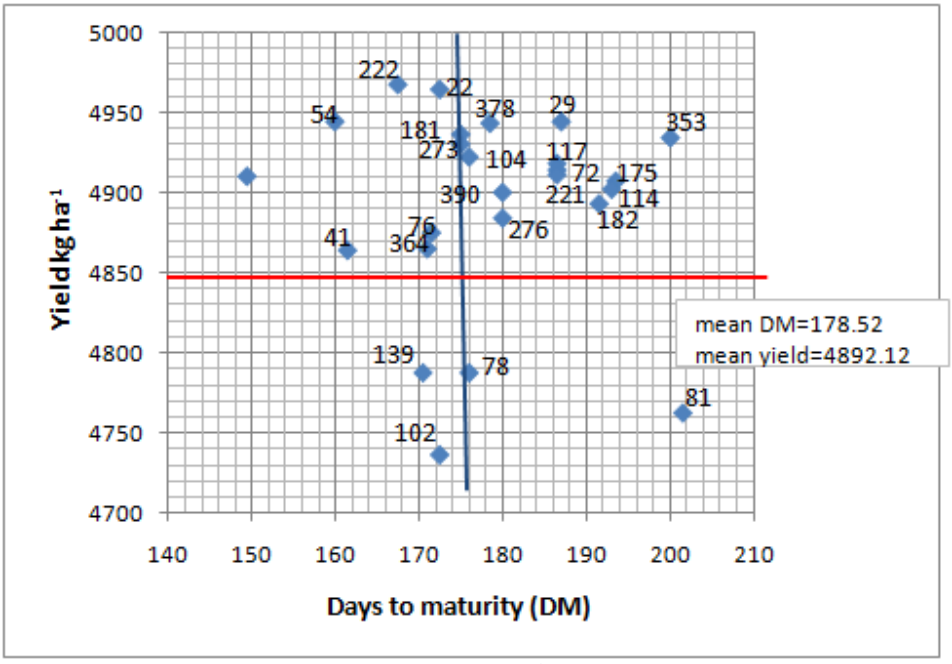

Figure 3.4 Yield against days to maturity of the best rice genotypes under soil N+P- conditions.

The scatter plot of genotypes under N+P+ experimental fertility conditions by days to maturity versus yield displayed line 356 (WAB 450-11-1-P31-1-HB) as the most desirable (Figure 3.5).

Line 39 (Caiapo) although it was early it had low yields a case observed also for line 355 (WAB 450-11-1-1-P41-HB).

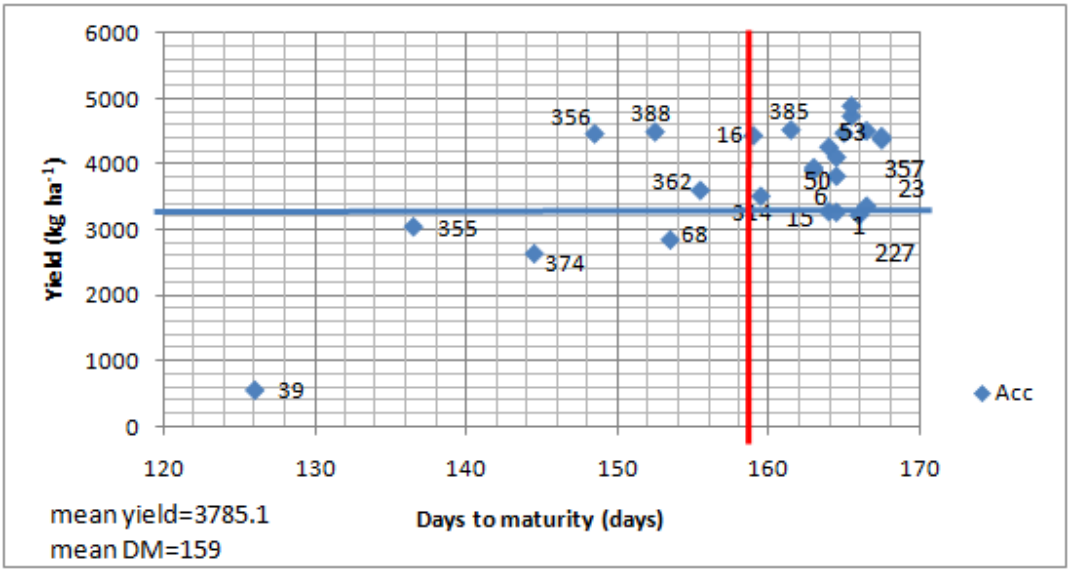

Figure 3.5 Analysis of yield and days to maturity of the best rice genotypes under soil N+P+ conditions.

3.4.4 The distribution of the 390 rice lines for days to maturity under different soil N and P conditions

The distribution of the three hundred and ninety genotypes under soil N-P- condition was towards lateness with majority of the lines maturing around 170 and 190 days (Fig 3.6). Very few lines matured below 140 days.

Under soil N-P+ condition, some genotypes were quite early below 140 days compared to soil N-P- condition (Fig. 3.7). However, the majority of genotypes matured between 170 and 190 days, but proposition of genotypes maturing later than 200 days was higher compared to soil N-P- condition.

The distribution of days to maturity under soil N+P- condition was centred around 180 days, with some lines maturing earlier than 140 days (Fig. 3.8). The proportion of lines maturing below 150 days was highest under this N+P- soil condition compared to soil N-P-, N-P+ and N+P+ condition. However, the proportion of lines maturing beyond 200 days was high compared to the other three soil conditions.

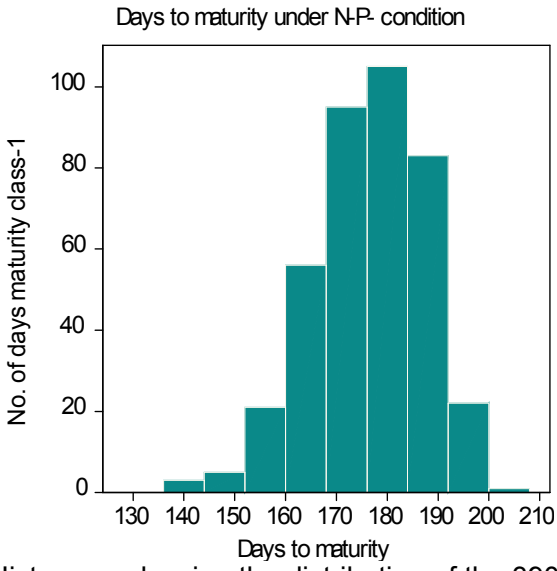

Figure 3.6 Histogram showing the distribution of the 390 rice lines according to maturity under soil N-P- condition.

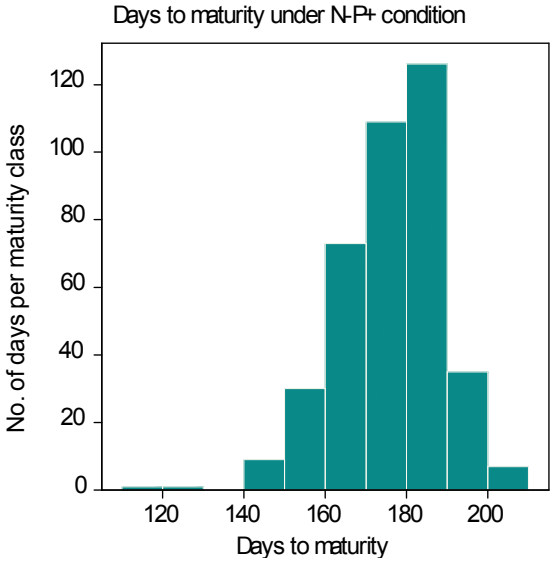

Figure 3.7 Histogram showing the distribution of the 390 rice lines according to maturity under soil N-P+ condition.

The days to maturity indicated negative skew towards the left, implying some of the lines were early in maturity (Figure 3.9.). However, some lines were quite late in maturity, but majority of lines matured in around 190 days.

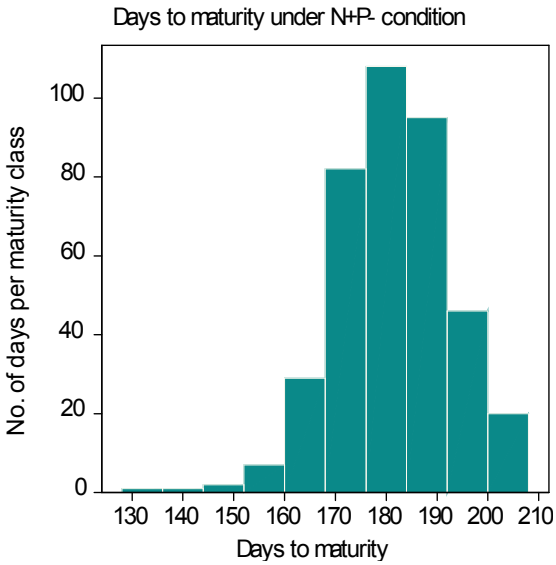

Figure 3.8 Histogram showing the distribution of the 390 rice lines according to maturity under soil N+P- condition.

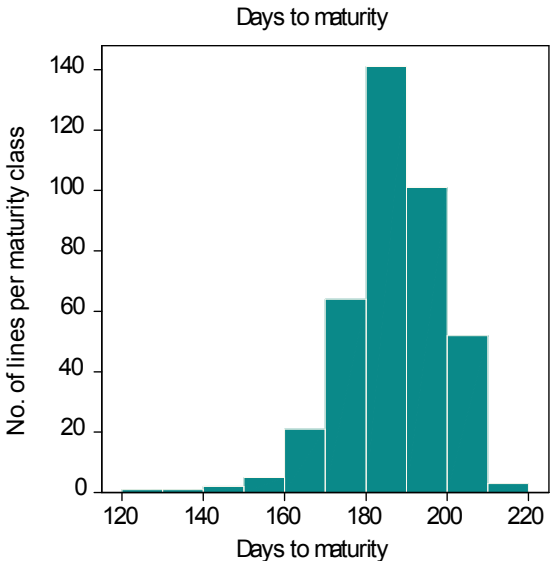

Figure 3.9 Histogram showing the distribution of the 390 rice lines according to maturity under soil N+P+ condition.

3.4.5 The distribution of the 390 rice genotypes for grain yield under different soil N and P conditions

The distribution of yield under soil N-P- was toward the right with majority of the genotypes showing relatively high yields (Fig 3.10), but about eight genotypes had yields below 1000 kg ha^{-1}.

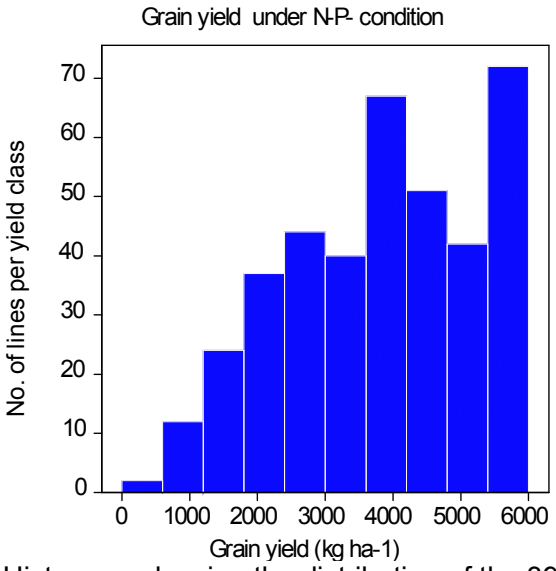

Figure 3.10 Histogram showing the distribution of the 390 rice lines for grain yield under soil N-P- conditions

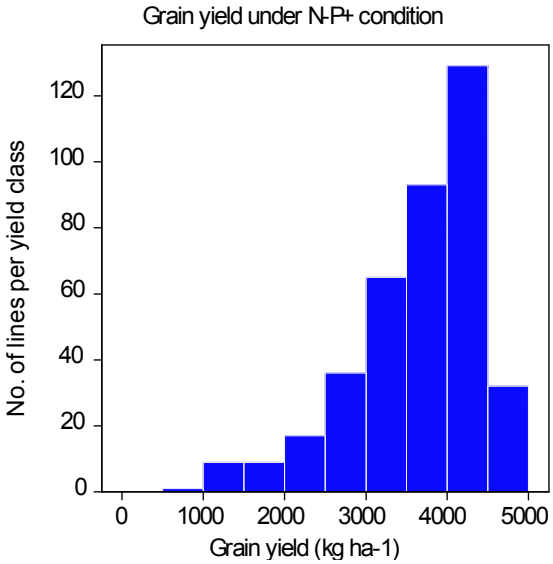

Figure 3.11 Histogram showing the distribution of the 390 rice lines for grain yield under soil N-P+ conditions

The distribution of lines under N-P+ had very few lines below 1000 kg ha^{-1} and majority of the other lines had yield clustering around 3500 to 4500 kg ha^{-1} (Fig. 3.11). However compared to soil N-P- condition, no genotype exceeded yield of 5000 kg ha^{-1}.

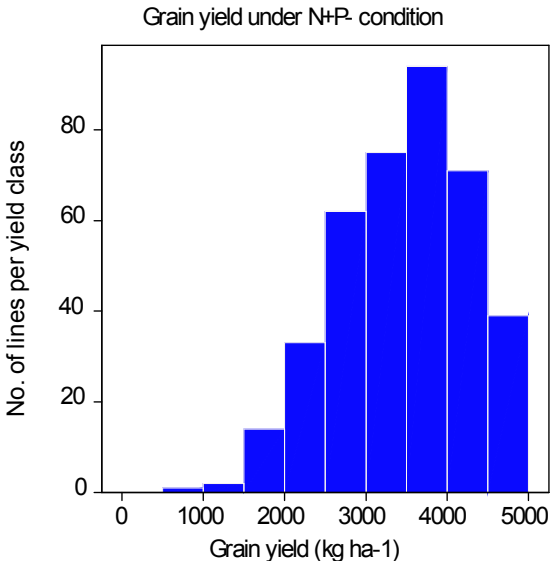

Figure 3.12 Histogram showing the distribution of the 390 rice lines for grain yield under soil N+P- conditions

The yield under soil N+P- condition were largely below 4000 kg ha^{-1} and none exceeded yield of 5000 kg ha^{-1} (Fig. 3.12). There were about two genotypes that had yields below 1000 kg ha^{-1}.

The yield for the 390 lines clustered towards the right indicating majority of the lines were high yielding under soil N+P+ condition (Figure 3.13). Majority of lines had yields around 3500 to 4500 kg ha^{-1}, but none exceeded 5000 kg ha^{-1}.

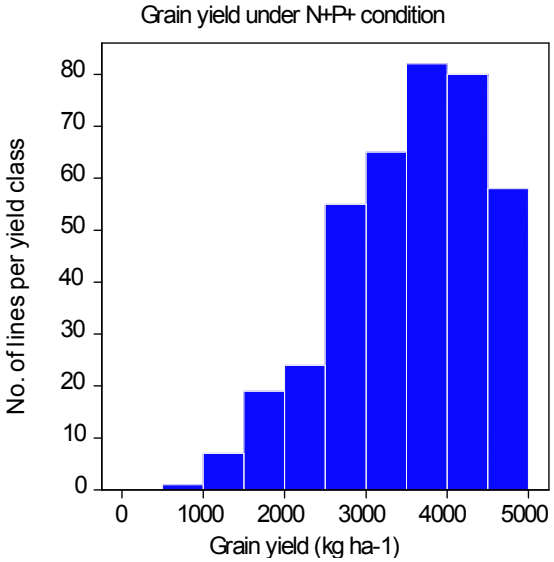

Figure 3.13 Histogram showing the distribution of the 390 rice lines for grain yield under soil N+P+ conditions

3.4.6 The scattering of the 390 rice genotypes for grain yield against days to maturity under different soil N and P conditions

Generally under soil N-P- condition, the lines were widely scattered and the quadrant of the low yielding but early maturing lines have less lines compared to the other three quadrants (Fig. 3.14). Genotypes 370, 54, 378, 341 (pedigree names are in the Appendix 3.1) were high yielding and fall below the mean for maturity. These genotypes are promising because they show adaptation to low soil N and P conditions. However lines 291, 270, 363 were very early maturing but very low yielding, thus they are undesirable.

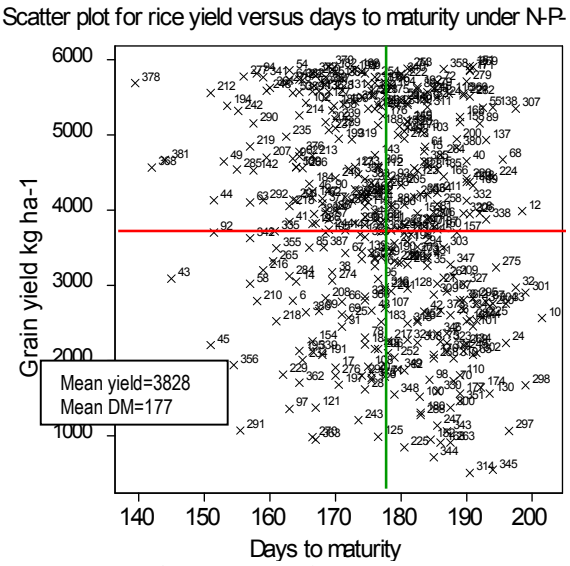

Figure 3.14 Scatter plot for rice yield versus days to maturity under N-P-

The performance of the lines under soil N-P+ had most of the genotypes in the high yielding but late maturing quadrant (Fig. 3.15). The adapted genotypes for this condition include 340, 371, 382, 217. These had high yield and were below the mean for days to maturity. The worst genotypes were 310, 301, 216, 180 among others. These were low yielding and late maturing and thus poorly adapted to this soil condition.

The genotype scattered mostly in the two late quadrants and about equally for yield with major variation occurring under low yielding quadrant (Fig. 3.16). The promising lines under this soil environment are 96, 54, 41, 22, 222 and 388 to name just a few. Poorly adapted lines were 130, 218, 216, 313 and 209. The majority of the lines congregated toward the higher two yielding quadrants, but skewed towards lateness.

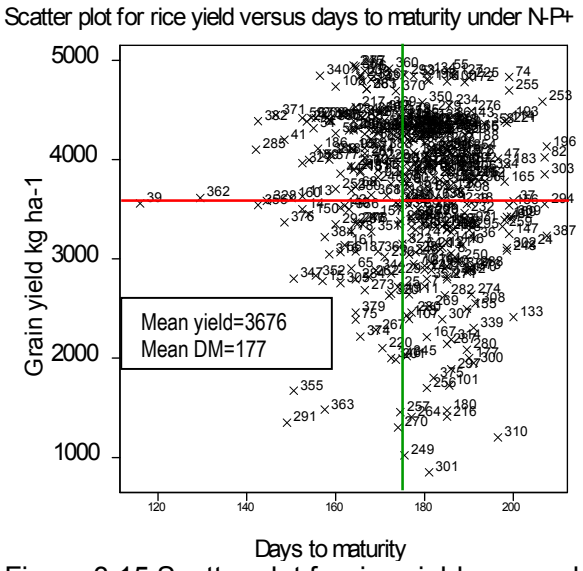

Figure 3.15 Scatter plot for rice yield versus days to maturity under N-P+

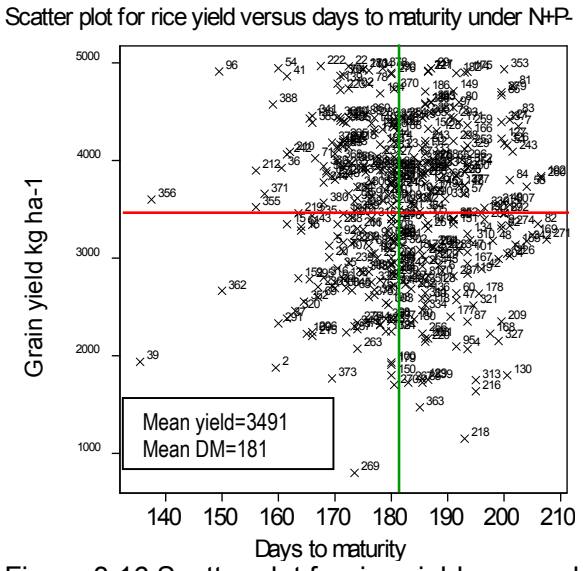

Figure 3.16 Scatter plot for rice yield versus days to maturity under N+P-

The scatter plot for the 390 lines under N+P+ showed that majority of the lines were early and a good number of them had desirable yield (Figure 3.17). The population mean for days to maturity was 187 while yield was 3559.5 kg ha^{-1}. Generally the majority of the lines had yields above the mean yield but to the right. The promising genotypes were 370, 222, 212, 64, 54, 41, 388, 78 and 96. The low yielding genotypes were 39, 246 and 263.

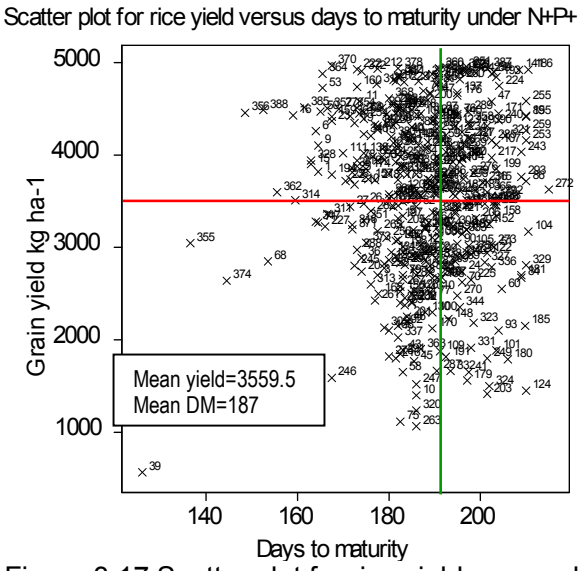

Figure 3.17 Scatter plot for rice yield versus days to maturity under N+P+

3.4.7 The scattering of the 25 best rice genotypes for grain yield against different soil N and P conditions

When the genotypes were displayed for yield versus soil nitrogen (N) and phosphorous (P) level the majority of the twenty five lines were skewed towards less N tolerance two quadrants (Fig. 3.18). The best genotype was 151 because it was the highest yielding and tolerant, although it was not the most tolerant. The most tolerant lines were 340, 7, 260 and 251 but these were below the mean yield. The least favourable genotype was 382 as it was least tolerant and had the lowest yield among the group.

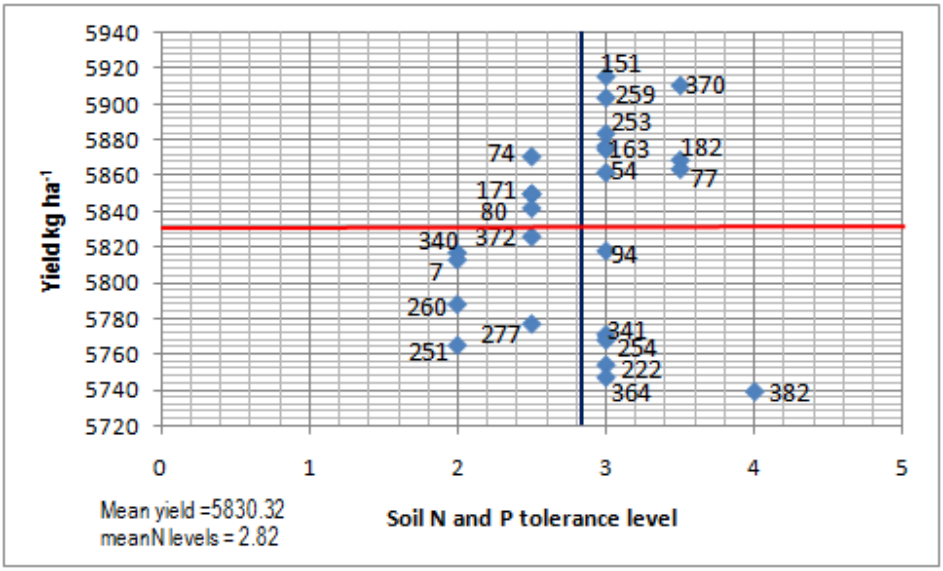

Figure 3.18 Head to head plot of the best 25 rice lines for yield versus soil N and P condition.

The majority of the lines scattered towards the left showing more tolerance under soil N-P+ condition (Fig.3.19). The best genotype was 277 although line 245 had the highest yield, it was less tolerant than 277. The lines 255 and 361 were the least adapted in terms of yield but were tolerant. The best tolerant lines had yields just slightly above the mean yield.

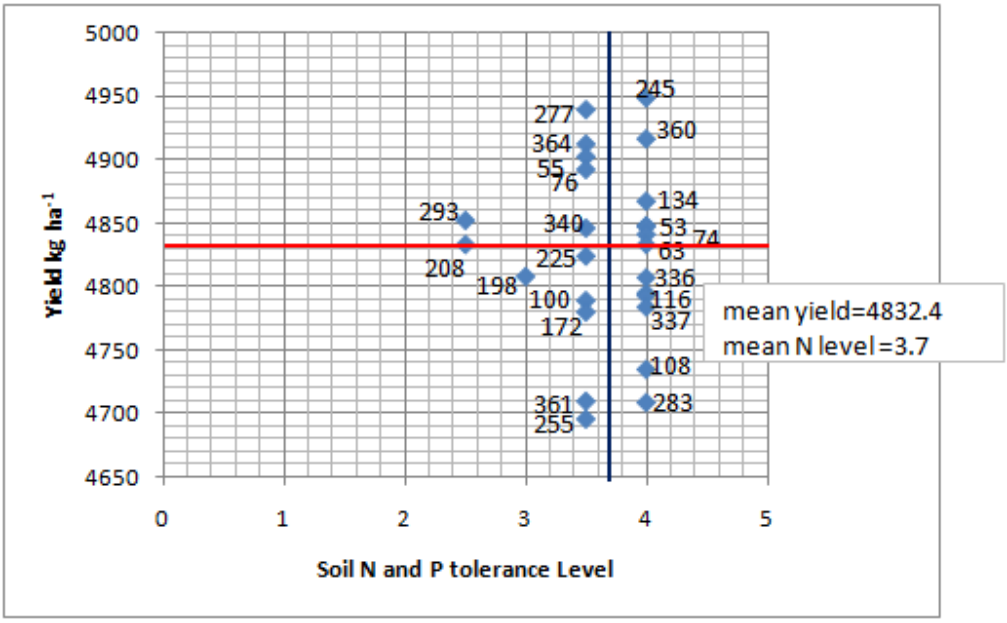

Figure 3.19 Head to head plot of the best 25 rice lines for yield versus soil N and P condition.

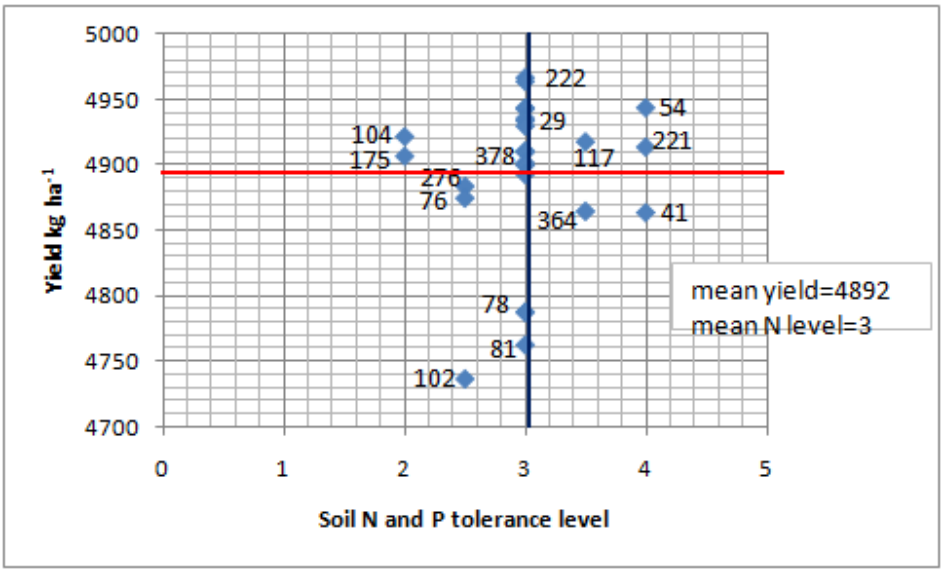

Figure 3.20 Head to head plot of the best 25 rice lines for yield versus soil N and P condition.

The best adapted lines were 222 and 29 in terms of both yield and tolerance but they were at the demarcation line for tolerance (Fig.3.20). The least adapted lines were 102 and 81 because they

were low yielding although tolerant to soil N and P condition. The majority of the lines were at the medium tolerance line but many were above the mean yield.

The best line (370) in terms of yield was less adapted to soil N and P condition, while the best tolerant lines (94, 342 and 334) had yields below the average (Fig.3.21). The majority of the lines congregated towards high yielding but less tolerant and low yielding but more tolerant quadrants.

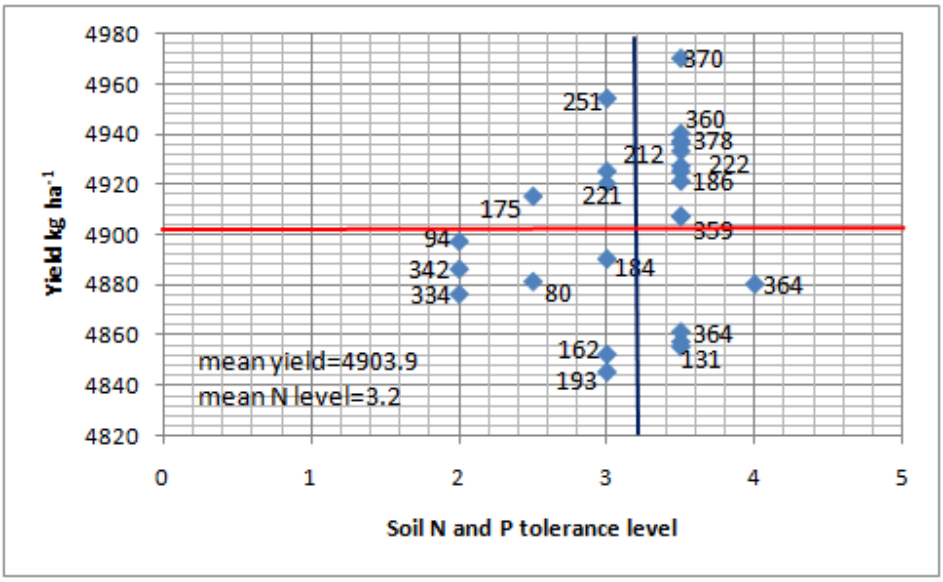

Figure 3.21 Head to head plot of the best 25 rice lines for yield versus soil N and P condition.

3.4.8 The correlation of grain yield against different soil N and P conditions

Generally the correlation of yield with different soil N and P conditions produced values that were low, although some were significant (Table 3.6). The highest and very highly significant correlation figures were between yield under N+P+ and P tolerance under N+P+ (0.528, $P<0.001$), yield under N-P+ and P tolerance under N-P+ (0.4781, $P<0.001$) and yield under N-P+ and Yield under N-P- with a very highly correlation value of 0.4421. The results indicate variability of genotype performance under various soil N and P condition. Some of the interactions were significant between yield and various soil N and P conditions as indicated by significant correlations.

Table 3.6 Correlation of rice yield with four levels of soil nitrogen and phosphorous fertility tolerance levels

	P tolerance N-P	P tolerance N+P	P tolerance N+P+	Yield under N-P-	Yield under N-P+
P tolerance N-P+	-		*, **, *** Significant at P<0.05, 0.01 and 0.001		
P tolerance N+P-	0.2242***	-	ns- nonsignificant P>0.05		
P tolerance N+P+	0.1318**	-0.0457ns	-		
Yield under N-P-	-0.2153***	0.0175ns	-0.2037***	-	
Yield under N-P+	-0.4781***	0.0014ns	-0.1753***	0.4421***	-
Yield under N+P-	-0.1433**	0.0014ns	-0.2462***	0.4266***	0.4051***
Yield under N+P+	-0.196***	0.0702ns	-0.528***	0.3962***	0.3112***
N tolerance N-P+	0.0006ns	-0.1128*	0.1768***	0.1164*	0.0679ns
N tolerance N-P-	-0.0704ns	-0.1305**	0.1215**	0.0672ns	0.1539**
N tolerance N+P-	-0.0126ns	0.0926ns	0.0357ns	0.1329**	0.1366**
N tolerance N+P+	0.025ns	0.0752ns	0.0734ns	0.0592ns	0.1415**
P tolerance N-P-	0.1243**	-0.0222ns	0.1535**	-0.5337***	-0.2159***

Table 3.6 (continued) Correlation of rice yield with four levels of soil nitrogen and phosphorous fertility tolerance levels

	Yield under N+P-	Yield under N+P+	N tolerance N-P+	N tolerance N-P-	N tolerance N+P-	N tolerance N+P+	P tolerance N-P-
P tolerance N-P+							
P tolerance N+P-		*, **, *** Significant at P<0.05, 0.01 and 0.001					
P tolerance N+P+		ns- nonsignificant P>0.05					
Yield under N-P-							
Yield under N-P+							
Yield under N+P-	-						
Yield under N+P+	0.3775***	-					
N tolerance N-P+	-0.0572ns	-0.0131ns	-				
N tolerance N-P-	0.0737ns	0.0354ns	0.2401***	-			
N tolerance N+P-	-0.0302ns	-0.0129ns	0.4034***	0.2076***	-		
N tolerance N+P+	-0.0238ns	0.0042ns	0.3634***	0.1566**	0.439***	-	
P tolerance N-P-	-0.2986***	-0.1895***	-0.0267ns	-0.0681ns	-0.0893ns	-0.0275ns	-

3.5 Discussion

The germplasm under study showed good genetic variability for all the traits studied partly because these were accessions from diverse origins. The germplasm was also well adapted to the local conditions and this might have been contributed by the use of *Oryza glaberrima* as one of the parents in the development of some of these materials. This species is native to western Africa and is known to be tolerant to a wide range of abiotic and biotic factors (Sarla and Swamy, 2005; WARDA, 2006). The broad sense heritability, genetic advance and genetic advance as percent of mean had positive values indicating that breeding for the traits is feasible (Karim *et al.*, 2007). It means then that selection of the parents with the desirable traits of interest (as guided by genotypic variance) to farmers and use of these in a breeding programme can enhance the performance of the resulting progenies when evaluated under the stress environment.

3.5.1 The days to heading, anthesis and maturity

The days to heading showed high variability exhibiting a range of 69 for Caiapo under N-P+ and 167 days for 272 (CT16345-CA-12-M) under N+P+ experimental conditions. This is a gap of 98 days and if the general belief that late genotypes tend to yield higher holds, then assuming this late genotype is high yielding, its days to maturity may be lowered by crossing to Caiapo or any other early maturing genotype. In this case, CT16345-CA-12-M had moderate yields (3627 kg ha^{-1}) under N+P+ condition. Its lateness is thus not conferring any yield advantage. Homma et al. (2004) have indicated the important role this trait plays in developing drought tolerant varieties and problem soils. Since heading stage is a critical period, any nutritional deficiency or water stress leads to adverse effects on the grain formation and thus yields. At this heading stage, any stress nutritional or otherwise can greatly affect pollen formation and thus lead to empty spikelet's in rice which may result again into low yields. Thus, genotypes with high nutrient use efficiency are preferred as they can maintain the balance between soil reserve and tissue demand, thus resulting into more filled spikelet's according to Dobermann and Fairhurst (2000).

The days to anthesis had wide ranges thus showing potential for reducing days to maturity in a breeding programme. The earliest was 39 (Caiapo) (73 days) under N-P+ conditions while 378 (WAB905-B-4A1.1) had 97 days under N-P- experimental environment. Kirk et al. (1998) and others have observed that such a gap of 24 days can be utilized to develop varieties with escape properties against late drought when nutrient availability is low due to reduced mobility as the

water medium for their transport in soil is reduced (Edmeades et al., 1997; Ekanayake et al., 1985; Fukai and Copper, 1995). According to Edmeades et al. (1997), Bolanos and Edmeades (1996), Saxena and O'Toole (2002) and Lafitte et al. (2002) the interval between heading and anthesis can play an important role in breeding against stresses such as drought and late stage nutrient deficiency, especially the one resulting from water stress. In rice genotypes that have anthesis within a narrow range in a genotype should be selected to reduce prolonged maturity and thus escape terminal drought. In maize, the anthesis-silking interval has been exploited to develop drought and nitrogen use efficient varieties (Bolanos and Edmeades, 1996). Rice, although it is a self pollinated crop, the wide gap of heading and anthesis is variable and this is not a good trait. This heading-anthesis gap can lead to differential maturity with consequent problems such as grain shattering for the earliest panicles, grain discolouration and loss of quality due to over drying in the field and in case of late drought, the materials with later anthesis may not set good grains. Generally this gap should be between 1 to 5 days for uniform crop maturity resulting to good grain quality because harvesting can be carried out at the right physiological stage for a crop.

The maturity period varied greatly with a range of 116 days for 39 (Caiapo) and 140 days for 378 (WAB 905-B-4A 1.1) and this was under N-P+ and N-P- experimental environments, respectively for earliest selected genotypes. The range of 24 days can be exploited by breeding varieties that mature early and thus escape terminal drought (Atlin et al., 2006b; Bing et al., 2005; Blum, 2000; Boonjung and Fukai, 1996). Since the broad sense heritability was low at 23.9% for days to maturity, modified bulk method without selection until the materials are fairly homozygous at about F_5 to F_6 generation, should be emphasized in selection as simple mass selection could not be efficient in this case. Heritability is used to establish the expected improvement or progress after selection of genotypes from a given population (Nyquist, 1991).

From the display of scatter plot of yield versus days to maturity under soil N-P- condition (Fig. 3.2) among the best high yielding genotypes, a number of them were in the desired quadrant of high yielding and early maturing (lines 378, 212, 381 and 368). However majority of the genotypes congregated in the high yielding but late genotypes confirming that late genotypes tend to be high yielding. The performance under soil N-P+ condition had different genotypes in the early and high yielding quadrant from those obtained under soil N-P- condition (Fig. 3.3). Probably the reason for this behaviour is that different gene system or quantitative trait loci (QTL) are operating for each of the two soil N and P conditions, thus the need to breed specific genotypes for each soil N and

P condition. The performance under soil N+P- had two genotype (76,364) occurring in the desired quadrant just as under soil N-P+ condition but was under soil N-P+ condition. The two lines may be having the same adaptation mechanism because the lest of the 23 genotypes were in different quadrants. The quadrant for early and high yielding lines under soil N+P+ condition (Fig. 3.5) had different genotypes from all the other three soil condition cases. This indicates that different adaptation mechanisms are in use for each of the four soil N and P conditions. The worst genotype was 39 as it was poorly adapted as indicated by its low yield although it was quite early. The foregoing clearly indicate the need to breed different genotypes to different soil N and P conditions, as none of the genotype had broad adaptation cutting across the four soil environments.

The days to maturity for the three hundred and ninety germplasm were congregated towards lateness (Fig. 3.6 to 3.9) to the right. This implies that there is need to introgress genes for earliness from such parents as line 39 (Caiapo) that is early but low yielding. The challenge is that high yield and earliness seem to be negative correlated such that imparting earliness may result to a yield penalty. However, backcrossing may help break some of this linkage and probably develop a compromise variety with desirable earliness and also high yielding.

3.5.2 The plant height and above ground biomass production

Plant height is an important parameter to consider as some farmers indicated their preference for tall plant height. The top genotypes had a range of 108 cm to 115 cm under N-P- and N+P- experimental conditions. This is in contrast to the shortest rice plants, which had a range of 46 to 79 cm under N+P- and N-P+ conditions (Table 3.5). This diversity can be harnessed through breeding to produce the preferred height by farmers. Farmers, in a participatory plant breeding trial, pointed out during focus group discussion and key informants, that tall plants are easy to harvest, a finding also observed in West Africa (Efisue et al., 2008), collect their culms and use them for livestock feed, making farm yard manure and thatching sheds. They also argued that short rice plants are normally prone to damage by flooding and splash water, rodents, ground birds and termites. They also indicated that they are tiresome due to excessive bending during harvesting, cutting and threshing, views that were also found in West Africa (Efisue et al., 2008). The H^2 value for this trait was 27.3% and since it is selected visually, this trait can be improved easily provided the various sources of the height and yield genes are present in the parents used for crossing (Simmonds and Smartt, 1999).

The values for top biomass (TB) for the top genotypes ranged from 2495g to 3889g under N+P+ and N-P- conditions. The difference was 1394g thus exhibiting wide variation among the genotypes for this trait. The lowest top biomass weight values observed for experimental environments had a range of 12.5g under N-P- to 45g under N-P+ condition (Table 3.5). Comparing these two groups reveals that the genetic diversity for culm biomass was high. The general trend appeared to be that the CT series materials from CIAT Columbia tended to have more biomass and occupied much of the top ten (Table 3.5), while Africa Rice Centre germplasm (ARC and WAB series) occupied the bottom ten band. It therefore implies that the CT series materials were more adapted to varying conditions of P and N. Selection for this trait may not be difficult, since visual observation can partly be used to carry out selections. The degree of genetic determination (H^2) (Falconer and Mackay, 1996) was highest (26.7%) for top biomass among all the other characters, further backing up the fact that, the trait is fairly heritable and its breeding may not pose much challenge. The genotypes that tended to have high biomass also had generally high yields, indicating high possibility of breeding varieties that combine the two traits.

3.5.3 The tolerance of genotypes under different soil P and N condition

The phosphorous tolerance (PT) values ranged from an overall mean of 1.703 (N+P-) and 2.62 (N+P+), while that of nitrogen tolerance (NT) was 2.7 (N-P-) and 3.391 (N-P+). Generally the top ten genotypes had a value of 1.0 for PT, but those of NT ranged from 1.0 to 1.5. This diversity in tolerance range can be utilized to develop genotypes with high nutrient use efficiency under the prevailing production environments and take advantage of any applied inputs. This could entail breeding for specific adaptation instead of broad adaptation (Ceccarelli, 1994; Christiansen and Lewis, 1982; Dudal, 1976; Fukai *et al.*, 1999a; Kimani and Derera, 2009; Kimani *et al.*, 2007; Pinheiro *et al.*, 2006; Yoji *et al.*, 1992). The majority of the modern cultivars have been bred for high input environments, but the cost of the inputs is prohibitive to the majority of the farmers in Kenya. Further, the farming systems that encourage soil replenishment have been abandoned or proved inapplicable mainly because of the population pressure, infrastructure development and climate change (Roder et al., 1995; Saito et al., 2006); thus aggravating the problem of low soil N and P and therefore the need for input efficient genotypes. These systems were slash and burn, shifting cultivation and crop rotation. It is no longer possible to practice these elementary and subsistence systems and since farming is nowadays highly commercial (Kirk et al., 1998; Smaling et al., 1997), the fields are rarely left fallow or rotated with other crops as an effort to maintain soil health (Donovan *et al.*, 1999; Fukai *et al.*, 1999a; Kirk *et al.*, 1998; Wonprasaid *et al.*, 1996). The

fallow periods may be long and thus unrealistic, the uplands are poorly managed thus eroded resulting in poor soil fertility (Kirk et al., 1998). It is now imperative that the crop improvement programmes should undergo a paradigm shift from concentrating on high input dependent varieties to screening for adaptation and selecting the efficient varieties for development or improving the cultivars in order to exploit the vast unexploited problem soil areas. Upland rice has immense potential in Kenya as much of the land is unexploited, this therefore, calls for a shift from high input varieties to efficient varieties targeted to the prevailing specific environments used by farmers for production.

The scatter plots of yield versus soil N and P tolerance levels had varied results (Fig. 3.18 to 3.21). Under soil N-P- the line 74 was the most desirable because it was tolerant to low soil N and P and had the highest yield under high yielding and tolerant quadrant. This means it is easy to select genotypes according to their adaptability. Under N-P+ soil condition, line 277 was the highest yielding although not the most adapted. The line 104 was the best but it was not the highest yielding under soil N+P- condition. Under the optimum soil condition the best genotype was 251 although it was the most adapted (Fig. 3.21). It is clear that different lines are specifically adapted to certain soil N and P conditions, and that breeding for a super variety with broad adaptation is not quite easy. It seems therefore that development of varieties should aim for specific adaptation (Ceccarelli, 1994; Fukai *et al.*, 1999a).

3.5.4 Yield under varying soil N and P conditions

The number of panicles per plant is an important yield parameter as grain yield is a function of panicles area^{-1} *spikelets panicle^{-1} * fertility of spikelets * weight of grains. Farmers are quite aware of the panicle characteristic and in a participatory plant breeding (PPB) trial, they preferred long well filled clean or shiny panicles with moderate grain shattering. The best genotypes had number of panicle range of 133 (N-P-) to 263 (N-P+), while the worst had 4 (N+P-) to 16 (N-P+) panicles under experimental environments in parenthesis. This diversity of number of panicle can be exploited visually in a breeding programme. The H^2 for this trait was 22.6% being second from that of top biomass, thus indicating fairly good degree of genetic determination (Falconer, 1989).

Some of these materials had superior yields under low soil fertility conditions thus they can be used for improvement of the local cultivar. The overall mean yield was 3639 kg ha^{-1}, which was high by any standard. However, some materials gave low yield as they were poorly adapted to

some of the experimental environments, but the majority of the materials having been bred for drought tolerance and problem soils had high yield, though their performance varied depending on the experimental environments (Table 3.4). The top yielding genotypes and their experimental environments were 151 (CT16328-CA-18-M) (N-P-) at 5916 kg ha^{-1}, 245 (CT16340-CA-9-M) (N-P+) 4948 kg ha^{-1}, 222 (CT16337-CA-3-M) (N+P-) 4967 kg ha^{-1}, 370 (WAB880-1-38-20-28-P1 HB) (N+P+) 4970 kg ha^{-1}. The materials from CIAT Columbia (CT series) dominated four top slots across the soil N and P conditions, while Africa Rice Centre materials (WAB) were represented by only one under high fertility condition. The best overall high yielding genotype was under low soil fertility conditions (N-P-), indicating the fact that breeding rice for problem soil adaptation is a reality as observed also by Gregorio (2002) and Saito et al (2006).

