Genetic Enhancement of Pearl Millet (*Pennisetum glaucum* [L.] R. Br.) for Resistance to *Striga hermonthica* (Del.) Benth and Compatibility to *Fusarium oxysporum* f.sp. *Strigae* in Burkina Faso

By

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Thesis Abstract

Pearl millet (*Pennisetum glaucum* [L.] R. Br. 2n = 2x = 14) is one of the most important cereal crops cultivated in the semi-arid tropics of sub-Saharan Africa and India, serving millions of households, and local and regional markets. It is a staple food crop in Burkina Faso, widely grown in the Sahelian and Sudano-Sahelian zones, characterised by poor soil conditions and erratic rainfall, and high temperatures. However, the potential production and productivity of pearl millet in Africa, including Burkina Faso, is constrained by the parasitic weed [*Striga hermonthica* (Del.) Bentham], bird damage, downy mildew, head miner, and low-yielding landraces. Developing *S. hermonthica*-resistant pearl millet varieties adapted to semi-arid regions with the desirable farmer and market-preferred traits would enhance yield gains and sustainable production. Therefore, the overall objective of this study was to improve pearl millet production and productivity in Burkina Faso by developing pearl millet varieties with *Striga*-resistance, compatibility with a biocontrol agent, *Fusarium oxysporum* f.sp. *Strigae* (*FOS*) and adapted to local agroecologies. The specific objectives of this study were to: (i) investigate the constraints affecting pearl millet production and farmers' approaches to *S. hermonthica* management in Burkina Faso to guide breeding and production, (ii) screen pearl millet genotypes for resistance to *S. hermonthica* and compatibility with a biocontrol agent, *FOS*, in the Sahel to select contrasting and promising parents for resistance breeding and production, (iii) determine the genome-wide association analyses of agronomic traits and *S. hermonthica* resistance in pearl millet to identify genetic markers for marker-assisted breeding and trait introgression, (iv) determine the generation mean analysis of *S. hermonthica* resistance in pearl millet to guide selection, genetic advancement and variety development, and (v) determine the combining ability effects and the response of pearl millet genotypes for agronomic traits and *S. hermonthica* resistance for selecting superior parents and hybrids.

The first study employed a participatory rural appraisal (PRA) and was conducted in the Sahel and Sudano-Sahelian zones of Burkina Faso, involving 492 farmers to document farmers' perceptions of the prevailing constraints affecting pearl millet production and related approaches to manage *S. hermonthica*. Recurrent drought, *S. hermonthica* infestation, shortage of labour, lack of fertilisers, lack of cash, and the use of low-yielding varieties were the main challenges hindering pearl millet production and productivity in the study areas. The study revealed a high population growth rate in rural areas, with 40% of respondents reporting families of up to 20 individuals per household. The majority of the respondents (40%) ranked *S. hermonthica* infestation as the primary constraint affecting pearl millet production, with yield losses of up to 80%. About 61.4% of the respondents in the study areas had achieved mean pearl millet yields of < 1.00 ton ha^{-1}. Poor access, the high cost of improved seed, and a lack of farmers' preferred traits in the existing improved pearl millet varieties were the main reasons for their low adoption, as 32% of respondents reported. *S. hermonthica* management options in pearl millet

production fields included moisture conservation using terraces, manual hoeing, hand weeding, use of micro-plots locally referred to as 'zaï', crop rotation and mulching. These management techniques were ineffective because they do not suppress the below-ground *S. hermonthica* seed and are difficult to implement. Integrated management practices employing breeding for *S. hermonthica*-resistant varieties with the aforementioned control measures could offer a sustainable solution for *Striga* management and improved pearl millet productivity in Burkina Faso.

The second study evaluated 150 pearl millet genotypes in *S. hermonthica* hotspot fields in rain-fed and greenhouse conditions using a 10 × 15 alpha lattice design in two replications in Burkina Faso. Significant differences were recorded among the tested pearl millet genotypes for the assessed agro-morphological and *Striga* resistance traits. Days to flowering were significantly delayed due to *S. hermonthica* infestation. Applying *FOS* on pearl millet seed significantly reduced the mean emerged *Striga* number in *S. hermonthica*-infested conditions. IP-3098, IP-6112, IP-9242, IP-10579, and IP-11358 were identified exhibiting *S. hermonthica* resistance and were compatible to *FOS*. The pearl millet genotypes supported few to none *S. hermonthica* emerged plants and had relatively low values under the Area under *Striga* Number Progress Curve (ASNPC). The selected genotypes are useful parents for breeding and integrated *Striga* management in Burkina Faso and related agro-ecologies.

In the third chapter, 150 pearl millet genotypes were assayed in genome-wide association analyses study for agronomic and *S. hermonthica* resistance traits to identify genetic markers for marker-assisted breeding and trait introgression. 256 K single nucleotide polymorphisms (SNPs) were used in the study. Significant differences ($P < 0.001$) were detected among the assessed pearl millet genotypes for *S. hermonthica* parameters and agronomic traits. Further, there were significant genotype by *S. hermonthica* interaction for the number of *S. hermonthica* and ASNPC. Twenty-eight SNPs were significantly associated with a low number of emerged *S. hermonthica* located on chromosomes 1, 2, 3, 4, 6, and 7. Four SNPs were associated with days-to-50%-flowering on chromosomes 3, 5, 6, and 7, while five were associated with panicle length on chromosomes 2, 3, and 4. Seven SNPs were linked to thousand-grain weight on chromosomes 2, 3, and 6. The putative SNP markers associated with a low number of emerged *S. hermonthica* and agronomic traits in the assessed genotypes are valuable genomic resources for accelerated breeding and variety deployment of pearl millet with *Striga* resistance and farmer-and market-preferred agronomic traits.

