THE ROLE OF *POTAMOGETON CRISPUS* L. IN THE PONGOLO RIVER FLOODPLAIN ECOSYSTEM

VOLUME I, TEXT

By

KEVIN HUGH ROGERS

Contents: V.1 Text. - V.2 Figures, tables and plates.

Submitted in partial fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in the

DEPARTMENT OF BOTANY,
UNIVERSITY OF NATAL,
PIETERMARITZBURG.

DECEMBER 1984

The author hereby declares that this whole thesis, unless specifically indicated to the contrary, is his own original work and that it has not been submitted in any form to another University.

To my family (all generations) who have so selflessly watched me spend so much of their time on this thesis.

Sheila Giles, who typed this thesis, cheerfully accepted my many alterations to the text and corrected some atrocious spelling.

The Council for Scientific and Industrial Research, through the Co-operative Scientific Programmes, provided the financial support for this study, except during the first year, when Charles Breen generously provided funds for a grateful student.

The Natal Parks Game and Fish Preservation Board, The Kwa-Zulu Department of Nature Conservation and South African Defence Force provided necessary permits and welcome logistic support.

My parents have given me fantastic encouragement, moral and other support throughout my studies. Their carefully considered guidance and advice have, and always will be, of great value to me.

Lastly to my wife, Flea, go my warmest thanks. Her assistance, advice, encouragement and thought provoking discussion in both the field and laboratory, have only been surpassed by the companionship and love she has provided since this study's inception.

SUMMARY

1. Aquatic macrophytes generally dominate energy and nutrient transfers in wetland ecosystems. They provide a diverse habitat for other organisms but each species or life-form, has a different role in determining ecosystem structure and function. A multidisciplinary research project on the Pongolo River Floodplain, Zululand, South Africa, provided a good opportunity to study the role of a submerged species, *Potamogeton crispus* L. in a wetland ecosystem.

2. The role of a plant species in ecosystem structure and functioning is contingent primarily upon its adaptations to the interactive biotic and abiotic components of the multifactorial environment. This role is manifest in the contribution the species makes both to the sum total of transfers of resources within the ecosystem and to the nature of the physical and chemical environment. These contributions can be to both the conservative energy-matter transfers of the ecosystem and to the information network which regulates ecosystem functioning.

3. This study set out, using Tete pan as the main field site, to:
   i) Characterise the major physical, chemical and biotic variables of the floodplain ecosystem which are most likely to affect the acquisition of resources by *P. crispus*.
   ii) Determine the way the species influences the environment.
   iii) Assess the species adaptations to environmental characteristics.
   iv) Assess transfers of resources from *P. crispus* to other ecosystem components, the factors affecting them and the contributions they make to ecosystem structure and functioning.
   v) Outline the implications of the findings for management of the ecosystem which is threatened by the contruction of an upstream dam.

4. Annual flooding of the Pongolo river and resultant poor light climate and fluctuating water levels create an unfavourable habitat for submerged plant growth in Tete pan during summer. During autumn through spring, however, stable water levels and good light penetration are favourable for plant growth. The duration of favourable and unfavourable periods varies annually, and on a longer time scale periodic droughts cause the pan to dry up completely. Nutrient concentrations and salinity of the water were favourable for freshwater plant growth during the study.

5. *Potamogeton crispus* on the Pongolo river floodplain is a winter producing annual which reproduces both sexually (achenes) and asexually (turions). Winter growth is initiated by turion germination each year and achenes ensure survival after drought. If floods continue into autumn young plants remain dormant until the light climate improves. Individual plants have a life span of 4 - 5 months but staggered germination of turions from April to June ensured that the population was present for up to 8 months. *Potamogeton crispus* was classified as a competitive-ruderal with multiple regenerative strategies. This life history enables the species to exploit the favourable period between floods and survive both summer flooding of unpredictable duration and intermittent droughts.

6. The major source of nutrients for *P. crispus* is the sediment pool and plant growth brings large amounts of nitrogen and phosphorus into circulation each year. The rapid completion of the life cycle ensures that in most years N and P released to the water during decay are taken up by other components of the ecosystem before the next summer floods. Thus, despite a potential for flushing of nutrient rich water by floods, pans such as Tete experienced a net gain in nutrients between flood periods during the study period.

7. *Potamogeton crispus* was the major primary producer in Tete pan during this study and although production was seasonal it was high (126 gm^{-3}) in comparison to other species reported in the literature.

8. The presence of an abundant and nutritious food source in the form of *P. crispus* turions, attracts a large and diverse waterfowl population to the floodplain each winter. During feeding the waterfowl uproot *P. crispus* plants and remove almost 90% of the turions. This represents a potentially unstable grazing system as the birds utilize the "residual growth potential" of the plant population. The hypothesis was formulated that stability of the grazing system and maintenance of *P. crispus* reproduction may be achieved by production of small turions which are energetically unrewarding for the waterfowl but form viable propagules. Overall, transfer of nutrients and organic matter to this grazing food chain represents a small ($<$10%) proportion of *P. crispus* production.

9. The growth of *P. crispus* in Tete pan provides a large surface area for epiphyton growth which increases in density and species diversity as plants age. Experiments showed that the host plant epidermis was invaded by necrotrophic bacteria but grazing of epiphyton by snails retarded this process in young leaves. However, as leaves aged the action of the bacteria softened (conditioned) the host tissues and promoted consumption of the leaves by snails. The co-existence of epiphyton and host plant is therefore achieved through a complex set of interacting attributes of the epiphyton community, the host plant and grazing animals. Comparisons with previously published hypotheses of the macrophyte-host relationship indicated that attempts to find a single controlling factor may be misleading and that adaptation for co-existence should be sought in a number of interacting variables.

10. Since conditioning of *P. crispus* by epiphytes and consumption of plants by snails follows a succession which reaches a climax during host senescence, it was important to develop a method of studying decomposition which included these processes. Experiments showed that both snails and bacterial conditioning had marked effects on the rates and pathways of dry matter and nutrient transfer during decomposition and that no single technique (eg. litter bags) will permit a thorough understanding of decomposition processes.

11. Conservative transfers of organic matter, nitrogen and phosphorus in Tete pan are dominated by the detrital food web with only a small proportion going to the grazing food chain. The consumption of *P. crispus* and its epiphyton by snails in winter and spring provides the major pathway of allochthonous production to the benthic detrital aggregate and detrital food web. These transfers are separated in both time and space from the allochthonous inputs of *C. dactylon* detritus which occur as a result of decay in the flooded pan margins during summer. The major input of phosphorus to the pans appears to occur by deposition of silt during floods but fixation of di-nitrogen by the epiphyton and in the detrital aggregate greatly exceed flood related inputs of nitrogen.

12. The continued functioning of the detritus dominated foodweb of the floodplain pans is dependent upon a sequence of resource transfers which are dominated, during periods between floods, by *P. crispus* and its epiphyton. The processes which regulate these conservative transfers show characteristics typical of the information network of cybernetic ecosystem functioning and hence it was hypothesised that the Pongolo floodplain ecosystem has the potential to buffer changes in resource input which will occur now that a dam has been constructed upstream. While the hydrological regime of the Pongolo river forms the primary determinant of the floodplain ecosystem, structure and function management of the system must also account for the "managerial" role of animals and temperature which initiate and rate regulate major ecosystem processes.

Page

LIST OF CONTENTS

ACKNOWLEDGEMENTS		i
SUMMARY		iii
LIST OF CONTENTS		vii
CHAPTER 1	INTRODUCTION	1
1.1	INTRODUCTION TO THE STUDY	1
1.2	REVIEW OF PERTINENT LITERATURE	3
1.2.1	"The role of plants in ecosystems": Theoretical appraisal	3
1.2.2	The floodplain environment	5
1.2.3	Plant life-history adaptations: A conceptual basis	7
1.2.3.1	Life-histories and reproduction of aquatic plants	10
1.2.4	Submerged aquatic plant production	12
1.2.5	Organic matter transfers	15
1.2.5.1	Transfers during growth	15
	Release of dissolved organic matter	15
	Grazing of submerged aquatic plants	16
	Losses due to damage	16
1.2.5.2	Transfers during senescence and decay	17
1.2.6	The acquisition and transfer of nutrients	19
1.2.7	The relationship between submerged plants and their epiphyton	20
1.2.8	Ecosystem structure and functioning	22
1.3	STUDY AREA	25
1.3.1	Geographical location and description	25
1.3.2	Geology and geomorphology	26
1.3.3	Climate	26
1.3.4	Hydrological regime	27
1.3.5	The effects of the Pongolapoort dam on flooding	29

Page

1.3.6 Biological components 29
1.3.7 Human utilization 32
1.3.8 Tete pan 33
1.4 *POTAMOGETON CRISPUS* L. 34
1.4.1 Morphology 34
1.4.2 Growth and reproduction 35

CHAPTER 2 MATERIALS AND METHODS 37
2.1 PHYSICAL AND CHEMICAL ENVIRONMENT OF TETE PAN 37
2.1.1 Pan depth and area 37
2.1.2 Light penetration 38
2.1.3 Salinity and conductivity 38
2.1.4 Temperature and dissolved oxygen concentration 38
2.1.5 pH 39
2.1.6 Water nutrient analyses 39
2.2 GROWTH, PRODUCTION AND REPRODUCTION OF *P. CRISPUS* 40
2.2.1 Standing crop 40
2.2.2 Turion and achene banks,and germination in the field 41
2.2.3 Effects of temperature and light on turion germination 42
2.2.4 Chlorophyll concentration 42
2.2.5 Oxygen production by shoot tips 43
2.3 THE ANALYSIS OF PLANT TISSUES 44
2.3.1 Analytical procedure for 1976 44
2.3.2 Analytical procedure after 1976 44
2.4 *POTAMOGETON CRISPUS*/WATERFOWL INTERACTIONS IN THE GRAZING FOODCHAIN 45
2.4.1 Waterfowl population estimates 45
2.4.2 Food consumed by waterfowl 45
2.4.3 The nutritive value of *P. crispus* turions and achenes 46
2.4.4 The estimation of turion consumption by means of the Wiens/Innes model of mean energy demand 48
2.4.5 Mass and condition of White-faced Duck 50

Page

2.4.6 Effects of waterfowl grazing on turion production in the field 50
2.4.7 Effects of waterfowl grazing on *P. crispus* standing crop 51
2.4.8 The production of large and small turions by detached plants 52
2.5 THE EPIPHYTON, GRAZER, HOST PLANT ASSOCIATION 53
2.5.1 Epiphyton colonization of *P. crispus* 53
2.5.2 Ultrastructure of the epiphyton/host interface 54
2.5.3 Effects of snail grazing on the epiphyton/host association 54
2.5.4 Numbers and standing crop of *Bulinus natalensis* 55
2.6 DECOMPOSITION AND DETRITUS FORMATION 55
2.6.1 Field studies 55
2.6.2 Laboratory studies 57

CHAPTER 3 THE PHYSICAL AND CHEMICAL ENVIRONMENT OF TETE PAN 59
3.1 RESULTS 59
3.1.1 Pan depth and area 59
3.1.2 Light penetration 60
3.1.3 Temperature 60
3.1.4 Oxygen concentration and pH 61
3.1.5 Conductivity and salinity 61
3.1.6 Nitrogen and phosphorus 62
3.2 DISCUSSION 64
3.2.1 Annual fluctuations in physical and chemical environments 65
3.2.2 Long term wet and dry cycles 66
3.2.3 Tete pan as a submerged plant habitat 67

CHAPTER 4 ADAPTATION OF GROWTH, REPRODUCTION AND NUTRIENT RELATIONS OF *POTAMOGETON CRISPUS* TO FLOODPLAIN CONDITIONS 69
4.1 RESULTS 69
4.1.1 Achene and turion germination, and the annual initiation of *P. crispus* growth 69

Page

4.1.2 Growth and decline of the *P. crispus* population 70

Changes in *P. crispus* standing crop in relation to leaf chlorophyll and shoot tip oxygen production during 1976 71

4.1.3 Replenishment of turion and achene banks 73

Turions 73

Achenes 73

4.1.4 Growth and reproduction during 1979 74

The summer standing crop 74

Winter growth and effects of drought 75

4.1.5 Nutrient relations 76

Tissue concentrations as an indication of nutrient availability 76

Accumulation of nutrient stocks in the standing crop 77

4.2 DISCUSSION 78

4.2.1 Life-history strategy of *Potamogeton crispus* 78

The established phase 79

Regenerative strategies 80

Potential failure of establishment and regeneration 83

4.2.2 Nutrient relations 84

4.2.3 The annual net production of *Potamogeton crispus* 85

4.2.4 Summary and conclusions 88

CHAPTER 5 *POTAMOGETON CRISPUS*/WATERFOWL INTERACTIONS IN THE GRAZING FOODCHAIN 89

5.1 THE WATERFOWL COMMUNITY AND IMPORTANCE OF *P. CRISPUS* AS A FOOD SOURCE 89

5.1.1 Results 89

Waterfowl community composition and numbers 89

Food and feeding behaviour of waterfowl 91

Nutritional value of turions and achenes and its influence on waterfowl condition 93

Page

5.1.2 Discussion 94

Waterfowl community composition and continental affiliations 94

The Pongolo floodplain as a waterfowl habitat 95

Implications of waterfowl grazing for *P. crispus* regeneration 96

5.2 EFFECTS OF WATERFOWL GRAZING ON THE *P. CRISPUS* POPULATION IN TETE PAN 97

5.2.1 Results 97

The quantity of turions consumed 97

Selection of turions and damage to standing crop by waterfowl 100

Turion formation by detached plants 101

Implications of turion size and number for standing crop development 102

5.2.2 Discussion 102

The influence of waterfowl on transfer of *P. crispus* production 102

The influence of waterfowl on nutrient transfers 104

Maintenance of *P. crispus* regenerative potential and stability of the grazing system: A hypothesis of adaptation viewed in an ecosystem context 104

CHAPTER 6 THE EPIPHYTON/GRAZER/HOST (*P. CRISPUS*) ASSOCIATION 108

6.1 THE EPIPHYTON/HOST ASSOCIATION 108

6.1.1 Results 108

Colonization by epiphyton 108

Ultrastructure of the epiphyton/host interface 108

6.1.2 Discussion 111

6.2 EFFECTS OF SNAIL GRAZING ON THE EPIPHYTON/ HOST ASSOCIATION 113

6.2.1 Results 114

The pattern of snail grazing on leaves 114

"Conditioning" and "edibility" of leaves and stems 115

The *Bulinus natalensis* population in Tete pan 116

Page

6.2.2 Discussion 116

Adaptation for co-existence of host and epiphyton 116

Implications of necrotroph/grazer interactions for transfer of resources 119

CHAPTER 7 DECOMPOSITION AND DETRITUS FORMATION 120

7.1 THE EFFECTS OF DRYING ON THE PATTERN OF MASS AND NUTRIENT LOSS FROM SENESCENT *P. CRISPUS* 120

7.1.1 Results 120

1976 experiments 120

1977 experiments 121

7.1.2 Discussion 123

7.2 EFFECTS OF GRAZING SNAILS AND EPIPHYTES ON DETRITUS FORMATION AND NUTRIENT TRANSFER 126

7.2.1 Results 127

Mass and nutrient loss from large mesh decomposition bags 127

Effects of grazing snails and epiphytes on detritus formation 128

Effects of grazing snails and epiphytes on nutrient transfers 129

7.2.2 Discussion 130

CHAPTER 8 THE ROLE OF *POTAMOGETON CRISPUS* IN CONSERVATIVE TRANSFERS OF ORGANIC MATTER AND NUTRIENTS IN TETE PAN 134

8.1 ORGANIC MATTER POOLS AND TROPHIC PATHWAYS 134

8.1.1 Autochthonous production 135

8.1.2 Allochthonous inputs 136

8.1.3 Other higher trophic levels 138

8.2 NUTRIENT TRANSFERS 139

8.2.1 A preliminary nutrient budget for Tete pan 140

8.2.2 Internal nutrient transfers 143

8.3 PERIODICITY OF ORGANIC MATTER AND NUTRIENT TRANSFERS 144

Page

CHAPTER 9 GENERAL DISCUSSION 147
9.1 INTRODUCTION 147
9.2 ECOSYSTEM ADAPTATION AND FUNCTIONING 150
9.2.1 The role of animal/plant interactions 150
9.2.2 Grazing versus detrital food webs 153
9.2.3 Nutrient cycling in an open system 155
9.2.4 Ecosystem adaptation to seasonal flooding 157
9.3 CONSIDERATIONS FOR MANAGEMENT OF THE PONGOLO FLOODPLAIN ECOSYSTEM 159
9.3.1 The hydrological regime 160
9.3.2 The managerial role of animals and temperature 161
9.4 FUTURE RESEARCH DIRECTIONS 162
9.4.1 *Potamogeton crispus* 162
9.4.2 During flood processes 163
9.4.3 Ecosystem response 163

REFERENCES 164
PERSONAL COMMUNICATIONS: ADDRESSES 198

CHAPTER 1

INTRODUCTION

1.1 INTRODUCTION TO THE STUDY

In wetland ecosystems such as marshes, swamps, floodplains and the littoral of lakes, aquatic macrophytes generally dominate energy and nutrient transfers, and provide a diverse habitat for animals, algae and bacteria (Wetzel and Hough, 1973; Gaudet, 1977; Howard-Williams and Lenton, 1975; Welcomme, 1979; Wetzel, 1979; Adams and Prentki, 1982). The major communities of macrophytes, the emergent, floating, floating leaved and submerged plants, play different roles in the different wetlands, with their respective roles being contingent mainly upon the prevailing hydrological regime, the light climate and nutrient availability (Wetzel and Hough, 1973; Welcomme, 1979; Brinson *et al.*,1981).

It is, however, difficult to define relationships between any one of these variables and particular ecosystem processes because many other factors may act either independently or interactively to mask the relationship (Brinson *et al.*, 1979). Our inability to account for these interactions seems to result from an over-emphasis on describing macrophyte distribution and quantifying production and nutrient transfers, rather than assessing cause and effect relationships (Wetzel and Hough, 1973; Spence, 1982). Thus, while there is a reasonable literature on the distribution of macrophytes and the quantities of nutrients and energy they store or transfer, there are few holistic accounts which assess the way these processes respond to different components of the multifactorial environment.

Although the same criticism has been levelled at terrestrial plant ecology (Patten and Odum, 1981) this branch of the science has, without doubt, a more predictive understanding of plant/environment interactions than its aquatic counterpart. This seems to arise largely from a paucity

of studies in wetland ecosystems (Stearns, 1978) of, (i) the life-history adaptations (McNaughton, 1975; Grime, 1979) which permit plants to survive in and exploit their environment, and (ii) biotic interactions, such as grazing, which, because they have important consequences in both evolutionary and ecological time, select for adaptation in a broader ecosystem context (Wiegert and Owen, 1971; Chew, 1974; McNaughton *et al.*, 1983).

A consequence of the lack of understanding of these factors and interactions is evident in the conflicting conclusions drawn in two recent reviews: Wetzel (1979) claims that "Any biotic utilization by animals has small impact on the overall metabolism of the system" while Brinson *et al.*, (1981) suggests that animal/plant interactions may have "a managerial influence --- on primary productivity, successional stages and/or homeostasis in the wetland ecosystem". Clearly such vastly different views should be resolved if we are to effectively manage freshwater wetlands. The onus is therefore on ecologists to adopt a more holistic approach to the study of aquatic plants and wetland ecosystem functioning in order to develop a more predictive understanding for use in wetland management (Stearns, 1978).

A multidisciplinary research project on the Pongolo River floodplain ecosystem in Zululand, South Africa, provided a good opportunity to study the role of a submerged species *Potamogeton crispus*, against this background.

On the coastal plain of northern Zululand, South Africa, flooding of the Pongolo River has formed an extensive (10 000 ha) floodplain of seasonally inundated grasslands and marshes dotted with shallow lakes or pans (Heeg and Breen, 1982). In 1972 a dam was completed in the Pongolapoort, upstream of the floodplain, to impound the river and divert water to an irrigation scheme on the nearby Makatini flats. Since the floodplain ecosystem, which has previously been dependent on this water, supports some 40 000 Thonga people (Heeg and Breen, 1982), a detailed research programme was initiated to pin-point the major determinants of the floodplain ecosystem functioning and to develop a management programme which would maintain it as a renewable natural resource.

The primary energy base of this ecosystem has been identified as arising from three main communities; (1) the semi-terrestrial, seasonally inundated, floodplain vegetation, (2) floating and rooted floating leaved plants which occur at the margins of some pans and (3) extensive, often monospecific, stands of the submerged macrophyte *Potamogeton crispus*, which occur in most pans that retain water through the winter (Musil, 1972; Rogers, 1980; Furness, 1981). Furness (1981) has studied the semi-terrestrial floodplain vegetation and the objectives of this study were; (1) to assess the role of *P. crispus* in the trophic and nutrient transfers of the floodplain pans and define the species' adaptations to the major biotic and abiotic factors influencing this role, (2) consider these findings in relation to our present understanding of submerged aquatic plant ecology and wetland ecosystem functioning and (3) outline the usefulness of these studies in the management of the Pongolo River floodplain ecosystem.

1.2 REVIEW OF PERTINENT LITERATURE

1.2.1 "The role of plants in ecosystems": Theoretical appraisal

The expression "the role of plants in ecosystems" is frequently used in one sense or another (Wetzel and Hough, 1973; Gaudet, 1974: Howard-Williams and Lenton, 1975; McNaughton *et al.*, 1983) but does not seem to have been defined. It is therefore useful to consider, at the outset, some theoretical aspects of this concept and its application in ecosystem management.

To formulate the concept one might ask "What does a plant do in an ecosystem?" Calow and Townsend (1981) suggest that organisms acquire resources and transform them into forms available to others in the food web. In this sense, plants can be considered to act as the initial gatherers of resources which, after modification, are transferred through the food web. However, in addition to this, the physical presence and metabolic activity of plants modifies the environment and so influences the presence and metabolism of other organisms. The role of a plant

could therefore be demonstrated by both the contribution it makes to the sum total of transfers of resources within the ecosystem, and the degree to which it modifies the environment.

Different species will clearly play different roles in an ecosystem and an assessment of the respective roles will provide a solid base for development of management goals and policies. The management strategies used to implement these policies, however, rely largely on manipulation of environmental (biotic and abiotic) factors to achieve the desired results, and the end product depends upon the way in which the individual species respond to the altered environment. Thus, for an assessment of the role of a species to be useful to the manager it must include information on the way the species responds to environmental factors.

This response is difficult to assess since each physical, chemical or biotic factor of the environment may affect some aspect of the plant's role in the ecosystem (McNaughton *et al.*, 1983). Furthermore, these factors do not necessarily act independently or deterministically but are often interactive in a probabalistic manner (McNaughton, 1983). Thus, the effects of individual forces may be minor but because the cumulative effects are large they should be assessed by the researcher and appreciated by the manager.

McNaughton (1983) has emphasised that attempting an empirical evaluation of the importance of each of the many environmental factors is technically impossible at present, although clearly an holistic approach to the study of a plant's role in an ecosystem is required. The practicalities of elucidation and quantification of the role of a plant species in an ecosystem are therefore formidable and it is likely that any one study of defined duration will raise more questions, than provide answers. Nevertheless, it is suggested that if the basic approach outlined below is followed, bearing in mind the theoretical background above, valuable contributions could be made to our understanding of the role of plants in ecosystem functioning and our ability to manage ecosystems for express purposes.

1. Characterise the major environmental (physical, chemical and biotic) variables of the ecosystem and evaluate (a) the factors most likely to affect the acquisition of resources and so plant growth and (b) the influence of the species concerned on the environment.

2. Determine the life-history adaptations (Grime, 1979; Calow and Townsend, 1981) of the species which permit it to survive in and exploit (Howard-Williams and Ganf, 1980) the habitat.

3. Assess the transfers of resources from this species to other components of the food web in relation to those of other primary producers in the ecosystem. Such an assessment leads to an appreciation of the species adaptation in a broader ecosystem context.

This review of pertinent literature follows this sequence and expands upon each component in the context of the role of submerged plants in wetland ecosystems in general and floodplains in particular.

1.2.2 The floodplain environment

As is the case with all wetlands, the form of a particular floodplain depends upon the hydrological regime of influent waters and the local topography. Floodplains occur in mature rivers which have attained grade (the minimum slope possible under existing conditions) over a considerable length of their course (King, 1967). The decrease in flow rate of water moving onto the graded river course results in an accumulation of water which, during high flow periods, overspills the river banks (King, 1967).

Where the catchment of the river is large and very distant from the floodplain it may have a reservoir effect and deliver only one major flood of long duration which may, as in the case of the Okavango Delta, Botswana, be out of phase with local rainfall and so arrive during the dry season (Hutchinson and Midgley, 1973). When the catchment is close to the floodplain a series of frequent short duration floods may characterise

the flood season which coincides with the period of local rainfall. In such instances (eg. Pongolo floodplain) long dry periods separate the annual floods (Welcomme, 1979; Heeg and Breen, 1982). Thus, alternate wetting and drying is a characteristic feature of these floodplains but its periodicity varies greatly in relation to over-spill floods arising from the catchment, local rainfall and floodplain topography.

The load of silt and organic detritus carried by flood waters is a major factor determining floodplain topography. When the river overflows its banks the reduction in flow rate causes deposition of silt in lines parallel to the river. Such "levees" are raised above the surrounding floodplain and tend to dictate the river course. However, lateral corrosion of the river bank, another important modifier of the floodplain topography, has an opposing effect. Lateral corrosion takes place by erosion of the outer bank of a curve in the river, with concomitant deposition on the inner bank or slip-off slope. This process continues until the ends of the loop which is formed, meet, and the river cuts off the loop to form an ox-bow lake (Gregory and Walling, 1973). The continual movement of the river across the easily eroded alluvial plain results in many other floodplain features such as; interfluvial depressions between old levees; point bars which form by deposition of sand on slip-off slopes; back swamp deposits of fine sediments between the levees and floodplain margins, and lakes formed by sediment deposition across the mouths of tributary rivers. The more mature the river and the broader its floodplain, the greater the diversity of these features (King, 1967; Gregory and Walling, 1973; Welcomme, 1979) which, when coupled with the hydrological regime, create a wide variety of conditions of substratum type, water depth and duration of inundation. These in turn lead to a mosaic of habitat types over the floodplain ranging from rapidly draining grasslands, to swamps and open water bodies which may support submerged plant species.

The hydrological regime of the river which modifies the floodplain topography and dictates the frequency, depth and duration of flooding also has important influences on the gains and losses of nutrients for the system. The two main sources of nutrient input to floodplains are

considered to be those dissolved in the water and those adsorbed onto silt (Welcomme, 1979). The latter is the most important source of phosphorus to the system (Mitch *et al.*, 1979) but the flood waters may also act more to flush salts from the system (Furness, 1981; Heeg and Breen, 1982). This has led to the suggestion that construction of dams in the catchment will reduce silt inputs but maintain a flushing action and so reduce productivity (Furness, 1981). This remains an hypothesis, however, and the ability of floodplain ecosystems to adjust (see section 1.2.8) to the changes in hydrological regime and silt and nutrient inputs is unknown.

1.2.3 Plant life-history adaptations: A conceptual basis

The most significant work in the development of an holistic approach to the study of life cycles was that of MacArthur and Wilson (1967) who originally proposed the r/K concept of life histories. This work recognises two types of organism at opposite ends of the evolutionary spectrum: (i) K- selected organisms inhabit stable, non-fluctuating environments; they have a long life span and devote a small amount of energy to reproduction in order to produce few offspring with a high probability of survival, and (ii) r- selected species are considered opportunistic species which exploit fluctuating environments, have short life spans and expend a large amount of energy in reproductive effort (Collier *et al.*, 1973; Grime, 1979).

Although very influential in the development of ideas on life-history adaptations (Calow and Townsend, 1981) the r/K concept has been found to present an oversimplified model (Whittaker and Goodman, 1979) which cannot provide a complete explanation of plant life-history phenomena. The main criticism is that it attempts to explain life-histories as the outcome of a single selection pressure, resource availability. As a result separate populations of the same species may occupy very different positions on the r-K continuum (Whittaker and Goodman, 1979) as may juvenile and adult components of one population (Stearns, 1976). This led Grime (1977 and 1979) to propose the more detailed C-R-S model of life-history strategies in which he recognises that plants

have evolved three primary or vegetative strategies (C, R and S) which operate in the mature or established phase of the life cycle and five regenerative strategies for reproduction.

Grime bases his model on the assumption that two sets of environmental conditions limit plant biomass in any one habitat; those which restrict production of biomass are termed "stressful" while "disturbances" effect the partial or total destruction of biomass in a productive environment. There are four permutations of high and low stress or disturbance but because severe stress would exclude recovery in a very disturbed habitat, only three are habitable (Grime, 1977; Calow and Townsend, 1981). Thus, three basic strategies have evolved: C or competitive plants (low stress, low disturbance); S or stress tolerant plants (high stress, low disturbance) and R or ruderal plants (low stress, high disturbance). Grime's regenerative strategies are based on modes of reproduction and survival during the juvenile stage. These are; (i) Vegetative expansion (V), (ii) Seasonal regeneration (S), (iii) Persistent seed banks (B), (iv) Wind dispersal (W) and (v) Persistent seedlings (B_r).

This broader system of classification of both environmental conditions and the mechanism of plant response to them, can be of more use to the manager than that of the r-K concept. In most instances management decisions must be based on a paucity of information but if there is a classification system into which the species or system can be placed, the information base can be broadened. An example is that having categorised a particular habitat and the life-history strategies of plants in it, one can use Grime's system to consider whether or not a change in environmental conditions will cause failure of species to regenerate or establish and so adapt management accordingly. The environmental and biological basis of the r-K concept is too broad to be as useful in this context.

Recently the C-R-S model has received some criticism from two main fronts. Firstly, because of the interactive nature of environmental variables, a factor which constitutes a stress under one set of conditions can well be a disturbance under another. Thus, his classification

of the environment is somewhat narrow (Menges and Weller, 1983) but it could undoubtedly be improved. A second, stronger criticism is levelled at Grime's *a posteriori* approach in classifying a previously "uncoordinated collection of natural history observations" (Calow and Townsend, 1981). These authors favour a more *a priori* approach which will increase predictability since it permits the formulation of "hypotheses ---- which can be tested in true Popperian fashion --- (Pōpper, 1959)". Detailed examination of this argument is not considered necessary here; suffice it to say that it may also be claimed that, since a number of interacting variables are involved in ecological problems there is generally no single null converse of an hypothesis. Thus, it cannot be tested in the true Popperian sense (Quin and Dunham, 1983).

Calow and Townsend's (1981) alternative approach, that of resource acquisition and reallocation, nevertheless provides a good basis for scientific investigation of a species adaptation in both the life-history and ecosystem context. It is based on the optimal use of limited resources and an organism's life-history adaptations are assessed quantitatively as its ability to acquire resources and then partition them between maintenance, growth, storage, repair, defence and reproduction. This ties in with the concept of the role of plants in ecosystems expressed earlier since it is the stored resources which are transferred to other components of the ecosystem. If more than the stored resources are transferred, then the ability of the plant to persist in and exploit the ecosystem may be impaired. Thus, this sort of approach seems to lend itself well to the study of the role of plants in ecosystems as discussed in section 2.1 above. However, our knowledge of how plants function in the multifactorial environment is so limited that the optimal adaptive strategy of a plant in any one habitat cannot be predicted *a priori* (Solbrig, 1981). While this does not detract from the scientific worth of this approach it does limit its applicability to studies orientated towards providing answers to immediate or short-term management problems. In such cases it is probably best to draw from both Grime's (1979) and Calow and Townsend's (1981) approaches in a manner suitable to the problem and study in hand. This suggestion gains merit from the discussion of ecosystem

functioning (section 1.2.8) which points out the need for both quantitative information on the acquisition and transfer of energy and nutrients (resources) as championed by Calow and Townsend (1981) and an understanding of natural history phenomena which Grime's (1979) CRS model provides.

1.2.3.1 Life-histories and reproduction of aquatic plants

Attempts to classify wetland, or in particular floodplain, conditions in terms of the selective forces of stress and disturbance as advocated by Grime (1979) indicate that all four combinations (Section 1.2.3.1) occur in both the aquatic and seasonally inundated areas. Thus, all four categories of stress tolerant, ruderal and competitive plants and combinations of these can be expected within the diverse range of habitats (Menges and Weller, 1983). Perhaps more important, however, is to recognise that individual species respond differently to particular selective forces of the environment (Menges and Weller, 1983). A flood may therefore stress some aquatic plants by reducing light penetration but act as a disturbance to others by causing physical destruction of biomass. Similarly a perennial species is adapted to seasonal desiccation but an annual may respond to dry periods as a disturbance by dying back. The interpretation of stress and disturbance must therefore be based on each species' traits and life-history adaptations assessed for each species in relation to its particular habitat.

Detailed studies of adaptation of aquatic plants are few and have generally only considered aspects of r and K selection (McNaughton, 1975; Brock, 1983). It is therefore more pertinent to review life-histories and reproduction of aquatic plants in general terms.

The relative uniformity of the aquatic, in contrast to the terrestrial, environment is held to encourage vegetative growth (Sculthorpe, 1967) and thus perennial species with predominantly asexual reproduction (Hutchinson, 1975). Many wetlands, particularly in the sub-tropics, however, experience alternate periods of wetting and drying which would

select for annuals with desiccation resistant propagules (Howard-Williams and Ganf, 1981). Both types of life-history are therefore common in floodplain habitats (Menges and Waller, 1983).

A variety of means for asexual reproduction have evolved including the production of underground rhizomes, tubers and stolons. Many species have developed specialised buds or dwarf stems, termed turions, which become detached from the parent plant and usually germinate only after a period of dormancy (Arber, 1920; Hutchinson, 1975). In this way many perennials act as annuals with the non-reproductive portions dying back and the turions surviving the unfavourable season.

The initiation of both production and germination of asexual propagules is generally attributed to environmental stimuli such as day length, light, temperature and redox potential (Hutchinson, 1975; Haller *et al.*, 1976; Weber and Nooden, 1976; Sastoutomo, 1980). The physiological basis of such stimulation is not well understood, but hormonal reactions similar to those of terrestrial seeds appear to be operative (Weber and Nooden, 1976) and permit the species to regulate their growth to favourable seasons.

This marked tendency for asexual reproduction in aquatic macrophytes has resulted in the development of clonal populations, ecotypes, (McNaughton, 1966; Hutchinson, 1975) which permit species to occupy widely differing habitats and take advantage of locally favourable growing seasons. For example, only particular clones of *Spirodela polyrhiza* (L.) Schleid. produce turions and different sets of environmental factors promote production and germination according to local climatic conditions (Perry, 1968).

Many asexual reproductive organs cannot survive dehydration so that, in the sub-tropics in particular, species must have some other means of surviving dry periods. Sexual reproduction appears to play an important role in this regard. The production of seeds and fruits by most species provides a propagule with a tough outer covering which not only withstands desiccation but often requires it in order to break dormancy (Meunchner, 1936; Telcherova and Hejný, 1973; Everson,

1980). Even under wet conditions it may take several years to break the dormancy imposed by the thick coat (Hutchinson, 1975) with the result that large seed banks develop, reducing the risk of local extinction during dry periods.

Fruits and seeds are also important for dispersal of both annual and perennial species and the hard coat ensures survival during the rigorous passage through the gut of dispersal agents such as duck (Ridley, 1930). Others float until ready to germinate and are dispersed by wind and wave action (Spence *et al.*, 1971).

1.2.4 Submerged aquatic plant production

The role of a plant species in an ecosystem is primarily determined by its ability to acquire energy through the process of photosynthesis and to transform this into the chemical energy of organic matter which may be utilized by higher trophic levels. Estimates of net organic matter production are therefore prerequisites to understanding the role of plants in an ecosystem.

The productivity of submerged plants has been determined by methods which measure the rates of carbon assimilation (using the ^{14}C isotope) or evolution of oxygen (Vollenweider, 1969; Wetzel and Likens, 1979; Moss, 1980). Both methods are generally assumed to measure net productivity (Westlake, 1975) and while the highest rates recorded are 13 - 18 mg C g^{-1} dry wt. hr^{-1} or 38 - 51 mg O_2 g^{-1} dry wt. hr^{-1} (Ikusima, 1965) the average lies between 2 - 10 mg C g^{-1} hr^{-1} or 5 - 25 mg O_2 g^{-1} hr^{-1} (Westlake, 1975). Neither method, however, accurately measures net productivity.

The use of ^{14}C actually provides a measure somewhere between net and gross productivity since some respiratory CO_2 is recycled internally for use in photosynthesis (Moss, 1980) and the use of O_2 evolution rates has been the subject of much debate. Hartman and Brown (1967) argued that the presence of lacunae containing gas in submerged water plants provides storage capacity for oxygen which could be revitalized during

respiration. Thus, measurements of changes in oxygen concentration in the surrounding water do not give an accurate assessment of oxygen metabolism. However, Westlake (1967; 1978) has shown that there is no evidence for a high resistance to outward diffusion of O_2 into the medium, and that provided plants are incubated in a stirred or flowing medium, measured changes in oxygen concentration can be easily corrected for the fraction retained in the lacunae, thus providing an accurate measure of productivity. It appears that under unstirred conditions an indication of photosynthetic potential is achieved but results should be treated with caution.

These two methods, however, have two important disadvantages which should be considered when studying the role of submerged plants in an ecosystem. The first is that attached algal epiphytes which have high rates of production will also assimilate ^{14}C and produce O_2 giving an overestimation of host plant productivity, and it is often difficult to remove them without damaging the host. Secondly while these methods give estimates of quantities produced they do not permit evaluation of the quality of the production; a very important factor determining the use of plant production by higher trophic levels (Boyd and Goodyear, 1971). For example both the C:N ratio and particle size are important factors determining invertebrate consumption of plant detritus (Cummins and Klug, 1979; Cummins *et al.*, 1980), and waterfowl preferentially select reproductive organs (Smith and Odum, 1981) high in carbohydrates and lipids. More direct estimates of organic matter production may therefore be preferable when studying the role of plants in ecosystem functioning. Quality can readily be assessed from the same samples and epiphyte biomass remaining after gentle washing is relatively very small.

Organic matter production can be estimated by following changes in standing crop over the growing season (Westlake, 1965; 1975). In annual plants, standing crop changes generally follow a typical sigmoid growth curve and decrease once the plants become senescent (Figure 1.1). In this idealised example gross productivity reaches a plateau towards the end of the exponential growth phase and decreases only when senescence sets in. Net productivity, on the other

hand, decreases late in the exponential phase and becomes negative as respiration rate begins to exceed gross productivity. Maximum standing crop is reached when current net productivity reaches zero and subsequently decreases as the rate of respiration exceeds gross productivity.

If the initial standing crop (propagules) and losses other than respiration are negligible, the seasonal maximum standing crop equals the annual net production. When much of the plant survives by means of rhizomes or tubers into the next growing season, initial biomass is not negligible, but provided it persists without appreciable losses until after the seasonal maximum, the annual net production may be obtained by difference between initial and final standing crop. More commonly,however, some of the initial standing crop is lost or translocated into the next season's growth and losses by death or grazing occur before seasonal maximum standing crop is reached (Rich *et al.*, 1971; Howard-Williams, 1978).

Matthews and Westlake (1969) overcame these problems when studying the emergent species *Glyceria maxima* by using the Allen-curve technique where the fate of all the individuals of a particular cohort of new shoots was followed. Recently Howard-Williams (1978) adapted this approach to the study of a submerged *Potamogeton pectinatus* community in the eastern Cape by tagging plants and measuring their growth rates with the aid of SCUBA*; linear growths were converted to biomass changes from length/mass regressions. This method is undoubtedly the most thorough and should be pursued wherever conditions in the field are suitable and time permits.

The roots of submerged plants generally form a small (2 - 10%) but significant proportion of the total standing crop (Westlake, 1965) but this may be larger if tubers or other underground storage organs are produced. Determination of underground standing crop is difficult but has been achieved by estimating mass in randomised cores (Westlake, 1968; Everson, 1980). Root production has not been accurately measured.

* Self Contained Underwater Breathing Apparatus

1.2.5 Organic matter transfers

While the amount of plant production indicates the potential role the species can play in ecosystem processes, the actual role is demonstrated by the subsequent proportional distribution of the production amongst the different trophic levels and storage compartments (sections 1.2.1 and 1.2.8).

The transfers of submerged plant production can be conveniently divided into those which occur during the growing period and those which occur during senescence and decay of the remaining organic matter.

1.2.5.1 Transfers during growth

Release of Dissolved Organic Matter

A small, but at times significant, proportion (0.9 - 10%) of the carbon fixed photosynthetically by submerged plants is released extracellularly during growth as dissolved organic matter (DOM) (Wetzel, 1969; Wetzel and Manny, 1972; Hough and Wetzel, 1975; Søndergaard, 1981).
The compounds released are mostly of low molecular mass (eg. glucose, sucrose, fructose, glycine) (Allen, 1971; Søndergaard, 1981) and thus readily catabolized by bacteria and some algae. Heterotrophic micro-organisms convert this non-living, detrital DOM (Rich and Wetzel, 1978) to a living particulate form (Paerl, 1978) which has greater nutritional value and can then be utilized by higher trophic levels.