In contrast, the worst performers were 314 (CT16350-CA-7-M) (N-P-) 509 kg ha^{-1}, 301 (CT16350-CA-2-M) (N-P+) 850 kg ha^{-1}, 269 (CT16344-CA-8-M) (N+P-) 800 kg ha^{-1}, and 39 (Caiapo) (N+P+) 567 kg ha^{-1}. Caiapo seems to be poorly adapted to low soil fertility, unlike the other parent *O. glaberrima* (line 353) that appeared twice in the top ten yielders under N-P+ and N+P+ optimum experimental environment and had yield above 4925 kg ha^{-1}. Problem soils are widespread throughout the world and breeding rice varieties that are capable of extracting the most fixed nutrients like phosphorous is very important, cost effective and environmentally friendly (Wissuwa and Ae, 2001a). The fact that the progenies of these two materials were far above their parents in yield is a clear manifestation that breeding for higher yields may be met with high success. This can be fairly easy if heritability for yield under low soil P and N is high as mass selection can be applied (Borojevi'c, 1990). However, if heritabilities are low, other methods of handling segregating populations that include pedigree, bulk, backcross, and modified bulk method can be used for progress in breeding work (Fasoula et al., 1993; Fawole et al., 1982; Holland et al., 2003; Li et al., 1997; Nyquist, 1991; Verma and Srivastava, 2004).

The distribution of yield for the three hundred and ninety lines under the four soil conditions scattered yield towards the right (Fig.3.10 to 3.13). Some genotypes were high yielding above 5000 kg ha^{-1} under soil N-P- condition. Otherwise yield under soil N+P- condition tended to have a better distribution curve than the other conditions. In all soil N and P conditions some genotypes had less than 1000 kg ha^{-1}, especially under soil N-P- condition. When yield was scattered against days to maturity, there were a number of promising genotypes that appeared in the high yielding and early quadrant (Fig. 3.14 to 3.17). Fewer genotypes seemed to congregate in the undesirable low yielding but early quadrant across all the soil N and P conditions, but higher

proportion of lines scattered in the least desirable quadrant of low yielding and late maturing. Generally none of the genotypes came out outstandingly as having wide adaptability across the soil N and P conditions. This is negative behaviour in breeding programmes because no single variety seem to be widely adapted and thus breeders have to develop different varieties for each unique soil N and P environments. This may be expensive and where varieties are to be processed, they may pose problems of standardization, because most likely they will be different, for example in grain traits and morphology in each environment. However, this may be a positive thing especially in cases of pests or disease outbreaks and buffering against environmental problems such as drought, floods, low temperature, because their levels of resilience may be different.

The 1000 grain weight (unhulled) is another important trait that indicates seed size and yield, where weight is used to sell the produce. The best top genotype had a weight range of 25.79g (N-P+) to 29.2g (N+P+), while the lowest performers had a range of 3.83g (N-P-) to 10.2g (N+P+) under the conditions in parenthesis (Table 3.4). The degree of genetic determination was low at 8% indicating that bulk breeding method where lines are advanced without selection until they become more homogeneous, may be the procedure to use (Allard, 1960; Chahal and Gosal, 2002; Hallauer and Miranda, 1989; Holland *et al.*, 2003; Li *et al.*, 1997; Nyquist, 1991; Rabiei *et al.*, 2004a; Smith and Kinman, 1965; Verma and Srivastava, 2004; Wu, 2003). The grain types preferred by Kenyan farmers are the slender long white types characteristic of basmati rice. Aroma is another key attribute as aromatic grains fetch premium prices in the market. However, these aromatic types have low yields and the trait seems to be strongly linked to low yield (Karim et al., 2007; Singh, 2005). The performance of the genotypes was observed to generally have high yields for those lines with poorer grain quality. The line like Duorado and NERICA1 that have high grain quality had a tendency to have low yields.

The correlation of yield to different soil N and P conditions indicated some case where it was significant thus indicating existence of interaction and possibly crossovers. This confirms findings from the two ways scatter plots that different genotypes were better adapted to different soil N and P environments. This implies that breeding programmes should strive to put genotypes to the environment that they are best adapted to for better yield under the prevailing stress conditions.

Generally, the notion held by some that development of plants with high extracting ability of nutrients such as P can be detrimental, especially with no external P supply, because they may

deplete soil reserves is farfetched. A part from these plants benefiting from applied nutrients, the soil reservoirs for an element like P can be available for centuries, assuming that the plants are able to extract it. Kirk et al. (1998) have argued on the complex intricacies involved in nutrients dynamics and concluded that development of efficient varieties is the best option available, not only on environmental concerns but also economically.

3.6 Conclusion and Implication

The accessions were found to be well adapted to the local conditions as indicated by their characterization data of traits like days to maturity, plant height and yield. The variability found in the study traits like biomass and the high values of H^2 obtained is an indication that their heritability was contributed partly by the heritable additive genetic effects. The combined use of H^2 estimates, CVP, GA and GAM can be utilized to improve phosphorous, nitrogen tolerance and other yield related components from the population by selecting promising genotypes under the prevailing farmers conditions. The high CVP values or phenotypic variability for traits like top biomass, number of panicles, phosphorous tolerance, yield and 1000 seed weight implies that visual appraisal can be utilized. This can be so in selections from the segregating progenies from crosses made for their improvement. The high GAM values for TB, NP and yield is an indicator of their heritability in the progenies from the parents. Very few genotypes performed well across the soil N and P experimental environments. Thus indicating that different genotypes are adapted differently to the environments and that different gene or quantitative trait loci may be involved singly or in groups. This is a clear case of broad adaptation. One of the genotype, Caiapo, which was one of the parents in the CIAT materials ranked number one for days to heading, days to anthesis and days to maturity in terms of earliness. This is an indication and a confirmation that it is possessing genes for earliness and it is therefore, a good choice for parent, where earliness is the breeding objective. The N-P- environment was found to discriminate well the genes for yield better than N+P+ condition. These materials therefore, can be used to develop varieties adapted to low soil fertility and with the end user desired traits. The correlation of yield and the two way biplots have shown that genotypes are adapted differently in different soil N and P environments.

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Appendix 3.1 The 390 lines from WARDA and CIAT-Colombia evaluated for adaptability

1	ARCCU1 Fa1 0-L4P2-HB
2	ARCCU1 Fa4-L3P6-3-HB
3	ARCCU1 Fa4-L5P2-1-HB
4	ARCCU1 Fa4-L5P2-3-HB
5	ARCCU1 Fa5-L2P3-HB
6	ARCCU1 Fa5-L4P1-HB
7	ARCCU1Fa1-L4P3-HB
8	ARCCU2Fa10-L2P4-HB
9	ARCCU2Fa11-L4P3
10	ARCCU2Fa11-L6P1-HB
11	ARCCU2Fa11L3P1-HB
12	ARCCU2Fa4-L7P1-HB
13	ARCCU2Fa5-L8P2-HB
14	ARCCU2Fa9-L4P8-HB
15	ARCCU2Fa9-L6P2-HB
16	ARCCU3Fa10-L7P1-HB
17	ARCCU3Fa12-L 11 P82-HB
18	ARCCU3Fa12-L 11P1-HB
19	ARCCU3Fa12-L 12P1-HB
20	ARCCU3Fa12-L 13P1-HB
21	ARCCU3Fa12-L12P2
22	ARCCU3Fa12-L2P1-HB
23	ARCCU3Fa12-L2P14-HB
24	ARCCU3Fa12-L8P6-HB
25	ARCCU3Fa3-L 13P2-2-HB
26	ARCCU3Fa3-L4P3-HB
27	ARCCU3Fa3-L7P1-HB
28	ARCCU3Fa5-L8P2-HB
29	ARCCU3Fa6-L3P9
30	ARCCU3Fa7-L 16P5-HB
31	ARCCU3Fa7-L3P3-HB
32	ARCCU3Fa7-L9P8-HB
33	ARCCU3Fa8-L2P4-1
34	ARCCU3Fa8-L3P1
35	ARCCU3Fa8-L7P8
36	ARCCU3Fa9-L6P1-HB
37	ARCCU3Fa9-L6P2-HB
38	ARCCUI Fa4-L3P6-2-HB
39	Caiapo
40	CT16307(1)-CA-14-M
41	CT16307(1)-CA-15-M
42	CT16307(1)-CA-2-M
43	CT16307(1)-CA-3-M
44	CT16307(1)-CA-4-M
45	CT16307(1)-CA-5-M
46	CT16307(1)-CA-6-M
47	CT16307(1)-CA-8-M
48	CT16307-CA-11-M
49	CT16307-CA-13-M
50	CT16307-CA-14-M
51	CT16307-CA-15-M
52	CT16307-CA-19-M
53	CT16307-CA-2-M
54	CT16307-CA-5-M
55	CT16307-CA-7-M
56	CT16308-CA-2-M
57	CT16308-CA-5-M
58	CT16308-CA-6-M
59	CT16310(2)-CA-3-M
60	CT16310(2)-CA-5-M
61	CT16310(2)-CA-7-M
62	CT16311(1)-CA-1-M
63	CT16311(1)-CA-6-M
64	CT16311(1)-CA-8-M
65	CT16311(2)-CA-1-M
66	CT16311(2)-CA-3-M
67	CT16312(1)-CA-1-M
68	CT16312(1)-CA-2-M
69	CT16312(2)-CA-1-M
70	CT16312(2)-CA-5-M
71	CT16312(2)-CA-6-M
72	CT16313-CA-10-M
73	CT16313-CA-11-M
74	CT16313-CA-15-M
75	CT16313-CA-17-M
76	CT16313-CA-19-M
77	CT16313-CA-3-M
78	CT16313-CA-4-M
79	CT16313-CA-6-M
80	CT16313-CA-8-M
81	CT16315(1)-CA-1-M
82	CT16315(1)-CA-10-M
83	CT16315(1)-CA-11-M
84	CT16315(1)-CA-14-M
85	CT16315(1)-CA-16-M
86	CT16315(1)-CA-19-M
87	CT16315(1)-CA-2-M
88	CT16315(1)-CA-22-M
89	CT16315(1)-CA-5-M
90	CT16316-CA-2-M
91	CT16316-CA-3-M
92	CT16316-CA-6-M
93	CT16316-CA-7-M
94	CT16316-CA-8-M
95	CT16317-CA-1-M
96	CT16317-CA-4-M
97	CT16318-CA-1-M
98	CT16318-CA-2-M
99	CT16319-CA-1-M
100	CT16319-CA-11-M
101	CT16319-CA-12-M
102	CT16319-CA-13-M
103	CT16319-CA-2-M
104	CT16319-CA-4-M
105	CT16319-CA-8-M
106	CT16319-CA-9-M
107	CT16321-CA-1-M
108	CT16322-CA-11-M
109	CT16322-CA-16-M
110	CT16322-CA-7-M
111	CT16322-CA-9-M
112	CT16323-CA-1-M
113	CT16323-CA-11-M
114	CT16323-CA-13-M
115	CT16323-CA-2-M
116	CT16323-CA-20-M
117	CT16323-CA-23-M
118	CT16323-CA-25-M
119	CT16323-CA-27-M
120	CT16323-CA-3-M
121	CT16323-CA-30-M
122	CT16323-CA-4-M
123	CT16323-CA-6-M
124	CT16323-CA-9-M
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127	CT16324-CA-11-M
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129	CT16324-CA-17-M
130	CT16324-CA-3-M
131	CT16324-CA-8-M
132	CT16324-CA-9-M
133	CT16325-CA-2-M
134	CT16325-CA-3-M
135	CT16326-CA-3-M
136	CT16326-CA-4-M

137	CT16327-CA-1-M
138	CT16327-CA-15-M
139	CT16327-CA-2-M
140	CT16327-CA-20-M
141	CT16327-CA-22-M
142	CT16327-CA-6-M
143	CT16327-CA-7-M
144	CT16327-CA-8-M
145	CT16327-CA-9-M
146	CT16328-CA-1-M
147	CT16328-CA-10-M
148	CT16328-CA-11-M
149	CT16328-CA-12-M
150	CT16328-CA-15-M
151	CT16328-CA-18-M
152	CT16328-CA-2-M
153	CT16328-CA-20-M
154	CT16328-CA-22-M
155	CT16328-CA-3-M
156	CT16328-CA-7-M
157	CT16328-CA-8-M
158	CT16328-CA-9-M
159	CT16329-CA-10-M
160	CT16329-CA-3-M
161	CT16329-CA-5-M
162	CT16329-CA-7-M
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165	CT16330(1)-CA-12-M
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168	CT16330(1)-CA-2-M
169	CT16330(1)-CA-3-M
170	CT16330(1)-CA-4-M
171	CT16330(1)-CA-5-M
172	CT16330(1)-CA-6-M
173	CT16330(1)-CA-8-M
174	CT16331-CA-5-M
175	CT16331-CA-8-M
176	CT16333(1)-CA-1-M
177	CT16333(1)-CA-10-M
178	CT16333(1)-CA-11-M
179	CT16333(1)-CA-15-M
180	CT16333(1)-CA-16-M
181	CT16333(1)-CA-18-M
182	CT16333(1)-CA-20-M
183	CT16333(1)-CA-21-M
184	CT16333(1)-CA-22-M
185	CT16333(1)-CA-23-M
186	CT16333(1)-CA-24-M
187	CT16333(1)-CA-3-M
188	CT16333(1)-CA-7-M
189	CT16333(1)-CA-9-M
190	CT16333(2)-CA-1-M
191	CT16333(2)-CA-11-M
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193	CT16333(2)-CA-15-M
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195	CT16333(2)-CA-18-M
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199	CT16333(2)-CA-3-M
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201	CT16334(1)-CA-13-M
202	CT16334(1)-CA-14-M
203	CT16334(1)-CA-16-M
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205	CT16334(1)-CA-19-M
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225	CT16337-CA-7-M
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235	CT16338-CA-28-M
236	CT16338-CA-29-M
237	CT16338-CA-3-M
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244	CT16340-CA-5-M
245	CT16340-CA-9-M
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249	CT16341-CA-8-M
250	CT16341-CA-9-M
251	CT16342-CA-13-M
252	CT16342-CA-17-M
253	CT16342-CA-18-M
254	CT16342-CA-19-M
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264	CT16344-CA-14-M
265	CT16344-CA-17-M
266	CT16344-CA-20-M
267	CT16344-CA-3-M
268	CT16344-CA-4-M
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345	CT16356(1)-CA-7-M
346	CT16356(1)-CA-8-M
347	CT16356(2)-CA-11-M
348	CT16356(2)-CA-3-M
349	CT16356(2)-CA-4-M
350	CT16356(2)-CA-8-M
351	CT16356(2)-CA-9-M
352	Dourado precoce
353	O.glaberrima
354	WAB 450-1-BL 1-136-HB
355	WAB 450-11-1-1-P41-HB
356	WAB 450-11-1-P31-1-HB
357	WAB 450-16-2-BL2-DV1
358	WAB 450-B-136-HB
359	WAB 450-I-B-P-160-HB
360	WAB 450-I-B-P-20-HB
361	WAB 450-I-B-P-28-HB
362	WAB 450-I-B-P-38-HB
363	WAB 450-I-B-P-422-HB
364	WAB 450-I-B-P-91-HB
365	WAB 616-53-4-3-1-1-

	HB
366	WAB 880 SG50
367	WAB 880-1-32-1-2-P1-HB
368	WAB 880-1-38-20-15-P2-HB
369	WAB 880-1-38-20-17-P1-HB
370	WAB 880-1-38-20-28-P1 HB
371	WAB 881-10-.37-18-12-P3-HB
372	WAB 881-10-37-18-13-P1-HB
373	WAB 881-10-37-18-3-P1-HB
374	WAB 881-10-37-18-9-P1-HB
375	WAB 881-SG1
376	WAB 897-B-B-B-B-24
377	WAB 901-7A2.1
378	WAB 905-B-4A 1.1
379	WAB 91 0-B-4AB.1
380	WAB 915-B-3A 1.1
381	WAB 919-72-4-1-HB
382	WAB 952-B-47AB.1
383	WAB 960-B-11A1.1
384	WAB 963-B-12A1.2
385	WAB450-12-2-BL1-DV1
386	WAB902-B-14A1.1
387	WAB951-B-181AB.1
388	WAB963-3A 1.1
389	WAB964-B-3A 1.2
390	WAB969-40-1-HB

CHAPTER FOUR.

Combining Ability and Performance of Rice Genotypes Under Four Different Soil Fertility Environments

Abstract

This study was conducted to establish the genetic factors controlling some upland rice metric traits. Nine parents were selected after evaluating three hundred and ninety (390) lines for adaptability under four different soil nitrogen and phosphorous conditions that are prevalent in farmers' production environments. A 9 by 9 full diallel mating design was used and the F_2 populations and their parents were evaluated for their performance under contrasting soil N and P conditions; at Mwea, Alupe and Matuga locations in Kenya. These soil conditions were N-P- (no P no N applied), N-P+ (P only applied), N+P- (N only applied) and N+P+ (both P and N applied). The genotype mean squares and the interaction with environment had significant mean squares for most of the soil N and P conditions. The GCA and SCA effects mean squares were also significant and their interactions with environment were highly significant. The magnitude of GCA and SCA indicated that the SCA effects were more important, imply nonadditive effects were predominant. The GCA:SCA ratios were mostly less than 1.0 for the majority of the traits under the soil N and P conditions, thus indicating greater contribution of nonadditive genetic effects. The reciprocal effects were significant and further analysis revealed that nonmaternal effects were slightly more important over the maternal effects. The maternal and nonmaternal mean squares were found to be significantly different from zero ($P<0.05$) for most of the ten traits under this study. This implies that the nonheritable effects were higher in control of the traits under the four soil N and P conditions. The GCA effects for the parents were significant under different soil N and P conditions, and NERICA and G8-WAB964-B-3A 1.2 were the best combiners for earliness and a 1000 seed weight. The genotype when ranked indicated lack of broad adaptation across locations and soil N and P conditions, thus generally exhibiting specific adaptation. The biplots indicated that different genotypes were occurring in different quadrants thus showing specific adaptation under given soil N and P condition. The correlation of yield for the different soil N and P conditions indicated both positive and negative values, of which some were significant. This shows interaction and possibly crossovers were present. The conclusion is that the exploitation of the nonheritable effects can best be utilized by breeding hybrid rice as is the case in China and other countries and that exploitable genetic variability exist in the genotypes.

4.1 Introduction

There is widespread occurrence of low soil phosphorous and nitrogen in many of the farmers' fields in Sub-Sahara Africa, with consequent low yields (Atlin *et al.*, 2006b; Christiansen and Lewis, 1982; Donovan *et al.*, 1999; Kirk *et al.*, 1998; Smaling *et al.*, 1997; Wonprasaid *et al.*, 1996). One sustainable strategy to attempt to solve this problem is to develop adapted varieties with superior P and N utilization. Many farmers are unable to access credit and thus inputs and hence soil amendment through application of inorganic fertilizers is not affordable. Further, not all genotype are responsive to added inputs, and these will normally continue to perform dismally even when nutrients are applied (Fageria et al., 1988; Saito et al., 2006; Smaling et al., 1997; Wade et al., 1999a). The use of N is particularly tricky because inappropriate use of it can lead to grain quality deterioration but cool temperature are experienced during flowering and maturation, grain quality may be enhanced (Chaturvedi, 2005; Efferson, 1985), thus low market value. It therefore, calls for strategies of nitrogen (N) management as the correct N level leads to high grain quality traits like aroma (Bhattacharjee et al., 2002; Bradbury, 2009). The use of efficient varieties in N utilization normally enhances grain quality, as these are less chalky, remain intact after shelling or milling with high head rice value. It is important that adapted and low phosphorous (P) and N tolerant varieties be breed to capture these novel traits intrinsic in farmers' cultivars. The N utilization efficiency and recovery in rice is very low at 30% despite adequate supply from both external sources like inorganic fertilizer or from organic sources such as decayed and mineralized crop residues (Dobermann and Fairhurst, 2000; Roberts, 2006; Shukla et al., 2004).

Based on P or N-use efficiency and grain yield at a low soil P or N level, rice genotypes have been classified into four groups. Fageria and Baligar (2003) classified the first genotype group as efficient and responsive (ER) and that these are genotypes that produce above the average yield compared to all the genotypes tested in the experiment at low P or N level and had higher P or N-use efficiency than the average of all the genotypes. The second group are the genotypes that are efficient and non-responsive (ENR). These genotypes produce more than the average yield of genotypes tested at low P or N level, but P or N-use efficiency is lower than the average of all genotypes classified in this group. The third group are the non-efficient and responsive (NER) genotypes that produce less than average grain yield at low P or N level, but P or N use efficiency is above the average of the genotypes tested. The fourth group are genotypes that produce less than the average yield of genotypes tested at low P or N level and

response to applied P or N (P or N use efficiency) is also less than the average of those genotypes. These types are classified as non-efficient and non-responsive (NENR) genotypes. Fageria and Baligar (2003) from a practical point of view, argued that the genotypes which fall into ER group are the most desirable, because they can produce high yield at low soil P or N levels and also respond well to applied P or N. Thus, this group can be utilized with low as well as high input technology with reasonably good yield.

Phosphorus (P) deficiency is a major abiotic stress that limits crop productivity on farmers' fields. The majority of the regions have low absolute soil-P content, mainly because P in the soils is strongly bound to soil particles (Fageria et al., 1988; Fawole et al., 1982). This tendency to form insoluble complexes leads to a very low mobility of P in soils and this condition is exacerbated by low soil pH prevalent in most farmers fields (Christiansen and Lewis, 1982; Clark and Duncan, 1991; Dambroth and El Bassam, 1983; Donovan et al., 1999; Fageria and Baligar, 2003; Fageria et al., 1988; Fawole et al., 1982; Harpstead and Adams, 1976; Smaling et al., 1997). A high biomass output has also been used as an indicator of efficient plants. The breeding of P use-efficient cultivar has been studied and reported to be under genetic control and that genotypes do show great variability in this traits (Kirk et al., 1998; Manske et al., 2000; Rebetzke et al., 2004; Saito et al., 2006).

In Kenya, no research has been conducted on genetics of low and high soil N and P tolerance or development of varieties adapted to low soil N and P conditions. However, various studies have been conducted elsewhere which have indicated that nitrogen and phosphorous tolerance and use efficiency and response in rice and even wheat is widely varied among genotypes and it is heritable. These studies have reported that the trait is controlled quantitatively (major genes) and that major quantitative trait loci have been identified that confer tolerance to low soil N and P (Baligar et al., 2001; Cassman et al., 1998; Chaturvedi, 2005; Clark and Duncan, 1991; Dambroth and El Bassam, 1983; De-Datta, 1981; Donovan et al., 1999; Ju et al., 2009; Manske et al., 2000; Ortiz-Monasterio et al., 2003). There is no information of combining ability and maternal effects on the existing varieties and no work has been conducted in breeding and understanding genetic for the varieties found in Kenya. There is also limited information on combining ability and maternal effects from elsewhere in relation to low and high soil N and P tolerance. Therefore the breeding of cultivars that perform well under the inherent or added nutrients have not been undertaken in Kenya for the rice crop despite the existent of poorly adapted and low yielding cultivars. This work was therefore, intended to study the combining

ability and maternal effects in development of new genotypes with enhanced adaptation to low and high soil P and N and with better yields in upland environments.

4.1.1 Study objectives

The main objective of this study was to establish the genetic control of low soil phosphorous and nitrogen tolerance under environments prevalent in farmers' upland rice fields.

The specific objectives were to:

i. establish the magnitude and role of GCA, SCA and interaction effects conditioning and contributing to inheritance of various traits for tolerance to low soil P and N conditions,
ii. estimate the magnitude of reciprocal effects in control of the studied traits, and
iii. establish the genotypes performance for various agronomic traits under low and high soil P and N conditions.

4.1.2 Study hypothesis

The study hypothesis was that tolerance to low and high soil P and N was conferred by additive and dominance genetic effects and that different genotypes ranked differently under different soil N and P environments.

4.2 Materials and Methods

4.2.1 Germplasm assemblage and parents selection

The selected parents from the adaptation trial were planted in a crossing block as a full nine parent diallel mating design. The features of these parents are indicated in Table 4.1.

Table 4.1 Rice parents used in the diallel and their characteristics

Serial No.	Pedigree	Source*	Primary selection criteria
G1	NERICA1	ARC	High grain quality, early, blast resistant
G2	Duorado	Kenya	Local cultivar (Adapted)
G3	IR79913-B-176-B-4	IRRI	Early, low soil N & P Tolerant
G4	CT16333(1)-CA-20-M	CIAT	Medium maturity, high yielding
G5	CT16333(1)-CA-22-M	CIAT	Low soil N and P tolerant
G6	CT16333(2)-CA-18-M	CIAT	Low soil P tolerant
G7	CT16313-CA-19-M	CIAT	Early, blast tolerant
G8	WAB964-B-3A 1.2	ARC	Early, high yielding
G9	CT16317-CA-4-M	CIAT	Low soil N tolerant

*IRRI-International Rice Research Institute G1-G9 means also parents 1 to 9
CIAT- International Center for Tropical Agriculture ARC-Africa Rice Centre (WARDA)

4.2.2 Diallel mating

A steel and mesh wire screen house was constructed to be used as a crossing block structure with high sunlight infiltration for optimal photosynthesis, where the selected parents were planted for hybridization. This was at KARI-Mwea Tebere, and three sets of parents were planted on staggered dates; 18th July, 21st August and 24th September 2009 as potted plants. The staggered planting was to ensure synchronization of the parents as they had different flowering dates; this was established during an earlier adaptation and characterization trial of these accessions. The hybridization was performed in a full nine parent diallel mating scheme. The emasculation of parents was effected by use of a suction vacuum emasculator that was constructed at African Centre for Crop Improvement, University of KwaZulu Natal as described by Lamo (2010). Hand emasculation was also used. Optimum conditions were ensured such as watering to avoid water stress, weeding and control of pests. The emasculation and pollination was carried out from the mid morning around 8.00 am to the afternoon up to 4.00 pm. This was the period when the female flowers had not opened and from around noon the male flowers had freshly opened spikelets and the panicles were lax thus facilitating collection of fresh pollen for pollinating the emasculated female spikelets. A crossing data sheet was used to monitor successive crosses and those that were few, hence requiring further crossing and therefore have a complete F_1 seed set.

Once the emasculation and pollination had been effected, the flowers were covered by a soda straw (Appendix 4.1) of the correct width and length to prevent cross pollination and at the same time rise the relative humidity for better fertilization as recommended by Fehr and Hadley (1980). A manila tie on tag indicating the cross, date and pollinator initials were tied on the emasculated and pollinated flowers. The ground was kept moist to raise humidity and thus minimize emasculated flower, stigma and pollen desiccation. The crossing block structure was made of small diameter mesh wire to keep birds away. The seeds were carefully harvested and placed in well-labelled medical envelops and dried under shade condition. The seed set realized were few to establish a field trial in most of the crosses, hence it was important to increase the F_2 seed. The F_1 seeds were planted in the screen house as potted plants to ensure maximum care and keep any pests away. These were selfed to increase the F_2 seeds then harvested and stored in well-labelled medical envelops.

4.2.3 Environmental locations for evaluation of the F_2 plants

The F_2 seeds were evaluated in three regions, namely Central at KARI-Mwea Tebere, western at Lake Basin Development Authority (LBDA-Alupe) and Coast region at KARI-Matuga. Their characteristic are as described below: KARI-Mwea Tebere (National Rice and Fibre Research Centre (NRFRC)) is located in Mwea Division, Kirinyaga South District, Central Province, 112 km East of Nairobi in Kenya. It lies on Latitude 00^o 37' S and Longitude 37^o 20' E at an elevation of 1159 m above sea level (masl). The average rainfall is about 850 mm with a range of 500 - 1250 mm divided into long rains (March – June with an average of 450 mm) and short rains (Mid-October to December with an average of 350 mm). The rainfall is characterized by uneven distribution in total amounts, time and space. The temperature ranges from 15.6º C to 28.6º C with a mean of about 22º C. The soil are nitosol, which are deep, well drained dusky-red to dark reddish-brown, friable clay with low fertility (FURP, 1987; Jaetzold and Schmidt, 1983).

Lake Basin Development Authority (LBDA) Alupe is located on Latitude 0° 30' 0 N; Longitude 34° 7' 50 E; on an elevation of 1170 meters above sea level (masl) in the western part of Kenya. The soils at Alupe have been characterized as Ferralo-orthic Acrisol with pH of 5.0 (FURP, 1987). The total annual rainfall at Alupe was 1,398 mm and temperature ranged from 16-34°C during the year 2009.

KARI- Matuga is situated 15 km South of Mombasa from the Likoni ferry in Kwale District. The centre is at Latitude 4^o 9' 52 S and Longitude 39^o 34' 23 E at an elevation of 132 masl. Annual mean temperatures are between 24.4^{o}C and 26^{o}C and the area receives mean annual rainfall of about 800mm. The site lies in Agro- Ecological Zone CL3 referred to as the coconut-cassava zone and is suitable for conventional agriculture. The soils are derived from Pliocene sandstones and are commonly referred to as Magarini sands (Jaetzold and Schmidt, 1983). They are low in C, N, P, K and are moderately acidic.

The soil was sampled in the 0-30 cm top soil layer over the experimental block. It was sampled in both diagonals at the four corners, at the middle, then between the corners, and between the middle of diagonals and corners making a total of 17 samples. These samples were analyzed separately and since they had almost the same values, these were composited and averaged. The soil analysis was carried out at JomoKenyatta University of Agriculture and technology (JKCUAT) and had the properties indicated in Table 4.2.

Table 4.2 Soil analysis results for the Mwea, Alupe and Matuga regions

Parameter	Mwea	Alupe	Matuga
$pH_{1:1}$	5.53	4.69	5.7
ECe (Electrical conductivity)	0.11	0.18	0.07
% N	0.16	0.73	0.05
Available P (ppm)	1.35	0.14	0.46
Extractable-Zn (ppm)	1.65	1.75	11.8
Extractable-Cu (ppm)	8.52	5.66	9.47
Extractable-Mn (ppm)	360	48	380.7
Extractable-Fe (ppm)	379	479	190.3

4.2.4 The experimental design and management

The 72 populations (F_2s generation) seed and the 9 parent made up eighty one entries which were planted at KARI-Mwea on the 18th August, at KARI-Matuga on the 25th August and LBDA on the 10th September 2009. These were planted in an alpha lattice design arrangement of 9x9 within the fertility treatment, and were replicated twice at Mwea and three times at Alupe and Matuga. The overall arrangement was a split plot experimental design where fertility treatment was the main plot and the genotypes the subplot. The experimental plot was 1.6 m^2 consisting of 40 plants. The inter- and intra-row spacing was 20 cm. Three seeds were sown per hill and later thinned to one. Normal cultural practices such as weeding, spraying and harvesting were carried out manually. Supplementary sprinkler irrigation was only undertaken at Mwea and Matuga when necessary, but at Alupe no additional moisture was applied and hence the trial was purely rainfed given that the rainfall was adequate. The experimental environments were N-P- (no P and N applied), N-P+ (P applied), N+P- (N applied) and N+P+ (both P and N applied).

The source of P and N were inorganic fertilizers triple super phosphate (TSP-($CaHPO_4$) 32.5% - 60kg P ha^{-1}) applied as basal and calcium ammonium nitrate (CAN -90 kg N per ha^{-1}), applied as splits of 45 kg ha^{-1} at planting and at maximum tillering. These were applied in the designated treatment blocks arranged in such a way that N due to it high mobility does not flow to unintended block and thus introduce unwanted interference.

The following data was collected. Days to heading (days), anthesis and maturity, P tolerance (scale, 1-5) and N tolerance (scale, 1-5), plant height (cm), top biomass (g), number of panicles (absolute numbers per ten plants), days to maturity (days), 1000 grain wt (g), and grain weight ha^{-1} (kg). The nitrogen scale of 1-5 is widely used to measure leaf colour intensity which is related to leaf N status (Shukla et al., 2004) as follows; the leaf colour chart (LCC) developed at

International Rice research Institute (IRRI, 2003) was used at flowering stage. Ten disease free plants were selected randomly and the middle part of the top most fully opened leaf from each plant was placed on the LCC to compare the leaf colour and the LCC colour. The value on LCC that matched the leaf colour was recorded and if the leaf colour fell between two LCC shades, the two value were added together and divided by two to get the average. The values for the ten plants were summed up and then divided by ten to get the final score. This method is non-destructive and readings were taken under the body shade if it was sunny to minimise its effects on the colour reading. To standardize readings, only one person took the data at the same day time when it was bright. Plant that were N tolerant were given a score of one and those that were least tolerant were given a score of five. The score of three was taken as moderate tolerance. The P tolerant scale was developed based on the following visual parameters of P deficiency that include; stunted growth, dull-green or blue-green colour, possible purple coloration on some part of the plant, reduced flowering, delayed maturity, leaf tips look burnt, followed by older leaves turning a dark green, and reddish-purple colour. The most P tolerant plants were rate one and these had normal vigorous growth without deficiency symptoms. The least tolerant ones were rated five and these had high deficiency symptoms, while the moderately tolerant ones were rated three. These values of N and P tolerance were tested for normality using SAS proc univariate normal plot and were found to be normally distributed.

For the agronomic traits, thirty six plants were randomly selected for data collection and the early maturing lines were tagged with a different colour code of netting string, one colour per week for three weeks. The top biomass was taken from an area of 1.6 m^2 in grams (g) by cutting the culms at the ground level with a sickle. The culms without panicles were dried to constant moisture and then weighed and data recorded. Plant height was measured as whole numbers (cm) from soil surface to tip of the tallest panicle (awns excluded) (IRRI, 2002). Days to maturity were counted as number of days from seeding to grain ripening (85% of grains on panicle were mature). 1000 seeds were weighed in grams of 1000 well-developed whole grains that were dried to 13% moisture content and then weighed on a precision balance. The yield was taken as the weight of unhulled grains harvested from an area of 1.6 m^2 and then converted to kg ha^{-1} at 14% moisture content.

4.2.5 Data analysis

The data for the ten traits was analyzed using SAS software version 9.2 using Diallel SAS 05 program (Kang, 2003; SAS-Institute, 2003; Zhang et al., 2005). The genetical model applied was:

$X_{ijklc} = \mu + \alpha_l + b_{kl} + v_{ij} [g_i + g_j + s_{ij} + r_{ij} (m_i + m_j + n_{ij})] + (\alpha v)_{ijl} [(\alpha g)_{il} + (\alpha g)_{jl} + (\alpha s)_{ijl} + (\alpha r)_{ijl} ((\alpha m)_{il} + (\alpha m)_{jl} + (\alpha n)_{ijl}] + e_{ijk}$.

Where μ is the population mean, α_l is the environment effect,

b_{kl} is block effect in each environment, v_{ij} cross effect,

g_i and g_j are GCA effects for i^{th} and j^{th} parent, r_{ij} is the reciprocal effects for ij^{th} cross,

$(\alpha v)_{ijl}$ is the interaction between environment and the cross, s_{ij} is SCA effect for ij^{th} cross,

$(\alpha g)_{il}$ is the interaction effect between GCA effect for the i^{th} parent and environment,

$(\alpha g)_{jl}$ is the interaction between GCA effect for j^{th} parent and environment,

$(\alpha s)_{ijl}$ is the interaction between SCA effect for ij^{th} cross and environment,

$(\alpha r)_{ijl}$ is the interaction between reciprocal effects for ij^{th} or ji^{th} cross and environment,

m_i is the maternal effect of the parental line i,

m_j is the maternal effect of the parental line j,

n_{ij} is the non-maternal effect of ij^{th} or ji^{th} cross,

$(\alpha m)_{il}$ is the interaction between environments and maternal effects of parent i,

$(\alpha m)_{jl}$ is the interaction between environments and maternal effects of parent j,

$(\alpha n)_{ijl}$ is the interaction between environments and nonmaternal effects of ij^{th} or ji^{th} cross.

e_{ijk} is experimental error or residue effect for the X_{ijklc} observation (k=1, 2,…, r; i=j=1, 2,…, n).

4.3 Results

4.3.1 Genotype x environment interaction

The genotypes across the environment showed highly significant mean squares (P<0.001) (Table 4.3). The mean squares for mega-environments were highly significant; except for days to heading and nitrogen tolerance which had significant values at P<0.01 both under experimental environment N+P+, while days to heading (N-P+) had non-significant values. The environment mean squares were only non-significant under N+P+ for 1000 seed weight, while genotypes (entries) were very highly significant for number of panicles, plant height, 1000 seed weight and grain yield (Table 4.4). The genotype by environment interactions (GEI) were not significant for number of panicles under N-P-, 1000 seed weight under N-P- and N-P+ conditions. The GEI were highly significant (P<0.001); except for days to maturity (N+P+) which

were significant at P<0.01. The days to heading (N-P-), phosphorous tolerance (N-P+) and top biomass (N-P-) were significant at P<0.05. Days to anthesis (N-P-) and days to maturity (N-P-) were not significant (0.05<P).

The GCA x environment interactions were significant for days to heading, maturity and top biomass in all the four soil N and P conditions. For the other traits, under some soil N and P they were not significant (Table 4.3 and 4.4). The SCA x environment interactions were significant for nitrogen (N) and phosphorous (P) tolerance and grain yield under all the four soil N and P conditions. The other metric traits had one or more soil N or P condition having nonsignificant value. The reciprocal x environments interactions were very highly significant for grain yield, except under N-P+ condition where they were highly significant. They were however nonsignificant for at least one soil N or P condition for the other metric traits. The maternal x environment interaction were very highly significant for top biomass (except N-P- condition, P<0.05) and grain yield for all the four soil N and P conditions. The interactions however were nonsignificant in one or two of the soil N or P condition. None of the metric traits had significant nonmaternal x environment interactions for all the four soil N and P conditions. However top biomass had very highly significant interactions except for N-P- soil condition.

4.3.2 The genetic component effects for the ten traits under different soil N and P experimental environments

The general combining ability (GCA) mean squares were very highly significant for days to maturity, anthesis and maturity; top biomass and plant height for all four soil N and P conditions. The 1000 grain weight and grain yield had significant values under the four soil conditions (Table 4.3 and 4.4). The SCA were very highly significant for days to heading and maturity; N and P tolerance, top biomass and plant height for the four soil conditions, however, number of panicles per plant and grain yield had significant values for all the soil conditions. The reciprocal mean squares were very highly significant for days to heading, anthesis, N tolerance, top biomass plant height, number of panicles and grain yield for the four soil N and P environments.

The maternal mean squares were highly significant for days to heading, anthesis, N tolerance, top biomass, plant height, 1000 seed weight and grain yield for the four N and P soil conditions. Nonmaternal mean squares were very highly significant for days to heading, N tolerance, top biomass, plant height and grain yield under the four soil N and P environments.

Table 4.3 Mean squares components for rice days to heading, anthesis, maturity; N and P tolerance and top biomass under four soil conditions

Traits		Days to heading (days)				Days to anthesis (days)				Days to maturity (day)			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	436.10***	347.67***	440.21***	467.71***	1861.91***	34839***	417.26***	450.33***	83.57***	52.26***	177.24***	76.33***
ENV	2	10161.12***	192.90ns	11370.59***	18205.00***	30017.68***	1091.05***	7879.43***	17147.84***	680.29***	1839.57***	6629.30***	3430.29***
REP(ENV)	5	1818.54***	1682.34***	4683.49***	3889.87***	58995.58***	2164.61***	5000.12***	4016.06***	218.87***	99.72***	634.63***	322.91***
ENTRY	80	617.00***	549.58***	560.66***	443.11***	829.36***	518.17***	555.95***	422.81***	213.39***	44.95***	210.19***	63.60***
GCA	8	949.83***	1155.77***	1488.61***	868.23***	2782.78***	1117.83***	1475.55***	800.81***	338.85***	80.85***	165.96***	110.22***
SCA	36	483.46***	432.98***	262.22***	289.85***	372.35ns	399.77***	258.52***	292.11***	167.42***	34.28***	366.31***	75.82***
REC	36	676.57***	532.37***	652.9***	501.90***	852.27***	503.32***	649.02***	469.51***	231.49***	47.64***	63.90***	41.02*
MAT	8	1553.39***	1094.70***	1588.84***	1407.19***	2578.43***	1046.42***	1549.81***	1308.65***	534.17***	40.85*	91.78**	37.42ns
NMAT	28	426.05***	371.71***	385.48***	243.25***	359.08ns	348.14***	391.65***	229.75***	145.01***	49.58***	55.93**	42.05*
ENV*ENTRY	160	180.89*	206.74***	110.75***	151.35***	240.81ns	197.46***	111.42***	143.95***	6.97ns	32.09***	65.83***	33.06**
GCA*ENV	16	378.20***	387.96***	156.49**	316.64***	442.94ns	362.00***	141.67*	309.36***	9.84ns	17.56ns	38.06ns	50.85*
SCA*ENV	72	145.15ns	146.20*	88.97ns	115.58*	214.77ns	143.28*	92.42*	108.97*	6.33ns	29.94***	113.43***	25.31ns
REC*ENV	72	172.79ns	227.00***	122.37***	150.39***	221.93ns	215.07***	123.7***	142.17***	6.98ns	37.47***	24.40ns	36.86**
MAT*ENV	16	114.27ns	410.61***	117.3*	311.59***	247.24ns	390.68***	122.87*	289.01***	9.06ns	56.97***	44.79*	78.06***
NMAT*ENV	56	189.51*	174.54**	123.81**	104.33ns	214.7ns	164.9*	123.94**	100.21ns	6.38ns	31.89***	18.57ns	25.08ns
R-Square		0.67	0.69	0.8	0.79	0.78	0.7	0.79	0.79	0.86	0.66	0.81	0.67
Coeff Var		11.72	9.82	7.81	8.43	19.66	9.19	7.46	8.02	1.85	2.46	3.1	2.88
Mean		97.98	100.67	106.08	104.72	91.38	105.05	110.2	108.02	156.8	165.67	164.04	167.41
GCASS/Entry SS		15.39	21.03	26.55	19.59	33.55	21.57	26.54	18.94	15.88	17.99	7.90	17.33
SCASS/Entry SS		35.26	35.45	21.05	29.44	20.20	34.72	20.93	31.09	35.31	34.32	78.42	53.65
GCA:SCA Ratio		0.44	0.59	1.26	0.67	1.66	0.62	1.27	0.61	0.45	0.52	0.10	0.32
RecSS/EntrySS		49.34	43.59	52.40	50.97	46.24	43.71	52.53	49.97	48.82	47.69	13.68	29.02
MSS/RecSS		51.02	45.70	54.08	62.31	67.23	46.20	53.06	61.94	51.28	19.05	31.92	20.27
NMSS/RecSS		48.98	54.31	45.92	37.70	32.77	53.80	46.93	38.06	48.72	80.95	68.08	79.73

Traits		Nitrogen tolerance (scale)				Phosphorous tolerance (scale)				Top biomass (g)			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	1.60***	1.23***	1.31***	1.31***	1.46***	1.04***	1.15***	1.41***	313518.70***	322789.60***	418933.00***	437643.40***
ENV	2	4.74***	13.37***	4.65***	2.58**	31.93***	29.85***	22.28***	2.14***	3105***	8949963.69***	9277101.37***	15639235.20***
REP(ENV)	5	10.79***	3.99***	2.30***	0.47ns	3.26***	4.41***	1.03ns	0.18ns	343991.88***	95202.81***	323873.86***	92631.41***
ENTRY	80	2.70***	1.61***	2.24***	1.82***	1.71***	1.07***	0.96***	1.85***	720418.39***	535581.84***	673688.24***	627251.45***
GCA	8	2.09***	1.60***	0.77ns	1.10*	1.15*	0.56ns	0.89ns	0.91**	602938.63***	666017.56***	1345109.60***	1154118.55***
SCA	36	2.82***	1.77***	2.88***	2.11***	1.34***	1.45***	1.03***	1.74***	508891.99***	307621.38***	362073.13***	353761.20***
REC	36	2.72***	1.44***	1.93***	1.68***	2.21***	0.79**	0.91**	2.18***	958051.40***	734556.59***	836098.61***	783660.13***
MAT	8	4.18***	2.23***	3.79***	2.29***	3.19***	0.68ns	0.78ns	2.34***	1716621.93***	1858253.89***	2450926.23***	2427770.42***
NMAT	28	2.30***	1.22***	1.40***	1.51***	1.93***	0.82**	0.94**	2.13***	741316.96***	413500.21***	374719.29***	313914.34***
ENV*ENTRY	160	0.72***	0.80***	0.78***	1.07***	0.89***	0.56*	0.99***	1.22***	74221.39*	115665.90***	183798.84***	163601.14***
GCA*ENV	16	0.48ns	0.57ns	0.96*	2.11***	0.75*	0.69ns	1.39***	1.26***	108355.98*	169667.47***	274089.17***	224246.13***
SCA*ENV	72	0.85***	1.04***	0.76*	1.05***	0.91***	0.78***	0.85***	1.41***	67482.13ns	121167.35***	187411.92***	180580.86***
REC*ENV	72	0.63*	0.61ns	0.76*	0.86***	0.89***	0.31ns	1.03***	1.02***	73375.18ns	98164.09***	160121.23***	133144.75***
MAT*ENV	16	1.09**	0.91*	0.67ns	0.75*	1.08**	0.44ns	1.05*	1.83***	107863.48*	110615.29***	171104.00***	151592.72***
NMAT*ENV	56	0.50ns	0.52ns	0.78*	0.89***	0.84***	0.27ns	1.03***	0.79***	63521.38ns	94606.61***	156983.30***	127873.91***
R-Square		0.7	0.62	0.61	0.67	0.68	0.61	0.65	0.76	0.76	0.93	0.91	0.94
Coeff Var		26.82	25.52	24.76	21.37	32.47	35.89	25.73	26.76	35.78	15.17	18.58	13.62
Mean		2.13	1.9	2.06	2.03	2.01	1.8	1.95	1.97	683.8	801.63	879.21	1001.53
GCASS/Entry SS		7.74	9.94	3.44	6.04	6.73	5.23	9.27	4.92	8.37	12.44	19.97	18.40
SCASS/Entry SS		47.00	49.47	57.86	52.17	35.26	60.98	48.28	42.32	31.79	25.85	24.19	25.38
GCA:SCA Ratio		0.16	0.20	0.06	0.12	0.19	0.09	0.19	0.12	0.26	0.48	0.83	0.72
RecSS/EntrySS		45.33	40.25	38.77	41.54	58.16	33.22	42.66	53.03	59.84	61.72	55.85	56.22
MSS/RecSS		34.15	34.41	43.64	30.29	32.08	19.13	19.05	23.85	39.82	56.22	65.14	68.84
NMSS/RecSS		65.77	65.90	56.42	69.91	67.92	80.73	80.34	75.99	60.18	43.78	34.86	31.16

The magnitude of GCA mean squares (% GCA SS/Genotypic SS) ranged from 3.44% for N tolerance under N+P- soil condition to 33.55% for days to heading under N-P- condition (Table 4.3 and 4.4). The SCA ranged from 20.20% for days to anthesis under N-P- condition to 78.42% for days to maturity under N+P- soil condition. The GCA:SCA ratio from the GCA and SCA magnitudes ranged from 0.06 for N tolerance under N+P- to 1.66 for days to anthesis under N-P- condition. The metric traits with a ratio of more than one were days to heading (1.26 for N+P- condition), days to anthesis (1.66 for N-P-, 1.27 for N+P-), N tolerance (1.06 for N+P+) and plant height 1.8 for N+P- soil condition. The magnitude of reciprocal effects ranged from

13.68% (N+P-) to 61.72% (N-P+) for days to maturity. The contribution of reciprocal effects exceeded 50% in the following traits and soil conditions; days to heading (N+P-, N+P+), anthesis (N+P-), P tolerance (N-P-, N+P+), all top biomass N and P conditions, number of panicles (N+P-), plant height (N-P+, N+P+), 1000 seed weight (N-P+, N+P-) and grain yield under N-P+ and N+P+ soil conditions. The maternal effects had range of 15.63% for number of panicles (N+P-) to 68.84% for top biomass under N+P+ soil condition. However the following metric traits had more than 50% contribution to the reciprocal effects; days to heading (N-P-, N+P-, N+P+), anthesis (N-P-, N+P-, N+P+), maturity (N-P-), top biomass (N-P+, N+P-, N+P+), 1000 seed weight (N+P+) and plant height under N-P+ and N+P+ soil conditions. Nonmaternal effects range was 31.16% for top biomass (N+P+) to 80.95% for days to maturity for N-P+ soil condition. The magnitude was however more than 50% over maternal effects in most cases (Table 4.3 and 4.4).