The fourth study determined the gene action and inheritance of *S. hermonthica* resistance in newly developed pearl millet populations to guide selection and genetic advancement. Bi-parental crosses were derived from contrasting pairs of *Striga*-resistant/*Striga*-susceptible of pearl millet lines. Two sets of parental lines and their subsequent F_1s, F_2s, and backcross generations were evaluated under greenhouse

and *S. hermonthica* infested field conditions using a randomised complete block design with three replications. The analysis of variance showed significant ($P < 0.001$) differences among the generations across sets for *Striga* parameters. *Striga* resistance is quantitatively inherited and governed by multiple genes. Duplicate gene action controlled the inheritance of the number of emerged *S. hermonthica*. Unique F_2 individuals with *S. hermonthica* resistance were selected from the two sets for genetic advancement through recurrent selection method for pearl millet variety development by integrating desirable agronomic and farmer-preferred traits.

The last study assessed the combining ability effects of pearl millet genotypes for *S. hermonthica* resistance and agronomic traits. The analysis of variance for combining ability effects showed significant ($P < 0.01$) differences among parents for days to flowering, panicle diameter, and grain yield. The difference between lines and testers were significant ($P < 0.001$) for panicle length and the number of emerged *Striga*. The genotype IP-11358 had high and positive general combining ability (GCA) effects (158.99) for grain yield. Negative GCA effects of -6.99, -6.40, and -134.08 were recorded for *Striga* count 60 days after planting, *Striga* count 80 days after planting, and ASNPC in that order for genotype IP-11358 in the greenhouse under *S. hermonthica* conditions. The hybrid IP-11358 × ICMB177111 displayed a higher specific combining ability (SCA) effect and standard heterosis for grain yield. The selected pearl millet genotypes are suitable for breeding high-yielding and *Striga*-resistant open-pollinated and hybrid varieties for *Striga*-prone areas in Burkina Faso and related agro-ecologies of sub-Saharan Africa.

Overall, the study identified *S. hermonthica* as the most critical pearl millet production constraint in Burkina Faso. Also, the study highlighted significant genetic diversity among 150 genotypes for *S. hermonthica* resistance when assessed using economic traits and SNP markers under *Striga* hotspot areas. Best-performing genotypes such as IP-3098, IP-6112, IP-9242, IP-10579 and IP-11358 were selected as suitable parents for *S. hermonthica* resistance breeding. The family IP-11358 × ICMB177111 was identified as having high-yielding and *Striga*-resistance. The selected genotypes are recommended for production and as donor parents for new population improvement in pearl millet *Striga* resistance breeding.

Declaration

I, Armel ROUAMBA, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other University.

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

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Signed

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……..

Armel Rouamba

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

[redacted]

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Prof. Hussein Shimelis (Supervisor)

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Dedication

This thesis work is dedicated to my

Late-Brother, Sambo Rouamba

Late-Father, Tibo Rouamba

Late-Mother, Gompoko Pauline Nikièma

Family

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Publications pertaining to this Thesis

Chapter One

Rouamba A.; Shimelis H.; Drabo I.; Shamuyarira K.W.; Mrema E. Management of the *Striga* epidemics in pearl millet production – A Review. Published in *CABI Agriculture and Bioscience*, 5:11, https://doi.org/10.1186/s43170-023-00210-1.

Chapter Two

Rouamba, A.; Shimelis, H.; Drabo, I.; Laing, M.; Gangashetty, P.; Mathew, I.; Mrema, E.; Shayanowako, A.I.T. Constraints to Pearl Millet (*Pennisetum glaucum*) Production and Farmers' Approaches to *Striga hermonthica* Management in Burkina Faso. Published in *Sustainability* 2021, 13, 8460. https://doi.org/10.3390/su13158460.

Chapter Three

Rouamba, A.; Shimelis, H.; Drabo, I.; Mrema, E.; Gangashetty, P.I. Screening of pearl millet genotypes for resistance to *Striga hermonthica* and compatibility to a biocontrol agent, *Fusarium oxysporum* f.sp. *Strigae*, in the Sahel. Published in *Crop Protection, 178 (2024) 106573, https://doi.org/10.1016/j.cropro.2024.106573.*

Chapter Four

Rouamba, A.; Shimelis, H.; Drabo, I.; Mrema, E.; Ojiewo, O.C.; Mwadzingeni, L.; Rathore, A. Genome-wide association analyses of agronomic traits and *Striga hermonthica* resistance in pearl millet. Published in *Scientific Reports*. 13:17152. https://doi.org/10.1038/s41598-023-44046-1.

Chapter Five

Rouamba, A.; Shimelis, H.; Drabo, I.; Shayanowako, A.I.T.; Mrema, E.; Gangashetty, P.I. Generation mean analysis of *Striga hermonthica* resistance in pearl millet (*Pennisetum glaucum* [L.] R. Br.). Published in the *Journal of Crop Improvement*. 37 (6), 834-852. https://doi.org/10.1080/15427528.2022.2156960.

Thesis introduction

Background

Pearl millet (*Pennisetum glaucum* [L.] R. Br., 2n = 2x = 14) is the world's sixth most important cereal crop after wheat, rice, maize, barley and sorghum. It is widely cultivated in the arid and semi-arid regions of Africa and Southern Asia, where other crops like wheat and maize may not thrive (FAOSTAT 2022; Gupta et al. 2022). Pearl millet is commonly grown under rain-fed agricultural systems. In sub-Saharan Africa, pearl millet grains are used as a staple food, whereas stover is used for livestock feed, fuelwood, and construction material (Burgarella et al. 2018). It is rich in protein, calcium, phosphorous and iron, with a relatively high amount of thiamine, riboflavin and niacin (Gupta et al. 2022). Furthermore, it has been attributed to having several health benefits on various diet-related diseases/disorders and deficiencies such as anaemia, constipation, cancer, diabetes, celiac, and diarrhoea (Gupta et al. 2022).

Almost all global production of pearl millet grains comes from sub-Saharan Africa and Asia (FAOSTAT 2022). In West Africa, pearl millet is grown in an estimated area of 19.7 million hectares with a mean productivity of < 0.74 tons ha^{-1}. In Burkina Faso, pearl millet is cultivated by small-scale farmers on an estimated area of 1.2 million hectares with low productivity (mean national production ≤ 0.81 tons ha^{-1}) compared to Asia, where smallholder farmers achieve high yields (1.4 tons ha^{-1}) (FAOSTAT 2022). Pearl millet constituted a daily diet for many people in the rural area of Burkina Faso. The main pearl millet dishes include tosafi, foura, gapal, couscous, zom-kom, gonre and gnon (Drabo 2016). It is also used in the processing industry, especially in preparing infant food. Pearl millet is the most expensive cereal on the national market for the last five years (Govt. Burkina Faso, WFP 2023).