Extracellular release from submerged plants, however, probably contributes little to the total DOM pool in freshwaters (Søndergaard, 1981) since much larger quantities are released during senescence and decay (Otsuki and Wetzel, 1974; Godshalk and Wetzel, 1978c).

Grazing of submerged aquatic plants

In general, little of the annual primary production (10 - 20%) of a freshwater body enters the grazing foodchain (Wetzel, 1979). Furthermore, while animals ingest, on average, 10 - 20% of the annual particulate organic matter (POM) production, they assimilate only some 50% of this; the rest is egested and enters the particulate and dissolved detrital pools along with the ungrazed production (Wetzel, 1979).

Similarly, less than 20% of submerged plant production is thought to be consumed by animals (Hutchinson, 1975; Wetzel, 1975) and thus the contribution of these plants to the overall grazing food chain is often considered small or insignificant (Wetzel, 1979). It is important to realise, however, that even if a small proportion of the production is grazed, it may be sufficient to support large populations of animals, such as waterfowl which have nutritional and aesthetic value to man.

While insects (Wetzel, 1975), some mammals (Weller, 1978) and molluscs (Pip and Stewart, 1976) consume living submerged plants, the major grazers are waterfowl (Anderson and Low, 1976; Kiøboe, 1980; Smith and Odum, 1981) which feed mainly on the nutritious reproductive organs. Such selective feeding by waterfowl has considerable potential for impact on the reproductive capacity of the population in that it reduces input to the propagule/seed bank. Indeed, in annual species in particular, this may become an important factor governing population growth and production in successive years (Noy-Meir, 1975). Few studies have, however, considered grazing from this point of view and thus the full effect of waterfowl grazing on wetland submerged plant communities is not understood (Smith and Odum, 1981).

Losses due to damage

Submerged plants have reduced supportive tissues and are thus susceptible to damage (Sculthorpe, 1967) by physical and mechanical forces such as wave action and large animal movements. In general,

the effects of wave action, however, restrict submerged plants to sheltered sites where such losses are small in relation to total production (Jupp and Spence, 1977). The effects of waterfowl, which uproot and breakup plants while feeding would seem to be a more important source of loss from plant communities. Smith and Odum (1981) demonstrated marked reductions in biomass and net production of grasses in a salt marsh as a result of goose feeding activities. Such damage has also been reported for submerged plants (see Smith and Odum, 1981) but the effects on production and the pathways of transfer of the detached organic matter need to be assessed.

1.2.5.2 Transfers during senescence and decay

Since a small proportion of the submerged plant production is grazed, most senesces and dies thus entering the detritus pool (Wetzel, 1979). The elucidation of this important trophic pathway has stimulated detailed investigations over the last decade, of the fate of aquatic plants during the decomposition process. Present understanding is based largely on the study of the disappearance of particulate matter and nutrients from dead plant material, either contained in mesh bags and incubated in the field (Boyd, 1970; Howard-Williams and Junk, 1976; Godshalk and Wetzel, 1978 b; Danell and Sjöberg, 1979; Howard-Williams and Davies, 1979) or incubated in the laboratory, *in vitro* (Jewell, 1971; Godshalk and Wetzel, 1978,a,b,c; Carpenter and Adams, 1979).

Godshalk and Wetzel (1978,a,b,c), after an extensive review of the literature and detailed *in vitro* studies recognised three phases in the decomposition of dead aquatic macrophytes:

1. During the initial phase decay rates are rapid and attributed to losses of DOM and nutrients by leaching. Much of this DOM is labile and is rapidly metabolized by heterotrophic micro-organisms.

2. The second phase of decomposition is characterised by a decreasing decay rate and the major cause of mass loss is microbial catabolism of the plant tissues. During this phase there is a progressive reduction in particle size of the POM which provides a greater area for microbial colonization. The potential of the larger population to increase decay rate is, however, limited by increased resistance of the tissues to decay as the more labile substrates are progressively catabolised. Since microbial metabolism is the major agent of mass loss, environmental factors which affect microbial activity such as temperature and the availability of oxygen and nutrients, are thought to have their greatest influence during this phase.

3. During the final phase of decomposition the declining rate of decay approaches an asymptote of zero. The major factor controlling mass loss is the refractility (resistance to decay) of the remaining detritus and plants with more structural tissues have, overall, slower decay rates which result in more detritus remaining as the asymptote approaches zero. The patterns of decay of aquatic macrophyte POM are therefore highly species specific.

Godshalk and Wetzel (1978 c) and more recently Wetzel (1979) suggest that animals play an almost insignificant role in the decomposition of autochthonous organic matter. Their hypothesis is that 99% of the organic matter has three possible fates which in order of magnitude are: decomposition by micro-flora and release as CO_2, sedimentation as POM, or export from the system as DOM or POM.

The studies which lead to this description of the decomposition process and later studies which support it (Howard-Williams and Davies, 1979; Carpenter and Adams, 1979) have,however,been based on the use of plant material which was killed either by drying (Wohler *et al.*, 1975; Howard-Williams and Junk, 1976; Howard-Williams and Davies, 1979) or lyophilization followed by drying (Godshalk and Wetzel, 1978 b; Carpenter and Adams, 1979). This was done to prevent the growth of plants during experiments and also to permit storage until experiments

could be carried out. While this may approach the natural system for many emergent species, most submerged plant production senesces and dies in the aqueous environment.

Natural senescence is an orderly and programmed sequence of events which leads to the death of a plant or a plant part (Woolhouse, 1967). It includes events such as the gradual loss of cell membrane integrity and the resultant slow leaching of dissolved substances (Eilam, 1965) and could therefore be an important aspect of decomposition (Gallagher, 1978). In particular a slow rate of leaching, as opposed to the rapid leaching experienced when plants are dried, would provide a very different organic substratum for colonization of micro-organisms and the retention of nutrients in the plant tissues could also increase microbial activity. Harrison and Mann (1975) alluded to such effects when they found that drying appears "to alter the organic matter (of *Zostera marina* L. leaves) in such a way that it was less rapidly attacked by microbes".

Exclusion of the process of senescence from decomposition studies could therefore markedly alter the rates and patterns of decay and so bias interpretations of the role submerged plants play in the detrital food chain.

1.2.6 The acquisition and transfer of nutrients

In aquatic ecosystems the major pools of nutrients required for plant growth are those situated in the sediment, the water phase, and in the living and dead biota. The main factors affecting transfer between these pools are changes in chemical equilibria (Welch, 1980) microbial metabolism and the rates of primary production and decay (Wetzel, 1979). Since rooted macrophytes can be highly productive (section 1.2.2) and have access to nutrients in both the sediment and water they can play an important role in these transfers (Wetzel, 1975; Howard-Williams and Allanson, 1978).

The role of submerged macrophyte rooting systems in the acquisition of nutrients was a point of debate for many years (Pond, 1905; Sculthorpe, 1967; Denny, 1972; Bristow, 1974; Denny, 1980).

Many earlier studies (reviewed by Hutchinson, 1975; Spence, 1982) held the view that the roots served only to anchor the plants and that nutrient absorption was foliar; later studies showed that sediment type and nutrient status significantly affected plant growth and concluded that nutrients were absorbed mainly through the roots. More recently, however, particularly with the advent of radio tracer studies, it has been shown that both root and shoot absorption take place in the same plant (McRoy and Barsdale, 1970; Bristowe and Whitcombe, 1971; Nichols and Keeney, 1976; Carignan and Kalff, 1979). Furthermore, translocation of nutrients occurs in both directions, and both release of root absorbed nutrients into the water (McRoy and Barsdale, 1970; De Morte and Hartman, 1974) and transfer of water absorbed nutrients directly to the sediment (Swanepoel and Vermaak, 1977) have been described.

In general it appears that roots act as the major site of nutrient absorption (Welsh and Denny, 1979; Carignan and Kalff, 1980) with acropetal translocation and the release of some nutrients from the foliage occurring.

Although this release is generally small (*c*.5% of total uptake) it may have important consequences for the associated epiphyton community (Section 1.2.7) and should not be ignored in the face of the quantitatively much longer transfers which take place during senescence and decay.

1.2.7 The relationship between submerged plants and their epiphyton

Submerged aquatic plants like all other underwater surfaces receiving enough light provide substrata for colonization by communities of algae, bacteria and other micro-organisms (Moss, 1980; Wetzel, 1983). Unlike most other surfaces, however, the macrophytes are metabolically active and release a variety of dissolved organic substances and inorganic nutrients (section 1.2.6; Wetzel and Manny, 1972; McRoy and Goering, 1974; Penhale and Thayer, 1980) to the surrounding water.

The epiphytic algae and bacteria at the plant/water interface have ready access to these substances and their use may stimulate epiphyton growth (Wetzel and Allen, 1971; Moss, 1980; Rogers, 1981). This relationship between epiphytes and the host plant is saprotrophic or, as described by Allen (1971), chemo-organotrophic.

The presence of the epiphytic organisms and the detritus and inorganic particles which collect among them, however, must also affect the host plant; for example by restricting the passage of light (Sand-Jensen and Søndergaard, 1981; Phillips *et al.*, 1978; Lossee and Wetzel, 1983) and carbon dioxide (Wetzel, 1983) from the water to the plant. Such competition for resources has led some authors to express surprise in the fact that plants have not, in the course of their evolution, acquired some means of restricting epiphyton development (Hutchinson. 1975; Moss, 1980). Examples of adaptations, such as the secretion of protective mucilage sheaths (Pond, 1918) and sulphur compounds which inhibit algal growth (Wium-Andersen *et al.*, 1982), are therefore usually considered the exception rather than the rule. This has led to the formulation of more general hypotheses to explain the significance of the relationship between epiphytes and their host plants.

Hutchinson (1975) suggested that since epiphyton growth provides an easily available and nutritious food source for grazing invertebrates, it diverts them from consuming and damaging the host plant. He postulated that epiphytes play the same role in aquatic systems as do chemical adaptations which prevent excessive grazing in terrestrial systems. Thus, release, by the host plant, of dissolved nutrients and organic compounds which stimulate epiphyton growth might be considered as part of the plant's overall adaptive strategy.

Phillips *et al.* (1978) and Eminson and Moss (1980) also consider the release of nutrients and DOM by the plants to be a major factor determining the balance which develops between epiphytes and the host plants. Their hypothesis, in the context of this discussion, is that this balance is maintained by the magnitude of fluxes (usually small) of substances at the host/epiphyton interface such that the epiphyton provides maximum benefit to the host by diverting grazing but is

prevented from becoming so dense as to interfere with light and CO_2 reception. They further suggest that the balance may be upset when the fertility of the water increases to the point where it has greater influence on the epiphyton than the fluxes at the host/epiphyton interface. Under these conditions the growth of epiphyton may become so dense as to outcompete the host for inorganic carbon and light. Thus, submerged plant populations decline in highly eutrophic conditions.

Neither of these hypotheses have been tested and although there is some evidence to support aspects of both, Wetzel (1983 a) suggests that our understanding of the relationships is so poor that it is "premature to state ---- how the actors in this complex community --- are affecting each other". He favours the view that the microfloral complex and host plant are a highly integrated system metabolically and that experiments at the microlevel are needed before understanding can be improved. This does not necessarily conflict with the Phillips *et al.* (1978) and Eminson and Moss (1980) hypothesis but perhaps suggests that, with a multifactorial environment acting on both epiphyton and host plant, a complex set of strategies, adapted for different levels of co-existence in different habitats, might occur.

1.2.8 Ecosystem structure and functioning

Studies of floodplain ecosystems are so limited (Welcomme, 1979; Mitsch *et al.*, 1979) that an attempt to outline concepts of their structure and functioning by comparing systems would be fruitless. A more informative approach would be to consider theoretical concepts of ecosystem structure and function and their implications for management.

An ecosystem can be described as a unit of the biosphere within which chemical substances (organic matter and nutrients) are cycled and recycled while energy, transported as part of those substances, continually passes through the system (Welch, 1980). The ability of the ecosystem to continue cycling these substances is maintained by a continual input of energy, equal to losses from the system. The

variability of energy flow and nutrient cycling processes, however, generally prevents assignment of clear-cut boundaries to ecosystems (Welch, 1980) although units such as lakes, streams and wetlands are often considered ecosystems for study and management purposes. However, in this context it is important to recognise the role of the catchment in providing inputs of water, energy and nutrients, and also that both chemical substances and energy may be lost through the outflow.

Clearly, if an ecosystem is to continue functioning, inputs must at least balance losses, and the question arises as to whether ecosystems can, in response to inputs, adjust their structure and function to regulate losses. In other words, is the behaviour of ecosystems guided by future or desired goals? Do they act as cybernetic systems in a true teleological sense (Engelberg and Bayarsky, 1979; Jordan, 1981; Patten and Odum, 1981)?

This has been the subject of some argument, but for the purposes of this discussion ecosystems can be considered as units of co-evolution which consist of biotic and abiotic components that change and evolve together (Patten, 1975; Jordan, 1981). In this sense ecosystems respond on the basis of an input/output model with a series of internal feedbacks which maintain its orderly function and absorb some change in input to dampen change in output (Patten and Odum, 1981). As such, ecosystems respond to inputs and entities and thus the study of ecosystems has implications for management (Welch, 1980).

Patten and Odum (1981) consider that the principal function of an ecosystem is to make possible the orderly cycle of life. This means using energy to clean up residues from past cycles and converting them into forms that can initiate and support new cycles. Thus, ecosystems possess a primary network of "conservative energy and inorganic energy-matter" flows resulting from a variety of transformation and exchange processes. These authors suggest that the processes are mainly trophic and so knowledge of the food web is fundamental to understanding the network. Important constituent processes of the primary conservative network are primary production, decomposition, nutrient cycling, growth and development, and feeding.

To achieve orderliness in the transformation and exchange of energy and energy-matter, a secondary information network is required to regulate the primary conservative processes (Jordan, 1981; Patten and Odum, 1981). This network is vast and complex but, put most simply, all the processes and interactions known collectively as "natural history", serve to mediate the conservative exchange and transformation processes. It is not their energy or matter contribution to interactions which is important but the way in which they initiate, catalyse, rate limit or otherwise regulate transfers. They include non-conservative uses by organisms of the physical media(air, water, soil), sight, sound, smell, temperature and other sensory cues provided by the physical, chemical and biotic environments(Patten and Odum, 1981). To this could be added the physical attributes of organisms, such as hard seed coats, thickened cell walls, sharp teeth or spines which,qualitatively rather than quantitatively, allow them to exploit a habitat.

Interactions between the primary conservative and secondary informational networks form the machinery which has evolved to maintain the structural and functional integrity of the ecosystem.

Like much ecological theory this hypothesis of ecosystem structure and function is difficult to test scientifically. The qualitative significance of aspects of the information network which maintains order in the system, compounds the problem. However, this discussion does emphasise that when studying the role of a plant species in an ecosystem one must consider both the transfers of energy-matter (production, grazing, decomposition and associated nutrient cycling) and the manner in which these are initiated and regulated by interactions which may be qualitatively rather than quantitatively important (the information network). Furthermore it is important to recognise that the sum of these interactions infers the evolution of adaptation of a species to whole ecosystem functioning (McNaughton *et al.*, 1983) which is more than the life-history adaptation that permits the plant to exploit a habitat. Without this sort of understanding effects of environmental change on the role of a plant in ecosystem functioning are difficult to predict. This in turn means that management options are limited and their effects difficult to predict.

1.3 STUDY AREA

A general description of the physical, chemical and biotic factors of the Pongolo river floodplain provides the background for characterizing, in subsequent chapters, the major factors affecting the role of *P. crispus* in the floodplain ecosystem.

1.3.1 Geographical location and description

The Pongolo River floodplain is situated on the coastal plain of north eastern South Africa (27°30'S; 32°15'E) (Figure 1.2) and comprises that part of the Makatini flats which is seasonally flooded by the Pongolo river (Figure 1.3).

The river arises near Wakkerstroom in the south eastern Transvaal (Figures 1.2 and 1.4) at 2200 m above mean sea level (a.m.s.l.) and flows due east for approximately 340 km through a catchment of 7830 km^2 until it reaches the Lebombo mountains. The Pongolapoort dam has been constructed in the gorge through the Lebombo mountains at about 75 m a.m.s.l. On emerging from the gorge the river turns northwards and flows across the Makatini flats to join the Usutu river at Ndumu on the South African - Moçambique border (20 m a.m.s.l.). The Pongolo River floodplain has been formed on this section of the river which has attained grade and has a gradient of 1:3000.

The floodplain is approximately 60 km long, between 0.8 and 4.8 km wide and covers 10416 ha. It includes some riparian forest, rapidly-draining hygrophilous grasslands, marshes (Furness and Breen, 1980) and a series of depressions, the floodplain pans (Hutchinson *et al.*,1932), which capture and retain water when the river overflows its banks. Most of the pans are shallow (< 3 m deep, Breen *et al.*,1978), and have formed in old river courses (ox-bow lakes), interfluvial depressions and valleys of old tributaries which have been dammed by the deposition

of silt at their confluence with the Pongolo River (Walley, 1980; Heeg and Breen, 1982). There are 26 major and about 60 minor pans (Figure 1.3) with an area of approximately 2200 ha (Breen *et al.*, 1978) when the floodwaters subside and the pans lose contact with the river.

1.3.2 Geology and geomorphology

Successive decreases in sea level during the Pleistocene glaciations have resulted in exposure of the continental shelf which now forms the Moçambique coastal plain (Hill, 1975). During this period a series of long-shore dunes developed and formed a barrier to the eastward flow of the Pongolo River thus setting it on its present northerly course parallel to the Lebombo mountains. These are formed from acidic volcanic rocks particularly rhyolite and dacite (Figure 1.5).

The floodplain therefore lies on marine Cretaceous deposits of the continental shelf onto which the river has, over 30 000 years, deposited its sediment load to form the alluvial soils of the floodplain. The marine deposits have considerable influence over water quality on the floodplain (Heeg *et al.*, 1978). The water retained in the pans differs from that of the river, not only in having a higher TDS, but also in the composition of the solutes which approximate to seawater in their equivalent ionic proportions. The annual flooding of the floodplain flushes the system thus reducing the salinities of the pans. Changes in the flooding regime as a result of the construction of the Pongolapoort dam could cause an increase in salinity if flooding is reduced.

1.3.3 Climate

The Pongolo floodplain lies at the northern extreme of the "warm to hot, humid sub-tropical" climatic region of South Africa (Schulze, 1965). During the summer (December to March), the mean monthly maximum temperature ranges from 30,5^{o} - 32,5^{o}C (Table 1.1) and temperatures

of over 40°C are frequently attained. Relative humidity at 08h00 is greater than 72% and at 14h00 is approximately 52% (Table 1.1). Winters (May to August) are somewhat cooler (mean monthly maximum 25.0° - 26.8°C; Table 1.1) but relative humidity remains high (Relative humidity at 08h00 is 78 - 86% and at 14h00 is 39 - 48%; Table 1.1).

Mean annual rainfall on the floodplain is 572 mm and while some rain falls throughout the year, the winters are considerably drier than the summers (Table 1.1).

Evaporation is very high and at 2 388 mm p.a. is far in excess of precipitation (Breen *et al.*, 1978). Heeg and Breen (1982) suggest that this is due to a large advective component caused by arid surroundings. high temperatures and a very high run of wind. The area is subjected to considerable wind, particularly during the period September to December when the average daily run is greater than 230 km day^{-1} (Table 1.1).

1.3.4. Hydrological regime

The abrupt change in gradient of the river as it flows onto the Makatini flats (Figure 1.3) markedly reduces flow rate, causing partial deposition of the sediment load and flooding of extensive areas adjacent to the river. Flooding is therefore dependent on rainfall in the catchment west of the Lebombo mountains (Figure 1.2) and the degree of flooding is determined by; (1) the volume of water delivered to the floodplain; (2) the rate of flow;(3) duration of high flow and (4) the volume of water in the pans when flooding commences. Data for the first three factors are available from a gauging station (N^{0}W4M06, Dept. of Water Affairs) operative since 1929 but the volume of water in most pans is not known.

Monthly records for the period 1929 to 1976, in a statistically corrected form (Figure 1.6; Heeg and Breen, 1978) show that 70% of the total annual flow occurred during the period November to March with the greatest volume (17.5%) during February. Lowest flow occurred during the period June to September (approximately 10.5% of the total) and although floods have been recorded during this period they are infrequent.

Summer flooding is characterised by several floods of relatively short duration (Heeg and Breen, 1982), which may be grouped into two peak periods; December and to a greater extent February (Figure 1.6). High flood level (HFL) has been defined as the highest level attained by floodwater during an average year and thus marks the boundary of the floodplain (Breen *et al.*, 1978). The level of water remaining in the pans after the floods have subsided is maximum retention level (MRL). The depth of water in the pans is reduced considerably between flood seasons by evaporation so that some pans dry out annually. The permanence of water in the floodplain pans is determined by their MRL in relation to river height and pan depth, and has important consequences for the biota they support (Section 1.3.6).

With the construction of the Pongolapoort dam the need to conserve water for irrigation purposes now exists. A number of studies (Phélines *et al.*, 1972; Coke, 1980; Kok, 1980; Furness, 1981; Heeg and Breen, 1982) have therefore attempted to; (1) predict the minimum flow rates required to flood particular pans and (2) derive estimates of the duration of flooding at different flow rates. The computational techniques have, however, been very simple and have not taken such factors as previous flood histories that season, changes in infiltration rate and volume of water remaining in the pans into account. The figures they derived therefore have limited use and should be treated with caution until corroborated by more detailed analyses (Alexander, pers. comm.).

Pitman and Weiss (1979) have provided the means of corroboration in the form of a detailed mathematical model of the floodplain hydrology. However, this model still requires calibration with detailed data collected in the field during actual floods.

At present it is therefore not possible to accurately predict the extent of inundation of the floodplain by particular discharges from the dam. Since the hydrological regime is the principal determinant of floodplain ecosystem productivity (Furness, 1981; Heeg and Breen, 1982) this places considerable constraints on the development of management options for the floodplain.

1.3.5 The effects of the Pongolapoort dam on flooding

The Pongolapoort dam first affected flow in the Pongolo river in March 1970 when construction openings in the dam wall were closed (Phélines *et al.*, 1972). For various reasons, however, the dam has never been filled and has remained at less than 25% full capacity for the last ten years. The maximum flow which could be released under these conditions was 200 cumecs which is considerably less than the 690 cumec flood proposed by Pitman and Weiss (1979) as an "average" summer flood.

Natural floods have therefore been attenuated by the dam and durations extended (Figure 1.7) but the river gradient is so small that the floodwaters have still backed up and reached HFL (Furness, 1981; Section 3.1.1). The timing of releases from the dam, however, have generally followed the natural flood pattern and few unseasonal floods have been released. The main effect of the dam has thus been to extend the period of inundation during summer. While this altered flooding regime may have important effects on the seasonally flooded communities (Furness, 1981), the direct effects on winter producing aquatic plants such as *P. crispus* are probably small.

An additional and probably more serious problem however, is that the dam acts as a silt trap (D. Toerien, pers. comm.; W. Alexander, pers. comm.; Heeg and Breen, 1982) and reduces the amount of sediment and associated nutrients now deposited on the floodplain. Furthermore, the water leaving the dam tends to re-acquire a silt load resulting in erosion of levees and channels and hence may change the MRL in affected pans. The changed flooding regime could therefore have several indirect effects on the aquatic and seasonally flooded communities.

1.3.6 Biological components

The Pongolo floodplain is inhabited by an essentially tropical fauna and flora and many species find their southern limit here.

The primary producers on the floodplain are distributed according to their tolerance of periods of exposure and inundation and can be divided into two types: the seasonally flooded and aquatic communities. Six seasonally flooded communities have been recognised (Furness and Breen, 1980; Furness, 1981; Figure 1.8):

1. The *Acacia xanthophloea* Benth. - *Dyschoriste depressa* Nees community occurs on 128 ha at the edge of the floodplain and is inundated only when the river is in flood.

2. The *Ficus sycomorus* L. - *Rauvolfia caffra* Sond. community grows only along the levees of the river where the water table is always high but inundation occurs only when the river reaches HFL. It is an extensive community covering 406 ha.

3. The *Cynodon dactylon* (L.) Pers. community covers 171 ha and forms extensive lawns around some pans where it experiences regular inundation and gradually becomes exposed as the floods subside.

4. The *Cyperus fastigiatus* Rottb. - *Echinochloa pyramidalis* (Lam.) Hitch. & Chase community covers the largest area, 2471 ha, and occurs in marshy areas which remain wet for most of the dry season.

5. Two *Phragmites* species occupy the wettest areas and cover c. 234 ha of the floodplain. The *P. australis* (Cav.) Trin. ex Steud. community grows in flat, swampy areas while *P. mauritianus* Kunth occurs on river banks, inlet-outlet channels and pan margins where there is a marked fluctuation in water level.

When the communities become flooded during summer they contribute allochthonous inputs of nutrients and energy to the aquatic system (Furness, 1981). To date, however, only those inputs from *C. dactylon* have been quantified, making it difficult to assess the relative importance of allochthonous and autochthonous inputs to the pans.

The aquatic flora which provide the autochthonous inputs to the pans can be broadly divided into two types:

1. The algal communities comprise the phytoplankton and the periphyton. The phytoplankton, which consists essentially of cyanobacteria and the diatom *Melosira granulata* Ehrenberg, is generally sparse (Colvin, 1972) and appears to contribute little to the primary energy of the system as a whole (Rogers and Breen, 1980; Furness, 1981; Heeg and Breen, 1982).

Substantial amounts of periphyton occur on most submerged surfaces in the floodplain pans but the major community is that occurring on *P. crispus* during the winter months (Rogers, 1981; Heeg and Breen, 1982). This community forms a small biomass compared to the host plant (19% of *P. crispus* non-reproductive standing crop) but considering that it is continuously grazed by invertebrates and a rapid turnover time of *c.* 15 days can be expected (Rogers, 1981), its contribution to the annual autochthonous production of the system is likely to be important.

2. The aquatic plant communities may be either perennial or seasonal.

The perennial community of free-floating and rooted species forms dense stands in pans such as Ntujanini, Sivunguvungu, Mhlolo and Mzinyeni.

The main species are *Trapa natans* var. *bispinosa* (Roxb.) Makino and *Nymphaea caerulea* Sav. but dominance differs between localities and many other species such as *Pistia stratiotes* L. and *Azolla pinnata* R. Br. are important local contributors to the community in certain pans (Rogers, 1980). While these communities provide inputs to the floodplain pans throughout the year their contribution to the overall productivity of the system is probably small as they do not usually form very extensive stands (Heeg and Breen, 1982).

Two seasonally producing communities of submerged plants occur in those pans which do not dry out in winter (Breen *et al.*, 1978). During summer, *Najas pectinata* (Paerl.) Magnus forms dense stands in a few pans such as Bumbe and Mthikeni (Rogers, 1980). In saline pans such as Nyamithi (Heeg *et al.*, 1978) this species may be replaced by *N. marina* L. which is more tolerant of such conditions.

The major inputs from the aquatic commnities are likely to come from the winter growth of the dominant submerged plant *Potamogeton crispus* which forms extensive almost monospecific stands in many of the floodplain pans (Musil, 1972; Rogers, 1981; Heeg and Breen, 1982). These inputs are particularly important as they occur in winter when other inputs are at a minimum

The aquatic invertebrate fauna, which has been studied in some detail (Colvin, 1972; Walley, 1980), varies from pan to pan. Snails are abundant in the floodplain pans with large populations of *Bulinus (Bulinus) natalensis* (Küst.) occuring on *P. crispus* in winter. These are the main grazers of the epiphyton on *P. crispus* (Walley, 1980; Rogers, 1981). In addition *Bulinus (Physopsis) globosus* (Morel.) and *Biomphalaria pfeifferi* (Krauss), the intermediate hosts of bilharziasis, occur in many pans (Heeg and Breen, 1982).

Fifty species of fish have been recorded from the Pongolo floodplain (Kok, 1980), each exploiting a number of different food resources. The only truly herbivorous fish in the system is *Tilapia rendalli*, Gilchrist and Thompson. Both *P. crispus* and its epiphyton form a part of its diet in winter. In general the fish population forms a part of the detritus foodchain, either by utilizing detritus production directly, or by feeding on the numerous invertebrate detritivores.

The floodplain is noted for its avifauna, particularly wildfowl, which are most abundant during the winter when water levels are low. Large concentrations of waterfowl are found on pans containing *P. crispus* (Dutton, 1972). A number of other vertebrates, including crocodile and hippopotamus, occur on the floodplain. The hippopotamus occur in a few pans and feed off the floodplain by night but defaecate in the pans during the day. They thus provide a substantial but very localised, allochthonous input of energy and nutrients to the aquatic system (Heeg and Breen, 1982).

1.3.7 Human utilization

Approximately 40 000 people living around the floodplain are dependent upon it to varying degrees for their subsistence agriculture and fishing (Poultney, 1980; Rogers, 1981; Heeg and Breen, 1982).

1. Large herds of domestic stock graze on the *Cynodon dactylon* and *Cyperus fastigiatus* - *Echinochloa pyramidalis* communities as these become exposed during the dry season. Grazing on the surrounding Makatini flats is sparse at this time.

2. The people grow a variety of subsistence crops on those areas of the floodplain flooded for only short periods of time. In these areas the water table is higher than on the surrounding Makatini flats and the alluvial soil deposited by the floods is richer in nutrients.

3. The fish on the floodplain are extensively exploited by the people for whom they form a major source of animal protein. Fish are caught in a number of ways including the use of gill nets, basket traps and line and hook. The traditional *isi Fonya* is also an important method of catching fish once water levels in the pan are sufficiently low.

The floodplain forms an important source of water for domestic purposes and in addition the people use a number of species from the seasonally flooded terrestrial communities for building and thatching.

1.3.8 Tete pan

Most of this study was conducted on Tete pan (Figure 1.9) which is typical of the floodplain pans in that it is shallow with a depth of 1.5 m at MRL and *c.* 3.8 m at HFL (Figure 1.10). The pan has an area of 110 ha at MRL.

Between MRL and HFL the shore tends to slope gently (Figure 1.10) so that small changes in depth result in large changes in surface area. The vegetation of this area is also typical (Figure 1.9) with the *A. xanthophloea* - *D. depressa* and *C. dactylon* fringing the pan to the east and extensive marshland communities of *C. fastigiatus* and *E. pyramidalis* to the west. The riparian forest has been largely cleared to provide suitable areas for cultivation.

Below MRL the pan sides slope relatively steeply (Figure 1.10) so that decrease in depth results in little change in surface area until water level falls below 0.5 m. During an average year evaporative demand seldom reduces the water level below 0.5 m (Pitman and Weiss, 1979).

Perennial communities dominated by *Nymphaea* spp. and *Ceratophyllum demersum* occur in two small protected bays but the dominant plant is *P. crispus* which covers approximately 100 ha of the pan in winter.

1.4. *POTAMOGETON CRISPUS* L.

Potamogeton crispus L., a cosmopolitan member of the Potamogetonaceae (Dandy, 1937; Stucky, 1979), is one of 7 species of the genus which occur in South Africa. It is common in the summer rainfall areas (Obermeyer, 1966) and is confined to fresh or brackish waters since it is not tolerant of "high" salinities (Stephenson *et al.*, 1980).

1.4.1 Morphology

Growth is sympodial from a branched rhizome which bears few unbranched roots at each node (Obermeyer, 1966). The shoots arise from most nodes (Figure 1.11) and grow up to the surface of the water. Lower shoot internodes are long but as the shoot reaches the surface, internodes become shorter and a compact fan of sessile, linear-lanceolate leaves is formed, with the youngest in the centre. Although the leaves from the lowest nodes may be lost as the plant ages they are not replaced, so that the youngest leaves occur at the apex and oldest at the base (Rogers and Breen, 1981 a).

The flower spike is terminal, simple and emergent, and bears 5 - 10 wind pollinated flowers (Arber, 1920; Obermeyer, 1966). The flowers are bisexual with 4 carpels , each having a single ovary. The fruit has a hard pericarp and forms an achene (Everson, 1980).

1.4.2 Growth and reproduction

The achenes have a long after-ripening period before germination (Meunschner, 1936) which is generally poor (Teltsherová and Hejný, 1973). They can, however, survive dry periods of up to 18 months and may be important in surviving drought conditions (Everson, 1980; Rogers and Breen, 1980).

In the north temperate regions of America and Europe *P. crispus* is a summer producing species and overwinters by one, or a combination, of three vegetative means; as dormant rhizomes, as dwarf shoots or by the production of dormant apices termed turions (Arber, 1920; Sculthorpe, 1967; Stuckey *et al.*, 1978). Such perennation, with the year round presence of a vegetative form, led Stuckey (1979) to term *P. crispus* a perennial but other authors (Arber, 1920; Sculthorpe, 1967; Hutchinson, 1975) refer to it as an annual since most of the vegetative production dies back each year.

In sub-tropical Israel *P. crispus* is a winter producing plant which survives the summer by the production of turions only. Waisel (1971) attributes this seasonality of growth to the temperature control of both turion production and germination, and suggests the annual die off of *P. crispus* in early summer is caused by increasing temperatures. He thus terms the species "thermophobic".

The turions of *P. crispus* (Figure 1.11) can be up to 5 cm long and bear 3 - 7 small, thickened, triangular leaves (Sculthorpe, 1967) with dormant buds in their axils. These turions differ from those of other submerged macrophytes in that they develop by the production of axillary branches from the buds rather than elongation of the axis (Arber, 1920). Furthermore, although some may "germinate" without a resting period, they have become more a means of reproduction than perennation (Arber, 1920).

It is difficult on the basis of this information to describe an adaptive strategy for *P. crispus* but clearly it has a number of regenerative strategies which permit it to exploit a wide range of habitats. An aim of this study will be to describe the adaptive strategy of *P. crispus* on the Pongolo floodplain.

Little is known of the factors controlling growth and reproduction of *P. crispus* on the Pongolo floodplain. Everson (1980) has reported that achene germination is very low, and while turion germination may be high, it is completely inhibited at salinities of 5 parts per thousand (Kennedy, 1976). Much more detailed information on the factors affecting growth and reproduction in this system is therefore required.

CHAPTER 2

MATERIALS AND METHODS

2.1 PHYSICAL AND CHEMICAL ENVIRONMENT OF TETE PAN

Some of the more important physical and chemical factors which affect the growth, reproduction and decay of submerged macrophytes were measured at approximately monthly intervals at three stations (Figure 1.8). Measurements were taken at two levels (10 cm below the water surface and 10 cm above the sediment) and, in most instances, averaged to obtain a mean value for each factor in the shallow water column.

Pan depth, light penetration, temperature, salinity, conductivity, pH and dissolved oxygen concentrations were measured in the field and water samples were returned to the laboratory for nutrient analysis.

2.1.1 Pan depth and area

Fluctuating water levels can have marked effects on the temporal and spatial distribution of littoral plants (Spence, 1982) and hence their growth.

The level of the water below a permanent bench marker reference point on the shore was measured with a self-levelling dumpy level. Pan depth was then calculated by subtracting the estimate of water level from the known height of the bench marker above the flat bottom (Section 1.3.8) of the pan (Breen *et al.*, 1978).

Changes in the surface area of Tete were determined from the curve of change in the area with depth modified from Breen *et al.*(1978) (Figure 1.10).

2.1.2 Light penetration

Light penetration into a water-body is the single most important factor affecting the distribution of photosynthetic organisms. Secchi disc transparency which provides "an approximate evaluation of the transparency of water to light" (Wetzel, 1975) and represents between 10 and 15% transmission, was therefore monitored at each station.

2.1.3 Salinity and conductivity

Salinity provides a measure of the concentration (parts per thousand) of dissolved salts (Yellow Springs Instrument Co., 1981) while the conductivity (specific conductance) of the water solution is a measure of both the concentration and extent of dissociation of the dissolved salts.

Measurements of the seasonal changes in salinity and conductivity were expected to contribute to the understanding of the effects of leaching of salts from the Cretaceous marine deposits (section 1.3.2) on pan water quality. They were measured with a YSI model 33 S-C-T meter (Yellow Springs Instrument Co.).

2.1.4 Temperature and dissolved oxygen concentration

Production of oxygen during photosynthesis results in an increase in the O_2 concentration in the water so that during periods of high productivity this may increase above 100 percent saturation. Dissolved oxygen concentration not only provides an indication of primary productivity but, with temperature, markedly affects rates of growth and decay of aquatic organisms (Wetzel and Likens, 1979). Temperature also has marked influences on the solubility of substances in water and hence on their availability to aquatic organisms.
A YSI model 51B oxygen/temperature meter and YSI 5739 oxygen/temperature probe (Yellow Springs Instrument Co.) were used in the field.

2.1.5 pH

The pH of a waterbody is a measure of the hydrogen ion concentration and as such is affected by the equilibrium

$$H_2O + CO_2 \rightleftharpoons HCO_3^- + H^+ \rightleftharpoons CO_3^= + H^+$$

which results from the dissolution of CO_2 in water. In most lakes changes in pH are regulated largely by the buffering effects which additional carbonates have on this equilibrium (Wetzel, 1975).

The uptake of CO_2 during photosynthesis, however, also causes a shift in the equilibrium resulting in an increase in the proportion of HCO_3^- and $CO_3^=$ and a reduction in the concentration of hydrogen ions (Cole, 1975). Thus, during periods of high productivity pH increases while it decreases during periods of low productivity. Diel changes in pH may therefore provide an indication of primary productivity in a waterbody. A Polymetron Type 55B pH meter was used to measure pH in the field.

2.1.6 Water nutrient analyses

Since phosphorus and nitrogen are the two nutrients most likely to limit productivity (Wetzel, 1975) these were monitored during the study period. Water for chemical analysis was collected in preleached (10% HCl) bottles and filtered through a preleached (distilled water) 0.45 um membrane filter (Golterman, 1969).

Facilities for these analyses were not available at the field station so that filtered and unfiltered samples were frozen (Golterman, 1969) and transported to Pietermaritzburg for analysis. As a result a period of up to six months elapsed between collection and analysis of samples.

Freezing of samples results in the development of high local concentrations which may cause precipitation of silica in neutral to acidic waters and metal salts in alkaline waters (Stainton *et al.*, 1974). Total phosphorus is unaffected by freezing and may still be measured after lengthy storage (Golterman, 1969). In general the nutrient data of this

study should be considered only as an indication of trends in nutrient concentrations.

Soluble reactive phosphorus (SRP) was measured by the molybdate - blue method (modification 'a' of Golterman, 1969) using filtered water. Absorbance at 882 um was read on a Beckman DB-G spectrophotometer.

Total phosphorus concentrations were obtained by analysing an unfiltered water sample after all soluble and particulate organic phosphorus had been oxidised by persulphate digestion (Menzel and Corwin, 1960).

Nitrate - nitrogen (NO_3 - N) was measured by the salicylate method (Anon., 1969) during 1976 and 1977 but interference by high chloride concentrations during 1978 and 1979 led to the use of the cadmium reduction method (Strickland and Parsons, 1972) later in the study.

2.2 GROWTH, PRODUCTION AND REPRODUCTION OF *P. CRISPUS*

Attempts to measure growth rates and production of cohorts of *P. crispus* plants by the method of Howard-Williams (1978) were unsuccessful because turbid water early and late in the growing season and uprooting of plants by waterfowl, made it impossible to locate and measure the tagged plants. The growth pattern of the *P. crispus* community was therefore followed by sequential estimates of standing crop and production was estimated by measuring particulate matter losses from the community and adding these to the seasonal maximum standing crop.

One loss from the community which was not measured was the extra-cellular release of DOM. No facilities were available at the field station for such measurements.

2.2.1 Standing crop

Standing crop of the above - sediment phytomass was estimated at about monthly intervals from random, 810 cm^2 samples taken with an electromechanical sampler (Breen *et al.*, 1976). The sampler, which was lowered from the side of a boat, cut a column (16.1 cm diameter)

of plant material from the community to a depth of approximately 5 cm below the sediment surface.

Sample points were randomised by selecting them in a stratified manner along arbitrarily placed transect lines which differed in origin and direction on each sampling occasion.

Twenty samples were washed in pan water to remove sediment and epiphyton, dried in a commercial spin dryer and weighed fresh in the field. The standard error was calculated immediately and, if necessary, more samples were taken until the standard error was less than 10% of the mean. Turions and inflorescences were removed from the plants and counted and weighed separately to determine their contribution to the total standing crop. This could then be divided into the reproductive (asexual turions and achenes) and non-reproductive portions. Samples were then dried in a forced draft oven at 60°C for 48 hours, cooled in a desiccator and weighed.

2.2.2 Turion and achene banks, and germination in the field

The turion and achene banks in the sediment were determined in February or March of each year, just prior to germination. The density of achenes and turions in the sediment was determined from between 90 and 120 samples collected with a Van Veen grab which sampled an area of 504 cm^2. Sampling was randomised as for standing crop samples and continued until a standard error of less than 10% of the mean number per unit area was obtained.