4.3.3 General combining ability effects for the parents under the four soils N and P experimental environments

The general combining ability effects (GCA) of NERICA 1 (G1) were highly significant ($P<0.001$) and negative for days to heading and anthesis and days to maturity (Table 4.5) under all the experimental environments, but days to maturity had higher but very highly significant GCA effects. The GCA effects for *Duorado precoce* (cultivar-G2) were not significant ($P>0.05$). The entry G3 (IR9913-B-176-B-4) had varied reaction; it had positive and significant GCA effects for days to heading and anthesis except under N-P- and days to maturity. G4 (CT16333(1)-CA-20-M) had non-significant days to maturity under all the fertility environments. Entry G5 (CT16333(1)-CA-22-M) and G6 (CT16333(1)-CA-18-M) had non-significant GCA effects for days to heading and maturity. Entry CT1631-CA-19-M (G7) had highly heterogeneous GCA effects being positive and significant for days to heading, anthesis and maturity. Entry G8 (WAB964-B-3A 1.2) and G9 (CT16317-CA-4-M) GCA effects were non-significant for days to maturity, except under N-P- condition. The GCA:SCA ratio for the days to heading (N+P-, 1.26) and anthesis (N-P-, 1.66 and N+P-, 1.27) was more than one under the indicated soil N and P conditions. This indicates that generally nonadditive effects were more important than additive effects, except where the ratio of GCA:SCA is more than one.

The GCA effects were significant for G1 (NERICA1) for Phosphorous tolerance (PT) under N-P-, while G2 (Duorado) was significant for nitrogen tolerance (NT) except under N+P- conditions where G4 (CT16333(1)-CA-20-M)) was significant.

Parent G6 (CT16333(2)-CA-18-M) was significant for NT under N-P+, while G7 (CT16313-CA-19-M) was significant under N-P- and N-P+ conditions, but WAB964-B-3A 1.2 was significant for NT under N-P- condition.

Table 4.4 The genetic mean square parameters for rice number of panicles, plant height, 1000 seed wt and grain yield under four soil conditions

Traits		Number of panicles (numbers)				Plant height (cm)			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	195.45***	335.37***	631.16***	891.40***	344.29***	643.60***	318.83***	421.98***
ENV	2	954.24***	19947.26***	34665.85***	17945.50***	9166.11***	46018.07***	3413.51***	17042.82***
REP(ENV)	5	859.28***	356.72**	4417.10***	3039.00***	3802.78***	1396.82***	803.25***	356.28***
ENTRY	80	279.69***	227.22***	253.47***	1230.76***	394.57***	587.68***	649.62***	658.67***
GCA	8	452.51***	337.38***	196.42ns	1764.87***	751.82***	1072.38***	1843.02***	1274.16***
SCA	36	299.74***	233.80***	227.09*	1011.47***	295.08***	289.43***	347.05***	427.07***
REC	36	221.24***	196.16***	292.52**	1331.35***	414.68***	778.23***	687.00***	753.49***
MAT	8	324.65*	310.70***	205.74ns	1682.77***	882.61***	2013.31***	1496.80***	2038.22***
NMAT	28	191.69*	163.43**	317.31**	1230.95***	280.98***	425.35***	455.63***	386.43***
ENV*ENTRY	160	123.11ns	143.63***	276.27***	441.43*	100.80***	80.83***	99.62ns	97.93***
GCA*ENV	16	156.34ns	180.84**	383.98**	590.3*	190.88***	113.81**	177.97***	57.47ns
SCA*ENV	72	132.80ns	118.26*	275.14***	388.45ns	78.01***	66.71*	96.54ns	80.69*
REC*ENV	72	106.03ns	160.73***	253.47**	461.33*	103.56***	87.63***	85.28ns	124.16***
MAT*ENV	16	78.72ns	407.02***	220.62ns	634.57*	241.92***	129.98***	77.37ns	280.49***
NMAT*ENV	56	113.84ns	90.36ns	262.85**	411.84ns	64.03**	75.53**	87.54ns	79.49*
R-Square		0.65	0.72	0.73	0.63	0.86	0.9	0.7	0.83
Coeff Var		22.69	37.49	34.62	56.9	9.57	10.27	11.7	9.08
Mean		19.34	24.21	35.04	21.41	62.39	66.22	79.2	81.17
GCASS/Entry SS		16.18	14.85	7.75	14.34	19.05	18.25	28.37	19.34
SCASS/Entry SS		48.23	46.30	40.32	36.98	33.65	22.16	24.04	29.18
GCA:SCA Ratio		0.34	0.32	0.19	0.39	0.57	0.82	1.18	0.66
RecSS/EntrySS		35.60	38.85	51.93	48.68	47.29	59.59	47.59	51.48
MSS/RecSS		32.61	35.20	15.63	28.09	47.30	57.49	48.42	60.11
NMSS/RecSS		67.39	64.80	84.37	71.91	52.70	42.51	51.58	39.89

Traits		1000 seed weight (g)				Yield (kg ha$^{-1)}$			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	30.84***	19.26***	25.02***	20.61***	3280743.00***	2952930.00***	2310665.10***	2910699.00**
ENV	2	303.51***	116.28***	114.03***	9.98ns	22943494.50***	14604653.50***	38594033.30***	52001185.30***
REP(ENV)	5	266.07***	29.19*	42.32**	84.32***	15984672.60***	15957779.30***	2763696.60**	1766207.10ns
ENTRY	80	44.09***	40.32***	41.39***	33.69***	3593149.90***	3490553.70***	2678734.60***	2713260.00***
GCA	8	83.52***	56.37***	32.56**	92.94***	2883485.10*	3384441.13*	4158269.79***	3030135.69**
SCA	36	40.42***	20.92***	34.36***	19.47**	3729251.43***	2506759.55**	2957753.25***	1919261.69**
REC	36	38.99***	56.15***	50.38***	34.74***	3614751.55***	4497928.45***	2070930.37***	3436841.41***
MAT	8	64.44***	76.09***	68.41***	88.87***	6359163.93***	5710896.38***	3090183.70***	6201006.76***
NMAT	28	31.72***	50.45***	45.23***	19.27*	2830633.73***	4151366.18***	1779715.13***	2647079.88***
ENV*ENTRY	160	13.45ns	7.20ns	15.19**	12.22ns	2481757.70***	2132069.90***	1658931.00***	2431552.60***
GCA*ENV	16	20.36*	4.76ns	19.85*	17.05ns	2989545.94**	3345072.58**	976829.41ns	3696263.00***
SCA*ENV	72	12.19ns	6.69ns	13.99*	12.98ns	2562777.91***	1886700.76*	1415194.78***	2411777.85***
REC*ENV	72	13.19ns	8.27ns	15.35*	10.38ns	2287895.62***	2107882.90**	2054245.42***	2170280.57***
MAT*ENV	16	28.48**	11.24ns	9.31ns	19.68*	4339864.27***	4820621.64***	2579482.97***	3995439.40***
NMAT*ENV	56	8.82ns	7.42ns	17.08**	7.72ns	1701618.86ns	1332814.69ns	1904177.55***	1648806.61*
R-Square		0.63	0.67	0.69	0.65	0.62	0.68	0.65	0.63
Coeff Var		13.77	11.1	12.91	12.71	24.63	27.41	23.13	34.23
Mean		24.26	26.75	24.95	25.23	2514.53	2401.37	2663.59	2979.53
GCASS/Entry SS		18.94	13.98	7.87	27.59	8.02	9.70	15.52	11.17
SCASS/Entry SS		41.25	23.35	37.36	26.01	46.70	32.32	49.69	31.83
GCA:SCA Ratio		0.46	0.60	0.21	1.06	0.17	0.30	0.31	0.35
RecSS/EntrySS		39.79	62.67	54.77	46.40	45.27	57.99	34.79	57.00
MSS/RecSS		36.73	30.11	30.18	56.85	39.09	28.21	33.16	40.09
NMSS/RecSS		63.28	69.88	69.83	43.14	60.91	71.79	66.84	59.91

Entry G9 (CT16317-CA-4M) GCA effects were significant for PT under N-P- and N+P+, and for NT under N-P- condition. The GCA:SCA ratios for PT and NT were generally below under all the soil N and P conditions indicating preponderance of non-additive over additive effects. NERICA1 (G1) had significant but negative GCA effects for plant height, top biomass across all conditions, but number of panicles had positive but non-significant values under N-P+ and N+P- conditions (Table 4.5).

Genotypes IR79913-176-B-4, CT16333(2)-CA-18-M and CT16313-CA-19-M had nonsignificant values for number of panicles across all fertility conditions, while G4 had positive and very highly significant values for top biomass under all conditions. Genotypes G5 and G8 had non-significant values for plant height and top biomass, respectively under all fertility conditions. The GCA:SCA ratio for top biomass, number of panicles (NP) and plant height were less than one except for plant height under N+P- where it was 1.18. Overall for these traits, the nonadditive gene action was predominant in the control of their inheritance under all the four soil N and P experimental environments.

The NERICA1 had significant GCA effects for 1000 seed weight under N+P+, while G2 were under N-P+ and N+P- conditions. The parent G3 had significant but negatives values for 1000 seed weight except under N+P- and for yield under N-P- and N-P+ conditions. Parent G8 displayed positive and highly significant values for 1000 seed weight except under N+P- condition, while G9 had significant values under N-P- and N+P- for 1000 seed weight and yield, respectively. The GCA:SCA ratios for 1000 seed weight and grain yield were less than one except for 1000 seed weight under N+P+ where it was 1.06. This indicates nonadditive gene action were preponderant over the additive effects.

4.3.4 Genotypic rankings under three experimental environments and three mega-environments.

The ranking of genotypes across the four fertility experimental environments and mega-environments varied with crossover types being observed. For days to heading genotype 8 (NERICA 1 x WAB964-B-3A1.2) was among the top 15 best genotype in all the experimental conditions and mega-environments, although its rank varied but it was ranked top at Mwea under N-P+ and N+P+ and at Matuga under N+P- conditions (Table 4.6). Genotype 5 (NERICA 1 x CT16333(1)-CA-22-M) also appeared in all the conditions and ranked top at Alupe and Matuga under N+P- and N+P+ experimental conditions, respectively. Parent 10 (Dourado) was ranked top 15 six times followed by 1 (NERICA 1) that ranked top in both of its appearances.

Table 4.5 The GCA effects of rice parents for days to heading, anthesis, maturity; N and P tolerance, plant height, top biomass, number of panicles, 1000 seed wt and grain yield under four soil conditions

Traits	Days to heading (days)				Days to anthesis (days)				Days to maturity (day)				Phosphorous tolerance (scale)				Nitrogen tolerance (scale)			
Source	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
#G1	-4.76***	-4.72***	-6.24***	-4.26***	-10.35***	-4.69***	-6.03***	-4.04***	-3.58***	-1.70***	-2.54***	-2.16***	0.14*	-0.04ns	0.02ns	-0.01ns	0.06ns	-0.01ns	0.02ns	-0.004ns
G2	1.59ns	1.18ns	1.03ns	0.08ns	-0.51ns	1.05ns	1.16ns	0.03ns	0.18ns	-0.06ns	0.36ns	0.45ns	0.01ns	0.05ns	0.06ns	0.052ns	0.06**	0.01***	-0.11ns	-0.13*
G3	1.99ns	3.78***	3.36***	4.45***	-0.62ns	3.72***	3.23***	4.42***	-0.14ns	-0.11ns	0.05ns	0.02ns	-0.005ns	0.07ns	0.13ns	0.09ns	0.06ns	0.10ns	0.03ns	0.09ns
G4	3.20**	-0.33ns	2.26*	1.54ns	1.74ns	-0.22ns	2.41*	1.33ns	0.38ns	0.029ns	-0.29ns	0.41ns	0.093ns	0.09ns	0.05ns	0.05ns	0.06ns	0.04ns	-0.13*	-0.03ns
G5	-1.14ns	0.61ns	1.50ns	1.37ns	-1.46ns	0.75ns	1.52ns	1.19ns	1.01***	0.05ns	0.62ns	0.41ns	-0.04ns	-0.01ns	0.01ns	-0.04ns	0.06ns	-0.05ns	0.01ns	-0.02ns
G6	-1.33ns	3.21***	3.30ns	0.67ns	0.75ns	3.21***	3.25***	0.71ns	0.47ns	0.67ns	0.57ns	0.31ns	0.002ns	-0.10ns	-0.04ns	-0.05ns	0.06ns	-0.21**	0.05ns	-0.12ns
G7	2.74*	1.43ns	-1.93*	-0.71ns	4.94*	1.24ns	-2.10*	-0.67ns	1.59***	1.05*	1.34*	0.64ns	-0.06ns	0.01ns	-0.003ns	0.11ns	0.06**	0.17*	-0.02ns	0.11ns
G8	-1.40ns	-2.52*	-0.22ns	-1.80ns	1.85ns	-2.57**	-0.15ns	-1.66ns	-0.98***	0.14ns	-0.20ns	-0.50ns	0.03ns	-0.02ns	-0.13ns	-0.09ns	0.06*	-0.002ns	0.07ns	0.10ns
G9	-0.90ns	-2.66**	-3.07**	-1.35ns	3.66*	-2.48*	-3.29***	-1.30ns	1.06***	-0.07ns	0.07ns	0.43ns	-0.17*	-0.05ns	-0.09ns	-0.12*	0.06**	-0.05ns	0.08ns	-0.01ns

Traits	Plant height (cm)				Top biomass (g)				Number of panicles (numbers)				1000 seed weight (g)				Yield (kg ha^{-1})			
Source	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
G1	-2.50**	-5.42***	-7.70***	-7.07***	-68.14**	-90.42***	-108.44***	-96.02***	1.93*	0.79ns	0.44ns	6.00***	-0.56ns	-0.06ns	-0.21ns	-0.62*	-35.29ns	63.41ns	-118.63ns	-156.92ns
G2	4.32***	0.51ns	2.20*	0.97ns	43.47*	-16.64ns	-12.03ns	-21.64ns	-1.20ns	2.37*	-0.05ns	-2.87ns	0.54ns	0.81**	-0.67*	0.02ns	202.98ns	-100.27ns	-144.55ns	-25.37ns
G3	-1.95*	-1.74ns	-2.58**	-1.55ns	-59.72*	4.06ns	55.28*	41.53ns	-1.31ns	0.64ns	-0.58ns	-2.06ns	-1.18***	-1.22***	0.003ns	-1.13***	1.69ns	-111.16ns	-202.47*	-204.04*
G4	-2.54**	-1.69ns	-0.90ns	-0.52ns	100.02***	138.52***	232.16***	218.61***	-0.81ns	-2.25*	0.19ns	-2.24ns	-0.20ns	-0.03ns	0.41ns	-0.38ns	-47.94ns	-177.46ns	35.28ns	-106.45ns
G5	0.05ns	1.23ns	-0.17ns	1.44ns	44.17*	49.63*	-45.65ns	-48.70ns	3.67***	1.25ns	-1.90ns	-2.92ns	-0.24ns	-0.54*	-0.29ns	-0.23ns	-206.60*	-111.35ns	-68.17ns	175.49ns
G6	-0.46ns	1.91ns	4.01***	0.15ns	-44.43*	-29.22ns	-30.44ns	-21.91ns	-0.001ns	0.57ns	0.09ns	0.26ns	0.39ns	-0.09ns	-0.07ns	0.98***	-98.47ns	-101.06ns	-26.20ns	226.33*
G7	2.48**	4.12***	2.01*	2.79**	-83.06***	-76.17***	-28.45ns	-38.24ns	-0.11ns	-1.91ns	-1.33ns	-0.69ns	0.73*	0.28ns	0.88**	0.33ns	242.51*	254.16*	2.81ns	-28.84ns
G8	0.19ns	1.36ns	3.27***	1.61ns	22.005ns	6.77ns	-38.31ns	-21.02ns	-0.16ns	-0.23ns	1.53ns	5.82***	1.19***	0.76**	0.35ns	1.44***	-64.95ns	178.25ns	339.29***	66.33ns
G9	0.40ns	-0.27ns	-0.15ns	2.17*	45.68*	13.47ns	-24.12ns	-12.61ns	-2.02*	-1.22ns	1.62ns	-1.30***	-0.67*	0.09ns	-0.40ns	-0.41ns	6.08ns	105.46ns	182.63*	53.46ns

*significant at P<0.05
**significant at P<0.01
***significant at P<0.001
ns-not significant

#G1-NERICA 1
G2-Duorado
G3-IR79913-176-B-4
G4-CT16333(1)-CA-20-M
G5-CT16333(1)-CA-22-M
G6-CT16333(2)-CA-18-M
G7-CT16313-CA-19-M
G8-WAB964-B-3A 1.2
G9-CT16317-CA-4-M

Genotype 46 (CT16333(2)-CA-18-M x CT16333(2)-CA-18-M) and 73 (CT16317-CA-4-M) appeared four and three times, respectively among the best 15 for phosphorous tolerance, although they did not rank at the top. Genotype 55 (CT16313-CA-19-M) also appeared three times among the 15 best P tolerant lines. The genotype 14 (Dourado x CT16333(1)-CA-22-M) was ranked at the top 6 times and in fact it was the most tolerant under N+P+ experimental condition across all the mega-environments. Matuga (N+P-) and Mwea (N+P+) did not have any parent ranked top 15 meaning progenies were better adapted that their parents for P tolerance. For nitrogen tolerance, the most adapted was genotype 46 (CT16333(2)-CA-18-M x CT16333(2)-CA-18-M) followed by parents 73 (CT16317-CA-4-M) and 55 (CT16313-CA-19-M) each appearing four times with parent (CT16313-CA-19-M) being the best at Alupe under N+P- condition. For this trait, all the fertility conditions and mega-environments had at least an adapted parent. The days to maturity showed the highest variability with parent 1 (NERICA1) appearing seven and genotype 6 (NERICA 1 x CT16333(2)-CA-18-M) two times at the first position. Parent 28 (CT16333(1)-CA-20-M) and 73 (CT16317-CA-4-M) appeared six and five times respectively among the best top 15. The mega-environments Mwea (N-P+ and N+P-) had eight of the 9 parents appearing among the best 15 adapted and early maturing genotypes. At Matuga under N+P- experimental condition, all the nine parents occupied the top place but under N+P+ condition, six parents appeared among the best 15 genotypes.

The most adapted parents for top biomass were 28 (CT16333(1)-CA-20-M) and parent 10 (Dourado) appearing four times each among the top best 15 genotypes. Genotypes 36 (CT16333(1)-CA-20-M x CT16317-CA-4-M) and 33 (CT16333(1)-CA-20-M x CT16333(2)-CA-18-M) appeared at the top four times. Mwea under N-P+ and N+P- and Matuga under N+P- and N+P+ had no adapted parent indicating superiority of progenies over their parents (Table 4.7). Genotype 55 (CT16313-CA-19-M) appeared six times, while line 28 (CT16333(1)-CA-20-M) appeared 3 time as the best genotypes for the 1000 seed weight. Genotype 69 (WAB964-B-3A1.2 x CT16333(1)-CA-22-M) ranked at the top under N-P+ at Matuga and N+P- at Alupe. Genotype 66 (WAB964-B-3A1.2 x Dourado) appeared 6 times in the best ranked genotypes in different positions and under different soil fertility experimental conditions. The progeny of cross 74 (CT16317-CA-4-M x NERICA 1) ranked top under N-P+ at Mwea and N+P+ at Matuga for grain yield (Table 4.7). The following three parents; 28 (CT16333(1)-CA-20-M), 64 (WAB964-B-3A1.2) and 73 (CT16317-CA-4-M) regardless of their position among the best 15 genotypes appeared each three times. The genotype 70 (WAB964-B-3A1.2 x CT16333(2)-CA-18-M) appeared six times despite being a product of exotic germplasm. A gain genotype 2 (NERICA 1 x Dourado) appeared five times and 54 (CT16333(2)-CA-18-M x CT16317-CA-4-M) appeared 4 times for grain yield.

Table 4.6 Means of the best 15 F_2 segregants for days to heading, maturity; N and P tolerance, under four soil conditions (red are parents)

Trait	Days to heading (days)																	
	Top 15 crosses																	
Exptal Envt	N-P+						N+P-						N+P+					
MegaEnvt	Mwea		Alupe		Matuga		Mwea		Alupe		Matuga		Mwea		Alupe		Matuga	
	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value
1	8	77.0	1	75.3	74	83.0	60	79.0	5	74.3	8	81.7	8	74.0	1	79.3	5	84.7
2	81	78.0	76	97.7	60	83.3	74	79.0	76	75.7	5	82.3	5	75.5	10	102.7	68	85.0
3	5	79.0	11	99.7	68	84.7	68	83.0	8	76.0	4	82.7	77	76.0	8	104.7	10	86.3
4	60	79.0	5	100.7	41	85.0	6	84.0	15	76.3	60	83.0	67	77.5	3	105.0	77	87.7
5	80	79.5	9	101.0	10	85.7	34	84.5	9	76.7	9	83.3	10	78.5	9	105.3	3	88.7
6	4	80.0	10	101.7	36	87.7	41	85.0	13	77.3	81	84.0	4	80.0	11	106.0	75	90.7
7	9	81.0	21	101.7	6	88.0	5	85.5	34	79.0	77	84.7	75	80.5	7	106.0	61	91.0
8	77	81.5	73	102.0	5	88.7	36	87.0	72	80.0	80	85.3	48	81.0	6	110.0	36	91.7
9	3	82.5	7	102.3	34	88.7	10	88.0	1	80.7	3	86.0	60	81.0	5	110.0	60	91.7
10	7	82.5	8	103.0	81	89.7	81	89.0	80	81.0	7	86.3	68	81.5	4	114.3	65	91.7
11	6	84.0	74	103.3	8	91.3	8	89.5	4	82.3	6	87.3	6	82.0	13	116.7	7	92.3
12	35	86.0	3	104.7	71	91.3	77	89.5	44	82.3	74	88.7	9	83.0	14	117.7	8	92.3
13	74	86.0	26	104.7	35	92.0	9	90.5	11	83.7	35	92.0	12	83.5	15	119.3	4	92.7
14	62	88.5	72	104.7	61	92.0	35	90.5	3	84.0	52	92.3	39	83.5	12	119.3	74	92.7
15	78	88.5	6	106.0	77	92.3	63	90.5	6	85.7	62	93.3	61	84.5	2	122.7	76	93.7

Trait	Phosphorous tolerance (Scale 1-5)																	
	Top 15 crosses																	
Exptal Envt	N-P+						N+P-						N+P+					
MegaEnvt	Mwea		Alupe		Matuga		Mwea		Alupe		Matuga		Mwea		Alupe		Matuga	
	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value
1	16	1.0	36	1.0	14	1.0	14	1.0	14	1.0	17	1.0	14	1.0	14	1.0	14	1.0
2	17	1.0	37	1.0	46	1.0	16	1.0	11	1.0	36	1.0	16	1.0	11	1.0	16	1.0
3	18	1.0	50	1.0	53	1.0	17	1.0	9	1.0	39	1.0	17	1.0	8	1.0	18	1.0
4	36	1.0	51	1.0	58	1.0	18	1.0	7	1.0	15	1.3	18	1.0	6	1.0	38	1.0
5	38	1.0	54	1.0	6	1.3	30	1.0	6	1.0	47	1.3	36	1.0	3	1.0	39	1.0
6	39	1.0	55	1.0	8	1.3	36	1.0	15	1.3	52	1.3	39	1.0	13	1.3	52	1.0
7	46	1.0	58	1.0	30	1.3	38	1.0	5	1.3	54	1.3	53	1.0	4	1.3	58	1.0
8	52	1.0	59	1.0	38	1.3	39	1.0	3	1.3	57	1.3	54	1.0	1	1.3	73	1.0
9	53	1.0	64	1.0	39	1.3	46	1.0	12	1.7	66	1.3	58	1.0	7	1.7	21	1.3
10	54	1.0	65	1.0	54	1.3	52	1.0	10	1.7	68	1.3	72	1.0	12	2.0	24	1.3
11	58	1.0	69	1.0	73	1.3	53	1.0	8	1.7	70	1.3	38	1.7	10	2.0	46	1.3
12	55	1	72	1.0	24	1.7	54	1.0	1	1.7	72	1.3	75	1.7	9	2.0	53	1.3
13	37	1.5	76	1.0	28	1.7	58	1.0	13	2.0	74	1.3	77	1.7	2	2.0	76	1.3
14	57	1.5	77	1.0	55	1.7	72	1.0	2	2.0	50	1.7	80	2.0	15	2.3	78	1.7
15	62	1.5	78	1.0	60	1.7	73	1.0	4	3.0	63	1.7	81	2.0	5	2.7	80	1.7

Trait	Days to maturity (days)																	
	Top 15 crosses																	
Exptal Envt	N-P+						N+P-						N+P+					
MegaEnvt	Mwea		Alupe		Matuga		Mwea		Alupe		Matuga		Mwea		Alupe		Matuga	
	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value
1	1	135.5	6	147.3	1	153.0	1	130.5	6	142.3	1	134.7	1	145.0	1	147.0	1	148.3
2	2	140.5	1	154.3	10	158.0	2	140.5	2	156.3	28	139.0	48	154.5	6	151.7	28	157.3
3	5	142.5	72	159.7	76	160.7	5	141.5	21	157.3	73	142.0	3	155.5	2	166.0	73	158.0
4	28	143.5	21	161.0	44	161.0	28	141.5	37	157.3	10	142.3	49	156.5	3	166.0	74	158.7
5	64	144.5	35	161.3	74	161.3	64	144.0	35	158.3	64	144.0	17	157.0	21	167.0	55	159.0
6	73	145.5	56	161.7	2	161.7	73	145.5	72	158.3	46	146.3	45	157.0	72	167.0	68	159.3
7	46	146.5	69	162.0	8	163.0	46	146.5	3	159.0	19	148.0	44	159.0	65	167.3	49	160.3
8	55	148.0	25	162.3	5	163.3	55	147.0	25	159.3	55	153.3	51	159.0	9	167.7	64	160.7
9	19	149.5	28	162.3	67	163.7	19	149.0	28	159.3	37	153.7	72	159.0	35	167.7	48	161.3
10	37	150.0	37	162.3	22	164.0	37	150.0	29	159.3	74	162.7	13	159.5	37	167.7	71	161.7
11	56	151.5	38	162.3	29	164.3	56	151.0	38	159.3	16	163.3	37	159.5	38	167.7	27	162.0
12	6	152.0	2	163.0	80	164.3	6	152.0	56	159.3	8	165.3	46	159.5	56	167.7	50	162.3
13	9	152.5	29	163.0	20	165.0	9	152.0	44	160.3	30	165.3	77	159.5	74	168.0	72	162.3
14	3	153.0	3	163.3	14	166.0	3	152.5	74	160.3	31	165.3	29	160.0	29	168.3	19	162.7
15	35	153.5	74	163.3	68	166.0	35	153.5	61	160.7	48	165.3	73	160.0	69	168.3	56	163.7

Trait	Nitrogen tolerance (Scale 1-5)																	
	Top 15 crosses																	
Exptal Envt	N-P+						N+P-						N+P+					
MegaEnvt	Mwea		Alupe		Matuga		Mwea		Alupe		Matuga		Mwea		Alupe		Matuga	
	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value
1	16	1.0	3	1.0	14	1.0	14	1.0	55	1.0	36	1.0	14	1.0	21	1.0	18	1.0
2	18	1.0	9	1.0	5	1.7	16	1.0	56	1.0	37	1.0	16	1.0	26	1.0	39	1.0
3	36	1.0	13	1.0	3	1.7	17	1.0	58	1.0	42	1.0	17	1.0	34	1.0	46	1.0
4	39	1.0	16	1.0	12	2.0	18	1.0	59	1.0	45	1.0	18	1.0	36	1.0	52	1.0
5	46	1.0	20	1.0	9	2.0	36	1.0	61	1.0	50	1.0	36	1.0	37	1.0	53	1.0
6	52	1.0	34	1.0	11	2.3	38	1.0	64	1.0	51	1.0	38	1.0	41	1.0	72	1.0
7	58	1.0	36	1.0	8	2.3	39	1.0	65	1.0	54	1.0	39	1.0	45	1.0	5	1.3
8	72	1.0	41	1.0	7	2.3	46	1.0	67	1.0	55	1.0	46	1.0	46	1.0	7	1.3
9	73	1.0	45	1.0	6	2.3	52	1.0	69	1.0	58	1.0	52	1.0	49	1.0	10	1.3
10	6	1.5	55	1.0	4	2.3	54	1.0	72	1.0	59	1.0	53	1.0	50	1.0	15	1.3
11	38	1.5	58	1.0	2	2.3	58	1.0	74	1.0	66	1.0	54	1.0	55	1.0	16	1.3
12	75	2.0	59	1.0	1	2.3	72	1.0	76	1.0	68	1.0	58	1.0	59	1.0	20	1.3
13	77	2.0	66	1.0	13	2.7	73	1.0	77	1.0	72	1.0	72	1.0	66	1.0	37	1.3
14	78	2.0	77	1.0	10	2.7	42	1.5	78	1.0	76	1.0	73	1.0	77	1.0	73	1.3
15	80	2.0	81	1.0	15	3.0	53	1.5	80	1.0	79	1.0	81	2.0	81	1.0	79	1.7

Table 4.7 Mean of the best 15 F_2 segregants for top biomass, 1000 seed wt and grain yield under four soil conditions (red are the parents)

Trait	Top biomass (g)																	
	Top 15 crosses																	
Exptal Envt	N-P+						N+P-						N+P+					
MegaEnvt	Mwea		Alupe		Matuga		Mwea		Alupe		Matuga		Mwea		Alupe		Matuga	
	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value
1	33	2789.2	36	3090.4	36	1783.3	34	1770.5	36	2432.2	33	2169.7	33	2643.5	36	3133.2	33	2273.4
2	22	1695.5	38	2325.3	38	1606.6	33	1632.9	38	2293.4	22	1537.0	22	1671.2	38	2528.2	22	1503.0
3	34	1456.4	35	2149.7	35	1259.8	22	1335	35	2123.5	34	1343.4	34	1565.1	35	2292.4	34	1353.5
4	20	1333.8	42	1578.7	39	1242.5	21	1267.5	42	1454.3	61	1253.7	32	1394.8	42	1788.1	38	1245.0
5	21	1286.0	28	1521.6	28	1135.1	35	1228.9	17	1413.4	20	1242.4	21	1394.7	41	1650.7	65	1239.0
6	38	1236.8	10	1472.7	10	1072.7	20	1124.5	28	1394.9	38	1211.5	38	1383.0	39	1641.0	67	1223.7
7	32	1233.7	17	1441.9	23	1003.9	38	1106.9	10	1346.5	21	1209.8	20	1355.1	28	1633.6	21	1213.0
8	30	1225.9	41	1441.5	41	996.8	31	1103.5	41	1315.0	31	1179.5	30	1315.4	17	1582.6	36	1208.2
9	25	1215.8	39	1431.7	46	991.7	39	1100.3	25	1312.4	30	1170.9	18	1294.6	61	1538.1	59	1208.0
10	36	1136.8	25	1338.9	25	967.3	32	1094.4	39	1305.4	32	1146.6	36	1283.0	40	1536.7	35	1206.7
11	59	1110.2	40	1332.4	40	921.2	26	1092.3	40	1299.4	25	1114.0	25	1281.2	21	1516.8	32	1186.7
12	26	1110.0	61	1328.9	17	915.4	27	1053.2	61	1236.9	60	1104.9	59	1229.8	25	1514.8	18	1176.3
13	18	1092.9	34	1308.7	16	873.5	36	1050.3	34	1236.8	36	1078.0	26	1218.7	10	1482.1	30	1175.6
14	31	1092.3	21	1274.0	79	853.4	30	1043.5	76	1224.5	50	1075.3	31	1201.0	34	1451.5	20	1165.9
15	35	1086.1	78	1261.4	11	824.8	59	1018.3	23	1209.2	59	1060.4	65	1195.3	23	1411.7	39	1156.7

Trait	Grain yield (kg ha^{-1})																	
	Top 15 crosses																	
Exptal Envt	N-P+						N+P-						N+P+					
MegaEnvt	Mwea		Alupe		Matuga		Mwea		Alupe		Matuga		Mwea		Alupe		Matuga	
	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value
1	74	4809.0	75	5362.8	54	4492.9	76	4342.4	58	5119.3	74	3792.5	70	4622.3	49	5338.1	17	4128.6
2	18	4664.5	71	4929.2	5	4094.9	54	4317.0	40	5025.2	78	3768.1	53	4488.9	17	5271.1	34	3757.0
3	78	4609.0	68	4626.8	57	4036.1	57	4316.8	74	4521.8	64	3668.1	17	4201.7	51	4769.9	19	3746.8
4	51	4481.2	28	4476.4	64	3981.6	17	4082.0	81	4423.0	51	3655.5	54	4166.7	65	4755.1	70	3733.5
5	53	4306.2	60	4398.8	28	3939.3	53	4065.2	47	4318.1	76	3622.1	4	4145.5	6	4585.5	7	3690.3
6	49	4228.8	61	4339.5	58	3918.8	73	4033.0	77	4046.0	49	3618.3	39	4133.4	45	4544.9	75	3639.7
7	44	4227.2	2	4301.4	47	3889.7	67	4012.1	78	3988.8	60	3516.0	25	4103.7	63	4468.2	15	3608.8
8	64	4197.9	53	4023.5	8	3777.5	15	4012.1	75	3907.6	44	3456.5	35	4083.3	36	4330.4	28	3591.9
9	76	4114.5	36	3940.2	17	3773.6	1	3976.7	69	3828.3	22	3418.7	68	4077.8	23	4285.4	72	3571.8
10	36	4070.1	19	3781.0	15	3715.6	58	3961.9	59	3586.0	36	3418.4	56	4033.2	43	4229.6	52	3545.9
11	41	4041.9	38	3548.3	41	3586.2	60	3928.1	55	3489.7	70	3406.2	2	4027.8	52	4211.9	54	3534.8
12	70	4025.6	42	3506.7	73	3520.3	41	3882.4	60	3480.1	40	3346.5	52	4022.8	26	4093.4	2	3490.3
13	2	4007.1	55	3487.0	56	3394.5	62	3815.2	67	3454.6	16	3344.1	71	4012.1	48	4055.5	4	3445.1
14	60	3933.1	65	3460.7	4	3361.5	56	3780.7	68	3369.6	2	3327.1	80	3955.6	50	4008.1	73	3327.4
15	22	3930.6	70	3401.3	70	3357.8	8	3770.4	37	3365.3	29	3325.8	61	3947.8	47	3984.3	37	3321.1

Trait	1000 seed weight (g)																	
	Top 15 crosses																	
Exptal Envt	N-P+						N+P-						N+P+					
MegaEnvt	Mwea		Alupe		Matuga		Mwea		Alupe		Matuga		Mwea		Alupe		Matuga	
	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value	F_2 line	Value
1	5	31.9	75	5362.8	69	31.2	35	31.4	69	33.2	49	30.5	53	31.7	11	180.0	53	30.9
2	49	30.9	71	4929.2	35	31.1	69	30.9	66	33.1	61	29.1	64	31.0	54	177.3	66	29.9
3	18	30.9	68	4626.8	45	30.4	25	30.9	51	32.7	29	29.1	48	30.9	77	177.3	48	29.7
4	51	30.7	28	4476.4	31	30.4	15	30.8	2	32.2	3	29.0	52	30.5	42	177.0	52	29.5
5	70	30.4	60	4398.8	26	30.4	18	30.3	65	32.2	32	29.0	66	30.5	57	177.0	49	29.4
6	28	29.9	61	4339.5	18	30.3	26	30.3	75	32.2	70	28.5	67	30.4	41	176.7	64	29.1
7	38	29.6	2	4301.4	33	30.2	31	30.0	18	31.8	18	28.4	49	29.6	50	176.7	70	29.0
8	3	29.4	53	4023.5	15	30.0	6	29.9	29	31.2	36	28.3	63	29.3	40	176.3	63	28.8
9	29	29.4	36	3940.2	13	29.9	33	29.9	68	30.9	55	28.3	70	29.3	76	174.7	72	28.7
10	55	29.35	19	3781.0	6	29.5	13	29.8	45	30.7	58	28.3	35	29.2	46	173.7	35	28.4
11	61	29.05	38	3548.3	55	29.1	20	29.8	48	30.6	66	28.2	6	29.0	49	173.7	6	28.4
12	13	28.9	42	3506.7	66	28.9	55	29.4	60	30.5	13	28.1	72	28.9	52	173.7	38	28.1
13	32	28.8	55	3487.0	47	28.5	28	28.9	71	30.3	51	27.8	19	27.8	80	173.7	67	27.9
14	58	28.7	65	3460.7	10	28.5	45	28.9	16	30.1	26	27.5	60	27.8	7	173.3	55	27.7
15	66	28.65	70	3401.3	62	28.4	65	28.9	53	29.8	16	27.4	38	27.7	43	173.3	1	27.6

4.4 Discussion

For any meaningful progress in the development of superior cultivars, genetic variability has to be present to enable selection in the desired direction (Atlin *et al.*, 2000; Bugbee, 1999; Falconer and Mackay, 1996; Fukai *et al.*, 1999a). In the present case, high variability existed in the genotypes and their reactions under different experimental conditions.

4.4.1 The genetic effects, their interactions and its significance.

The GCA, SCA and reciprocal mean squares were generally significant for all the traits under the four soil N and P conditions. However, the magnitude (%) of GCA was generally less than for SCA indicating the importance of nonadditive effects over additive effects (Tables 4.3 and 4.4) and these finding are in agreement with Andrzej et al. (2011) with similar results in wheat. Consequently, the GCA:SCA ratio was only above one for days to heading (N+P-, 1.26), anthesis (N-P-, 1.66, N+P-, 1.27), plant height (N+P-, 1.18) and 1000 seed weight (N+P+, 1.06) as indicated in Table 4.3 and 4.4. This clearly demonstrates the predominant role of nonadditive gene action were playing in inheritance of the traits with a ratio less than one. This means inheritance was low and probably environments played a major role.

Further portioning of SCA mean squares revealed that the reciprocal effects were high in most case around 40% and up to more than 60% indicating that the maternal effects were important in inheritance or control of these traits. The analysis of reciprocal effects into maternal and nonmaternal effects revealed that these in many case were nearly equal but nonmaternal effects seem to be more dominating than maternal effects over the soil N and P conditions and traits.

From the above discussion, the presence of significant reciprocal and maternal effects interaction with environment implies that, in a breeding program, the choice of parent to use as male or female and for what environment is important. This is because cytoplasmic genes play a role in the inheritance of the particular trait under the contrasting experimental environments as was demonstrated above (Ao et al., 2000; Chen et al., 1998; Shi et al., 2000; Shi et al., 2002; Swaminathan, 1993; Wade et al., 1999b; Wu et al., 2004; Zhang et al., 2002). Where maternal effects are significant, it means that one parent will specifically be used as the female, by virtues of the egg being larger than the pollen means that it has more

cytoplasm and hence bodies and structures such as the mitochondria and Golgi bodies or apparatus that may influence the behaviour of the progenies (Deborah, 1987).

The significance of nonadditive effects has serious implication in rice breeding because the heritable additive gene action is of less importance. According to Andrzej *et al* (2011) selection procedures that remove the dominating non-additive effects and hence promote and utilize the fixable additive effects should be used to improve the traits. This implies breeding of rice in order to exploit these nonheritable effects will have to be towards hybrid varieties as is the case in China, where more than 50% of rice production comes from hybrid rice (Virmani *et al.*, 2003). China and many other countries are now growing hybrid rice and they have been able to reach nearly to 10 t ha^{-1}. The much held belief that hybrid are for open pollinated crops may not make much sense in right of these results and the fact that hybrid rice is now widely being grown and it has been even introduced into Kenya. In the survey conducted, farmers had preference for hybrid rice and thus these may have wider adoption if introduced. However the issue of seed production will have to be addressed so that enough seeds can be produced sustainably and also the issue of farms inputs because these varieties may require more inputs that farmers indicated they may not afford.

The general combining ability effects had varied reactions for both traits and soil N and P conditions (Table 4.3 and 4.4). NERICA1 was the best general combiner for earliness as it had negative but very highly significant GCA values ($P<0.001$) for days to heading, anthesis and maturity. NERICA1 which is a short variety was also effective in reducing plant height and top biomass, however farmers' preferences were for taller and high biomass, thus it may not be the parent to use here. Parent G8 (WAB964-B-3A 1.2) is a good general combiner for a 1000 seed weight and may be used to improve on seed quality. Generally different parents were good combiner under different soil N and P, thus displaying lack of universal good combiners across all traits and soil N and P conditions. The fact that GCA effects magnitudes were not generally high than SCA effect in control of given traits means that it is difficult to predict performance of yield or other traits based on parents GCA. This implies progress in breeding for specific traits and soil condition will be slow and much emphasis need to be placed on specific adaptability and hybrids development.

4.4.2 The genotypic and environment interactions and their significance.

The ANOVA showed varying degrees of variability of the genotypes and their interactions with the mega-environments. This genotype by environment interaction (GEI) indicates that

some genotypes for days to heading such as NERICA 1x WAB964-B-3A1.2, NERICA 1 x CT16333(1)-CA-22-M, had specific adaptation to Mwea, while NERICA1 was adapted to Alupe and CT16317-CA-4-M x NERICA 1 was adapted to Matuga environments across the four soil fertility conditions. Probably this could be exploited to develop varieties adapted to low and high soil phosphorous and nitrogen soil conditions. Dourado, which is a cultivar, was broadly adapted to all the three-mega-environments for days to maturity. This means that desirable genotypes with a given adaptation can be bred by using the stress environment and selection of the promising materials or progenies (Alam et al., 2004; Chahal and Gosal, 2002; De-Datta, 1981; Jiang et al., 1994; Simmonds and Smartt, 1999). The line 14 (Dourado x CT16333(1)-CA-22-M) was ranked top in the three mega-environments but for different experimental conditions indicating that it had broad adaptation for P tolerance. This probably is because the cultivar Duorado was used as a female in this line, thus the genes for adaptation were transmitted to the progeny. In contrast genotype 17 (Dourado x WAB964-B-3A1.2) was adapted to Mwea conditions for the three fertility conditions. This is a case of specific adaptation that can be exploited. This again is a cross involving the cultivar Duorado and the fact that this genotype ranked among the top three best, is a manifestation of its superiority (Ceccarelli, 1994).

There were cases of specific adaptation such as genotype 2 (NERICA 1 x Dourado) that was only adapted to N+P+ at Alupe for P tolerance. Two parents, 46 (CT16333(2)-CA-18-M) and 73 (CT16317-CA-4-M) were accessions that showed specific adapted to Mwea under the three experimental environment conditions for nitrogen tolerance. The same case was observed for parent 55 (CT16313-CA-19-M) for Alupe for nitrogen tolerance and many of the genotypes in general showed crossover type of interaction where one genotype ranked differently in different environments. For top biomass, genotype 33 (CT16333(1)-CA-20-M x CT16333(2)-CA-18-M) and 22 (IR79913-B-176-B-4 x CT16333(1)-CA-20-M) had specific adaptation in that order for the three experimental environment. The case for Alupe was more striking where the top four genotypes, 36 (CT16333(1)-CA-20-M x CT16317-CA-4-M), 38 (CT16333(1)-CA-22-M x NERICA 1), 35 (CT16333(1)-CA-20-M x WAB964-B-3A1.2) and 42 (CT16333(1)-CA-22-M x CT16333(2)-CA-18-M) were ranked top for the three soil fertility conditions. This shows that, despite the parents having been accessions that were evaluated and characterized for only one season, the selected parents progenies had high level of adaptation even in regions where the materials were not evaluated. Therefore, these materials seem to have wide adaptation, not only for fertility condition, but also for the prevailing environments for top biomass.