The low grain yields in farmers' fields are caused by various biotic factors such as *S. hermonthica* (Del.) Bentham infestation, bird damage, insect pests, and diseases and abiotic stresses (such as heat and drought) and socio-economic factors (such as the use of low-yielding landraces and limited access to production inputs) (Drabo et al. 2018; Rouamba et al. 2021). *Striga* is widely distributed in most agricultural fields in Africa, including Burkina Faso, due to the production of millions of seeds per plant and its quick dispersal via animals, admixture in crop seeds, water runoff, wind, and farming tools. The seeds can remain viable in the soils for more than 14 years (Emechebe et al. 2004). Damages caused by *Striga* on its host were about 75% before its emergence (Parker and Riches 1993). The magnitude of yield losses incurred by *Striga* depends on the varieties grown, the level of the infestation, the prevailing climatic conditions, and the control measures (Mrema et al. 2016). Integrated *Striga* management options involving host resistance and biological control are the best strategies for controlling *Striga* (Mrema et al. 2017). Breeding pearl millet varieties resistant to *Striga* and compatible with a biocontrol agent such as *Fusarium oxysporum* f.sp. *Strigae* (*FOS*) will significantly increase pearl millet production in Burkina Faso.

Progress and gap of pearl millet breeding in Burkina Faso

International research and development projects and national breeding programs are striving to develop new, locally adapted pearl millet varieties with high yield potential and tolerance to major biotic and abiotic stresses (Ojiewo and Gekanana 2018). Notable international collaborative pearl millet projects include the pearl millet and sorghum improvement (PROMISO), harnessing opportunities for productivity enhancement (HOPE I and II) for sorghum and millets and accelerated varietal improvement and seed delivery of legumes and cereals in Africa (AVISA) which are led by the International Crops Research Institute for the Semiarid Tropics (ICRISAT). For instance, the research collaboration of ICRISAT with the Institute of Environment and Agricultural Research/Burkina Faso strengthened pearl millet breeding and capacity development. The collaboration enabled the development and release of pearl millet varieties such as Laada, Konkosbouga, Somkèta, Doumoukafa, which are open-pollinated-varieties and the first hybrid variety Nafagnon in 2019 (ECOWAS-UEMOA-CILSS 2021) adapted to the local agroecological zones.

Despite the past collaborative research efforts, pearl millet production and productivity remained low in Burkina Faso due to various constraints (Drabo et al. 2018; Azare et al. 2020; Rouamba et al. 2021). These include using low-yielding landraces, inadequate support from research and policy, a poor seed system, and biotic and abiotic stresses such as *Striga* and drought stress (Drabo et al. 2018; Rouamba et al. 2021). Farmers must be involved in setting the breeding goals so that the new improved varieties that will be developed respond to the constraints prevailing in the production areas and meet their preferences (Drabo et al. 2018). Several studies reported that farmer's participation in plant breeding has improved the acceptability of developed varieties under challenging environments by including their preferences in breeding objectives (Ceccarelli et al. 2009). Modern pearl millet breeding methods and technologies can substantially increase the current yield gaps in Africa by developing *Striga*-resistant and locally adapted genetic materials to deliver climate-smart and resilient varieties with farmer's preferred traits. There is a need for breeding programmes to consider the value chain to develop *Striga*-resistant varieties to mitigate the effects of *Striga* and improve pearl millet production in sub-Saharan Africa, including Burkina Faso.

***Striga hermonthica* as a challenge to pearl millet production in Burkina Faso**

Striga species are notorious parasitic weeds affecting pearl millet production in the Sahel and Sudano-Sahel regions (Emechebe et al. 2004). There are 13 *Striga* species reported in Burkina Faso, with *S. hermonthica* (Del.) Bentham and *S. gesneroïdes* (Willd) Vatke are the most devastating cereal and legume crop weeds, respectively (Boussim et al. 2011). Yield losses due to *S. hermonthica* vary between 7 and 41% in the central zones, while up to 55% losses have been reported in the eastern zones of Burkina Faso (Zombré and Nikiéma 1992 Traoré and Yonli 2001). The parasitic weed has a wide range of hosts, including rice (*Oryza glaberrima* Steudel and *O. Sativa* L.), maize (*Zea mays* L.), sorghum (*Sorghum bicolor* [L.] Moench), pearl millet, and fonio (*Digitaria exilis* (Kippist) Stapf) (Boussim et al. 2011; Mrema et al. 2017).

Farmers employ hand weeding, crop rotation, and botanicals such as a concoction powder prepared from pods of the African locust bean (Parkia biglobosa (Jacq.) R. Br. ex G. Don) and almonds of the shea tree (*Vitellaria paradoxa* C.F. Gaertn.) to control *S. hermonthica* (Boussim et al. 2011). These methods reduce the amount of *S. hermonthica* seed in the soil and improve soil fertility, but they have high labour requirements that limit their implementation and use. The use of chemical herbicides is not widely reported among smallholder farmers due to their high cost, limited access, and potential environmental hazards. In addition, the use of host plant resistance against *S. hermonthica* is limited by poor access to or the unavailability of resistant varieties. A combination of effective *S. hermonthica* control methods is required to reduce *S. hermonthica* on pearl millet production in SSA.

Conventional plant breeding, based on natural and induced genetic variability, selection and testing of new varieties, has benefited farmers in high-potential production environments (Drabo et al. 2018). However, the research outcome emanated from high-potential environments and was not adopted by resource-poor farmers for several reasons. Small-scale farmers have limited access to external production inputs and depend on their traditional varieties for multiple reasons, such as intrinsic quality traits and to avert crop losses.