Sediment was removed from the samples by washing in gauze (1 mm^2 mesh size) bags, whereafter the achenes and turions were picked from the debris, counted, dried (60°C) and weighed.

The percentage germination of achenes and turions in the field was estimated from 5 - 10 grab samples taken each month.

2.2.3 Effects of temperature and light on turion germination

The effects of temperature and light on turion germination were investigated by placing turions in glass bottles which were either transparent (light) or painted (dark). Five bottles were placed in each of 5 aquaria at temperatures of 15°, 20°, 25°, 30° and 35°C. This covered the range of temperatures experienced in the field (section 3.1.3). Twenty five turions and 200 mls of filtered pan water were placed in each bottle and aerated continuously. Light (16 hour light and 8 hour dark cycle) was provided by fluorescent lights giving a radiant flux density of 16.1 $W \cdot m^{-2}$. Turions were collected from the sediment surface on 9th January 1977, when the water temperature was 29°C. They were stored in a polystyrene box at 29 $\pm$ 1°C for 3 days until the experiment was started. The number germinated was counted twenty-nine days later, after which no further germination took place.

2.2.4 Chlorophyll concentration

The concentrations of chlorophylls *a* and *b* in *P. crispus* leaves were determined each time the standing crop was estimated in order to give an indication of change in photosynthetic potential during the life span of the community. A *c.* 50 g sample of leaves, stripped from the stems, was collected from each of the three sampling stations on Tete pan and transported to the laboratory (1 to 1½ hrs) in plastic bags in a cool, dark polystyrene box. The samples were then washed to remove epiphyton, spun dry and subsampled for immediate chlorophyll extraction. Leaves were homogenised in acetone made basic with $MgCO_3$ (Westlake, 1969) and extracted in the dark at -7°C for 12 hrs. The samples were then filtered through glass-fibre filters and the acetone diluted to 90% with distilled water after allowing for the water in the fresh leaves; this was approximately 80% of fresh mass. Preliminary tests showed that no adjustment was required for turbidity of the samples. Absorbance was measured at 665 and 645 um.

Additional samples were used to estimate the fresh mass: dry mass

ratio of the leaves so that the concentration of chlorophyll could be expressed per unit of dry mass.

2.2.5 Oxygen production by shoot tips

The rate of oxygen production by 4 - 5 cm long shoot tips was estimated in 1976 each time standing crop was sampled. In view of the problems associated with this approach (section 1.3.2) the results could not be used for reliable estimates of plant production but were used, in association with the chlorophyll estimates to indicate changes in the photosynthetic potential and metabolism of the plants.

Although very little epiphyton colonised shoot tips (section 6.1.1) they were washed gently before incubation to remove all but the very firmly attached epiphytes. The shoot tips were placed in 250 ml "light" and "dark" bottles and incubated for 2 - 3 hrs at the depth from which they came, on clear, sunny, windless days between 09.00 and 12.00 hours. Each incubation comprised twelve bottles: three light and three dark, with and without shoot tips. The bottles were filled with unfiltered pan water and the oxygen concentration before and after incubation was estimated using a standard Winkler technique (Strickland and Parsons, 1972). The results from bottles without shoot tips were subtracted from those with shoots to allow for changes resulting from plankton in the water. After O_2 determination the shoot tips were dried ($60^{o}C$) and weighed so that production rates could be expressed per unit of plant mass.

2.3 THE ANALYSIS OF PLANT TISSUES

Plant tissue analyses were required:

1. As indicators of nutrient availability for plant growth.

2. For the estimation of a nutrient budget for Tete pan.

3. For the estimation of rates of nutrient loss during decomposition.

Dried samples were ground to a fine powder and bulked. Three sub-samples were used for analysis of total N and P. In decomposition studies the concentrations of the cations K, Ca and Mg were also measured.

2.3.1 Analytical procedure for 1976

Total N was determined by titration after digestion and Kjeldahl distillation (Paech and Tracey, 1955). After ashing at 490°C for 4 hrs and acid-extraction (Paech and Tracey, 1955), total P was determined by the molybdate-blue method (Golterman, 1969) and cations by atomic-absorption spectrophotometry (Allen, 1974).

2.3.2 Analytical procedure after 1976

After 1976 tissue analyses were performed in the Department of Soil Science, University of Natal, Pietermaritzburg. Each sample was analysed individually for P, K, Ca and Mg by emission spectrometry using a Phillips 1410 Semi Automatic X-Ray Spectrometer (Kubota and Lazar, 1967). Total N was determined as ammonia with a Beckman ion specific electrode (Meldal-Johnsen, 1975) following Kjeldahl digestion (Paech and Tracey, 1955).

2.4 *POTAMOGETON CRISPUS*/WATERFOWL INTERACTIONS IN THE GRAZING FOODCHAIN

2.4.1 Waterfowl population estimates

The number of waterfowl of different species using Tete pan as a feeding ground, was counted during the evening feeding periods (16h00 to sunset). Counts, made over 3 - 6 consecutive days at approximately monthly intervals, were expressed as mean monthly counts.

During 1978 counts were also made on 10 other pans every second month. The pans were; Mtikheni, Mhlolo, Sivunguvungu, Bumbe, Ntujanene, Mzinyeni, Mandlankunzi, Kangazini, Namanini and Sukunti (Figure 1.3). To complete these counts in as short a period as possible,they were made at different lakes at different times of day. Some were counted during the morning feed between sunrise and 09h00 and others during the evening feeding period. It took up to 3 days to estimate the populations on these lakes and it is stressed that because of inter-pan movements the counts provide only a general index of waterfowl distribution and numbers.

2.4.2 Food consumed by waterfowl

The types of food consumed by waterfowl were determined by examination of oesophageal contents of birds shot during both morning and evening feeding periods.

Swanson and Bartoneck (1970) suggest that to ensure fresh food in the bird's crops and also a reliable quantitative measure of the species ingested, birds should be observed feeding for at least 10 minutes before being shot. The most abundant duck on the Pongolo floodplain, *Dendrocygna viduata* L. (White-faced duck), however, fed in flocks by diving, making it impossible to observe a single individual for any length of time. Birds collected from feeding or flying flocks during the feeding periods contained undigested and easily identifiable food in the oesophagus and this sampling procedure was therefore adopted. Occasional birds that had apparently not fed recently were excluded from the analysis.

The oesophagi containing food were removed from the birds as soon after collection as possible and preserved in 5% formaldehyde (Owen, 1972) containing 5 mg ℓ^{-1} of Phloxine dye. The latter protein stain permitted easy identification and recovery of animal remains, while the preservative prevented post-mortem digestion of the food.

The contents of the oesophagi were sorted into species with the naked eye, oven dried (60°C) and weighed. Mass was used in preference to the usual volumetric methods (Swanson *et al.*, 1974; Geldenhuys, 1977) for two reasons:

1. Food items such as soft bodied invertebrates and carbohydrate filled seeds differ markedly in their relative water contents and thus in energy stored per unit volume. Volume is therefore expected to be less well correlated with organic matter and energy content than dry mass (Westlake, 1965). As such,mass is a better index of food value.

2. Since dry mass per unit area (standing crop) is a basic currency of plant and animal production studies (Westlake, 1965), comparisons between food consumption and food supply are facilitated.

The data were analysed by the aggregate percent method (Martin *et al.*, 1946; Swanson *et al.*, 1974) where the percentage contribution by weight of each food species in each bird is calculated and then expressed as the mean percent contribution for each food species, for each sampling interval. Swanson *et al.* (1974) consider that when birds are collected while feeding and the oesophagi are well filled, the aggregate percent method provides the least biased results; particularly when presented with other information such as frequency of occurrence of each food item.

2.4.3 The nutritive value of *P. crispus* turions and achenes

Turions and achenes were picked from plant material, obtained by dragging an anchor through the water, each time the *P. crispus* standing

crop was estimated during 1977.

Phosphorus and total nitrogen content were determined (section 2.3) and crude protein estimated as 6.25 x total N (Boyd and Goodyear, 1971). Total available carbohydrate was estimated by an enzymatic (Takadiastase) method for plant material containing starch (Marais, 1969) at the analytical laboratories of the Cedara Agricultural College, Hilton, 3245, Natal.

Oven dried ($60^{o}C$) material was ground and extracted with ether (boiling point 40 - $60^{o}C$) in a Soxhlet apparatus to determine the total lipid content (Paech and Tracey, 1956).

The gross energy content was determined by bomb calorimetry following the method of Walley (1980).

Available dietary energy is best expressed as metabolizable energy (ME) of a particular food item (Burton *et al.*, 1979). This is the gross energy content (joules g^{-1}) of the food consumed minus the amount of energy voided in faecal and urinary excretions. Since bird species differ in their ability to assimilate the same food source (Sugden, 1974), ME is best measured by feeding captive birds of the species under study on the particular food source. However, since facilities for such experimentation were not available, an estimate of the "Apparent" Metabolizable Energy (AME) of turions was made using the formula of Carpenter and Clegg (1956) as outlined by Sibbald *et al.* (1963). This formula is based on the crude protein,lipid and non-structural carbohydrate content of the foods and, although originally developed for domestic fowl foods, it has been shown to be applicable to cereal grains and foods of similar composition eaten by duck (Sugden, 1971). Since *P. crispus* turions had a high starch content, a non- structural component which is easily digested (Gous, pers. comm.) it was considered reasonable to apply the Carpenter-Clegg formula to the determination of the AME of turions.

2.4.4 The estimation of turion consumption by means of the Wiens / Innis model of mean energy demand.

The existence energy (M_t) is the sum of the energy expended in standard metabolism, specific dynamic action and limited locomotor activity per square metre per day at temperature "t" (Kendeigh, 1970). Existence energy for non-passerine birds of body weight $W(g)_1$ at ambient temperatures of 30^oC and 0^oC, have been calculated by Kendeigh as:

$$M_{30} \text{ (k cal/bird day)} = 0.540\ W^{0.75}$$

and

$$M_0 \text{ (k cal/bird day)} = 4.337\ W^{0.53}$$

The M_t requirements for any temperature within this range are obtained by linear extrapolation through these values (Wiens and Innis, 1974). Conversion to SI units of mechanical energy can be made by using 1 calorie = 4.2 joules (Phillipson, 1966).

Free living adult birds are, however, more active than allowed for by this model, and may have metabolic demands of approximately 40% above the existence level (Schartz and Zimmerman, 1971). Thus the total energy requirement (MT) of a free living bird (Wiens and Innis, 1974) is approximated by:

$$MT = M_t + 0.4\ M_t$$

Further correction factors may be used for periods when birds are moulting or breeding (Wiens and Innis, 1974). Neither of these activities occurred during the period when *P. crispus* produced turions and so corrections were not required.

Wiens and Innis (1974) assumed that 70% of the ingested food is metabolically available and hence calculated the total energy intake (MA, joules $bird^{-1}$ day^{-1}) of a free living adult bird, which is neither moulting nor breeding, at ambient temperature as:

$$MA \text{ (joules bird}^{-1} \text{ day}^{-1}) = (M_t + 0.40\ M_t)\ 1.43$$

They do, however, suggest that digestive efficiency (or metabolizable energy of the food) be treated as a variable since it may vary between both bird and food type. In this study the AME of turions was 75.5% of the gross energy content and so it was assumed that 75.5% of the dry mass of turions would be assimilated. Thus, if turions were the only items consumed:

$$MA_i = (M_t + 0.4\ M_t)\ 1.32$$

where t is the averaged mean daily temperature (obtained from Heeg and Breen, 1982) for the interval i between population censuses of duck on Tete pan and M_t calculated using the mean mass of duck (as determined in 1978, section 2.4.4) for the interval i.

The total energy intake for a particular duck species on Tete pan during the period in which turions were consumed each year could therefore be calculated as:

$$(MA_{i1} + \text{duck days}_{i1}) + (MA_{i2} + \text{duck days}_{i2}) \ldots (MA_{in} + \text{duck day}$$

that is: $\sum (\ MA_i + \text{duck days}_i)$

The total turion intake by duck could then be calculated and converted to a dry mass basis using estimates of;

1. the contribution of turions to the total diet (i.e. the total energy intake) (section 2.4.2)
2. turion gross energy per unit dry mass

   and

3. turion AME per unit dry mass.

This assumes that other food items have the same AME as turions but since they generally formed less than 10% of the diet the error in calculation was probably small and could be ignored. In view of the many assumptions made in using this model the results should be viewed as rough estimates only. They were, however, the best obtainable since even with considerably more effort little improvement could be gained.

2.4.5 Mass and condition of White-faced Duck

The condition of White-faced duck on the floodplain was assessed as the percent contribution of the perivisceral and sub-cutaneous fat deposits to total body mass (Wypkema and Ankney, 1979). Five to twelve birds, collected every second month during 1978, were dried with paper towel and weighed fresh to the nearest 1 g. After the birds had been skinned, the sub-cutaneous and perivisceral fat deposits were removed and weighed.

High summer temperatures often made the sub-cutaneous fat too soft to remove easily and accurately in the field. In these cases the skins were returned to the laboratory and frozen in sealed plastic bags so that the cold, solidified, fat could be easily removed. Perivisceral fat, being loosely connected to the viscera, was always easily removed and weighed in the field.

2.4.6 Effects of waterfowl grazing on turion production in the field

The method of excluding grazers from sub-units of the grazing area (Brown, 1954) was used to study the effects of duck grazing on turion production at Tete pan during 1976 and 1978.

In 1976 the exclosures consisted of a frame (2 x 2 x 2 m) of steel reinforcing rod (1.26 cm diameter) bounded by 20% plastic shade netting on the four vertical sides. The frame was pressed into the sediment such that the bottom of the shade cloth was 5 - 10 cm below the sediment surface and the top 10 cm above the water. Aerial entry of the duck was prevented by a 1 m high fence of upright wire (4 mm diameter) bars, 15 cm apart, around the top of the exclosure. Since duck glide in to the water on a low flight path they did not land in the exclosure. The thin upright bars also prevented other birds from settling on the exclosure.

The exclosures were, however, too small to allow entry in a boat and this made sampling of the turion and seed banks within them difficult.

In 1978, therefore, larger exclosures of 25 m^2 (5 x 5 m) were constructed of untreated, wooden poles bounded by galvanized wire mesh 5.5 x 5.5 cm) stretched from 0.5 m below, to 1 m above water level. This was sufficient to exclude duck from the exclosure and spikes on the poles prevented other birds from roosting on them.

The exclosures (3 in 1976 and 4 in 1978) were positioned in the pan before growth of *P. crispus* commenced. In February of the following year, after the plants had died down and before turion germination began, the sediment samples were taken in each enclosure with the Van Veen grab. The samples were washed and turions and seeds removed, counted, oven dried and weighed as described in section 2.2.2.

The effects of duck grazing on turion and seed production were assessed by submitting the difference between the sizes of the turion and achene banks inside and outside the exclosure to a "t" test (Parker, 1973).

2.4.7 Effects of waterfowl grazing on *P. crispus* standing crop

The most abundant species of waterfowl on Tete pan, the White-faced duck, fed in dense flocks or "rafts" of up to 1 000 birds. The area utilized at each feed was easily distinguished by damaged plants and turbid waters. Similarly, early in the season, areas where birds had not yet fed were distinguishable by an absence of damaged plants.

To quantify the proportion of standing crop broken or uprooted by feeding waterfowl, a portion of the community was sampled immediately after it was grazed for the first time. On the 23/7/78 areas of the *P. crispus* population which did not show signs of grazing damage were pinpointed. Observation then continued until the 26/7/78 when a flock of 500 birds (to the nearest 20) fed over one of the areas which had not been previously grazed. The feeding birds covered an area of *c.* 3 000 m^2 (100 x 30 m) during the single morning feeding period.

Immediately the birds had ceased feeding the detached plants were collected by hand from a small boat within each of three 25 m^2 quadrats, spaced at 25 m intervals along the length of the feeding area.

Since some detached plants could have entered the area by wave and wind action after earlier feeding in other areas, three control quadrats were set up in the area immediately adjacent to the sample area where birds had not previously fed.

The detached plants were then oven dried and weighed and the number of turions remaining on the plants counted. The turions were divided into two groups:

1. Large turions: Large starch-filled turions which consisted of swollen stems with dormant buds in the axils of swollen leaf bases (Plate 2 a).

2. Small turions: The stems of these turions were only slightly swollen and the leaf bases were either absent or so reduced that the dormant buds protruded beyond them (Plate 2 b).

2.4.8 The production of large and small turions by detached plants

Plants detached by feeding waterfowl on the 21/7/78 were spun dry and four 100 g (fresh weight) subsamples were obtained. The numbers of large and small turions remaining in each subsample was recorded before the plants were placed in glass tanks containing 35ℓ of unfiltered pan water and incubated in shaded sunlight.

Plants were incubated for 20 days and the numbers of large and small turions were counted. At this stage much of the vegetative material had been consumed by snails *(Bulinus natalensis)* and no further turions were produced.

2.5 THE EPIPHYTON, GRAZER, HOST PLANT ASSOCIATION

2.5.1 Epiphyton colonization of *P. crispus*

The pattern of epiphyton colonization of *P. crispus* leaves and stems of different ages was studied by scanning electron microscopy. Leaves and stems of different ages were collected from the base of plants (oldest) to the shoot tip (youngest) (see Section 1.4).

Five mature plants at the same stage of development were collected from Tete pan shortly after the population reached maximum standing crop in 1977. Plants were carefully cut at the sediment and gently transferred to a trough of lake water. Two leaves were removed from each of four zones (Figure 1.11); 'youngest' leaves, which were not fully expanded, near the apex; 'young' leaves, fully expanded near the apex; 'mature' leaves, midway down the stem and showing no evidence of senescence; 'oldest' leaves, near the bottom of the stem, showing yellowing. Two sections of stem 3 cm long and bearing at least one internode were also removed from the base, middle and tip of each plant.

Leaves and stems were transferred to cold (4°C) 5% phosphate-buffered glutaraldehyde. Despite care in handling, loose 'detrital aggregate' (Bowen, 1979) was dislodged and this study therefore considered only the more securely attached epiphyton.

Because snails graze the senescing plants (Section 6.1) no very old or decaying leaves or stems could be found in the field. To simulate the later stages of senescence 'oldest' leaves and basal stem sections were incubated in unfiltered lake water at room temperature until they were flaccid (12 days). They were then transferred to glutaraldehyde.

The distal 0.5 - 1 cm portion of five leaves and stems from each age group were soaked twice in 0.05 M sodium cacodylate buffer for 10 mins. to remove preservative, before fixing in 1% osmium tetroxide. The tissue was dehydrated by passing through a graded acetone series (10, 20, 30, 60 and 100%). Material was critical point dried after the method of Cross *et al.* (1977), coated with gold and viewed under a Jeol JSM 35 scanning electron microscope.

2.5.2 Ultrastructure of the epiphyton/host interface

The ultrastructure of the epiphyton/host interface was investigated by transmission electron microscopy. Distal sections of the preserved leaf and stem material remaining from the previous investigation (section 2.5.1) were soaked (30 mins.) in three changes of 0.05 M cacodylate buffer, before being fixed in 2% osmium tetroxide. They were then dehydrated in acetone, soaked in propylene oxide and embedded in araldite resin. Polymerisation was for 48 h at 70°C.

Transverse sections (*c.* 70 um) were cut with a diamond knife on an LKB microtome and stained with uranyl acetate and lead citrate (Reynolds, 1963). A Hitachi HU, 11, E was used for viewing.

2.5.3 Effects of snail grazing on the epiphyton/host association

Leaves and stem sections of different ages were collected from 100 mature plants of *P. crispus* (section 2.5.1) and placed in separate polythene buckets containing unfiltered lake water. Despite care in handling during transport to the laboratory loose detrital aggregate and associated microflora were dislodged. It was not, however, removed from the buckets but left as a possible source for recolonization of the plant material.

The leaves and stems were incubated in the buckets, on a laboratory bench, to allow epiphyte colonization to continue in the absence of grazers for 20 days. The effects of snail grazing on the epiphyton and host were then determined in two ways;

1. On the day of collection four leaves and four stems of each age category were presented to 8 snails of uniform size (shell diameter 2.5 - 3.0 mm) contained in 2 glass jars. The jars were filled with 75 mls of unfiltered lake water and incubated on the laboratory bench. After 24 hours the plant material from one set of jars was preserved for viewing by SEM (section 2.5.1).

The condition of the remaining leaves was recorded photographically after 20 days.

2. Changes in the rates of consumption ("edibility"; Nicotri, 1977) of *P. crispus* were assessed after presenting leaves and stems to snails on the day of collection and after 2, 4, 6, 8, 10, 12 and 18 days of incubation in the absence of grazers. The experiment was terminated after 18 days.

2.5.4 Numbers and standing crop of *Bulinus natalensis*

Estimates of seasonal changes in the *B. natalensis* population were made by sorting all snails from the *P. crispus* standing crop samples. The snails were preserved in 5% formaldehyde in the field and on return to the laboratory were oven dried (60°C), weighed and counted.

2.6. DECOMPOSITION AND DETRITUS FORMATION

The initial decomposition experiments were designed to establish a method of study using the decomposition or "litter" bag technique (Boyd, 1970) to follow mass and nutrient loss in the field.

Thereafter, studies were conducted in the laboratory to assess the role of snails and necrotroph conditioning in the natural process of detritus production.

2.6.1 Field studies

Since waterfowl broke and uprooted the plants before they died the use of detached plants in decomposition studies would represent the natural situation.

Material was collected by dragging an anchor behind the boat just above

the sediment surface. The sample thus included both undamaged and duck-damaged plants of various ages. To ensure a study of the entire process of senescence, death and decay, only apparently healthy plants were selected, while those already showing evidence of senescence were discarded. Sediment was removed by gentle washing in lake water and all invertebrates, roots and reproductive structures were removed. The excess water was then removed by spin-drying and subsamples (100g, about 10 g dry mass) were rapidly weighed and transferred to plastic-coated, fibre-glass gauze bags (400 x 250 mm, 2.25 mm^2 mesh size). The bags were kept standing in lake water to prevent the plants drying out. Additional subsamples were air-dried before being placed in the decomposition bags. Further subsamples, of different mass, were oven dried at 60^oC. These data were used to determine the fresh mass : dry mass ratio so that all fresh mass estimates could be converted to an oven dry mass basis.

The bags were transferred to four stations on the lake, situated 30 m apart within the area colonized by *P. crispus*. They were attached to a marker by a cord long enough to permit them to sink to the bottom. Bags containing plants which were not dried tended to float for 1 - 2 days before sinking to the sediment, as do naturally uprooted plants.

One bag of "fresh" and one of dried material was collected from each station at approximately five day intervals. The contents of the bags were rinsed rapidly in distilled water and the snails and other invertebrates which had entered the bags during incubation were removed and counted. All material was dried at 60^oC and weighed.

The four samples for each treatment were then bulked, ground and analysed for total nitrogen, phosphorus, potassium, calcium and magnesium as described in section 2.3.

In 1977 a set of decomposition bags of mesh size 5 x 5 mm was also used as described above. This mesh size did not restrict the movement of the snail population into and out of the bags and provided an indication of the effects of snails on the rate of mass loss.

2.6.2 Laboratory studies

While litter bags provided an indication of mass loss in the field the nature and amount of detritus lost from the bags could not be assessed. Experiments to determine the role of epiphyton and snails in detritus production were therefore assessed *in vitro*.

Uprooted plants were collected from the field, washed gently in lake water to remove sediment, and all invertebrates, roots and reproductive structures were separated. The excess water was then removed by spinning the material in a commercial spin-drier.

Sixty-four subsamples of 30 g each (about 3 g dry weight) were weighed rapidly and transferred to plastic bags before being transported to the laboratory. The subsamples were placed in glass jars containing 2 *l* of aerated unfiltered water and divided into four treatments of sixteen jars each:

1. No snails: *P. crispus* plants incubated without snails as described above.

2. Snails: Forty snails of 0.35 g fresh weight were added to each jar. This represented the density and mass of snails per gram of *P. crispus* in the field at the time.

3. No snails plus EDA: Since preparation of subsamples would have dislodged much of the epiphyton, 20 ml (0.025 g dry weight) of epiphytic detrital aggregate (EDA) was added to act as a source of bacteria during incubation. The EDA was washed from other plants.

4. Snails plus EDA: Both snails and EDA were added to the jars.

The effects of the treatments were assessed by following mass loss of the plant material and detritus accumulation over a period of 24 days. Four replicates of each treatment were harvested at 6 day intervals and

the remaining plant material separated from the detritus by pouring the contents of the jars through a 1 mm^2 sieve. The water was filtered through pre-weighed glass-fibre filters to remove the detritus and both detritus and remaining plant material were oven dried (60^oC) and weighed.

Results were fitted to an exponential function ($y = ae^{-bk}$, where y = mass of plant material remaining after time interval b, a is the initial mass and k the rate constant) which was then linearised to $\ln y = a - bk$ (where a is the natural log of the initial mass). Differences in rates of mass loss were tested for significance by following the "Simultaneous Test Procedure" for differences between regression co-efficients (k) (Sokal and Rohlf, 1969).

Total nitrogen and phosphorus concentrations of the plant material and detritus remaining at each harvest were determined as described in section 2.3.2.

Total dissolved P in the water was measured by the molybdate-blue method (Golterman, 1969) in a filtered sample after digestion with persulfate (Menzel and Corwin, 1960).

Total dissolved N was measured by micro-Kjeldahl digestion and distillation (Golterman, 1969).

CHAPTER 3

THE PHYSICAL AND CHEMICAL ENVIRONMENT OF TETE PAN

The potential contribution of *P. crispus* to nutrient and energy transfers in the floodplain ecosystem is governed largely by the suitability of the environment for plant growth (section 1.2.1). This chapter describes the physical and chemical environment of the floodplain pans with particular reference to Tete pan.

3.1 RESULTS

3.1.1 Pan depth and area

During the summer months periodic flooding caused the water level in Tete pan (Figure 3.1) to fluctuate rapidly and irregularly between maximum retention level (MRL, 1.5 m) and high flood level (3.8 m). The first floods occurred in December (1976 and '77) and October (1978) and drainage to MRL occurred in May, March, April and January in 1976, '77, '78 and '79 respectively. Thus the pan and river were separated for between 6 and 8 months from autumn to spring during 1976 - '78 but for 13 months from January 1979 until floods again entered Tete in February 1980 (P. Louw, pers. comm.).

During the dry months of autumn through spring, water level decreased by evaporation and seepage at approximately 0.1 m per month (Figure 3.1) with the result that in 1976, '77 and '78 the water depth in early summer, shortly before the next season's floods, was between 0.7 and 0.9 m. During 1979, however, the pan and river were separated during the summer months when the increased evaporative demand caused water levels to drop at about 0.22 m per month. Consequently, by mid October, the pan had almost dried out (Figure 1.10) and only a small (1 ha) area of water about 0.1 m deep remained.

Changes in surface area of Tete pan (Figure 3.2) were also marked and irregular during summer floods but because of the relatively steep

sides of the pan (Figure 1.10), were small and gradual during the dry autumn to spring period. Thus, while the area available for colonization by rooted, submerged plants was very variable during summer, it usually changed only slightly (from 106 ha to 90 ha) over the 6 - 8 month period that the river and pan were separated. Even during the 1979 drought the surface area remained above 80 ha until early September, after which it decreased rapidly to less than 1 ha by mid October.

3.1.2. Light penetration

Secchi disc transparency (Figure 3.1) was low (0.15 - 0.3 m) during floods but once the pan and river lost contact, the water cleared rapidly and the pan bottom was usually visible by early winter.

Since Tete is shallow, wind-induced turbulence at times disturbed the sediments and caused an increase in turbidity. Such periods were, however, short lived as the resuspended material settled rapidly, and they were not reflected in the data except in late spring (October, November; Figure 3.1) when water levels were lowest and wind runs longest (Table 1.1).

3.1.3 Temperature

Midday water temperatures, at both the surface and bottom of the pan, were maximal (30 - 31°C; Figure 3.3) during summer (January and February) but declined rapidly to 16 - 18°C in June and July. Temperatures then began to increase again before the end of August each year.

Although the pan was at times isothermal, the bottom waters were usually slightly (up to 2°C) cooler than the surface at midday. At the high temperatures experienced on the floodplain a 2°C difference in temperature would create a large density difference between surface and bottom waters, thus providing considerable resistance to mixing (Beadle, 1981; Wetzel, 1975). Monitoring over three 24 hour periods during 1976, however, showed that these temperature differences were

caused by daily heating of surface waters (Figure 3.4) and that heat loss at night permitted mixing throughout the water column.

During 1979 seasonal changes in temperature followed the same pattern as previous years until the pan was very shallow (10 cm, mid-October) when the midday temperature reached 35°C.

3.1.4 Oxygen concentration and pH

Both oxygen concentration and pH, at midday, (Figure 3.5) showed marked seasonal fluctuations. During winter and early spring (June to October) supersaturation of oxygen occurred and pH rose to between 8.4 and 9.5. During periods of flooding, however, oxygen concentrations dropped to well below saturation, reaching 52% in February 1978, and pH dropped to below pH 7.5.

Both oxygen concentration and pH may be indicators of production within a waterbody with both parameters rising during periods of high productivity (Wetzel, 1975; Cole, 1979; Wetzel and Likens, 1979). The data therefore, indicate a net use of oxygen over production during floods when waters are turbid and detrital inputs large (Furness, 1981) but high primary productivity during the winter months. During 1979 oxygen concentrations and pH followed similar trends to previous years until August when there was a rapid decline in both variables, shortly before the pan dried out, indicating a sudden decrease in primary production.

The periods of high pH and oxygen concentration coincided with the presence of *P. crispus* in the pan (Figure 3.5; Chapter 4) during all four years of study indicating that this plant's metabolism had a marked influence on the chemical environment of the pan.

3.1.5 Conductivity and salinity

Conductivity was low (100 to 500 u S cm^{-2}; Figure 3.6) during periods of flooding but increased gradually as water levels decreased by evaporation after the river and pan were separated. Maximum conductivities reached during 1976, '77 and '78 were 800, 1500 and 1800 u S cm^{-2} respectively while in 1979 conductivity rose from 1900 in August to reach 4500 in October shortly before the pan dried out.

Salinity (Figure 3.6) followed a similar trend to conductivity; during periods of flooding it was undetectable but as water levels declined by evaporation, salinity rose to 0.7, 0.85, 1.0 and 2.0°/₀₀ in 1976, '77, '78 and '79 respectively.

Conductivity and salinity were therefore both markedly affected by flooding, which flushed salts from the system, and by evaporation during the dry months (March to October) which increased the concentrations of salts. The salt content may also have been increased by the presence of seepage water from the underlying marine Cretaceous deposits (Heeg *et al.*, 1978), but there is insufficient information to indicate how important this may be.

A plot of conductivity against percentage decrease in volume of the pan (Figure 3.7) shows a non-linear relationship where there is little change in conductivity until some 60 - 70% of the volume has been lost. This indicates that increased conductivity is not simply a function of concentration of salts and that the system is fairly well buffered against changes in conductivity until reduction in water volume is large. Such buffering has been noted in a number of shallow African lakes (Howard-Williams and Ganf, 1981) and is attributed to a wide range of hydrological, chemical and biotic interactions. On the Pongolo floodplain it is probably due, at least in part, to precipitation of certain elements early in the annual drying cycle and to the duration of flooding in the previous season which would leach salts from the sediment and flush them from the system. Uptake of elements by macrophytes may have influenced conductivity but the lack of a consistent relationship between annual changes in *P. crispus* standing crop and conductivity (Figure 3.7) suggests that this was not a major buffering mechanism.

3.1.6 Nitrogen and phosphorus

Nitrate-nitrogen (NO_3-N) concentrations (Figure 3.8) showed distinct bimodal fluctuations each year. Levels were high (up to 152 ug ℓ^{-1} in 1976) at the end of the flooding period whereafter they declined rapidly during the growth period of *P. crispus* to reach low (8 ug ℓ^{-1}, 1976) or undetectable levels in midwinter. This was followed by a rise in concentration each year in spring, which Rogers (1981) attributes to N_2 - fixation by epiphytic cyanobacteria and subsequent excretion by

snails which graze upon them. There is a later decrease in these high levels with the advent of the first floods which are low in NO_3-N (Archibald *et al.*, 1969). The rise in NO_3-N as floods continue into summer probably results from leaching of inundated soils and the oxidation of NH_4^+ released during decay of drowned semi-terrestrial vegetation.

The maximum concentrations of NO_3-N varied from year to year (Figure 3.8) but were always near the lower limit for the concentrations normally expected in unpolluted waters (Wetzel, 1975). Everson (1980), however, showed the total N concentrations in the sediment were high and changed very little over an annual cycle.

Soluble reactive phosphorus (SRP) concentrations (Figure 3.9) tended to be higher (up to 35 ug ℓ^{-1}) during floods and lower (5 ug ℓ^{-1}) when the river and pan were separated but there was no consistent pattern during the study period.

Total phosphorus concentrations (Figure 3.9) in Tete pan also varied markedly from year to year, but showed a more consistent pattern of high levels (60 - 100 ug ℓ^{-1}) during floods and lower levels during the winter months.

While silt-adsorbed P and soluble P leached from inundated terrestrial vegetation probably contribute to high concentrations during floods it is difficult to fully assess the factors affecting P concentrations and fluxes in this system from the information available because:

1. Lake sediments may buffer changes in soluble phosphorus by net adsorption during periods of low biological demand and net release of P when demand increases. Thus concentrations in the water may remain steady although significant exchanges are taking place (Twinch and Breen, 1980).

2. The depth of the oxidised microzone at the sediment/water interface is very important in determining the P exchange kinetics between sediment and water (Syers *et al.*, 1973; Klopatek, 1978). Wind induced turbulence in shallow, highly oxygenated systems such as Tete

pan will frequently disturb the sediments and increase the depth of the microzone. Initially, this will result in a release of P from the pore water of the reduced sediments but the increased depth of oxidised sediment which results, will slow down further release.

3. All biological components of a water-body are important factors in phosphorus cycling and their rates of P uptake from the sediments or water, excretion and release of P on death cause marked changes in the concentrations of all forms of phosphorus (Twinch and Breen, 1980). The effect of a single flux of P may therefore not be clearly evident.

4. Orthophosphate-phosphorus (PO_4-P) is the only form of phosphorus freely available to primary producers and SRP levels do not accurately indicate the quantities of this nutrient present (Section 2). Furthermore, SRP concentrations can be affected by lengthy storage of samples (Section 2.1.2).

Phosphate-phosphorus, is however, only one of the important phosphorus components in water which include colloidal P, low molecular weight organic P, particulate P and PO_4-P (Twinch and Breen, 1980). All of these compartments would directly or indirectly influence growth of *P. crispus* and its epiphyton. However, elucidation of the various pathways of flux would require very detailed research beyond the scope of this study.

The data presented do, however, suggest that, on the basis of P concentrations in the water, Tete pan can be classed as mesotrophic to eutrophic (Wetzel, 1975) and since available P in the sediments is high (Everson, 1980) phosphorus does not appear to be in short supply for rooted submerged macrophytes and their epiphyton.

3.2 DISCUSSION

The flooding regime of the Pongolo River during 1976, '77 and '78 broadly followed the usual pattern of seasonal events (Section 1.3.4)

with early floods in spring followed by further floods during summer. The absence of floods during 1979 was unusual and caused by fluctuations in rainfall which occur on a longer time scale (Tyson and Dyer, 1978). The parallel occurrence of annual, small magnitude and longer time scale, large magnitude fluctuations in environmental conditions is an important determinant of shallow lake functioning in the tropics and sub-tropics (Beadle, 1981; Howard-Williams and Ganf, 1981; Brock and Lane, 1983). The large surface area to volume ratio of these lakes means that the capacity of the water body to buffer environmental effects which act over the surface area, is small. Thus both short and long term extremes in environmental conditons occur and the biota of shallow lakes are adapted to these. This discussion considers the implications of seasonal flooding regimes and long term wet and dry cycles on the Pongolo floodplain for growth and reproduction of submerged macrophytes.

3.2.1 Annual fluctuations in physical and chemical environments

During 1976, '77 and '78 there were two distinct phases of physical and chemical conditions each year.

1. A summer (November to March) period of flooding when water depth and surface area fluctuated frequently and widely, and silt loads reduced light penetration to a few centimetres. Thus, despite low salinity and conductivity, warm temperatures and a tendency for higher nutrient levels than at other times of the year, summer conditions were not favourable for the growth of rooted submerged macrophytes. The low O_2 concentrations and pH during this period indicate that during summer the aquatic phase of the floodplain is dominated by a heterotrophic metabolism. The major energy source of the floodplain fauna at this time is detritus, formed when the semi-terrestrial vegetation is inundated.

2. During autumn through spring (April to October) pan depth and area were more stable and decreased slowly as water was lost by evaporation and seepage. Light penetration was good and although temperatures were lower than in summer, and conductivity and salinity increased, they did not exceed the range reported for other habitats

of *P. crispus* (Waisel, 1979; Stephenson *et al.*, 1980). Thus, although nutrient concentrations, particularly NO_3-N, tended to be lower, nutrients were available in the sediments and conditions were suitable for the growth of rooted submerged plants such as *P. crispus*. Indeed, supersaturation of oxygen and high pH indicated high rates of primary production during this period.

Although floods create unfavourable conditions for submerged macrophytes during summer they are instrumental in ensuring that growth can take place in winter, in three main ways;

(a) they recharge the pans with water and in doing so they
(b) flush out accumulated salts (Heeg and Breen, 1982) which could reduce growth of *P. crispus* and germination of the turions (Kennedy, 1976) if salinity exceeded 5 parts per thousand;
(c) floods also act in transferring nutrients from inundated semi-terrestrial vegetation to the aquatic phase (Furness, 1981).

Periods of flooding are therefore as important as stable water level periods in providing an environment suitable for sustained submerged plant production. Plant life-cycles would, however, need to be adapted to the winter/spring favourable period.

3.2.2 Long term wet and dry cycles

Tyson and Dyer (1978) have proposed that an 18 year wet and dry cycle occurs in the summer rainfall area of South Africa. Their data have shown a drought period during the 1960's followed by above average rainfall during the 1970's, and they predicted another drought in the early 1980's. This cycle clearly affects the Pongolo floodplain as Coke (1970) described Tete pan as being "almost dry and salinity high" in 1968/69, Furness (1981) reported extended duration floods in summer 1975/76, and Tete pan was again almost dry in 1979 and dried out completely in 1983 (C.M. Breen, pers. comm.).

Extended periods of flooding in wet years, and unseasonal floods such as occurred in July 1963, will have the effect of shortening the winter/ spring period favourable for primary producers but droughts are likely to have most impact on submerged plants and their role in ecosystem functioning.

The absence of floods during January and February 1979 resulted in stable depth, clear water conditions in Tete pan which were favourable for the growth of submerged macrophytes. Unseasonal production was accompanied by an increase in pH at this time (Figure 3.5). Despite the marked drop in water level during winter, however, conditions of light and surface area remained favourable until early September when the area available for colonization was rapidly reduced. Most important, however, was that although salinity and conductivity increased markedly,they did not exceed the general limits (5°/$_{oo}$ and 5000 u S cm^{-1} sec^{-1} respectively) of tolerance of freshwater organisms (Beadle, 1981).

Increased salinity appears to be one of the major causes of death of freshwater organisms during a drought phase in shallow lakes (Kalk *et al.*, 1979; Beadle, 1981; Howard-Williams and Ganf, 1981) and may be more important on the Pongolo floodplain than indicated by conditions in Tete pan. Others pans such as Mhlolo and Nyamithi which have small saline catchment areas of their own (Heeg *et al.*, 1978) normally have higher salinities (2 - 4°/$_{oo}$) and thus may be more affected by concentration of salts during droughts. Heeg *et al.* (1978) and Walley (1980) suggest that this may be the reason for a complete absence of lamellibranchs and reduced oligochaete biomass in these pans which both contain dense stands of *P. crispus*.

3.2.3 Tete pan as a submerged plant habitat

Since individual plant species respond differently to particular environmental variables (section 1.2.3.2) there is no point in attempting to clarify the conditions in floodplain pans such as Tete in terms of stress or disturbance until more detailed studies of *P. crispus* growth and reproduction are discussed. However, it is recognised that for an organism to survive in, and exploit, a shallow water habitat it must

have a life cycle which, (a) provides for an inoculum to survive unfavourable periods and (b) ensures growth and reproduction during favourable periods. On the Pongolo floodplain, if plants such as *P. crispus* are to play an important role in ecosystem functioning they must:

1. Produce inoculae to survive the unfavourable light climate in summer which varies in both timing and duration each year in relation to seasonal flooding.

2. Produce inoculae which will survive drought conditions occurring on a longer time scale.

3. Have the ability to grow and reproduce in a variable and short (6 - 8 months) period during winter and spring each year.