The days to maturity showed high level of variability, especially for the parents. The Mwea environment for N-P+, and N+P- had eight parents and in fact, all the genotypes had the same rank. This is where the accessions were evaluated and parental materials selected with farmers input; probably this had contributed to the unique ranking that was not in any other fertility conditions or mega-environments. Matuga environment had all the nine parents under N+P- ranking top nine positions, while under N+P+ condition three parents (1, 28 and 73) had same rank similar to N+P- and the other three (55, 64 and 19) were crossover type for days to maturity. The 1000 seed weight did not show any systematic ranking and generally crossovers were predominant and although a number of parents appeared in the top 15 best rank, none of them was at rank one. It is only Alupe environment under N+P- that did not rank any parent among the best 15 genotypes, indicting its discriminating power (Table 4.7). The grain yield had strong crossover types of ranking for both soil fertility experimental environments and mega-environments. The data obtained indicates that it would be difficult to bred for wide adaptation and therefore, specific adaptation to given environment approach should be used to develop varieties with high performance for a given environment. This is likely to be of benefit because better performance could be realized under the prevailing farmers conditions.

The above analysis indicate that GEI was quite significant (Peyman *et al.*, 2009) and any attempt to breed cultivars for low and high soil P and N has to be based on the premises of correct source of tolerance genes, presence of the correct stress and proper mating, environmental and analysis designs. This will most probably lead to identification and isolation of the promising genotypes with the desirable performance for the target environments (Allard and Bradshaw, 1964; Borojevi'c, 1990; Ceccarelli, 1994; Chahal and Gosal, 2002; Christiansen and Lewis, 1982; Fasoula and Fasoula, 1995; Fasoula and Fasoula, 1997; Hallauer and Miranda, 1989). Holland et al. (2003) and Nyquist (1991) have detailed the environments that crop grow in and their level of control or management, while Christiansen and Lewis (1982) have explained the issue of low soil P and N and the breeding options available. Cassman et al. (1998) have discussed and argued on the various intricacies involved in crop productivity in problem soils. Saal *et al*. (2010) while working with barley found that quantitative trait loci by nitrogen interaction were best discriminated when N was used and that yield had ambiguous performance under N environment but more clear over environments. One thing that seems to be agreeable is that use of inorganic fertilizers is not an end by itself. This is further confirmed by the fact that their use can be an environmental hazard and hence their use require careful management, especially given not

all of it is used by the crops under production. What is emerging is that crops and genotypes within the crop population have varied levels and abilities to acquire and utilize the nutrients under the prevailing conditions as was indicated by crossover in genotypes performance. Further, some genotypes are good at acquiring soil nutrients and having luxurious growth at the expense of yields. Other genotypes acquire and efficiently use nutrient thereby resulting in higher yields or economic returns. These types of genotypes, it is agreeable that, they can be bred using phenotypic traits under the stress of interest. For example, some genotypes in this study yielded well under low soil P and N than when the nutrients were optimal. This is a case of efficient progenies, which were able to utilize the available nutrients irrespective of their level in the soil to give economic returns.

4.5 Conclusion

The significant GCA and SCA's and other genetic parameters is indication of presence of genetic diversity for the parents used which can be exploited by selection of the promising progenies from the segregating populations under the diverse environments prevalent in farmers production ecologies. The nonadditive gene action were more important than the heritable additive gene effects. The preponderant gene action for the traits under most of the soil N and P conditions was the nonadditive genetic effects as the GCA:SCA ratios were mostly less than one except for days to heading (N+P-), anthesis (N-P- and N+P-), plant height (N+P-) and a 1000 seed weight (N+P+). The reciprocal effects were important and further partitioning indicated that the nonmaternal effects were actually more important than the maternal effects, although the % difference was not generally large. The best general combiner for earliness was NERICA1, while G8-WAB964-B-3A 1.2 was the best combiner for 1000 seed weight among the selected parents. The performance of the lines and selected parents was largely dependent on mega-environment and the experimental environments as was indicated by the varied ranks of genotypes, thus exhibiting significant GEI. The different rankings of yield with in different soil N and P conditions suggested probability of occurrence of crossover ranks for various genotypes for given traits. The biplots analysis have indicated specific adaptation rather than broad or wide adaptation of genotypes under different soil N and P conditions. It therefore, follows that with proper progeny screening under the desirable stress, genotypes with enhanced performance under low and high soil P and N can be developed.

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Appendix 4.1 The pictorials of procedures used for pollinations

Plate 4.1 Crossing block with 2nd parent set

Plate 4.2 Emasculation for hybridization being effected

Plate 4.3 A cross covered by straw and a tag

Plate 4.4 A fertile cross between Dourado and NERICA1

CHAPTER FIVE.

Genetic mechanisms controlling Soil Phosphorous and Nitrogen Tolerance Determined by Leaf and Seed Content in the F_2 and F_3 Rice Populations

Abstract

An experiment was conducted to determine the relation between leaf and grain nitrogen and phosphorous with tolerance to low and high soil nitrogen and phosphorous fertility conditions. The seventy two each of F_2 and F_3 families and nine parents were evaluated in three main rice growing regions in Kenya. These were laid out in 9x9 alpha lattice design and replicated two (Mwea) and three times at Matuga and Alupe. Leaf and seed samples were taken for nitrogen and phosphorous content analysis. Results indicated significant genotypes, environments and genotypes by environments interactions. The analysis of genetic components gave highly significant GCA and SCA mean squares for the days to heading, anthesis and maturity, phosphorous and nitrogen tolerance, top biomass, plant height, number of panicles, 1000 seed weight and grain yield under the four soil experimental environments. The GCA:SCA ratios were less than one for all the traits, except grain yield under soil N+P+ condition where it was 1.17. This indicate that nonadditive effects were more important that additive effects. The reciprocal effects were significant and generally larger than GCA effects in magnitude, while nonmaternal effects were in most cases larger than maternal effects indicating interactions of cytoplasm with nuclear genes was more important that additive gene action. The general combining ability effects (GCA) for parents were significant for both F_2 and F_3 materials for the above ten traits and under the experimental conditions. The leaf and seed N and P contents gave significant genotypic mean squares values for the three mega-environments. The GCA and SCA mean squares were significant for leaf and seed N and P for the three locations. The same case was observed for GCA effects for the parents, with all the nine parents showing significant values for leaf nitrogen and phosphorous for the three locations. The GCA:SCA mean square ratios had larger values of more than 1.0 for the majority of the traits under the four soil N and P conditions, except for leaf P and grain N for all the three locations. This was a clear manifestation of the dominant role of additive gene action over the dominance effects and that improvement for low soil P and N fertility tolerance is practical. The reciprocal effects were significant and nonmaternal effects were larger than maternal effects except for grain yield for all the three

locations. This implies cytoplasmic interactions with nuclear genes were predominant over cytoplasmic per se effects.

5.1 Introduction

5.1. Phosphorous (P) and nitrogen (N) concentration in rice leaves and grains

There is scant information on P and N accumulation in grains and leaves (culms) and their genetics in relation to rice variety P and N use efficiencies. Ju et al. (2009) while working with cultivars with high nutrient use efficiency for dry matter accumulation (NUEd) observed that rice with high grain yield showed higher total dry matter accumulation (TDMA = TNA*NUEd) and harvest index (HI), but rising TDMA depressed HI. They reported that increase in grain yield should be on increasing TDMA (increased by better NUEd) rather than HI. The TDMA is a function of total N absorption (TNA) and NUEd, implying yield can be increased by improving TNA, NUEd, HI or all of them. Ju et al.(2009) found significance difference in TNA among rice lines and that high yielding lines tended to have high TNA, however, a negative correlation was observed between TNA and NUEd. They reported that 97.1% of the variation in grain yield was explained by TNA, NUEd and HI.

The yield of rice is largely dependent on accumulation of dry matter and especially effective partitioning to plant parts of economic importance especially in stressful environments (Kumar et al., 2006). In cereals the grains constitute the most important sink for N after anthesis and thus grain yields. Kumar et al. (2006) reported that redistribution of assimilates from stem and leave contributed to grain yield in favourable environments but under water stress, but not unfavourable ones. Inthapanya et al. (2000b) have observed that low yielding genotypes were associated with low grain P and N, and that nutrient uptake by genotypes varied for both low and high fertility conditions. They observed that grain yield, total P and N content under both fertilized and non-fertilized conditions had low values in late maturing lines, with greater penalty being for yield. The high yielding lines were generally found to have high nitrogen (NUEg) and phosphorous (PUEg) use efficiency for grains, but not high nitrogen (NUEp) and phosphorous use efficiency for plants (PUEp) (Inthapanya et al., 2000b). The high yielding genotypes had low N concentration in the grain and location had significant effect for culms and grain P and N. The application of fertilizer had insignificant effect except for culms P concentration and N concentration in grains was two to three times that of culms, but the ration for P was higher. Grain N was negatively related to NUEg at two

locations. The relationship between HI and PUEg was found to be positive across three locations and two fertilizer levels. The PUEg was found to decrease with increase in plant P content (Inthapanya et al., 2000b). Saito et al. (2006) observed that little response of grain yields to only P application was consistent across all locations and that the regression coefficient of 1.55 for the improved cultivars was particularly suitable for high-yielding environments, but these cultivars also were highest-yielding in the least productive environments. Plant species and cultivars within species differ in efficiency in nutrient uptake. This, along with differences in dry matter accumulation per unit time and growth duration, results in differences in nutrient content. Further, there are genotypic differences in the efficiency with which nutrients are used in the production of TDM, and in the proportion and quantity of nutrients translocated to the grain (Clark, 1990). Tirol-Padre et al. (1996) reported that late-maturing cultivars accumulated a larger amount of N in the plants, perhaps as a result of increased N mineralisation, and produced a higher grain yield. Generally, early-maturing cultivars were found to have a higher N concentration in grain and stem, and this was associated with low N use efficiency. Some lines were found to be inferior as they did not yield well with increasing rates of N application due to inherently low yield potential while others were inefficient in capturing low soil available N resulting in low grain yield, and that grain yield was related to total P and N content in the plant (Singh et al., 1998). Fukai et al. (1999a) has reported that there was a positive relationship between harvest index (HI) and PUEg (r^2=0.41), but not between HI and N use efficiency for grain production (NUEg) (grain yield/plant N content) (r^2=0.06). They found that NUEg was negatively related to grain N concentration with r^2 of 0.36. In general the amount of leave and grain P and N content in relation to grain yield under different soil fertility conditions and environments was highly variable, and opportunity exists for development of varieties suited to particular production conditions and environments.

The objective of this study was to determine the relationship between rice P and N tissue content in relation to soil available amounts in determining yields and their physiology in the F_2 and F_3 populations and their parents.

5.1.1 The objectives

The specific objectives were to:

i). determine the mode of gene action conditioning leaves and grain P and N inheritance, and

ii). determine the physiological factors governing leaves and grain P and N in relation to grain yield.

5.1.2 The study hypothesis

The leaf and grain N and P content is genetically controlled and efficient genotypes have low N and P content in the leaf and grain, and that different physiological factors control the expression of N and P content in these tissues.

5.2 Materials and Methods

5.2.1 Evaluation of F_2 and F_3 populations at three locations, KARI-Mwea, KARI-Matuga and LBDA Alupe

The F_2 and F_3 plants were evaluated in three regions, namely Central at KARI-Mwea Tebere, western at Lake Basin Development Authority (LBDA-Alupe) and Coastal region at KARI-Matuga. There characteristic are as described below: KARI-Mwea Tebere (National Rice and Fibre Research Centre (NRFRC)) is located in Mwea Division, Kirinyaga South District, Central Province, 112 km East of Nairobi in Kenya. It lies on Latitude 00^o 37' S and Longitude 37^o 20' E at an elevation of 1159 m above sea level (masl). The average rainfall is about 850 mm with a range of 500 - 1250 mm divided into long rains (March – June with an average of 450 mm) and short rains (Mid-October to December with an average of 350 mm). The rainfall is characterized by uneven distribution in total amounts, time and space. The temperature ranges from 15.6º C to 28.6º C with a mean of about 22º C. The soil are nitosol, which are deep, well drained dusky-red to dark reddish-brown, friable clay with low fertility (FURP, 1987; Jaetzold and Schmidt, 1983).

Lake Basin Development Authority (LBDA) Alupe is located on Latitude 0° 30' 0 N; Longitude 34° 7' 50 E; on an elevation of 1170 meters above sea level (masl) in the western part of Kenya. The soils at Alupe have been characterized as Ferralo-orthic Acrisol with pH of 5.0 (FURP, 1987). The total annual rainfall at Alupe was 1,398 mm and temperature ranged from 16-34°C during the year 2009.

The remnants of F_2 seeds and seeds harvested from the preceding F_2 plants (F_3) from a full nine parent diallel mating design were used for study of tolerance to low and high soil P and N, tissue analysis for leaves and grain N and P content. The upland rice materials used did not have seed dormancy problem, thus it was possible to plant them immediately after harvesting.

These materials were planted on 9th February 2010 at KARI-Mwea Tebere and LBDA-Alupe on 17th February 2010. The site characteristics had been earlier given in chapter four. The eighty one lines (Parents included) were laid out in 9x9 alpha lattice design and replicated two and three times at Mwea and Alupe, respectively. The overall arrangement was a split plot experimental design where fertility treatment was the main plot and the genotypes the subplot. The experimental plot was 1.6 m^2 consisting of 40 plants. The inter- and intra-row spacing was 20 cm. Three seeds were sown per hill and later thinned to one. The experimental environment consisted of blocks with no P and N application (N-P-), P application (N-P+), N application (N+P-) and both P and N application (N+P+). The P was applied as triple super phosphate (TSP) at the rate of 60 kg ha^{-1} at planting, while N (CAN) was applied at the rate of 90 kg ha^{-1} but in two equal splits at planting and maximum tillering stage.

The 81 samples were used for determination of N and P in grain and leaves at maturity as explained by Tirol-Padre et al. (1996), and (Fageria et al., 1988). Phosphorous use efficiency for grain (PUEg) was determined as grain yield per given P content, likewise for the N content. The nitrogen use efficiency for grain (NUEg) was obtained as shoot dry weight per given N content. The relationship between harvest index (HI) and PUE, NUE; grain N and P concentration and NUEg and PUEg was determined.

The plots were kept weed free by manual weeding and all other cultural practices were followed, with sprinkler irrigation being used to supplement rainfall when necessary. Bird and monkey scarers were used at crop maturity and until harvest.

5.2.2 Data collection

Procedures described by IRRI (2002) were used to collect data on both morphological and yield parameters. At physiological maturity, plants from twenty hills were cut at ground level and their number of panicles determined, dry weight of leaf and stem, and grain plus yield components were determined. Samples of leaf, stem + panicle rachis, and grain (caryopsis+hull) were ground and analysed separately for both N and P content as explained by (Fageria et al., 1988; Lyness, 1936; Tirol-Padre et al., 1996). Grain (unhulled) yield was determined from two row plots for F_2s and F_3s and per plant for F_2s. Total straw weight was determined after drying for five days in the sun to a constant weight (Shu et al., 2005). At

maturity, 5g per sample of seed for F_3s were weighed for P and N determination. The leaves and seed P and N analysis was carried out at JomoKenya University of Agriculture and Technology using Uv-vis spectrophotometer (model Shimadzu Mini 1240) for P and Block digester (Macro kjeldahl) model Sibata for N analysis.

Mean seed yield in high and low fertility, and percent reduction due to low fertility was used as the selection criteria. The formulae of Fischer and Maurer (1978) was used to calculate low soil fertility intensity index (LFII) $\{1-\frac{\bar{x}lf}{\bar{x}hf}\}$ and Low fertility susceptibility index (LFSI) $[\frac{\bar{x}g}{LSFII}]$ for each genotype. Where $\bar{x}$ is the mean of genotype under low (lf) and high fertility (hf) condition. The field screening results were interpreted using grain yield efficiency index (GYEI) defined as

$$\frac{(yield\ under\ nutrient\ use)(yield\ under\ no\ nutrient\ use)}{(Experimsntal\ mean\ yield\ at\ low\ nutrient\ level)(Experimsntal\ mean\ yield\ at\ high\ nutrient\ !evel)}$$

The GYEI is useful in helping separate genotypes into high yielding, stable, nutrient efficient, low yielding, unstable, and nutrient inefficient genotypes (Fageria and Baligar, 2003). Tolerant genotypes have GYEI of 1.0 and above, inefficient genotypes have a value of 0.0 - 0.5 and genotypes between 0.5-0.9 are considered intermediate. GYEI is very good for separation where two nutrient levels have been used, as it is the case here.

5.3 Data analysis

The testing of differences between genotypes and mega-environments was carried out as explained by (Daljit, 1973) according to the following model;

$Y_{ijkm} = \mu + v_i + l_j + (vl)_{ij} + (lb)_{jk} + (vlb)_{ijk} + \varepsilon_{ijkm}$;

where Y_{ijkm}=observed value for ith genotype in the l^{th} mega-environment in the k^{th} block for m^{th} individual

μ=overall mean; v=genotypes; v_i=effect of i^{th} genotype or variety; l=mega-environments; l_j=effect of j^{th} environment; $(vl)_{ij}$=interaction of i^{th} variety and j^{th} environment; $(lb)_{jk}$=effect of k^{th} block within j^{th} environment; vlb_{ijk}=interaction of i^{th} genotype with k^{th} block in j^{th} mega-environment;

b=blocks per environment; m=individuals in each of the vlb plots

ε_{ijkm}=effect of i^{th} genotype, k^{th} block in j^{th} environment specific to m^{th} individual.

The data was analyzed for genetic components for each of the ten traits studied; leaves and seed P and N content by using SAS software version 9.2 option SAS diallel (Kang, 2003; SAS-Institute, 2003; Zhang et al., 2005). The following genetical model I method 1 was applied:

$X_{ijklc} = \mu + \alpha_l + b_{kl} + v_{ij} [g_i + g_j + s_{ij} + r_{ij} (m_i + m_j + n_{ij})] + (\alpha v)_{ijl} [(\alpha g)_{il} + (\alpha g)_{jl} + (\alpha s)_{ijl} + (\alpha r)_{ijl} ((\alpha m)_{il} + (\alpha m)_{jl} + (\alpha n)_{ijl}] + e_{ijklc}$.

Where μ is the population mean, α_l is the environment effect,

b_{kl} is block effect in each environment, v_{ij} cross effect,

s_{ij} is SCA effect for ij^{th} cross, r_{ij} is the reciprocal effects for ij^{th} cross,

m_i is the maternal effect of the parental line i, m_j is the maternal effect of the parental line j,

n_{ij} is the non-maternal effect of ij^{th} or ji^{th} cross,

$(\alpha v)_{ijl}$ is the interaction between environment and the cross, g_i and g_j are GCA effects for i^{th} and j^{th} parent,

$(\alpha g)_{il}$ is the interaction effect between GCA effect for the i^{th} parent and environment,

$(\alpha g)_{jl}$ is the interaction between GCA effect for j^{th} parent and environment,

$(\alpha s)_{ijl}$ is the interaction between SCA effect for ij^{th} cross and environment,

$(\alpha r)_{ijl}$ is the interaction between reciprocal effects for ij^{th} or ji^{th} cross and environment,

$(\alpha m)_{il}$ is the interaction between environments and maternal effects of parent i,

$(\alpha m)_{jl}$ is the interaction between environments and maternal effects of parent j, and

$(\alpha n)_{ijl}$ is the interaction between environments and nonmaternal effects of ij^{th} or ji^{th} cross.

e_{ijklc} is experimental error or residue effect for the X_{ijklc} observation (k=1,2,…, r; i=j=1,2,…, n).

5.4 Results

5.4.1 Gene action of the F_2s materials under contrasting soil N and P conditions

The means squares for entries and mega-environments were generally highly significant ($P<0.001$) under various soil N and P experimental environments (Table 5.1 and 5.2). The GCA and SCA mean squares were also significant across various soil N and P for given traits in most cases. In many cases the percentage SCA mean squares were higher in magnitude than for GCA, indicating the importance of nonadditive effects over additive effects for the traits studied. The GCA:SCA ratios were less than one, except for yield under N+P+ where it was 1.17. This implies further that the additive effects were not as important as for the nonadditive effects in inheritance or control of the traits studied. The reciprocal mean squares were generally around 50% indicating their important role in control of the traits under given

soil N and P conditions. The maternal effects were in most cases less in magnitude than the nonmaternal effects under various soil N and P conditions for the traits studied.

Table 5.1 Source of variation and mean squares on 10 rice traits studied under four soil N and P conditions

		Days to heading (days)				Days to anthesis (days)				Days to maturity (day)			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	126.31***	149.90***	103.83	129.96***	538.05	1099.08***	98.45***	1268.14***	139.62***	100.24	162.05***	165.13***
ENV	2	150.63*	289.68***	151.13***	138.91***	7207.50***	43396.03***	152.63***	66479.05***	3990.53***	3625.11***	8068.80***	1455.41***
REP(ENV)	5	181.14	141.3	220.29	412.98	12060.37	20158.19	185.29	29015.6	972.71	509.91	981.65	806.2
ENTRY	80	102.69***	145.72***	86.49***	137.93***	302.20**	605.45***	82.59***	353.35***	111.75***	55.35***	107.95***	133.18***
GCA	8	171.79***	165.00***	207.16***	426.82***	238.71ns	1928.65***	195.93***	1521.86***	257.62***	91.82***	141.63**	109.49**
SCA	36	83.59**	144.19***	62.78***	117.87***	291.20*	437.33ns	60.91***	139.25ns	66.12***	53.71***	85.23**	126.57***
REC	36	106.43***	142.97***	83.38***	93.80***	327.31*	479.52*	79.08***	307.78ns	124.95***	48.88***	123.18***	145.06***
MAT	8	139.41***	159.24***	116.09***	84.78***	323.16ns	916.34*	110.66***	858.59**	280.04***	54.77**	213.98***	161.15***
NMAT	28	97.01***	138.32***	74.04***	96.38***	328.49*	354.72ns	70.06***	150.41ns	80.64***	47.19***	97.24***	140.47***
ENV*ENTRY	160	147.57***	152.65***	116.22***	111.26***	258.45*	349.29ns	110.37***	327.26***	88.11***	85.71***	86.58***	156.92***
GCA*ENV	16	132.47***	130.30***	145.83***	223.10***	393.211*	1091.63**	134.02***	1169.30***	119.55***	73.83***	105.68*	155.14***
SCA*ENV	72	116.75***	140.33***	63.65***	72.83***	233.60ns	258.96ns	59.29***	119.35ns	69.27***	106.12***	98.02***	227.55***
REC*ENV	72	181.74***	169.93***	162.20***	124.83***	253.35ns	274.65ns	156.20***	348.06ns	99.96***	67.94***	70.89*	86.68***
MAT*ENV	16	241.47***	278.06***	143.63***	176.90***	335.11ns	599.76ns	139.10***	636.34*	177.92***	19.36ns	72.60ns	60.23ns
NMAT*ENV	56	164.68***	139.04***	167.51***	109.96***	229.99ns	181.76ns	161.08***	265.70ns	77.68***	81.81***	70.40*	94.23***
R-Square		0.82	0.89	0.9	0.9	0.66	0.7	0.89	0.75	0.81	0.79	0.73	0.76
Coeff Var		4.74	4.02	3.17	3.48	14.99	22.28	3.08	21.73	3	2.61	4.22	3.87
Mean		93.17	89.91	90.64	89.68	91.44	8097	93.49	77.4	157.93	163.79	153.61	152.41
GCASSS/Entry SS		16.73	11.32	23.95	30.94	7.90	31.85	23.72	43.07	23.05	16.59	13.12	8.22
SCASS/Entry SS		36.63	44.53	32.66	38.46	43.36	32.50	33.19	17.73	26.63	43.67	35.53	42.77
GCA:SCA Ratio		0.46	0.25	0.73	0.80	0.18	0.98	0.71	2.43	0.87	0.38	0.37	0.19
RecSS/EntrySS		46.64	44.15	43.38	30.60	48.74	35.64	43.09	39.20	50.32	39.74	51.35	49.01
MSS/RecSS		29.11	24.75	30.94	20.09	21.94	42.47	31.10	61.99	49.80	24.90	38.60	24.69
NMSS/RecSS		70.89	75.25	69.07	79.92	78.06	57.54	68.91	38.01	50.20	75.09	61.40	75.32

		Top biomass (g)				Number of panicles (numbers)				Phosphorous tolerance (scale)			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	175196.54***	233946.95***	165852.87***	268684.99***	4226.28***	4664.64***	933.92***	833.83***	2.08***	1.54***	1.94	1.47***
ENV	2	406132.60***	8804274.21***	70479.15***	21387563.75***	417536.47***	713946.13***	83002.80***	66688.44***	53.33***	16.30***	41.62***	5.44***
REP(ENV)	5	232864.75	102808.24	20972.93	104346.29	68536.07	2913.25	127.23	784.78	2.35	0.05	1.51	0.48
ENTRY	80	207437.50***	218406.77***	202017.52***	167138.48***	499.84***	320.97***	467.58***	485.71***	1.93***	1.58***	1.95***	1.50***
GCA	8	270010.01***	281223.36***	240749.91***	237078.47***	192.52ns	304.74***	895.70***	118.23***	2.89***	0.86***	3.26***	2.60***
SCA	36	157582.19***	155229.22***	163201.94***	123954.47***	705.29***	261.49***	435.96***	466.86***	1.61***	1.46***	1.88***	1.57***
REC	36	243387.81***	267625.08***	232225.91***	194780.27***	362.68*	384.06***	404.06***	586.21***	2.04***	1.86***	1.72***	1.17***
MAT	8	463933.20***	628372.05***	421042.40***	394240.21***	526.19*	754.09***	968.55***	842.71***	2.62***	2.96***	1.99***	1.83***
NMAT	28	180374.84***	164554.51***	178278.34***	137791.72***	315.96ns	278.33***	242.78***	512.93***	1.87***	1.55***	1.64***	0.99***
ENV*ENTRY	160	137906.33***	147275.74***	136313.39***	112408.22***	374.73**	207.97***	404.66***	360.62***	1.58***	1.38***	1.46***	1.44***
GCA*ENV	16	175287.06***	193636.26***	164886.54***	161134.35***	291.82ns	330.002***	500.04***	480.54***	1.87***	1.25***	2.85***	3.31***
SCA*ENV	72	106050.05***	104324.94***	109838.06***	83207.09***	438.81**	203.71***	341.39***	239.31***	0.96***	0.93***	1.50***	1.35***
REC*ENV	72	161455.77***	179924.20***	156439.12***	130781.32***	329.08ns	185.12***	446.73***	455.29***	2.14***	1.85***	1.12***	1.11***
MAT*ENV	16	306722.82***	424252.47***	286275.17***	262825.85***	441.73ns	437.67***	1121.90***	609.22***	3.74***	1.26***	1.39***	2.25***
NMAT*ENV	56	119950.90***	110116.12***	119343.11***	93054.31***	296.90ns	112.96***	253.82***	411.31***	1.68***	2.01***	1.04***	0.78***
R-Square		0.98	0.97	0.99	0.97	0.93	0.99	0.92	0.93	0.84	0.83	0.87	0.89
Coeff Var		3.36	5.59	3	5.21	24.62	7.28	15.37	12.98	28.78	28.79	25.22	23.62
Mean		1303.53	1281.94	1333.82	1470.74	61.42	80.03	47.24	50.69	1.84	1.62	1.79	1.53
GCASSS/Entry SS		13.02	12.88	11.92	14.18	3.85	9.49	19.16	2.43	14.97	5.44	16.72	17.33
SCASS/Entry SS		34.18	31.98	36.35	33.37	63.50	36.66	41.96	43.25	37.54	41.58	43.38	47.10
GCA:SCA Ratio		0.38	0.40	0.33	0.43	0.06	0.26	0.46	0.06	0.40	0.13	0.39	0.37
RecSS/EntrySS		52.80	55.14	51.73	52.44	32.65	53.85	38.89	54.31	47.56	52.97	39.69	35.10
MSS/RecSS		42.36	52.18	40.29	44.98	32.24	43.63	53.27	31.95	28.54	35.36	25.71	34.76
NMSS/RecSS		57.64	47.82	59.71	55.02	67.76	56.37	46.73	68.06	71.30	64.81	74.16	65.81

*significant at P<0.05 **significant at P<0.01 ***significant at P<0.001 ns-not significant

Table 5.2 Source of variation and mean squares for genetic components of F_2 ten rice traits under four soil N and P conditions

		Nitrogen tolerance (scale)				Plant height (cm)			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	2.19***	1.74***	1.08***	1.56***	151758***	1680.61	507.91	447.73***
ENV	2	0.87ns	14.08***	5.16***	0.76ns	193407.01***	211437.40***	46702.23***	2929.31***
REP(ENV)	5	1.7	1.93	1.3	0.83	3356.6	441.5	743.9	199.39
ENTRY	80	2.72***	2.03***	0.97***	1.8***	319.97***	433.11***	252.50***	505.68***
GCA	8	2.95***	2.61***	1.44***	1.65***	367.67***	773.51***	345.40***	1113.97***
SCA	36	2.97***	1.75***	0.95***	2.08***	330.30***	450.68***	150.40***	460.14***
REC	36	2.43***	2.19***	0.89***	1.56***	299.04***	339.89***	333.95***	416.05***
MAT	8	1.98***	1.84***	0.91**	1.25***	770.99***	728.63***	813.58***	512.08***
NMAT	28	2.56***	2.29***	0.89***	1.64***	164.20***	228.83***	196.92***	388.62***
ENV*ENTRY	160	1.70***	1.28***	1.12***	1.36***	247.60***	352.61***	177.03***	368.06***
GCA*ENV	16	1.60***	1.26***	0.51ns	2.80***	235.47***	333.59***	303.81***	675.77***
SCA*ENV	72	2.00***	1.27***	1.03***	1.06***	240.34***	291.38***	107.99***	311.03***
REC*ENV	72	1.41***	1.30***	1.36***	1.33***	257.57***	418.06***	217.90***	356.72***
MAT*ENV	16	0.96***	1.21***	3.15***	1.60***	504.70***	743.00***	523.99***	492.86***
NMAT*ENV	56	1.54***	1.33***	0.85***	1.25***	186.96***	325.22***	130.45***	317.82***
R-Square		0.83	0.8	0.74	0.83	0.96	0.98	0.95	0.92
Coeff Var		23.8	26.54	24.08	27.95	8.2	5.51	3.83	4.08
Mean		2.33	2.07	1.77	1.68	81.59	81.55	117.63	126.48
GCASSS/Entry SS		10.85	12.86	14.85	9.17	11.49	17.86	13.68	22.03
SCASS/Entry SS		49.14	38.79	44.07	52.00	46.45	46.83	26.80	40.95
GCA:SCA Ratio		0.22	0.33	0.34	0.18	0.25	0.38	0.51	0.54
RecSS/EntrySS		40.20	48.55	41.29	39.00	42.06	35.31	59.52	37.02
MSS/RecSS		18.11	18.67	22.72	17.81	57.29	47.64	54.14	27.35
NMSS/RecSS		81.94	81.33	77.78	81.77	42.71	52.36	45.86	72.65

		1000 seed weight (g)				Yield (kg ha$^{-1)}$			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	23.91***	27.42***	23.51***	17.11***	2795069.80***	1893861.10***	2362050.00***	1441338.30***
ENV	2	674.87***	1213.91***	662.18***	428.40***	15787170.40***	79304753.90***	58758691.70***	19789523.70***
REP(ENV)	5	20.7	0.35	15.81	2.52	389691.2	1272733.9	247371.1	1280770.9
ENTRY	80	24.65***	27.65***	23.62***	20.07***	3397834.20***	1561437.40***	2148526.80***	1641079.20***
GCA	8	27.52***	57.70***	42.37***	20.29***	4574679.33***	3523712.34***	3216642.18***	4372069.92***
SCA	36	24.25***	20.25***	13.54***	18.05***	3077395.05***	894411.48***	1745364.94***	832764.89***
REC	36	24.40***	28.38***	29.54***	22.05***	3456752.11***	1792402.22***	2314329.70***	1842506.70***
MAT	8	37.01***	38.77***	36.53***	28.78***	3862816.88***	1899737.62***	1373990.54***	3895787.34***
NMAT	28	20.80***	25.41***	27.54***	20.13***	3340733.60***	1761734.96***	2582998.03***	1255855.09***
ENV*ENTRY	160	15.15***	13.38***	15.70***	9.56**	2120105.90***	1281940.90***	1949915.50***	1018266.30***
GCA*ENV	16	11.46*	16.79**	27.57***	12.16*	2842940.14***	564805.31*	2920334.48***	1158007.19***
SCA*ENV	72	11.58***	11.01***	13.50***	8.20*	1989353.13***	1194156.25***	1546974.24***	840549.08***
REC*ENV	72	19.54***	15.00***	15.25***	10.33**	2090228.78***	1529088.96***	2137208.21***	1164929.92***
MAT*ENV	16	24.39***	32.49***	15.09***	12.74*	2409215.48***	828774.80**	2865939.68***	1418277.73***
NMAT*ENV	56	18.15***	10.00**	15.30***	9.65**	1999089.72***	1729178.72***	1928999.22***	1092544.83***
R-Square		0.78	0.79	0.83	0.68	0.8	0.82	0.89	0.86
Coeff Var		7.91	8.09	6.64	8.6	18.77	11.58	10.12	8.94
Mean		27.56	27.4	27.69	27.35	3635.49	4607.807	4419.03	4516.18
GCASSS/Entry SS		11.16	20.87	17.94	10.11	13.46	22.57	14.97	26.64
SCASS/Entry SS		44.27	32.96	25.80	40.47	40.76	25.78	36.56	22.84
GCA:SCA Ratio		0.25	0.63	0.70	0.25	0.33	0.88	0.41	1.17
RecSS/EntrySS		44.54	46.19	56.28	49.44	45.78	51.66	48.47	50.52
MSS/RecSS		33.71	30.36	27.48	29.00	24.83	23.55	13.19	46.99
NMSS/RecSS		66.30	69.64	72.51	71.01	75.17	76.45	86.81	53.01

*significant at P<0.05 **significant at P<0.01 ***significant at P<0.001 ns-not significant

Table 5.3 Mean squares of general combining ability effects for the nine rice parents under four soil N and P conditions

	Days to heading (days)				Days to anthesis (days)				Phosphorous tolerance (scale)				Nitrogen tolerance (scale)				Plant height (cm)			
	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
#G1	-1.97*	-2.03**	-3.42***	-3.22***	-2.26ns	-10.16***	-3.29***	-7.34**	0.05ns	-0.01ns	0.12ns	0.17*	-0.14ns	0.08*	-0.16*	0.08ns	-2.89ns	-5.26*	-2.57ns	-5.33***
G2	-0.12ns	-0.93ns	-0.02ns	-1.51*	-2.74ns	-2.72ns	-0.03ns	-4.68ns	-0.17ns	-0.01ns	-0.24**	0.05ns	0.20*	0.08ns	0.08ns	-0.01ns	0.004ns	2.00ns	1.24ns	-0.37ns
G3	1.06ns	2.11**	1.94**	2.58***	0.03ns	-1.49ns	1.83**	-0.88ns	0.32***	0.10ns	0.19*	-0.03ns	0.15ns	0.08ns	0.08ns	-0.09ns	-0.42ns	-1.69ns	1.124ns	1.04ns
G4	1.25ns	1.55*	1.03ns	1.58*	1.26ns	0.73ns	1.04ns	-1.13ns	0.21*	0.03ns	-0.28**	0.13ns	0.23*	0.08*	0.13ns	0.13ns	0.15ns	1.28ns	3.88*	5.19***
G5	0.09ns	1.05ns	0.17ns	1.17ns	0.42ns	-0.34ns	0.29ns	0.61ns	-0.07ns	-0.17*	-0.02ns	-0.31***	-0.09ns	0.08***	-0.24**	-0.12ns	-2.45ns	-1.68ns	-0.30***	4.38***
G6	1.34ns	-0.30ns	1.01ns	1.72*	1.72ns	1.12ns	1.06ns	0.93ns	0.06ns	-0.14*	0.05ns	-0.23**	0.16*	0.08ns	0.10ns	-0.13ns	-0.97ns	-1.87ns	-1.82ns	0.16ns
G7	1.33ns	-0.29ns	-0.26ns	1.33*	1.94ns	5.10*	-0.22ns	3.35ns	-0.04ns	0.02ns	-0.15ns	-0.03ns	-0.24*	0.08ns	0.01ns	-0.18**	1.17ns	1.45ns	0.18ns	0.65ns
G8	-0.91ns	0.08ns	0.36ns	-0.53ns	-0.08ns	3.31ns	0.27ns	3.34ns	-0.25**	0.10ns	0.27**	0.14*	-0.13ns	0.07ns	-0.07ns	0.19*	3.48ns	4.83ns	-1.69ns	-1.07ns
G9	-2.07**	-1.24ns	-0.83ns	-3.13***	-0.30ns	4.45ns	-0.94ns	5.82*	-0.10ns	0.08ns	0.07***	0.13ns	-0.15ns	0.07ns	0.07ns	0.12ns	1.93ns	0.93ns	-0.04ns	-4.65***

	Top biomass (g)				Number of panicles (numbers)				Days to maturity (day)				1000 seed weight (g)				Yield (kg ha^{-1})			
	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
G1	-53.57*	24.76*	-40.43*	-44.96ns	-2.02ns	-0.77ns	-5.44**	-0.11ns	-3.66***	-0.11ns	0.52ns	-0.52ns	-0.058ns	-0.35ns	-0.15ns	0.004ns	-258.01*	-337.45***	-283.57**	-563.22***
G2	-40.83*	24.76ns	-21.15ns	-33.23ns	-1.01ns	2.83ns	-0.30ns	0.88ns	-1.43ns	-0.15ns	-0.71ns	0.59ns	-0.09ns	0.57ns	0.24ns	0.36ns	148.57ns	18.51ns	-24.16ns	32.49ns
G3	-40.27*	24.76ns	-44.06*	-21.20ns	1.03ns	3.20ns	1.57ns	2.29ns	-0.13ns	1.15ns	-0.42ns	1.14ns	-0.70*	-1.31***	-1.13***	-0.76*	258.84*	234.77*	141.14ns	152.48**
G4	113.19***	24.76***	109.04***	108.20***	-0.99ns	-0.89ns	-2.78ns	-0.95ns	0.68ns	-0.83ns	-2.87**	-1.84*	-0.06ns	0.08ns	-0.03ns	-0.20ns	68.35ns	7.42ns	-37.55ns	106.43ns
G5	47.40*	24.76**	50.05*	51.61ns	-0.56ns	-2.07ns	0.56ns	-1.45ns	0.37ns	-1.08ns	1.23ns	1.60ns	-0.71*	-1.01**	-0.18ns	-0.67*	135.89ns	98.17ns	262.27**	71.77ns
G6	-8.93ns	24.76ns	-10.20ns	-17.61ns	0.49ns	0.08ns	-0.39ns	-0.19ns	0.90ns	1.001ns	1.06ns	-1.05ns	0.77*	0.69ns	1.07***	0.30ns	-302.35**	196.43*	42.10ns	152.75**
G7	-46.13*	24.76ns	-52.63**	-51.86ns	2.66ns	-0.80ns	0.51ns	0.80ns	0.69ns	1.60*	0.56ns	-0.11ns	-0.07ns	0.45ns	-0.06ns	0.43ns	-74.36ns	-226.74*	-199.11*	4.79ns
G8	5.91ns	24.76ns	-0.95ns	-2.08ns	1.27ns	-1.59ns	0.03ns	-0.48ns	2.34**	-0.51ns	-0.03ns	-0.52ns	0.92**	1.10**	0.89**	0.59*	267.12*	153.03ns	-135.63*	77.717ns
G9	23.24ns	24.76ns	10.33ns	11.13ns	-0.87ns	0.01ns	6.24**	-0.78ns	0.25ns	-1.07ns	0.67ns	0.71ns	-0.01ns	-0.21ns	-0.66*	-0.04ns	-244.05*	-144.16ns	234.5146	-35.20ns

*significant at P<0.05 **significant at P<0.01 ***significant at P<0.001 ns-not significant

#G1-NERICA 1 G2-Duorado G3-IR79913-176-B-4 G4-CT16333(1)-CA-20-M G5-CT16333(1)-CA-22-M G6-CT16333(2)-CA-18-M G7-CT16313-CA-19- G8-WAB964-B-3A 1.2 G9-CT16317-CA-4-M

5.4.2 General combining ability effects for the nine rice parents.

The general combining ability (GCA) effects for the nine parents had very varied behaviour across the different soil N and P experimental environments (Table 5.3). The following instances were notable, parent G1 (NERICA 1) had significant but negative values for days to heading and grain yield (0.05>P<0.001) across the four experimental environments. NERICA1 is fragrant and early maturing variety, but with relatively low yields. Since it is good combiner for earliness, it can be used for breeding early maturing varieties.

Parent G4 (CT16333(1)-CA-20-M) reacted in the opposite direction to NERICA 1, it had positive and highly significant GCA effects for top biomass under the four experimental environments. Entry G8 (WAB964-B-3A 1.2) had significant values for 1000 seed weight under all the four soil N and P experimental environments. However, parent G3 (IR79913-B-176-B-4) on the other hand, displayed significant but negative GCA effects. Number of panicles had seven of the nine parents having non-significant GCA effects under all the four soil N and P experimental environments, and only under N+P- did parents G1 and G9 (CT16317-CA-4-M) have significant values (P<0.01). Seven parents under N+P+ had significant GCA effects values for days to heading, with entry G5 (CT16333(1)-CA-22-M) and G8 having non-significant GCA effects under the four soil N and P experimental conditions for the same trait.

5.4.3 The F_2 population means for the best ten rice lines for five traits under four soil N and P conditions

Genotype 36 (CT16333(1)-CA-20-M x CT16317-CA-4-M) had consistent performance for top biomass under all four soil N and P experimental environments and was ranked top, while line 38 (CT16333(1)-CA-22-M x NERICA 1) was ranked 2nd except under N-P+ (Table 5.4). The line 35 (CT16333(1)-CA-20-M x WAB964-B-3A1.2) was ranked 3rd among the highest top ten except under N-P+ soil condition (the line pedigree names for the means are in Table 5.10). The genotypes were variable for phosphorous tolerance with line 2 (NERICA 1 x Dourado) being the most tolerant under N-P+ and N+P- soil condition conditions and line 15 (Dourado x CT16333(2)-CA-18-M) under N-P- and N+P+ soil conditions. Line 2 again was the most tolerant for nitrogen except under N-P- soil condition. Grain yield had varied line performance with no consistent line having across fertility consistency. However, lines 46 (CT16333(2)-CA-18-M x CT16333(2)-CA-18-M), 42 (CT16333(1)-CA-22-M x CT16333(2)-CA-18-M), 70 (WAB964-B-3A1.2 x CT16333(2)-CA-18-M) and 53 (CT16333(2)-CA-18-M x WAB964-B-3A1.2) appeared

twice among the top highest yielders under any one of the conditions. The lines had varied performance for days to maturity with none of the lines showing consistency.

Table 5.4 The mean values for the best top ten F_2 rice lines under four soil N and P conditions

	Phosphorous tolerance (1-5 scale)								Nitrogen tolerance (1-5 scale)								Grain yield (kg ha^{-1})							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	8	1.0	2	1.0	2	1.0	3	1.0	19	1.0	2	1.0	2	1.0	2	1.0	31	5106.5	64	5498.6	26	5293.9	12	5418.3
	15	1.0	5	1.0	10	1.0	15	1.0	56	1.0	37	1.0	38	1.0	16	1.0	44	5085.7	31	5497.7	21	5203.9	69	5235.8
	16	1.0	6	1.0	11	1.0	16	1.0	29	1.3	56	1.0	44	1.0	28	1.0	22	4981.9	49	5344.2	47	5130.4	53	5146.0
	43	1.0	10	1.0	13	1.0	18	1.0	37	1.5	62	1.0	56	1.0	35	1.0	66	4813.4	46	5304.5	18	5130.2	46	5113.0
	44	1.0	13	1.0	16	1.0	25	1.0	59	1.5	19	1.3	71	1.0	40	1.0	39	4733.9	42	5283.5	42	5128.3	58	5102.6
	45	1.0	14	1.0	18	1.0	29	1.0	40	1.6	40	1.3	76	1.0	42	1.0	48	4682.3	19	5274.4	37	5082.6	28	5100.9
	58	1.0	28	1.0	30	1.0	37	1.0	73	1.6	30	1.3	5	1.3	43	1.0	70	4653.1	13	5233.7	66	5077.5	70	5089.9
	59	1.0	34	1.0	41	1.0	40	1.0	28	1.7	6	1.5	43	1.3	45	1.0	5	4629.4	11	5155.7	31	5008.4	66	5084.7
	60	1.0	38	1.0	46	1.0	42	1.0	43	1.7	14	1.5	46	1.3	55	1.0	43	4611.4	53	5143.1	58	4990.0	40	5062.7
	63	1.0	40	1.0	56	1.0	43	1.0	64	1.7	16	1.5	60	1.3	56	1.0	4	4588.3	47	5136.1	16	4978.8	51	5051.2
Mean		1.8		1.6		1.8		1.5		2.3		2.1		1.8		1.7		3635.5		4607.8		4419.0		4516.2

	Top biomass (g)								Days to maturity (days)							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	36	2275.8	36	2185.9	36	2285.7	36	2337.7	53	163.1	47	152.7	11	142.6	1	140.9
	38	1895.3	35	1860.7	38	1939.4	38	2105.5	36	163.3	78	155.8	42	145.2	28	140.9
	35	1839.0	38	1838.3	35	1834.7	35	2032.0	60	163.5	77	156.2	36	145.7	46	142.8
	42	1508.0	39	1494.1	42	1577.2	42	1698.2	48	164.0	66	157	64	146.4	55	143.5
	28	1482.5	42	1479.0	39	1520.3	28	1673.5	44	164.1	59	157.3	68	146.4	24	144.5
	40	1433.5	40	1444.4	17	1514.6	25	1669.4	39	164.2	65	157.7	34	146.9	9	145.3
	39	1432.4	41	1429.5	41	1514.4	39	1662.0	49	164.3	5	157.8	48	147.3	10	145.5
	17	1432.1	28	1392.8	40	1457.3	41	1649.1	51	164.4	42	158.3	15	148.4	57	146.0
	61	1424.2	43	1362.7	28	1445.3	10	1612.8	71	164.7	28	158.6	47	148.5	36	146.2
	41	1417.8	54	1354.7	25	1444.8	21	1612.1	33	167.0	18	159.1	24	149.6	75	146.3
Mean		1303.5		1281.9		1333.8		1470.7		157.9		163.8		153.6		152.4

5.4.4 Leaf and seed tissue phosphorous and nitrogen genetic analysis for rice F_3 populations.

The analysis of leaves and seed tissue for phosphorous (P) and nitrogen (N) gave generally very highly significant ($P<0.001$) mean squares across all mega-environments (Table 5.5). The only exception was the GCA which had highly significant values ($P<0.001$) except grain nitrogen at Mwea where it was significant at $P<0.05$, and the SCA at Mwea and Matuga ($P<0.01$). Reciprocal, maternal and nonmaternal components were very highly significant ($P<0.001$) except for grain nitrogen that had highly significant values at Matuga, which was again the case for maternal, and nonmaternal factors that had significant value ($P<0.05$). The GCA:SCA ratio analysis gave values larger than 1 for leaf N and grain P across the three locations. The

magnitude of reciprocal effects were generally greater than GCA effects in all cases, except for leaf P at all location. The proportion of nonmaternal effects was larger than maternal effects in all the cases, except for grain P for the three locations.