Breeding for *Striga* resistance is the most economical and sustainable strategy for smallholder pearl millet producers. However, the *Striga*-pearl millet relationship is complex due to the continuous increase of *Striga* host range and its ability to overcome resistance, making long-term *Striga* resistance breeding difficult (Cotter et al. 2012). Pyramiding multiple resistance genes in a single variety is the most durable control method against the parasite. Polygenic resistance provides a broad-spectrum control of the parasite (Mbuvi et al. 2017). The complex life cycle of *Striga*, its ability to adapt to diverse environments, and the mixed cropping systems of smallholder farmers have made using a single-control approach ineffective. As a result, the combined use of two or more methods has been advocated for

effective *Striga* control. These methods included cultural practices (e.g., hand-weeding, crop rotation, trap crops) (Kanampiu et al. 2018; Midega et al. 2010), moisture conservation practices (Rouamba et al. 2021), *Striga* resistant crops (Cissoko et al. 2011), and biocontrol agent (Shayanowako et al. 2020; Joel 2000; Oswald 2005). The most sustainable way to cope with *Striga* damage is through Integrated *Striga* Management (ISM), incorporating various *Striga* control methods (Oswald 2005; Ejeta and Gressel 2007; Elzein et al. 2008). ISM reduce *Striga* infestation significantly under farmer's fields conditions. An evaluation of a genetically diverse pearl millet germplasm for resistance to *S. hermonthica* and compatibility to *FOS* would be necessary for genetic enhancement and breeding. Subsequently, the pearl millet genotypes resistant to *Striga* and compatible with *FOS* are useful for trait integration and integrated *Striga* management in Burkina Faso and related agro-ecologies. Detailed information, such as the genome-wide association analyses study (GWAS) and the generation mean analysis (GMA) of the selected parental lines, is needed for breeding. Therefore, there was a need to study the combining ability effects after the systematic crossing of selected parents in a line-by-tester mating design, using family evaluations in several *Striga*-infested environments. This would enable the selection of promising parents and families for further genetic advancement and cultivar release.

Overall research goal

This study's overall objective was to improve pearl millet production and productivity in Burkina Faso by developing varieties with *Striga*-resistance and compatibility with a biocontrol agent, *Fusarium oxysporum* f.sp. *Strigae* (*FOS*) and adapted to the local agro-ecologies.

Specific objectives

The specific objectives of the study were:

i) To investigate the constraints affecting pearl millet production and farmers' approaches to *S. hermonthica* management in Burkina Faso to guide breeding and production.

ii) To screen pearl millet genotypes for resistance to *S. hermonthica* and compatibility with a biocontrol agent, *FOS*, in the Sahel to select contrasting and promising parents for resistance breeding and production.

iii) To determine the genome-wide association analyses of agronomic traits and *S. hermonthica* resistance in pearl millet to identify genetic markers for marker-assisted breeding and trait introgression.

iv) To determine the generation means analysis of *S. hermonthica* resistance in pearl millet to guide selection, genetic advancement and variety development.

v) To determine the combining ability effects and heterosis of pearl millet genotypes for agronomic traits and *S. hermonthica* resistance for selecting superior parents and hybrids.

Research hypotheses.

The main hypotheses of the study are summarised below.

i) Smallholder farmers in Burkina Faso have varied pearl millet production constraints and *Striga* management approaches that can guide future breeding and production.
ii) Significant genetic variation exists among pearl millet genotypes that can be selected for *S. hermonthica* resistance and compatibility with *FOS* to be used as donor parents in *Striga* resistance breeding.
iii) The genotypes assessed in the study are genetically divergent for *S. hermonthica* resistance when subjected to selection using phenotypic traits and single nucleotide polymorphism (SNP) markers.
iv) Crosses between selected pearl millet lines differ in genetic factors for *S. hermonthica* resistance to guide selection, genetic advancement and variety development.
v) The selected parents and their crosses exhibit different levels and magnitude of combining ability effects for yield and yield components when evaluated with and without *S. hermonthica* infestation to select superior parents and hybrids.

Thesis outline

This thesis comprises six chapters (see Table below), developed according to the objectives set above. Chapter 1 is written as a separate review paper, while Chapters 2 to 6 are written as discrete research papers, each following a stand-alone research paper format, followed by a general overview of the research and its implications. The literature review and five experimental chapters of the study made the thesis chapters that were condensed into discrete but inter-dependant papers according to the University of KwaZulu-Natal's dominant thesis format. For this reason, there is some inevitable repetition of references and some information between chapters. Chapter 2 was published in Sustainability (2021, 13, 8460. https://doi.org/10.3390/su13158460); Chapter 5 in Journal of Crop Improvement (2022, https://doi.org/10.1080/15427528.2022.2156960).

Table 0.1 The outline of the thesis is, therefore, as follows:

Chapters	Titles
-	Thesis introduction
1	Review of the literature
2	Constraints to pearl millet production and farmers' approaches to *S. hermonthica* management in Burkina Faso
3	Screening of pearl millet genotypes for resistance to *S. hermonthica* and compatibility to a biocontrol agent, *Fusarium oxysporum* f.sp. *Strigae*, in the Sahel
4	Genome-wide association analyses of agronomic traits and *S. hermonthica* resistance in pearl millet
5	Generation means analysis of *S. hermonthica* resistance in pearl millet (*Pennisetum glaucum* [L.] R. Br.)
6	Combining ability and hybrid breeding in pearl millet (*Pennisetum glaucum* [L.] R. Br.) for agronomic traits and resistance to *S. hermonthica* (Del.) Bentham

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Chapter 1. Review of the Literature