CHAPTER 4

ADAPTATION OF GROWTH, REPRODUCTION AND NUTRIENT RELATIONS OF *POTAMOGETON CRISPUS* TO FLOODPLAIN CONDITIONS

The life history and adaptive strategy* of *P. crispus* needs to be carefully attuned to the major environmental fluctuations which occur on the Pongolo floodplain if it is to successfully exploit its habitat and play a predictable role in ecosystem functioning.

Plants must acquire resources (energy and nutrients) and allocate them to growth and reproduction during the favourable periods of the year such that some may be stored over the unfavourable periods in order to ensure an inoculum when conditions for growth subsequently improve.

This chapter considers the adaptations of *P. crispus* growth, reproduction and nutrient relations to the floodplain environment.

4.1 RESULTS

To facilitate interpretation, results for growth and reproduction during the wet period (1976-78) are presented first (Sections 4.1.1 - 4 1 3), followed by those for the drought year 1979 (Section 4.1.4). Nutrient relations for both periods are presented in section 4.1.5.

4.1.1 Achene and turion germination, and the annual initiation of *P. crispus* growth

Achene germination was very low each year, ranging between 0 and 0.005% of the bank in the sediment and most plants arose from turions each year.

Turion germination (Figure 4.1) was first recorded in April and reached maxima of 60%, 84% and 91% in mid-July 1976, '77 and '78 respectively. The estimate of 60% in 1976 is, however, considered low

* This controversial term is used (*sensu* Grime, 1979) as it implies a suite of interdependent adaptations which promote functioning of the plant in a multifactorial, interactive environment. This implication, fundamental to the general theme of this thesis, is lacking from other terms in common usage.

as it was based on the number of turions with attached plants only and did not account for detachment of plants during sampling. During the latter two years the turions with empty bud scales in the axils of leaves, indicating the loss of the attached plant, were included and so a germination of 85% to 95% by mid-July would appear more accurate.

The initiation of turion germination occurred at a time of decreasing temperature (Figure 3.3) and increasing light penetration (Figure 3.1); two factors which have been identified as important stimuli for germination in other submerged plants (Hutchinson, 1975; Section 1.2.1). This was confirmed by laboratory experiments which showed that both temperature and light had significant effects on turion germination (Table 4.1). Germination was maximal at 15°C, significantly ($p = 0.01$) reduced at 25°C and did not occur at 30°C. Light had no significant effect on percentage germination at low temperatures but markedly increased germination at 25°C.

The summer conditions of high temperature and low light penetration (Section 3.1) therefore inhibited germination but when temperature dropped below 25°C in April germination was stimulated. Since light is not important in promoting germination below 25°C, germination can occur before light reaches the sediment as must have occurred in 1976 (Figures 3.1 and 4.1).

Temperature therefore appears to be a major factor controlling turion germination and thus the initiation of *P. crispus* growth at the onset of the favourable winter season.

4.1.2 Growth and decline of the *P. crispus* population

Growth of young plants, as indicated by increases in standing crop (Figure 4.2a) and rates of dry matter production (Figure 4.2b), was slow initially but increased rapidly during June and July each year. The formation of reproductive structures (turions and inflorescences) by mature plants in August coincided with a reduction in vegetative growth and maximum standing crop occurred in late August/early September (Figure 4.2a and b).

The decline of standing crop was not as predictable as the initiation or growth phases and plants disappeared by the beginning of November 1978, late November 1977 and mid-December 1976. During 1976 and 1977 *P. crispus* had therefore disappeared before the floodwaters filled the pan to above MRL (Figure 4.2a) but during 1978, 41 g m^{-2} or 62% of maximum standing crop remained in October when the pan was flooded by very turbid water (Figure 3.1; Section 3.0.0). Thus, the life cycle of *P. crispus* on the Pongolo floodplain has usually been completed before the onset of summer floods but early floods may inundate the population and cause its rapid decline (Figure 4.2).

Waisel (1971) has described *P. crispus* in Israel as "thermophobic" and suggests that the annual decline of winter-growing populations is caused by increasing summer temperatures. More detailed studies of *P. crispus* on the Pongolo floodplain during 1976, however, suggest that this is not so.

Changes in *P. crispus* standing crop in relation to leaf chlorophyll and shoot tip oxygen production during 1976

In April 1976 plants began to grow below the euphotic zone (i.e. at 2.5 times Secchi disc depth) in darkness or very dim light (Figure 3.1) and they contained no measurable chlorophyll (Figure 4.3). Thereafter, the chlorophyll *(a + b)* content increased rapidly to a maximum in May and June but declined in July after the maximum rates of dry matter production had occurred (Figure 4.2b). Rates of dry matter production and leaf chlorophyll concentration therefore decreased before temperatures began to rise. A similar sequence of events occurred during 1977 and '78 (Figures 4.2 and 4.3).

Shoot tips were first incubated in bottles at their natural depth, just above the sediment surface, during April 1976. The young plants which lacked chlorophyll showed a small net uptake of oxygen (Figure 4.4) indicating that growth must have been at the expense of the turion reserves. By May, however, the plants were 1 m tall and water depth had decreased to 1.5 m. Thus despite continuing turbidity (Secchi disc depth 0.4 m) the plants had reached the euphotic zone. The rate of O_2 production by shoot tips incubated at 1 m was 5 mg O_2 g^{-1} hr^{-1} but four times

greater (20 mg O_2 g^{-1} hr^{-1}) at the surface, indicating that the rate of photosynthesis was reduced by light attenuation in the turbid water.

The maximum rate of O_2 production by shoot tips was measured in early June but then decreased markedly to a minimum in late August (3 mg O_2 g^{-1} hr^{-1}) shortly after the water temperature (Figure 3.3) had begun to rise (17°C to 19°C). More important, however, was that during this period of decreasing production, gross rates of O_2 production showed a smaller decrease than net production (Figure 4.4) indicating an increased respiratory demand and that the shoot tips were beginning to senesce (refer to discussion in Section 1.2.2. and Figure 1.1). This occurred at the same time as the decrease in the rate of dry matter production (Figure 4.2b) and chlorophyll concentration (Figure 4.3) and demonstrates that growth, and the potential for growth, decreased before the onset of increasing temperatures, turbidity and conductivity associated with spring.

By mid-September, however, both net and gross rates of oxygen production by shoot tips (Figure 4.4) had increased significantly and this trend was maintained into November despite increasing temperatures and a general decrease in the standing crop (Figure 4.2). This is at least partly explained by the fact that waterfowl uproot older plants while feeding on the turions thereby improving light penetration and favouring the growth of younger and shorter plants. These were used in later experiments and showed increased rates of photosynthesis with increasing temperatures as has been demonstrated for *P. cripsus* in Japan (Saitoh *et al.*, 1970).

These results show that on the Pongolo River floodplain the annual decline of *P. crispus* is not brought about by increasing temperatures but probably reflects the normal cycle of an annual species. The decline in the population, 4 - 5 months after germination began, therefore appears to be inherent; the plants reach maturity, flower, set seed, produce turions and then senesce. If this interpretation is correct, then *P. crispus* plants on the floodplain have a life span of 4 - 5 months and the period over which germination takes place, 3 - 4 months, permits the population to grow for approximately 8 months during the winter/ spring period. The ratio of production to biomass (maximum standing crop) would therefore be considerably greater than one (Section 4.2.3).

4.1.3 Replenishment of turion and achene banks

Turions

Approximately 90% of the turions present on the sediment in autumn each year germinated and observations in the field indicated that those remaining were not viable and decayed before the next autumn. An annual replenishment of the turion bank must therefore have occurred.

Turions were first formed in June of 1976, '77 and '78 and maximum numbers (270, 770, 722 m^{-2} respectively) and mass (9, 21, 29 g m^{-2} respectively) were recorded in late August, early September (Figure 4.5a). These maxima do not, however, represent the total production of turions for each year since:

1. Mature turions became detached from the parent plant and, on sinking to the sediment, became rapidly indistinguishable from the previous seasons turions.

2. Turions were grazed by waterfowl (Section 5.1).

3. Additional turions were produced after maximum number per unit area was measured.

The most meaningful estimate of the turion bank available for each season's growth was the number of turions on the sediment in February or March shortly before germination began. This turion bank increased each year (Table 4.2) from 1129 m^{-2} ($\pm$ 195, $p = 0.05$) in 1976 to 2100 ($\pm$ 273) in 1979. The mass of these turions, which also showed a general increase from 40 g m^{-2} in 1976 to 60 g m^{-2} in 1979 (Table 4.2), represented the total production of turions minus that removed by grazers (Section 5.1).

Achenes

Although achene germination was small, it was important in propagation after dry years (Sections 1.2.3 and 4.1.4). Since losses of achenes from the sediment bank may occur through death and decay in the unpredictable period between droughts, they will need to be regularly replaced.

Inflorescences were first produced in August each year and reached a maximum in September (Figure 4.5b). In contrast to turions this maximum did represent a reasonable estimate of total numbers of inflorescences produced since:

1. Very few new inflorescences were produced after September.
2. Inflorescences were retained on plants until after senescence
3. Consumption by waterfowl was small (Section 5.2).
4. Inflorescences which settled on the sediment remained recognisable until well into summer.

Also in contrast to turions, the number and mass of inflorescences produced decreased significantly ($p = 0.05$) from 38 m^{-2} at 1.2 g m^{-2} in 1976 to 11.5 m^{-2} at 0.38 g m^{-2} in 1978.

Twenty to twenty four ovaries ($\bar{x}$ 21 $\pm$ 3; $p = 0.01$) were produced per inflorescence of which 77% matured to form achenes. This yielded 561, 240 and 180 achenes m^{-2} during 1976, '77 and '78 respectively. However, despite this small production (Hunt and Lutz, 1959) the achene bank increased from 1976 to 1978 indicating that losses each year were small.

4.1.4 Growth and reproduction during 1979

The summer standing crop

All the plants of the 1978 standing crop had disappeared by the end of November but a second crop of small (2 - 3 cm) plants with a standing crop of 0.8 g m^{-2} was collected on the 7th December 1978. These plants remained small throughout the early summer floods and growth was resumed in early 1979 when the floods subsided and light penetration improved (Figure 3.1). Thus, on the 4th April 1979 a standing crop of 12.7 g m^{-2}, consisting of mature plants bearing turions, was sampled (Figure 4.2).

The origin of these plants is uncertain but both turion and achene germination may be implicated. Examination of the turion and achene

banks showed that 14% (341 m^{-2}) of the turions had germinated and the achene bank had decreased by 49%. The small percentage germination of turions was consistent with the small standing crop of plants but the large loss of achenes was not. This latter loss is therefore difficult to explain.

The cause of this unseasonal appearance of *P. crispus* is also difficult to explain although it does seem related to the early flooding and inundation of the 1978 standing crop. One possible explanation is that the floods consisted mainly of cold hypolimnetic water from the Pongolapoort dam and that this stimulated germination of some turions. There are, however, no data to support this hypothesis.

Few inflorescences were produced by this summer growth but a maximum of 54 turions m^{-2} was recorded in April (Figure 4.5a). All plants had disappeared by late May.

This summer growth supports the hypothesis that *P. crispus* is not adversely affected by high temperature on the Pongolo River floodplain but has a short life span and senesces after reproduction.

Winter growth and effects of drought

The growth of *P. crispus* in winter 1979 was initiated by the germination of turions in April as in previous years (Figure 4.1). Overlap of the summer and winter standing crops prevented calculation of the rates of dry matter production until May, whereafter it was clear that production followed the same pattern as in previous years (Figure 4.2b).

Maximum production (0.79 g m^{-2} day^{-1}) was recorded in June with a decline in July. These changes in production coincided with a typical rise and fall in chlorophyll concentrations (Figure 4.3).

Standing crop (Figure 4.2a) also followed established trends until July when it reached 38 g m^{-2} and turions and inflorescences were first produced in June (Figure 4.5). However, despite this apparently normal growth of *P. crispus* there was a sudden unseasonal cessation of measurable dry matter production in late July followed by a rapid decline

in standing crop during August (Figure 4.2). All plants had disappeared by 6th September 1979.

Although in July the water level was low (Figure 3.) there was no indication of adverse environmental conditions (Section 3.0) which might have caused the unseasonal disappearance of plants. Field observations at the time, however, indicated that excessive damaging and uprooting of plants by feeding waterfowl was the major cause of standing crop decline. Waterfowl normally fed on the current seasons turions produced on plants (Section 5.1) but the low water level permitted the birds to upend and dig up the "parent" turions which had given rise to the standing crop. In doing so, waterfowl rapidly destroyed the *P. crispus* population during August before reproduction was completed, thus reducing recruitment to the turion and achene banks in the sediment.

The fate of these turion and achene banks during the drought which followed was not determined but studies on Khangazini pan showed that while turions did not survive des ication (unpublished data), achene germination was stimulated (Rogers and Breen, 1980). Thus, the plants which were growing in turbid water in September 1980 (field observation) probably arose from achenes.

4.1.5 Nutrient relations

Tissue concentrations as an indication of nutrient availability

The overall ability of a plant to accumulate mineral elements is reflected in the ash content of the dry mass (Brinson and Davies, 1976). The ash content of *P. crispus* over the four year study period varied between 12% and 18% dry mass (Table 4.3) which was within the range for submerged macrophytes reported in the literature (reviewed by Hutchinson, 1975). Ash content does not, however, reflect the proportions in which nutrients occur and despite a high ash content individual nutrients such as nitrogen and phosphorus may be in short supply.

During 1976 - '78 nitrogen content was highest (2.5 - 3.3%) in young plants each year and decreased steadily to 1.4 - 1.7% in senescent plants

at the end of the season. Such a decrease is common and can be attributed to the accumulation of "non-growing tissues" as the plants age (Howard-Williams and Allanson, 1978). These nitrogen concentrations fall within the range reported in the literature (Reimer and Toth, 1969; Howard-Williams and Allanson, 1978) and are much higher than the "critical concentration" (1.3%) of Gerloff and Krombholz (1966). This suggests that the plants contained more nitrogen than was required for growth, the critical amount, and that luxury uptake and storage was taking place.

Phosphorus concentrations (0.7 - 0.21%; Table 4.3) in the tissue during 1976 - 78 followed the same pattern of decrease with age as nitrogen, and were not only higher than the 0.13% critical concentration (Gerloff and Krombholz, 1966) but were among the highest reported in the literature (Hutchinson, 1975). Thus luxury amounts of P were probably also taken up.

In contrast to the wet years, during 1979 the concentrations of both nitrogen and phosphorus (Table 4.3) in plant tissues were below the critical concentrations (p = 0.08 - 0.13% and N = 0.36 - 0.49%). While this might indicate nutrient limitation of growth rates, rates of dry matter production (Figure 4.2b) do not support this as they were not markedly lower than previous years.

Accumulation of nutrient stocks in the standing crop

Temporal changes in standing stock of both nitrogen and phosphorus (Figure 4.6) in the plant tissues followed those of plant standing crop but the maxima reached each year differed. During 1976 - '78 maximum nitrogen stocks varied little and remained between 1200 and 1400 mg N m^{-2} while stocks of phosphorus decreased each year from 300 mg P m^{-2} in 1976 to 160 mg P m^{-2} in 1978. During 1979 both nitrogen and phosphorus maximum stocks were very low at 300 mg m^{-2} and 40 mg m^{-2} respectively but this is a reflection of both the low standing crop and low concentrations of nutrients in the plants.

During 1976 - '78 the nitrogen (NO_3-N) and phosphorus (TP) present in the water when Tete pan and the river first lost contact (Table 4.4)

would only have accounted for 10 - 20% of that accumulated in the plant population at maximum standing crop. This suggests that the major nutrient pool for *P. crispus* is in the sediments and supports studies by Everson (1980) which indicated that most P uptake occurred via the root system.

4.2 DISCUSSION

Three major points for discussion arise from these results:

1. The life-history strategy of *P. crispus* on the Pongolo floodplain and the manner in which this permits the species to persist in and exploit the floodplain environment.

2. Nutrient relations of *P. crispus* and their potential influence on losses from and gains to the floodplain pans.

3. The relationship between standing crop of *P. crispus* and net production which represents the amount of organic matter, energy and nutrients available to other trophic levels.

4.2.1 Life-history strategy of *Potamogeton crispus*

The data available do not permit a quantitative estimation of *P. crispus*' life-history strategy in terms of resource acquisition and reallocation as advocated by Calow and Townsend (1981). The more qualitative CRS model of Grime (1979) is therefore used as a basis for describing the attributes of *P. crispus* life-history which permit it to survive in, and,exploit the pans of the Pongolo river floodplain.

Grime recognises that plants have evolved 3 primary adaptive strategies (C,R and S) which operate in the mature or established phase of the life-cycle and 5 regenerative strategies for reproduction. These strategies represent the extremes and different combinations are found in intermediate environments.

The established phase

The different types of organisms which have evolved the three primary adaptive strategies are described by Grime (1977 and 1979) as:

1. Competitors in which C- selection has involved selection for high competitive ability which depends upon plant characteristics which maximise the capture of resources in productive, relatively undisturbed environments.

2. Stress tolerators in which S- selection has brought about reductions in both vegetative and reproductive vigours, to permit endurance of environments in which stresses such as low light, poor nutrient availability or water supply limit productivity.

3. Ruderals in which R- selection has resulted in the evolution of short life cycles and large reproductive effort in potentially productive environments where severe disturbance creates intermittently favourable conditions for plant growth.

The CRS model of life-history strategies has largely been developed on the basis of terrestrial plant ecology and the little that is known of emergent aquatic plants such as *Typha* (McNaughton, 1975). Submerged aquatic angiosperms have not been considered but the model provides a useful framework for description of both established and regenerative (see below) strategies of *P. crispus* on the Pongolo floodplain.

The floodplain environment would favour R- selected species as it is potentially productive but experiences alternating unfavourable and favourable seasons for plant growth. Although *P. crispus* growth is usually restricted to the favourable period, the severe attenuation of light during unfavourable floods appears to act as a disturbance to the established phase. This was observed when the early flood of October 1978 resulted in the rapid death of *P. crispus*.

The high rate of production of *P. crispus*, its short life span and large annual reproductive effort could all represent adaptations to R-selection pressures placing this species in the ruderal category.

However, the monospecific nature of most stands of *P. crispus* in the floodplain pans might also indicate that it is an extremely successful competitor which avoids periods of disturbance. *P. crispus* on the Pongolo floodplain is probably therefore best classified as a competitive -ruderal but much more information is required to verify its competitive abilities.

Regenerative strategies

The five regenerative strategies described by Grime (1979) can be summarised as follows:

1. Vegetative expansion (V) where a low risk of offspring mortality is achieved by prolonged attachment to the parent plant and mobilization of resources from parent to offspring. As the parent must survive the period of offspring establishment this strategy has usually evolved in undisturbed habitats.

2. Seasonal regeneration (S) from an annual, large seed production, usually occurs when seasonally predictable disturbances, such as flooding and snow, create unfavourable and favourable growing periods. This strategy is common in temperate regions where seasonal cycles are marked.

3. Persistent seed banks (B) which may represent many years of accumulation, are usually found in habitats which experience intermittent "catastrophic" environmental perturbations such as fire and drought. There are 3 main mechanisms operative in persistent seed banks: (i) The prevention of germination between the time of seed production and burial; (ii) burial of seeds and maintenance of dormancy and (iii) promotion of germination.

4. Wind dispersal (W) of numerous seeds has evolved in plants which exploit areas subject to erratic and large-scale disturbances.

5. A persistent seedling bank (B_r) usually occurs in forests where conditions for recruitment occur infrequently. Seedlings persist in a stunted or etiolated condition where factors such as light are deficient. They are often dependent on large seed reserves during this period and become established only when death of trees creates a gap in the canopy

Grime (1979) points out that the major selective forces resulting in differentiation of these regenerative strategies have been intensity, periodicity and spatial distribution of environmental disturbances. Thus, since more than one disturbance can occur in an ecosystem and they can be on different time scales, any one phenotype or genotype might exhibit several regenerative strategies. *P. crispus* possesses 3 different strategies, S, B_r and B_s, which seem to have evolved in response to the three main environmental features of the floodplain; predictable seasonal growth periods, unpredictable flood durations and intermittent "catastrophic" droughts, respectively.

P. crispus seasonal regeneration

Although turions are asexual reproductive organs their seasonal production, summer dormancy and temperature trigger of germination in autumn present a mechanism of seasonal regeneration which regulates the established ruderal phase to the favourable growing season. While the established phase has a life span of only 4 - 5 months, staggered germination as temperature declines permits the population to exploit the full 8 - 9 months of the favourable winter/spring period.

P. crispus persistent "seedling" strategy

Turions contain large energy reserves which maintain the young plants when there is insufficient light for photosynthesis. The persistent seedling strategy of *P. crispus* occurs in cold temperate lakes where germination of turions occurs in autumn but ice cover limits light penetration and prevents plant growth. The young plants remain stunted

until spring thaw and growth occurs in spring and summer (Stuckey *et al.*, 1978). On the Pongolo floodplain the ability of seedlings to persist under dark conditions allows the species to survive irregularities in the flooding cycle and exploit the favourable periods which inevitably follow. Thus, seedlings survived the turbid conditions after late floods in 1976 and the floods which followed an unseasonal germination of turions in December 1978.

The *P. crispus* persistent "seed" bank

The persistent "seed" bank of *P. crispus* consists of achenes formed during sexual reproduction. The achenes require an after ripening period (Mayer and Poljakoff-Mayber, 1963; Everson, 1980) which suppresses germination before burial in the sediments. The main factor maintaining dormancy of buried achenes appears to be the hard, impermeable pericarp. Rupture of the pericarp during desiccation breaks dormancy (Everson, 1980) and hence the achene bank has evolved as an effective strategy for persistence of the species after droughts. Guppy (in Meunschner, 1936) found that achenes can survive up to 18 months of dessication.

Although the main functional significance of persistent seed banks is to ensure regeneration *in situ* after a major environmental disturbance they may also facilitate dispersal by animals (Grime, 1979). The protection provided by the hard pericarp of *P. crispus* achenes during passage through the gut of waterfowl (Section 5.1) would represent such a strategy and promote gene flow between populations on the floodplain.

The strategies of both the established and regenerative phases of *P. crispus* life cycle are therefore well adapted to floodplain conditions and permit effective exploitation of the favourable growth periods. Under the natural flooding regime of the Pongolo river *P. crispus* may therefore play a predictable role in the annual cycle of organic matter and nutrient transfers. However, as construction of the Pongolapoort Dam will affect the flooding regime and alter environmental conditions on the floodplain it is important to identify factors which might cause "failure" (Grime, 1979) to establish or regenerate.

Potential failure of establishment and regeneration

The most likely causes of failure to establish would be drying out or flooding of the pans during the winter months, after most turions had germinated but before the plants had begun to reproduce. The staggered timing of germination and growth, effectively reduces this most critical period to the months of June and July. Although natural floods have occurred during this time (Heeg and Breen, 1982) they have a very low frequency of occurrence.

Partial failure to establish may also occur as a result of destructive feeding by waterfowl on parent turions, as occurred in 1979. Since waterfowl presence on the pans appears to be mostly a response to the availability of turions (Chapter 5), many plants would mature before the bird's arrival and only those which germinated late in the season would not become established.

Failure in the regenerative phase is more difficult to predict, particularly as both turion and achene production and germination must be considered. Consumption by waterfowl may also affect regeneration.

Grime (1979) considers that a change in the environment of species with multiple regeneration strategies will tend to reduce the effectiveness of some strategies and, if one form of disturbance predominates over the others, reduce the effective number of strategies to one. Controlled releases of floods from the Pongolapoort Dam in the immediate future (10 - 20 years) are likely to be of very regular duration and timing (Alexander, 1982) thus eliminating droughts. In the long term, however, as irrigation demands increase, frequent "droughts" could be experienced on the floodplain.

Over the next 20 years, therefore, an absence of 'droughts' may favour seasonal turion regeneration and reduce achene production. The fact that, during the wet years of this study turion production increased and achene production decreased, would tend to support this hypothesis. A decrease in achene production would not result in regenerative failure but if the

achene bank were to be markedly depleted by death and decay during this period, failure to regenerate could occur when irrigation demands eventually result in a 'drought' on the floodplain. Monitoring programmes designed to assess the effects of controlled discharges on the floodplain ecosystem (Alexander, 1982; Breen, 1983) should therefore follow changes in turion and achene banks and adapt management accordingly.

Two other major environmental factors which could result in regeneration failure are an increase in salinity to above 5% and droughts which extend beyond the period of achene survival under desiccated conditions. Guppy (in Meunschner, 1936) suggests that this is 18 months, but further studies should verify this for the Pongolo floodplain populations.

Excessive grazing of the regenerative phase can have a major impact on a plant's ability to exploit a particular habitat (Grime, 1979). The major grazers of *P. crispus* are waterfowl which feed on turions, but studies on the floodplain (Section 5.2) suggest that grazing acts to stimulate turion production rather than decrease regenerative potential.

Change in the flooding regime of the Pongolo river could therefore be a major factor affecting the ability of *P. crispus* to exploit the floodplain environment.

4.2.2 Nutrient relations

Growth of *P. crispus* brings large amounts of nitrogen and phosphorus from the sediment pool into circulation each year and much of this is transferred to the water phase during decomposition (Section 7.2.1). Thus, during the annual decline in standing crop when the non-reproductive portions of *P. crispus* decomposed, there was a general increase in N and P concentrations in the water (Figures 3.8, 3.9). This indicates that release from the decaying plants exceeded rates of uptake by other components of the system and that nutrients may accumulate in the water at a time when flooding is likely. However, although concentrations of N and P increased, because of reduced volume, the actual amounts in the water (Table 4.4) at this time each year were lower than when the pan and river

lost contact after the previous floods. Overall therefore, the pan ecosystem, with *P. crispus* and its epiphyton as the major primary producers, acted as a nutrient trap during the period of isolation from the river each year. During the three wet years there was a total net transfer of *c.* 170 kg P as total phosphorus and *c.* 190 kg N as total NO_3-N from the water to the various components of the ecosystem.

The potential fate of the nitrogen is difficult to assess since biochemical reactions may have resulted in retention in the biota or sediments, or losses to the atmosphere by denitrification (Wetzel, 1975). The sediments, however, seem the most likely component for phosphorus retention in view of their role as a sink for phosphorus (Syers *et al.*, 1973). As the major primary producers, *P. crispus* and its epiphyton undoubtedly played an important role in taking up and transferring these nutrients in the ecosystem.

In October 1978, 44 kg P and 400 kg N remained in the plant standing crop when floods exceeded MRL and caused rapid decay of the plant tissues.

Release of these nutrients to the water phase during decomposition could result in their being flushed from the system by floodwaters. Thus, if floods are early there may be a loss of nutrients from, rather than gain to the pan. Studies of nutrient transfers during decomposition (Chapter 7) are therefore required to assess the magnitude of losses to the water phase and their significance to ecosystem functioning (Chapters 8 and 9).

4.2.3. The annual net production of *Potamogeton crispus*

The importance of aquatic plant production to system metabolism can be assessed by its contribution to the gross energy flow through the food web (Wetzel and Hough, 1973).

The amount of energy or matter available to other trophic levels is the net production of the plants (Phillipson, 1966) and in many earlier studies of annual species (reviewed in Westlake, 1965; Wetzel, 1975) this was considered to be represented by the maximum standing crop

achieved in a season. However, this is so only if the following conditions apply:

1. Propagule germination must take place within a short period of time.
2. There must be no loss of plants or plant parts by natural death, abscission or grazing before maximum standing crop.
3. Respiration of all plants must equal or exceed gross production after maximum standing crop.

Clearly growth of *P. crispus* on the Pongolo floodplain does not meet these requirements and, since dry matter production could not be measured by the mark and measure technique of Howard-Williams (1978), an alternative approach was adopted. This involved making separate estimates of annual net production of the non-reproductive shoot material, roots, turions and achenes based on the following information and assumptions:

1. Non-reproductive shoot material: The staggered germination of turions, a plant life span of 4 - 5 months (Section 4.2.1) and the fact that as older plants disappear they appear to be replaced by younger plants which are very productive (Section 4.1.2), suggests that *P. crispus* shoot production greatly exceeds maximum standing crop. In this light, assuming that there are no major losses to grazing or leaf fall before death of plants, the presence of a standing crop for 8 - 9 months (twice a plants life span) indicates that annual net shoot production can be approximated by twice the maximum standing crop.

2. Roots: Everson (1980) estimated the root mass at maximum standing crop to be approximately 4.3% of the non-reproductive plant mass. By applying the same reasoning as for shoots, root net production can be estimated as twice that present at maximum standing crop.

3. Turions: A proportion of the turion production is grazed each year (Section 5.2). Assuming other losses of turions

are small, the turion net production will equal the mass of turions present on the sediment after standing crop decline plus the mass grazed.

4. Achenes: Achene production could be estimated from the maximum standing crop of inflorescences each year (Section 4.1.3).

5. Although young plants may grow at the expense of turion reserves most plants of only 1 - 2 cm in height were photosynthetic. The plant mass derived from the previous years production is therefore assumed to have contributed little to the maximum standing crop and so to annual net production.

Thus it was calculated (Table 4.5) that the annual net production of *P. crispus* in Tete pan was 120, 187 and 158 g m^{-2} dry mass for 1976, '77 and '78 respectively and that the production:maximum biomass ratio (P/B ratio) ranged from 2.5 to 2.8. Therefore, although *P. crispus* has a short life span and low maximum standing crop, the high P/B ratio (Table 4.6) results in an annual net production which falls in the middle of the range reported in the literature (Table 4.6). The high reproductive effort of *P. crispus*, *c.* 40% of net production, is evident from these data.

Few studies have demonstrated the significance of macrophyte production to overall ecosystem functioning but in South Africa Howard-Williams and Allanson (1978, 1981) have shown *Potamogeton pectinatus* L. production to be very important in energy and nutrient dynamics of the Swartvlei lake ecosystem. Although *P. pectinatus* is highly productive it occupies only 7.3% of the lake area and using their data it can be calculated that this plant contributes *c.* 34 g m^{-3} dry mass to the system on a unit volume basis. This represents *c.* 50% of the total primary production of the system.

Potamogeton crispus has a lower annual net production but occupies nearly 90% of the area of Tete pan and contributed an average of *c.* 126 g m^{-3} to the system per annum between 1976 and 1978. Phytoplankton production during winter is very small (Rogers and Breen, 1980) and primary production in summer also appears low (Section 3.2). Thus, although

P. crispus growth is highly seasonal, its contribution to trophic and nutrient dynamics of floodplain pans such as Tete is likely to be extremely important. In addition it acts as a substratum for epiphyton which contributes *c.* 23 g m^{-3} per annum (Section 8.1.2).

4.2.4 Summary and conclusions

Potamogeton crispus is a winter producing ruderal with multiple regenerative strategies. It is well adapted to exploiting the short winter/spring period favourable for submerged plant growth and surviving both summer flooding of unpredictable duration and intermittent catastrophic droughts. This suggests that *P. crispus* can play a predictable role in the Pongolo river floodplain ecosystem.

The major source of nutrients for *P. crispus* is the sediment pool and plant growth brings large amounts of nitrogen and phosphorus into circulation each year. The rapid completion of the life cycle ensures that in most years N and P released to the water during decay can be taken up by other components of the ecosystem before the summer floods. Thus, despite a potential for flushing of nutrient rich water when floods arrive, pans such as Tete appear to experience a net gain in nutrients in most winter/spring periods. As the major primary producer in these pans, *P. crispus* shows important adaptation to nutrient cycling in an ecosystem context. More detailed studies of the transfers of nutrients through the food web are, however, required before this adaptation can be fully ellucidated.

The annual net production of *P. crispus* in Tete pan is very high on a unit volume basis and thus, although growth is very seasonal, its contribution to trophic dynamics in similar floodplain pans is likely to be extremely important.

The transfers of *P. crispus* production and accumulated nutrients to other components of the ecosystem and factors affecting them, form the basis of discussion in succeeding chapters.

CHAPTER 5

POTAMOGETON CRISPUS/WATERFOWL INTERACTIONS IN THE GRAZING FOODCHAIN

Large flocks of waterfowl inhabit the Pongolo floodplain (Dutton, 1972; Clark, 1974; Cyrus and Robson, 1980) with peak numbers occurring during winter and spring (Dutton, 1972). Although the achenes of *P. crispus* form an important food source for waterfowl in north America (Hunt and Lutz, 1959), Dutton (1972) working on Nyamithi pan, suggested that waterfowl were attracted to the floodplain by the large number of gastropods associated with the *P. crsipus* and not the plant itself. His work thus supported the hypothesis (Section 1.2.5.1) that submerged macrophytes do not make a significant contribution to the grazing foodchain.

This part of the study investigates this hypothesis and considers (1) the role of *P. crispus* in maintaining a diverse waterfowl community on the floodplain and (2) the influence of waterfowl feeding on the *P. crispus* population under both wet and drought conditions.

5.1 THE WATERFOWL COMMUNITY AND IMPORTANCE OF *P. CRISPUS* AS A FOOD SOURCE

5.1.1 Results

Waterfowl community composition and numbers

Eleven pans of widely differing physico-chemical characteristics (Table 5.1) and representing a cross-section of floodplain waterbodies, were visited every second month during 1978 to assess the species composition and relative abundance of the waterfowl community on the floodplain as a whole. The pans could be divided into three groups according to a subjective estimate of the cover of *P. crispus* at maximum standing crop:

(1) "Abundant" *P. crispus*; 80% or more of the pan surface area was colonized by *P. crispus* at maximum standing crop.

(2) "Sparse" *P. crispus*; scattered plants or colonies covering less than 10% of the pan area.

(3) "No" *P. crispus*; *P. crispus* did not occur in these pans.

A total of 12 waterfowl species were recorded (Table 5.2) over the year with the White-faced Duck (*Dendrocygna viduata* (L.)) being the most common (73.5%) followed by the Spurwing Goose (*Plectropterus gambensis* (L.)) (9.4%), Yellow-billed Duck (*Anas undulata*, Dubois) (4.4%) and Knob-billed Duck (*Sarkidornis melanotus* (Pennant)) (4.0%). Two species, the Cape Teal (*Anas capensis*, Gmelin) and White-backed Duck (*Thalassornis leuconatus*, Eyton) were observed only once each.

All species, except the Red-billed Teal (*Anas erythrorhyncha*, Gmelin), were most abundant (No. of birds ha^{-1}) on pans colonized by *P. crispus*. Most species showed a marked preference for pans with abundant *P. crispus* and seasonal changes in number also followed the growth and decline of the plants. In general the numbers of White-faced Duck and of the other species (considered together; Figure 5.1) were low during summer but after increasing rapidly during June remained high (*c.* 5700 and *c.* 2700 respectively) during winter and spring. The number of birds declined rapidly during November with the onset of summer floods.

Although about 85% (5000) of the winter White-faced Duck population occurred on pans with abundant *P. crispus* there was a movement of some birds (*c.* 1500) to pans with sparse *P. crispus* during October before the onset of floods (Figure 5.1).

This study confirms the findings of Dutton (1972) that the White-faced Duck are the most common species on the floodplain and that waterfowl concentrate on the pans during winter and spring. No evidence was, however, found to support his view that the birds dispersed over the floodplain during summer floods to breed. Most species, particularly the White-faced Duck, migrated from the floodplain during the summer

breeding season. Some White-faced Duck do, however, breed on the floodplain and females containing eggs were shot during January 1977 (1), January 1978 (2) and December 1978 (2). Broods of flightless juveniles were observed during both April and May, 1978.

The waterfowl community on Tete pan, where most detailed studies on waterfowl/*P. crispus* interactions were undertaken, was typical of that found on pans with abundant *P. crispus* (Table 5.3). One further species, the Cape Shoveler (*Anas smithii* (Hartet)) was observed in small flocks during 1979 increasing the total number of species observed to 13.

The maximum number of waterfowl on Tete pan was reached in August or September of each year (Figure 5.2) at approximately the time of *P. crispus* maximum standing crops (Figure 4.1). The birds did not, however, all remain on the pan and numbers declined rapidly in late September/early October. This was after maximum plant standing crop but before that of turions and achenes was reached. White-faced Duck numbers reached maxima of 3009, 4210 and 2635 birds in 1976, '77 and '78 while the total number of birds of other species were 790, 495 and 385 respectively.

In summer 1979 during the unusual growth of *P. crispus*, both the White-faced Duck (300) and other species (450) (Figure 5.2) congregated at Tete pan to a greater extent than in previous summers. During the winter drought, however, White-faced Duck numbers were markedly reduced over previous winters with a maximum of 490 occurring in August. The total number of birds of other species did not change (Figure 5.2) but there was a shift in the proportional species composition (Table 5.3); while the Knob-billed Duck was scarce and the Pygmy Goose (*Nettopus auritus* (Boddaert)) absent, both the Red-billed Teal and Yellow-billed Duck appeared to be attracted by the low water conditions.

Food and feeding behaviour of waterfowl

Analysis of the oesophagus contents of White-faced Duck from 11 different pans on the floodplain showed distinct seasonal differences in the types of food consumed (Table 5.4). During summer and autumn,

when the few birds present were dispersed over the whole floodplain, their food was varied with 15 different types being selected. In most cases the food was obtained by dabbling in the shallows and the major food item was inundated *Heliotropium indicum* L. nutlets. Insects and the reproductive organs of plants, such as *E. pyramidalis*, *Polygonum* spp. and *Cyperus* spp., which occur along the margins of pans also occurred frequently in the diet. During winter and spring, however, only 9 different food items were consumed with *P. crispus* turions forming 63.5% of the diet and occurring in 83% of the samples. The reproductive organs of *Nymphaea* spp., *Cyperus* spp. and *E. pyramidalis* were also consumed but mostly by birds collected from pans where *P. crispus* was sparse or absent.

White-faced Duck which fed on Tete pan where there was abundant *P. crispus* similarly ingested a variety of food in summer (Table 5.5) but in winter and spring diet was dominated (80 - 100%) by turions. Turions were obtained by dabbling or upending during mid-winter but as spring progressed and duck numbers declined (Figure 5.2) the birds began diving and uprooting the *P. crispus* plants in order to obtain turions. The only other items eaten frequently in winter and spring were *P. crispus* achenes and aquatic insect larvae but these did not form a large proportion of the total diet mass.

The winter and spring diets of the Knob-billed Duck, Spur-winged Goose, Egyptian Goose (*Alopchen aegypticus* (L.)) and Fulvous Whistling Duck (*Dendrocygna bicolor* (Viellot)) on Tete pan were also dominated by *P. crispus* turions while the Hottentot Teal fed predominantly on the mollusc *Bulinus natalensis* (Table 5.6). Three Yellow-billed Duck and two Red-billed Teal collected on Tete during winter had empty crops although their gizzards contained a large proportion of turion fragments.

Most of the major species of waterfowl on the Pongolo floodplain therefore feed selectively on *P. crispus* turions when they are abundant during winter but are more opportunistic in their feeding habits in summer when large portions of the floodplain are inundated.

This pattern was altered slightly during the drought of 1979 when two birdscollected on Tete pan during the unusual summer growth of *P. crispus* contained only turions in their crops. Furthermore, during winter when water levels were very low, the White-faced Duck began digging in the sediment and removing turions from the previous seasons production which had, or were in the process of producing new shoots. Thus the crops of five duck shot in late July contained both the current (73%) and previous (20%) season's turions.

Nutritional value of turions and achenes and its influence on waterfowl condition

Potamogeton crispus turions (Table 5.7) are very rich in available carbohydrate (50%) but have low lipid (1.5%) and protein (3.8%) contents (Sugden, 1971; Krull, 1970). Electron micrographs (Plate 5.1) indicate that the major carbohydrate is starch which is accumulated in the parenchymatous tissues of the thickened leaf bases and stems.

Achenes, on the other hand, have a much lower available carbohydrate content (18.8%) but contain more lipid (15.6%) and protein (5.9%) which have higher energy yielding potentials than carbohydrate. The gross energy content of achenes (18.9 kj g^{-1}) is therefore higher than that of turions (16.4 kj g^{-1}) but since the thick pericarp of the achene (Everson, 1980) is not readily digested the apparent metabolizable energy content (Sibbald *et al.*, 1963) is similar to that of turions.

Field observations during this study, however, indicated that the pericarp is so hard that many, perhaps most, achenes pass through the gut intact. Thus, although achenes are apparently nutritious they would provide a much lower energy reward per unit of effort than the turions, which waterfowl select as their major food source. The value of achenes as a waterfowl food source is further reduced by their small standing crop (Figure 4.5).

White-faced Duck present on the floodplain during autumn 1979 and more importantly those arriving in early winter (June and July) had small body mass (*c.*6.25 g) and low fat reserves (1 - 2.5%) (Figure 5.3) but

by mid-October both mass and fat reserves had increased significantly ($p = 0.05$) to 780 g and 5.3% respectively. Thus, birds which left the floodplain at the beginning of the breeding season (November) were in good condition.

The decrease in condition of those birds remaining during summer is probably attributable to a greater energy expenditure in obtaining food which is less available under flooded conditions. This is supported by both the lower food intake (Table 5.5) and wide variety of foods eaten (Tables 5.4 and 5.5).