The general combining ability (GCA) effects had varied values for both tissue nitrogen and phosphorous as well as the mega-environments. Leaf nitrogen and phosphorous had very highly significant effects for all the parents at the three mega-environments, but sign for some was negative (Table 5.5). However, at Mwea parents G9 (CT16317-CA-4-M) and G8 (WAB964-B-3A 1.2) had significant and highly significant values for leaf N and P, respectively. For grain nitrogen, parents G1 (NERICA1), G2 (*Duorado precoce*), G3 (IR79913-176-B4), G4 (CT16333(1)-CA-20M), G5 (CT16333(1)-CA-22-M), G7 (CT16313-CA-19-M) and G8 had non-significant values.

Entry 44 (CT16333(1)-CA-22-M xWAB964-B-3A1.2) had the highest leaf nitrogen for Alupe and Matuga, while entry 12 (Dourado x IR79913-B-176-B-4) had the highest leaf phosphorous for the three mega-environments (data not shown for the means). Grain nitrogen was highest for entry 76 (CT16317-CA-4-M x IR79913-B-176-B-4) at Mwea and Alupe, while entry 22 (IR79913-B-176-B-4 x CT16333(1)-CA-20-M) had the highest grain phosphorous at Alupe and Matuga. Entry 28 (CT16333(1)-CA-20-M x CT16333(1)-CA-20-M) had the lowest values for leaf nitrogen across the three mega-environments, while entry 9 (NERICA 1 x CT16317-CA-4-M) had the lowest leaf phosphorous and grain phosphorous across the three mega-environments.

5.4.5 Mean squares of genetic components for the F_3 rice populations under the four soil N and P conditions

The mean square values due to entries, mega-environments and their interactions were highly significant in most cases for the traits under the four experimental environments (Tables 5.6 and 5.7). The GCA, SCA, reciprocal, maternal and nonmaternal effects were highly significant in almost all the soil N and P conditions. The GCA:SCA ratios were less than one, except for days to maturity for soil N+P- condition. The proportion of reciprocal effects was generally greater than GCA for most of the soil N and P conditions. The partitioning of reciprocal effects revealed that the nonmaternal effects were in most cases for most of the soil N and P condition larger than the maternal effects (Tables 5.6 and 5.7).

Table 5.5 Mean squares of genetic components for rice leaf and grain N and P for Mwea, Alupe and Matuga locations

Trait		Leaf Nitrogen			Leaf Phosphorous			Grain Nitrogen			Grain Phosphorous		
Mega environments		Mwea	Alupe	Matuga	Mwea	Alupe	Matuga	Mwea	Alupe	Matuga	Mwea	Alupe	Matuga
Source	DF												
REP	1	1.596	1.387	0.816	5.675	1.656	2.264	0.005	0.005	0.481	0.046	0.017	0.096
ENTRY	80	0.203***	0.203***	0.210***	0.090***	0.092***	0.0896***	0.037***	0.038***	0.041***	0.079***	0.069***	0.072***
GCA	8	0.675***	0.754***	0.785***	0.256***	0.276***	0.254***	0.032*	0.034***	0.088***	0.301***	0.266***	0.272***
SCA	36	0.129***	0.135***	0.129***	0.103***	0.098***	0.097***	0.029**	0.036***	0.035**	0.034***	0.028***	0.031***
REC	36	0.173***	0.148***	0.164***	0.040***	0.045***	0.045***	0.045***	0.041***	0.036**	0.075***	0.067***	0.067***
MAT	8	0.368***	0.284***	0.322***	0.058***	0.056***	0.063***	0.064***	0.074***	0.055**	0.234***	0.213***	0.212***
NMAT	28	0.117***	0.109***	0.118***	0.035***	0.042***	0.040***	0.040***	0.032***	0.031*	0.029***	0.026***	0.026***
GCASSS/Entry SS		33.25	37.14	37.38	28.44	30.00	28.35	8.65	8.95	21.46	38.10	38.55	37.78
SCASS/Entry SS		28.60	29.93	27.64	51.50	47.93	48.72	35.27	42.63	38.41	19.37	18.26	19.38
GCA:SCA Ratio		1.16	1.24	1.35	0.55	0.63	0.58	0.25	0.21	0.56	1.97	2.11	1.95
RecSS/EntrySS		38.35	32.81	35.14	20.00	22.01	22.60	54.73	48.55	39.51	42.72	43.70	41.88
MSS/RecSS		47.27	42.64	43.63	32.22	27.65	31.11	31.60	40.11	33.95	69.33	70.65	70.32
NMSS/RecSS		52.60	57.28	55.96	68.06	72.59	69.14	69.14	60.70	66.98	30.07	30.18	30.18
	#G1	-0.023***	-0.089***	-0.060***	0.148***	-0.153***	-0.156***	-0.029ns	-0.008ns	-0.031ns	-0.039***	-0.039**	-0.032*
	G2	0.079***	0.028***	0.055***	0.048***	0.061***	0.056***	0.007ns	-0.015ns	-0.018ns	-0.023*	-0.022ns	-0.027*
	G3	-0.190***	-0.221***	-0.197***	0.041***	0.036***	0.040***	0.001ns	-0.004ns	0.004ns	0.215***	0.209***	0.210***
	G4	-0.226***	-0.179***	-0.221***	0.107***	-0.113***	-0.101***	0.019ns	0.063***	0.059**	-0.017*	-0.009ns	-0.015ns
	G5	0.217***	0.230***	0.242***	0.053***	0.055***	0.048***	-0.001ns	-0.024ns	-0.082***	0.023*	0.016ns	0.014ns
	G6	0.049***	0.0406***	0.078***	0.095***	0.099***	0.092***	-0.037*	-0.025ns	-0.019ns	-0.089***	0.071***	0.077***
	G7	0.062***	0.095***	0.065***	0.058***	0.060***	0.058***	-0.003ns	-0.020ns	-0.006ns	-0.087***	0.082***	0.082***
	G8	0.047***	0.118***	0.092***	0.019**	0.013***	0.018***	-0.020ns	-0.008ns	0.007ns	-0.025*	-0.027*	-0.024*
	G9	-0.014*	-0.023***	-0.054***	0.060***	-0.058***	-0.053***	0.064**	0.042*	0.086***	0.041***	0.025*	0.033*
R-Square		0.993	0.996	0.993	0.991	0.997	0.999	0.735	0.819	0.752	0.945	0.926	0.925
Coefficient Variation		2.715	2.263	3.416	1.367	0.706	0.392	10.248	7.995	11.991	7.759	8.136	9.343
Mean		1.510	1.392	1.174	2.848	2.413	2.554	1.123	1.150	1.036	0.878	0.913	0.819
GCA:SCA ratio		5.23	5.59	6.09	2.49	2.82	2.62	1.10	0.94	2.51	8.85	9.50	8.77
*significant at P<0.05			#G1-NERICA 1			G5-CT16333(1)-CA-22-M			G9-CT16317-CA-4-M				
**significant at P<0.01			G2-Duorado			G6-CT16333(2)-CA-18-M							
***significant at P<0.001			G3-IR79913-176-B-4			G7-CT16313-CA-19-M							
ns-not significant			G4-CT16333(1)-CA-20-M			G8-WAB964-B-3A 1.2							

The general combining ability (GCA) effects were variable for the traits under the four soil N and P experimental environments (Table 5.8). Parent G1 had significant but negative GCA for days to heading, anthesis and maturity under the four experimental environments. Parent G4 (CT16333(1)-CA-20-M) had very highly significant (P<0.001) GCA effects for top biomass under the four soil N and P condition.

Genotype IR79913-176-B-4 had negative but significant GCA effects for 1000 seed weight under the four soil conditions. Five parents had significant GCA effects for top biomass and grain yield under soil N+P+ experimental condition. None of the parents had significant GCA effects for phosphorous tolerance (N+P+), nitrogen tolerance (N+P+) and plant height (N-P+, N+P-), but there effects varied on different soil N and P environments.

Table 5.6 Mean squares for genetic components of ten rice traits under four soil N and P conditions

		Days to heading (days)				Days to anthesis (days)				Days to maturity (day)			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	155.38***	131.06***	139.03***	141.95***	142.90***	118.09***	132.89***	127.58	69.88***	99.04***	66.06***	99.40***
ENV	2	1199.11***	6294.62***	0.004ns	613.51***	1590.60***	5796.30***	21.96ns	801.98***	1749.73***	7952.60***	957.05***	3753.25***
REP(ENV)	5	164.62	148.86	112.32	459.23	144.12	58.10	153.49	566.09	1105.57	517.62	483.85	847.59
ENTRY	80	183.06***	76.65***	143.62***	127.90***	165.58***	72.00**	135.86***	110.45***	40.81***	37.98***	48.96***	63.81***
GCA	8	285.35***	231.08***	276.32***	226.26***	262.29***	206.22***	257.25***	236.72***	86.43***	107.29***	126.34***	174.36***
SCA	36	165.93***	70.79***	117.36***	94.64***	156.61***	59.16***	110.91***	85.23***	46.04***	28.92**	25.76***	39.56***
REC	36	177.45***	48.19***	140.38***	139.29***	153.07***	42.71***	133.82***	107.62***	25.44*	31.64***	35.58***	63.49***
MAT	8	268.53***	96.29***	147.67***	180.88***	220.46***	79.40***	144.14***	198.09***	50.28**	48.14**	73.56***	163.97***
NMAT	28	151.43***	34.44***	138.30***	127.41***	133.81***	32.23***	130.87***	81.77***	18.34ns	26.93*	24.73*	34.79***
ENV*ENTRY	160	114.31***	107.75***	137.19***	138.22***	102.07***	101.00***	130.53***	119.84***	39.11***	46.23***	65.07***	61.27***
GCA*ENV	16	135.82***	100.81***	203.68***	94.21***	138.79***	93.85***	198.72***	95.73***	55.41**	64.28***	149.68***	107.71***
SCA*ENV	72	81.95***	60.20***	74.89***	91.13***	76.09***	57.86***	78.25***	61.13***	32.85**	46.19***	55.13***	57.08***
REC*ENV	72	141.88***	156.85***	184.72***	195.09***	119.90***	145.70***	167.66***	183.90***	41.74***	42.25***	56.21***	55.13***
MAT*ENV	16	125.93***	325.00***	285.15***	273.55***	84.39***	279.38***	235.46***	299.58***	57.24**	53.49***	77.92***	71.48***
NMAT*ENV	56	146.44***	108.81***	156.02***	172.67***		107.50***	148.29***	150.85***	37.31**	39.04***	50.01***	50.46***
R-Square		0.91	0.86	0.89	0.89	0.90	0.86	0.88	0.85	0.74	0.82	0.77	0.86
Coeff Var		3.58	4.35	3.78	4.00	3.38	4.02	3.84	4.26	3.14	2.95	2.81	2.50
Mean		92.87	87.20	88.29	89.09	95.57	90.32	91.38	92.03	131.56	130.08	129.74	132.44
GCASSS/Entry SS		15.59	30.15	19.24	17.69	15.84	28.64	18.93	21.43	21.18	28.25	25.80	27.32
SCASS/Entry SS		40.79	41.56	36.77	33.30	42.56	36.98	36.74	34.72	50.77	34.27	23.68	27.90
GCA:SCA Ratio		0.38	0.73	0.52	0.53	0.37	0.77	0.52	0.62	0.42	0.82	1.09	0.98
RecSS/EntrySS		43.62	28.29	43.98	49.01	41.60	26.69	44.32	43.85	28.05	37.49	32.70	44.77
MSS/RecSS		33.63	44.40	23.38	28.86	32.01	41.31	23.94	40.90	43.92	33.81	45.94	57.39
NMSS/RecSS		66.37	55.59	76.63	71.14	67.99	58.69	76.06	59.10	56.07	66.20	54.06	42.62

		Phosphorous tolerance (scale)				Nitrogen tolerance (scale)				Plant height (cm)			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	2.76***	2.00***	2.61***	2.40***	2.15***	2.28***	2.16***	2.30***	2094.55***	2349.40***	466.18***	960.76***
ENV	2	13.63***	8.77***	1.58*	4.98***	2.07*	1.11ns	4.89***	0.56ns	288011.12***	302137.13***	28274.70***	91730.41***
REP(ENV)	5	0.38	0.18	0.51	0.22	2.85	0.60	1.47	0.76	292.28	486.83	2843.73	1144.40
ENTRY	80	2.68***	2.38***	3.08***	2.32***	2.61***	2.38***	2.37***	2.36***	416.29***	538.71***	251.24***	420.91***
GCA	8	2.54***	1.97***	2.90***	1.06***	2.82***	1.30***	1.83***	0.89***	1012.12***	645.75***	142.77*	469.01***
SCA	36	2.25***	2.49***	2.99***	2.79***	2.45***	2.92***	2.45***	2.33***	325.11***	566.52***	347.86***	516.58***
REC	36	3.13***	2.36***	3.21***	2.13***	2.72***	2.08***	2.40***	2.71***	375.07***	487.10***	178.73***	314.54***
MAT	8	2.18***	2.25***	3.71***	4.28***	7.68***	4.03***	4.13***	4.99***	958.02***	634.78***	359.72***	746.79***
NMAT	28	3.41***	2.39***	3.07***	1.51***	1.30***	1.52***	1.91***	2.06***	208.51***	444.91***	127.02**	191.04***
ENV*ENTRY	160	2.80***	1.60***	2.23***	2.54***	1.67***	2.25***	1.94***	2.32***	266.44***	482.60***	244.35***	359.11***
GCA*ENV	16	6.89***	3.57***	1.69***	3.87***	0.68ns	1.49***	1.26***	1.97***	544.85***	696.21***	342.53***	318.06***
SCA*ENV	72	2.27***	1.66***	2.00***	2.91***	1.98***	2.47***	2.25***	2.47***	211.17***	501.37***	279.83***	273.41***
REC*ENV	72	2.41***	1.09***	2.57***	1.87***	1.58***	2.19***	1.78***	2.25***	259.84***	416.36***	187.05**	453.93***
MAT*ENV	16	0.89**	0.47**	1.23**	1.80***	1.04*	3.38***	1.30***	3.46***	547.97***	615.98***	195.16**	1208.27***
NMAT*ENV	56	2.85***	1.27***	2.95***	1.88***	1.74***	1.85***	1.91***	1.90***	177.52***	359.32***	184.73***	238.40***
R-Square		0.84	0.84	0.83	0.85	0.79	0.84	0.81	0.87	0.98	0.98	0.83	0.94
Coeff Var		35.07	22.64	32.61	23.13	28.69	30.39	21.56	28.04	5.68	5.11	7.96	6.89
Mean		1.72	1.58	1.83	1.64	2.15	1.82	1.87	1.73	86.80	92.82	100.49	92.17
GCASSS/Entry SS		9.48	8.28	9.42	4.57	10.80	5.46	7.72	3.77	24.31	11.99	5.68	11.14
SCASS/Entry SS		37.78	47.08	43.69	54.12	42.24	55.21	46.52	44.43	35.14	47.32	62.31	55.23
GCA:SCA Ratio		0.25	0.18	0.22	0.08	0.26	0.10	0.17	0.08	0.69	0.25	0.09	0.20
RecSS/EntrySS		52.56	44.62	46.90	41.31	46.90	39.33	45.57	51.67	40.54	40.69	32.01	33.63
MSS/RecSS		15.48	21.19	25.68	44.65	62.75	43.06	38.24	40.92	56.76	28.96	44.73	52.76
NMSS/RecSS		84.74	78.77	74.39	55.14	37.17	56.84	61.90	59.12	43.24	71.04	55.28	47.24

*significant at P<0.05 **significant at P<0.01 ***significant at P<0.001 ns-not significant

Table 5.7 Mean squares for genetic components of the F_3 rice populations 10 traits under four soil N and P conditions

		Top biomass (g)				Number of panicles (numbers)			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	194739.74***	84842.22***	64287.18***	166828.43***	996.91***	1936.83***	1795.74***	2193.90***
ENV	2	8707846.18***	2511914.87***	182265.29***	36628.77**	29120.06***	97939.23***	116826.67***	145061.99***
REP(ENV)	5	112775.22	471165.96	27279.26	122335.24	236.16	500.56	708.4	207.76
ENTRY	80	162002.11***	74443.14***	77580.45***	205312.50***	820.49***	983.89***	1038.13***	1111.052***
GCA	8	230902.75***	94415.05***	108800.72***	264997.29***	837.05***	973.99**	1592.21***	852.44**
SCA	36	111907.71***	61759.56***	57798.63***	157625.87***	649.90***	1055.55***	1345.17***	1191.03***
REC	36	196785.26***	82688.52***	90424.43***	239735.84***	987.40***	914.43***	607.97***	1088.54***
MAT	8	309508.04***	92534.94***	135979.00***	455364.26***	2285.49***	887.48***	979.66***	1294.67***
NMAT	28	164578.75***	79875.26***	77408.84***	178127.72***	616.52***	922.13***	501.77**	1029.65***
ENV*ENTRY	160	124137.21***	50415.76***	50906.98***	131640.34***	850.33***	1743.61***	1156.24***	1565.37***
GCA*ENV	16	146964.45***	66893.55***	67924.87***	169525.35***	1625.43***	1745.14***	1422.07***	776.71**
SCA*ENV	72	90843.80***	37081.22***	44963.03***	110788.65***	855.91***	1594.69***	1169.59***	1481.31***
REC*ENV	72	152357.90***	60088.57***	53069.17***	144073.15***	672.49***	1892.19***	1083.82***	1824.69***
MAT*ENV	16	249284.21***	75651.89***	52565.15***	248047.40***	808.19***	1177.38***	916.16***	458.99ns
NMAT*ENV	56	124664.66***	55641.90***	53213.17***	114366.22***	633.72***	2096.42***	1131.73***	2214.89***
R-Square		0.94	0.98	0.94	0.96	0.77	0.81	0.84	0.86
Coeff Var		7.57	2.95	4.16	4.76	27.06	32.92	30.87	30.73
Mean		1173.57	1176.88	1277.24	1352.27	38.2	52.73	42.16	51.01
GCASSS/Entry SS		14.25	12.68	14.02	12.91	10.20	9.90	15.34	7.67
SCASS/Entry SS		31.09	37.33	33.53	34.55	35.64	48.28	58.31	48.24
GCA:SCA Ratio		0.46	0.34	0.42	0.37	0.29	0.21	0.26	0.16
RecSS/EntrySS		54.66	49.98	52.45	52.54	54.15	41.82	26.35	44.09
MSS/RecSS		34.95	24.87	33.42	42.21	51.44	21.57	35.81	26.43
NMSS/RecSS		65.05	75.13	66.58	57.79	48.56	78.43	64.19	73.57

		1000 seed weight				Yield (kg ha^{-1})			
Source	DF	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
Model	247	25.12***	19.90***	23.09***	23.34***	1995500.70***	2327307.30***	2751787.30***	2109743.20***
ENV	2	1580.03***	753.22***	942.67***	439.38***	47455536.40***	47653651.50***	48424825.20***	3827731.40***
REP(ENV)	5	4.44	1.3	62.65	54	591258.9	1391201.8	2117761.9	191115.7
ENTRY	80	19.69***	18.46***	18.33***	24.81***	1767165.90***	1947789.40***	2265988.40***	2511645.00***
GCA	8	53.22***	23.80***	18.046***	13.84***	2977058.39***	2101797.90***	1778416.25***	4505407.98***
SCA	36	18.21***	20.92***	12.77***	28.39***	1265776.41***	1625602.38***	2897804.43***	2137500.49***
REC	36	13.72***	14.81***	23.95***	23.68***	1999690.31***	2235752.22***	2367274.81***	2442731.00***
MAT	8	9.96**	19.58***	27.62***	37.69***	1724168.50***	3101934.30***	3352648.07***	4028447.58***
NMAT	28	14.79***	13.45***	22.91***	19.67***	2078410.83***	1988271.63***	2085739.6***	1989669.13***
ENV*ENTRY	160	11.89***	12.88***	14.87***	15.51***	1708244.30***	2175349.90***	2409310.30***	1758315.10***
GCA*ENV	16	15.06***	17.70***	13.01**	15.57***	1632403.97***	2049725.54***	4453575.34***	2439898.89***
SCA*ENV	72	11.69***	12.98***	16.36***	18.20***	2322491.79***	2298713.18***	2006764.74***	1440128.59***
REC*ENV	72	11.38***	11.70***	13.79***	12.81***	1110850.11***	2079903.15***	2357574.72***	1925038.64***
MAT*ENV	16	8.16*	10.44***	22.16***	25.78***	1259639.92**	1575123.34***	3233555.90***	3473628.56***
NMAT*ENV	56	12.29***	12.07***	11.39***	9.11***	1068338.74***	2224125.95***	2107294.39***	1482584.38***
R-Square		0.82	0.87	0.78	0.85	0.76	0.85	0.86	0.88
Coeff Var		7.2	5	7.52	5.87	17.03	11.97	13.16	10.59
Mean		27.41	28.01	28.31	28.2	3900.66	4500.23	4181.32	4130.79
GCASSS/Entry SS		27.03	12.89	9.85	5.58	16.85	10.79	7.85	17.94
SCASS/Entry SS		41.62	51.00	31.35	51.49	32.23	37.56	57.55	38.30
GCA:SCA Ratio		0.65	0.25	0.31	0.11	0.52	0.29	0.14	0.47
RecSS/EntrySS		31.36	36.10	58.80	42.95	50.92	51.65	47.01	43.77
MSS/RecSS		16.13	29.38	25.63	35.37	19.16	30.83	31.47	36.65
NMSS/RecSS		83.84	70.64	74.40	64.61	80.84	69.17	68.53	63.35

*significant at P<0.05 **significant at P<0.01 ***significant at P<0.001 ns-not significant

Table 5.8 General combining ability effects for nine rice parents for ten traits under four soil N and P conditions

	Days to heading (days)				Days to anthesis (days)				Days to maturity (day)				Phosphorous tolerance (scale)				Nitrogen tolerance (scale)			
Source	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
#G1	-3.32***	-2.38**	-3.78***	-2.83***	-3.10***	-2.16**	-3.77***	- 3.02***	-1.61**	-1.42*	-2.97***	-2.98***	0.13ns	-0.11ns	-0.03ns	-0.03ns	0.069ns	0.03ns	0.08ns	0.103ns
G2	1.84**	0.36ns	-0.10ns	0.01ns	1.75**	0.39ns	-0.10ns	-0.20ns	-0.88ns	-0.77ns	0.64ns	0.97ns	-0.24*	-0.24**	-0.17ns	-0.06ns	-0.19*	-0.07ns	-0.24*	-0.06ns
G3	0.12ns	2.49**	1.26ns	2.54***	0.05ns	2.39**	1.26ns	2.10**	-0.56ns	1.11ns	0.48ns	0.93ns	0.08ns	-0.03ns	-0.16ns	-0.06ns	-0.16ns	-0.05ns	0.07ns	0.08ns
G4	0.82ns	1.35ns	1.49*	0.24ns	0.57ns	0.92ns	1.46*	0.86ns	1.72**	0.42ns	0.03ns	-1.06ns	0.03ns	0.07ns	0.015ns	0.05ns	-0.12ns	0.005ns	-0.04ns	-0.086ns
G5	0.10ns	0.40ns	0.58ns	0.75ns	0.04ns	0.38ns	0.72ns	0.89ns	-0.06ns	0.66ns	1.10*	0.56ns	-0.25*	-0.13ns	-0.19*	-0.16ns	-0.15ns	0.04ns	0.03ns	0.114ns
G6	0.44ns	0.68ns	1.37*	1.36ns	0.76ns	0.68ns	1.24ns	1.32ns	0.63ns	1.03ns	-0.36ns	1.40*	-0.04ns	0.05ns	0.004ns	0.01ns	0.36***	0.24*	0.20*	-0.11ns
G7	-2.59***	-2.04*	-1.25ns	-1.09ns	-2.57***	-2.19**	-0.90ns	-0.59ns	0.12ns	0.22ns	0.38ns	-0.14ns	0.03ns	0.14ns	-0.03ns	0.24ns	0.11ns	0.09ns	0.10ns	0.11ns
G8	1.45*	0.46ns	1.36*	0.38ns	1.36*	0.67ns	1.07ns	0.52ns	0.78ns	0.64ns	0.38ns	0.99ns	-0.007ns	0.014ns	0.23**	0.01ns	0.01ns	-0.16ns	-0.20*	-0.098ns
G9	1.15ns	-1.32ns	-0.93ns	-1.36ns	1.14ns	-1.07ns	-0.98ns	-1.89*	-0.14ns	-1.89**	0.33ns	-0.67ns	0.28**	0.25**	0.34ns	0.013ns	0.07ns	-0.12ns	-0.005ns	-0.05ns

Traits	Plant height (cm)				Top biomass (g)				Number of panicles (numbers)				1000 seed weight (g)				Yield (kg ha^{-1})			
	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+	N-P-	N-P+	N+P-	N+P+
G1	-6.64*	-0.62ns	-2.07ns	-2.77ns	-20.12ns	-26.89ns	-37.91**	-9.19ns	0.45ns	2.76ns	9.76**	6.17*	-0.66*	0.08ns	0.26ns	0.25ns	-62.81ns	-217.76*	163.64ns	160.67*
G2	1.99ns	-1.47ns	1.53ns	4.26*	-12.27ns	-13.86ns	-2.39ns	-26.50ns	1.13ns	0.10ns	-1.07ns	-0.001ns	0.42ns	0.11ns	-0.07ns	0.21ns	-133.43ns	26.52ns	79.24ns	339.58***
G3	4.80ns	2.02ns	0.01ns	1.78ns	-34.47ns	-11.84ns	-11.29ns	-41.24*	2.39ns	-6.20**	-5.41ns	-2.80ns	-1.37***	-0.97***	-0.87**	-0.68**	108.88ns	140.92ns	216.40*	-18.11ns
G4	3.19ns	5.41ns	0.42ns	-0.17ns	106.27***	75.67***	78.26***	120.35***	-0.65ns	-3.77ns	2.24ns	3.49ns	0.27ns	-0.31ns	0.11ns	0.041ns	137.96ns	-38.93ns	57.42ns	196.24*
G5	-0.11ns	-2.54ns	1.79ns	-0.08ns	26.01ns	4.18ns	0.75ns	41.14*	1.74ns	0.75ns	-2.36ns	-2.42ns	-0.02ns	-0.12ns	-0.19ns	-0.19ns	380.22***	142.89ns	-24.65ns	-36.55ns
G6	-1.29ns	1.94ns	-0.88ns	-2.47ns	-56.47*	-21.16ns	-9.79ns	-51.10*	-3.24ns	3.63ns	-2.14ns	-0.23ns	1.17***	0.97***	0.30ns	0.61*	2.37ns	171.20ns	-26.53ns	-55.53ns
G7	-0.48ns	-1.27ns	-0.63ns	-1.83ns	-51.79*	-12.40ns	-5.26ns	-45.63*	4.99*	1.76ns	0.09ns	-2.92ns	0.08ns	0.05ns	0.34ns	-0.39ns	-110.03ns	88.67ns	-177.78ns	-332.75***
G8	-2.44ns	-3.08ns	0.78ns	-0.44ns	24.67ns	25.21ns	23.62ns	13.96ns	-5.01*	-1.63ns	-0.81ns	-1.75ns	0.68*	0.32ns	0.57ns	0.30ns	-200.96*	-229.57*	-161.02ns	64.56ns
G9	0.99ns	-0.40ns	-0.96ns	1.73ns	18.17ns	-18.92ns	-35.99**	-1.78ns	-1.81ns	2.60ns	-0.30ns	0.48ns	-0.58ns	-0.12ns	-0.44ns	-0.15ns	-122.19ns	-83.93ns	-126.72ns	-318.12***

*significant at P<0.05	#G1-NERICA 1	G5-CT16333(1)-CA-22-M	G9-CT16317-CA-4-M
**significant at P<0.01	G2-Duorado	G6-CT16333(2)-CA-18-M	
***significant at P<0.001	G3-IR79913-176-B-4	G7-CT16313-CA-19-M	
ns-not significant	G4-CT16333(1)-CA-20-M	G8-WAB964-B-3A 1.2	

5.4.6 The mean values for five traits for the ten best F_3 rice populations under four soil N and P conditions

The performance of genotypes for phosphorous tolerance was varied and lines 7 (NERICA1 x CT16313-CA-19-M), 8 (NERICA1 x WAB964-B-3A1.2), 10 (Dourado), 16 (Dourado x CT16313-CA-19-M) and 21 (IR79913-B-176-B-4 x Dourado) appeared twice among the best lines regardless of their ranking (Table 5.9). Line 3 (NERICA1 x IR79913-B-176-B-4), 7, and 31 (CT16333(1)-CA-20-M x IR79913-B-176-B-4) appeared at least twice for best nitrogen tolerant lines. The top biomass line performance was varied but some lines showed some consistency in at least two soil N and P conditions like lines; 35 (CT16333(1)-CA-20-M x WAB964-B-3A1.2), 36 (CT16333(1)-CA-20-M x CT16317-CA-4-M), 29 (CT16333(1)-CA-20-M x NERICA 1), 21 (IR79913-B-176-B-4 x Dourado), 17 (Dourado x WAB964-B-3A1.2) and 28 (CT16333(1)-CA-20-M). Grain yield had no consistent line performance, although lines 43 (CT16333(1)-CA-22-M x CT16313-CA-19-M), 28 (CT16333(1)-CA-20-M), 39 (CT16333(1)-CA-22-M x Dourado), 33 (CT16333(1)-CA-20-M x CT16333(2)-CA-18-M) did appear at least twice among the best ten irrespective of individual ranking.

Table 5.9 Mean values for the ten best rice genotypes for five traits under four soil N and P conditions

	Phosphorous tolerance (1-5 scale)							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	3	1.0	2	1.0	4	1.0	5	1.0
	5	1.0	4	1.0	8	1.0	7	1.0
	7	1.0	7	1.0	13	1.0	8	1.0
	8	1.0	8	1.0	17	1.0	9	1.0
	10	1.0	13	1.0	21	1.0	10	1.0
	13	1.0	15	1.0	31	1.0	16	1.0
	15	1.0	17	1.0	36	1.0	17	1.0
	16	1.0	19	1.0	37	1.0	31	1.0
	17	1.0	21	1.0	43	1.0	33	1.0
	31	1.0	33	1.0	52	1.0	34	1.0
Mean		1.7		1.6		1.8		1.6

	Nitrogen tolerance (1-5 scale)							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	3	1.25	3	1.0	16	1.0	4	1.0
	7	1.25	7	1.0	26	1.0	6	1.0
	13	1.25	8	1.0	77	1.0	8	1.0
	25	1.25	18	1.0	8	1.2	16	1.0
	31	1.3	31	1.0	44	1.2	31	1.0
	68	1.3	35	1.0	2	1.3	36	1.0
	4	1.5	37	1.0	12	1.3	39	1.0
	8	1.5	63	1.0	14	1.3	45	1.0
	10	1.5	64	1.0	18	1.3	46	1.0
	12	1.5	65	1.0	35	1.3	49	1.0
Mean		2.2		1.8		1.9		1.7

	Grain yield (kg ha^{-1})							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	32	5292.3	6	5226.9	28	5289.9	39	5204.2
	28	4878.7	8	5217.3	37	5240.9	11	5106.5
	25	4798.3	46	5216.3	80	5064.1	33	5102.2
	31	4739.6	3	5182.5	5	5037.7	64	5087.7
	39	4723.6	7	5180.5	19	5028.5	5	5043.2
	78	4685.7	80	5167.8	33	4981.0	6	5027.2
	6	4670.7	36	5140.1	18	4977.6	38	5001.9
	71	4663.6	55	5133.1	6	4965.8	4	4991.6
	43	4610.6	43	5123.6	12	4925.7	31	4977.6
	49	4520.6	67	5087.2	39	4917.0	34	4926.9
Mean		3900.7		4500.2		4181.3		4130.8

	Top biomass (g)							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	36	1884.2	35	1643.6	35	1770.5	36	2252.4
	38	1708.9	28	1332.9	28	1475.5	38	2047.8
	35	1633.4	39	1331.9	10	1446.4	35	1820.2
	29	1321.3	40	1329.9	39	1443.2	29	1569.8
	23	1268.0	38	1318.4	40	1443.1	21	1551.4
	21	1263.1	34	1312.8	38	1432.7	42	1504.0
	25	1258.9	9	1295.6	4	1414.2	39	1492.4
	9	1249.2	21	1294.3	34	1413.3	23	1490.7
	70	1248.6	17	1291.3	17	1407.1	34	1470.1
	39	1244.0	4	1286.2	9	1402.8	41	1469.1
Mean		1173.6		1176.9		1277.2		1352.3

	Days to maturity (days)							
	lines	N-P-	lines	N-P+	lines	N+P-	lines	N+P+
	1	123.8	18	121.8	7	121.3	6	122.3
	21	123.8	8	122.0	9	121.5	77	122.8
	19	126.0	7	122.5	5	121.8	4	123.1
	60	126.2	9	122.5	8	122.0	8	123.2
	12	126.4	77	122.5	77	122.3	60	123.3
	11	126.6	60	123.5	61	122.3	7	124.5
	6	126.8	5	123.8	4	124.0	9	124.8
	2	127.0	4	123.9	20	124.8	11	125.3
	20	127.1	75	124.0	11	125.3	34	125.3
	61	127.1	6	124.2	1	125.5	5	126.0
Mean		131.6		130.1		129.7		132.4

5.4.7 The physiological factors for low soil P and N tolerance for parents and F_3 generations

The physiological indices used to measure genotypes for nutrient tolerance or efficiency according to Fischer and Maurer (1978) and Ouk et al. (2006) were used and therefore, are explained. The low soil fertility intensity index (LSFII) is calculated as 1- $\frac{\bar{x}lf}{\bar{x}hf}$ where $\bar{x}$ is mean of all genotypes under lf (low fertility) and hf (high fertility). The lower values are associated with high tolerance. The low susceptibility index (LFSI) = $\frac{\bar{x}g}{LSFII}$, where $\bar{x}g$ is the mean of genotype. The harvest index = grain yield (at 11% moisture content(mc))/Biomass (at 11% mc) (Singh et al., 2003).

Agronomic N-use efficiency (ANUE) = $\frac{yield\ under\ nutrient\ use - yield\ under\ no\ nutrient\ use}{Amount\ of\ nutrient\ applied}$

The agronomic efficiency measures increment of yield per unit of applied nutrient (Ohnishi et al., 1999).

The partial factor productivity for applied nutrient (PFP) = $\frac{yield\ under\ nutrient\ use}{nutrient\ applied}$.

Grain yield efficiency index (GYEI) =

$$\frac{yield\ under\ no\ nutrient * yield\ under\ nutrient\ use}{experimental\ mean\ under\ no\ nutrient\ use * experimental\ mean\ under\ nutrient\ use}$$

The line 80 (CT16317-CA-4-M) x (CT16313-CA-19-M) had the lowest and negative value for low soil fertility intensity index (LSFII) of -0.73, while line 9 (NERICA 1x CT16317-CA-4-M) had the highest index of 0.40 for nitrogen (Table 5.10). For phosphorous nutrient, line 80 had the lowest value (-0.70), while line 35 had the highest value of 0.49 under phosphorous condition. The low fertility susceptibility index (LFSI) for nitrogen had the highest value for line 77 (13.03), however line 4 had the lowest value (-10.11). For phosphorous condition, the highest value was for line 5 (8.79) and lowest value for line 79 (-0.77). The highest harvest index (HI) was obtained from line 6, while the lowest HI was for line 9 under nitrogen condition.

Table 5.10 Physiological efficiency indices for the 72 rice F_3 and parents across two mega-environments

No.	Parents and F_3s'			LSFII-N	LSFII-P	LSFI-N	LSFI-P	HI-N	HI-P	ANUE-N	ANUE-P	PFP-N	PFP-P	GYEI-N	GYEI-P
1	NERICA 1	x	NERICA 1	0.13	-0.27	-0.52	-0.04	0.34	0.46	5.02	-15.61	48.85	50.14	0.56	0.88
2	NERICA 1	x	Dourado	0.03	-0.04	-2.06	-0.27	0.59	0.56	1.56	-2.58	49.47	69.28	0.96	1.11
3	NERICA 1	x	IR79913-B-176-B-4	-0.18	0.07	0.37	0.15	0.56	0.41	-8.86	4.79	45.53	86.38	1.22	1.04
4	NERICA 1	x	CT16333(1)-CA-20-M	0.01	0.14	-10.11	0.07	0.46	0.36	0.37	11.72	47.65	82.64	1.33	1.24
5	NERICA 1	x	CT16333(1)-CA-22-M	0.05	0.00	-1.41	8.79	0.51	0.54	2.68	0.09	55.97	80.03	1.30	1.47
6	NERICA 1	x	CT16333(2)-CA-18-M	-0.04	0.01	1.70	0.79	0.62	0.53	-2.22	1.02	55.18	87.11	1.41	1.45
7	NERICA 1	x	CT16313-CA-19-M	-0.23	0.00	0.29	2.78	0.54	0.40	-10.82	0.24	46.58	86.34	1.17	1.02
8	NERICA 1	x	WAB964-B-3A1.2	-0.31	-0.23	0.22	-0.04	0.53	0.47	-13.82	-15.40	54.42	86.96	1.12	1.13
9	NERICA 1	x	CT16317-CA-4-M	0.40	0.10	-0.17	0.09	0.26	0.37	21.34	8.19	47.47	47.38	0.73	1.18
10	Dourado	x	Dourado	0.02	0.14	-4.19	0.07	0.43	0.32	0.81	10.89	43.21	74.49	1.09	1.02
11	Dourado	x	NERICA 1	0.10	0.27	-0.66	0.04	0.46	0.34	5.80	23.32	41.19	76.41	1.26	1.10
12	Dourado	x	IR79913-B-176-B-4	-0.07	-0.07	1.00	-0.13	0.53	0.47	-3.44	-5.57	54.73	81.68	1.21	1.31
13	Dourado	x	CT16333(1)-CA-20-M	0.16	0.01	-0.43	0.72	0.40	0.43	8.53	1.10	53.96	69.25	1.10	1.38
14	Dourado	x	CT16333(1)-CA-22-M	0.09	0.16	-0.73	0.06	0.52	0.41	4.97	12.87	45.42	73.54	1.15	1.15
15	Dourado	x	CT16333(2)-CA-18-M	0.06	0.22	-1.06	0.04	0.50	0.37	3.36	17.60	41.15	74.29	1.14	1.02
16	Dourado	x	CT16313-CA-19-M	-0.06	0.06	1.15	0.15	0.53	0.40	-3.06	4.96	48.88	82.87	1.26	1.20
17	Dourado	x	WAB964-B-3A1.2	0.10	0.13	-0.65	0.08	0.38	0.34	5.25	9.64	44.17	68.03	1.00	1.05
18	Dourado	x	CT16317-CA-4-M	0.02	-0.02	-3.16	-0.42	0.51	0.45	1.15	-1.84	55.31	79.39	1.25	1.40
19	IR79913-B-176-B-4	x	IR79913-B176-B-6	-0.20	-0.28	0.33	-0.03	0.50	0.49	-8.84	-18.44	55.87	78.64	1.00	1.14
20	IR79913-B-176-B-4	x	NERICA 1	0.03	0.03	-2.65	0.29	0.45	0.37	1.21	2.38	45.98	69.54	0.96	1.03
21	IR79913-B-176-B-4	x	Dourado	0.13	0.08	-0.54	0.12	0.39	0.38	6.68	6.52	49.08	70.12	1.09	1.23
22	IR79913-B-176-B-4	x	CT16333(1)-CA-20-M	0.04	0.11	-1.69	0.09	0.44	0.35	1.77	7.11	39.63	63.91	0.82	0.82
23	IR79913-B-176-B-4	x	CT16333(1)-CA-22-M	-0.26	0.02	0.26	0.54	0.46	0.34	-11.04	1.13	41.36	79.74	0.98	0.82
24	IR79913-B-176-B-4	x	CT16333(2)-CA-18-M	-0.36	-0.50	0.19	-0.02	0.43	0.42	-11.83	-24.83	49.68	67.44	0.65	0.77
25	IR79913-B-176-B-4	x	CT16313-CA-19-M	-0.04	0.27	1.56	0.04	0.42	0.27	-1.96	18.69	33.04	71.19	0.94	0.70
26	IR79913-B-176-B-4	x	WAB964-B-3A1.2	0.10	-0.01	-0.69	-0.65	0.41	0.41	4.55	-1.02	47.09	62.78	0.85	1.02
27	IR79913-B-176-B-4	x	CT16317-CA-4-M	-0.33	-0.17	0.20	-0.06	0.46	0.36	-12.49	-9.63	43.75	74.73	0.81	0.77
28	CT16333(1)-CA-20-M	x	CT16333(1)-CA-20-M	0.13	-0.24	-0.53	-0.04	0.33	0.43	6.06	-17.10	58.78	61.97	0.85	1.31
29	CT16333(1)-CA-20-M	x	NERICA 1	0.05	-0.11	-1.48	-0.09	0.37	0.39	2.05	-7.62	50.15	64.52	0.84	1.06
30	CT16333(1)-CA-20-M	x	Dourado	-0.40	-0.59	0.17	-0.02	0.42	0.42	-11.99	-26.63	47.86	63.15	0.55	0.68
31	CT16333(1)-CA-20-M	x	IR79913-B-176-B-4	-0.02	0.02	4.05	0.43	0.54	0.48	-0.92	1.85	54.07	84.34	1.36	1.40
32	CT16333(1)-CA-20-M	x	CT16333(1)-CA-22-M	0.13	0.22	-0.50	0.04	0.43	0.35	7.25	17.57	42.07	69.79	1.09	1.06
33	CT16333(1)-CA-20-M	x	CT16333(2)-CA-18-M	0.03	0.02	-2.04	0.40	0.46	0.43	1.88	2.02	55.34	82.22	1.35	1.47
34	CT16333(1)-CA-20-M	x	CT16313-CA-19-M	0.13	0.25	-0.52	0.04	0.39	0.31	7.10	20.41	41.14	71.46	1.14	1.06
35	CT16333(1)-CA-20-M	x	WAB964-B-3A1.2	-0.11	0.49	0.59	0.02	0.36	0.15	-5.61	35.65	25.16	81.80	1.16	0.58
36	CT16333(1)-CA-20-M	x	CT16317-CA-4-M	-0.06	0.08	1.12	0.12	0.54	0.42	-3.25	6.53	49.50	85.67	1.34	1.25
37	CT16333(1)-CA-22-M	x	CT16333(1)-CA-22-M	-0.07	-0.31	1.02	-0.03	0.48	0.51	-2.93	-20.58	58.23	71.16	0.92	1.22
38	CT16333(1)-CA-22-M	x	NERICA 1	-0.01	0.10	5.46	0.10	0.46	0.38	-0.68	7.97	50.26	84.39	1.36	1.31
39	CT16333(1)-CA-22-M	x	Dourado	0.08	0.06	-0.80	0.17	0.43	0.41	4.85	4.79	54.63	79.46	1.33	1.48
40	CT16333(1)-CA-22-M	x	IR79913-B-176-B-4	-0.04	0.03	1.85	0.35	0.43	0.37	-1.86	2.11	49.66	79.38	1.18	1.19