Abstract

Pearl millet (*Pennisetum glaucum* [L.] R. Br.) is a drought-resilient and nutritious staple food crop widely cultivated in arid and semi-arid regions. Worldwide pearl millet is ranked the 6th widely produced cereal crop after wheat, rice, maize, barley, and sorghum, with a total production of 30.5 million tons on 32.1 million hectares. In Burkina Faso, it is the 3rd widely cultivated crop next to sorghum and maize, with a mean yield of 0.8 ton ha^{-1}, far below the potential yield of 3.0 tons ha^{-1} attributable to various production challenges. Among the production constraints, the parasitic weed *Striga* species, particularly *S. hermonthica* is endemic and causes up to 80% yield losses under heavy infestation. Different control methods (e.g., cultural practices, chemicals and bio-herbicides) have been recommended, but they have been largely ineffective due to diverse and complex problems, including the life cycle, fecundity, and prolonged seed dormancy of *S. hermonthica*; poor access and cost of implementation. Breeding for host plant resistance presents a cost-effective, environmentally friendly and affordable method for smallholder farmers to control and reduce *Striga* infestations and improve pearl millet yields. Therefore, the objectives of this study were to present the impact of *S. hermonthica* damage on pearl millet production and productivity and assess the effectiveness of different management methods of *S. hermonthica* with an emphasis on host plant resistance. The first section of the review assesses the impact of *Striga* infestation on pearl millet production, followed by the developmental stages of *Striga*, *Striga* infestation and damage management strategies, breeding for *Striga* resistance and other *Striga* control methods. The paper summarises genetic resources, new breeding technologies, and innovations for the precision and speed breeding of *Striga*-resistant cultivars. Information presented in this review will guide the use of the best breeding strategies and accelerate the development of new pearl millet cultivars that are high yielding and resistant to *S. hermonthica* to reduce damage incurred by *Striga* infestations on farmers' fields in Burkina Faso and similar agro-ecologies.

Keywords: breeding methods, pearl millet, *Striga* control methods, *Striga hermonthica*, witchweed

1.1. Introduction

Pearl millet (*Pennisetum glaucum* [L.] R. Br., 2n= 2x = 14) is one of the most nutritious and hardy cereal crops in arid and semi-arid regions. In Burkina Faso, pearl millet is the most widely cultivated cereal crop after sorghum and maize (INSD 2021). Pearl millet is highly tolerant to drought, low soil fertility, salinity, and high temperatures making it the most reliable food supply in dry regions worldwide. Pearl millet is valued for its nutritional profiles and quality food and feed for human wellbeing. For instance, when compared to maize, pearl millet grain has 11 to 12.5% bio-available protein. The grain comprises higher concentrations of iron, zinc and micro-minerals, including magnesium, calcium, sodium and potassium (Ghatak et al. 2016; Owheruo et al. 2019).

The average productivity of pearl millet is generally low in Africa. In Burkina Faso, a mean grain yield of 0.8 ton ha^{-1} is reported, comparatively lower than that for maize (1.7 ton ha^{-1}) and sorghum (1.0 ton ha^{-1}) (FAOSTAT 2022). The low productivity of pearl millet is attributable to the combined effect of several production constraints, including lack of improved varieties, *S. hermonthica* infestation, bird damage, severe drought, and poor soil health (Drabo et al. 2018; Rouamba et al. 2021). Rouamba et al. (2021) reported that *S. hermonthica* (Del.) Benth. was identified to be the major constraint to pearl millet production in five regions of Burkina Faso.

The parasitic weed, *Striga* species, is the primary constraint to cereal and legume crop production in sub-Saharan Africa (SSA). It is the most noxious weed affecting sorghum, pearl millet, maize and cowpea (Ali et al. 2009). The following *Striga* species are mainly recognised: *S. hermonthica* and *S. asiatica* inflicting heavy damage to the major cereal crops in SSA. Over 50 million hectares of soils under cereal cultivation in SSA have been infested by *Striga* spp. (Dafaallah 2019). The yield losses in cereals due to *Striga* damage can rise to 80% depending on cultivar susceptibility and the degree of the infestation. Crop failures and abandonment of cereal production are common in SSA due to high parasitism (Kamara et al. 2020). Most crop damage in *Striga*-infested fields occurs before *Striga* emergence, complicating effective parasite control (Dafaallah 2019).

Striga-resistant pearl millet cultivars are yet to be developed and deployed in SSA (Jamil et al. 2021; Rouamba et al. 2022). Six pearl millet varieties (i.e., M141, M239, M029, M197, M017, and KBH) (Kountche et al. 2013) and 29Aw (Dayou et al. 2021) were identified with relatively high yields and moderate resistance to *Striga*.

The management of the *Striga* epidemics in pearl millet includes cultural practices (e.g., crop rotation, intercropping, optimal soil fertilisation, moisture conservation methods, hand-weeding), herbicides, biological control agents (e.g., *Fusarium oxysporum* f.sp. *Strigae* [*FOS*]), resistance breeding and

integrated *Striga* management (Kountche et al. 2013; Jamil et al. 2021; Rouamba et al. 2021; Rouamba et al. 2022). Although most cultural practices are less expensive and helpful in reducing *Striga* seed bank and infestation they are not widely adopted due to limited access, low farmer acceptance associated with labour shortage, less effective in reducing crop damage and the need for financial resources (Murage et al. 2011; Goldwasser and Rodenburg 2013; Mahuku et al. 2017; Franke et al. 2018). According to Hearne (2009), Yoder and Scholes (2010) and Mandumbu et al. (2019), host-plant resistant deployment is considered the most economical, practical, and suitable long-term approach for managing *Striga* under smallholder conditions.

Integrating different approaches enables effective *Striga* management. The combination of host plant resistance with a biological control agent (e.g., *FOS*) effectively reduces *Striga* counts and emergence (Mrema et al. 2020; Shayanowako et al. 2020; Dossa et al. 2023). The bio-control agent has been successfully used and integrated with resistance breeding in maize (Hassan et al. 2018; Baiyegunhi et al. 2019); Lobulu et al. 2019; Shayanowako et al. 2020; Yacoubou et al. 2021; David et al. 2022) and sorghum (Rebeka et al. 2013; Mrema et al. 2017; Belay 2018; Mrema et al. 2020; Begna 2021). However, this technology is yet to be explored in pearl millet production solo or combination with other control methods in Burkina Faso and elsewhere. Therefore, the objectives of this study were to present the impact of *S. hermonthica* damage on pearl millet production and assess the effectiveness of different management methods of *S. hermonthica* with an emphasis on host plant resistance. The review discusses the impact of *Striga* infestation on pearl millet production, followed by the developmental stages of *Striga*, infestation and management strategies, breeding for *Striga* resistance and other *Striga* control methods. The paper summarises genetic resources, new breeding technologies, and innovations for the development of *Striga*-resistant cultivars with precision and speed breeding methods.