5.1.2 Discussion

Waterfowl community composition and continental affiliations

The waterfowl community of the Pongolo floodplain is typical of that described by Winterbottom (1967) as "East African Tropical Aquatic Avifauna" in that the major species include the White-faced Duck, Spurwing Goose, Knob-billed Duck and the ubiquitous Egyptian Goose. The presence of the Yellow-billed Duck at some density, however, indicates a degree of overlap with the "South Temperate" species distribution. In all, 13 of the 16 species which breed in South Africa (Siegfried, 1970) and one of the few regular migrants (the Cape Teal) are represented on the floodplain. Thus, the Pongolo floodplain provides a habitat for one of the most diverse waterfowl communities in South Africa. This is enhanced further by the presence of many other water-associated birds of which 15 species are of restricted distribution and listed as "endangered" in the South African Red Data Book (Siegfried *et al.*, 1976; Heeg and Breen, 1982).

The most abundant waterfowl on the Pongolo floodplain, the White-faced Duck, is essentially a tropical species which occurs in large flocks (up to 24000) on floodplains of Zambia (Douthwaite, 1977) through to Senegal (Treca, 1981) but has been recorded in small numbers as far south as the Orange Free State goldfields (Liversidge, 1962; Geldenhuys, 1976). In most areas but particularly the floodplains of tropical

Africa, White-faced Duck occur in large flocks in winter and spring (Winterbottom, 1964; Dowsett, 1971; Dutton, 1972; Douthwaite, 1977; Skead and Dean, 1977) but seem to disperse to ephemeral water bodies to breed during the wet season (field observations).

Clark (1974) suggests that the White-faced Duck is expanding its range into the more temperate areas of southern Africa and this may be so on the Pongolo floodplain where it increased in numbers from flocks of *c.* 300 in 1961 to 1000 - 2000 in 1972. Counts of over 4000 in this study (1977) support this hypothesis and further studies may reveal that the Pongolo floodplain is becoming an increasingly important habitat as this species, and perhaps others, spread further south into temperate Africa.

The Pongolo floodplain as a waterfowl habitat

Although the Pongolo floodplain is one of a number of wetland areas on the coastal plain of northern Natal, it appears to be the most important habitat for waterfowl in the area. Certainly the same numbers and in some cases diversity, are not seen on the Muzi swamps, the coastal lakes and vleis to the east (field observations) or on the Umfolozi River floodplain at the southern limit of the coastal plain (Rogers, 1978).

The presence of an abundant winter food source in the form of *P. crispus* turions is undoubtedly the major factor attracting waterfowl to the Pongolo floodplain. The high carbohydrate content of turions provides a food with an A.M.E. higher than the average wild seeds and almost equivalent to cultivated grains such as barley and wheat (Sugden, 1971). Thus the waterfowl can replenish their fat reserves in a short period during winter and spring, and return to summer breeding grounds in good condition.

The Pongolo floodplain does not seem to form an important breeding ground for waterfowl probably because rapidly fluctuating water levels in summer (Section 1.3.11) inundate potential nesting sites and create conditions of low and changeable food supply.

In winter, however, the relatively stable water levels in many pans and warm climate permit the growth of aquatic plants, in particular *P. crispus*, and associated invertebrates at a time when most other waterbodies in South Africa are either too cold, or have too little water, to encourage such growth. Since the winter flocks of East African tropical species of waterfowl on the floodplain are far larger than those reported for other parts of the country it would seem that the Pongolo floodplain acts as an important overwintering area for these birds.

The exact role of the floodplain in maintaining a large and diverse waterfowl community at the southern limit of the tropical species range cannot, however, be elucidated without more detailed studies. In particular the factors limiting population growth in the summer breeding grounds must be identified (Flake, 1979; Kroodsma, 1979) before our ability to conserve or manage the waterfowl populations can be improved.

Implications of waterfowl grazing for *P. crispus* regeneration

Noy-Meir (1975) illustrated, theoretically, the ways in which the stability of a terrestrial grazing system can be affected by different characteristics of the herbivores and plants concerned. Smith and Odum (1981) have suggested that aspects of this theory may be applicable to goose grazing of rhizomatous salt marsh plants.

Plant species which possess both grazeable and ungrazeable fractions to their total biomass may impart stability to the system, since herbivore populations fluctuate in relation to the availability of the grazeable fraction only and leave a "reserve biomass" which provides a "residual growth potential" from which the plants can regenerate. In terrestrial systems the residual growth potential usually takes the form of asexual reproductive organs such as tubers and rhizomes (Noy-Meir, 1975) but presumably a seed bank or annually produced seed reserve would provide the same potential for regeneration in species with predominantly sexual reproduction.

Most birds (Grime, 1979) and in particular waterfowl (Skead, 1980; Smith and Odum, 1981) consume the (sexual and asexual) reproductive structures of aquatic plants rather than the "non reserve" biomass. As such they are utilizing the "residual growth potential" which could affect the ability of the resource (plant population) to renew itself, and so reduce the stability of the system. Such "unstable" systems would be more prone to overgrazing and extinction of the resource. The adaptation of a plant species to grazing would therefore have important implications for stability in the ecosystem context.

Waterfowl on the Pongolo floodplain feed on both the sexual and asexual "residual growth potentials" of their principal food resource *P. crispus* and, furthermore, in obtaining their food they uproot the growing plants and remove them from their major source of nutrients, the sediment. A potentially unstable grazing system therefore exists and further studies were directed towards assessing the adaptation of *P. crispus* to waterfowl grazing and the potential for overgrazing.

5.2 EFFECTS OF WATERFOWL GRAZING ON THE *P. CRISPUS* POPULATION IN TETE PAN

Grazing waterfowl would exert their influence on *P. crispus* in two ways: (1) direct effects of turion and achene removal on the plant and (2) indirect effects of reduction in propagule number on subsequent development of *P. crispus* populations. In either event the effect on stability of the grazing system would depend largely on the proportion of turion production removed by waterfowl.

5.2.1 Results

The quantity of turions consumed

Three different methods were used to obtain an estimate of turion consumption (Section 2.4.5); (1) the exclosure technique (2) culling of birds immediately after feed and (3) stochastically, by means of the Wiens/Innis model (Section 2.4.4).

Exclosures

In 1976 three exclosures were set up in Tete pan to estimate the proportion of turion and achene production which was consumed by waterfowl (Section 2.4.6).

In early 1977 when all the *P. crispus* plants had disappeared there was no significant difference (Table 5.8) in the number of achenes inside or outside the exclosures, confirming earlier observations (Section 5.1.1) that the waterfowl did not consume a large proportion of the sexual reproductive reserve. At the same time there were more turions ($p = 0.001$) on the sediment outside the exclosures than within (Table 5.8). The mass of turions was, however, not significantly greater, indicating that the turions within the exclosures were larger than those in the pan. Two possible explanations for these observations are:

1. The enclosure of *P. crispus* influenced the size and number of the turions produced.

2. Grazing removed large turions and stimulated production of many smaller ones.

In both cases, however, exclosures were unsuitable for estimation of turion consumption. No attempt was made to establish the effect of exclosures on turion production but later studies (this section) considered the selection of large turions by grazers and subsequent production of small turions.

Culling after feeding

The White-faced Duck had two distinct feeding times, in the early morning and late evening. It was hoped that, by culling birds immediately after feeds, an estimate of the total amount consumed could be made by multiplying the mean mass of turions in the crops by the number of birds on the pan. This was repeated morning and evening to estimate daily consumption on four occasions during winter and spring 1977 and knowing the changes in duck numbers with time, the total amount of turions consumed could be calculated.

It was estimated that between the 15/6/77 and 29/11/77 approximately 3 g dry weight m^{-2} of turions was consumed. This represented a total of 2724 kg, yielding a total energy intake (based on A.M.E., Section 5.1.1) of 59.9 x 10^6 kj. However, even the "existence energy requirement" (Section 2.4.4) of the 1977 White-faced Duck population (calculated by the formulae of Kendeigh (1970)) would have been nearly three times greater (160 x 10^6 kj or 8.36 g m^{-2} turions). Although Kendeigh's method may be subject to some error (Laseiwski and Dawson, 1967) there is clearly no energy deficit in the population as the birds gain in mass and improve in condition while feeding on *P. crispus* turions. Thus this method did not appear to give an accurate assessment of turion consumption by the waterfowl.

The weaknesses of the method were probably that the duck digested a large proportion of the food during feeding and before they were shot, and that it did not account for nocturnal feeding by the White-faced Duck.

An estimate of the quantity of turions consumed by all duck was therefore made using the deterministic model of Wiens and Innis (1974) (Section 2.4.4).

Estimation using the Wiens/Innis model

Consumption of turions by White-faced Duck as calculated in this way varied from 7.9 g m^{-2} in 1976 to 14.3 g m^{-2} in 1977 and 10.0 g m^{-2} in 1978 (Table 5.9), Since consumption by all other species was estimated as 3.4, 4.1 and 2.1 g m^{-2} respectively, it was calculated that between 15 and 25% of the turion production was consumed by the waterfowl during each of these years. During the winter drought of 1979 the waterfowl consumed less than half (5.3 g m^{-2}) that of previous years. Thus, since grazing by waterfowl may have stimulated turion formation, at least 75% of the turion production was not consumed in any one year and remained to form a large "reserve growth potential".

The size of a reserve is not, however, indicative of its long term stability nor of the potential for overgrazing if the waterfowl population were to increase. Overgrazing of *P. crispus* turions was not evident during this study but nevertheless, each year, waterfowl moved away from Tete pan (Figure 5.2) to others with abundant *P. crispus* before turion number and standing crop reached a maximum in spring. Since such a migration could effectively reduce the potential for overgrazing of the turion reserve and so impart stability to the grazing system its cause required investigation.

It was noted that, at the time the migration began each year, there was a marked reduction in the mean size (mass) of turions (Table 5.10). The hypothesis was thus developed that smaller turions would be difficult to locate and so the reward to waterfowl per unit of feeding effort would be reduced, causing some birds to move to other feeding grounds. Further studies were directed towards determining the cause of this decline in turion size and the implications of this in maintaining the stability of the grazing system.

Selection of turions and damage to standing crop by waterfowl

The reduction in turion size in early spring could have arisen in two ways: (1) a preferential selection of large turions by feeding birds or, (2) through an increased production of small turions, possibly by detached plants.

In the field "small" turions could be easily distinguished from "large" turions in that stems of small turions were only slightly swollen and leaf bases were so reduced that the dormant buds protruded beyond them (Plates 2.1 and 2.2).

To determine the extent of uprooting and breaking of plants, and the selection of large turions by waterfowl a comparison was made between an area of Tete pan in which duck had recently fed and one in which no feeding had occurred (Section 2.4.7).

On the morning of the 26/7/78 a flock of *c*.500 White-faced Duck were observed feeding in a dense "raft" in an area (*c*. 3000 m^2) which had not been previously utilized that season. The effects of duck feeding on *P. crispus* standing crop and turion numbers were determined by comparison of samples within the feeding area and immediately adjacent to it.

Sixty seven percent of the *P. crispus* standing crop in this area was detached from the sediment during the morning feed. Since duck feed twice a day, 500 duck could detach 67% of the standing crop from 6000 m^2. It was estimated by extrapolation of these results that during each year of study half the number of duck present could have uprooted all the plant material present at maximum standing crop. This supported field observations that duck progressively detached almost the entire standing crop each year.

Furthermore, the duck had removed 89% of the turions from the detached plants and where there had been 7.8 ($\pm$ 0.9, $p = 0.05$) large turions and 1.4 ($\pm$ 0.4) small turions per gram of non-reproductive *P. crispus* before feeding, only 1.0 ($\pm$ 0.5) large turion, but 0.8 ($\pm$ 0.3) small turions per gram remained. Thus, while feeding the duck uprooted many plants and selected a high proportion of the large turions but few small ones. The overall high proportion removed (89%) contradicts previous evidence that only 15 - 25% of the turion production was consumed. The possibility that the detached plants continued to produce turions was therefore investigated.

Turion formation by detached plants

Detached plants were transferred to glass tanks (Section 2.4.8) and within 20 days they had produced 3.3 ($\pm$ 0.9) large and 61.0 ($\pm$ 3.2) small turions per gram of non-reproductive material. In the field where some plants had been detached but others were still rooted there was also a marked increase in small turions from 1.4($\pm$ 0.4) g^{-1} to 12.5 ($\pm$ 3.1) g^{-1} but only a small change in the number of large turions (7.8 ($\pm$ 0.9) g^{-1} to 11.3 ($\pm$2.6) g^{-1}), during the 20 day interval. Thus, not only do the waterfowl selectively graze large turions but by uprooting plants they appear to promote a rapid production of small turions.

This was tested in the field by setting up exclosures which prevented the removal of large turions and the uprooting of plants by grazing waterfowl. By the end of the season large turions were significantly ($p = 0.001$) more abundant inside the exclosure whilst small turions were more abundant in the pan where grazing and uprooting had occurred (Table 5.11). The total number of turions inside and outside the exclosures was, however, the same and apparently did not show the stimulation of turion production by grazing seen in earlier exclosures (Table 5.8). This can be at least partly explained by the fact that these second exclosures had a large mesh size (5.5 x 5.5 cm) which permitted wind action to move some detached plants into the exclosures. These became entangled amongst the rooted plants and produced small turions which settled to the sediment.

Field observations therefore suggest that grazing stimulated production of turions but the effect was masked by poor experimental design.

Implications of turion size and number for standing crop development

The annual standing crop of *P. crispus* develops largely from germination of turions. Although grazing may stimulate an increase in turion numbers, their value in perennation from one year to the next depends on their viability. When incubated at 20°C in the light 64.9% germination was achieved for small turions. This was some 10% (significant at $p = 0.05$) less than for large turions (75%) but the reduction in viability would be offset by the *c.* 45% increase in turion production stimulated by grazing (Table 5.8).

5.2.2 Discussion

The influence of waterfowl on transfer of *P. crispus* production

Waterfowl appear to be the major grazers of *P. crispus* production on the Pongolo floodplain. The only other potential grazer of aquatic plants is the fish *Tilapia rendalli* (Heeg and Breen, 1982) but this species is not abundant and no visual evidence of grazing of *P. crispus* was found.

Consumption of 15 - 20% of turion production by waterfowl represented only 6 - 10% of the total *P. crispus* dry matter net production (6.5; 9.8; 7.6% in 1976, '77 and '78 respectively); thus a significant but small amount of *P. crispus* production enters the grazing food chain. The proportion of this amount which is metabolized by the birds (about 75% by mass) will be exported from the system (4.5 - 7.5% of P_n) as CO_2 from respiration or as biomass when the birds migrate to the summer breeding grounds. The remainder of that ingested (1.5 - 2.5% P_n) would enter the detritus food chain as faeces, either directly to the aquatic phase during winter or during floods, after being deposited on the floodplain by roosting birds. In either event this amount is small in relation to other autochthonous (e.g. non-reproductive *P. crispus* and epiphyton) and allochthonous (e.g. *Cynodon dactylon*) inputs to the aquatic system of the floodplain (Heeg and Breen, 1982; Section 8.1).

Very few studies of waterfowl have attempted to estimate the proportion of plant production removed during grazing (Anderson and Low, 1976; Smith and Odum, 1981) but it appears that between 2% (Dobrowolski, 1973) and 58% (Smith and Odum, 1981) can be utilized. Smith and Odum (1981) and Smith (1982) suggest that waterfowl grazing, particularly when it is of a short duration but destructive nature, stimulates annual net production by the food plant and may affect the type and amount of detritus formed. In their studies *Spartina* rhizomes dug up by Snow Geese, supplement the amount of organic matter which enters the detrital food chain.

Since there was no difference in turion standing crop inside and outside exclosures at the end of a season and waterfowl removed 15 - 25% of the production, grazing also increases *P. crispus* production to a small extent on the Pongolo floodplain. More important, however, is that by uprooting and breaking up most of the *P. crispus* production, waterfowl could have considerable effect on the processes of decomposition and detritus formation. This is considered in Chapter 7.

The influence of waterfowl on nutrient transfers

Some studies suggest that waterfowl can provide a pulse of nutrients to the lake water during peak feeding seasons (Kalbe, 1976; Dobrowolski, 1973; Ryther and Dunston, 1971). During the first years of this study, waterfowl on Tete pan consumed an average of 7.5 kg N and 2.0 kg P each season. This represented 1.0% and 1.5% of the N and P in *P. crispus* at maximum standing crop, and 10% of the N (as NO_3 -N) and 2.6% of the P in the pan water when floods subsided to MRL (Section 4.2.2).

This amount would be transferred over a period of 5 months and some of it deposited on dry land. Transfer of nutrients by waterfowl is therefore unlikely to be an important factor affecting aquatic primary production on the Pongolo floodplain. Loss of nutrients from the system by bird migration in summer and by flushing when floods inundate faeces on the floodplain will therefore also be small in comparison to other inputs and losses during floods (Section 8.2.1).

Maintenance of *P. crispus* regenerative potential and stability of the grazing system: An hypothesis of adaptation viewed in an ecosystem context

Potamogeton crispus on the Pongolo floodplain supports a large waterfowl population although less than 10% of the annual net production of the plant is consumed. As it is the reproductive organs, turions and to a lesser extent achenes, which are eaten,this could represent an unstable grazing system (Noy-Meir, 1975; Smith and Odum, 1981) and so be prone to overgrazing. Since the waterfowl population appears to be increasing and construction of the dam upstream may affect the pattern of environmental disturbances to which *P. crispus* is adapted (Section 4.2.1), it is important to consider the stability of this grazing system which provides an important winter food resource to the birds.

Results of the studies on interactions of waterfowl and *P. crispus* indicate that grazing may in fact enhance turion production, and also that a sudden reduction in mean turion size may cause birds to leave a pan and thereby reduce grazing pressure. Thus, at least in wet years, a mechanism which controls grazing pressure seems to operate and maintain *P. crispus* regenerative potential.

An hypothesis was formulated to explain these interactions and the main effects they have on stability of the grazing system under wet and dry conditions. This is summarised in the conceptual model in Figure 5.4.

Since the reproductive and not non-reproductive tissues of *P. crispus* are consumed by waterfowl, these annual plants always mature and enter the regenerative phase (Section 4.2.1) before grazing has any impact on the population. Few achenes are eaten by waterfowl and most enter the persistent achene bank in the sediment where they ensure the persistence of the species after drought (Section 4.2.1).

Most of the achenes ingested, however, pass through the gut and Everson (1980) suggests that the resulting scarification of the pericarp actually stimulates germination. Waterfowl may therefore be important in dispersal of *P. crispus*.

During mid-winter (July) waterfowl feed on the large turions near the surface but as the duck population increases these become scarce and the birds begin to dive and uproot plants in order to obtain turions. The object of diving appears to be to bring the plant to the surface where the lower turions can be easily removed. Approximately 90% of the first formed turions are removed in this way.

A second crop of turions is then initiated in the axils of most leaves of the detached plants, but since the plants no longer have access to their nutrient supply they begin to senesce and less photosynthate is available for turion formation. The second crop of turions is thus small and because they are more difficult to locate the waterfowl obtain a lower energetic reward per unit of effort.

As the season progresses the waterfowl continue to selectively graze the large turions and reduce the ratio of large to small turions even further. It would thus become increasingly difficult for the birds to match effort with reward.

Then, during wet years, as the energetic reward per unit effort approaches some critical point (probably *c.* 1) many duck leave that population of *P. crispus* and move to another (Figure 5.4). This movement would decrease the competition for food which is experienced by the remaining birds permitting a greater reward per unit effort. Thus the duck population stabilizes at a lower density during spring. This density is probably regulated by the rate of production of both large and small turions by rooted and uprooted plants respectively.

Uprooted plants remain floating for a few days but soon senesce, sink and decay (Section 7.1.1). Most of the small turions produced by these plants sink to the sediment along with turions (large and small) dislodged from the plants by the activity of feeding waterfowl. Once turions are scattered and partly buried in the soft sediment their retrieval appears energetically unrewarding for the waterfowl which leave for the summer breeding grounds once *P. crispus* standing crop has declined.

The production of small viable turions appears to provide an "ungrazeable reserve biomass" which stabilizes the waterfowl/*P. crispus* grazing system by providing the "residual growth potential" for the next season. Grazing during wet seasons does not therefore reduce the seasonal regenerative potential of *P. crispus* and is unlikely to result in regenerative failure (Section 4.2.1).

During a drought year, water levels are low and turions in the sediment are accessible to upending and dabbling waterfowl. Thus, when reward per unit of feeding effort decreases the duck dig up these turions causing rapid destruction of the standing crop before all plants have matured (Figure 5.4) and entered the regenerative phase (Section 4.2.1). The result is a decreased turion production and seasonal regenerative potential. Even such destructive grazing is, however, unlikely to reduce turion production or turion numbers in the sediment to zero in any one season as the waterfowl are likely to leave when the reward per unit of feeding effort is reduced. A small regenerative potential will therefore probably always exist in pans such as Tete. In the event of the pan drying up, the achene bank, which does not seem to be markedly affected by grazing, becomes the major means of regeneration (Section 4.2.1).

Potamogeton crispus therefore appears to exhibit remarkable adaptation in an ecosystem context (McNaughton *et al.*, 1983) in that, even under a complex hydrological regime, it can support a dense and diverse waterfowl population which, by feeding on the plants' main reproductive organs, induces a potentially "unstable" grazing system.

This adaptation results in a small conservative (Section 1.2.8) transfer of *P. crispus* production (6- 10 %) to the waterfowl trophic level and is clearly governed by an intricate information network (Figure 5.4) which acts to maintain regenerative potential.

CHAPTER 6

THE EPIPHYTON/GRAZER/HOST (*P. crispus*) ASSOCIATION

Eminson and Moss (1980) proposed that a delicate balance develops between macrophyte and epiphyton such that the epiphyton provides maximum benefit to the host by diverting grazing without becoming so dense as to interfere with light and CO_2 reception. The nature of the association and stability of the balance which develops may affect macrophyte production and so the role of the host in the ecosystem. This study describes the association between epiphytes and the host, *P. crispus*, assesses the effects of snail (*Bulinus natalensis*) grazers on the association and discusses adaptations for co-existence of epiphyton and host plants.

6.1 THE EPIPHYTON/HOST ASSOCIATION

Scanning electron microscopy was used to determine the species composition and succession of colonization of *P. crispus* by epiphyton while the transmission electron microscope permitted an ultrastructural study of the effects of epiphyton on the host plant.

6.1.1 Results

Colonization by epiphyton

The patterns of colonization were examined on both adaxial and abaxial leaf surfaces. As no consistent differences could be detected, the processes were regarded as relatively unaffected by leaf orientation.

The youngest leaves at the tip of the plant were devoid of epiphyton (Plate 6.1a), although some fine debris adhered to the surface (Plate 6.1b). A sparse epiphyton, comprising *Cocconeis placentula* (Ehrenberg) Cleve (Plates 6.1c and d) and occasional groups of short stout bacteria (*c.* 1 um long, Plates 6.1d and 6.2a) had colonized the young leaves by the time they had expanded fully. The bacteria appeared to be attached to the leaf surface by a web-like structure (Plate 6.2a) resembling the

acidic polysaccharide fimbriate webs described by Floodgate (1972).

With increasing age the epiphyton became more dense and included a greater variety of species (Plate 6.1 e and f). On mature leaves *C. placentula* was dominant with *Gomphonema* spp. (Plate 6.1e) and *Navicula* spp. (Plate 6.1g) also present. Filamentous cyanobacteria, enclosed in mucilaginous sheaths, and colonies of short stout bacteria were common. Scattered upright, rough-walled bacilli were also present and could be seen at higher magnification (Plate 6.2b).

The density of *C. placentula* increased markedly on the oldest leaves as did the bacterial component (Plate 6.1g and h). Whilst diversity of diatoms did not appear to change, the bacteria included prostrate smooth-walled rods (0.25 um x 2 um, Plates 6.1h and 6.2c) and short filaments (0.3 - 0.8 um diameter, Plate 6.1h).

Incubation of the oldest leaves in pan water for 12 days to simulate the later stages of senescence did not cause any visible change in the species present in the epiphyton but did increase the density, particularly of the bacteria. The filamentous bacteria were abundant (Plates 6.1i and j).

The composition of epiphyton on stems was the same as that on leaves. The upper 3 cm of stem was devoid of epiphyton but, as in leaves, the density and species number increased down the stem so that the most dense and diverse epiphyton was found at the base of the plant.

Incubation of the basal 3 cm stem sections in pan water for 12 days also resulted in a marked increase in density but no detectable change in species composition (Plate 6.3a and b) of the epiphyton.

Ultrastructure of the epiphyton/host interface

Epidermal cells of the youngest leaves had a thin cuticle overlying a layered cell wall (Plate 6.4a). The cytoplasm was dense and vacuoles were absent. The first bacterial colonisers of the leaf surface were

evident in sections of young leaves, but they did not appear to disrupt the cell structure (Plate 6.4b). The dense cytoplasm was highly vacuolated and chloroplasts and mitochondria were closely packed together (Plate 6.4b and c). A broad electron translucent zone occurred between the cytoplasm and the dense adaxial cell wall (Plate 6.4b). This zone contained no organelles (Plate 6.4c) and since it was not separated from the dense wall by a membrane, it was probably of cell wall rather than cytoplasmic origin. It appears to have arisen by dissolution of the pectic matrix, allowing the wall to swell and the microfibrils to become disorganised. These changes were not evident in the mesophyll of abaxial epidermal cells.

In both the adaxial and abaxial epidermal cells of mature leaves electron translucent areas, also comprised of sparse disorganised micro-fibrils, were evident just beneath the cuticle (Plate 6.5a - c). Within each of these areas were small organisms having well-defined cell walls, a granular cytoplasm and fibrous nuclear material within an electron translucent area (Plate 6.5d), indicating that they were bacteria. The electron translucent areas around them may, therefore, represent degradation of the cell wall by extra cellular enzymes (Byrde, 1980).

Occasionally the plant cuticle was ruptured and the underlying cell wall digested away (Plate 6.5b). The cell walls of the mesophyll (Plate 6.5c) and abaxial epidermis (not shown) had, by this stage, also become swollen with loosely arranged microfibrils.

The oldest leaves from the field supported a dense epiphyton. The cuticle was almost completely absent and most of the epidermal cell walls, both adaxial and abaxial, were disorganised (Plate 6.6a). The epidermal cells showed typical signs of advanced senescence (Baddeley, 1967) in that they were highly vacuolated, most organelles were absent and the remaining chloroplasts swollen with ill-defined grana stacks. The tonoplast was also swollen and ill-defined. The mesophyll cells (Plate 6.6b) showed less advanced senescence, being vacuolated and with occasional swollen chloroplasts. The walls of these cells were disorganised and swollen (Plate 6.6b and inset) with a markedly invaginated plasmalemma resembling that of transfer cells (Pate and Gunning, 1972).

After 12 days in the laboratory the cells lacked cytoplasm and only the disorganised cell walls and plasmalemma of the leaf cells remained (Plate 6.7). Bacteria had penetrated into both the epidermal (Plate 6.7a) and mesophyll cells (Plate 6.7b) and the walls of both tissues had been extensively degraded.

Ultrastructure of the upper 3 cm of stems was similar to the youngest leaves in that there was no evidence of attached epiphyton or penetration of epidermal cells by bacteria. Mid-way down the stem, however, occasional bacteria were evident within the outer epidermal wall (Plate 6.8a). Although the bacteria were surrounded by electron translucent areas indicative of enzymatic degradation, there was only slight inward swelling of the cell wall. Epidermal cells of the basal 3 cm stem sections, however, showed swelling typical of that in leaf cells (Plate 6.8b).

After incubation in pan water for 12 days basal stem sections showed little change in ultrastructure although bacteria had invaded the intercellular spaces of the cortex (Plate 6.8c). Entry may have been gained via the cut ends of the stems.

6.1.2. Discussion

Two patterns of colonisation of submerged macrophytes by epiphyton have been reported. In freshwater macrophytes and many marine macroalgae, new species replace earlier colonisers as the host ages (Ballantine, 1979; Cattaneo and Kalff, 1978; Howard-Williams *et al.*, 1978), whilst in other marine macroalgae (Ballantine, 1979) and on *P. crispus*, as shown in this study, pioneer epiphyton species may persist. In all cases however, there is both an increase in epiphyton density and species diversity during ageing of the host. Thus although the pattern of colonisation by epiphyton may differ, the result in all cases, is an increase in epiphyton density and species diversity during ageing of the host. There is, however, little information on the fate of the epiphyton after death of the host. Robb *et al.*(1979) observed marked differences in the diversity of bacteria on living and decomposing *P. pectinatus* leaves, while Newell and Fell (1980) showed gradual

changes in the mycoflora of *Thalassia testudinum* König after death. Clearly the death of *P. crispus* leaves and stems during incubation in lake water did not affect epiphyte diversity while the density, particularly of bacteria, increased.

The swelling and disruption of the epidermal wall of fairly young leaves and the bases of rooted stems of *P. crispus*, which results in a reduction in cell volume and thus also in internal cell wall area, has not been reported in other submerged plants. It is, however, a common feature of cells infected by bacteria (Wallis, 1977) and other pathogens (Beckman, 1964).

The disorganisation of the microfibrils in cell walls has been ascribed to an increase in acidity, or to cationic complexing as a result of the secretion of organic acids by the invading pathogen. This weakens and loosens the lattice structure of the polymeric substances in the primary wall of the invaded cell (Beckman, 1964) and, often, in adjacent cells as well (Wallis, 1977; Wallis and Truter, 1978). In *P. crispus* swelling and disorganisation occur before any pathogens are observed within the tissues. The host response might, therefore, be attributed to organic acids secreted by the epiphytes, particularly the bacteria, before penetration. This is supported by the gradual extension of these conditions into the mesophyll and abaxial leaf epidermis before bacteria are evident in them. Why the response was not observed on the abaxial epidermis at the same time as the adaxial, when both had similar epiphyton, is not clear.

The characteristics of transfer cells seen in the older mesophyll cells are also difficult to interpret, since, although they have been known to occur in response to nematode parasitism in some plants (Whitfield, 1979) they also occur normally in many submerged macrophytes (Pate and Gunning, 1972).

Invasion and degradation of stems by bacteria appeared to take place more slowly than in leaves. This is probably attributable to the greater degree of thickening and lignification of the stem cell walls (Everson, 1980) and would explain the lack of extensive degradation during incubation in lake water.

Bacteria are only known to enter hosts through natural openings (e.g stomata and lenticels) and lesions. Since the former are absent in *P. crispus*, the pathogens probably gained entry to the epidermal cell wall through wounds which could have been caused by a variety of factors. Once within the epidermis, however, they spread rapidly and actively degraded the surrounding cell wall. It is likely that these activities were, at least partly, responsible for the concomitant senescence of leaf and stem cells since senescence caused by pathogens is known to manifest itself in the same way as natural senescence (Butler and Simon, 1967).

The results of this study support those of Howard-Williams *et al.* (1978), and suggest that the host/epiphyton relationship is more complex than the essentially saprophytic relationship described as chemo-organotrophic by Allen (1971). In *P. crispus* since it may cause the death of the host by promoting senescence, it could be considered necrotrophic and as such forms a further factor which may affect the delicate balance between macrophyte and epiphyton proposed by Eminson and Moss (1980). Bacteria, by degrading the cell walls would probably soften them making the plant more susceptible to damage and consumption by invertebrate grazers, rather than protecting it by diverting grazers as Hutchinson (1975) proposed. Degradation of plant tissues by bacterial and fungal action also occurs in autumn shed leaves in streams and is termed "conditioning" (Cummins, 1974). Such conditioning softens the tissues and permits increased rates of consumption by invertebrates (Cummins and Klug, 1979).

6.2 EFFECTS OF SNAIL GRAZING ON EPIPHYTON/HOST ASSOCIATION

The gastropod *Bulinus natalensis*, is the most abundant macro-invertebrate associated with the *P. crispus* community (Walley, 1980) and, like most gastropods (Calow, 1974), is a periphyton feeder (Stiglingh and Van Eden, 1970; Walley, 1980). The influence of grazing by *B. natalensis* on the epiphyton/host association of *P. crispus* was therefore investigated.

6.2.1 Results

The pattern of snail grazing on leaves

Scanning electron microscopy was used to study the pattern of snail grazing on leaves of different ages (section 2.5.3).

After 24 hours exposure to snails the surface of the youngest leaves remained apparently unchanged. Thus if the snails had been grazing on the leaves they caused little or no damage. The surface of young leaves (Plate 6.9a and b) was also unaffected by the grazing action of snails, although most of the epiphyton had been removed, leaving debris and the ventral valves of some diatoms behind. Grazing snails had, however, removed the epiphyton and parts of the outer walls of some epidermal cells of mature leaves (Plate 6.9c and d). This exposed numerous canals (Plate 6.9d, arrowed) which are thought to have been caused by necrotrophic action of the bacterial epiphytes within the cell walls. The incidence of canals increased in the vicinity of damaged cells, indicating a correlation between heavy localised infections of bacteria and cell damage caused by snail grazing.

Senescent leaves, having almost entirely electron translucent epidermal cell walls as a result of bacterial degradation (section 6.1.2), were extensively damaged by snail grazing within the 24 hour period (Plate 6.9e and f).

After 6 days in the presence of snails, all the youngest leaves (Plate 6.10a) and most young leaves (Plate 6.10b) were still intact and showed no macroscopic evidence of damage. Furthermore, while most mature leaves had been damaged (Plate 6.10c), the few senescent leaves remaining were extensively damaged (Plate 6.10d). Microscopical examination of the leaf surfaces showed them to be devoid of epiphyton and while the youngest leaves were undamaged, damage increased with leaf age.

Grazing snails therefore fed primarily on epiphytes but in older leaves, those parts which had been degraded by epiphytic, necrotrophic bacteria were also consumed. Grazing *in vitro* also, however, controlled the extent of recolonization by epiphytes. It is suggested that this would have the effect of reducing conditioning by necrotrophs which would

retard consumption by snails. Support for this hypothesis was sought in the laboratory by comparing the change in "edibility" (rate of consumption; Nicotri, 1980) of leaves of different ages with increasing time allowed for conditioning before grazers were introduced.

"Conditioning" and "edibility" of leaves and stems

When leaves of the two youngest categories (youngest and young) were presented to snails immediately after collection, they were inedible and remained so until the experiment was terminated 20 days later (Figure 6.1a and b). Even when these leaves were incubated with detrital aggregate in the absence of snails for 2, 4 and 8 days before being introduced to snails, they remained apparently unconditioned and inedible.

Mature and senescent leaves, however, had been conditioned *in situ* before collection and edibility, which was always greatest in the oldest senescent leaves, increased with time of conditioning in the laboratory (Figure 6.1a and b).

After 18 days conditioning all leaves were similarly edible and most had been consumed by the 20th day (Figure 6.1b). Thus, the number of leaves remaining after 20 days was greatest when conditioning was least and when snail grazing continuously removed the developing epiphyton. The results show that although the degree of conditioning of leaves controls edibility and thus consumption by snails, grazing, by controlling the development of epiphyton, arrests conditioning and curtails consumption of the leaves.

The consumption of sections of stems taken from the tip, middle and base of mature plants similarly increased with time allowed for necrotroph conditioning (Figure 6.2a). The edibility was, however, only slightly affected by position of the stem on the plant for the first four days, thereafter all sections were consumed at equal rates. The rate of consumption was generally slower than for leaves, and, in contrast to leaves, the number remaining at the end of the experiment decreased slightly with time for which snail grazing occurred (Figure 6.2b).

Necrotrophic conditioning appeared therefore to be less efficient than in leaves. This confirms the observations made by transmission electron microscopy (Section 6.1.2) which were attributed to the greater proportion of structural material in stems than leaves.

Nevertheless the number of stems remaining when the experiment was terminated was greatest when conditioning was controlled by the continuous removal of epiphyton by grazing snails.

The *Bulinus natalensis* population in Tete pan

The numbers and standing crops of snails in Tete pan (Figure 6.3) were high in winter and spring but low during the summer months. The number and mass of snails per gram of *P. crispus* did not remain constant but increased to a maximum on senescing plants which support the most epiphyton (Rogers, 1981).

Appleton (1978) suggests that temperature is the major factor governing seasonal changes in Bulinid populations and that snails are favoured by warm summer temperatures and decline in winter. Careful searches of marginal and mid-pan habitats in Tete pan, however, showed that the population declined in summer and did not simply migrate from the *P. crispus* community to other areas. Thus, on the sub-tropical Pongolo floodplain where winter temperatures are warm, the availability of epiphyton and *P. crispus* as a food source and habitat, and not temperature,appear to be the main factors determining the seasonality of the *B. natalensis* population.

6.2.2 Discussion

Adaptation for co-existence of host and epiphyton

The "delicate balance", which Eminson and Moss (1980) suggest develops between epiphyton and the host plant, is thought to be controlled by fluxes of nutrients and DOM at the host/epiphyte interface. It is thus dependent on host metabolism and topography, and manifested in a

host-specific epiphyton. Although their hypothesis is based on algal epiphytons, the mechanisms they proposed might also apply to bacteria, especially as they are also universal contributors to the epiphyton.

The epiphyton developing on artificial substrata in the pans of the Pongolo system shows distinct differences in species composition, biomass and nutrition from those on *P. crispus* (Rogers, 1981), indicating that host metabolism does influence the epiphyton. However, in contrast to the situation proposed by Eminson and Moss (1980) the epiphyton does not prevent damage to the host by diverting grazing since the host cells are resistant to grazing until conditioned by necrotrophic bacterial epiphytes. It may be correct that snail grazing prevents excessive growth of epiphyton on *P. crispus* but, perhaps of greater significance is the reduction in the rate of attack by necrotrophs which appears to extend the life span of the plant. These data thus support the hypothesis of Eminson and Moss (1980) in that both host metabolism and grazing seem to be important factors regulating the structure and function of the epiphyton/host association but it does not support the hypothesis (Hutchinson, 1975) that the epiphyton protects the host from grazers. Instead, aspects of the host's life-history strategy, structural resistance to grazers and a short life-span, which is completed before conditioning facilitates grazing, are important factors in its own defence.

The important concept that arises from this discussion is that co-existence of epiphyton and host in the floodplain pans is achieved through a complex set of interacting attributes of the epiphyton community, the host plant and the grazing animals. This suggests that in other environments, factors such as allelopathy (Wium-Anderson *et al.*, 1982) the production of mucilage (Hutchinson, 1975) and replacement of leaves in perennial species could also form important components of overall adaptations for co-existence. Attempts to find ubiquitous factors which have an overriding control of the association (see Wetzel, 1983 and 1983a) could be misleading. The concept of a number of interacting variables, of which one or more plays a predominant role under a certain set of environmental conditions, would seem more consistent with the theory of organism and community adaptation within ecosystems (Sections 1.2.1; 1.2.2; 1.2.8). This does not, however, mean that existing hypotheses are either premature (Wetzel, 1983a) or should be discarded.

They are, after all, hypotheses and thus more experiments should be designed to test them under a range of conditions. Progress in our understanding of the roles of epiphyton and aquatic plants in wetland ecosystems and the factors permitting co-existence will remain slow until a more experimental approach is adapted (Sand-Jensen, 1983; Wetzel, 1983a). This study indicates that the concept of organism and community adaptation within ecosystems (Grime, 1979; Calow and Townsend, 1981; Solbrig, 1981; McNaughton *et al.*, 1983) could provide a useful basis for formulating and testing hypotheses.

The epiphyton of *P. crispus* has a dual role; it does provide grazing for snails but, when once the bacterial component has gained entry into the cell wall, it serves also to enhance grazing of the macrophyte rather than divert it. The rapid growth and very short life cycle of *P. crispus* (4 - 5 months; Section 4.3.1) ensures that reproduction can take place before the plants are consumed but if the balance were upset necrotrophic processes could cause the destruction of the plants before reproduction occurred. The question therefore arises as to how easily the natural balance between epiphyte and host can be upset.

Eminson and Moss (1980) consider that the balance between epiphyton and host may be upset when the fertility of the water increases to the point where it has a greater influence on the epiphyton than the relatively small fluxes at the host/epiphyte interface. Epiphyton growth is thus stimulated and the attached organisms outcompete the host for nutrients, inorganic carbon and light, resulting in a decline in macrophyte populations in highly eutrophic waters (Phillips *et al.*, 1978). While this may be important in the particular context of eutrophication, the above discussion clearly shows that many other factors may also be important. For example in the case of *P. crispus* on the Pongolo floodplain, necrotrophic bacteria/grazer interactions may be as important. If lake fertility were increased, a decrease in the host's influence on the epiphyton may lead to a rate of invasion by necrotrophic micro-organisms which exceeds the rate of grazing earlier in the host's life-cycle. A decline in both growth and reproduction which results more from bacterial attack than competition for resources, could thus lead to a loss of macrophytes from the system. The possibility of a similar set of circumstances arising from the eradication of the snails in an anti-bilharzia

campaign provides a further example.