No.	Parents and F_3s'			LSFII-N	LSFII-P	LSFI-N	LSFI-P	HI-N	HI-P	ANUE-N	ANUE-P	PFP-N	PFP-P	GYEI-N	GYEI-P
41	CT16333(1)-CA-22-M	x	CT16333(1)-CA-20-M	0.08	0.24	-0.88	0.04	0.38	0.28	3.51	16.54	34.55	63.12	0.84	0.74
42	CT16333(1)-CA-22-M	x	CT16333(2)-CA-18-M	-0.26	-0.09	0.26	-0.11	0.51	0.39	-11.41	-5.67	47.55	82.77	1.05	0.98
43	CT16333(1)-CA-22-M	x	CT16313-CA-19-M	-0.67	-0.17	0.10	-0.06	0.54	0.34	-22.78	-8.64	39.91	85.39	0.85	0.64
44	CT16333(1)-CA-22-M	x	WAB964-B-3A1.2	0.07	0.07	-0.94	0.14	0.44	0.39	3.54	5.24	46.08	69.03	0.99	1.07
45	CT16333(1)-CA-22-M	x	CT16317-CA-4-M	-0.71	-0.08	0.09	-0.12	0.55	0.30	-22.53	-3.73	34.26	81.45	0.75	0.51
46	CT16333(2)-CA-18-M	x	CT16333(2)-CA-18-M	-0.15	-0.05	0.44	-0.19	0.54	0.44	-7.77	-3.76	52.70	86.94	1.27	1.24
47	CT16333(2)-CA-18-M	x	NERICA 1	-0.29	-0.10	0.23	-0.10	0.51	0.39	-12.45	-6.37	46.86	82.60	1.02	0.94
48	CT16333(2)-CA-18-M	x	Dourado	0.08	0.03	-0.82	0.36	0.46	0.43	4.41	2.16	52.46	74.24	1.16	1.33
49	CT16333(2)-CA-18-M	x	IR79913-B-176-B-4	-0.05	0.18	1.32	0.05	0.52	0.35	-2.44	13.10	39.17	75.50	1.05	0.88
50	CT16333(2)-CA-18-M	x	CT16333(1)-CA-20-M	-0.33	0.37	0.21	0.03	0.44	0.19	-12.15	20.44	23.54	73.98	0.80	0.41
51	CT16333(2)-CA-18-M	x	CT16333(1)-CA-22-M	-0.32	0.02	0.21	0.42	0.54	0.37	-13.19	1.41	40.68	82.22	0.99	0.79
52	CT16333(2)-CA-18-M	x	CT16313-CA-19-M	-0.19	0.02	0.35	0.61	0.51	0.37	-8.77	1.08	45.48	82.46	1.11	0.99
53	CT16333(2)-CA-18-M	x	WAB964-B-3A1.2	-0.28	0.21	0.24	0.05	0.51	0.28	-12.18	13.23	34.08	82.62	1.03	0.69
54	CT16333(2)-CA-18-M	x	CT16317-CA-4-M	0.12	-0.07	-0.57	-0.13	0.36	0.39	5.15	-4.84	46.70	57.48	0.73	0.95
55	CT16313-CA-19-M		CT16313-CA-19-M	-0.20	0.00	0.34	2.00	0.52	0.39	-9.40	0.34	47.40	85.55	1.18	1.06
56	CT16313-CA-19-M	x	NERICA 1	-0.15	-0.53	0.45	-0.02	0.35	0.41	-4.25	-22.43	43.21	48.76	0.40	0.57
57	CT16313-CA-19-M	x	Dourado	-0.33	0.13	0.20	0.08	0.47	0.28	-10.60	6.03	27.71	63.50	0.59	0.41
58	CT16313-CA-19-M	x	IR79913-B-176-B-4	-0.07	-0.02	0.96	-0.63	0.47	0.41	-3.43	-1.13	49.92	78.90	1.13	1.15
59	CT16313-CA-19-M	x	CT16333(1)-CA-20-M	-0.10	-0.05	0.64	-0.18	0.56	0.47	-5.19	-4.03	52.24	82.11	1.18	1.21
60	CT16313-CA-19-M	x	CT16333(1)-CA-22-M	0.02	-0.01	-2.81	-0.67	0.36	0.34	0.97	-0.88	41.13	59.36	0.70	0.78
61	CT16313-CA-19-M	x	CT16333(2)-CA-18-M	-0.41	-0.12	0.16	-0.08	0.47	0.33	-14.55	-6.57	39.92	75.14	0.78	0.67
62	CT16313-CA-19-M	x	WAB964-B-3A1.2	-0.27	0.08	0.25	0.11	0.44	0.28	-9.82	4.55	33.10	68.93	0.72	0.56
63	CT16313-CA-19-M	x	CT16317-CA-4-M	-0.65	-0.64	0.10	-0.02	0.48	0.42	-20.51	-29.91	51.32	77.85	0.71	0.76
64	WAB964-B-3A1.2		WAB964-B-3A1.2	0.22	0.05	-0.31	0.19	0.41	0.44	12.33	4.36	53.62	66.31	1.09	1.42
65	WAB964-B-3A1.2	x	NERICA 1	0.25	0.05	-0.27	0.18	0.36	0.41	13.10	4.27	49.02	58.15	0.88	1.19
66	WAB964-B-3A1.2	x	Dourado	-0.26	-0.08	0.26	-0.12	0.48	0.37	-10.88	-4.82	44.43	78.15	0.94	0.86
67	WAB964-B-3A1.2	x	IR79913-B-176-B-4	-0.35	-0.10	0.19	-0.09	0.55	0.40	-14.71	-6.54	46.18	84.79	1.03	0.91
68	WAB964-B-3A1.2	x	CT16333(1)-CA-20-M	-0.12	0.07	0.56	0.14	0.47	0.36	-5.35	4.64	41.39	74.74	0.97	0.86
69	WAB964-B-3A1.2	x	CT16333(1)-CA-22-M	-0.27	-0.18	0.25	-0.05	0.50	0.42	-10.83	-10.96	48.09	77.43	0.92	0.92
70	WAB964-B-3A1.2	x	CT16333(2)-CA-18-M	0.31	-0.03	-0.22	-0.32	0.30	0.41	14.66	-2.11	48.81	49.11	0.68	1.09
71	WAB964-B-3A1.2	x	WAB964-B-3A1.2	0.08	0.16	-0.85	0.06	0.42	0.34	3.97	12.25	42.19	69.58	1.02	1.00
72	WAB964-B-3A1.2	x	CT16317-CA-4-M	0.13	0.07	-0.51	0.13	0.42	0.40	6.11	5.03	42.73	59.96	0.80	0.92
73	CT16317-CA-4-M		CT16317-CA-4-M	-0.31	-0.10	0.22	-0.09	0.50	0.43	-12.93	-6.40	46.05	82.07	1.00	0.90
74	CT16317-CA-4-M	x	NERICA 1	-0.01	0.21	5.57	0.05	0.39	0.27	-0.49	12.71	32.07	61.56	0.73	0.61
75	CT16317-CA-4-M	x	Dourado	-0.06	0.08	1.05	0.13	0.53	0.45	-3.16	5.64	45.61	78.79	1.13	1.06
76	CT16317-CA-4-M	x	IR79913-B-176-B-4	-0.30	-0.21	0.23	-0.05	0.49	0.44	-11.72	-12.55	47.77	76.69	0.88	0.88
77	CT16317-CA-4-M	x	CT16333(1)-CA-20-M	-0.01	-0.14	13.03	-0.07	0.39	0.41	-0.22	-8.88	48.01	63.46	0.78	0.95
78	CT16317-CA-4-M	x	CT16333(1)-CA-22-M	-0.31	0.38	0.22	0.03	0.49	0.22	-12.26	22.48	24.75	77.99	0.90	0.46
79	CT16317-CA-4-M	x	CT16333(2)-CA-18-M	-0.14	-0.01	0.47	-0.77	0.50	0.40	-6.70	-0.88	47.14	79.89	1.08	1.03
80	CT16317-CA-4-M	x	CT16313-CA-19-M	-0.73	-0.70	0.09	-0.01	0.54	0.50	-24.30	-34.73	56.27	86.13	0.83	0.87
81	CT16317-CA-4-M	x	WAB964-B-3A1.2	0.18	0.13	-0.38	0.07	0.39	0.38	9.01	9.86	44.07	62.45	0.92	1.05
	LSFII_Low soil fertility intensity index; LFSI_Low fertility susceptibility index; HI_Harvest index;														
	ANUE_ Agronomic N-use efficiency; PFP_Partial factor productivity for applied N or P; GYEI_Grain yield efficiency index														

The lowest harvest index under phosphorous condition was obtained from line 35 (0.15), while line 2 (0.56) had the highest value. Agronomic nutrient use efficiency highest value was obtained from line 9 (21.34), but the lowest value was obtained from line 80 (-24.30) for nitrogen nutrient. For the phosphorous condition, the highest and lowest values were for line 35 (35.65) and line 80 (-34.73). The partial factor productivity index (PFP) had the highest values in line 28 (58.78) and the lowest value for line 50 (23.54) for nitrogen fertilization, while under phosphorous condition line 9 (47.38) had the lowest PFP and line 6 gave the highest value of 87.11. The line 56 (0.40) had the lowest grain yield efficiency index but line 6 had the highest value of 1.41 for nitrogen condition. For phosphorous, the highest value was obtained from line 39 (1.48) and the lowest was from line 50 with a GYEI of 0.41.

5.5 Discussion

5.5.1 Gene action for the F_2 and F_3 populations for the traits under four soil N and P environments

The significance of environment, GCA, SCA, reciprocal, maternal and nonmaternal mean squares indicate that there were differences in the way the environment influenced the performance of genotypes. The genotypes were found to rank differently in different soil N and P conditions, meaning specific rather than broad adaptation occurred. This implies breeding should be geared towards development of varieties with specific adaptation to given soil N and P conditions. According to Andrzej *et al*. (2011). The significance of genotype by environments had implication that the best genotype under one environment were not necessary the best in another environment. The significant of GCA, SCA, reciprocal, maternal and nonmaternal mean squares is an indication of significant genetic control in inheritance of the traits over and above the environmental contribution. This implies there is adequate genetic variability that can be exploited for variety development. However, the low GCA:SCA ratio (less than 1.0) for the traits under most of the soil N and P condition has implications in rice variety development. The magnitude of SCA was more important that the contribution of the heritable effects, implying that the desirable additive effects were low compared to nonheritable nonadditive genetic effects (Peyman *et al.*, 2009). This further implies that the environmental effects had a bigger role than additive effects contribution to inheritance of the traits. The cases where the GCA:SCA ratio was more than one, the environmental influence was less and additive effects were playing big role in traits inheritance, hence selection can lead to breeding of superior cultivars (Andrzej *et al.*, 2011). The preponderance of the GCA effects over the SCA imply that selection by exploiting additive effects can lead to development of desirable varieties, since environment effects influencing the trait were low. The partitioning of SCA into maternal and nonmaternal effects revealed that the proportion of nonmaternal effects was higher in magnitude than the maternal effects, and this was more pronounced in F_3 populations. This has serious implication, given that the magnitude of reciprocal effects was generally greater than GCA. Since progress cannot be highly achieved by exploiting additive effects, the breeding programmes could have to turn to hybrid development in order to exploit the large nonadditive genetic effects. This is if other studies with different parents find similar results. Other with the present parents, the hybrid varieties seem to be the way to go. This could

mean that issues of hybrid seed and how to produce it could have to be addressed given that China and many other Asian countries have embraced hybrid rice production with yield nearing the 10 t ha^{-1} (Virmani *et al.*, 2003).

The Maternal effects in this study were found to be significant and they are known to contribute substantially to the phenotype of an individual as explained by Deborah (1987). The influence though mainly is maternal, paternal effects do also occur and probably this accounted for the large nonmaternal effects observed here. The fact that reciprocal pairs do have similar nuclear genetic contributions, any difference in performance of reciprocal pairs is then due to maternal or in some cases paternal effects. This means that the selection of female or male during hybridization is important. Genetic studies done elsewhere, have also demonstrated various types of maternal effects on traits like mineral composition of seeds, seed oil in *Lupinus*, fatty acid content in maize, and protein content in dry beans and soybeans (Deborah, 1987). However, in some cases these differences do not persevere beyond the second filial generation, pointing that in these instances they are noncytoplasmic maternal effects. In this study, differences between reciprocal crosses were influenced probably by the environment. This indicates that some parents used as females were better adapted to exploit the prevailing experimental environment than others. It is reported that some of the maternal parents may actually have more influence than the male parent on the progeny phenotype. In some extreme cases, the maternal phenotype can for some traits have greater influence than the offspring, on the offspring's own phenotype (Deborah, 1987). The fact that the parents have the same cytoplasm and thus there should not be reciprocal differences does not hold as mtDNA differences have been observed (Deborah, 1987). The materials under study being F_2 and F_3 progenies were heterozygous and still segregating thus may have contributed to maternal effects. Melchinger et al. (1986) has observed maternal effects due to heterozygosity in seed parent for grain and forage yield in maize. The great variability shown in the materials in terms of genetic components and highly significant values of GCA effects, proves that improvement of traits such as adaptation to low soil fertility, desired maturity period, 1000 seed weight and yield can be accomplished. This is because these traits are heritable and thus can be passed on from parents with high GCA effects and even those displaying positive SCA effects by recurrent selection to fix them.

5.5.2 The general combining ability (GCA) for the ten traits for F_2 and F_3 populations under different soil N and P conditions

The parental GCA effects were varied under the different soil N and P conditions and that NERICA1 (G1) was a good general combiner for earliness. Thus it can be used in a breeding programme where earliness is a priority. Parent G8 (G8-WAB964-B-3A 1.2) can be used to improve a 1000 seed weight, while parent G4 (G4-CT16333(1)-CA-20-M) can be used to breed for higher top biomass preferred by farmers. Parent G6 may also be used to breed for higher 1000 seed weight (Tables 5.3 and 5.8). The breeding of top biomass and tall rice plant that farmers considered to be important to them could be fairly easily as the GCA of the best combiners can be relied on to predict the performance in the progenies.

5.5.3. Mean values of ten traits for parents, F_2 and F_3 rice populations under different soil N and P conditions

Tillering and panicle initiation are the critical phenological periods when N deficiency is well expressed due to high N demand and thus are the best stages to monitor N. Hall (2007) and Smaling (1997) have cited nitrogen and phosphorous as the major limiting factor for crops productivity in the Sub-Sahara Africa. However, various workers have reported the variability and ability of some genotype to extract phosphorous from poor soil (Baligar et al., 2001; Fageria and Baligar, 2003; Fageria et al., 1988; Hall, 2007). In this study, variability was observed for both genotype and environment together with their interactions across various fertility gradients created by different nitrogen and phosphorous treatments. This exemplifies the fact that different genotypes do perform preferentially in given soil N and P fertility conditions and mega-environments. The mean squares for genotypes and environments and their interactions were highly significant for the four fertility conditions (Tables 5.1, 5.2, 5.6 and 5.7). This implies that the genotypes performances were different and that under given soil fertility conditions, genotypes performances were also varied. This indicates that certain genotypes were adapted to specific environments. This is confirmed by performance of mean grain yield that capture the general trend of the majority of the genotypes across a given environment. The yield at near optimum fertility condition (N+P+) were not the highest, and in fact the highest mean was under N-P+ (4607.8), followed by N+P+ (4516.2), and finally N-P- (Table 5.4). Among the highest ten genotypes, none of the genotypes had a consistent ranking and therefore, different lines appeared to be suited to given soil N and P fertility

conditions. However, for top biomass line 36 (CT16333(1)-CA-20-M x CT16317-CA-4-M) consistently was ranked number 1 across the four soil conditions, thus indicating superior performance. The 1000 seed weight showed different results with soil N+P-, N-P-, N-P+ and N+P+ experimental environments having the highest and lowest weight, respectively. For F_3 populations the same or less trend was observed of specific adaptation rather than broad adaptation (Table 5.9). Evidence of stagnation or decline in the productivity of rice even with application of the correct and recommended amounts of NPK fertilizers has been reported by Sharma and Prasad (2003). The fact that in this study best mean yield were not obtained under optimal condition (N+P+) they confirm this reaction. Previous studies conducted (Wissuwa and Ae, 2001b; Wissuwa *et al.*, 2002) have lead to identification and isolation of a major quantitative trait locus (QTL) responsible for P uptake in rice.

5.5.4 F_2 genetics of leaves and seed nitrogen and phosphorous control

The analysis of leaves and seed tissue for N and P contents showed highly significant genotypic mean squares (Table 5.5) under the three mega-environments. The GCA and SCA components, the reciprocal, maternal and nonmaternal effects were all significant. In this study, the GCA effects contributed to the inheritance of leaf N and grain P concentration because they were of higher magnitude than SCA effects. The GCA effects are an indication of presence of heritable additive effects, and thus give an estimate of improvement of a particular trait. Andrzej *et al*. (2011) have reported that although rice is highly self pollinated, the significant SCA effects imply that certain parental combinations can lead to development of high performing crosses. The selfing of such a cross may ultimately lead to fixation of the positive effects that enhance a particular trait. However, if the non-additive component is huge, the improvement of a stable genotype may be elusive especially if environment plays a major role in the expression of the trait. In this study, the GCA effects were larger than SCA effects for leaf N and grain P for the three location. This means that the inheritance of these traits is under additive gene action, while leaf P and grain N are under nonadditive effects. The partitioning of SCA effects revealed that nonmaternal effects were greater for leaf N and P and grain N; but the maternal effects dominate the control of grain P. The presence of large nonadditive gene action portend the use of hybrid in rice to exploit these genetic effects.

The GCA effects for all the parents were significant for leaf nitrogen and leaf phosphorous for all the three mega-environments. However, their signs were either positive or negative and their magnitude also differed. At Mwea, parent G5 (CT16333(1)-CA-22-M) and G2 (Duorado) contributed to enhanced N content in the leaf; while G4 (CT16333(1)-CA-20-M) and G3 (IR79913-B176-B-6) combined to reduce leaf N accumulation (Table 5.5). At Alupe, G5 and G8 (WAB964-B-3A1.2) can be used to enhance N accumulation, while G3 and G4 will act to reduce leaf N content. This simple analysis shows that different parents were more effective in enhancing a given trait in given mega-environments and that the reverse also occurred. Some progenies had values better than either of their parents, thus indicating transgressive segregation. For example in case of N tolerance, cross 13 (Dourado x CT16333(1)-CA-20-M) had a value of 1.25, while 10 (Duorado) had a value of 1.50 under soil N-P- condition (Table 5.9).

Wissuwa et al. (2005) reported that the distribution of P and dry matter between the root and shoot was mostly affected by P supply and that a clear distinction between excess P and P-deficiency could be made. In the case of excess P, they found that plants had very high root and shoot tissue P. They observed plants grown under P deficiency, had highly suboptimal P concentrations in root (<0.5 mg P g^{-1} RDM) and shoot tissue (<0.75 mg P g^{-1} SDM). They noted that despite allocating relatively more P to shoots and maintaining higher P concentrations in leaves, a tolerant variety, Nipponbare, did not show an increase in net photosynthetic capacity and thus yields were not significantly increased. Slaton et al. (2002) further found that phosphorus concentration in the harvested grain was not affected by the time or rate of P fertilizer application. This could probably explain why in the present study some genotypes that were expected to have higher grain yield under optimal condition failed to do so. Instead yielding higher under suboptimal conditions and these probably are highly promising for use in the target low input farmers conditions prevalent in most of their farms.
Zeigler and Adam (2008) have observed that improvements in crop management incorporating such practices as site-specific nutrient use efficiency and conservation agriculture have had demonstrable impact in farmers' fields. Dat Van (2005) and Jiang et al (2007) have indicated that "as the major force of evolution, variance exhibits plants' perfect adaptation to environments. Thousands of different traits and alleles emerge, because of genetic variance; they form a large germplasm pool from which people can select varieties with morphologies of interest and other important agronomic traits that best serve crop modification and plant breeding".

5.5.5 The physiological indices used for nutrient use efficiency for the ten traits

The low soil fertility intensity index (LSFII) had values ranging from -0.73 (80) to +0.4 (9) and mean -0.01 (4, 38, 74, 77) for nitrogen, and -0.70 (80) to +0.49 (35) and a mean of 0.00 (**55**, 5, 7) for phosphorous Table 5.10. The figures in parenthesis are the crosses while bolded values within the parenthesis are the parents. The positive figures indicate those cross and parents that had better performance under low soil N or P and hence tolerant as explained by singh et al. (2003). The genotype 80 (CT16317-CA-4-M (low soil N tolerant) x CT16313-CA-19-M (early)) had poor adaptation in both low soil N and P as indicated by its low values. The low soil tolerance ability of the female parent seemed to be over shadowed by the early male parent in the F_3 progenies. The following lines 5, 6, 16, 25 and 31 generally seem to be well adapted across the fertility conditions when their LSFII and LFSI values are considered. However, there were better specific adaptations when LSFII (line 9) and LFSI (line 31) are considered individually.

Low fertility susceptibility index (LFSI) was also variable, the performance range of values were 13.03 (7) to -10.11 (4) with a mean of 0.06 under nitrogen experimental environment. Under P the range was 0.49 (35) to -0.70 (80) and mean of -0.01 (79, 60). The range was narrower for P compared to N, probably indicating poorer performance of the progenies. The higher values are preferred because they indicate higher tolerance and therefore, line 4 and 35 for N and P tolerance were the most tolerant and adapted to low soil fertility conditions. The lines with negative values were poorly adapted to low soil fertility conditions.

Harvest index had a range of 0.26 (9) to 0.62 (6) and a mean of 0.47 (68) and 0.46 (33) under N experimental environment. For P, the range was 0.15 (35) to 0.56 (2) and mean 0.39 (29, 42, 44, 47, 54, **55**,). The overall performance under low P condition appears to be inferior compared to N experimental environment. A possible explanation may be that inherent soil P was very low and thus had reduced effect on yield, or the response of genotypes to available P was not good for many of the genotypes. Since the genotype by environment interactions were significant, the environment effects might have contributed to this low performance.

The agronomic nutrient use efficiency (ANUE) for N experimental environment had range values of -24.30 (80) to 21.34 (9) and mean of -2.44 (**46**). For P the range span between -34.73 (80) to 35.65 (35), and mean of 1.41 (51). The N range can be fitted within the P range

meaning the operation range of N was better than for P. The phosphorous (P) range displays great diversity in genotype reaction to low soil P condition and thus selection though possible could be slow in cultivar development compared to N range. The genotype 80, (CT16317-CA-4-M (low soil N tolerant) x CT16313-CA-19-M (early)), by the look of its performance is a good one and probably should be included in future work. The higher values for ANUE are not desirable and hence the lower values are indicator of better performance per unit of applied nutrient and thus higher efficiency and responsiveness. The genotypes with high positive values are undesirable such as line 81 (CT16317-CA-4-M x WAB964-B-3A1.2) for both N and P. For N the following lines are inefficient, 70 (WAB964-B-3A1.2 x CT16333(2)-CA-18-M), 65 (WAB964-B-3A1.2 x NERICA 1); anf for P lines 78 (CT16317-CA-4-M x CT16333(1)-CA-22-M), 34 (CT16333(1)-CA-20-M x CT16313-CA-19-M) and 25 (IR79913-B-176-B-4 x CT16313-CA-19-M).

Partial factor for productivity of applied nutrient (PFP) under nitrogen experimental environment had values within 23.54 (50) and 58.78 (**28**) with a mean of 46.86 (47). For P the bounds were 47.38 (9) and 87.11 (6) and mean of 76.41 (11). Clearly, the majority of the genotypes tended to cluster around the upper performance for both N and P situation and line 6 seem to be a good candidate for source of desirable tolerance together with line 16, 28, 37, 80, 519 33 and 18 among others (Table 5.10). This direct efficiency measure for a given nutrient discriminated genotypes for both N and P and indicated specific lines that were better in either one or both of the elements. Line 35 was efficient under P while line **28** was efficient under N soil fertility conditions.

Grain yield efficiency index (GYEI) is another good parameter for measuring the use efficiency of genotypes in converting nutrients into usable and economic products. The range for N situation was, 0.40 (56) to 1.41 (6) and a mean of 1.00 (17, **73**). For the P environments, the range spanned between 0.41 (50) to 1.48 (39) with mean of 1.03 (20, 79) (Table 5.10). The genotypes were divided or distributed almost equally between the upper and lower of the mean. The wide range of phosphorous (P) tolerance case implies better yield performance compared to N values. This probably indicates a wide buffering capacity against adverse low soil P environments with some yields. This wide buffering may not be realized with the narrower band found in nitrogen tolerance, probably this call for broadening of the band by infusion of new and genetically broadly based genotypes. However, more variability may be created by conducting more crosses and backcrossing of some of the

parents to pyramid genes for low soil N tolerance and other desirable traits by farmers. The higher values are preferred as they indicate higher efficiency and therefore, across the N and P soil fertility conditions, lines 6, 33, 39, 5, and 18 had higher efficiencies, while lines 56, 30 and 57 were inefficient.

5.6 Conclusion

The findings have demonstrated wide genetic variability that can be judiciously exploited to develop varieties with end user traits. The GCA, SCA, reciprocal, maternal and nonmaternal effects were highly significant under the different soil N and P conditions. The GCA:SCA ratio exhibited the dominant effects of the nonfixable nonadditive gene action over the additive effects. The reciprocal effects were of larger magnitude than GCA effects, confirming the importance of nonadditive effects. The nonmaternal effects were greater than maternal effects indicating the need for hybrid varieties to exploit these nonfixable genetic effects. The GCA effects for parents were generally significant with good combiners like NERICA1 for earliness. The mean ranking indicated specific adaptation rather than broad adaptation to different soil N and P conditions. The physiological factors used to determine genotypes efficiencies in nutrient use were varied, but generally indicated that while some genotypes were specific in their adaptation, others had a broad adaptation across the soil fertility experimental environments.

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CHAPTER SIX.

Association of Phenotypic traits and Variations in SSR Markers for Fragrance and Metric Traits under different soil fertility regimes

Abstract

Fragrance in rice is an important quality trait. This study was conducted to determine the association between variations in fragrance and in SSR markers that had earlier been reported to be linked to the fragrance (fgr) gene for possible use in marker assisted selection, and to establish gene action for fragrance. Nine parents and 72 F_2 populations generated by full diallel mating design, planted in a 9 by 9 alpha lattice design at KARI-Mwea Tebere Research Centre, were used for the study. During growth, various traits were recorded including phosphorous tolerance (PT), nitrogen tolerance (NT), plant height (PH), number of panicles (NP), days to maturity (DM), 1000 seed weight (SDWT) and grain yield (YLD)). Plant leaves of the parental genotypes were sampled for DNA analysis using SSR markers RM223 and RM284. The results indicated that RM223 was polymorphic among the parents, while RM 284 gave monomorphic results. Four alleles of RM223 (146, 155, 161, and 163) were detected. Test for independence using Chi-square indicated that there was no association between fragrance phenotype and RM223 marker. The additive gene action was greater for the fragrance score. The general combining ability was about one and half times higher than interactions (SCA). The performance of the fragrant lines was generally lower than that of nonfragrant lines. There was generally negative relationship between fragrant score and other agronomic traits such as grain yield across the three soil N and P fertility environments. The NERICA1 was found to be a good donor for fragrant based on phenotypic (sensory) tests and can be exploited in a breeding programme.

6.1 Introduction

Rice is the third most important crop in Kenya after maize and wheat. The crop plays an important role both economically and in terms of food security. Its widespread production is limited by various factors including poor grain quality, low soil fertility, drought, salinity, phosphorus and nitrogen deficiency; insect pests and diseases.

Rice grain quality is determined by a number of factors such as fragrance, whiteness and slenderness. The term “fragrance” is rooted from the fact that resine, oils and balsams are

distinguished as fragrant compounds by a market odour (smell) (Nguyen and Buu, 2008). Fragrant rice emits a definite odour in the fields, during harvesting, storage, milling, cooking and eating (Efferson, 1985) and it is best developed in cooler temperatures during maturity.
Xiangli *et al*. (2008) reported that fragrant rice is popular worldwide and consumers normally pay higher prices for this. Application of phosphorous has been shown to favourably influence rice grain quality, fragrance, softness, fluffiness, whiteness, and glossiness (Suwanarit et al., 1997). Organic manure however, has not been found to affect the rice cooking qualities (Jeong et al., 1996).

Several volatile compounds have been shown to be responsible for the fragrance identified within three of the distinct genetic subpopulations of rice, including *Group V* (i.e., "Basmati" and "Sadri" varieties), *indica* (i.e., "Jasmine" varieties), and tropical japonica (Yajima *et al.*, 1979) and (Mahatheeranont *et al*., 2001). Over 100 volatile compounds have been detected in fragrant rice varieties, but the major compound responsible for the characteristic fragrant is 2-acetyl-1-pyrroline (2AP) (Buttery *et al.*, 1983; Itani *et al.*, 2004; Lorieux *et al.*, 1996). This compound is produced in all parts of the rice plant except the roots (Yoshihashi, 2002), has a very low odour threshold, allowing humans to detect it at minute concentrations in field-grown plants or crushed leaf tissue, as well as in the grain before, during, and after cooking.
Michael *et al*. (2009) observed that fragrance is a highly valued grain quality trait in rice, yet the origin and evolution of the gene underlying this trait remains unclear. Mahatheeranont *et al*. (2001), Shu Xia *et al*. (2008) and others, further found that a single allele (badh2.1) is largely responsible for fragrance in rice. Examination of the occurrence of the *BADH2.1* allele in 280 accessions of wild rice (*Oryza rufipogon/Oryza nivara*), showed that the allele was absent from all wild genotypes, except for a single accession that was heterozygous for the allele (Ahn *et al*., 1992; Kibria *et al*., 2008; Wanchana *et al*., 2005; Yoshihashi, 2002). Using haplotype analysis Michael *et al*. (2009) established the single origin of *badh2.1* allele within the *Japonica* varietal group and demonstrated the introgression of this allele from *Japonica* to *Indica*. A single locus on chromosome 8 (*fgr*) has been further associated with fragrance. Fine mapping and subsequent sequence analysis identified a betaine aldehyde dehydrogenase gene, *BADH2,* to be associated with the fragrant phenotype. Buttery *et al* (1983) has explained that the functional mutation creating the recessive *badh2.1* allele was first described as three single nucleotide polymorphisms (SNPs) and an 8-bp deletion in the seventh exon of the gene that resulted in a premature stop codon and putatively truncated the *BADH2* protein. Recent surveys of diverse fragrant germplasm support the association of

badh2.1 with fragrance and transformation of a fragrant variety with the dominant non-fragrant allele has been shown to abolish fragrance confirming that *BADH2* is the major genetic determinant of fragrance in rice (Chen *et al.*, 2006; Jain *et al.*, 2004; Kibria *et al.*, 2008). A second mutation in the *BADH2* gene, *BADH2.2*, has been associated with fragrance within a set of germplasm from China (Wongpornchai *et al.*, 2004): those have elevated levels of 2AP but do not carry the *BADH2.1* allele (Shu Xia *et al.*, 2008).

Inheritance of fragrant has been reported to vary depending with materials used in the research. A major nuclear recessive gene has been reported to control fragrance in rice (Bradbury, 2009). The first molecular marker for grain fragrance was discovered by Ahn (1992). Using RFLP analysis he showed that the fragrance locus was linked to a single copy DNA clone, RG28, on chromosome 8 of rice, at a distance of 4.5 cM. Since then a number of PCR-based markers have been developed to detect fragrance and assist breeders in their selection of this trait through marker assisted selection (MAS) (Bradbury *et al.*, 2005).

Shu Xia (2008) investigated fragrance inheritance and carried out fine mapping of the fragrance gene in crosses between the fragrant elite hybrid rice *Oryza sativa indica* variety Chuanxiang-29B (Ch-29B) and the non-fragrant rice *O. sativa indica* variety R2 and *O. sativa japonica* Lemont (Le). The F_1 grains and leaves were found to be non-fragrant while the F_2 nonfragrant to fragrant segregation pattern was 3:1. He found F_3 segregation ratio was consistent with the expected 1:2:1 for a single recessive fragrant gene in Ch-29B. Linkage analysis between simple sequence repeat (SSR) markers and the fragrant locus for the fragrant F_2 plants mapped the Ch-29B fragrant gene to a chromosome 8 region flanked by SSR markers RM23120 at 0.52 cM and RM3459 at 1.23 cM, The flanking markers Aro7, RM23120 and RM3459 identified could greatly accelerate the efficiency and precision of fragrant rice breeding programs. Other studies have reported varying nonfragrant to fragrant F_2 segregation patterns, such as 15:1 (Pinson, 1994), 37:27 (Reddy and Sathyanarayanaiah, 1980) and 175:81 (Dhulappanavar, 1976).

Nguyen and Bui (2002) reported two markers, RG28 and RM223 as being closely linked to extremely fragrant phenotypes. To examine the power of the identified SSR markers in predicting the phenotype of the fgr locus, they determined the genotypes of the F_2 individuals at this locus by performing progeny testing for fgr in the F_3 generation. Molecular markers that are closely linked to the fragrant gene could be used for indirect selection for the

presence or absence of scent, and may also be useful for the rapid incorporation of the scent character into breeding lines.

In Kenya, despite the importance of rice and the enormous potential that exists, its productivity is low and no breeding work has been carried out to develop fragrant varieties with tolerance to the low soil N and P conditions prevalent in the farmers production environments. The fragrant rice fetches premium prices in the market. No studies have been conducted on fragrant rice varieties in the country and hence, this study was proposed.

6.1.1 Study objectives

The specific objectives were to:

i. determine association of variations in SSR marker with that for fragrance,
ii. determine the gene action for fragrance,
iii. determine the performance of fragrant line under N and P fertility conditions, and
iv. determine the role of reciprocal effects on agronomic traits.

6.1.2 Study hypothesis:

The hypothesis is that there is association between the markers and the fragrance, additive gene action predominates over nonadditive effects, and that fragrant genotypes have negative effects on metric traits.

6.2 Materials and Methods

6.2.1 Plant materials

The plant materials included nine parents and 72 F_2 populations generated by full diallel mating design. The parents were selected for different traits, among which included tolerance to low soil N and P and fragrance (Table 6.1). One parent, NERICA 1, was fragrant but low yielding. It was included in order to donate the fragrant genes. The 72 F_1 seeds were planted and selfed to generate F_2 populations for the field experiment at KARI-Mwea Tebere. The F_2 seed were planted on 9th February 2010 in two replicates, at intra- and inter-row spacing of 20 cm.

Table 6.1 Rice parents used in the diallel and their characteristics

Serial No.	Pedigree	Source*	Primary selection criteria
G1	NERICA 1	ARC	Fragrant, early maturity, blast resistant
G2	Duorado	Kenya	Local cultivar (Adapted)
G3	IR79913-B-176-B-4	IRRI	Early, low soil N & P Tolerant
G4	CT16333(1)-CA-20-M	CIAT	Medium maturity, high yielding
G5	CT16333(1)-CA-22-M	CIAT	Low soil N and P tolerant
G6	CT16333(2)-CA-18-M	CIAT	Low soil P tolerant
G7	CT16313-CA-19-M	CIAT	Early, blast tolerant
G8	WAB964-B-3A 1.2	ARC	Early, high yielding
G9	CT16317-CA-4-M	CIAT	Low soil N tolerant

*IRRI-International Rice Research Institute
ARC-Africa Rice Centre (formerly WARDA)
CIAT- International Center for Tropical Agriculture
G1-G9 means also parents 1 to 9
Middle name is the genotype pedigree e.g. IR79913-B-4 is parent 3

Fertilizer at 60 kg P ha^{-1} and 45 kg N ha^{-1} was applied as basal application. Additional 45 kg N was applied at maximum tillering and panicle initiation stage by hand broadcast. Normal agronomic practices were observed such as manual weeding, spraying against insect pests, especially aphids, supplemental sprinkler irrigation and guarding against birds and monkeys.

6.2.2 Sensory fragrance evaluation

6.2.3 Leaf samples

Phenotyping for fragrance in the leaves was determined according to the method described by Sood and Siddiq (1978). When the plants were at tillering stage, 2 g were excised from two or three leaves from each parent. The leaf tissues were cut into small pieces of about 5 mm and placed into petri dishes containing 10 mL of 1.7% (w/v) potassium hydroxide (KOH). The petri dishes were covered with the lid and kept at room temperature (25^0 C) for about 10 minutes. They were then opened one by one and the samples sniffed and scored for the presence or absence of fragrance emission (Xiangli et al., 2008). Five well trained panelists were asked to classify the samples using the following fragrance numerical scale ranging from 0 to 3 (0 = non-fragrance, 1 = mild fragrance, 2 = moderate fragrance and 3 = strong fragrance) (Louis et al., 2005; Nguyen and Bui, 2002).

6.2.4 Seed samples

Fragrance phenotyping in the seeds was determined according to the method described by Nguyen and Bui (2002). Twenty grains harvested from parents were placed into 5-ml screw-cap tube containing 1 ml of distilled water and were then incubated at 65°C for 60 minutes with the tubes closed. The fragrance was evaluated after storage at 4°C for 20 min to allow the samples to cool. The samples were then separately opened for smelling by five well-trained panelists with experience in fragrance evaluation. The fragrance was evaluated using numerical scores ranging from 0 to 3 (0 = non-fragrance, 1 = mild fragrance, 2 = moderate fragrance and 3 = strong fragrance) (Louis et al., 2005; Nguyen and Bui, 2002).

6.2.5 DNA extraction

DNA suitable for PCR analysis was prepared using a simplified miniscale procedure described by Nguyen and Bui (2002). A piece of young rice leaf (2 cm), those that have just emerged, were collected and placed in a labeled sealed polypropylene bag. The leaf was ground using a polished glass rod in a well of a Spot Test Plate (Thomas Scientific) after adding 400 µl of extraction buffer (50 mM Tris-HCl pH 8.0, 25mM EDTA, 300mM NaCl and 1% SDS). Grinding was done until the buffer turned green, which is an indication of cell breakage and release of chloroplasts and cell contents. Another 400 µl of the extraction buffer was added and mixed into the well by pipetting. 400 µl of the lysate was transferred to the 1.5 ml centrifuge tube. The lysate was deproteinized using 400 µl of chloroform. The aqueous supernatant was transferred to a new 1.5 ml tube and DNA precipitated using absolute ethanol. DNA was air-dried and resuspended in 50 µl of TE buffer (10mM Tris-HCl pH 8.0, 1mM EDTA pH 8.0). An aliquot of 1 µl was used for PCR analysis. The remaining DNA was stored at -20^0 C for any later use.

6.2.6. PCR - DNA markers analysis for fragrance rice gene

Two SSR markers (RM 223, RM 284) were analyzed at BecA ILRI, Nairobi using protocols optimized by Susan McCouch at Cornell University (Michael *et al*., 2009; Semagn *et al*., 2006). The markers have been known to be linked to the fragrant recessive gene (*fgr*) on chromosome 8 of rice. Sequences for the two primers were:

RM284	Fwd: atctctgatactccatccatcc	Rev: cctgtacgttgatccgaagc
RM223	Fwd: gagtgagcttgggctgaaac	Rev: gaaggcaagtcttggcactg

For the microsatellite assay, PCR amplification was performed in 50 µl volumes containing 10mM Tris-HCL (pH 8), 50mM KCl, 1.5 mM MgCl, 2.1 unit of TAKARA Taq, 4 nmol dNTP, 10 pmol primer and 50ng genomic DNA. The sample was covered with one drop of mineral oil. The PCR reactions were denatured at 95^0 C for 5 min, followed by 35 cycles of 94^0 C for 60 seconds, 55^0 C for 30 seconds and 72^0 C for 60 seconds. The final extension was at 72^0 C for 5 min. After PCR, 13µl of loading buffer (98% formamide, 10mm EDTA, 0.025% bromophenol blue, 0.025% xylene cyanol) were added. PCR products were sequenced by the ILRI BecA Genome Research Facility at Nairobi, Kenya.

6.2.7 Phenotypic data collection

The following seven biometric traits were recorded from the field experiment; phosphorous tolerance (PT), nitrogen tolerance (NT), plant height (PH), number of panicles (NP), days to maturity (DM), 1000 seed weight (SDWT) and grain yield (YLD) according to IRRI standards evaluation procedures (IRRI, 2002).

6.2.8 Analysis of data

A contingency Chi-Square test for association between alleles and fragrance score was performed on the parents data, while the metric traits were subjected to statistical analysis using Diallel SAS software program (Zhang *et al.*, 2005). This was to produce Analysis of variance (ANOVA), the means, the genetic variances relating to general combining ability (GCA), specific combining ability (SCA), reciprocal effects (REC), maternal effects (MAT), non-maternal effects (NMAT). Chi square was used to test for association between fragrance and the variation in SSR marker (RM223).

6.3 Results

6.3.1 Association of variation in SSR marker (RM223) with fragrance

SSR marker RM 284 was monomorphic while RM223 was polymorphic among the parent genotypes used in this study (Table 6.2). A total of four alleles (146, 155, 161 and 163) were detected. The fragrant genotype (NERICA1) had allele 155. This allele was also present in IR79913-176-B-4 which is nonfragrant. The mildly fragrant genotypes CT16313-CA-19-M and WAB964-B-3A 1.2 had allele 161. This allele was also present in CT16333(1)-CA-20-M, CT16333(1)-CA-22-M, and CT16333(2)-CA-18-M which are nonfragrant. Test for association

between variation in RM223 and fragrance indicated that the two traits were independent (P=0.9016) and X^2 (df=6, n=9)=5.55. There is hence need to test a larger number of genotypes and markers.

Table 6.2 The crosses, marker, alleles and rice fragrance scores for the parents at KARI-Mwea

Parents	Pedigree	Sample ID	Marker	Allele 1	Allele 2	Aroma score	Classification
G1	NERICA 1	A1	RM223	155	155	3.0	Fragrant
G2	Dourado	A10	RM223	163	163	0.0	Nonfragrant
G3	IR79913-B-176-B-4	A19	RM223	155	155	0.0	Nonfragrant
G4	CT16333(1)-CA-20-M	A28	RM223	161	161	0.0	Nonfragrant
G5	CT16333(1)-CA-22-M	A37	RM223	161	161	0.0	Nonfragrant
G6	CT16333(2)-CA-18-M	A46	RM223	161	161	0.0	Nonfragrant
G7	CT16313-CA-19-M	A55	RM223	161	161	0.7	Slightly fragrant
G8	WAB964-B-3A1.2	A64	RM223	161	161	0.7	Slightly fragrant
G9	CT16317-CA-4-M	A73	RM223	146	146	0.0	Nonfragrant
G1-NERICA1		G5-CT16333(1)-CA-22-M			G9-CT16317-CA-4-M		
G2-Duorado		G6-CT16333(2)-CA-18-M					
G3-IR79913-176-B-4		G7-CT16313-CA-19-M					
G4-CT16333(1)-CA-20-M		G8-WAB964-B-3A 1.2					

6.3.2 Gene action for fragrance

The mean squares for entries for GCA, SCA, REC, MAT were very highly significant P≤0.001 but non-maternal had highly significant values at P≤0.01 Table 6.3. The GCA effects for the parents G1 (NERICA 1) and G6 (CT16333(2)-CA-18-M were very highly significant but negative for parent 6. Only NERICA 1 had positive and very highly significant mean squares. The other genotypes had negative and nonsignificant mean square values. The GCA variances was very highly significant and also in magnitude (GCA:SCA ratio is 1.48). The reciprocal effects were less than GCA in amounts and the nonmaternal effects were larger than maternal effects.

The reciprocal, maternal and non-maternal effects were significant and positive. The SCA effects for parents were mainly negative and only a few were significant P≤0.05 (Table 6.3). Line S19 (NERICA 1 x CT16313-CA-19-M) had highly but negative SCA value. Few reciprocal cases had significant effects at P≤0.001, only reciprocal 49 (CT16333(1)-CA—20-M x CT16317-CA-4-M) had negative but very highly significant values. Maternal effects were significant for parent 1 (NERICA 1) and 4 (CT16333(1)-CA—20-M). The non-maternal effects

were significant in six cases and only line N49 CT16333(1)-CA-20-M x CT16317-CA-4-M) and N12 (NERICA1 x Duorado) had very highly significant but negative values.

Table 6.3 Mean square values, rice parental GCA, SCA, Reciprocals, maternal and nonmaternal effects of the parents and F_2 rice lines

Trait				Fragrance				
			The 9 parent GCAs'		SCA, Reciprocal, Maternal and nonmaternal effects			
Source	DF	MS	Intercept	0.288***	#11	S11	1.387***	SCA
Model	80	0.87***	REP	0.012ns	12	S12	-0.447**	
REP	1	0.214	G1	0.650***	15	S15	-0.354*	
ENTRY	80	0.886***	G2	-0.183**	17	S17	-0.391*	
R-Square		0.68	G3	-0.109ns	18	S18	0.350*	
Mean		0.313	G4	-0.109ns	2	S19	-1.463***	
Root MS		0.453	G5	-0.109ns	5	S49	0.611*	
GCA	8	3.72***	G6	-0.202***	44	S77	0.498*	
SCA	36	0.56***	G7	-0.072ns	8	S79	-0.685*	
REC	36	0.58***	G8	0.021ns	10	S99	1.519*	
MAT	8	1.09***	G9	0.113ns	48	R13	0.667***	reciprocal
NMAT	28	0.43**			50	R15	0.500**	
					51	R16	0.667***	
GCASSS/Entry SS		41.99			52	R17	0.500**	
SCASS/Entry SS		28.44			72	R49	-0.833***	
GCA:SCA Ratio		1.48			47	M1	0.333***	maternal
					50	M4	-0.130*	
RecSS/EntrySS		29.46			55	N12	-0.611***	nonmaternal
MSS/RecSS		41.76			61	N18	-0.333*	
NMSS/RecSS		57.66			62	N23	-0.444**	
					69	N35	-0.370*	
					75	N47	0.407*	
					15	N49	-0.648***	

G1-NERICA 1	G5-CT16333(1)-CA-22-M	* significant at P≤0.05
G2-Duorado	G6-CT16333(2)-CA-18-M	** significant at P≤0.01
G3-IR79913-176-B-4	G7-CT16313-CA-19-M	*** significant at P≤0.001
G4-CT16333(1)-CA-20-M	G8-WAB964-B-3A 1.2	ns nonsignificant
	G9-CT16317-CA-4-M	# only significan effects are shown

6.3.3 The mean performance values for the eight rice traits at KARI-Mwea

Genotype CT16333(2)-CA-18-M was the most tolerant to low soil phosphorous (P) and nitrogen (N) parent across the three fertility levels (Table 6.4). However NERICA1 was not adapted to the low soil N and P. Genotypes CT16313-CA-19-M and Duorado were the tallest genotypes, a trait preferred by the farmers, when averaged over the three soil fertility experimental environments. NERICA1 although preferred for fragrant, was short across the three soil fertility conditions. Genotypes Duorado and CT16333(1)-CA-20-M had the highest biomass across the soil conditions while NERICA1 had the lowest biomass. Genotype CT16333(1)-CA-20-M and WAB964-B-3A 1.2 had the highest yields across the three soil

environments. Genotype CT16333(1)-CA-20-M and CT16313-CA-19-M had the highest number of panicles when compared across the three soil fertility environments. Line CT16333(1)-CA-20-M was the earliest in terms of days to maturity, while WAB964-B-3A 1.2 had the highest 1000 seed weight across the three soil N and P conditions.