1.2. The Impact of *Striga* on Crop Production

Striga hermonthica is an obligate and hemiparasitic weed that parasitizes the root systems of cereals and legumes. It is becoming a persistent threat to crop production in sub-Saharan Africa, the Middle East, and Asia (Parker 2012). *Striga* is affecting the livelihoods of more than 300 million people in Africa and causing annual yield loss with a monetary value of 7 to 10 billion US$ (Scholes and Press 2008; Rodenburg et al. 2010). The parasite causes significant crop damage and reduces the productivity of cereals, including pearl millet (Dafaallah 2019). In sorghum and pearl millets, annual yield losses due to *Striga* parasitism were estimated to be 8.6 million tons (Mallu et al. 2021).

Striga hermonthica infestation is estimated to cause up to 80% yield losses in pearl millet production in Burkina Faso (Rouamba et al. 2021). Wilson et al. (2004) reported grain losses in pearl millet due to *Striga*

ranging between 10 - 95% depending on susceptibility of the variety, agroecology and cultural practices. The visible effects of *S. hermonthica* on crops range from stunted growth through wilting, yellowing, and scorching of leaves to death of many affected plants (Sibhatu 2016; Rouamba et al. 2021). A total crop loss with heavy infestations has been reported due to its pervasive nature of the weed (Mbuvi et al. 2017; Menkir et al. 2020). The most severely *Striga*-infested countries in West Africa are Burkina Faso, Gambia, Mali, Niger, Nigeria, Senegal, and Togo (Jamil et al. 2022). Dawud (2018) reported an increasing trend in *S. hermonthica* incidence and severity in pearl millet growing areas in Nigeria. Early-generation *Striga* control reduces yield losses and prevents subsequent spread to previously unaffected areas (Scholes and Press 2008; Kountche et al. 2016).

1.3. Developmental Stages of *Striga*

The parasite depends on its host plant for survival and growth, since it cannot survive at any stage (Cimmino et al. 2018). It takes about 10 weeks for *Striga* spp. to complete its life cycle (Yacoubou et al. 2021). Seed germination in *Striga* is initiated after the perception of germination stimulants, mainly strigolactones (SLs), released by roots of the host plants (Yoneyama et al. 2010; Joel and Bar 2013; Al-Babili and Bouwmeester 2015). Following germination, the *Striga* radicle grows toward host roots. The perception of host-derived haustorium-inducing factors, such as 2,6-dimethoxy-1,4-benzoquinone, prevents further growth of the radicle and induces cell expansion and division, and proliferation of hair cells at its tip, forming a haustorium, a special invasive organ that penetrates host (Goyet et al. 2019). Penetration of the host epidermis is mediated by the elongation of distal cells of the haustorium in the protoderm or epidermis of the host root and underlying ground tissue (Spallek et al. 2013). This is followed by rounds of periclinal and anticlinal divisions of haustorium cells, leading to growth into the cortex of host plants siphoning water and nutrients (Hood et al. 1998, Yoshida et al. 2010). A single *Striga* plant can yield up to 500,000 seeds, which are capable of remaining dormant in the soil for up to 20 years (Lobulu et al. 2019).

1.4. Management Strategies of *Striga* Infestation and Damage

Striga is a major problem in areas with low moisture and where soil fertility is eroded through cereal monocropping, decreased fallow, and minimal use of organic or inorganic fertilisers (De Groote et al. 2005). Several measures have been recommended to control *Striga*. The control measures can be grouped into cultural, chemical, biological, genetic and a combination of these (Mbwika et al. 2011; Sibhatu 2016).

1.4.1. Cultural Control Method

Various cultural management strategies have been proposed to manage *Striga*. The strategies include hand-weeding (Rouamba et al. 2021), intercropping of cereals with legumes (Lee and Thierfelder 2017; Mutyambai et al. 2019; Jamil et al. 2021), water management (Rouamba et al. 2021), mixed cropping, crop rotation (Kuyah et al. 2021), cover cropping (Randrianjafizanaka et al. 2018; Rich 2020), push-pull technology (Niassy et al. 2022), and soil fertilization (Dawud 2017). These strategies aid in reducing *Striga* seed proliferation and slow down seed germination and growth (Silberg et al. 2021). Push-pull' is an approach that involves intercropping fields with a repellent and an attractive trap plant. It was developed to control *Striga* weed in resource-poor farming systems repelling *Striga* from the major food crops while simultaneously attracting it to a trap crop (Ndayisaba et al. 2020). The mechanism underpinning this is an allelopathic effect of intercrop root exudates in suppressing germination of *Striga* and hence only requires the intercrop component of the push–pull system (Khan et al. 2010). The *Desmodium* root secretes compounds that promote the germination and development of parasitic *Striga* weeds prevent them from adhering to host roots through radical growth inhibition, which causes the depletion of *Striga* seed bank, below one *Striga*/m^2 in five years under push-pull conditions, and at least four *Striga*/m^2 in non-push-pull conditions (Ndayisaba et al. 2020). However, most cultural control strategies are perceived as unaffordable, labour-intensive, impractical, or incompatible with other farm operations (Sibhatu 2016) and have thus been scarcely adopted.

1.4.2. Chemical Control

Chemical compounds that imitate SLs actions present a rising advancement in *Striga* management in pearl millet and sorghum production. This method involves the use of different chemicals such as dihydrosorogoleone, sesquiterpene and kinetin (Babalola and Odhiambo 2008; Cardoso et al. 2011; Zwanenburg et al. 2016). Known as germination stimulants for parasitic plants, SLs constitute a new class of plant hormones essential for *Striga* control (Zwanenburg et al. 2016). The SL analogue MP16 was able to cause a maximum reduction of *Striga* emergence by 97% under greenhouse evaluation, while Nijmegen-1 analogue was able to cause 40% and 60% reduction of *Striga* emergence in pearl millet and sorghum fields, respectively, compared to the standard chemical GR-24. Though this method has been highly successful in greenhouse trials, it is still expensive for small-scale farmers (Samejima et al. 2016; Zwanenburg et al. 2016; Kountche et al. 2019).