Implications of necrotroph/grazer interactions for transfer of resources

Under natural conditions on the Pongolo floodplain, snail numbers are maximal on senescing plants which support the most epiphyton. Thus it might be expected that the effects of conditioning by epiphytes and of snail grazing on the host plant in the field, would be most pronounced at this time.

A number of studies have suggested that although living plants are not eaten, snails do consume senescing or dead ti ssues (Azevedo and Medeiras, 1955; Stiglingh and van Eden, 1970; Lamens and van der Velde, 1978; Cattaneo and Kalff, 1980). Similarly, freshly shed autumn leaves are not consumed by stream invertebrates (Kaushik and Hynes, 1971) but once partly conditioned by microbes,large amounts of leaf tissue are ingested. However, invertebrate assimilation is inefficient (Wetzel, 1979) and most of the biomass consumed is voided as faeces and enters the detrital pool as dissolved and particulate organic matter. The microbial conditioning and invertebrate grazing may thus have a profound effect on the fate of allochthonous organic matter production.

This study indicates that necrotrophic bacteria/snail grazer interactions may also play an important role in determining the transfers of *P. crispus* production and accumulated nutrients during senescence and decay.

CHAPTER 7

DECOMPOSITION AND DETRITUS FORMATION

Present understanding of the decomposition of aquatic macrophytes is based largely on the study of the disappearance of particulate matter and nutrients from dead plant material, either contained in mesh bags and incubated in the field (Boyd, 1970; Wohler *et al.*, 1975; Howard-Williams and Junk, 1976; Godshalk and Wetzel, 1978b; Danell and Sjöberg, 1979; Howard-Williams and Davies, 1979), or incubated in the laboratory *in vitro* (Jewell, 1971; Wohler *et al.*, 1975; Godshalk and Wetzel, 1978a, b,c; Carpenter and Adams, 1979).

The plant material, actively growing or senescent, has usually been killed by drying or lyophilization (Section 1.2.3.2) and hence studies have not included senescence and the action of necrotrophic bacteria in the decay process. The initial decomposition experiments were therefore designed to establish a method which included natural senescence (1976) and to compare the results with those obtained when plants were dried. Further experiments assessed the role of necrotrophic bacteria/grazer interactions in detritus formation and nutrient cycling in more detail.

7.1 THE EFFECTS OF DRYING ON THE PATTERN OF MASS AND NUTRIENT LOSS FROM SENESCENT *P. CRISPUS*

7.1.1 Results

1976 Experiments

These experiments were designed to establish a routine for collection of material that was about to enter the senescent phase so that neither young actively growing nor partly decomposed plants were used in the decomposition studies.

Plants were uprooted from the sediment to simulate damage caused by waterfowl and those in which senescence and decay was evident were

discarded (Section 2.6.1). The remainder were transferred as fresh (undried) material to the decomposition bags.

Material placed into decomposition bags on the 21 August (1976), just before the population began its annual decline (Figure 7.1;e_1), lost mass rapidly (83%) during the first 17 days and then mass increased significantly ($p = 0.05$, Figure 7.2). Inspection showed that some of the shoots in the bags had started to grow and it was evident that not all of the material placed in the bags had been entering the senescent phase. However, when apparently healthy material (i.e plants already senescing were discarded) was collected 30 days after maximum standing crop (Figure 7.1;e_2) and the experiment repeated, there was a rapid loss of mass which continued at a constant rate of *c.* 4% day^{-1}, until only 9% remained after 27 days (Figure 7.2b). Since no growth of plants was evident in the bags all material was considered to have been about to senesce when the experiment was initiated. Thus it appeared that the pattern of mass loss of *P. crispus* during natural senescence and decay could be followed when material was collected *c.* 30 days after maximum standing crop had been attained.

1977 Experiments

Material was collected at the same stage of the annual cycle (Figure 7.1;e_3) for a comparison of the pattern of natural senescence and decay with that obtained when plants were killed by drying. To facilitate discussion the terms "senescent" and "dried" plants are used to describe the material used in the two sets of litter bags.

Senescent plants did not show a significant reduction in mass during the first 24 hours (Figure 7.3) but thereafter loss proceeded at a constant rate, *c.* 4% of the original mass per day, and after 24 days only 10% of the original mass remained. The rate of mass loss was thus the same as that measured in 1976 (Figure 7.2b).

Dried material lost 18% of its mass within two hours (Figure 7.3). No significant loss occurred during the next 23 hours after which it proceeded at a constant rate, 2% of the original mass per day. This was slower than the loss from senescent material and, after 24 days,

a significantly greater proportion of the original mass (35%) remained in the bags containing dried material.

Nutrient concentration in senescent material remaining in the bags showed little change during decomposition, although phosphorus and magnesium decreased slightly (Figure 7.4a). All nutrients were therefore, lost from the bags at similar rates. Significant reduction in nutrient stock could not be detected after 24 hours, but loss proceeded at a constant rate of *c.* 4% day^{-1} during the following 24 days (Figure 7.4b).

Nitrogen concentration in the dried material remained fairly constant during decomposition and was thus similar to that in senescent material (Figure 7.4a). Phosphorus and potassium concentrations decreased during the first two hours whilst those of calcium and magnesium each increased by almost two thirds. During the period 1 - 24 days the concentrations of phosphorus and magnesium declined slightly with calcium and potassium remaining fairly constant.

The rapid loss of mass during the first 2 hours, associated with differential rates of nutrient loss, resulted in marked differences between the nutrient stocks remaining in decomposing senescent and dried material. The stocks of nitrogen, phosphorus and potassium in dried plant material decreased by 7%, 54% and 95% respectively within two hours (Figure 7.4b). Thereafter nitrogen and phosphorus stocks were reduced at constant rates(*c.* 3.7% and 3.3% day^{-1} respectively) whilst no further losses in potassium were recorded. Reduction of nitrogen stocks between 2 hours and 24 days were more rapid in the case of senescent than dried material, so that after 24 days dried material contained more nitrogen than did senescent material. In contrast, after the initial rapid loss of phosphorus, the rate of loss was slower than that from senescent material and at the end of the experiment the amounts remaining were similar.

The stocks of calcium and magnesium in dried material increased markedly during the first 24 hours before declining at almost constant rates of 3.3% of the original mass per day (Figure 7.4b). The stocks of calcium and magnesium were consistently higher in dried than in senescent material.

The decomposing senescent and dried plant material both attracted snails (*Bulinus natalensis*) with numbers and mass initially higher on the dried material. However, by the eighteenth day the senescent material supported more than twice the number and mass of snails (Table 7.1).

7.1.2 Discussion

The rate and pattern of mass loss from dried plant material was similar to that observed for a variety of aquatic plants (Boyd, 1970; 1971; Mason and Bryant, 1975; Howard-Williams and Junk, 1976; Howard-Williams and Davies, 1979; Godshalk and Wetzel, 1978b). The initial rapid loss of mass has been attributed mainly to the solubilization and leaching of minerals and organic substances (Planter 1970; Kaushik and Hynes, 1971; Godshalk and Wetzel, 1978a; Swift *et al.*, 1979) and the later, slower loss of mass is attributed to the breakdown or catabolism of plant material by heterotrophic micro-organisms (Howard-Williams and Junk, 1976; Saunders, 1976; Godshalk and Wetzel, 1978c). However, when decomposition bags are used, mass loss during the latter phase is also related to the loss of particulate matter by comminution (Swift *et al.*,1979) from the bags and the rate of catabolism of these particles is not recorded. Thus as decomposition is the sum of leaching, comminution and catabolism (Swift *et al.*, 1979) the pattern of mass loss from decomposition bags in the field reflects the rates of production of both the particulate and dissolved organic detritus (Rich and Wetzel, 1978),and not the rate of complete decomposition.

Since dried *P. crispus* lost a greater proportion of its phosphorus and potassium than of its mass during the first two hours, it is clear that these two nutrients were rapidly leached. In contrast, the rate of loss of the nitrogen stock was the same as the rate of mass loss indicating that leaching was not important. This has been observed in other studies (Odum and de la Cruz, 1967; de la Cruz, 1975; Howard-Williams and Davies, 1979) and is attributed to the rapid binding of any soluble nitrogen that is released by either the microflora associated with the decomposing material, or as protein complexes on the dead material. As decomposition proceeds these processes can also result in an increase in the concentration of nitrogen (Howard-Williams and Davies, 1979)

but this was not evident in the present study, possibly because its duration was so short.

Howard-Williams and Junk (1976) observed a marked increase in the concentration of calcium during the early stages of decomposition and attributed it to the adsorption of Ca^{++} onto the surface of the plant material by cation exchange. The increase in stocks and concentration of both calcium and magnesium within two hours during this study, suggests that dried *P. crispus* is also acting as a cation exchange surface.

Despite the close similarity between the patterns of nutrient and mass loss reported elsewhere and those shown here for dried *P. crispus*, they deviate markedly in most respects from those occurring in senescent material.

Thus detached, senescent plant material did not act as a cation exchange surface and the loss of mass from senescent material did not show the initial rapid leaching. The latter might be expected since during natural ageing, leaching would be an extended process as individual cells senesce, die and lyse (Godshalk and Wetzel, 1978c) whereas when dried material is used, all cells are dead on re-immersion.

However, since leaching is a more rapid process than microbial breakdown of structural material, certain nutrients such as P and K, would be expected to show a decrease in concentration during decomposition (Swift *et al.*, 1979). As this was not observed in the case of senescent material it is concluded that leaching was dependent on structural breakdown and thus nutrient loss by leaching was concurrent with loss of particulate matter by comminution. The presence of large numbers of snails which preferentially consume senescing plant material (Section 6.2.1) implicates them in this process.

It is clear,however, that the mechanisms leading to a loss of mass and nutrients during these experiments were markedly altered by drying of the plant material. Harrison and Mann (1975) and Godshalk and Wetzel (1978a) have also observed that drying increased the rate of leaching, and the former authors commented that drying appeared to alter the organic matter in such a way that it was less rapidly attacked by microbes. The overall slower rate of mass loss from dried material in

this study might also therefore be a result of a change in the pattern of microbial breakdown.

Until recently, it was considered that colonization by microflora responsible for decomposition began after death of the plant or plant part (Oláh, 1972). However, this study (Section 6.1) and those of Howard-Williams *et al.* (1978) and Robb *et al.* (1979) have demonstrated microfloral successions which begin on young plants and continue after death. Furthermore, in this study it was apparent that necrotrophic bacteria, which formed an integral part of the natural epiphyton succession, were responsible for both hastening senescence and initiating the decomposition process.

When decomposition was studied using senescent material, the microflora would have remained living and relatively undisturbed but when dried material was used it would, like the plant cells, have been killed by the drying process. Dried material would therefore have to be recolonized before decomposition could proceed. Since nutrients and dissolved organic matter are leached rapidly during the first two hours and they are known to influence the rate of bacterial production (Fenchel and Harrison, 1976; Paerl, 1978) it is likely that recolonization would be nutrient limited. Drying must therefore be expected to alter both the type of micro-organisms colonizing the material, and the rate of catabolism; hence the slower overall rate of mass loss from dried plants.

Furthermore, since snails such as *B. natalensis* grazed both the senescent plants (Section 6.2.1) and the epiphyton which promote senescence, it must be expected that drying would influence snail numbers and the consequent pattern of comminution and detritus formation. The larger snail mass which was supported on the decomposing senescent material emphasises the different pathways of energy and nutrient transfer which become operative if the material is dried prior to experimentation.

Rates of decomposition have usually been modelled by an exponential function of the type $y = ae^{-bk}$ where y is the mass remaining after a time interval b, a is the initial mass and k is the rate constant (Jewell, 1971; Howard-Williams and Davies, 1979; Carpenter and Adams, 1979). Although an exponential model of this type fits the data for decomposition of dried *P. crispus* (coefficient of determination 0.99,

Figure 7.5a), inspection shows that in common with data from other workers (Howard-Williams and Davies, 1979; Godshalk and Wetzel, 1978b), it does not fully account for the initial rapid loss by leaching. In a modification, Godshalk and Wetzel (1978b) noted that if k was considered to decrease exponentially (an exponential model of the type $dW/dt = kW$ where $k = ae^{-bt}$, W = percent of the initial mass remaining and t = days of decomposition) then no such discrepancy occurred. However, k did not decrease exponentially in this study but rather changed very abruptly between 2 and 24 hours.

The loss of mass from senescent material, in both 1976 (not shown) and 1977 (Figure 7.5b) was best described by a linear model of the type $y = a_o - a_1 x$, (where y is the mass remaining after time x, a_o is the initial mass and a_1 the rate constant) with coefficients of determination of 0.995 and 0.997 respectively. However, despite its usefulness in describing the pattern of mass loss from the decomposition bags, it is limited in that it does not account for the fate of fine particulate or dissolved detritus. More detailed investigations of the factors affecting production and utilization of this detritus are required before a biologically meaningful model can be produced. Nevertheless the different functions required to describe the two sets of data suggest that drying of a submerged macrophyte such as *P. crispus* may bias a mathematical model of decomposition.

Since drying markedly affected the decomposition process many previous studies may have underestimated the rates of decomposition of submerged macrophytes as they did not account for the influence of epiphyton/grazer interactions during senescence.

7.2 EFFECTS OF GRAZING SNAILS AND EPIPHYTES ON DETRITUS FORMATION AND NUTRIENT TRANSFER

Once preliminary experiments to establish a routine for studying decomposition had been completed, the effects of epiphyte conditioning and snail grazing on decomposition were examined.

7.2.1 Results

Mass and nutrient loss from large mesh decomposition bags

During the preliminary experiments (Section 7.1) it was observed that the larger snails of the population were excluded from the bags with a mesh size of 1.5 x 1.5 mm. In 1977 a study of the size frequency distribution of the *B. natalensis* population, present 1 month after maximum *P. crispus* standing crop (Figure 7.6), showed that a mesh size of 5 x 5 mm would permit access by the whole population.

The loss of mass from senescent plants placed in these bags (Figure 7.7a) was similar to that from the smaller mesh bags incubated at the same time (Section 7.1.2) in that there was no significant leaching loss initially and about 10% of the original mass remained after 24 days.

The pattern of mass loss, however, was not linear as in the small mesh bags but exponential (Figure 7.7b, coefficient of determination 0. 98 and rate constant, k = 0.086).

Concentrations of N and P showed little change during decomposition (Figure 7.8a) and loss of nutrient stocks followed the pattern of mass loss (Figure 7.8b) confirming that a rapid leaching loss did not take place.

Two explanations for the different patterns of mass loss from the two mesh sizes are:

1. The larger mesh size permitted access to the plant material by a greater size range of snails (Table 7.1) so that total snail mass was greater. Since snails are implicated in the decomposition process this would have effected an increase in the rate of mass loss.

2. The larger mesh size would allow loss of larger detrital particles from the bags, thus enhancing the rate of mass loss from the bags.

The major disadvantage of the decomposition bag technique is that it is not possible to collect the detritus lost from the bags and so study its

formation and role in the decomposition processes. *In vitro* experiments were therefore conducted so that all detritus could be collected and the effects of conditioning by epiphytes and grazing by snails on detritus production assessed (Section 2.6.2).

Effects of grazing snails and epiphytes on detritus formation

Detached plants, incubated without snails, lost *c.* 38% of their mass in 12 days (Figure 7.9a) at which stage they were brown, flaccid and apparently dead. Thereafter mass loss continued exponentially (k = -0.033) (Figure 7.9a, Table 7.2) such that 50% loss (t ½) occurred within 20 days The pattern and rate of mass loss was not significantly ($p > 0.05$) affected by the addition of epiphytic detrital aggregate (EDA) when snails were absent (Figure 7.9a, Table 7.2). In contrast, plants incubated with snails, although showing the same exponential pattern of mass loss, lost mass significantly (p =0.05) more rapidly (k = 0.056 t ½ = 13) and this was greatly enhanced by addition of EDA. Despite the greater rates of mass loss in the presence of snails the plants did not become brown and flaccid.

Accumulation of a fine detritus (FPOM$<$1 mm^2),consisting mainly of snail faeces, was also significantly more rapid (Figure 7.9b) when EDA was added (1095 mg in 24 days) than in the presence of snails alone (600 mg). In the absence of snails, however, most of the dead plant material remained unfragmented and both with and without EDA less than 200 mg of fine detritus accumulated.

These results provide further evidence that snail grazing, by removing epiphytes, controls the spread of necrotrophic organisms which promote senescence in *P. crispus*. Consumption of conditioned plant parts, however, leads to a rapid loss of mass and production of fine detritus.

The rate and pattern of mass loss from plants with snails and EDA were the same as those obtained in the field using large mesh bags. Since the detritus produced by feeding snails is fine ($<$1 mm^2), loss of large particles from the bags is unlikely to be significant and both the field and laboratory studies (snails plus EDA) would appear to approximate the natural situation.

The exponential rates of mass loss, in contrast to the linear rate observed in the smaller mesh bags, can probably be attributed to the differences in the snail populations within the bags. In the small mesh bags snail entry was restricted so that the relative rates of grazing and conditioning would have differed from that in large mesh bags where grazer access was similar to the field situation.

Effects of grazing snails and epiphytes on nutrient transfers

Studies on the nutrient transfers during detritus formation were confined to the two treatments "Snails + EDA" which approximated the field situation and "No snails or EDA" which provided comparison.

Loss of N and P stocks from *P. crispus* plants *in vitro* followed the same patterns as mass loss (Table 7.3). Thus while 9 and 10% of the original stocks of N and P respectively remained after 24 days in the presence of snails 49% N and 60% P remained where snails were absent.

In the absence of snails, most of the P was lost as dissolved P to the water (27% after 24 days) and only 7% occurred in the FPOM. Only 3% of the N stocks occurred in the dissolved form after 24 days while 19% occurred as FPOM. In contrast, snail consumption of *P. crispus* resulted in more N and P being lost to the FPOM than to the water. The amount of N in the FPOM rose to 14.6% of the original stocks indicating that fixation of N occurred, increasing the total N stock by 67%.

When snails were absent the total nitrogen stocks decreased during the 24 day incubation period (Table 7.3). This can probably be attributed to inefficient removal of periphyton from the sides of the incubation jars at each harvest. Such periphytic growths were minimal in the presence of snails which grazed them continuously. The important point, however, is that consumption of *P. crispus* by snails had a marked effect on the rates and directions of nutrient transfers. In particular it resulted in a smaller proportion of nutrients entering the dissolved phase and a detritus very much richer in nitrogen (Table 7.4) than was produced by microbial decomposition alone.

The organic matter (ash free dry weight; Table 7.4) content of the snail faeces (FPOM), although lower (77%) than the parent plant material (85%), was higher than that produced by microbial decomposition (69%) and so too was the N:organic matter ratio. The large quantities of FPOM produced by snails were, therefore, the more nutritious detritus.

7.2.2 Discussion

Under natural conditions on the Pongolo floodplain,the effects of epiphytes and snails on the host plant are most important in determining the fate of plant production at the time of senescence, after the plants have been uprooted by waterfowl.

Before the plants are uprooted the invading bacteria are restricted to the outer epidermal wall even in the oldest leaves (Section 6.1). Once uprooted, however, the plant's combined strategy of defence against, or control of, epiphytes appears to break down and the invading bacteria spread rapidly. This supports the suggestion that host metabolism influences the epiphyton (Section 6.2.2).

Conditioning of the cell walls of *P. crispus* clearly permits the snails to consume the plants before they die and before the readily utilizable organic matter is leached out. This permits the rapid formation of a fine, nutritious detritus and so influences the rates and patterns of nutrient and energy transfer within the ecosystem.

Conservative transfers of energy-matter in the detrital pathway are large in comparison to the grazing food chain (Section 5. 2.2) but are also clearly governed by a complex set of interactions attributable to the ecosystem information network (Section 1.2.8).

This is similar to the pattern of decay of allochthonous plant litter which enters streams (Cummins *et al.*, 1973; Boling *et al.*, 1975; Anderson and Sedell, 1979) in that certain invertebrates (designated "shredders") have been shown to be very important in reducing dead, conditioned leaves to FPOM which is then utilized by other functional

groups (e.g. collectors). The rates of conditioning and hence FPOM production are primarily controlled by the refractility of the tissues (Cummins *et al.*, 1973) which differs between species.

On the Pongolo floodplain rates of conditioning are also dependent on the relative refractility of the tissues (leaves and stems) and although *B. natalensis* is morphologically a "scraper" (Stiglingh and Van Eeden, 1970), conditioning of *P. crispus* permits it to function as a "shredder" and produce a fine detritus. This forms a very valuable food source for the many detritivorous fish species (Heeg and Breen, 1982) and invertebrates (Walley, 1980) on the floodplain. The trophic relations of these detritivores are not well understood but Walley (1980) has shown that the production of the oligochaete *Branchiura sowerbyi*, an important collector species, is markedly increased by the seasonal input of *P. crispus* detritus each year.

Much attention has been paid in recent studies to the modelling of the decomposition process (Godshalk and Wetzel, 1978c; Carpenter, 1981). These have usually described the pattern of decay as an exponential function ($y = ae^{-bt}$; see discussion Section 7.1), and have not actually considered the way in which this rate is affected by biotic and abiotic factors. Godshalk and Wetzel (1978c) developed a simple model to describe the interactions of the major factors affecting the rate of decomposition:

$$k = \frac{T \times O \times N_1}{R \times S}$$

Where k = decomposition rate; T = temperature; O = oxygen; N_1 = nutrients; R = plant refractility; S = particle size

This was not considered to be a definitive model of the decomposition process but could be used to demonstrate future research needs. Godshalk and Wetzel pointed out that, since k would not respond linearly to changes in the other model components and that the components do not necessarily act independently of one another, little would be gained from more descriptive studies and further research should concentrate on:

(i) The significance of decomposition to aquatic ecosystems.

(ii) The importance of the various rates to system metabolism and stability over long periods of time.

(iii) The relations between detritus decomposition and the maintenance of higher trophic levels.

(iv) The role of decomposition as an agent by which mineral nutrients are regenerated.

The first of these priority research areas is not well defined and seems to be covered largely by the other three more specific areas. These areas can only be approached on the assumption that the basic decay rates of the plants can be reasonably accurately measured.

This study has shown that the techniques adopted in a study can markedly affect the rates of change of the model components and interactions between them. Thus, not only is the estimate of k affected but also the interpretation of which factors affect k and by how much. For example whe *P. crispus* plants were dried,the rate of leaching was accelerated such that the loss of nutrients (N_1 in model) and dissolved organic matter caused a marked change in the refractility (R) of the tissues. This reduced the rate of conditioning by necrotrophs and so the ability of snails to act as shredders and reduce particle size (S). Hence, nutrient loss was faster and k slower, and the role of *P. crispus* in nutrient regeneration and system metabolism may have been misinterpreted.

On the Pongolo floodplain the rate of *P. crispus* decay is rapid and so is probably not important in maintaining long term stability of the system as would more refractile tissues with a slower decay rate. However, the timing of the entry of detritus into the floodplain detrital pool each year appears very important. The formation of *P. crispus* detritus in spring comes at a time when other energy imputs are low and this serves to maintain higher trophic levels until the summer floods transfer allochthonous detritus to the pans (Heeg and Breen, 1982). This study demonstrates that the timing and rate of entry of *P. crispus* to the

CHAPTER 8

THE ROLE OF *POTAMOGETON CRISPUS* IN CONSERVATIVE TRANSFERS OF ORGANIC MATTER AND NUTRIENTS IN TETE PAN.

The general objective of this study was to gain an understanding of the role of *P. crispus* in the functioning of the Pongolo River floodplain ecosystem. The preceeding chapters have described the floodplain environment and the biology of *P. crispus* at the population and community levels. It now remains (Chapters 8 and 9) to integrate this information with other ecosystem characteristics and processes and to develop an understanding of the role of *P. crispus* in the functioning of the floodplain pans.

The purpose of this Chapter (8) is to describe the role of *P. crispus* in the conservative transfers of organic matter, nitrogen and phosphorus in Tete pan and to develop a framework on which to base a discussion (Chapter 9) of the adaptations which regulate functioning of the pans as aquatic ecosystems. The conceptual modelling approach adopted depicts ecosystem components and transfers semi-quantitatively and assists in identifying future research requirements.

8.1. ORGANIC MATTER POOLS AND TROPHIC PATHWAYS

The trophic pathways in Tete pan are illustrated (Figure 8.1) as transfers which occur between the major pools of organic matter (ash free dry mass) on an annual basis. Only transfers of organic matter are shown and not respiratory losses of CO_2 which would occur at all trophic levels but were not measured. The conventional symbol for a general storage compartment (a square box; Odum, 1971) is used to designate pools, and transfers are differentiated into those which could be quantified (solid lines) and those which are known only qualitatively (dotted lines).

Since the model deals with the pan or aquatic ecosystem and not the floodplain as a whole, inputs from the seasonally inundated vegetation are considered allochthonous and those generated by aquatic primary producers, autochthonous.

8.1.1 Autochthonous production

Potamogeton crispus production in winter and spring represents the largest autochthonous input of organic matter (OM) to Tete pan (Figure 8.1). The average annual net production over the study period was *c.* 130t of which 49% (63t) was shoot material, 3% (4t) roots and 48% (61t) turions and achenes. Transfer of this production to the grazing food chain is largely limited to waterfowl consumption of turions (10t or 7.8% P_n) and the remaining *c.* 95% senesces, dies and enters the detrital food web. There are 3 main pathways of transfer to the detritus pool:

1. The roots die and decay within the sediment. Since they are distributed between 1 and 20 cm deep (Everson, 1980) only a portion of the detritus will be available to trophic levels higher than decomposers. The contribution of roots to the detrital food web is thus considered small.

2. About 51t OM, as turions, remains in the surface sediments until the following year when, after germination and transfer of some mass to the developing plantlet (Section 4.2.3), they are conditioned by bacterial action and enter the detrital pool. The organic matter entering the detrital pool (30t) was calculated as the amount remaining in July each year after germination was complete. Since germination spans some months (Section 4.1.1) turions would be at different stages of decay in July; this figure (30t) is thus an underestimate but the best available.

3. The largest portion of production, 63t of shoot material, is conditioned by bacteria and converted to a fine detritus by snails (Section 7.2.1). The pool of snail biomass is small (0.7t) and since the assimilation of macrophyte tissues by such invertebrates is

low (< 10%; Calow, 1975; Smock and Harlow, 1983) and few generations of *B. natalensis* are produced each winter (Appleton, 1978) a small amount is transferred to the snails and most of the *P. crispus* shoot production enters the detrital pool on the sediment surface as faeces.

The other important autochthonous organic matter input to Tete pan is by epiphyton production (Rogers, 1981). The maximum standing crop of epiphyton is only 3t of organic matter but rapid turnover of these communities results in a much greater annual transfer. Rogers (1981) did not measure production but suggests that a turnover time of 15 days can be expected in a productive warm environment such as Tete pan. Using this figure and her data on change in OM standing crop, epiphyton annual production is estimated at 26t, most of which appears to be consumed by snail grazers (Section 6.2.1; Rogers, 1981). Other studies (Hunter, 1980; Kesler, 1981; Summer and McIntyre, 1982) have also shown that grazing invertebrates can remove most of the epiphyton production and since assimilation efficiency is low (*c.* 30%; Calow, 1975) a large proportion of this production also seems to enter the detritus pool on the sediment surface before being transferred to the detrital food web.

In general therefore, most autochthonous production in Tete pan enters the detritus pool on the sediment surface but not before it is processed by snails which represent only a small pool of organic matter with a low rate of assimilation. An important role of the snails therefore seems to be promoting the transfer of primary production to the detrital pool and the formation of a benthic detrital aggregate (BDA, Bowen, 1979a) on the sediment surface.

8.1.2 Allochthonous inputs

The *Cynodon dactylon* lawns which occur on the slopes draining directly into the pans (Figure 1.4) have potentially the largest allochthonous input to the aquatic phase (field observations; Breen, pers. comm.). Detritus from the *C. fastigiatus* / *E. pyramidalis* and *Phragmites*

communities appears to be largely trapped in the marshy depressions they inhabit, while the two higher lying communities (*F. sycomorus/R. caffra* and *A. xanthophloea/D. depressa* (Section 1.3.6)) are only flooded for short periods in very wet years and comprise plants which do not decay rapidly. Their contribution to detritus inputs to the pans is therefore considered small.

Approximately 130 ha of *C. dactylon* lawn drained into Tete pan during the study period. Furness (1981) showed that an aboveground standing crop of 644 kg ha^{-1} dry mass (Furness, 1981; pg. 97) or 570 kg ha^{-1} ash free dry mass, can be expected just before the summer floods and that 50% of this might be lost through decay during a 28 day flood. Thus, in Tete pan *C. dactylon* would contribute about 43t to the aquatic phase in this time. If inundated for 120 days the contribution would be 61t.

These figures are somewhat in contrast with Furness' (pg. 104) suggestion that *C. dactylon* contributes up to 10 times (per unit area) as much to the aquatic phase of the floodplain as *P. crispus*. Reasons for this contrast are:

1. He considered *P. crispus* net production to be equal to maximum standing crop and used the low figures of 1976 only.

2. Underground biomass of *C. dactylon* was included in his calculation but this is unlikely to reach the aquatic phase as it is buried in compact soils.

In addition it is important to realise that the significance of these two species to trophic relations in any pan will depend upon the area occupied by each and comparison on a unit area basis only may be misleading. It is clear, however, that both autochthonous and allochthonous sources provide large organic matter inputs to the detrital pool of the aquatic phase. The pathways by which allochthonous material is transferred have not, however, been assessed.

8.1.3 Other higher trophic levels

There are two pathways of organic matter transfer from the detritus pool; along the detrital food web or to permanent burial in the sediments. The latter, however, seems very small as decomposition of primary production is rapid (Section 7.1.2; Furness, 1981) and the organic matter content of the sediments is low (< 1.5%; Everson, 1980). Thus, as in most aquatic ecosystems (Odum and de la Cruz, 1963; Rich and Wetzel, 1980; Mann, 1980) the major pathway of energy flow in Tete pan is through the detrital food web.

A number of steps in this food web have been demonstrated qualitatively but few quantitatively (Kok, 1980; Walley, 1980; Heeg and Breen, 1982) so for the purposes of this study, the contributing organisms have been broadly grouped as either birds, benthic invertebrates or fish. The detrital food web is considered, in the model (Figure 8.1) to begin with the organic matter which collects in the detritus pool on the sediment surface. The snails are not included as their role appears to be in the preparation of the organic matter for transfer into the diverse detrital food web rather than consumption of detritus. Furthermore, very little of the organic matter consumed by the snails is transferred directly to other trophic levels since the only organism to predate upon them to any extent is the Hottentot Teal (Section 5.1.1). The few Teal which inhabit the floodplain do not seem to generate an important transfer of organic matter.

Standing crop data for duck and snails were obtained from this study but that for "other birds" and fish from Walley (1980) and Heeg and Breen (1982) and Kok (1980) respectively. Conversions from dry mass to ash-free dry mass were carried out using average values for these organisms supplied by Jorgenson (1979).

The most important point which can be gained from the limited knowledge of conservative transfers in the detrital food web, is that most organic matter is cycled within the pan ecosystem and little is exported beyond its boundaries (Figure 8.1).

Transfers of organic matter through the food web can result in losses from the ecosystem via consumer emigration and human exploitation. Emigration losses from wetlands are seldom large (Prentki *et al.*, 1978), particularly if the animals feed and roost within the ecosystem and there is no large emigration of juveniles each year. Since these criteria fit most consumers of the floodplain pans the net export of organic matter from Tete pan by consumer migration can be considered low. One exception to this rule may be the White Pelican (*Pelicanus onocrotalus* L. which transports fish to juveniles at lake St. Lucia to the south. Whitfield (pers. comm.) estimates that about 1t of organic matter may be exported from Tete pan by this means. The major loss therefore occurs through human exploitation of fish stocks which amount to *c.* 3t if 170 kg fresh mass ha^{-1} p.a. (or 400t from the floodplain) are harvested as suggested by Heeg and Breen (1982).

8.2 NUTRIENT TRANSFERS

The models of nutrient (N and P) transfers (Figures 8.2 and 8.3) were quantified in the same manner as the organic matter model and thus describe the amounts of nutrients moved from one pool to another over an annual cycle. Concentrations of nitrogen and phosphorus in fish and waterfowl tissues were not determined during this study and average values for these organisms were taken from Jorgenson (1979). The data for epiphyton nutrient relations were obtained from Rogers (1981).

In Chapter 4 it was suggested that when floods entered Tete pan after *P. crispus* standing crop had decayed there was a small net gain of nutrients (N and P) by the ecosystem during the period in which it was separated from the river. However, the floodplain as a whole is an open system with a through-flow of water and if floods are early it is also possible that nutrients released during decomposition could be flushed from the pan. Clearly if the productivity of the floodplain pans is to be maintained,exports of nutrients must at least be balanced by imports. An important objective of these models was therefore to attempt a nutrient budget of Tete pan and to use gaps in the budget to propose future research directions.

8.2.1 A preliminary nutrient budget for Tete pan

The main sources of nutrients for wetland ecosystems are atmospheric fall-out (wet and dry), inflowing water and nitrogen fixation. Birds and hippopotomuses which feed away from the wetland but return to its refuge after feeding may be important sources in some systems (Moss, 1980; Prentki *et al.*, 1978) but neither occur in Tete pan.

The contributions of wet and dry fall-out to the N and P budget of Tete pan have not been measured but in a rural area, far removed from industry, they are likely to be small in relation to other inputs ($<5\%$; Prentki *et al.*, 1978; Mitsch *et al.*, 1979).

Inflow of water to Tete pan during summer floods can contribute nutrients in three main ways; in the water retained in the pan when the flood subsides in autumn (76 kg P, Figure 8.2; 75 kg N as $NO_3^=$, Figure 8.3); by promoting decay of *C. dactylon* (114 kg P and 1050 kg N) and by deposition of silt to which nutrients are adsorbed. To date no estimate of silt load to the floodplain has been made, but studies of other floodplains (Welcomme, 1979; Mitsch *et al.*, 1979) indicate that this could be the major source of phosphorus to the pans. The generally higher concentrations of total P in the water of Tete pan during turbid summer floods (Section 3.1.2) would support the view that silt adsorbed P is an important input to the pan.

The largest source of nitrogen, on the other hand, appears to be N_2 fixation which has been observed to occur in the epiphyton (1140 kg; Rogers, 1981) and also in the detritus arising from snail processing of conditioned *P. crispus* (calculated from Section 7.2.1 to be *c.* 1300 kg p.a.).

In general therefore, phosphorus loading to Tete pan may be largely dependent on flooding but flood related nitrogen loads are strongly augmented by N_2 fixation which is associated with the growth and decay of *P. crispus*.

Loss of available N and P from wetlands occurs principally through permanent burial in the sediments, consumer emigration/exploitation, outflow and denitrification (Prentki *et al.*, 1978).

Permanent burial of N and P in the sediments of Tete pan has not been measured but is likely to be small in relation to incoming loads and internal transfers (Prentki *et al.*, 1978); especially as organic matter burial is small (Section 8.1) and growth of plants such as *P. crispus* tend to result in a net upward movement of nutrients from the sediment (see below; Prentki *et al.*, 1978). Exports via consumer emigration are also likely to be small (Section 8.1). The largest potential loss is from emigration of waterfowl (20 kg P and 400 kg N) each summer but as about the same quantities will be returned when birds arrive the next winter any net loss will be small. Export via pelican and human exploitation of fish stocks, however, may be as high as 66 kg P and 530 kg N per annum.

Export of N and P from Tete pan by outflow is also important but will depend, at least in part, on the timing of floods in relation to *P. crispus*' cycle of growth and decay. If floods occur in summer after *P. crispus* standing crop has declined and ecosystem processes have transferred the nutrients released during decomposition to other storage compartments, the average export will be only the 20 kg P and 11 kg N which remain in the water phase. However, if floods are earlier a larger stock of nutrients may be flushed downstream. For example when floods arrived in October 1978, some 44 kg P and 400 kg N remained in the standing crop. Decomposition studies (Section 7.2.1) showed that about 30% of the P and 10% of the N may be transferred to the water phase as dissolved N and P and so could be flushed from the system. These losses (*c.* 13 kg P and 40 kg N) were, however, less than the average gain from the water phase (76 kg P and 75 kg N as $NO_3^=$, see above) and so would not have markedly affected the size of the N and P pools in Tete pan. If, on the other hand floods were to arrive in early spring when *P. crispus* was at maximum standing crop, then total export, including the nutrients in the water, could increase to 146 kg P and 330 kg N.

While these losses of N, even when combined with fishing export (330 + 530 = total 860 kg p.a.), are small in comparison to total N inputs (3565 kg p.a.), an early flood,in conjunction with fishing,increases the total quantified P export to 212 kg. This is 22 kg higher than the annual import from water retention and *C. dactylon* decay (190 kg), but if floods occur after *P. crispus* decline P export will be much less at 86 kg p.a.. This serves to illustrate that the timing of floods may have important consequences for nutrient, especially P, loss but whether or not it will result in overall net import or export in the pan ecosystem may depend upon the difference between inputs of silt adsorbed P and losses which may occur during floods; neither of which have been measured to date. Of particular importance in the latter context is the release of P which may occur if there is a marked change in the chemical equilibrium at the sediment water interface during floods. As redox potentials decline nutrients tend to become more soluble (Wetzel, 1975) and may enter the water phase. This can particularly affect the phosphorus equilibrium since P release from the sediments to the water can occur even without complete annoxia (Stevenson and Gibson, 1976). In Tete pan reduced O_2 tensions above the sediment during floods (Section 3.1.4) may result in a release and subsequent flushing of P downstream. Thus, even when floods occur in summer, outflow exports could be much greater than concentrations in the water indicate.

The very large difference between the measured imports (3565 kg) and exports (860 kg) of N from the system, suggests, in the absence of evidence for permanent burial, that nitrification and denitrification are important processes in the N cycle of Tete pan; but neither have been measured to date. The seasonal change between highly oxidised conditions which develop in winter and spring as a result of *P. crispus* production and more reduced conditions in summer would favour these biochemical processes and so stimulate a dynamic N cycle.

Future studies aimed at deriving the nutrient budgets of floodplain pans, and indeed the floodplain ecosystem as a whole, should therefore concentrate on the nitrification/denitrification cycle with flood related additions and losses of P. In the past,floods were probably

the major factors affecting import and export of P in the pans but now the Pongolapoort dam will retain much of the silt and so markedly reduce imports. Researchers and managers should therefore ask what mechanisms exist to conserve nutrients and how can these be maintained? Clearly controlled flood releases from the dam in relation to the cycle of growth and decay of *P. crispus* could offer one management option but a greater understanding of internal transfers of nutrients is required if the P budget is to be balanced in future.

8.2.2 Internal nutrient transfers

The preceeding "black-box" nutrient budget for Tete pan ignored the internal ecosystem processes which, according to ecosystem theory (Section 1.2.8; Mann, 1980; Welch, 1980; Patten and Odum, 1981) should provide a buffer against change in external factors. Since change in nutrient, especially P, loads to the system will result from the Pongolapoort dam, it is important to determine the most important components of internal nutrient transfers (this section) and assess their significance for whole ecosystem functioning (Chapter 9).

The major source of nitrogen and phosphorus for *P. crispus* appears to be the sediment (Section 4.2.2; Everson, 1980) but that for the epiphyton may be from either or both the water and host plant (Figures 8.2 and 8.3). However, since the maximum combined size of the *P. crispus* and epiphyton N and P pools is much larger (11 and 3 times respectively) than the amount in the water at MRL, the sediment pool must represent the origin of most N and P taken up by autochthonous organic matter producers other than N_2 fixing cyanobacteria.

As can be expected (Welch, 1980) transfers of N and P taken up by primary producers in Tete pan largely follow the same pathways as organic matter. Thus, while small proportions are transferred to the deeper sediments by root decay (10 - 15%) and to waterfowl grazers ($<5\%$), the largest proportion ($>80\%$) is transferred through the small snail pool to the BDA on the sediment surface. *In vitro* studies of *P. crispus* decomposition

(Section 7.2.1) showed that, at least in the short term, about 30% of this P and 10% of the N accumulated in the water while the rest (70% and 90% respectively) remained in the detritus which settles to the sediment. The sediments, especially the surface detrital aggregate therefore seem to play a central role in nutrient transfers. An important observation in this context is that, if it is assumed that snail processing of *P. crispus* detritus promotes N_2 fixation in the field as it apparently did do *in vitro* (Section 7.2.1), then it can be calculated that N inputs to the detrital aggregate outweigh P inputs by about 18 : 1. Thus, the two large inputs of nitrogen to the system by N_2-fixation appear to generate internal transfers of N which are more than twice the average required per unit of phosphorus for primary production (Section 7.1; Wetzel, 1975). The possible significance of this for ecosystem functioning is discussed in Section 9.2.3.

8.3 PERIODICITY OF ORGANIC MATTER AND NUTRIENT TRANSFERS

The preceeding sections have outlined the magnitude and pathways of major pools and transfers of organic matter and nutrients in Tete pan but an important aspect of the functioning of this network lies in the timing or periodicity of these transfers over an annual cycle. Since most of the organic matter and nutrients transferred in Tete pan pass through the detrital pool on the sediment surface, changes in organic carbon, total nitrogen and available phosphorus concentrations of the surface sediments (Everson, 1980) should give an indication of the periodicity of major transfers in the system.