Table 6.4 The means of the rice parent lines for eight traits under the three soil N and P experimental environments

Table 6.4 The means for the PT, NT, PH, TB, NP, DM, SDWT and yield under the three experimental environments

Traits	Phosphorous tolerance (PT) (1-5 scale)			Nitrogen tolerance (NT) (1-5 scale)			Plant height(PH) (cm)			Top biomass (TB) (g)		
EXPT. ENVT.	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+
Serial No.												
G1	2.0	3.2	3.0	2.0	1.5	2.8	70.2	119.6	129.3	1188.1	1234.0	1436.5
G2	1.0	1.0	1.3	1.8	1.8	1.5	98.8	126.0	133.8	1314.7	1428.8	1612.8
G3	1.7	2.7	1.5	1.3	2.4	1.3	82.4	117.4	135.9	1186.4	1298.8	1502.3
G4	1.0	1.3	2.8	2.0	1.4	1.0	97.7	122.6	132.0	1392.8	1445.3	1673.5
G5	1.3	1.7	1.0	1.0	1.6	3.0	82.1	121.6	132.6	1172.5	1259.4	1473.8
G6	1.0	1.0	1.0	1.5	1.3	1.3	75.8	113.3	132.3	1205.0	1326.4	1518.3
G7	1.5	1.8	1.8	1.8	2.3	1.0	86.5	130.1	142.7	1241.9	1253.0	1455.9
G8	2.1	1.3	1.5	2.3	1.9	1.8	84.0	118.8	127.0	1240.7	1364.3	1523.0
G9	1.2	1.8	2.6	2.6	2.1	2.3	73.9	118.0	125.3	1257.5	1286.3	1507.0

	Number of panicles (NP) (numbers)			Days to maturity (DM) (days)			1000 Seed Weight (SDWT)(g)			Yield (Kgha$^{-1)}$		
EXPT. ENVT.	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+
Serial No.												
G1	94.7	48.2	41.1	166.2	155.4	140.9	27.1	28.0	27.4	3645.5	3481.9	2893.7
G2	80.2	56.6	48.0	162.7	156.5	145.5	24.1	28.6	26.2	4884.2	4783.7	4587.3
G3	90.5	44.1	45.4	168.9	151.2	146.8	25.4	27.6	26.8	5274.4	4219.9	4872.4
G4	89.7	48.0	57.8	158.6	153.3	140.9	26.9	28.3	28.4	4603.1	4623.3	5100.9
G5	79.9	60.7	50.2	160.2	154.9	152.0	25.7	27.7	29.2	4962.5	5082.6	4040.3
G6	79.1	44.7	53.4	170.8	166.4	142.8	28.8	31.3	26.0	5304.5	4443.4	5113.0
G7	94.9	69.2	56.3	172.6	153.3	143.5	28.3	30.5	30.7	4187.1	3584.0	4689.2
G8	86.3	49.2	43.5	166.2	146.4	148.0	30.5	30.8	30.1	5498.6	4935.3	4790.5
G9	86.8	57.4	43.5	162.9	152.3	152.3	25.3	25.8	24.5	4339.8	4889.2	4482.6

G1-NERICA 1	G5-CT16333(1)-CA-22-M	G9-CT16317-CA-4-M
G2-Duorado	G6-CT16333(2)-CA-18-M	
G3-IR79913-176-B-4	G7-CT16313-CA-19-M	
G4-CT16333(1)-CA-20-M	G8-WAB964-B-3A 1.2	

A number of F_2 lines from crosses involving the fragrant NERICA1 had superior performance across the three soil fertility conditions for phosphorous (P) and nitrogen (N) tolerance (Table 6.5). The progenies (NERICA 1 x Dourado), (NERICA 1 x IR79913-B-176-B-4) and (NERICA 1 x CT16333(1)-CA-22-M), were the most P tolerant and high tolerance was recorded for P than N. The most susceptible line was IR79913-B-176-B-4 x WAB964-B-3A1.2 under N+P- with a mean value of 3.3. For nitrogen tolerance, the lowest tolerant average range was 2.7 (line CT16333(1)-CA-20-M x CT16313-CA-19-M) to 3.5 for line CT16313-CA-19-M x CT16333(2)-CA-18-M under N-P+ experimental condition which had three lines with a score

of 1.0 (NERICA1 x Dourado, CT16313-CA-19-M x NERICA1 and CT16313-CA-19-M x WAB964-B-3A1.2 62). The plant height varied with N+P+ condition having the tallest 143.1cm for line IR79913-B-176-B-4 x CT16333(1)-CA-20-M under N+P+ condition. The shortest was 106.3cm for line NERICA 1 x CT16317-CA-4-M. The N-P+ experimental condition had short plants 58.7cm for line NERICA 1 x CT16313-CA-19-M. The lines CT16333(1)-CA-20-M x CT16317-CA-4-M and NERICA 1 x Dourado under both N-P+ and N+P+ soil fertility experimental environments showed the highest and lowest top biomass. However, better top biomass development was observed under N+P+ condition with best producer being line CT16333(1)-CA-20-M x CT16317-CA-4-M (2337.7g) and NERICA1 x Dourado (1204.2g) as the lowest producer. The NERICA1 and Dourado are grown by farmers and are generally short and low yielding.

The number of panicles per ten plants had the best expression under N-P+ condition with a range of 109.8 for line (Dourado x CT16333(1)-CA-22-M) and 75.5 for line CT16333(2)-CA-18-M x NERICA 1 (Table 6.5). The line Dourado x CT16333(1)-CA-22-M had also the highest value under N+P+ soil condition. The earliest maturing line 11 (Dourado x NERICA 1) was observed under N+P- conditions, and the latest line 47 (CT16333(2)-CA-18-M x NERICA 1) under N-P+ soil condition. The highest 1000 seed weight was obtained for line CT16333(2)-CA-18-M x Dourado which had 32.2g under N+P+ experimental condition. The lowest weight was recorded for line IR79913-B-176-B-4 x CT16333(1)-CA-22-M (19.7g) under N+P+ condition. This trait exhibited great variability. The highest yielding experimental environment was N-P+ which had parent WAB964-B-3A1.2 yielding the highest (5498.6 kg ha^{-1}), and its lowest yielding line was NERICA 1 x Dourado (2668.7 kg ha^{-1}). This is a cross between the two farmers' varieties and had low yields all through the three experimental environments, implies that it is inferior as it does not respond to applied nutrients. The progenies involving fragrant NERICA1 had varied level of fragrance and even those not involving fragrant had varied levels, although the levels were much lower than those involving NERICA1.

Table 6.5 The means for the phosphorous and nitrogen tolerance, plant height, top biomass, number of panicles, days to maturity, 1000 seed weight and grain yield for the F_2 rice populations under the three experimental environments

Traits			Phosphorous tolerance (PT)			Nitrogen tolerance (NT) (1-5 scale)			Plant height(PH) (cm)			Top biomass (TB) (g)			Number of panicles (numbers)			Days to maturity (days)			1000 Seed Weight (g)			Yield (Kgha^{-1})			Aroma
EXPT. ENVT.			N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	
Popns																											
1	NERICA 1	x Dourado	1.0	1.0	1.3	1.0	1.0	1.0	71.3	118.2	111.8	887.8	1002.0	1204.2	82.9	40.1	44.4	166.9	152.2	155.5	26.5	28.0	25.2	2668.7	2108.5	2596.2	0.0
2	NERICA 1	x IR79913-B-176-B-4	1.2	1.5	1.0	2.2	1.6	1.5	74.3	113.6	115.6	1036.4	1148.6	1353.6	76.5	41.0	44.3	163.7	152.3	156.6	26.0	25.1	26.3	5116.0	4031.3	3870.6	1.3
3	NERICA 1	x CT16333(1)-CA-20-M	2.0	1.2	1.2	2.8	1.8	1.8	75.2	113.2	132.5	1131.8	1299.4	1441.3	84.9	49.5	52.8	164.8	149.7	153.6	24.6	23.5	26.4	5125.4	4815.3	4152.7	1.3
4	NERICA 1	x CT16333(1)-CA-22-M	1.0	2.0	1.3	2.3	1.3	1.3	67.9	109.8	123.5	1168.1	1306.9	1479.7	84.5	46.3	54.3	157.8	167.7	164.8	27.4	22.8	27.0	4463.2	4305.7	4282.2	1.0
5	NERICA 1	x CT16333(2)-CA-18-M	1.0	2.3	1.3	1.5	1.6	1.5	67.6	117.0	119.3	1061.4	1231.2	1363.7	83.5	38.2	56.0	167.7	168.0	162.7	28.7	25.5	25.4	3771.4	3581.0	3259.5	1.3
6	NERICA 1	x CT16313-CA-19-M	1.8	1.3	1.3	2.4	2.0	1.3	58.7	110.7	111.3	1230.0	1341.6	1491.2	88.3	33.7	72.6	164.8	154.0	149.0	24.6	25.2	26.1	3679.6	4506.5	3727.8	1.0
7	NERICA 1	x WAB964-B-3A1.2	1.3	2.4	1.8	2.0	1.8	2.3	61.8	111.2	118.9	1236.1	1326.9	1481.1	89.8	40.6	46.1	164.2	159.5	164.8	27.6	26.5	28.0	3473.8	3921.7	4222.5	1.3
8	NERICA 1	x CT16317-CA-4-M	1.5	1.6	1.3	2.7	2.0	1.3	62.7	109.4	106.3	1183.8	1292.6	1491.6	95.6	35.7	46.0	164.4	150.2	145.3	27.5	26.9	30.5	3886.0	3984.0	3833.6	1.3
9	Dourado	x NERICA 1	2.3	1.0	2.3	2.6	1.8	2.4	91.6	121.8	116.6	1266.0	1349.5	1522.8	89.9	41.8	66.3	166.6	142.6	154.3	29.2	28.5	28.1	5155.7	4639.7	4876.2	0.7
10	Dourado	x IR79913-B-176-B-4	2.3	2.1	2.2	2.5	2.1	2.1	66.8	125.1	126.8	1186.1	1257.3	1487.2	100.9	54.0	67.3	167.3	155.3	157.6	21.9	21.6	23.1	4012.0	3674.2	5418.3	0.0
11	Dourado	x CT16333(1)-CA-20-M	1.0	1.0	1.5	1.8	2.2	2.2	71.8	125.3	127.2	1172.6	1279.6	1483.6	92.8	54.0	58.7	169.9	151.1	153.4	29.7	27.8	28.2	5233.7	4744.5	5000.4	0.0
12	Dourado	x CT16333(1)-CA-22-M	1.0	2.8	1.3	1.5	1.5	1.3	80.0	115.8	129.3	1108.8	1260.3	1411.7	109.8	59.8	78.7	162.1	156.8	152.1	27.1	22.2	25.8	4764.3	4719.3	4831.1	0.3
13	Dourado	x CT16333(2)-CA-18-M	1.5	1.3	1.0	2.3	1.7	1.3	75.9	129.2	138.8	1180.8	1269.4	1421.7	101.0	42.7	54.0	163.1	148.4	155.3	28.4	27.2	28.8	4876.4	4854.4	4219.4	0.3
14	Dourado	x CT16313-CA-19-M	1.5	1.0	1.0	1.5	1.5	1.0	71.3	117.5	132.3	1272.9	1381.1	1523.4	91.3	50.0	59.8	163.3	157.3	158.0	28.4	27.5	27.3	5113.2	4978.8	5042.1	0.3
15	Dourado	x WAB964-B-3A1.2	1.7	1.3	1.3	2.9	1.8	2.7	76.3	128.9	131.5	1322.0	1514.6	1578.1	94.8	48.3	51.1	164.1	150.4	156.8	29.4	28.1	28.2	4882.5	3827.6	4009.2	0.0
16	Dourado	x CT16317-CA-4-M	1.8	1.0	1.0	1.9	2.2	1.3	77.4	121.3	114.8	1183.0	1237.0	1440.4	85.2	44.5	58.5	159.1	157.7	163.0	31.3	30.2	28.5	4283.0	5130.2	4901.0	0.0
17	IR79913-B-176-B-4	x NERICA 1	2.2	2.3	2.5	2.8	1.8	2.5	72.5	122.4	123.5	1209.5	1230.2	1438.7	94.8	41.9	45.3	162.9	153.1	148.2	22.7	22.7	26.7	4584.4	4339.4	4442.6	0.0
18	IR79913-B-176-B-4	x Dourado	2.0	1.3	1.3	1.8	2.1	1.5	71.6	113.2	111.2	1342.4	1434.4	1612.1	84.8	53.8	51.8	164.8	158.9	158.3	29.5	29.4	27.5	4286.0	5203.9	4545.9	0.7
19	IR79913-B-176-B-4	x CT16333(1)-CA-20-M	2.5	2.7	2.0	2.4	2.0	2.5	74.3	120.9	143.1	1183.5	1239.1	1433.4	107.2	47.5	67.5	162.0	152.7	153.3	21.5	20.8	23.3	4909.5	4742.4	4152.7	0.0
20	IR79913-B-176-B-4	x CT16333(1)-CA-22-M	1.7	1.8	2.0	2.3	2.3	1.8	71.0	127.9	139.1	1290.8	1365.1	1607.8	90.9	44.0	47.4	165.8	153.8	155.0	23.5	21.3	19.7	4607.9	4294.7	4883.6	0.0
21	IR79913-B-176-B-4	x CT16333(2)-CA-18-M	2.3	2.5	1.9	2.3	2.0	1.8	74.5	125.8	138.7	1181.9	1256.9	1465.8	103.5	60.8	65.3	166.3	149.6	144.5	24.0	20.1	22.0	4074.0	4611.3	4169.3	0.0
22	IR79913-B-176-B-4	x CT16313-CA-19-M	2.3	1.4	1.0	2.0	1.9	1.8	71.5	129.2	121.8	1352.4	1444.8	1669.4	97.6	49.1	49.2	164.4	149.6	151.2	26.0	27.0	28.2	4530.3	3253.7	3552.3	0.0
23	IR79913-B-176-B-4	x WAB964-B-3A1.2	1.5	3.3	1.5	3.2	1.8	1.5	81.7	122.8	129.6	1218.3	1243.7	1459.6	90.6	51.5	57.9	159.7	151.3	153.3	29.8	29.6	29.9	4872.6	5293.9	4454.2	0.0
24	IR79913-B-176-B-4	x CT16317-CA-4-M	2.0	2.3	1.8	1.8	1.5	2.2	68.8	124.3	127.0	1248.4	1341.3	1566.1	107.8	49.2	51.3	163.9	150.1	160.0	23.6	22.8	23.7	4424.3	4498.6	4479.9	0.7
25	CT16333(1)-CA-20-M	x NERICA 1	1.6	1.7	1.0	2.8	2.0	1.5	78.5	134.3	140.3	1268.4	1381.4	1587.5	85.2	52.0	62.3	160.3	156.7	152.8	29.5	28.1	28.3	4793.7	3473.9	3647.6	0.0
26	CT16333(1)-CA-20-M	x Dourado	1.3	1.0	2.0	1.3	1.9	1.5	80.5	127.9	140.8	1219.2	1264.2	1471.1	91.1	49.9	49.8	164.4	154.4	152.8	25.8	28.5	28.6	4033.6	3150.6	3728.8	0.0
27	CT16333(1)-CA-20-M	x IR79913-B-176-B-4	1.5	1.3	1.3	2.8	2.0	1.3	79.5	128.3	131.8	1284.5	1355.6	1569.9	81.4	55.0	64.3	163.6	149.9	151.2	28.4	29.1	28.6	5497.7	5008.4	4658.6	0.0
28	CT16333(1)-CA-20-M	x CT16333(1)-CA-22-M	3.2	1.6	1.3	2.8	1.5	1.5	75.7	129.4	142.4	1253.4	1254.0	1468.5	85.0	43.3	41.7	162.7	152.4	156.5	27.2	25.6	24.8	4591.7	4770.7	4218.1	0.0
29	CT16333(1)-CA-20-M	x CT16333(2)-CA-18-M	1.5	1.3	1.3	1.8	2.5	3.3	75.4	126.0	130.0	1187.3	1390.2	1570.0	92.2	43.9	50.7	168.4	155.4	154.5	26.9	29.3	28.2	4754.0	4963.5	4741.2	0.0
30	CT16333(1)-CA-20-M	x CT16313-CA-19-M	1.0	2.3	1.5	3.0	2.7	2.0	76.3	119.8	125.7	1326.2	1437.2	1593.8	75.7	41.0	39.8	166.3	146.9	152.7	28.6	25.3	27.5	3880.9	4030.5	4573.0	0.7
31	CT16333(1)-CA-20-M	x WAB964-B-3A1.2	2.6	1.2	1.8	1.8	1.6	1.0	78.0	128.3	127.5	1860.7	1834.7	2032.0	91.7	44.3	46.1	163.2	155.0	151.3	27.8	29.8	27.2	3639.5	2801.4	4374.3	0.0
32	CT16333(1)-CA-20-M	x CT16317-CA-4-M	1.3	1.3	1.3	2.0	1.6	1.9	72.1	126.7	125.4	2185.9	2285.7	2337.7	92.0	46.3	57.9	159.7	145.7	146.2	29.2	29.6	27.2	4956.3	4751.2	5040.3	0.0
33	CT16333(1)-CA-22-M	x NERICA 1	1.0	2.1	1.5	2.1	1.0	1.5	63.0	119.1	122.8	1838.3	1939.4	2105.5	98.5	46.3	48.2	162.8	153.6	151.1	29.2	28.5	27.5	3585.2	3703.8	3729.4	0.0
34	CT16333(1)-CA-22-M	x Dourado	2.2	2.2	1.3	2.0	2.0	1.8	72.4	118.8	127.0	1494.1	1520.3	1662.0	88.2	50.3	57.3	161.8	155.0	150.8	27.0	28.0	25.6	4959.5	4689.6	4668.0	0.0
35	CT16333(1)-CA-22-M	x IR79913-B-176-B-4	1.0	1.6	1.0	1.3	1.5	1.0	75.2	118.9	139.3	1444.4	1457.3	1609.4	86.9	44.7	59.0	161.6	158.7	155.0	28.6	24.7	26.8	5044.1	4729.4	5062.7	0.7
36	CT16333(1)-CA-22-M	x CT16333(1)-CA-20-M	1.5	1.0	1.8	1.5	1.4	2.3	67.5	123.8	129.3	1429.5	1514.4	1649.1	86.8	49.3	44.9	163.3	151.9	153.2	28.4	28.8	27.3	4196.1	3387.2	4484.8	0.0
37	CT16333(1)-CA-22-M	x CT16333(2)-CA-18-M	1.5	1.5	1.0	1.5	1.8	1.0	77.9	111.7	128.0	1479.0	1577.2	1698.2	85.3	56.9	59.9	158.3	145.2	156.4	28.8	26.9	27.0	5283.5	5128.3	4996.7	0.0

Table 6.5 The means for the phosphorous and nitrogen tolerance, plant height, top biomass, number of panicles, days to maturity, 1000 seed weight and grain yield for the F_2 populations (popns) under the three experimental environments

Traits			Phosphorous tolerance (PT)			Nitrogen tolerance (NT) (1-5 scale)			Plant height(PH) (cm)			Top biomass (TB) (g)			Number of panicles (numbers)			Days to maturity (days)			1000 Seed Weight (g)			Yield (Kgha$^{-1)}$			Aroma
EXPT. ENV.			N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	N-P+	N+P-	N+P+	
Popns																											
38	CT16333(1)-CA-22-M	x CT16313-CA-19-M	1.0	1.3	1.0	2.2	1.3	1.0	70.8	112.6	125.4	1362.7	1293.1	1568.0	79.3	45.8	38.3	166.9	153.7	160.0	26.4	24.0	25.2	3626.0	4769.3	4841.7	0.0
39	CT16333(1)-CA-22-M	x WAB964-B-3A1.2	1.0	1.3	1.0	1.5	1.0	1.3	72.5	111.4	127.7	1227.0	1235.3	1438.2	82.9	42.6	54.3	163.8	160.7	156.0	24.0	23.6	24.4	4883.2	4742.9	4394.7	0.3
40	CT16333(1)-CA-22-M	x CT16317-CA-4-M	1.3	1.7	1.3	1.9	1.3	1.0	77.0	126.1	128.5	1287.1	1280.2	1489.4	78.4	49.6	42.5	164.2	159.7	146.5	24.2	25.6	28.5	4358.1	4700.8	3837.7	0.0
41	CT16333(2)-CA-18-M	x NERICA 1	2.3	1.8	1.5	2.6	2.3	2.0	64.6	112.8	120.8	1250.5	1321.3	1526.6	75.5	48.6	51.4	152.7	148.5	146.8	29.6	28.4	26.4	5136.1	5130.4	4932.4	0.0
42	CT16333(2)-CA-18-M	x Dourado	1.0	1.8	1.5	1.8	2.0	1.3	73.5	112.1	123.5	1312.7	1274.7	1505.5	98.3	50.0	40.4	161.4	147.3	157.5	31.9	29.8	32.2	4810.6	3455.5	4939.2	0.0
43	CT16333(2)-CA-18-M	x IR79913-B-176-B-4	1.3	1.5	1.7	2.8	1.8	1.8	81.5	117.2	134.8	1197.4	1256.8	1437.8	87.7	59.8	47.3	164.3	153.9	152.1	31.7	29.6	29.6	5344.2	4257.2	5009.1	0.0
44	CT16333(2)-CA-18-M	x CT16333(1)-CA-20-M	1.3	1.3	1.5	1.8	1.8	1.8	70.4	114.0	112.5	1159.5	1273.3	1499.9	88.3	51.9	46.2	163.1	150.9	157.8	29.1	26.5	27.0	3907.0	4820.7	4501.2	0.0
45	CT16333(2)-CA-18-M	x CT16333(1)-CA-22-M	1.0	1.3	1.0	2.4	2.5	1.5	78.8	126.9	131.3	1327.9	1336.2	1508.2	90.1	51.6	48.4	165.3	156.4	149.5	30.2	30.5	29.0	4635.7	4583.1	5051.2	0.0
46	CT16333(2)-CA-18-M	x CT16313-CA-19-M	1.8	2.6	1.7	1.7	1.9	1.8	70.8	116.4	128.1	1255.8	1300.2	1493.0	89.7	46.8	53.8	166.3	152.8	153.8	28.2	29.1	28.0	4614.9	4557.4	4615.9	0.0
47	CT16333(2)-CA-18-M	x WAB964-B-3A1.2	1.3	1.5	1.3	2.3	1.6	1.5	81.6	113.3	117.8	1272.6	1252.1	1457.2	92.8	51.5	63.6	164.9	157.7	151.3	30.5	29.8	27.2	5143.1	4456.2	5146.0	0.0
48	CT16333(2)-CA-18-M	x CT16317-CA-4-M	1.5	2.3	1.7	2.3	2.4	2.0	74.1	109.3	129.3	1354.7	1317.7	1474.4	89.2	56.2	56.9	160.3	155.5	148.9	26.0	24.3	27.8	4221.7	4182.5	4015.2	0.0
49	CT16313-CA-19-M	x NERICA 1	1.3	1.0	1.3	1.0	1.0	1.0	75.3	122.7	124.3	1097.2	1194.3	1388.9	89.5	56.3	38.5	166.5	157.2	155.0	28.0	27.0	28.1	3874.5	3880.8	4225.5	0.0
50	CT16313-CA-19-M	x Dourado	1.5	1.8	2.4	2.2	2.0	2.0	88.3	125.4	135.0	1090.2	1194.1	1359.7	92.8	50.9	42.7	162.3	155.7	146.0	29.4	27.0	28.3	3351.4	3587.7	3969.2	0.0
51	CT16313-CA-19-M	x IR79913-B-176-B-4	1.0	1.5	1.3	1.5	1.5	1.5	78.1	121.7	129.8	1011.7	1132.0	1327.6	84.4	46.8	69.1	164.1	157.4	158.3	25.3	26.3	26.8	4662.3	4990.0	5102.6	0.0
52	CT16313-CA-19-M	x CT16333(1)-CA-20-M	1.3	1.2	1.0	2.5	1.8	1.5	76.6	118.0	133.2	1188.6	1271.3	1441.5	89.3	47.3	60.2	157.3	150.5	155.3	25.9	25.6	25.4	4241.2	4823.2	5037.7	0.0
53	CT16313-CA-19-M	x CT16333(1)-CA-22-M	1.8	1.0	1.3	2.0	1.3	1.4	74.2	113.3	124.3	1120.8	1229.4	1443.5	85.5	45.3	50.7	161.5	159.7	159.3	28.5	26.3	26.0	4788.8	4241.7	4908.3	0.7
54	CT16313-CA-19-M	x CT16333(2)-CA-18-M	2.0	1.8	1.0	3.5	1.3	1.0	77.8	118.2	137.8	1342.0	1439.9	1559.4	88.5	45.6	54.3	165.0	161.4	148.3	28.7	27.0	28.2	4187.5	3744.9	3800.4	0.0
55	CT16313-CA-19-M	x WAB964-B-3A1.2	2.2	1.8	2.3	1.0	1.6	2.0	85.5	119.3	124.7	1121.8	1235.5	1442.6	88.6	45.8	50.4	160.5	157.1	150.1	30.4	28.3	26.3	4228.9	3811.1	3467.5	0.0
56	CT16313-CA-19-M	x CT16317-CA-4-M	1.0	1.0	1.0	2.0	2.0	1.8	76.0	117.8	113.8	1184.3	1231.6	1427.1	91.0	50.3	52.7	165.3	150.4	158.8	28.7	29.1	30.1	4559.6	4158.0	4430.8	0.3
57	WAB964-B-3A1.2	x NERICA 1	1.0	1.4	1.7	2.5	1.4	1.4	82.8	113.3	123.0	1186.4	1279.0	1459.7	90.2	49.8	61.2	157.7	154.3	147.5	30.7	30.6	27.0	4725.6	4433.7	4750.7	1.3
58	WAB964-B-3A1.2	x Dourado	1.8	2.0	2.0	3.0	2.0	2.0	79.8	110.2	115.5	1187.3	1293.8	1478.9	82.8	49.8	45.0	157.0	156.7	150.3	28.2	26.2	29.3	4813.8	5077.5	5084.7	0.0
59	WAB964-B-3A1.2	x IR79913-B-176-B-4	1.0	2.2	1.7	1.8	1.4	1.0	73.0	112.4	115.1	1188.6	1301.4	1494.2	87.1	57.0	67.7	163.3	161.7	156.3	30.5	28.6	30.0	4898.1	4453.0	4848.1	0.0
60	WAB964-B-3A1.2	x CT16333(1)-CA-20-M	1.7	1.9	1.3	2.6	2.3	2.6	80.9	124.5	133.3	1198.2	1292.4	1508.7	75.8	37.6	44.7	160.8	146.4	149.8	26.8	26.0	24.2	4919.6	2574.3	4430.5	0.0
61	WAB964-B-3A1.2	x CT16333(1)-CA-22-M	1.5	2.2	1.0	1.8	1.4	1.0	78.0	116.1	135.4	1235.0	1302.8	1518.0	87.7	46.3	59.5	161.7	153.1	152.8	29.8	28.6	28.2	4990.4	4872.1	5235.8	0.0
62	WAB964-B-3A1.2	x CT16333(2)-CA-18-M	1.5	3.0	1.0	1.5	2.0	1.0	83.4	127.4	133.5	1245.9	1331.6	1544.0	87.7	54.5	59.6	161.5	153.9	152.5	28.9	27.7	28.8	4674.6	4065.7	5089.9	0.0
63	WAB964-B-3A1.2	x WAB964-B-3A1.2	2.2	2.2	2.8	2.8	1.0	2.2	111.9	115.1	124.0	1222.1	1235.9	1412.6	81.0	58.3	66.3	161.0	155.4	152.0	25.8	31.5	28.2	4758.0	3703.5	5029.7	0.3
64	WAB964-B-3A1.2	x CT16317-CA-4-M	1.0	2.5	1.4	1.8	2.0	2.8	85.7	115.7	126.5	1092.0	1207.4	1427.0	86.6	49.8	49.4	166.3	155.3	150.8	27.8	27.1	26.8	4049.1	4869.0	4147.0	1.0
65	CT16317-CA-4-M	x NERICA 1	2.3	2.2	2.5	3.3	1.8	1.7	83.7	117.5	127.0	1165.3	1244.0	1438.4	77.7	47.1	68.8	165.1	158.9	152.0	25.8	25.5	25.6	4161.6	4489.8	4438.5	0.7
66	CT16317-CA-4-M	x Dourado	2.2	2.3	2.0	1.8	1.3	1.3	82.0	113.3	129.3	1136.6	1248.4	1425.2	91.3	55.1	58.7	159.8	160.1	146.3	26.5	29.2	26.3	4496.7	4502.3	4510.9	0.0
67	CT16317-CA-4-M	x IR79913-B-176-B-4	1.8	1.0	1.0	1.8	1.0	1.3	78.1	120.4	109.3	1166.0	1242.7	1467.7	85.1	81.1	54.7	159.8	162.9	163.8	26.8	26.9	28.2	4209.3	4644.4	4800.7	0.0
68	CT16317-CA-4-M	x CT16333(1)-CA-20-M	2.0	1.8	1.7	3.2	2.3	2.0	71.8	109.5	121.0	1219.2	1329.4	1502.8	81.7	46.0	45.7	156.2	152.8	150.0	28.3	29.0	26.9	3529.4	4577.2	4583.4	1.7
69	CT16317-CA-4-M	x CT16333(1)-CA-22-M	1.9	2.1	1.3	1.8	1.4	1.5	92.8	127.2	135.3	1210.4	1316.7	1484.9	89.5	71.8	53.3	155.8	157.9	161.0	28.6	26.7	26.9	4892.3	4671.8	4588.3	0.0
70	CT16317-CA-4-M	x CT16333(2)-CA-18-M	1.0	1.7	1.0	1.8	1.8	1.5	76.5	133.5	109.8	1219.2	1325.6	1492.5	88.8	50.1	50.2	164.3	158.4	154.3	25.9	24.8	26.8	4758.1	4553.4	4590.4	0.0
71	CT16317-CA-4-M	x CT16313-CA-19-M	2.1	2.0	1.3	2.8	2.3	1.6	72.0	124.3	121.5	1195.1	1303.6	1486.1	83.2	64.7	57.7	165.0	159.1	152.2	25.1	28.7	26.5	4519.5	4594.5	4675.9	0.0
72	CT16317-CA-4-M	x WAB964-B-3A1.2	2.5	1.8	2.0	3.1	1.4	2.5	88.3	122.4	137.1	1243.7	1336.7	1515.1	88.5	83.4	47.2	161.8	160.2	151.3	23.8	25.4	26.7	4235.9	3975.6	3707.9	1.0

6.4 Discussion

6.4.1 Association of variation in SSR marker to fragrance

One of the SSR markers, RM223, was found to be polymorphic among the parents and four alleles were identified. Fragrant genotypes had allele 155. This allele is also present in nonfragrant genotype. Mild fragrance had allele 161. This allele was also present in nonfragrant genotypes. Alleles 155 and 161 not solely present in fragrant rice. The chi square analysis of independence of the phenotypic and variation in SSR marker (RM223) among the parental genotypes indicated a probability (P=0.9016) and X^2 (df=6, n=9)=5.55. This shows lack of association. This is possible since SSR 223 is a flanking marker. There is need to test more genotypes and markers, especially gene markers for fragrance, since use of SSR markers for marker assisted selection may be more efficient. They are not affected by environment and fragrant plants can be identified at seedling stage thus reducing the volume of materials to be handled and hence cost (Abalo et al., 2009).

The F_2 populations of crosses involving NERICA1 had varied levels of fragrance though higher than those for crosses involving nonfragrant parents (Table 6.5). This probably may mean that the environment had some influence on the expression of fragrance as has been reported by other researchers (Jin *et al*., 2003; Michael *et al*., 2009). Kibria *et al*. (2008) have also reported occurrence of a wide range of intensity of fragrance among F_7 materials developed from a cross between fragrant and nonfragrant lines, and that many different deletions on the main fragrance locus occurred. Since fragrance is conferred by homozygous recessive gene (Lorieux *et al.*, 1996), the development of fragrant varieties could entail using a backcross breeding approach to transfer this gene to the desirable background.

Normally, conventional breeding program involves crossing whole genomes followed by selection of the superior recombinants from among the several segregating progenies. This is laborious and time consuming as it entails making several crosses, several generations of selection, and careful phenotypic selection. The tight linkage between the desired loci with the undesired loci obstructs the attainment of the desired objective. The advent of DNA marker technology; several types of DNA markers and molecular breeding strategies are now available to plant breeders and geneticists. These help breeders to surmount many of the problems faced during conventional breeding. It is essential for rice breeders to develop

reliable, fast and cost-effective evaluation tools for rice fragrance in breeding programs. As sensory quality has always been an important consideration in rice improvement, sensory methods including eluting fragrance from leaves with dilute KOH and chewing grains for fragrance. However, the detection of fragrance by sensory or chemical methods is by no means practical when processing large numbers of samples.

6.4.2 Fragrance genetics and phenotypic traits

The mean squares for fragrance sensory tests indicated highly significant values ($P \leq 0.001$) for the F_2 segregating population and that GCA, SCA, REC, MAT and NMAT variances were significant (Table 6.3). The GCA:SCA ratio was 1.48 indicating preponderance of the heritable and fixable additive effects. The reciprocal effects were less than GCA in magnitude thus emphasising the higher role of additive effects in fragrance control. The nonmaternal maternal effects were more important than maternal effects. The big role played by nonadditive effects cannot be ignored in aroma inheritance and its exploitation is hinged on hybrid development. The lager GCA effects over SCA effects is a clear indication that the fragrance trait is heritable, but its expression is greatly influenced by other cytoplasmic (significant maternal factors) and environmental factors as discussed in the preceding section. The parental GCA effects clearly showed that fragrance donor parent (NERICA1) had a major contribution ($P<0.001$) toward the inheritance of this trait and should, therefore be an excellent source of fragrance genes in breeding programmes. Other effects such as specific combining abilities of crosses, reciprocal, maternal and nonmaternal also played part in its inheritance. This further, demonstrate the complexity in fragrance breeding and thus the need to have marker tools to aid breeding work in selection of the progenies homozygous for the fragrance gene.

The phenotypic data for phosphorous tolerance, nitrogen tolerance, plant height, top biomass, number of panicles, days to maturity (DM), 1000 seed weight (SDWT) and grain yield indicated relatively poor performance for the fragrant genotypes as opposed to the nonfragrant ones. Louis *et al*. (2005), (Lee Crump, 1946) and Kibria *et al*. (2008) found a significant but a negative correlation between grain yield and fragrance. Obviously the present results are in agreement with these findings. Considering phenotypic and genotypic observations, the best four lines, for higher grain yield were nonfragrant (Table 6.5). The progenies arising from the crosses involving the fragrant NERICA1 parent and other

nonfragrant parents had better yields than the NERICA1 across all the fertility conditions, except for the progeny NERICA1 x Dourado (Table 6.5). The progenies of NERICA1 had different fragrance intensities, but higher than that involving nonfragrant parents. The wide range of expression of fragrant arising from segregating population between a fragrant and a nonfragrant genotype was also reported by Kibria *et al*. (2008). This may be an indication of promising yield improvement and with backcross breeding, the fragrance may be incorporated into these improved lines. The plant height was generally lower for progenies involving the fragrant line except for progeny NERICA1 x CT16333(1)-CA-20-M. Since farmers value taller plants for ease of harvesting and use of culms for livestock feed and making by product like hats, NERICA1 which is a short variety is not the ideal parent (Efisue et al., 2008). The top biomass was lower across the fertility conditions for progenies involving NERICA1 except for progenies NERICA1 x CT16313-CA-19-M and NERICA1 x WAB964-B-3A1.2 which had increased biomass. Parent NERICA1 although it posed the highly desirable fragrance, the association with other traits of agronomic importance was negative and therefore, this is a challenge in improvement of say yield and biomass. The trend for 1000 seed weight was a general reduction just like it was observed for grain yield and this confirms previous findings by Kibria et al. (2008).

Probably, as Jain *et al*. (2004) elaborated, marker selection (MAS) may change the selection criteria from selection of phenotypes towards selection of genes even in minute amounts and at all stages of plant growth. With availability of markers and genetic maps, it will be possible to exploit information and trace the flow of genes or quantitative trait loci (QTL) of interest in rice, and make prediction about crossing and selections that will increase the efficiency of variety development. In addition, microsatellite marker analysis can be automated and this feature is attractive for marker assisted selection programme. Compared to the phenotype, marker assisted selection for fragrance can improve the cost effectiveness and significantly speed up the introgression of fragrant gene to adapted rice genotypes.

6.4.3 Conclusion

This study has shown that fragrance is heritable from one generation to another, and the intensity of fragrance is affected by environment conditions and probably interactions between nuclear genes and cytoplasm. Fragrance is under additive genetic inheritance. The nonmaternal effects were observed that they play a big role in fragrance inheritance and

cannot be ignored. Metric traits studied were negatively related to fragrance. Use of markers though results showed no association, as opposed to phenotypic selection, could still be more accurate and reliable if a good gene marker is identified for the materials. Its adoption could greatly accelerate the breeding of new novel varieties within a shorter time frame because fragrance locus could be detected at the seedling stage and thus do early selections. It does not suffer from environmental vagaries unlike the phenotypic selection and thus more suited for quantitative traits breeding like fragrance which is a complex trait. However, the exact influence of nitrogen fertilization and temperature effect on fragrance development need to be determined in order to optimize its expression in production of quality grains.

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CHAPTER SEVEN.

Genetic Analyses of Rice Grain Yield under Low Soil Phosphorous (P) and Nitrogen (N) Conditions for Two Mega-Environments

Abstract

The genetic analysis of components governaning grain yield was investigated by use of a nine-parent (seven accessions and two local varieties) complete diallel mating design. The 72 F_2 populations and nine parents were planted in a 9x9 alpha lattice design replicated three and two times at Alupe and Mwea, respectively. The soil fertility environments were N-P+ (no N application), and N+P+ (N and P applied) to detect the effects of N and N+P- (no P applied) and N+P+ to discriminate the P effects. Hayman analysis was used to generate various components of variance and to elucidate their potential, utilization, and provide a thorough understanding of their role in grain yield development and improvement. The additive gene effects were significant for all cases of soil N and P environments and the two mega-environments. They were also more important than the dominant gene effects, indicating the need to use judiciously simple mass and pedigree selection in the early generations of segregating materials and bulk method for advance and near homogeneous lines. The maternal effects were signifcant, except for P effects at Mwea. This proves that cytoplasmic effects were important in contribution of yield under divergent soil N and conditions and locations. The genotypic effects were highly significant ($P<0.001$), except at Mwea where P effects were highly significant ($P<0.01$). The regression lines of covariance (W_r) against variance (V_r) under different soil N and P conditions for the two locations cut the W_r below the origin, except at Alupe for N condition. This indicates that the overdominance played a bigger role in genetic inheritance of yield. The mean potence was positive in all cases thus indicating desired direction and confirming overdominance and dominance were important in inheritance of yield. The heritability in narrow sense (h^2_{ns}) for upland rice grain yield was 21.52 and 4.22 under P and N deficiency, respectively at Alupe mega-environment.

7.1 Introduction

Rice in Kenya is the third most important staple food crop after maize and wheat (MoA, 2009; Rosemary et al., 2010). However, its production is constrained by low soil fertility due to continuous cultivation and unaffordability of inputs thus lack of replenishment of depleted nutrients. The other factors reported to contribute to low yields are high labour costs, lack of certified seeds and new improved cultivars, pests and diseases especially white stem borer

and rice blast (Newspaper, 2008). The yields are thus low, about 1 MT ha^{-1}, and lack of new improved and adapted genotypes to these environments complicate the situation further. Although rice plays an important role in food security and incomes to many people in agriculture, its production is still low and can only meet less than 20% of the local consumption (Rosemary et al., 2010). This is against the enormous potential that exist for exploiting both upland and irrigated rice to unlock the heavy imports of rice.

Although no work has been conducted on genetics of low soil tolerance inheritance, Many authors elsewhere, have reported that the control of grain yield is under polygenic control (Gao et al., 2004; Murai and Kinoshita, 1986; Yuan et al., 2003). It has also been reported that grain quality is mainly controlled by dominance gene effects and thus possibility of heterosis in rice (Verma and Srivastava, 2004; Verma et al., 2003). The research for development of adapted upland rice varieties has started in Kenya, against a background of lack of understanding of main genetic mechanisms responsible for low soil fertility tolerance. For a successful breeding programme, the genetics of low soil phosphorous (P) and nitrogen (N) in rice is pivotal. It is for this reason that Hayman analysis for genetic components was adopted to generate information on the genetics of low soil P and N control in rice. The Hayman analysis of genetical components is applied to test significance of treatment effects, hypothesis and to estimate the several variance components (Hayman, 1954; Lee Crump, 1946). The difference and understanding of genotype and phenotypic relationship, that is genetic structure and trait expression is the core of basic genetics.

The genetics and behaviour of the rice materials currently in Kenya has not been studied or documented despite the importance of this information in a rice breeding programme. It is thus quite imperative that a paradigm shift be urgently made to reverse the above situation as a counterproductive measure against the climate change and ever increasing depleted crop lands and lack of upland rice varieties both in diversity and adaptation to the local conditions. The upland rice offer enormous potential to reverse this situation of deficit to one of sufficiency as upland rice remains largely unexploited. The research work embodies useful information about gene action and inheritance pattern of grain yield in rice for developing breeding lines for enhanced performance under the prevalent low soil fertility, especially low N and P, in farmers' fields.

7.1.1 Study objectives and hypothesis

The specific objectives were to:

a) estimate the various variance components determining genetic control of grain yield,

b) estimate the narrow sense heritability for grain yield under contrasting soil N and P conditions, and
c) determine the nature of genes governing grain yield.

The study hypothesis is that yield is controlled by genes with increasing effects and that the narrow sense heritability is low with dominant gene effects playing the major role

7.2 Materials and Methods

7.2.1 F_2 populations evaluations under two contrasting phosphorous (P) and nitrogen (N) experimental environments at Mwea and Aupe

The F_1 seeds produced by crossing of the nine parents were advanced to produce F_2 seeds that were evaluated together with the parents. The features of parents are shown in Table 7.1. These were evaluated under contrasting soil P and N experimental environments at Mwea and Alupe that are different in terms of general weather patterns and soil types.

Table 7.1 The nine rice parents used in the diallel and their characteristics

Serial No.	Pedigree	Source*	Primary selection criteria
1	G1-NERICA1	ARC	High grain quality, early, blast resistant
2	G2-Duorado	Kenya	Local cultivar (Adapted)
3	G3-IR79913-B-176-B-4	IRRI	Early, low soil N & P Tolerant
4	G4-CT16333(1)-CA-20-M	CIAT	Medium maturity, high yielding
5	G5-CT16333(1)-CA-22-M	CIAT	Low soil N and P tolerant
6	G6-CT16333(2)-CA-18-M	CIAT	Low soil P tolerant
7	G7-CT16313-CA-19-M	CIAT	Early, blast tolerant
8	G8-WAB964-B-3A 1.2	ARC	Early, high yielding
9	G9-CT16317-CA-4-M	CIAT	Low soil N tolerant

*IRRI-International Rice Research Institute
ARC-Africa Rice Centre (WARDA)
CIAT- International Center for Tropical Agriculture
G1-G9 means also parents 1 to 9
=1 to =9 means also parents 1 to 9
Middle name is the genotype pedigree e.g. IR79913-B-4 is parent 3

KARI-Mwea Tebere (National Rice and Fibre Research Centre (NRFRC)) is located in Mwea Division, Kirinyaga South District, Central Province, 112 km East of Nairobi in Kenya. It lies on Latitude 00^o 37' S and Longitude 37^o 20' E at an elevation of 1159 m above sea level (masl). The average rainfall is about 850 mm with a range of 500 - 1250 mm divided into long rains (March – June with an average of 450 mm) and short rains (Mid-October to December with an average of 350 mm). The rainfall is characterized by uneven distribution in total amounts, time and space. The temperature ranges from 15.6º C to 28.6º C with a mean of about 22º C. The soil are nitosol, which are deep, well drained dusky-red to dark reddish-brown, friable clay with low fertility (FURP, 1987; Jaetzold and Schmidt, 1983).

Lake Basin Development Authority (LBDA) Alupe is located on Latitude 0° 30' 0 N; Longitude 34° 7' 50 E; on an elevation of 1170 meters above sea level (masl) in the western part of Kenya. The soils at Alupe have been characterized as Ferralo-orthic Acrisol with pH of 5.0 (FURP, 1987). The total annual rainfall at Alupe was 1,398 mm and temperature ranged from 16-34°C during the year 2009.

7.2.2 Evaluation experiment at KARI-Mwea and LBDA-Alupe

The eighty one upland lines (72 F_2 populations and nine parents) were planted out in an α lattice design replicated three and two times at Alupe and Mwea, respectively. The experimental environments were N-P+ (No N applied) and N+P+ to detect the effects of N and N+P- (no P applied) and N+P+ to discriminate the P effects. Triple super phosphate (TSP-($CaHPO_4$) 32.5% - 60kg P ha^{-1}) and calcium ammonium nitrate (CAN -90 kg N per ha^{-1}) were the source of elemental P and N. Nitrogen was applied as split of 45 kg ha^{-1} at planting and at maximum tillering stage, while P was applied as basal in the respective blocks. The trial was kept free of weeds by hand weeding and protected from pest and diseases by intermittent spraying when necessary. Supplementary sprinkler irrigation was only applied when necessary. The crop was harvested when it reached 90% physiological maturity in order to avoid grain shattering of the very early entries.

7.2.3 Data analysis

The data for yield was subjected to full diallel analysis using GenStat statistical program (Payne et al., 2009). The model for analysis was: Y=m + loc +a +b + c +d +loc*a + loc*b + loc*c +loc*d where,

Y = observed entry yield
m = grand mean,
loc= location effects,
a = additive effects,
b= dominance effects,
c = additive maternal effects,
d = maternal interaction effects,
The loc*a + loc*b + loc*c +loc*d are the model components interactions with locations

Data was arranged per experimental environment within the mega-environment and analyzed to obtain ‘a’, ‘b’ which is divided further into b_1 , b_2 and b_3; ‘c’ and ‘d’ components. Where significant of ‘a’ indicates significance of additive gene effects, ‘b’ the significant of dominance effects, ‘b_1’ show unidirectional dominance (it compares mean of F_1 and the mid-

parental value), 'b_2' indicates asymmetry of genes (whether gene are more positive, negative or are equal in influence), 'b_3' test dominance deviation not ascribable to b_1 and b_2; 'c' tests presence of maternal effects and 'd' tests reciprocal differences but not attributable to 'c'.
These, b1, b2 and b3 were tested against their individual error terms for significance and in case of homogeneity, they were tested with the pooled error (b x blocks term). Otherwise, if heterogeneous, these were tested against their error terms or interaction with the blocks. The 'a', 'b', 'c' and 'd' were tested also for their interaction with their blocks and in case of homogeneity, they were pooled together and their pooled error used to test each of them for their significance.

The assumptions or hypotheses on which the simple biometrical additive dominance model is based were elaborately discussed by Hayman (1954) and Mather and Jinks (1971) for diallel analysis and these include:

(i). Diploid segregation, (cause reciprocal difference, plus use of diverse inbred lines as parents)
(ii). Only environmental differences between reciprocal crosses,
(iii). Independent action of nonallelic genes and in the parents (no epistasis),
(iv). No multiple allelism,
(v). Homozygosity, and
(vi). Genes independently distributed (no linkage).