1.4.3. Biological Control

The quest for an eco-friendly approach to reduce the adverse effect of agrochemicals on plants and soils has led to the discovery of biocontrol agents to control major crop pests and diseases (Raklami et al. 2019; Jabborova et al. 2020). Biological control is the deliberate use of living organisms to suppress, reduce or eradicate a pest population. Biological control of weeds includes using herbivorous insects, microorganisms, especially fungi, and smothering plants. *Fusarium oxysporum* f.sp. *Strigae* [*FOS*], a host-specific fungi of the genus *Fusarium*, is highly pathogenic against *S. hermonthica* (Mrema et al. 2020). *FOS* is a soil-borne fungal pathogen that has shown immense potential in suppressing the emergence and fecundity of different *Striga* sp. (Zarafi et al. 2015). It has the ability to destroy *Striga* before it penetrates the roots of its host by producing phytotoxic compounds such as fumonisin B1 (Elzein and Kroschel 2004; Rebeka 2007). *FOS* is host specific, highly aggressive against *Striga*, easy to mass produce and shows high levels of genetic diversity (Ciotola et al. 2000). When host seeds are treated with *FOS* and planted, the fungus grows well in the rhizosphere of the emerging host plant, parasitizes *Striga* sp., inhibiting their growth and development, stopping them from parasitizing the roots of host plants (Rebeka 2007).

Arbuscular mycorrhizal (AM) fungus enhances cereal growth and performance against *Striga* and facilitates plant assimilation of phosphorus (P), water, and micronutrients from the soil. The inoculation of AM fungi on maize cultivars decreases the incidence of *S. hermonthica* and increases nitrogen (N) and P uptake of plants (Bonfante and Genre 2010; Samejima and Sugimoto 2018). *Bacillus subtilis*, *B. amyloliquefaciens*, and *Burkholderia phytofirmans* have been able to reduce *Striga* infestation on sorghum by 47% in a screening evaluation (Mounde et al. 2015). Enzymes, such as xylanases, pectinase, and amylases released by Bacillus and Streptomyces species, can directly cause the decay of *Striga* seeds.

1.4.4. Host Plant Resistance

Host plant resistance is the most economical approach to control *Striga* because resistant cultivars can be grown with limited production input (Hess et al. 1992). *Striga* resistance is the ability of the host genotype to forestall *Striga* attachment, growth, and development while producing a higher yield than the susceptible genotypes (Ramaiah 1987; Ejeta and Butler 1993). Tolerance, on the other hand, is the ability of the host plant to maintain high biomass and yield compared to susceptible genotypes under the same level of *Striga* parasitism (Haussmann et al. 2000; Rodenburg et al. 2005; Hearne 2009). Host resistance has not been fully deployed to date, with only partial resistance being reported in several genotypes (Ramaiah 1987; Wilson et al. 2004; Mwangangi et al. 2021; Rouamba et al. 2022). Plants employ different mechanisms to resist and tolerate *Striga* infestation (Anitha et al. (2020).

1.4.5. Integrated *Striga* Management

Integration of multiple control methods also referred to as integrated *Striga* management (ISM), can be efficient and economical with better control of *Striga* under smallholder farmers' conditions (Tesso et al. 2007). Figure 1.1 depicts tri-trophic interactions for integrated control of *Striga* through resistant host genotypes compatible with a biocontrol agent (*FOS*). The picture pot rays the underlying mechanisms and principles of integrating the *Striga*-resistant genotype with *FOS* treatment. The system reportedly enhances the effectiveness of the biocontrol agent with ultimate yield gains in sorghum and maize. An ISM is considered the most cost-effective and environmentally friendly and can quickly be adopted by smallholder pearl millet farmers (Joel 2000; Hearne 2009).

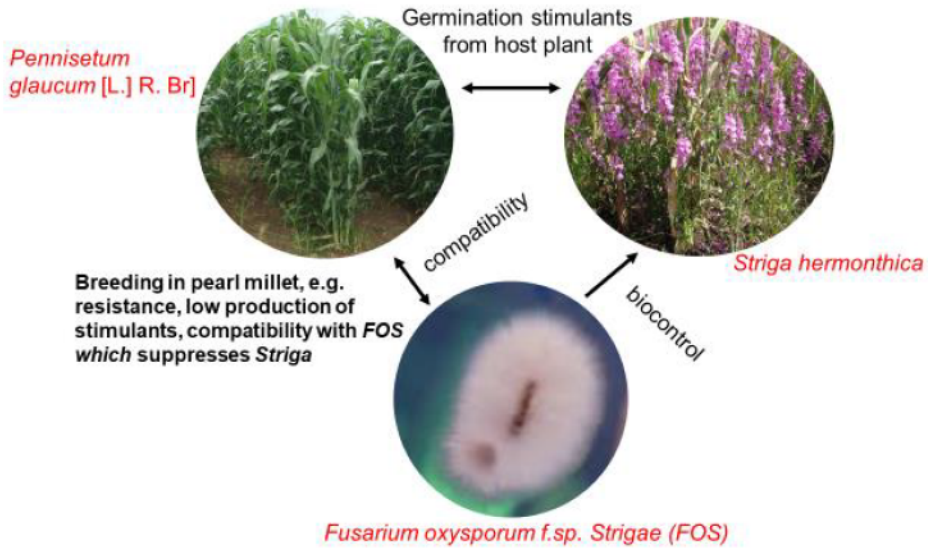

Figure 1.1. Schematic presentation of tri-trophic interactions for integrated control of *Striga* through resistant host genotypes compatible with a biocontrol agent (*FOS*).