Particulate detritus of aquatic macrophyte origin is mostly derived from the refractile, structural tissues and has a high C:N ratio and poor nutritive value (Wetzel, 1983). However, in the littoral zone of lakes algae, bacteria and fungi colonise the detritus and a complex, nutritious "benthic detrital aggregate" (BDA) develops (Bowen, 1978; 1979a,b,c) on the sediment surface. The growth and nutrient uptake of these

organisms decreases the C:N ratio and increases the nutritive value and thus seasonal change in the size and nutritional quality of the BDA pool is a major factor governing secondary production in shallow lakes (Bowen, 1979a,b,c). Although no studies have been conducted specifically on BDA in the floodplain pans, Eversons' (1980) study of sediment characteristics of Tete pan did include the top 1 cm which corresponds to the BDA.

Epiphyton production provides the major input of detritus to Tete pan during winter (Figure 8.4) but as spring progresses this is augmented by the decay of *P. crispus* which continues until early summer. Thereafter flooding inundates the *C. dactylon* community and further inputs of detritus to the pan sediments can be expected (Furness, 1981; Heeg and Breen, 1982). Epiphyton and *P. crispus* inputs to the pan are evident as marked increases in organic carbon and N concentrations in the BDA on the sediment surface (Figure 8.4) but during summer when *C. dactylon* decayed both concentrations declined steadily and did not reflect this input. Low inputs of N might be expected from allochthonous refractory detritus but the concomitant decline in OC concentration indicates that floods do not provide pulses of detritus to the sediment surface of the pan itself, but rather that *C. dactylon* decays *in situ* on the flooded margins. Thus, it seems the major ecosystem processes of the aquatic phase of the Pongolo floodplain ecosystem are separated temporally and also spatially such that they occur in the permanently flooded pan area during winter and spring (between floods) and on the seasonally flooded margins in summer (during floods).

Everson's (1980) data also show marked increases in OC and N in the BDA during autumn (Figure 8.4) which are not explained by studies on the Pongolo floodplain to date but are probably due to two main factors:

1. With the subsidence of pan water level to MRL at the end of summer, wind and wave action may disturb some of the now fine *C. dactylon* detritus in the shallows and re-distribute it to the pan sediments.

2. Increasing light penetration during autumn permits the growth of benthic algae and mats of heterocystous cyanobacteria were observed on the sediment surface in 1977,'78 and '79 (field obsv.).

Both the detritus and algal production would increase the OC content of the BDA but it is suggested that the marked increase in N concentration, which was not accompanied by a similar increase in P (Figure 8.4) was due to N-fixation by the cyanobacteria. Phosphorus concentrations decreased during the autumn to spring period, when demand by *P. crispus* and indirectly the epiphyton,was high and then increased during the period of *P. crispus* decay and detritus formation. Most importantly though P concentration increased markedly during the summer floods supporting the view that silt adsorbed P is an important import to the pan (Section 8.2.1).

Seasonal changes in the BDA thus indicate that four different communities, the benthic algae/cyanobacteria, epiphyton on *P. crispus*, *P. crispus* itself and *C. dactylon* , provide a series of organic matter and N inputs to the aquatic phase over an annual cycle. They therefore provide a continuous energy source for the detrital food web although the BDA pool shifts in importance from mid-pan to the seasonally flooded margins with the onset of floods. Furthermore, it appears that at least three separate events of N_2 fixation, spread over the annual cycle, act to maintain a low C:N ratio in the detritus pool and that silt carried by floods replenishes the P pool during summer.

The continued functioning of the detrital based food web and the small grazing food chain in Tete pan is dependent on a sequence of resource transfers which are dominated, during the periods between floods, by *P. crispus* and its epiphyton. It is important, from a management point of view, to assess the mechanisms, or adaptations, which maintain these conservative transfers and regulate their periodicity in an environment subject to annual flooding. This is discussed in Chapter 9.

CHAPTER 9

GENERAL DISCUSSION

9.1 INTRODUCTION

The preceding chapter demonstrates the extent of our knowledge of the conservative network of the aquatic phase of the Pongolo floodplain ecosystem, its links with the seasonally inundated component and the role of *P. crispus* in energy-matter transfers. A great deal of information, some of it very basic (eg. flood related inputs and outputs), is still required before a detailed understanding can be achieved but it is nevertheless important to now take stock of the situation and assess the usefulness of these data in predicting ecosystem response to change. The need for this assessment arises from construction of the Pongolapoort dam.

Many authors consider that one of the most important properties of an ecosystem is its ability to buffer changes in inputs or outputs of resources (see Odum, 1969; Jordan, 1981; Patten and Odum, 1981). Patten and Odum (1981) suggest that this ability is due to the cybernetic nature of ecosystem functioning which in turn lies in the way an information network directs and rate controls the ecosystem conservative transfers (Section 1.2.8). This final chapter is therefore concerned mostly with aspects of the information network and evidence of cybernetic properties in the functioning of the Pongolo floodplain ecosystem.

Cybernetic systems are a special class of cause-and-effect systems in which feedback of a portion of the potential output controls, at least in part, input (Figure 9.1). For feedback to operate the system requires an information network which connects all parts of the system into an integrated whole. Such networks regulate the system and are characterised by mapping (transcription of information from one physical entity to another) and amplification,in which low energy causes give

rise to high energy effects (Patten and Odum, 1981). Engelberg and Boyarsky (1979) have asserted that ecosystems are not cybernetic,but if one looks for properties in ecosystems which are analogous to engineered systems there is abundant evidence of cybernetic features (Patten and Odum, 1981). Ecosystems, however, tend to be "determinate" (Figure 9.1) rather than teleological because their "behaviour" is governed only by past causes rather than desired goals. Nevertheless "feedback structure may passively or emergently make - - - behaviour stable, regular, or otherwise predictable", and enable a system "to damp disturbance" or change (Patten and Odum, 1981).

Underlying the concept of a cybernetic ecosystem is that of the ecosystem as an evolutionary unit (Section 1.2.8), in which the sum of the interactions which maintains orderly function, represents an adaptation (Odum, 1969; Chew, 1974) to existence under a certain set of environmental constraints. Thus, it follows that the Pongolo floodplain ecosystem would be adapted to its specific flooding regime, as is *P. crispus*, but at the ecosystem level of organisation, adaptation must lie in the manner in which the conservative and information networks interact (Patten and Odum, 1981).

Unfortunately there has been no detailed theoretical treatment of wetland ecosystem functioning about which this discussion can be structured but some concepts outlined by Brinson *et al.* (1981) should be considered. They proposed that although the hydroperiod may be the major determinant of wetland ecosystem structure and function, other forcing functions, such as animal-animal and animal-plant interactions, markedly influence specific processes. As a result relationships between ecosystem properties and a single environmental variable, such as the hydrological regime, are difficult to find. Brinson *et al.*(1981) also recognise that open (exorheic) wetland ecosystems differ in the amount of flushing they experience and so differ in their patterns of storage, export and import of resources. But "like any organised ecosystem wetlands contain many complex pathways of energy flow" of different magnitudes and "feedback mechanisms" maintain their orderly functioning. Their concepts are therefore consistent with that of the cybernetic nature of ecosystems but lack the detail to confirm it.

In this chapter the pattern of storage, input and export of resources in the Pongolo floodplain pans is considered as an adaptation to the seasonal flooding regime. Particular attention is paid to the role of animal/plant (*P. crispus*) interactions in regulating this adaptation and to evidence of cybernetic properties which would imply an ecosystem capacity to buffer change. Finally the usefulness of this study in assessing future research and management policies is considered. Due to the complexity of the subject matter, the discussion takes the form of answers to questions which have arisen from the outline (Chapter 8) of the conservative structure of the ecosystem:

1. The role of animal/plant interactions.

Do animals have a small influence on system metabolism as held by Wetzel (1979; Section 1.2) for aquatic ecosystems in general or do they have a managerial influence on ecosystem processes Brinson *et al.* (1981)?

2. Grazing versus detrital food webs.

Why is so little *P. crispus* production transferred to the grazing foodchain and what is the significance of this for ecosystem adaptation and functioning?

3. Nutrient cycling in an open system.

What is the significance of the large, periodic N_2- fixation inputs from different sources and the high N:P ratio of inputs to the BDA, for ecosystem functioning?

4. Ecosystem adaptation to seasonal flooding.

Does the network of interactions which lead to the capture, transformation and transferral of resources by *P. crispus* have adaptive significance for ecosystem functioning and do the regulatory mechanisms indicate a potential to buffer change?

5. Management.

How can this information assist in future management and research policies?

9.2 ECOSYSTEM ADAPTATION AND FUNCTIONING

9.2.1 The role of animal/plant interactions

Wetzel's (1979) hypothesis that animals have a small influence on system metabolism is based on the assumption that they assimilate little of the organic matter synthesised by primary producers. As such, however, the hypothesis considers only the conservative transfers of energy - matter and not the information network of the ecosystem which regulates these transfers (Section 1.8). Brinson *et al.* (1981), however, suggest that animals act as "ecosystem managers" and may be very important in maintaining primary production, successional stages and ecosystem homeostasis. Their use of the term "ecosystem managers" implies a regulatory role and that they consider the effects of animals to be manifest through the information, rather than conservative, network. Reconciliation of the two hypotheses therefore seems to lie in adopting a more holistic ecosystem view of animal-plant interactions. This study has shown that two groups of animals, waterfowl and snails, affect the growth, reproduction and decay of *P. crispus* populations in Tete pan (Figure 9.2) but they are both small components of the conservative ecosystem network (Section 8.1). The question here is do they have a managerial role in the functioning of the pans of the floodplain ecosystem?

Waterfowl consume only a small proportion of *P. crispus* turion production in Tete pan and although this may stimulate further turion production to compensate for losses, it does not necessarily constitute a managerial influence on *P. crispus* populations. The same may not, however, apply in the shallower pans where upending waterfowl can dig in the sediments and remove parent turions, before the plants arising from them have reproduced. Some pans,such as Mgodo and Namanini,are shallow but because they are immediately adjacent to the river there is a high water table and they retain water all year round. Only occasional *P. crispus* plants are found in these pans, despite the fact that during periods of high water they are continuous with the deeper Bumbe pan which is extensively colonized.

Studies during the 1979 drought showed that low water levels alone did not reduce *P. crispus* growth or prevent reproduction (Section 4.1.4) in Tete pan; thus a hypothesis is that when the water level regularly drops to the up-ending depth of waterfowl (*c.* 30 cm) before the plants reproduce, grazing of parent turions induces an unstable grazing system (Noy-Meier, 1975) and the species fails to establish. Support for this hypothesis could be sought by transferring *P. crispus* turions to Namanini and planting them, at the same density per unit area, both within the protection of exclosures and in the pan where they are exposed to grazing. Since such an experiment would be contrasting the effects of hydrology (the rate of depth reduction) and animal influences, it would also provide information applicable to the hypothesis of Brinson *et al.*, (1983) that although hydrological regime is the primary determinant of wetland ecosystem functioning, other forces such as animals have a managerial influence on primary production and plant succession.

Other managerial influences of waterfowl lie in the indirect effects of their feeding activities in pans such as Tete. Waterfowl only consume a small proportion of *P. crispus* production (Section 8.1.1) but their impact on ecosystem processes lies in the fact that while feeding they uproot most, if not all (Section 5.2.1), mature plants. This increases the rates of necrotrophic attack and senescence (Section 7.2.2) which lead to the process of detritus formation (Figure 9.2). Although no quantitative data are available, observations in the field showed that a lack of grazing in exclosures led to a delay (by several weeks) in senescence and death of plants. Thus, although the conservative transfers are small, the physical activities of the birds appear to initiate the transfer of organic matter and nutrients to the dominant detrital pathway earlier than would natural senescence.

Waterfowl feeding activities can also be viewed as being indirectly responsible for a change in the managerial influence of snails (Figure 9.2). Before plants are uprooted feeding snails have a dual role of transforming epiphyton biomass into detritus (Rogers, 1981; Section 8.1.1) and controlling, at least partially, the rate of

necrotrophic attack on *P. crispus* (Section 6.2.2). Once the plants are uprooted by waterfowl, however, necrotrophic attack begins to exceed grazing and the plants are rapidly conditioned. It is difficult to assess the full mechanism leading to this imbalance in necrotroph attack and snail grazing, but two factors seem to be important either singly or, more likely, in combination. Firstly, detachment of the mature plants from their roots may lead to senescence with the concomitant increased release of DOM and nutrients, thus stimulating greater necrotroph growth. However, detachment from the roots cannot provide the full explanation since laboratory experiments (Section 6.2.1) showed that when grazing removed necrotrophs, detached leaves remained alive and healthy for more than 20 days. The second suggested mechanism, which is consistent with field observations, is that the vigorous feeding activities of the waterfowl dislodges snails from the plants and that in the time taken for recolonization, necrotroph attack begins to condition the plants. Under this hypothesis waterfowl activities interupt the managerial role of snails in controlling necrotroph attack and this indirectly feeds back to the recolonising snails by diverting their feeding activities to the host plant. Snail consumption thereafter regulates the pathways and rates of organic matter and nutrient transfer to the BDA and detrital food web (Section 8.1.1).

The managerial role of snails is complex but the main point is that animal-animal and animal-plant interactions have important regulatory effects on ecosystem processes which are divorced from any influence of the hydrological regime and thus these studies support the hypothesis of Brinson *et al.* (1981). Furthermore since the effects are large and arise out of small conservative transfers they may each constitute an amplification. Patten and Odum (1981) consider that indirect effects which arise from, or accompany, direct energy-matter transfers but are markedly more significant than the direct transfers, can be classed as "amplification". As such these interactions act in an informational sense to provide feedbacks. They have developed through evolutionary time to stabilize ecosystems and prevent catastrophic events such as "boom and bust herbivory" and large scale predator-prey oscillations (Patten and Odum, 1981).

Amplification effects are well known in the strict information network of cybernetic ecosystems (eg. the sight of a predator illicits a large energy response when prey run away) but some studies do recognise that they can arise as side effects of conservative transfers (Chew, 1974; O'Neill, 1976; Patten and Odum, 1981) as in Tete pan. The managerial influence of animals on primary production, succession and ecosystem homeostasis proposed by Brinson *et al.* (1981) therefore seems to operate, at least in part, through amplification, where the indirect effects of small conservative transfers act to trigger a response or regulate a rate, in an informational manner. Wetzel's (1979) proposal that animals have little effect on system metabolism does not seem to hold in an ecosystem context because it ignores information feedback and amplification.

9.2.2 Grazing versus detrital food webs

The details of transfers in the grazing and detrital food webs and the intricate sets of interactions which control these transfers are discussed elsewhere. Here attention is focussed on the significance of the proportional distribution of macrophyte production to the two food webs. That is, what significance has the small transfer to the grazing food web for functioning in an open floodplain ecosystem?

Many authors have pondered the question of why grazers do not eat aquatic macrophytes but only two (Hutchinson, 1975; Mann, 1980) have really attempted to formulate hypotheses. Hutchinson (1975) held the view that, since sodium content is favourably high in comparison to most terrestrial species and there is a general lack of secondary metabolites which might deter grazers, the answer did not lie in characteristics of the plant but in the covering of epiphyton which distracts invertebrate grazers. There are two problems with his view: Firstly, this study indicates that the structural nature of the plant rather than the epiphyton presence, prevents grazing of healthy *P. crispus* tissues by invertebrates and secondly, macro-grazers such as waterfowl, fish and larger animals would not be deterred by a layer of epiphyton if the plants provided an usable energy source.

Mann (1980) provides a more plausible explanation in his questioning of the distinction between grazing and detrital food chains. He points out that where grazing is heavy in terrestrial systems the dominant herbivores usually harbour a culture of microorganisms to assist digestion by converting structural plant tissues into readily assimilable carbohydrates. The process of "conditioning" of plant tissues in aquatic environments represents a similar process in that it makes indigestible plant tissues available to consumers but, since water is not limiting to bacterial metabolism in aquatic ecosystems, the process can take place in the external environment. Mann (1980) therefore implies that it is the nature of the plant material that regulates transfer to consumers in both environments and that certain adaptations have evolved to improve the transfer.

To assess the implications of this for ecosystem functioning the analogy can be taken further. In ruminants, the process represents an adaptation which increases the efficiency (Phillipson, 1966) of energy utilization by reducing the percentage of the energy intake which is not assimilated and thus exported from the organism. A hypothesis is that because plant material must be conditioned before it is transferred to consumers the process has the same overall result of reducing export from aquatic ecosystems as it does in ruminants. Because conditioning can take place more efficiently in the aquatic environment, selective forces may not have favoured the evolution of complex gut flora in aquatic organisms to the same extent as in terrestrial ones. Aquatic grazers of living tissues therefore only utilize readily assimilable organic matter such as the large energy reserves of reproductive organs. On the Pongolo floodplain certain waterfowl species only, appear to be adapted to using this type of food source efficiently and the export of organic matter through their feeding is small. The remaining *P. crispus* production requires conditioning before transfer to autochthonous consumers and only a small portion is exported from the system. Thus, other resources such as phosphorus which are associated with this organic matter are conserved within the system and transferred to storage compartments.

The evolution of a conservative network with small transfers of resources to allochthonous grazers and large transfers to an autochthonous detrital basal food web is a characteristic of aquatic ecosystems. Thus, although such a network provides a basis for reducing exports of resources from the Pongolo floodplain ecosystem it cannot be considered an adaptation* to the specific flooding regime. The question does arise, however, as to whether the specific characteristics of the floodplain conservative network and factors regulating it (information network) represent adaptations* to reduce the potential for flushing of resources from the system? This hypothesis* can be developed further by discussions of aspects of the nitrogen and phosphorus cycles in the Pongolo floodplain ecosystem (Section 9.2.3) and ecosystem adaptation (Section 9.2.4).

9.2.3 Nutrient cycling in an open system

Studies of Tete pan have shown that N_2- fixation may occur on at least three occasions over an annual cycle and that since a small amount of this nitrogen seems to be flushed from the pan during floods, the major exports of N appear to be through nitrification/denitrification (Section 8.2.1). In general the Pongolo floodplain ecosystem is characterised by a dynamic nitrogen cycle with transfers which are proportionally large in comparison to those of phosphorus.

At a population level the ability to fix N_2 clearly gives some organisms a competitive advantage over others when sources of available N are low (Welch, 1980) but why do inputs of N apparently exceed

* It is important to realise that "given a sufficiently inventive mind it is always possible to imagine what the selective advantage" of a particular phenomenon might be and that correlations should not be automatically taken as cause-effect relationships (Calow and Townsend, 1981). This sort of *a posteriori* approach can, however, be justified (Clutton-Brock and Harvey, 1979) if used to give order to observations from which one can generate research to accumulate or reduce support for the hypothesis.

the requirements of primary producers which are the main resource gatherers of the ecosystem? Is it that nitrification/denitrification is so rapid that recurring conditions of low N supply trigger frequent events of N_2-fixation? The nitrogen cycle in Tete pan is so poorly understood that this question could rapidly become circular as nitrification/denitrification could equally be triggered, or the rate increased, by improved N supply following N_2- fixation. However, if the question were considered in an ecosystem, rather than population, context, it could be rephrased to become "What is the significance of a dynamic N cycle to ecosystem functioning?"

One view of such a cycle may be that it increases the use of other resources in the ecosystem which may be potentially more limiting to organic matter production than is N which has a large atmospheric store . This in turn implies that an increased N supply permits the transfer of other resources,such as phosphorus,to storage compartments (detritus, sediments, living organisms; Sloey *et al.*, 1978) which are less subject to loss by flushing than the dissolved phase in the water. The development of a highly dynamic N cycle in ecosystems subject to flushing may thus have the indirect effect of buffering losses of other resources from the system.

Such a hypothesis of important side effects of a dynamic nitrogen cycle is consistent with the general theory of biochemical cycling in ecosystems and with cybernetic theory (Hutchinson, 1948; Patten *et al.*, 1976; Patten and Odum, 1981). Cycles of matter (not energy) in the conservative network are closed, and also "global" in the sense that they encompass the entire ecosystem. This permits conservative biochemical cycles, such as that of N, to act in an informational sense. For example, when changes in the availability of resources trigger events such as microbial blooms and new cycles of plant growth (Patten and Odum, 1981). The proposed transfer of phosphorus to storage compartments may therefore be only one of many side loops to co-evolve with a dynamic N cycle.

The important points in the context of this thesis, however, are; (1)

further indication of cybernetic features in the functioning of the Pongolo floodplain pan ecosystems and (2) a hypothesis that these are manifest in an ecosystem adaptation to conserve phosphorus under a flooding regime which would promote flushing. Such a hypothesis is probably impossible to test but a careful study of the spatial and temporal changes in N_2-fixation, nitrification and denitrification, while following similar changes in the amounts of P in various storage compartments, would provide useful evidence on the ability of the ecosystem to buffer the potential for flushing of resources.

9.2.4 Ecosystem adaptation to seasonal flooding

The question being asked here is: Does the network of interactions which lead to the capture, transformation and transferral of resources by *P. crispus* have adaptive significance for ecosystem functioning and do the regulatory mechanisms indicate a potential to buffer change? This section serves then to draw together the concepts and hypotheses of the preceding sections and to summarise and conclude the chapter.

Adaptation of a plant to a particular environment is viewed as its ability to reproduce in that environment (Solbrig, 1981). Similarly, in ecosystems the presence of an information network which regulates processes and so promotes continued existence, implies adaptation to a set of environmental constraints. Without such a network nature would be "chaotic, disorderly and unbalanced" but its presence imparts a cybernetic nature, at least to components of the system, if not to the system itself (Engelberg and Boyarsky, 1979; Patten and Odum, 1981). Thus, ecosystem adaptation can be recognised by identifying a set, or sets, of regulatory mechanisms which promote orderly transfer of energy-matter in such a way that it maximises, or at least promotes, the continual functioning of the ecosystem. Recognition of this adaptation leads to improved understanding of the ecosystem as a functional unit and to its ability to buffer the effects of change in input. This understanding in turn leads to

better management(Welch, 1980).

My thesis is that the floodplain ecosystem is adapted, as is *P. crispus*, to the seasonal flooding regime of the Pongolo river in a manner which permits it to capitalise on periods favourable to resource acquisition by primary producers. The principal need for adaptation arises from the effects that floods have on water depth, light penetration and the flushing of nutrients. The adaptation is manifest in the distinct separation of ecosystem processes into those which occur between floods and those which occur during floods, and in the complex set of feedback mechanisms, amplification and resource mapping which regulate this separation. Thus, although the hydrological regime (hydroperiod of Brinson *et al.*, 1981) is the major forcing function of ecosystem structure and function, the adaptation to it is regulated by a large number of other ecosystem components and processes which act in an informational sense. It is proposed that a consequence of this adaptation is that constituent cybernetic processes have led to the ability to dampen the effects of changes in input to the ecosystem.

This study has dealt with between flood processes, in particular the role of *P. crispus* in the capture, transformation and transfer of resources in the floodplain pans (Chapters 4 - 8). Figure 9.2 summarises these processes and the manner in which other biotic and abiotic ecosystem components initiate, direct and rate control them to form an adapted whole.

Growth of *P. crispus* is stimulated by a decrease in temperature but the differential response of turions to temperature staggers germination over a 3 month period and permits the population to capitalise on the entire period favourable for growth and reproduction. During this period *P. crispus'* physical presence and metabolic activities provide a suitable environment for a productive epiphyton. This makes substantial contributions to the acquisition and transfer of resources but at the same time has the potential to compete with the host for light and provides a micro-environment which favours the growth of necrotrophic organisms. Grazing of epiphyton by snails,

however, reduces this potential and so maintains high rates of production and nutrient cycling in the ecosystem. Once plants have begun to reproduce, interactions between waterfowl and snails regulate and direct the pathways and rates of transfer of resources acquired and transformed by *P. crispus*, to other ecosystem components in such a manner that it is largely completed before early summer when floods can be regularly expected. This network of interactions which regulates ecosystem processes between floods has clear cybernetic characteristics (Sections 9.2.1 - 9.2.3) and the effect of reducing exports of resources, particularly phosphorus, from the pans. The hypothesis is that this buffers the potential flushing effect of summer floods.

How important this buffering was under a natural flooding regime in which large imports of silt adsorbed phosphorus maintained productivity is uncertain but it could reduce the effects of a decreased P load now that a dam has been constructed upstream. In other words if management recognises that between flood processes can conserve resources, and permits the regulatory factors to operate effectively, a natural buffer to change in resource inputs will exist. Management of the Pongolo floodplain should therefore not only consider the seasonality of the hydrological regime but also the regulatory or informational processes which ensure completion of resource transfers before floods arrive.

9.3 CONSIDERATIONS FOR MANAGEMENT OF THE PONGOLO FLOODPLAIN ECOSYSTEM

This study has been concerned with achieving a holistic understanding of the role of *P. crispus* in the Pongolo floodplain ecosystem. This role is clearly important in maintaining ecosystem structure and functioning and should this be preserved by management as far as possible. To discuss the management of *P. crispus* alone however, would be counter to the general purpose of the study, management of the ecosystem as a whole is therefore included in this section. Two major issues are discussed; the hydrological regime

which forms as the major determinant/forcing function and the managerial roles of animals and temperature which initiate and rate regulate major ecosystem processes.

9.3.1 The hydrological regime

With the completion and filling of the Pongolapoort dam, future water requirements of the floodplain will have to come as controlled releases from the dam.

An important objective of management should be to maintain the seasonality of the hydrological regime and allow completion of all the annual between-flood processes in the pans. The last floods of the summer season should therefore occur before pan water temperatures reach 25°C (March - April) and *P. crispus* germinates. Occasional later floods (into May) would be acceptable as young plants can tolerate at least short periods of reduced light penetration (Section 4.2.1). The period between floods of successive summers can vary considerably but with two main considerations:

1. A water depth of about 35 cm (the up-ending depth of waterfowl) is required at the end of the dry period if a stable grazing system is to be maintained in pans colonised by *P. crispus*.

2. The first floods of the succeeding summer should not regularly occur before *P. crispus* standing crop has declined to zero. Earlier floods have the potential of flushing resources such as phosphorus from the pans before they are transferred to storage compartments.

In general therefore floods which flush, as opposed to fill, the pans should begin in November or early December with the last occurring about mid- to end- February. It is important to remember, however, that the ability of *P. crispus* to exploit this habitat as a ruderal, lies in its multiple regenerative strategies (including staggered germination) and short life cycle. Furthermore, the

flexibility of this species adaptations has probably been maintained by the variability of the flooding regime (Section 4.2.1) and could be reduced if artificial releases were made on a regular predetermined basis. This might not seem an important issue in the short term while water demands for agriculture are low but as these increase and water availability for the floodplain decreases flexibility in response to hydrological regime will be important. Artificial releases should therefore contain an element of variability which will not only maintain flexibility in the response of *P. crispus* but also of the ecosystem as a whole to enviromental changes.

Furness (1981), Heeg and Breen (1982) and Alexander (1982) have all proposed flooding regimes for the Pongolo floodplain which take seasonality as well as frequency, duration and magnitude into account. The latest proposal by Alexander (1982) incorporates the other two studies and came into effect in spring 1984. It is not necessary to discuss all the details of this proposal here as it incorporates the features discussed above. One of the main purposes of his proposal, however, was to provide the means to calibrate the Pitman/Weiss hydrological model (Section 1.3.4) of the floodplain. He therefore set specific dates in November (1984) and February (1985) for individual floods. Since variability in flooding is important these dates should not be carried through to future years and every effort should be made to incorporate variability into long term releases from the dam.

9.3.2 The managerial role of animals and temperature

A seasonally adjusted hydrological regime will provide an environment for *P. crispus* but this alone will not optimise the retention of resources such as phosphorus in the pans if rate regulatory and event initiating processes in the ecosystem are allowed to degenerate. Of particular importance to management in this context are the waterfowl and snail communities of the floodplain. If proposals for limited tourism in the area (Heeg and Breen, 1982) are implemented, then the hunting of waterfowl and eradication of bilharzia will become significant issues. Provided tourism is limited and hunting

controlled on a sustained yield basis waterfowl populations should not be affected but the use of molluscicides to combat bilharzia will affect all snail species including *B. natalensis*. They should not therefore be used, especially as they do not constitute a viable means of control (Appleton, pers. comm.).

The germination of turions in response to a temperature trigger may represent a good adaptation to a natural flooding regime but it does present problems for management under controlled floods as hypolimnial water in the dam is likely to be below 25°C during early summer (Furness, pers. comm.). Release of cold hypolimnial water during summer floods should therefore be avoided and floods should only be released from the radial gates of the Pongolapoort dam.

9.4 FUTURE RESEARCH DIRECTIONS

The purpose of this section is not to formulate a policy for future research on the Pongolo floodplain but rather to highlight some important issues which this study has brought to light. Numerous proposals for future research into aspects of the role of aquatic plants, including *P. crispus*, in aquatic ecosystems have been made throughout this dissertation. They will not be repeated here but rather the need to study the response of the ecosystem and its components, to changes in resource input will be emphasised. Most studies to date have been concerned with present day processes and not how they might change under future management practices.

9.4.1 *Potamogeton crispus*

Perhaps the most important information required about *P. crispus* in the above context is its response to changes in nutrient, particularly phosphorus, availability. What are the minimum requirements of this plant, and if nutrient supply is to be supplemented how can this be achieved without upsetting the epiphyte/host association?

9.4.2 During flood processes

To date there is very little information on processes which take place during floods and no understanding of how these processes operate in the context of ecosystem adaptation to flushing. Furness (1981) considered nutrient loss from decomposing, inundated *C. dactylon* and, although he did not study pathways of transfer, proposed that much of this could be flushed from the system. Is this so or are there other processes which act to retard flushing by transferral of nutrients to storage compartments? Does the same apply to other species of floodplain plants? A hypothesis, following this study, is that the rapid growth of epiphyton on inundated plants (Rogers, 1981), and consumption by invertebrates and juvenile fish, results in the retention of nutrients in storage compartments during floods. But how would this be affected by different durations, magnitudes and frequency of artificial floods? Studies should concentrate on decomposition of inundated vegetation, epiphyton production, grazing and the associated pathways nutrient transfer. These will improve understanding of adaptive processes, in particular rate regulating functions, which will assist in deciding on optimal characteristics of individual floods.

9.4.3 Ecosystem response

The need for management to consider the ecosystem as a functional adapted unit has been stressed in this study. Controlled floods provide the means for testing whole ecosystem response to different hydrological regimes and phosphorus would be a useful currency. How predictable is ecosystem response to hydrological regime? How finely does management of the regime have to be tuned? Measurements of the loads of phosphorus and other resources discharged from the dam and those leaving the floodplain, at a point such as Makanes drift where flow rate and depth can be measured, can provide a mass balance of P for the floodplain. If sampling is carried out at short intervals (hourly) a unique estimate of ecosystem response to flooding can be obtained and integrated into future management programmes.

REFERENCES

Adams, M.S. & Prentki, R.T. (1982). Biology, metabolism and function of littoral submersed weedbeds of Lake Wingra, Wisconsin, USA: A summary and review. *Archiv für Hydrobiologie* Suppl. 62: 333 - 409.

Alexander, W.J.R. (1982). Water requirements of the Pongolo floodplain system and recommended operating rules for the Pongolapoort Dam. Report of the Department of Environmental Affairs, Pretoria. pp. 28.

Allen, H.L. (1971). Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. *Ecological Monographs* 41: 97 - 127.

Allen, S.E. (Ed.) (1974). *Chemical Analysis of Ecological Materials*. Blackwell Scientific Publications, Oxford.

Anderson, M.G. & Low, J.B. (1976). Use of sago pondweed by waterfowl on the Delta Marsh, Manitoba. *Journal of Wildlife Management* 40: 233 - 242.

Anderson, N.H. & Sedell, J.R. (1979). Detrital processing by macro-invertebrates in stream ecosystems. *Annual Review of Entomology* 24: 351 - 377.

Anonymous (1969). Analytical guide, Part 2: Theoretical aspects and analytical methods. Internal report, Council for Scientific and Industrial Research, National Institute for Water Research, Pretoria. pp. 199.

Appleton, C.C. (1978). Review of literature on abiotic factors influencing the distribution and life cycles of bilharziasis intermediate host snails. *Malacological Review* 11: 1 - 25.

Arber, A. (1920). *Water Plants*. Cambridge University Press, London.

Archibald, C.G.M., Coetzee, O.J., Kemp, P.H., Pretorius, S.J. and Sibbald, R. (1969). The Rivers of Northern Natal and Zululand. Water Quality and Abatement of Pollution in Natal Rivers. Natal Town and Regional Planning Reports, Vol. 13, Part IV.

Azevedo, J. Fraga de & Medeiras, L. do C.M. de. (1955). Estudos ensaisos e documentas XIV: Os moluscos de áqua do ultramar Portugês. Minesterio do Ultramar, Lisboa.

Baddeley, M.S. (1967). Biochemical aspects of senescence. In: Preece, T.F. & Dickensen, C.H. (Eds.), *The Ecology of Leaf Surface Microorganisms*. Academic Press, New York.

Ballantine, D.L. (1979). The distribution of algal epiphytes on macrophyte hosts offshore from La Parguera, Puerto Rico. *Botanica Marina* 22: 107 - 111.

Beadle, L.C. (1981). *The Inland Waters of Tropical Africa: An introduction to tropical limnology*. Longman Inc., New York.

Beckman, C.H. (1964). Host responses to vascular infection. *Annual Review of Phytopathology* 2: 231 - 252.

Boling, R.H., Goodman, E.D., Zimmer, J.O., Cummins, K.W., Petersen, R.C., van Sickle, J.A. & Reice, S.R. (1975). Toward a model of detritus processing in a woodland stream. *Ecology* 56: 141 - 151.

Bowen, S.H. (1978). Benthic diatom distribution and grazing by *Sarotherodon mossambicus* in Lake Sibaya, South Africa. *Freshwater Biology* 8: 449 - 453.

Bowen, S.H. (1979a). A nutritional constraint in detritivory by fishes: The stunted population of *Saratherodon mossambicus* in Lake Sibaya, South Africa. *Ecological Monographs* 49: 17 - 31.

Bowen, S.H. (1979b). Determinants of the chemical composition of periphytic detrital aggregate in a tropical lake (Lake Valencia, Venezuela). *Archiv für Hydrobiologie* 87: 166 - 177.

Bowen, S.H. (1979c). Detritivorous fishes - What limits their growth? Unpublished manuscript, Department of Biological Sciences, Michigan Technological University, Houghton, Michigan. USA. pp. 12.

Boyd, C.E. (1970). Losses of mineral nutrients during decomposition of *Typha latifolia*. *Archiv für Hydrobiologie* 66: 511 - 517.

Boyd, C.E. (1971). The dynamics of dry matter and chemical substances in a *Juncus effusus* population. *American Midland Naturalist* 86: 28 - 45.

Boyd, C.E. & Goodyear, C.P. (1971). Nutritive quality of food in ecological systems. *Archiv für Hydrobiologie* 69: 256 - 270.

Breen, C.M. (1983). The Pongolo River Floodplain. An Overview of Monitoring Needs. Internal Report, Department of Botany, University of Natal, Pietermaritzburg, South Africa. pp. 6.

Breen, C.M., Furness, H.D., Heeg, J. & Kok, J. (1978). Bathymetric studies on the Pongolo river floodplain. *Journal of the Limnological Society of Southern Africa* 4: 95 - 100.

Breen, C.M., Lillig, C., Oliver, J. & Furness, H.D. (1976). A quantitative sampler for aquatic macrophytes. *Journal of the Limnological Society of Southern Africa* 2: 59 - 62.

Brinson, M.M. & Davis, G.J. (1976). *Primary Productivity and Mineral Cycling in Aquatic Macrophyte Communities of the Chowan River, North Carolina.* Report 120 of the Water Resources Research Institute, University of North Carolina, USA.

Brinson, M.M., Lugo, A.E. & Brown, S. (1981). Primary productivity, decomposition and consumer activity in freshwater wetlands. *Annual Review of Ecology and Systematics* 12: 123 - 161.

Bristow, J.M. (1974). The structure and function of roots in aquatic vascular plants. In: Torrey, J.G. & Clarkson, D.T. (Eds.), *The Development and Function of Roots.* Academic Press, New York.

Bristow, J.M. & Whitcombe, M. (1971). The role of roots in the nutrition of aquatic vascular plants. *American Journal of Botany* 58: 8 - 13.

Brock, M.A. (1983). Reproductive allocation in annual and perennial species of the submerged aquatic halophyte *Ruppia*. *Journal of Ecology* 71: 811 - 828.

Brock, M.A. & Lane, J.A.K. (1983). The aquatic macrophyte flora of saline wetlands in Western Australia in relation to salinity and performance. *Hydrobiologia* 105: 63 - 76.

Brown, D. (1954). Methods of Surveying and Measuring Vegetation. Commonwealth Bureau of Pastures and Field Crops, Bulletin 42, Farnham Royal, Bucks., England. pp. 223.

Burton, B.A., Hudson, R.J. & Bragg, D.D. (1979). Efficiency of utilization of bulrush rhizomes by lesser snow geese. *Journal of Wildlife Management* 43: 728 - 735.

Butler, R.D. & Simon, E.W. (1967). Ultrastructural aspects of senescence in plants. In: Strehler, B. (Ed.), *Advances in Gerontological Research*. Academic Press, London.

Byrde, R.J.W. (1980). Diseases in plants. In: Hawker, L.E. & Linton, A.H. (Eds.), *Microorganisms: Function, Form and Environment*. Edward Arnold, London.

Calow, P. (1974). Evidence for bacterial feeding in *Planorbis contortus* Linn. (Gastropoda : Pulmonata). *Proceedings of the Malacological Society of London* 41: 145 - 156.

Calow, P. (1975). The feeding strategies of two freshwater gastropods, *Ancylus fluviatilis* Müll and *Planorbis contortus* Linn. Pulmonata, in terms of ingestion rates and absorption efficiencies. *Oecologia* 20: 33 - 49.

Calow, P. & Townsend, C.R. (1981). Energy, Ecology and Evolution. In: Townsend, C.R. & Calow, P. (Eds.), *Physiological Ecology: An Evolutionary Approach to Resource Use*. Blackwell Scientific Publishers, Oxford.

Carignan, R. & Kalff, J. (1979). Quantification of the sediment phosphorus available to aquatic macrophytes. *Journal of the Fisheries Research Board of Canada* 36: 1002 - 1005.

Carignan, R. & Kalff, J. (1980). Phosphorus sources for aquatic weeds: Water or sediments. *Science* 207: 987 - 988.

Carpenter, S.R. (1981). Decay of heterogenous detritus: A general model. *Journal of Theoretical Biology* 89: 539 - 547.

Carpenter, S.R. & Adams, M.S. (1979). Effects of nutrients and temperature on decomposition of *Myriophyllum spicatum* L. in a hard water eutrophic lake. *Limnology and Oceanography* 24: 520 - 528.

Cattaneo, A. & Kalff, J. (1978). Seasonal changes in the epiphyte community of natural and artificial macrophytes in Lake Memphremagog (Que. and Vt.). *Hydrobiologia* 60: 135 - 144.

Cattaneo, A. & Kalff, J. (1980). The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnology and Oceanography* 25: 280 - 289.

Chew, R.M. (1974). Consumers as regulators of ecosystems. An alternative to energetics. *The Ohio Journal of Science* 74: 359 - 370.

Clark, A. (1974). The status of the whistling ducks in South Africa. *Ostrich* 45: 1 - 4.

Clutton-Brock, T.H. & Harvey, P.H. (1979). Comparison and adaptation. *Proceedings of the Royal Society London* 205: 547 - 565.

Coke, M. (1970). The water requirements of the Pongolo floodplain pans. Proceedings of the Convention: Water for the Future, Water Year 1970. pp. 6.

Coke, M. (1980). The natural flows of the lower Pongolo River. Unpublished report in "Man and the Pongolo Floodplain". National Programme for Environmental Sciences, Council for Scientific and Industrial Research, Pretoria, South Africa. Reference No. NP 14/106/7C.

Cole, G.A. (1979). *Textbook of Limnology*, 2nd edition. Mosby, St. Louis.

Collier, B.D., Cox, G.W., Johnson, A.W. & Miller, P.C. (1973). *Dynamic Ecology*. Prentice-Hall International, Inc., London.

Colvin, P.M. (1972). Sociological studies on the plankton of the Pongolo river floodplain. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Cross, R.H., Allanson, B.R., Davies, B.R. & Howard-Williams, C. (1977). Critical point drying as a preparative technique for scanning electron microscopy and its application in limnology. *Journal of the Limnological Society of Southern Africa* 3: 59 - 62.

Cummins, K.W. (1973). Trophic relations of aquatic insects. *Annual Review of Entomology* 18: 183 - 206.