These assumption hold and model is adequate only when regression coefficient (b) deviated significantly from zero and not from unity. The results obtained here pertain to the sample used.

The components of variation were calculated and test of validity of hypothesis conducted only if the ordinary analysis of variance (ANOVA) showed significant genotypic mean square. The covariance – variance (Wr-Vr) graphs and limiting parabola were drawn to the adequacy of the additive-dominance model, the degree of dominance (if complete, partial or overdominat) and direction of dominance depending on which genes dominant or recessive were predominant. The following terms were however, generated by the GenStat software; Wr, Vr and related items, VoLo, V_1L_2, VoL_2, $WoLo_1$, MLo, ML_2, regression coefficient, S.E. and 't' calculated with n-2 df. Where VoLo is the Variance of parents or VP; V_r is the variance of each array (crosses involving a given parent), these range from Vr_1, Vr_2,...Vr_n where n = number of parents in a diallel; V_1L_2 or ($\overline{V}_r$) is the mean variance of the arrays for the F_2 (sum of V_{r1} to V_{rn} divided by number of Replications); VoL_2 is the variance of the mean of arrays for F_2; W_r is the covariance between parents and their off-springs (covariance of the arrays with non-recurring parents), these range from W_{r1} to $W_{r....n}$; $WoLo_1$ is the mean covariance

between the parents and the arrays (sum of all $Wr_{1...n}$ divided by n); MLo is the mean of the parents and ML_2 is the mean of n^2 progeny of the F_2.

In order to test each of these components; E, D, F, H_1, H_2, h^2; the standard error (S.E.) of each was obtained as follows: Common multiplier is first obtained (s^2) as (½){Var(W_r-V_r)}, got easily by use of excel (fx function).The specific multipliers for each component are obtained as explained by Hayman (1954);

1. $D' = (n^5+n^4)/n^5$
2. $F' = (4n^5+20n^4-16n^3+16n^2)/n^5$
3. $H'_1 = (n^5+41n^4-12n^3+4n^2)/n^5$
4. $H'_2 = (36n^4)/n^5$
5. $h^{2'} = 16n^4+16n^2-32n+16)/n^5$
6. $E' = n^4/n^5$

Here n refers to the number of diallel parents and these are calculated simply as they are

7.3 Results

The analysis of variance gave the results indicated in Table 7.2. The components were only heterogeneous at Alupe under N effects, thus terms were tested against their pooled error for both b_1, b_2, b_3; and a, b, c and d.

Table 7.2 The mean square values of rice yield for components a, b_1, b_2, b_3, b, c and d for P and N effects at Alupe and Mwea.

Item	d.f.	m.s. (Alupe)		m.s. (Mwea)	
		P effects	N effects	P effects	N effects
a	8	2024426.1***	1834191.9***	1885313.7*	767464.2***
b1	1	1711881.5ns	6360.9ns	3978103.4ns	805528.2ns
b2	8	774382.9ns	624740.1*	692690.7ns	866478.1ns
b3	27	735370.0ns	471180.9ns	765055.1ns	576558.3ns
b	36	771164.8ns	492393.5*	838225.5ns	647345.2ns
c	8	1620670.3***	1745088.5**	2544903.6ns	1614472.1*
d	28	741856.8ns	473908.3ns	898221.6ns	692566.6ns
t	80	971183.7	745373.0	1134600.8	771897.3
block	1	456330.9	3006470.8	33048558.4	23948028.9
blka	8	645823.5	180798.9	2173701.3	591783.3
blkb1	1	478402.8	207553.1	1792523.8	624543.4
blkb2	8	547779.7	147969.8	1354146.8	1137761.6
blkb3	27	478745.1	446126.6	631234.5	513102.5
blkb	36	494076.6	373242.5	824139.7	655011.2
blkc	8	645755.3	217049.1	1755508.3	900884.7
blkd	28	594531.4	448891.4	543423.3	484351.1
blkt	80	559578.4	364855.9	953982.0	613544.7

*, **, *** P<0.05, 0.01 and 0.001 respectively; ns, non-significant P>0.05

The additive effects component was significant for yield across all the P and N effects and mega-environments Alupe and Mwea. This is a clear indication that the additive gene effects were operative for yield trait. The dominance effects 'b' (H_2) were significant at Alupe under N condition. The b_1, b_2, b_3 components were homogeneous under P experimental environments at both Alupe and Mwea, but under N conditions, these were homogeneous at Mwea and heterogeneous at Alupe. The unidirectional dominance 'b_1' (h^2) was not effective in all conditions, while the asymmetry of genes distribution was operative under N condition at Alupe. The dominance gene deviations (b_3) not accounted for by b_1 and b_2 (H_1-H_2) effects were not significant in all the cases (Murai and Kinoshita, 1986). The maternal effects (c) were operative in all cases except under P experimental environment at Mwea. The non-maternal effects (d) (Ferreira, 1985; Viana, 2000b) other than those explained by 'c' were insignificant (P>0.05) in all cases.

7.3.1 The components of variation estimation

The genotypic differences were found to be very highly significant in all cases except for P at Mwea where it was highly significant (P<0.01) as shown in Table 7.3 below, allowing further analysis for all the cases.

Table 7.3 The analysis of variance of rice yield under P and N effects at Alupe and Mwea mega-environments

	Alupe			Mwea		
		P effect	N effects	P effect		N effects
Source of variation	DF	MS	MS	DF	MS	MS
REP stratum	2	393003	202153	1	1461639	163
GENOTYPE	80	2747315***	2236116***	80	1465513**	1871871***
ENVT	1	135334*	9019426***	1	58766319***	25297467***
GENOTYPE.ENVT	80	1604627***	1094569***	80	1016579ns	1221204ns
Residual	322	22473	29573	161	922457	967178

*, **, *** P<0.05, 0.01 and 0.001 respectively; ns, non-significant P>0.05

7.3.2 The variances and covariances estimates

The variances (V_r), covariances (W_r) and array means were estimated and the parental means and variances are as indicated in Tables 7.4 to Table 7.7 below for both P, N conditions and Alupe and Mwea mega-environments.

Table 7.4 The variances, covariance, mean array and rice parents for P condition at Alupe.

Array	Vr	Wr	Wr-Vr	Wr+Vr	Array mean	Parent mean
NERICA1	320927.8	56534.6	-264393.3	377462.4	4253.6	3776.5
Duorado	298576.7	117610.8	-180965.9	416187.5	4827.6	5150.0
IR79913-B-176-B-4	139612.9	19770.4	-119842.5	159383.4	4709.4	4750.0
CT16333(1)-CA-20-M	88683.9	-2781.0	-91464.8	85902.9	5085.9	5106.5
CT16333(1)-CA-22-M	245310.2	157058.7	-88251.5	402369.0	4817.4	4750.5
CT16333(2)-CA-18-M	223820.4	134582.9	-89237.5	358403.2	4874.5	5222.5
CT16313-CA-19-M	591978.2	475584.1	-116394.1	1067562.4	4642.8	3075.0
WAB964-B-3A 1.2	210048.5	107634.2	-102414.2	317682.7	4536.9	3976.0
CT16317-CA-4-M	122268.8	-15202.7	-137471.5	107066.1	4843.7	4168.0
*Av. heterosis					327.1	

*Av. Heterosis (mean potence) is the mean of all crosses minus the man of all parents per trait

Table 7.5 The variances, covariance, mean array and rice parents for N condition at Alupe.

Array	Vr	Wr	Wr-Vr	Wr+Vr	Mean array	Mean Parent
NERICA1	266643.9	116473.0	-150170.9	383117.0	4356.6	3443.1
Duorado	230859.6	245661.7	14802.1	476521.3	4801.0	5529.3
IR79913-B-176-B-4	141945.0	208812.2	66867.2	350757.2	4875.8	4831.0
CT16333(1)-CA-20-M	47769.2	-5073.7	-52842.9	42695.5	5092.8	5243.1
CT16333(1)-CA-22-M	154758.0	216234.0	61476.0	370991.9	4780.6	5061.9
CT16333(2)-CA-18-M	106913.0	112327.9	5414.9	219240.9	5112.2	5381.7
CT16313-CA-19-M	329696.6	259732.6	-69963.9	589429.2	4690.6	3568.7
WAB964-B-3A 1.2	112082.8	44456.1	-67626.7	156538.9	4924.8	5297.5
CT16317-CA-4-M	175765.3	55189.8	-120575.5	230955.1	4861.6	4980.1
Av. heterosis					19.9	

Table 7.6 The variances, covariance, mean array and rice parents for P condition at Mwea.

Array	Vr	Wr	Wr-Vr	Wr+Vr	Array mean	Parent mean
NERICA1	200871.8	23161.9	-177709.9	224033.7	3908.2	3338.1
Duorado	311451.4	72901.4	-238550.0	384352.8	3355.0	2602.5
IR79913-B-176-B-4	235102.7	24376.4	-210726.3	259479.1	3602.7	2794.3
CT16333(1)-CA-20-M	300815.2	292577.8	-8237.4	593393.1	3882.6	4815.6
CT16333(1)-CA-22-M	414501.2	120972.9	-293528.3	535474.0	3775.5	3139.5
CT16333(2)-CA-18-M	161611.7	34235.2	-127376.5	195846.8	3870.4	3616.3
CT16313-CA-19-M	327528.2	196886.3	-130641.9	524414.5	3928.2	3475.5
WAB964-B-3A 1.2	149016.0	-73087.7	-222103.7	75928.4	4153.0	3594.7
CT16317-CA-4-M	256437.5	166843.0	-89594.6	423280.5	3668.7	2778.7
Av. heterosis					498.6	

Table 7.7 The variances, covariance, mean array and rice parents for N condition at Mwea.

Array	Vr	Wr	Wr-Vr	Wr+Vr	Array mean	Parent mean
NERICA1	212494.5	114611.7	-97882.8	327106.1	3843.4	2842.5
Duorado	224140.1	93912.3	-130227.8	318052.5	3698.5	3383.0
IR79913-B-176-B-4	85366.4	-54471.9	-139838.2	30894.5	3781.8	3740.7
CT16333(1)-CA-20-M	197001.0	87521.1	-109479.9	284522.1	3908.0	4848.4
CT16333(1)-CA-22-M	260789.0	42220.7	-218568.3	303009.7	3685.2	3079.3
CT16333(2)-CA-18-M	248462.8	12627.3	-235835.5	261090.1	3799.9	4030.1
CT16313-CA-19-M	133109.6	23442.9	-109666.7	156552.4	3771.5	3989.6
WAB964-B-3A 1.2	126403.1	-37806.8	-164209.9	88596.3	4015.5	3389.3
CT16317-CA-4-M	160626.3	88150.4	-72475.9	248776.6	3499.6	2905.5
Av. heterosis					224.4	

The average heterosis (mean potence) had positive values indicating predominance of overdominant and dominant genes in inheritance of grain yield under low soil N and P conditions. The array means compared to parental means were high, except for parents Dourado, IR79913-B-176-B-4, CT16333(1)-CA-20-M and CT16333(2)-CA-18-M indicating dominant genes were associated with increase in yield under P condition for Alupe. The differences over arrays (W_r-V_r) were all low, while parental order of dominance (W_r+V_r) were high indicating that recessive genes were controlling reduced inheritance of yield for all the cases. For Alupe under N condition the array means were large for parents NERICA1, IR79913-B-176-B-4 and CT16313-CA-19-M indicating these parents had dominant genes enhancing yield.

The testing of validity of hypothesis postulated by Hayman (1954) was undertaken for all the three tests; 't', b_o - b=0 and b_1 - b=1 as explained by Viana (2000a). The non-significance of 't', b_1 and significance of b_0 signifies adequacy of the additive-dominance model. The reverse of any of the above indicates failure and since the other two or one test signifies adequacy, as whole the model is then partially adequate (Marwat, 2002). However, failure of all hypotheses tests indicate complete inadequacy of the model. The N, (Alupe), P and N (Mwea) conditions showed partial adequacy of the model because bo test of hypothesis failure. However, under P experimental environment at Alupe, the additive-dominance model was completely adequate. Normally the W_r-V_r uniformity indicates validity of the assumptions.

7.3.3 The Covariance - Variance (W_r-V_r) graphs

Useful information is provided by plotting the relationship between covariance (W_r) and variance (V_r) (Hayman, 1954; viana et al., 1999). The parabola limits were plotted by

estimating the values W_{ri} (VoLo* V_{ri}) where i indicate genotypes 1 to n. The plot of W_{ri} against V_r values graphs are indicated in Figure 7.1 to Figure 7.4 below for Mwea and Alupe mega-environments. The standard regression line of unit slope was plotted by drawing W_{rei} against V_r. The distance between the origin (0,0) and the point of intersection of the limiting parabola and this regression line is was divided into four equal parts.

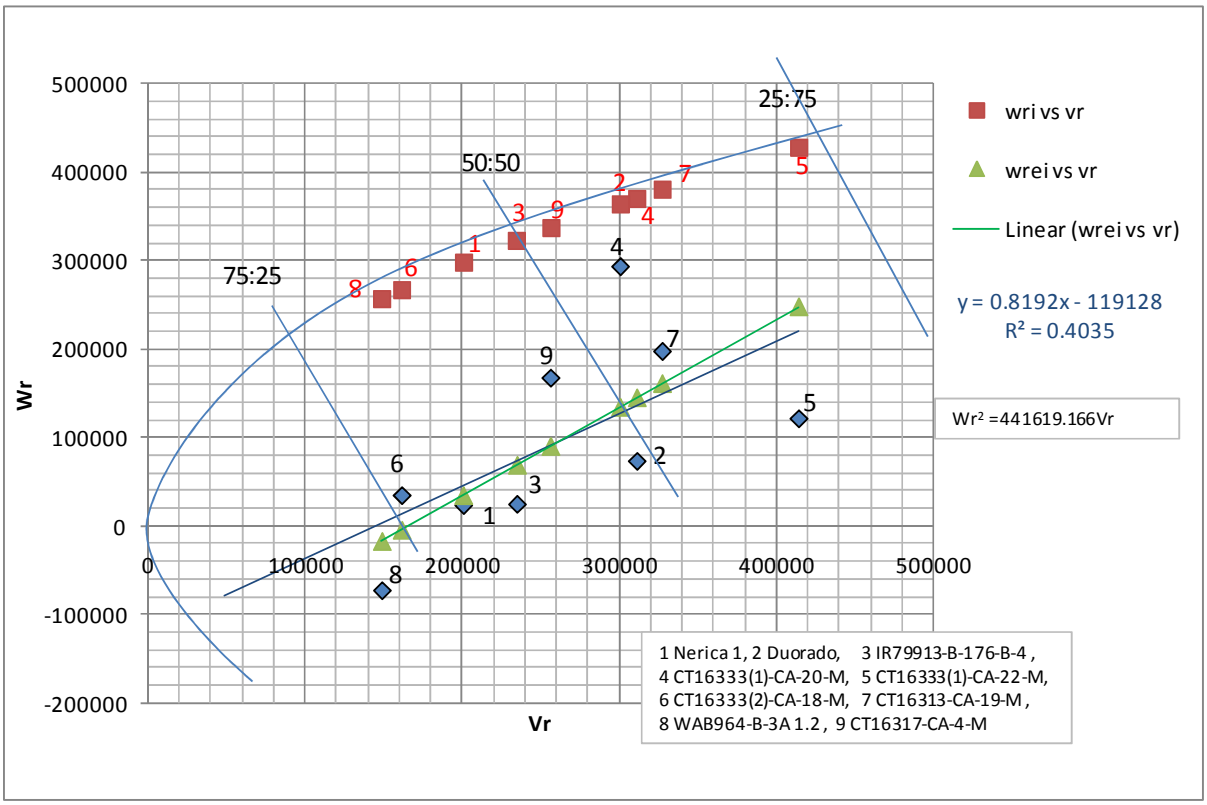

Figure 7.1 The $W_{r's}$ and V_r parabola and regression lines for rice grain yield under soil P condition at Mwea

The assumption of non-presence of non-allelic interaction was evidently met in all cases (Fig. 7.1 – 7.4) as the regression coefficient did not differ from unit in any considerable way. The regression line (triangles of unit slope) cut the covariance axis below the origin in all cases; except for N experimental environment at Alupe (Fig. 7.4), where it cut above the point of origin indicating partial dominance. Thus overdominance played a major role in genetic inheritance of yield under both P and N and mega-environments albeit for N condition at Alupe (Marwat, 2002; Viana, 2005).

The parents were variedly scattered along the regression line, thus exhibiting great variability (Dickinson and Jinks, 1956; Jinks, 1954). Parents 8 (Fig. 7.1) and 3 (Fig. 7.2) exhibited the most dominant genes for yield under soil P and N experimental environments respectively at Mwea.

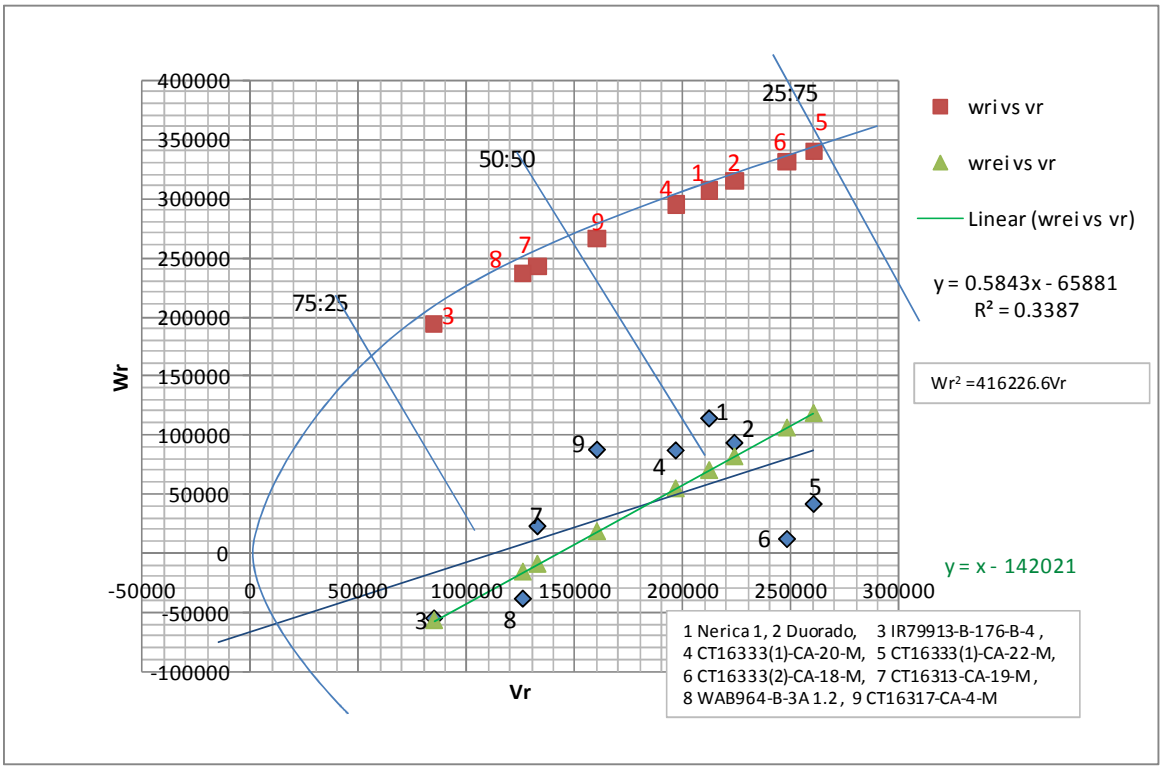

Figure 7.2 The $W_{r's}$ and V_r parabola and regression lines for rice yield under soil N condition at Mwea

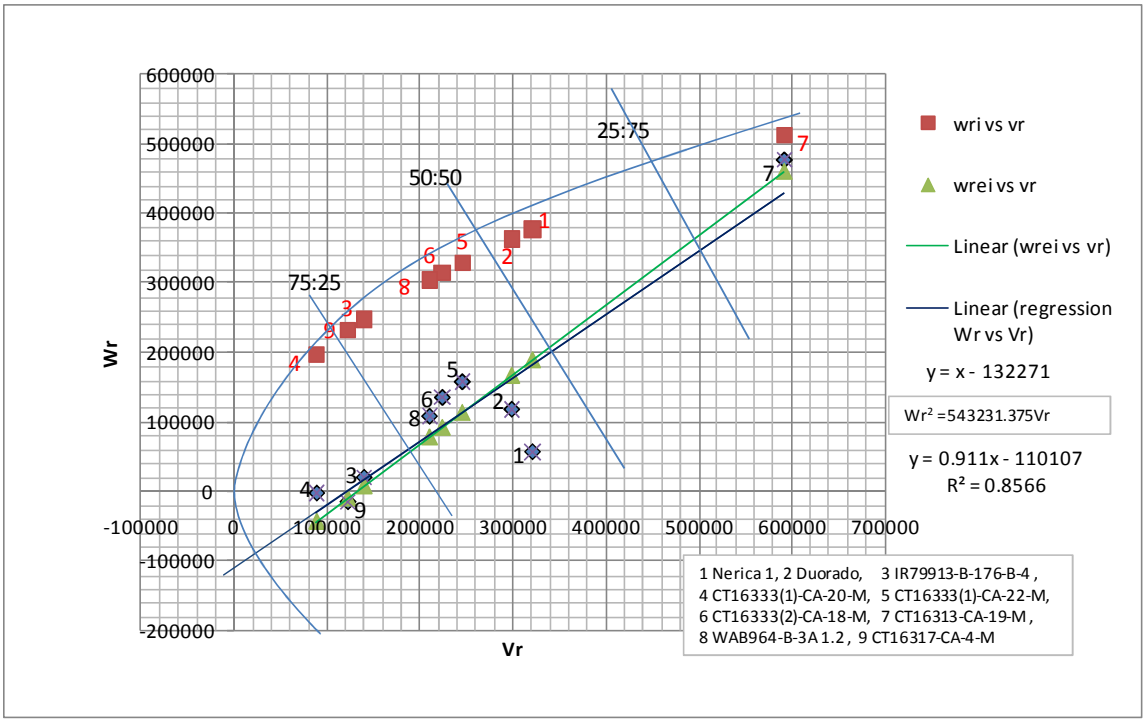

Figure 7.3 The $W_{r's}$ and V_r parabola and regression lines for rice yield under soil P condition at Alupe

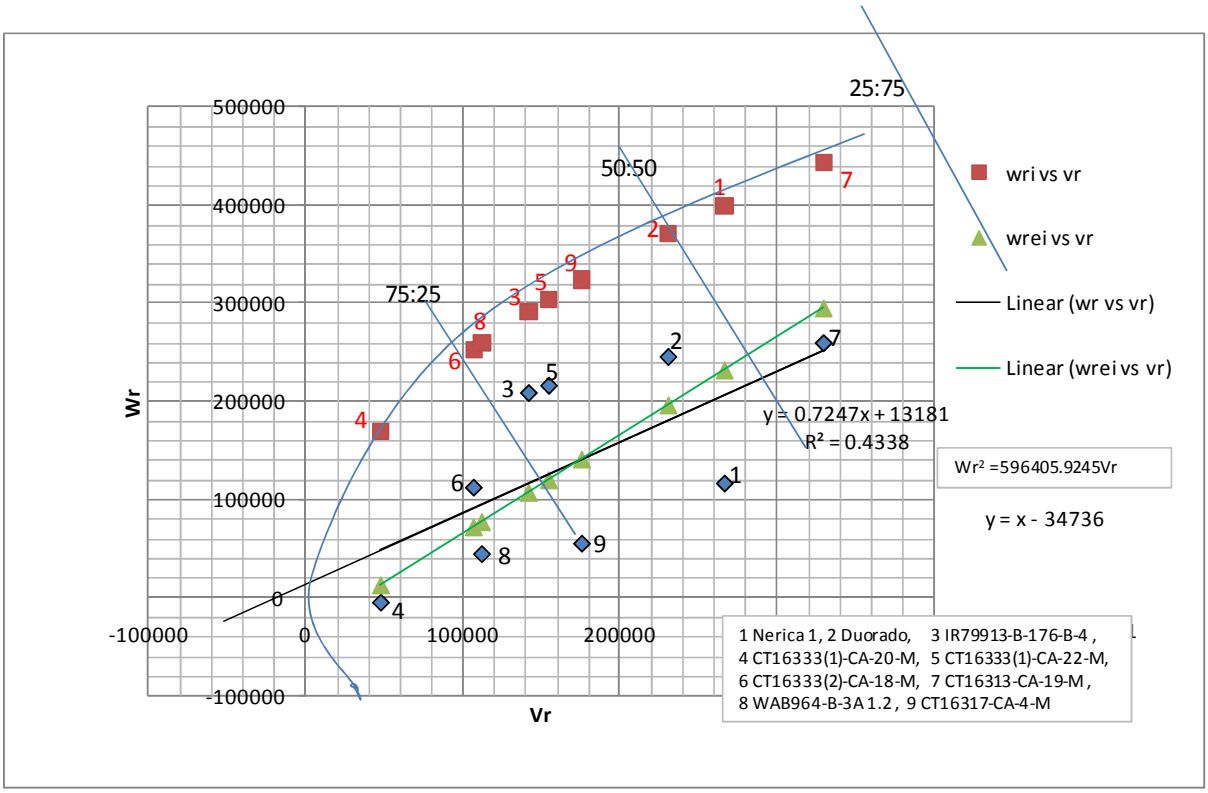

Figure 7.4 The $W_{r's}$ and V_r parabola and regression lines for rice yield under soil N condition at Alupe

The parent 4 in both P and N experimental environments at Alupe had the most dominant genes controlling grain yield. Parents 5 at Mwea and 7 at Alupe had excess recessive genes under both N and P conditions, respectively.

7.3.4 The components of variation estimation.

Rehman et al. (2010) using eight parent diallel on mungbean, Schuelter et al. (2010) using ten parent partial diallel on pepper, Marwat (2002) using a six full diallel on cotton, Murai and Kinoshita (1986) using a half five parent diallel, Johnson and Aksel (1959) using various forms of a fifteen diallel parents and Hayman (1954) using a eight parent full diallel of *Nicotiana rustica* have estimated the components of variation; D, H_1, H_2, F,h^2, E and E_2 and their ratios after proving the simple model to be adequate (Hayman, 1954; Jinks, 1956). Their values are presented in Table 7.8 for the nine parent full diallel, for both P and N soil fertility experimental environment conditions, and Alupe and Mwea mega-environments. The D, F, H_1, and H_2, are overall measures of gene action in the parents (Hayman, 1954; Hayman, 1958). The variation explained by additive effects (D) had positive values at Alupe and negative values at Mwea for both the P and N conditions. The covariance of additive and dominance effects (F) in a given array, was positive in all cases, indicating preponderance of dominant gene effects irrespective of whether they increased or decreased the effects (Mather and Jinks, 1971).

The standard errors for their test are also indicated in Table 7.8. The D component was significant for both P and N condition at Alupe (P<0.001), but not at Mwea. The F component of variation was significant except for Mwea under P experimental environment condition. It was however positive in all cases suggesting presence of more dominant alleles in parents than recessive alleles. H_1 component of variation due to dominance gene effect had negative and was only positive at Alupe under P condition. The H_1 was less than D in all cases indicating absence of overdominance. H_2 was greater than H_1 except under N at Alupe indicating equality of alleles. The H_2 component of variation indicates important information about the genes of the rare homozygotes, in the present case it had non-significant figure, being positive at Mwea and negative at Alupe. The dominance effects (h^2) when summed over all loci and crosses in heterozygous phase had negative values but highly significant figures at Mwea (P<0.001).

Table 7.8 The components *E, D, F, H_1, H_2, h^2 and their S.E. for rice yield under P and N conditions at Alupe and Mwea

Component	Alupe		Mwea		Test of components - Alupe		Test of components - Mwea	
	N effects	P effects	P effects	N effects	N effects	P effects	P effects	N effects
E	10212.9	8253.4	462892.6	480604.4	0.2ns	0.304ns	11.31***	18.5***
E_2	3404.3	4126.7	231446.3	240302.22				
D	586193.0	534977.9	-21273.5	-64377.8	10.3***	12.4***	-0.3ns	-1.6ns
F	649599.2	626373.3	890146.2	1071413.2	2.4*	3.2*	3.0ns	5.6***
H_1	-652791.6	-919785.7	-982043.9	-474948.2	-1.3ns	-2.4*	-1.7ns	-1.3ns
H_2	-760572.8	-450299.3	812404.1	326121.4	-1.8ns	-1.4ns	1.7ns	1.1ns
h^2	-48337.1	-57382.7	-3289686.5	-3416733.6	-0.2ns	-0.3ns	-10.0***	-16.4***
S.E.(D)	57124.6	42985.2	64699.5	40983.8				
S.E.(F)	266082.4	200221.9	301365.6	190899.6				
S.E.(H_1)	504335.2	379502.6	571211.4	361833.0				
S.E.(H_2)	433545.3	326234.5	491034.6	311045.1				
S.E.(h^2)	290436.5	218547.9	328949.2	208372.4				
S.E.(E)	18064.4	13593.1	20459.8	12960.2				

*D - variation on account of additive effects; E - component of experimental error
F - the covariance of additive and dominance effects in a single array (allele frequency),
H_1 - variation due to dominant gene effects,
H_2 - proportion of positive & negative genes in parents
h^2 - dominance effect as sum over all loci in heterozygous phase in all crosses

7.3.5 Estimation of important genetic parameters

Various variance components had varied ranges of values as shown in Table 7.9. The mean degree of dominance had the highest value at Mwea under N experimental environment. The contribution of genes with either increasing or decreasing effects were high under N conditions at Alupe, while the coefficient of correlation between the parental order of dominance (Wr+Vr) and the parental measurement Y_r had highest values at Mwea under N experimental condition. Prediction for measurement of completely dominant and recessive

parents for grain yield had a value of 0.3 at Alupe under N condition. The number of group of genes that show dominance and control yield tended to have a high negative value at Mwea under P condition. The heritability in narrow sense was most effective for yield under N condition at Alupe (Nelder, 1953; Viana, 2005). The values of completely dominant and recessive parents were 394465.2 and 535292.2 at Alupe under N and P experimental environments, respectively.

Table 7.9 Important genetic parameters estimated for rice yield under P and N condition at Alupe and Mwea mega-environments

Description	formulae	Alupe		Mwea	
		N effect	P effect	N effect	P effect
(mean degree of dominance)	$(1/4H_1/D)^{1/2}$	0.5	0.7	3.4	1.4
Proportion of genes with increasing or decreasing effects in Parents	(H2/4H1)	0.3	0.1	0.1	-0.2
Proportion of dominant and recessive genes with increasing and decreasing effects in Parents	$0.25*(4*DH1)^{1/2}$ +0.5*F)/(0.25*(4D H1)$^{1/2}$ -0.5*F)	-40.9	1.9	-1.4	-1.4
The coefficient of correlation between the parental order of dominance (Wr+Vr) and the parental measurement Yr	r	-0.6	-0.1	0.2	0.1
Prediction for measurement of completely dominant and recessive parents	r^2	0.3	0.01	0.1	0.01
Number of groups of genes that control the trait and show dominance	h^2/H_2	0.1	0.1	4.1	10.5
{1/4D}c/[1/4D+1/16H_1-1/8F+E]	h^2_{ns}	4.2	21.5	-0.02	-0.05
completely dominant parents value	Y_D	394465.2	-53644.5	32521.7	27067.8
completely recessive parents value	Y_R	-37929.1	535292.2	333673.1	251766.0

7.4 Discussion

The results showed that maternal effects (c) were significant except under P condition at Mwea. This implies that the selection of which parent to be used as the female matters (Deborah, 1987) and that if a locally adapted genotype has to be used as a male, then a problem may arise. This is probably because many of the genic traits unique to its local adaptation and quality (transmitted via cytoplasmic mitochondrials genes) in case of upland rice may be difficult to regain or recover. The same case was observed for reciprocal differences (d) apart from those ascribable to 'c'. This may imply that part of grain yield is controlled by cytoplasmic effects (Mather and Poysa, 1983).

7.4.1 The Covariance - Variance (W_r-V_r) graphs

The regression of W_r on V_r gives a line of unit slope for any dominance level, but in absence of dominance it regresses to a single point (Dickinson and Jinks, 1956). This did not happen and thus dominance was present in all cases and environments (Allard, 1956; Mather and Poysa, 1983). The array values for (W_r - V_r) were fairly homogeneous across the parental arrays thus dispelling epistasis, but (W_r + V_r) values were heterogeneous across the arrays thus supporting existence of dominance. The average heterosis in all cases was positive showing that the overdominant and dominat genes were important in inheritance of grain yield in the desired direction. The parents 3, 4, and 8 had lower Wr and Vr values hence they had greater proportion of dominant genes. The presence of some non-allelic interaction and particularly those of complementary gene action may have made parents 4, 6, 1 and 5 deviating further from the regression line . This made the regression lines to fail to fit into a completely unit slope (Figs.7.1 to 7.4) and this is hardly realized anyway (Dickinson and Jinks, 1956; Hayman, 1959). In this study no parent had complete heterozygosity (h=0), that is no dominance, as none of the parent fell on the limiting parabola line, further confirming adequacy of the simple model. Since the regression line was cutting the expected unit slope line, complementary gene action can be ruled out in this study on grain yield inheritance. Otherwise the regression line could lie to the right of that of unit slope (triangle points) (Mather, 1967; Nassar, 1965).

The genetic component of variation indicated that the additive (D) component was significant for the grain yield at Alupe, and this probably suggested yield improvement in upland rice may be carried out with simple methods like mass selection in the initial stages of segregating generation (Verma and Srivastava, 2004). The later use of recurrent selection can be adopted for homogeneous materials. The non-significance of D component at Mwea was further confirmed by the low h^2_{ns} estimates, and this behaviour signifies that the performance of the genotypes was different in the two mega-environments. Probably different sets of genes were in operation, which is indicated by Alupe site having few but positive values, while Mwea has higher but negative value for h^2/H_2 (Table 7.9). This probably can be interpreted as different genotype adaptation to different environments and thus need to adopt the approach of utilizing development of genotypes with specific adaptation to particular environmental stress like poor soil fertility, instead of widely adopted genotypes (Atlin *et al.*, 2006; Baligar *et al.*, 2001; Ceccarelli, 1994; Choo *et al.*, 1988; Dobermann and Fairhurst, 2000; Donovan *et al.*, 1999; Kimani and Derera, 2009). The estimate of H_2 was larger than H_1 indicating that positive and negative genes were symmetrically distributed. However, Verma and Srivastava (2004) in their study observed the

reverse for the gene governing grain yield. The negative and significant h^2 at Mwea imply more frequent distribution of recessive genes and probably this resulted in lower h^2_{ns} a case that was also observed by Verma and Srivastava (2004). This means that at Mwea, a rigorous breeding program should be used to identify parents with positive h^2 values for quicker genetic gains for grain yield under low soil ferility conditions and with low selection pressure. The F component was positive and significant in all cases, except under P condition at Mwea, thus verifying the distribution of genes as asymmetric in parents and this was further accentuated by the ratio of $H_2/4H_1$. The ratio of $H_2/4H_1$ at Alupe under N soil condition was 0.29 which is near a square of 0.5, thus indicating near equality of both positive and negative gene effects (Schuelter et al., 2010). The E component was non-significant at Alupe indicating that environment played a minor role, however, at Mwea, under both N and P experimental conditions, this component was highly significant ($P<0.001$) indicating the major role the environment played in grain yield (there were unusually high rainfall). The mean degree of dominance $(H_1/4D)^{0.5}$ had values greater than unity at Mwea thus exhibiting overdominance, a situation observed by Verma and Srivastava (2004) and Schuelter et al. (2010). However, at Alupe the values were below unity, signifying lack of overdominance in the parents. The values of completely dominant (Y_D) and recessive (Y_R) parents (Table 7.9), had positive values in all cases except under P and N experimental conditions at Alupe. These values Y_D and Y_R are the predicted possible limits of selection for the genes exhibiting dominance (Hayman, 1954; Murai and Kinoshita, 1986), and at Alupe P condition had the highest values, while at Mwea, N condition had the highest value. This indicates the possibility of selection and development of genotypes well adapted to low soil fertility conditions as far as grain yield is concerned.

7.5 Conclusion

1) The simple additive-dominance model was adequate for grain yield and estimation of various components and there ratios indicated potential for low soil fertility rice improvement for better yields.
2) The fixable additive gene effects were shown to be significant for yield under soil N and P experimental environments and the two mega-environments.
3) The narrow sense heritability reached 21% indicating although not as high, but nonetheless with the normal range, yield improvement is possible.
4) Overdominance was predominant and partial dominance was only observed at Alupe under soil N condition

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CHAPTER EIGHT.

Thesis Overview

8.1 Introduction

This chapter provides an overview of the thesis, highlighting the objectives and hypothesis and restating the major findings. It also states the implication of the results.

The general objectives were:

i) To establish the constraints and preferences for Kenya rice farmers,
ii) To evaluate and select adapted promising genotypes with desirable genes for tolerance to low soil P and N from the broad germplasm accession for hybridization with the local cultivar,
iii) To establish the genetic control of low soil phosphorous and nitrogen tolerance under environments prevalent in farmers' upland rice fields,
iv) To determine the relationship between rice P and N tissue content and soil available amounts in determining yields and their physiology in F_2 and F_3 segregants and their parents,
v) To relate the phenotypic sensory for fragrance to marker assisted selection for the fragrance rice (fgr) gene as a tool for frgrant upland rice breeding, and
vi) To generate information about gene action and inheritance pattern of yield in rice for developing breeding lines for enhanced performance under the prevalent low soil fertility, especially low N and P, in farmers' fields.

8.2 Summary and implications

The summary and implications are presented below.

Farmers Participation in Identification of Upland Rice Variety Preferences, Production Constraints, Socio-Economic Information

The survey conducted and supplemented with focus group discussion and key informants established the following:

- The farmers preferences in the rice varieties were high yielding, the need to have hybrid rice varieties cropping systems, nutrient use efficiency as the most preferred and these accounted for 53.7% of their wishes.
- Among the crops grown by the selected farmers, rice was the most important followed by maize, however, the hectarage of maize was the highest followed by rice.
- Farmers identified labour costs as a factor limiting production especially for irrigated rice and thus they preferred upland rice due to its less labour intensiveness.
- Farmers identified land preparation, inputs, planting, weeding and harvesting as the most expensive activities.
- Majority of the respondents grew irrigated rice, and 25.4% grew upland rice. This disparity was attributed to the fact that upland rice was new, the varieties having been officially released in 2009.
- The majority of the farmers expressed their desire to grow upland rice but lack of seeds, appropriate varieties and production knowledge was a major setback.
- The existing varieties were viewed as being high input based and farmers could not afford inputs, suggesting the need to have varieties with better response to inputs.
- The main fertilizers used were Diammonium Phosphate (DAP), Sulphate of Ammonia (SA), Calcium Ammonium Nitrate (CAN) and NPK (23:23:0), though the amounts used were very low and contributed little to any consequential yields. This was the case even after the farmers indicated that soil fertility was poor due to continuous cropping under irrigation.

It can be concluded that the farmers prefer varieties with high yield and good grain quality and efficient in nutrient use. They indicated preference for hybrid rice which should be considered in future and drought tolerant, insect pests (white stem borers) resistant varieties. Simple implement to aid in rice production were a necessity. There is therefore need to consistently involve farmers in participatory plant breeding in order to meet their desires in a variety and thus ensure wide adoption. There need to research on possibility of developing hybrid rice as is the case in China where more that 50% of rice area is under hybrid rice (Virmani et al., 2003).

Characterization and Selection of Upland Rice Germplasm under Low and High Soil Phosphorous (P) and Nitrogen (N) Environments

Accessions were acquired and evaluated under the prevailing conditions for characterization and selection of suitable parents for introgression of desirable genes into the local materials in a hybridization block. The following were the results:

- There existed good adaptation of the tested accessions with high variability. Seven accessions; IR79913-B-176-B-4, CT16333(1)-CA-20-M, CT16333(1)-CA-22-M, CT16333(2)-CA-18-M, CT16313-CA-19-M, WAB964-B-3A 1.2, CT16317-CA-4-M including NERICA1 and Duorado that had desirable traits were selected and used as parents in crossing block.
- The degree of genetic determination (H^2) ranged from 8.0% for 1000-grain weight to 26.7% for top biomass.
- The phenotypic coefficient of variation of genotypes ranged from 12.3% for days to maturity to 148.5% for top biomass, while, that of days to maturity ranged from 14.3% to 159.7% for top biomass.
- The genetic advance (GA) had values ranging from, 0.2 for phosphorous tolerance to 1080.5 for grain yield, while the genetic advance expressed as percent of the mean was 5.7% for days to maturity and 87.9% for top biomass.
- The mean values for the ten characters studied had wide variability under the four environments with days to maturity ranging from 188 for genotype ARCCU1Fa1-L4P3-HB under N+P+ to 177 days for genotype CT16333(1)-CA-1-M under N-P- condition.
- The highest yielding genotype was CT16328-CA-18-M under N-P- yielding 5916 kg ha^{-1}. The germplasm showed usable variability for low soil fertility adaptation, and hence improvement was possible to take advantage of the vast unexploited upland environments for increased rice productivity. The use of elite accessions can greatly broaden the local germplasm and lead to development of higher performing varieties under varied local environmental stresses.

Combining Ability and Performance of Rice Genotypes Under Four Different Soil Fertility Environments

The F_2 segregants resulting from a nine parent full diallel mating design (Griffing's, 1956) were evaluated and the following were the major findings:

- The GCA:SCA ratios were less than 1.0 for the majority of the traits under all the soil fertility environments, indicating greater proportion of nonadditive genetic effects that are not fixable. Thus hybrid rice may be developed to exploit heterosis.
- The maternal and nonmaternal mean squares were found to be significantly different from zero ($P<0.05$) for most the ten traits under study. This means that the nonfixable genetic effects were larger than the additive effects.

- The GCA effects for the parents were significant under different experimental environments but they had both positive and negative signs indicating different directions of influencing the trait of interest.
- The genotypes had both specific and broad adaptation as exhibited by their diverse rankings under different environments.

The preponderance of nonfixable nonadditive genetic effects means that their exploitation can be achieved by hybrid variety developments.

Genetic mechanisms controlling Leaf and Seed P and N Content in the F_2 and F_3 Rice Populations

The F_2 and F_3 leaf and grain samples for determination of N and P content (Griffing's, 1956b) and there relation with soil N and P was investigated and the results were:

- There was significant genotypes, environments and genotypes by environment interaction. This indicated that both genetic and environments were importance in governance of the traits
- The genetic components gave highly significant GCA and SCA mean squares for the days to heading, anthesis and maturity, phosphorous and nitrogen tolerance, top biomass, plant height, number of panicles, 1000 seed weight and grain yield under the four soil experimental environments. This implies that both additive and nonadditive effects were controlling inheritance of these traits
- The general combining ability effects (GCA) for parents were significant in both F_2 and F_3 materials for the ten traits studied and under all the experimental conditions.
- The leaf and seed N and P contents gave significant genotypic mean squares values for Mwea, Alupe and Matuga mega environment, implying additive effect were in control of seed N and P inheritance.
- The GCA and SCA mean squares were significant for leaf and seed N and P content for the three locations.
- The GCA effects for the nine parents had significant values for leaf nitrogen and phosphorous for the three locations. This implies performance of the progenies can be predicted from the mean of the parents.
- The GCA:SCA ratios had larger values of more than 1.0 for the majority of the traits under the four soil N and P conditions. This was a clear manifestation of the dominant role of additive gene action over the dominance effects and that improvement for low P and N soil fertility tolerance is practical.

The wide variability between stored N and P in the plant tissue and the actual performance of the metric traits can be exploited to develop more efficient varieties that can give economic yields under prevailing stress environment.

Association of Phenotypic traits and Variations in SSR Markers for Fragrance and Performance of Metric Traits for the Parents and F_2 progenies under different soil fertility regimes

The nine parents used in the diallel were evaluated phenotypically and by use of SSR marker for the fragrance while the F_2 materials were evaluated for metric traits performance in relation to fragrance. The following are the results:

- The SSR marker RM223 was polymorphic while, RM284 gave monomorphic results.
- Four alleles were detected including: 146, 155, 161, and 163.
- The GCA:SCA ratio was 1.48 indicating greater fixable additive effects over the nonadditive effects in fragrance inheritance.
- Test for independence using Chi-square indicated that there was no association between fragrance phenotypic and RM223 allele.
- The performance of the fragrant lines was generally lower than that of nonfragrant lines.
- There was negative association between fragrance score and other agronomic traits such as grain yield across the three soil N and P regimes.
- The NERICA1 was found to be a good donor for fragrance and can be exploited in a breeding programme.

The lack of association between fragrant phenotype and RM223 was probably use of few parents and flanking markers instead of gene markers. In future gene markers that are more specific should be used more parents should be used involving more parents. The sensory phenotyping may be limited by the fact that it may be affected by environment and thus give inconsistent results. The use of the more environment tolerant SSR markers may speed up breeding work as seedlings can be used to detect fragrance and thus discard the nonfragrant ones, hence reducing cost.

Genetic Analyses of Rice Grain Yield under Low Soil Phosphorous (P) and Nitrogen (N) Conditions for Two Mega-Environments

The F_2 segregants were analyzed using Hayman diallel analysis (Hayman, 1954; Mather and Jinks, 1977) to determine the magnitude, the nature of genes controlling grain yield under different soil and environments. The findings were:

- The additive gene action were found to be significant for all cases of N and P experimental environments and the two mega environments.
- The additive gene action were more important than the dominant gene effects, indicating the need to use judiciously simple mass selection and pedigree methods in the early generations and bulk method after segregating materials show uniformity.
- The h^2_{ns} for upland rice grain yield was 21.52% and 4.22% under P and N, respectively at Alupe.

The yield under the contrasting fertility and environments was shown to be under additive genetic effects and thus progress in grain yield improvement can be realized for the target environments. There is need to do deeper genetic analysis in order to fully understand the genes conferring certain traits of interest in a breeding programme. This could result in better breeding programme planning and determination of the best environmental designs to be applied to capture the intended outcomes.

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