Cummins, K.W. & Klug, J.M. (1979). Feeding ecology of stream invertebrates. *Annual Review of Ecology* 10: 147 - 172.

Cummins, K.W., Peterson, R.C., Howard, F.O., Wuycheck, J.C. & Holt, V.I. (1973). The utilization of leaf litter by stream detritivores *Ecology* 54: 336 - 345.

Cummins, K.W., Spengler, G.L., Wand, G.M., Speaker, R.M., Ovink, R.W., Mahan, D.C. & Mattingly, R.L. (1980). Processing of confined and naturally entrained leaf litter in a woodland stream ecosystem. *Limnology and Oceanography* 25: 952 - 957.

Cyrus, D.P. & Robson, N.F. (1980). *Bird Atlas of Natal.* University of Natal Press, Pietermaritzburg.

Dandy, J.E. (1937). The genus *Potamogeton* in tropical Africa. *Journal of the Linnean Society of Botany* I: 507 - 540.

Danell, K. & Sjöberg, K. (1979). Decomposition of *Carex* and *Equisetum* in a northern Swedish lake: dry weight loss and colonization by macro-invertebrates. *Journal of Ecology* 67: 191 - 200.

De la Cruz, A.A. (1975). Proximate nutrient changes during decomposition of salt marsh plants. *Hydrobiologia* 47: 475 - 480.

Denny, P. (1972). Sites of nutrient absorption in aquatic macrophytes. *Journal of Ecology* 60: 819 - 829.

Denny, P. (1980). Solute movement in submerged angiosperms. *Biological Review* 55: 65 - 92.

Dobrowolski, K.A. (1973). Role of birds in Polish wetland ecosystems. *Polskie Archiwum Hydrobiologii* 20: 217 - 221.

Douthwaite, R.J. (1977). Filter-feeding ducks on the Kafue flats, Zambia, 1971 - 1973. *Ibis* 119: 44 - 66.

Dowsett, R.J. (1971). A preliminary survey of Zambia's wetlands and waterfowl. *International Wildfowl Research Bureau Bulletin* 32: 75 - 84.

Dutton, T.P. (1972). Some factors affecting the fluctuations of waterfowl populations on Lake Nyamithi. Internal Report, Natal Parks Board, Pietermaritzburg, Republic of South Africa.

Eilam, Y. (1965). Permeability changes in senescing tissue. *Journal of Experimental Botany* 16: 614 - 627.

Eminson, D. & Moss, B. (1980). The composition and ecology of periphyton communities in freshwater. The influence of host type and external environment on community composition. *British Phycological Journal* 15: 429 - 446.

Engelberg, J. & Boyarsky, L.L. (1979). The noncybernetic nature of ecosystems. *The American Naturalist* 114: 317 - 324.

Everson, T.M. (1980). Germination and nutritional studies on *Potamogeton crispus* L.. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Fenchel, T. & Harrison, P. (1976). The significance of bacterial grazing and mineral cycling for the decomposition of particulate detritus. In: Anderson, J.M. & MacFadyen, A. (Eds.), *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*. Blackwell Scientific Publications, Oxford.

Flake, L.D. (1979). Wetland diversity and waterfowl. In: Greeson, P.E., Clark, J.R. & Clark, J.E. (Eds.), *Wetland Functions and Values: The State of our Understanding*. American Water Resources Association, Minneapolis.

Floodgate, G.D. (1972). The mechanisms of bacterial attachment to detritus in aquatic systems. IBP/UNESCO Symposium: Detritus and its role in aquatic ecosystems. *Memorie dell' Instituto Italiano di Idrobiologia* Suppl. 29: 309 - 323.

Furness, H.D. (1981). The plant ecology of seasonally flooded areas of the Pongolo River Floodplain, with particular reference to *Cynodon dactylon* (L.) Pers.. Ph.D. Thesis, University of Natal, Pietermaritzburg.

Furness, H.D. & Breen, C.M. (1980). The vegetation of the seasonally flooded areas of the Pongolo River Floodplain. *Bothalia* 13: 217 - 230.

Gallagher, J.L. (1978). Decomposition processes: Summary and recommendations. In: Good, R.E., Whigham, D.F & Simpson, R.L. (Eds.), *Freshwater Wetlands: Ecological Processes and Management Potential*. Academic Press, New York.

Gaudet, J.J. (1977). Uptake, accumulation, and loss of nutrients by papyrus in tropical swamps. *Ecology* 58: 415 - 422.

Geldenhuys, J.N. (1976). Relative abundance of waterfowl in the Orange Free State. *Ostrich* 47: 27 - 54.

Geldenhuys, J.N. (1977). Feeding habits of South African Shelduck. *South African Journal of Wildlife Research* 7: 5 - 9.

Gerloff, G.C. & Krombholz, P.H. (1966). Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. *Limnology and Oceanography* 11: 529 - 539.

Godshalk, G.L. & Wetzel, R.G. (1978a). Decomposition of aquatic angiosperms. I. Dissolved components. *Aquatic Botany* 5: 281 - 300.

Godshalk, G.L. & Wetzel, R.G. (1978b). Decomposition of aquatic angiosperms. II. Particulate components. *Aquatic Botany* 5: 301 - 327.

Godshalk, G.L. & Wetzel, R.G. (1978c). Decomposition of aquatic angiosperms. III. *Zostera marina* L. and a conceptual model of decomposition. *Aquatic Botany* 5: 329 - 354.

Godshalk, G.L. & Wetzel, R.G. (1978d). Decomposition of macrophytes and the metabolism of organic matter in sediments. In: Golterman, H.L. (Ed.), *Interactions Between Sediments and Water*. Dr. W. Junk, The Hague.

Golterman, H.L. (Ed.) (1969). *Methods for Chemical Analysis of Fresh Waters*. IBP Handbook No. 8. Blackwell Scientific Publications, Oxford.

Gregory, K.J. & Walling, D.E. (1973). *Drainage Basin Form and Process. A Geomorphological Approach*. Edward Arnold, London. pp. 456.

Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169 - 1184.

Grime, J.P. (1979). *Plant Strategies and Vegetation Processes.* John Wiley & Sons, Chichester.

Haller, W.T., Miller, J.L. & Garrard, L.A. (1976). Seasonal production and germination of *Hydrilla* vegetative propagules. *Journal of Aquatic Plant Management* 14: 26 - 29.

Harrison, P.G. & Mann, K.H. (1975). Detritus formation from eelgrass (*Zostera marina* L.): The relative effects of fragmentation, leaching and decay. *Limnology and Oceanography* 20: 924 - 934.

Hartman, R.T. & Brown, D.L. (1967). Changes in internal atmosphere of submersed vascular hydrophytes in relation to photosynthesis. *Ecology* 48: 252 - 258.

Heeg, J. & Breen, C.M. (1982). *Man and the Pongolo Floodplain.* South African National Scientific Programmes Report No. 56, Council for Scientific and Industrial Research, Pretoria, South Africa.

Heeg, J., Breen, C.M., Colvin, P.M., Furness, H.D. & Musil, C.F. (1978). On the dissolved solids of the Pongolo flood plain pans. *Journal of the Limnological Society of Southern Africa* 4: 59 - 64.

Hill, B.J. (1975). The origin of Southern African coastal lakes. *Transactions of the Royal Society of South Africa* 41: 225 - 250.

Hough, R.A. & Wetzel, R.G. (1975). The release of dissolved organic carbon from submersed aquatic macrophytes: Diel, seasonal and community relationships. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 19: 939 - 948.

Howard-Williams, C. (1978). Growth and production of aquatic macrophytes in a south temperate saline lake. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 20: 667 - 673.

Howard-Williams, C. & Allanson, B.R. (1978). The limnology of Swartvlei with special reference to production and nutrient dynamics in the littoral zone. Swartvlei Project Report Part 2.

Howard-Williams, C. & Allanson, B.R. (1981). An integrated study on littoral and pelagic primary production in a South African coastal lake. *Archiv für Hydrobiologie* 92: 507 - 534.

Howard-Williams, C. & Davies, B.R. (1979). The rates of dry matter and nutrient loss from decomposing *Potamogeton pectinatus* in a brackish south-temperate coastal lake. *Freshwater Biology* 9: 13 - 21.

Howard-Williams, C., Davies, B.R. & Cross, R.H.M. (1978). The influence of periphyton on the surface structure of a *Potamogeton pectinatus* L. leaf (An hypothesis). *Aquatic Botany* 5: 87 - 91.

Howard-Williams, C. & Ganf, G.G. (1981). Shallow Waters. In: Symoens, J.J., Burgis, M. & Gaudet, J.J. (Eds.), *The Ecology and Utilization of African Inland Waters*. United Nations Environmental Programme, Nairobi.

Howard-Williams, C. & Junk, W.J. (1976). The decomposition of aquatic macrophytes in the floating meadows of a central Amazonian Várzea Lake. *Biogeographica* 7: 115 - 123.

Howard-Williams, C. & Lenton, G.M. (1975). The role of the littoral zone in the functioning of a shallow tropical lake ecosystem. *Freshwater Biology* 5: 445 - 459.

Hunt, G.S. & Lutz, R.W. (1959). Seed production in curly leaved pondweed. *Journal of Wildlife Management* 23: 405 - 408.

Hunter, R.D. (1980). Effects of grazing on the quantity and quality of freshwater aufwuchs. *Hydrobiologia* 69: 251 - 260.

Hutchinson, G.E. (1948). Circular causal systems in ecology. *Annals of the New York Academy of Science* 50: 221 - 246.

Hutchinson, G.E. (1975). *A Treatise on Limnology Volume III. Limnological Botany.* John Wiley & Sons, New York.

Hutchinson, G.E., Pickford, G.E. & Schuurman, J.F.M. (1932). A contribution to the hydrobiology of pans and other inland waters of South Africa. *Archiv für Hydrobiologie* 24: 1 - 154.

Hutchinson, I.P.G. & Midgley, D.C. (1973). A mathematical model to aid management of outflow from the Okavango swamp Botswana. *Journal of Hydrology* 19: 93 - 112.

Ikusima, I. (1965). Ecological studies on the productivity of aquatic plant communities. I. Measurement of photosynthetic activity. *Botanical Magazine, Tokyo* 78: 202 - 211.

Jewell, W.J. (1971). Aquatic weed decay. Dissolved oxygen utilization and nitrogen and phosphorus regeneration. *Journal of the Water Pollution Control Federation* 43: 1457 - 1467.

Jordan, C.F. (1981). Do ecosystems exist? *The American Naturalist* 118: 284 - 287.

Jorgenson, S.E. (Ed.) (1979). *Handbook of Environmental Data and Ecological Parameters.* International Society for Ecological Modelling, Copenhagen.

Jupp, B.P. & Spence, D.H.N. (1977). Limitations of macrophytes in a eutrophic lake, Loch Leven. II. Wave action, sediments and waterfowl grazing. *Journal of Ecology* 65: 431 - 446.

Kalbe, L. (1976). Effect of intensive duck farming on primary production, oxygen balance and exploitation of freshwater lakes. *Limnologica* (Berlin) 10: 551 - 556.

Kalk, M., Howard-Williams, C. & McLaughlan, A.J. (Eds.) (1979). *Lake Chilwa: Studies of Change in a Tropical Ecosystem.* Monographiae Biologicae 35. Dr. W. Junk, The Hague.

Kaushik, N.K. & Hynes, H.B.N. (1971). The fate of the dead leaves that fall into streams. *Archiv für Hydrobiologie* 68: 465 - 515.

Kendeigh, S.C. (1970). Energy requirements for existence in relation to size of bird. *Condor* 72: 60 - 65.

Kennedy, T.M. (1976). Studies on *Potamogeton crispus* L. with particular reference to salinity. Unpublished report, Department of Botany, University of Natal, Pietermaritzburg.

Kesler, D.H. (1981). Grazing rate determination of *Corynoneura scutellata* Winnerty (Chironomidae : Diptera). *Hydrobiologia* 80: 63 - 66.

King, L.C. (1967). *South African Scenery: A Textbook of Geomorphology.* Oliver and Boyd, Edinburgh. pp. 308.

Kiørboe, T. (1980). Distribution and production of submerged macrophytes in Tipper Grund (Ring kobing - Fjord, Denmark) and the impact of waterfowl grazing. *Journal of Applied Ecology* 17: 675 - 688.

Klopatek, J.M. (1978). Nutrient dynamics of freshwater riverine marshes and the role of emergent macrophytes. In: Good, R.E., Whigham, D.F. & Simpson, R.L. (Eds.), *Freshwater Wetlands: Ecological Processes and Management Potential.* Academic Press, New York.

Kok, H.M. (1980). Ecological studies on some important fish species of the Pongolo floodplain, KwaZulu, South Africa. Ph.D. Thesis, University of Natal, Pietermaritzburg.

Kroodsma, D.E. (1979). Habitat values for nongame wetland birds. In: Greeson, P.E., Clark, J.R. & Clark, J.E. (Eds.), *Wetland Functions and Values: The State of Our Understanding.* American Water Resources Association, Minneapolis.

Krull, J.N. (1970). Aquatic plant - macroinvertebrate associations and waterfowl. *Journal of Wildlife Management* 34: 707 - 718.

Kubota, J. & Lasar, V.A. (1967). Routine X-Ray emission spectrographic analysis of common forage plants. In: *Soil Testing and Plant Analysis Part II.* Soil Science Society of America, Inc. Publishers, Madison.

Lammens, E.H. & van der Velde, G. (1978). Observations on the decomposition of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae) with special regard to the leaves. *Aquatic Botany* 4: 331 - 346.

Laseiwski, R.C. & Dawson, W.R. (1967). A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13 - 23.

Liversidge, R. (1962). Further notes on the wildfowl of the O.F.S. goldfields. *Ostrich* 33: 29 - 32.

Losee, R.F. & Wetzel, R.G. (1983). Selective light attenuation by the periphyton complex. In: Wetzel, R.G. (Ed.),*Periphyton of Freshwater Ecosystems*. Developments in Hydrobiology 17: 89 - 96.

MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton N.J.

Mann, K.H. (1980). The total aquatic system. In: Barnes, R.S.K. and Mann, K.H., (Eds.),*Fundamentals of Aquatic Ecosystems*. Blackwell Scientific Publications, Oxford.

Marais, J.P. (1969). The Weinmann method for the determination of total available carbohydrates in plant material containing starch. *Agroplantae* 1: 47 - 50.

Martin, A.C., Gensch, R.H. & Brown, C.P. (1946). Alternative methods in upland gamebird food analysis. *Journal of Wildlife Management* 10: 8 - 12.

Mason, C.F. and Bryant, R.J. (1975). Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L.. *Journal of Ecology* 63: 71 - 96.

Mathews, C.P. & Westlake, D.F. (1969). Estimation of production by populations of higher plants subject to high mortality. *Oikos* 20: 156 - 160.

Mayer, A.M. & Poljakoff-Mayber, A. (1963). *The Germination of Seeds*. Permagon Press, Oxford.

McLaughlin, G.R. & Liversidge, R. (1978). *Roberts Birds of South Africa*. John Voeleker Bird Book Fund: Cape Town.

McNaughton, S.J. (1966). Ecotype function in the *Typha* community - type. *Ecological Monographs* 66: 297 - 325.

McNaughton, S.J. (1975). r- and K- selection in *Typha*. *The American Naturalist* 109: 251 - 261.

McNaughton, S.M. (1983). Serengeti grasslands ecology: The role of composite environmental factors and contingency in community organization. *Ecological Monographs* 53: 291 - 320.

McNaughton, S.M., Wallace, L.L. & Coughenour, M.B. (1983). Plant adaptation in an ecosystem context: Effects of defoliation, nitrogen and water on growth of an African Sedge. *Ecology* 64: 307 - 318.

McRoy, C.P. & Barsdate, R.J. (1970). Phosphate absorption in eelgrass. *Limnology and Oceanography* 15: 6 - 13.

McRoy, C.P. & Goering, J.J. (1974). Nutrient transfer between the seagrass *Zostera marina* and its epiphytes. *Nature* 248: 173 - 174.

Meldal-Johnsen, A. (1975). An analysis of some factors influencing potato production. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Menges, E.S. & Waller, D.M. (1983). Plant strategies in relation to elevation and light in floodplain herbs. *The American Naturalist* 122: 454 - 473.

Menzel, D.W. & Corwin, N. (1960). The measurements of total phosphorus in seawater based on the liberation of organically bound fractions by persulphate oxidation. *Limnology and Oceanography* 10: 280 - 282.

Mitsch, W.J., Dorge, C.L. & Wiemhoff, J.R. (1979). Ecosystem dynamics and a phosphorus budget of an alluvial cypress swamp in southern Illinois. *Ecology* 60: 1116 - 1124.

Moss, B. (1980). *Ecology of Freshwaters*. Blackwell Scientific Publishers, London.

Muenchner, W.C.L. (1936). Storage and germination of seeds of aquatic plants. Cornell University Agricultural Experimental Station Bulletin No. 652.

Musil, C.F. (1972). Ecological Studies on the Aquatic Macrophytes of the Pongolo River Flood Plain Pans. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Newell, S.Y. & Fell, J.W. (1980). Mycoflora of turtlegrass (*Thalassia testudinum* König) as recorded after seawater incubation. *Botanica Marina* 23: 265 - 275.

Nichols, D.S. & Keeney, D.R. (1976). Nitrogen nutrition of *Myriophyllum spicatum*: Uptake and translocation of ^{15}N by shoots and roots. *Freshwater Biology* 6: 145 - 154.

Nicotri, M.E. (1977). Grazing effect of four marine intertidal herbivores on the microflora. *Ecology* 58: 1020 - 1032.

Nicotri, M.E. (1980). Factors involved in herbivore food preference. *Journal of Experimental Marine Biology and Ecology* 42: 13 - 26.

Noy-Meir, I. (1975). Stability of grazing systems: an application of predator-prey graphs. *Journal of Ecology* 63: 459 - 481.

Obermeyer, A.A. (1966). Potamogetonaceae. In: *Flora of Southern Africa, Volume 1.* Cape and Transvaal Printers Ltd., Republic of South Africa.

Odum, E.P. (1969). The strategy of ecosystem development. *Science:* 164: 262 - 270.

Odum, E.P. & de la Cruz, A.A. (1967). Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem. In: Lauff, G.H. (Ed.), *Estuaries.* American Association for Advancement of Science, Washington D.C..

Odum, H.T. (1971). *Environment, Power and Society.* Wiley-Interscience, New York.

Oláh, J. (1972). Leaching,colonization and stabilization during detritus formation. IBP/UNESCO Symposium: Detritus and its role in aquatic ecosystems. *Memorie dell ' Istituto Italiano di Idrobiologia* Suppl. 29: 129 - 147.

O'Neill, R.V. (1976). Ecosystem persistence and heterotrophic regulation. *Ecology* 57: 1244 - 1253.

Otsuki, A. & Wetzel, R.G. (1974). Release of dissolved organic matter by autolysis of a submerged macrophyte *Scirpus subterminalis*. *Limnology and Oceanography* 19: 842 - 845.

Owen, M. (1973). The winter feeding ecology of wigeon at Bridgewater Bay, Somerset. *Ibis* 115: 227 - 243.

Paech, K. & Tracey, M.V. (Eds.) (1955). *Modern Methods of Plant Analysis*, Volume 1. Springer, Berlin.

Paerl, H.W. (1978). Microbial organic carbon recovery in aquatic ecosystems. *Limnology and Oceanography* 23: 927 - 935.

Parker, R.E. (1973). *Introductory Statistics for Biology*. Studies in Biology No. 43. Edward Arnold, London.

Pate, J.S. & Gunning, B.E.S. (1972). Transfer cells. *Annual Review of Plant Physiology* 23: 173 - 196.

Patten, B.C. (1975). Ecosystem as a co-evolutionary unit: a theme for teaching systems ecology. In: Innis, G.S. (Ed.) *New Directions in the Analysis of Ecological Systems*. Part I. Society for Computer Simulation. La Jolla, California.

Patten, B.C., Bosserman, R.W., Finn, J.T. & Cole, W.G. (1976). Propagation of cause in ecosystems. In: Patten, B.C. (Ed.), *System Analysis and Simulation in Ecology, Vol. 4*. Academic Press, New York.

Patten, B.C. & Odum, E.P. (1981). The cybernetic nature of ecosystems. *The American Naturalist* 118: 886 - 895.

Penhale, P.A. & Thayer, G.W. (1980). Uptake and transfer of carbon and phosphorus by eelgrass (*Zostera marina* L.) and its epiphytes. *Journal of Experimental Marine Biology and Ecology* 42: 113 - 123.

Perry, T.O. (1968). Dormancy, turion formation and germination by different clones of *Spirodela polyrhiza*. *Plant Physiology* 43: 1866 - 1869.

Phelines, R.F., Coke, M.M. & Nicol, S.M. (1972). The biological consequences of the damming of the Pongolo River. Proceedings of the Conference of the International Commission on Large Dams, Madrid. pp. 175 - 190.

Phillips, G.L., Eminson, D. & Moss, B. (1978). A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquatic Botany* 4: 103 - 126.

Phillipson, J. (1966). *Ecological Energetics*. Studies in Biology Series No. 1, Edward Arnold, London.

Pip, E. & Stewart, J.M. (1976). The dynamics of two aquatic plant-snail assoications. *Canadian Journal of Zoology* 54: 1192 - 1205.

Pitman, W.V. & Weiss, H.W. (1979). A numerical hydraulic model of the Pongola floodplain. Report No. 2/79, Hydrological Research Unit, University of the Witwatersrand, Johannesburg.

Planter, M. (1970). Elution of mineral components out of dead reed *Phragmites communis* Trin.. *Polskie Archiwum Hydrobiologie* 17: 357 - 362.

Pond, R.H. (1905). The relation of aquatic plants to the substratum (contributions to the biology of the Great Lakes). Report of the U.S. Fisheries Commission 21: 483 - 526.

Pond, R.H. (1918). The larger aquatic vegetation. In: Ward, H.B. & Whipple, G.C. (Eds.), *Fresh-water Biology*. J. Wiley & Sons, New York.

Popper, K.R. (1959). *The Logic of Scientific Discovery*. Basic Books, New York.

Poultney, C. (1980). Subsistence and utilization of natural resources by the inhabitants of the Mtikheni/Nsimbi pan region of the Pongolo river floodplain: A preliminary appraisal. Internal Report, Department of African Studies, University of Natal, Durban.

Prentki, R.T., Gustafson, T.D. & Adams, M.S. (1978). Nutrient movements in lakeshore marshes. In: Good, R.E., Whigham, D.F. & Simpson, R.L. (Eds.), *Freshwater Wetlands: Ecological Processes and Management Potential*. Academic Press, New York.

Quinn, J.F. & Dunham, A.E. (1983). On hypothesis testing in ecology and evolution. *The American Naturalist* 122: 602 - 617.

Riemer, D.N. & Toth, S.J. (1968). A survey of the chemical composition of *Potamogeton* and *Myriophyllum* in New Jersey. *Weed Science* 17: 219 -223.

Reynolds, E.S. (1963). Use of lead citrate at high pH as an electron opaque stain. *Journal of Cell Biology* 17: 208 - 212.

Rich, P.H. & Wetzel, R.G. (1978). Detritus in the lake ecosystem. *The American Naturalist* 112: 57 - 71.

Rich, P.H., Wetzel, R.G. & Thuy, N.V. (1971). Distribution, production and role of aquatic macrophytes in a southern Michigan marl lake. *Freshwater Biology* 1: 3 - 21.

Ridley, H.N. (1930). *Dispersal of Plants Throughout the World.* L. Reeve & Co., Ashford, Kent.

Robb, F., Davies, B.R., Cross, R., Kenyon, C. & Howard-Williams, C. (1979). Cellulolytic bacteria as primary colonizers of *Potamogeton pectinatus* L. (sago pond weed) from a brackish south-temperate coastal lake. *Microbial Ecology* 4: 167 - 177.

Rogers, F.E.J. (1981). Studies on the epiphyton of *Potamogeton crispus* L.. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Rogers, K.H. (1978). Aquatic macrophytes and associated fauna. In: Breen, C.M. (Ed.), A report on the pans of the Umfolosi River. Department of Botany, University of Natal, Pietermaritzburg.

Rogers, K.H. (1980). The vegetation of the Pongolo floodplain: Distribution and utilization. In: Bruton, M.M. and Cooper, K.H. (Eds.), *Studies on the Ecology of Maputaland.* Rhodes University Press, Grahamstown.

Rogers, K.H. & Breen, C.M. (1980). Growth and reproduction of *Potamogeton crispus* in a South African lake. *Journal of Ecology* 68: 561 - 571.

Rogers, K.H. & Breen, C.M. (1981a). Effects of epiphyton on *Potamogeton crispus* L. leaves. *Microbial Ecology* 7: 351 - 363.

Rogers, K.H. & Breen, C.M. (1981b). A matrix of information on the Pongolo river floodplain pans. Internal report, Department of Botany, University of Natal, Pietermaritzburg. pp. 6.

Ryther, J.H. & Dunstan, W.M. (1971). Nitrogen, phosphorus, and eutrophication in the coastal marine environment. *Science* 171: 1008 - 1013.

Saitoh, M., Narita, K. & Isikawa, S. (1970). Photosynthesis of some aquatic plants in relation to temperature. *Botanical Magazine, Tokyo* 83: 10 - 12.

Sand-Jensen, K. (1983). Physical and chemical parameters regulating growth of periphytic communities. In: Wetzel, R.G. (Ed.), *Periphyton of Freshwater Ecosystems*. Dr. W. Junk, The Hague.

Sand-Jensen, K. & Søndergaard, M. (1981). Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Internationale Revue der gesamten Hydrobiologie* 66: 529 - 552.

Sastroutomo, S.S. (1980). Environmental control of turion formation in curly leaf pondweed *Potamogeton crispus*. *Physiologia Plantarum* 49: 261 - 264.

Saunders, G.W. (1976). Decomposition in fresh water. In: Anderson, J.M. & Macfadyen, A. (Eds.), *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*. Blackwell Scientific Publications, Oxford.

Schartz, R.L. & Zimmerman, J.L. (1971). The time and energy budget of the male Dickcissel *(Spiza americana)*. *Condor* 73: 65 - 76.

Schulze, B.R. (1965). *Climate in South Africa, Part 8. General Survey*. Weather Bureau, Department of Transport, South Africa.

Sculthorpe, L.D. (1967). *The Biology of Aquatic Vascular Plants*. Edward Arnold, London.

Sibbald, I.R., Czarnoki, J., Slinger, S.J. & Ashton, G.C. (1963). The predication of the metabolizable energy content of poultry feeding-stuffs from a knowledge of their chemical composition. *Poultry Science* 42: 486 - 492.

Siegfried, W.R. (1970). Wildfowl distribution, conservation and research in southern Africa. *Wildfowl* 21: 89 - 98.

Siegfried, W.R., Frost, P.G., Cooper, J. & Kemp, A.C. (1976). South African red data book - Aves. S.A. National Research Programmes Report No. 7. Council for Scientific and Industrial Research, Pretoria.

Skead, D.M. (1980). The ecological relationship of the Yellow-billed Duck to its habitat at Barberspan and vicinity. D.Sc. Thesis, University of Potchefstroom, Potchefstroom, South Africa.

Skead, D.M. & Dean, W.R.J. (1977). Seasonal abundance of Anatidae at Barberspan. *Ostrich Suppl.* 12: 49 - 57.

Sloey, W.E., Spangler, F.L. & Fetter, C.W., Jr. (1978). Management of freshwater wetlands for nutrient assimilation. In: Good, R.E., Whigham, D.F. & Simpson, R.L. (Eds.), *Freshwater Wetlands: Ecological Processes and Management Potential*. Academic Press, New York.

Smith, T.J. (1982). Herbivore induced changes in salt marsh community structure. In: Gopal, B., Turner, R.E., Wetzel, R.G. and Whigham, D.F. (Eds.), *Wetlands Ecology and Management*. International Scientific Publishers, Jaipur, India.

Smith, T.J. & Odum, W.E. (1981). The effects of grazing by snow geese on coastal salt marshes. *Ecology* 62: 98 - 106.

Smock, A.L. & Harlowe, K.L. (1983). Utilization and processing of freshwater wetland macrophytes by the detritivore *Asellus forbesi*. *Ecology* 64: 1556 - 1565.

Sokal, R.R. & Rohlf, F.J. (1969). *Biometry: The Principles and Practice of Statistics in Biological Research*. W.H. Freeman & Co., San Fransisco. pp. 776.

Solbrig, O.T. (1981). Energy, information and plant evolution. In: Townsend, C.R. & Calow, P. (Eds.), *Physiological Ecology: An Evolutionary Approach to Resource Use*. Blackwell Scientific Publishers, Oxford.

Søndergaard, M. (1981). Kinetics of extracellular release of ^{14}C labelled organic carbon by submerged macrophytes. *Oikos* 36: 331 - 347.

Spence, D.H.N. (1982). The zonation of plants in freshwater lakes. *Advances in Ecological Research* 12: 37 - 126.

Spence, D.H.N., Milburn, T.R., Ndawula-Senyimb, M. & Roberts, E. (1971). Fruit biology and germination of two tropical *Potamogeton* species. *New Phytologist* 70: 197 - 212.

Stainton, M.P., Capel, M.J. & Armstrong, F.A.J. (1974). *The Chemical Analysis of Fresh Water.* Department of the Environment, Fisheries and Marine Service, Research and Development Directorate, Miscellaneous Special Publication No. 25, Winnipeg, Manitoba.

Stephenson, M., Turner, G., Pope, P., Cole, J., Knight, A. & Tchobanoglous, G. (1980). The environmental requirements of aquatic plants. Appendix A, The Use and Potential of Aquatic Species for Wastewater Treatment. Publication 65, California State Water Resources Control Board, Sacremento, California.

Stearns, F. (1978). Management Potential: Summary and Recommendations. In: Good, R.E., Whigham, D.F. & Simpson, R.L. (Eds.), *Freshwater Wetlands: Ecological Processes and Management Potential.* Academic Press, New York.

Stearns, S.C. (1976). Life-history tactics: a review of ideas. *Quarterly Review of Biology* 51: 3 - 47.

Stevens, R.J. & Gibson, C.E. (1976). Sediment release of phosphorus in Lough Neagh, Northern Ireland. In: Golterman, H.L. (Ed.), *Interactions Between Sediments and Freshwater.* Junk & Pudoc, The Hague.

Stiglingh, I. & van Eeden, J.A. (1970). Notes on the feeding behaviour of *Bulinus (Bulinus) tropicus* (Krauss) Basommaptophora: Planorbidae. *Wetenskaplike Bydraes van die Potchefstroom se Universiteit vir Christelike Hoër Onderwys, Reeks B: Naturewetenskappe* 22.

Strickland, J.D. & Parsons, T.R. (1972). *A Practical Handbook of Seawater Analysis.* Fisheries Research Board of Canada, Ottawa.

Stuckey, R.L. (1979). Distributional history of *Potamogeton crispus* (curly pondweed) in North America. *Bartonia* 46: 22 - 42.

Stuckey, R.L., Wehrmeister, J.R. & Bartolotta, R.J. (1978). Submersed aquatic vascular plants in ice-covered ponds of central Ohio. *Rhodora* 80: 575 - 580.

Sugden, L.G. (1971). Metabolizable energy of small grains for mallards. *Journal of Wildlife Management* 35: 781 - 785.

Sugden, L.G. (1974). Energy metabolized by bantam chickens and blue-winged teal. *Poultry Science* 53: 2227 - 2228.

Sumner, W.T. & McIntire, C.D. (1982). Grazer-periphyton interactions in laboratory streams. *Archiv für Hydrobiologie* 93: 135 - 157.

Swanepoel, J.H. & Vermaak, J.F. (1977). Preliminary results on the uptake and release of ^{32}P by *Potamogeton pectinatus*. *Journal of the Limnological Society of Southern Africa* 3: 63 - 65.

Swanson, G.A. & Bartonek, J.C. (1970). Bias associated with food analysis in gizzards of blue-winged teal. *Journal of Wildlife Management* 34: 739 - 746.

Swanson, G.A., Krapu, G.L., Bartonek, J.C., Serie, J.R. & Johnson, D.H. (1974). Advantages in mathematical weighting of waterfowl food habits data. *Journal of Wildlife Management* 38: 302 - 307.

Swift, M.J., Heal, O.M. & Anderson, J.M. (1979). *Decomposition in Terrestrial Ecosystems*. Blackwell, Oxford.

Syers, J.K., Harris, R.F. & Armstrong, D.E. (1973). Phosphate chemistry in lake sediments. *Journal of Environmental Quality* 2: 1 - 14.

Teltscherova, L. & Hejný, S. (1973). The germination of some *Potamogeton* species from south Bohemian fishponds. *Folia Geobotanica and Phytotaxonomica* 8: 231 - 239.

Treca, B. (1981). Le régime alimentaire du Dendracygne veuf *(Dendrocygna viduata)* dans le delta du Sénégal. *L'Oiseau et la revue Française d'ornithologie* 51: 219 - 238.

Triska, F.J., Sedell, J.R., Cromack, K. & McCorison, F.M. (1984). Nitrogen budget for a small coniferous forest stream. *Ecological Monographs* 54: 119 - 140.

Twinch, A.J. & Breen, C.M. (1980). Advances in understanding phosphorus cycling in inland waters - their significance for South African Limnology. South African National Scientific Programmes Report No. 42.

Tyson, P.D. & Dyer, T.G.J. (1978). The predicted above-normal rainfall of the seventies and likelihood of droughts in the eighties in South Africa. *South African Journal of Science* 74: 372 - 377.

Vollenweider, R.A. (Ed.) (1969). *A Manual on Methods for Measuring Primary Production in Aquatic Environments.* IBP Handbook No. 12, Blackwell Scientific Publications, Oxford.

Waisel, Y. (1971). Seasonal activity and reproductive behaviour of some submerged hydrophytes in Israel. *Hidrobiologia* 12: 219 - 227.

Walley, G.C.B. (1980). Aspects of the benthic ecology of the Pongolo river floodplain. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Wallis, F.M. (1977). Ultrastructural histopathology of tomato plants infected with *Corynebacterium michiganense*. *Physiological Plant Pathology* 11: 333 - 342.

Wallis, F.M. & Truter, S.J. (1978). Histopathology of tomato plants infected with *Pseudomonas solanacearum* with emphasis on ultrastructure. *Physiological Plant Physiology* 13: 307 - 317.

Weber, J.A. & Nooden, L.D. (1976). Environmental and hormonal control of turion formation in *Myriophyllum verticillatum*. *American Journal of Botany* 63: 936 - 944.

Welch, E.B. (1980). *Ecological Effects of Waste Water*. Cambridge University Press, Cambridge.

Welcomme, R.L. (1974). *Fisheries Ecology of Floodplain Rivers*. Longman, N.Y. pp. 317.

Weller, M.W. (1978). Management of freshwater marshes for wildlife. In: Good, R.E., Whigham, D.F. and Simpson, R.L. (Eds.), *Freshwater Wetlands: Ecological Processes and Management Potential*. Academic Press, New York.

Welsh, R.P.H. & Denny, P. (1979). The translocation of ^{32}P in two submerged aquatic angiosperm species. *New Phytologist* 82: 645 - 656.

Westlake, D.F. (1965). Some basic data for investigation of the productivity of aquatic macrophytes. IBP Symposium: Primary Productivity in Aquatic Environments. *Memorie dell' Instituto Italiano di Idrobiologia* Suppl. 18: 229 - 248.

Westlake, D.F. (1967). Some effects of low-velocity currents on the metabolism of aquatic macrophytes. *Journal of Experimental Botany* 18: 187 - 205.

Westlake, D.F. (1968). The biology of aquatic weeds in relation to their management. Proceedings of the 9th British Weed Control Conference.

Westlake, D.F. (1969). Periphyton. In: Vollenweider, R.A. (Ed.), *A Manual on Methods for Measuring Primary Production in Aquatic Environments*. IBP Handbook No. 12, Blackwell Scientific Publications, Oxford.

Westlake, D.F. (1975). Primary production of freshwater macrophytes. In: *Photosynthesis and Productivity in Different Environments*. International Biological Programme, Cambridge University Press, Cambridge.

Westlake, D.F. (1978). Rapid exchange of oxygen between plant and water. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 20: 2363 - 2367.

Wetzel, R.G. (1964). A comparative study of the primary productivity of higher aquatic plants, periphyton and phytoplankton in a large shallow lake. *Internationale Revue der gesamten Hydrobiologie* 58: 893 - 901.

Wetzel, R.G. (1969). Factors influencing photosynthesis and excretion of dissolved organic matter by aquatic macrophytes in hard-water lakes. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 19: 2664 - 2668.

Wetzel, R.G. (1975). *Limnology*. W.B. Saunders Co., Philadelphia.

Wetzel, R.G. (1979). The role of the littoral zone and detritus in lake metabolism. *Archiv für Hydrobiologie, Ergebnisse der Limnologie* 13: 145 - 161.

Wetzel, R.G. (1983). *Limnology*. Second Edition. Saunders College Publishing, Philadelphia.

Wetzel, R.G. (1983a). Attached algal-substrate interactions: Fact or myth, and when and how? In: Wetzel, R.G. (Ed.), *Periphyton of Freshwater Ecosystems*. Dr. W. Junk, The Hague.

Wetzel. R.G. & Allen, H.L. (1971). Functions and interactions of dissolved organic matter and the littoral zone in lake metabolism and eutrophication. In: Kajak, Z. & Hillbricht-Ilkowska, A. (Eds.), *Productivity Problems of Freshwaters*. Polish Academy of Sciences, Warsaw.

Wetzel, R.G. & Hough, R.A. (1973). Productivity and the role of aquatic macrophytes in lakes. An assessment. *Polskie Archwum Hydrobiologie* 20: 9 - 19.

Wetzel, R.G. & Likens, G.E. (1979). *Limnological Analyses*. W.B. Saunders Co., Philadelphia. pp. 357.

Wetzel, R.G. & Manny, B.A. (1972). Secretion of dissolved organic carbon and nitrogen by aquatic macrophytes. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 18: 162 - 170.

Whitfield, A.K. (1977). Predation on fish in Lake St. Lucia, Zululand. Unpublished M.Sc. Thesis, University of Natal, Pietermaritzburg.

Whittaker, R.H. & Goodman, D. (1979). Classifying species according to their demographic strategy. I. Population fluctuations and environmental heterogeneity. *The American Naturalist* 113: 185 - 200.

Wiegert, R.G. & Owen, D.F. (1971). Trophic structure, available resources and population density in terrestrial vs. aquatic ecosystems. *Journal of Theoretical Biology* 30: 69 - 81.

Wiens, J.A. & Innis, G.S. (1974). Estimation of energy flow in bird communities: A population bioenergetics model. *Ecology* 55: 730 - 746.

Winterbottom, J.M. (1964). The migrations and local movements of some South African birds. In: Davis, D.H.S. (Ed.), *Ecological Studies in Southern Africa*. W. Junk, The Hague.

Winterbottom, J.M. (1967). The relationships of some African aquatic avifaunas. *Review of Zoology and Botany in Africa* 75: 150 - 155.

Wium-Anderson, S., Anthoni, U., Christophersen, C. & Houen, G. (1982). Allelopathic effects on phytoplankton by substances isolated from aquatic macrophytes (Charales). *Oikos* 39: 187 - 190.

Wohler, J.R., Robertson, D.B. & Laube, H.R. (1975). Studies on the decomposition of *Potamogeton diversifolius*. *Bulletin of the Torrey Botanical Club* 102: 76 - 78.

Woolhouse, H.W. (1967). The nature of senescence in plants. In: Woolhouse, H.W. (Ed.), *The Biology of Ageing*. University Press, Cambridge.

Wypkema, R.C.P. & Ankney, C.D. (1979). Nutrient reserve dynamics of lesser snow geese staging at James Bay, Ontario. *Canadian Journal of Zoology* 57: 213 - 219.

PERSONAL COMMUNICATIONS: ADDRESSES

Alexander, W.J.R. Manager: Scientific Services, Department of Environmental Affairs, Private Bag X209, Pretoria, 0001 Republic of South Africa.

Allanson, B.R. Institute of Freshwater Studies, Rhodes University, Grahamstown, 5140, Republic of South Africa.

Appleton, C.L. Research Institute for Disease in a Tropical Environment, South African Medical Research Council, P.O. Box 17120, Congella, 4013, Republic of South Africa.

Breen, C.M. Department of Botany, University of Natal, P.O. Box 375, Pietermaritzburg, 3200, Republic of South Africa.

Gous, S. Department of Poultry Science, Faculty of Agriculture, University of Natal, P.I. Box 375, Pietermaritzburg 3200, Republic of South Africa.

Louw, P. Department of Environmental Affairs, Operations Branch, Private Bag X209, Pretoria 0001, Republic of South Africa.

Torien, D.F. National Institute of Water Research, Council for Scientific and Industrial Research, P.O. Box 395, Pretoria 0001, Republic of South Africa.

Walley, G.C. B. c/o Zoology Department, University of Natal, P.O. Box 375, Pietermaritzburg 3200, Republic of South Africa.