1.5. Components of Host Plant Resistance

1.5.1. Root Architecture and stay-green trait

Field resistance to *Striga* parasites is attributed to root architecture and physiology. Plant roots serve as mechanical barriers that may resist haustorial attachment or avoid contact with pests held in seed banks (Ejeta 2000; Gurney et al. 2003). Antibiosis and hypersensitivity to *Striga* infection are due to active resistance functions in the host plants, barring the parasite from contact with the host. Haustorial interference with the host's root surface causes biochemical responses that cause histological changes, such as necrosis of the host's root cells to prevent penetration of distal cells of *Striga*. A genotype with hypersensitive resistant mechanisms inhibits parasitic attachment and growth and deprives its access to

nourishment to reach maturity (Ejeta 2000). However, the host in a given environment might succumb to one *Striga* population but resist another community of the same parasite (David et al. 2022). Hence, reliance on root architectural resistance alone may be insufficient and unreliable. Furthermore, host plants might escape infection by reduced root biomass and architecture that avoids the soil layer in which the parasite seeds are more common (Wegmann et al. 1991).

Although the physiology of the polygenic stay-green phenotype is not fully understood, there is evidence from studies in multiple species connecting aboveground stay-green phenotypes with root traits that have been measured ex-situ (Williams et al. 2022). In sorghum, multiple quantitative trait loci (QTL) for stay-green have co-located with QTL for nodal root angle (Borrell et al. 2014). Similarly, in barley, Gous et al. (2016) mapped QTL for stay-green traits located near QTL associated with root length, root dry weight, and root-to-shoot ratio (Arifuzzaman et al. 2014). Williams et al. (2022) demonstrated in barley, a trend in which stay-green lines had a higher percentage of their root length deeper in soil than non-stay-green lines.

High photo-inhibition rates per unit leaf are typical on most cereals infested by *Striga* spp. Therefore, maintaining high photosynthetic efficiency under heavy *Striga* infestation is critical to increasing tolerance levels to the parasite (Gurney et al. 2003). The stay-green or delayed senescence trait determines the ability of plants to keep their leaves in the active photosynthetic stage to sustain photo-assimilate production and reproductive efficiency under biotic and abiotic stress conditions. *Striga* damage and drought symptoms exhibit rapid leaf senescence and degeneration of leaf chlorophyll. Augmenting the stay-green trait with other *Striga* resistance components may increase host defence and boost yield gains. Ribaut et al. (2009) and Luche et al. (2015) reported that improvements in grain yield under *Striga* infestation have been associated with delayed senescence. Delayed senescence is expressed in two forms, namely functional and non-functional stay green characteristics. Practical stay-green plants continue to grow under conditions that lead to senescence in the wild type (Thomas and Howarth 2000). Non-functional stay-green plants are defective in the breakdown of chlorophyll and remain green even though chloroplasts are no longer photosynthetically active (Thomas and Howarth 2000). The former is relevant to *Striga* tolerance as mutants with functional "stay-green" have prolonged photosynthetic activity and delayed senescence compared to standard genotypes. In maize, genomic regions conferring stay-green have been mapped within the genome. Three stay-green QTLs, qsg-1, qsg-4, and qsg-8, have been identified under low nitrogen conditions (Ribeiro et al. 2018), showing the importance of the stay-green trait in *Striga* populations.

1.5.2 Escape

The ability of genotypes to complete reproductive life cycle before peak pest pressure, moisture deficit or disease outbreak is defined as ‘escape’. Selection for *Striga* escape through early maturity can reduce yield

loss due to the parasites and their derived phytotoxins (Rich and Ejeta 2008). Evaluating drought-tolerant extra early germplasm under *Striga* infestation is fundamental in breeding for early maturity. Ultra-early cultivars that complete their life cycle before the continuous effects of multiple *Striga* infestations are required where terminal drought stress jointly occurs with the parasite (Wegmann et al. 1991).

1.5.3. *Striga* Resistance Genes

Resistance to *Striga* appears to be complicated, based on a chain of resistance mechanisms deployed by the host plant. Efforts to understand the inheritance of traits associated with resistance to *Striga* have yielded mixed results, with relative success in sorghum and only brief progress in pearl millet. Kountche et al. (2013) reported the presence of quantitative resistance to *S. hermonthica* in a diversified gene pool of cultivated pearl millet under field conditions. Pearl millet landraces such as M141, M239, M029, M197, M017, and KBH have been reported to possess *Striga* resistance genes (Kountche et al. 2013). The introgression of multiple resistance genes in a single millet cultivar would provide stronger resistance to *Striga* (Kountche et al. 2016). Although conventional breeding has significantly contributed to crop improvement for *Striga* resistance, particularly in sorghum and pearl millet, this approach has generally been slowed when targeting the complex quantitative resistance trait to *Striga*. Thus, the development of molecular markers offers an opportunity to identify resistant genes in wild relatives and resistant varieties of related species (Ejeta and Gressel 2007; Rispail et al. 2007). This may facilitate the pyramiding of multiple resistance genes into the agronomically desirable elite and locally adapted *Striga* susceptible varieties (Kountche et al. 2016).

1.6. Screening for *Striga* Resistance in Pearl Millet

Several screening techniques were reported (Berner et al. 1997; Haussmann et al. 2000). These included double-pot, Pasteur pipette, root-slope, sandwich, and antihaustorial. Screening in pots requires growing the host in pots artificially inoculated with *Striga* seeds. *Striga* infestation in pots is more definite than in artificially infested fields (Rao et al. 1983). The agar-gel assay developed by Hess et al. (1992) provides a relatively easy means for screening host genotypes for low *Striga* seed germination stimulant production. These screening techniques used in other crops can be adapted to screen pearl millet for *Striga* resistance breeding.

1.7. Breeding for *Striga* Resistance

1.7.1. Conventional Breeding

Considerable efforts have been made in breeding for *Striga* resistance in cereals, and modest progress has been achieved in developing improved varieties (Yacoubou et al. 2021). The identification of

potential sources of resistance is the first step of all *Striga* breeding programmes. Crossing complementary parents with resistance genes and agronomic traits followed by recurrent selection increases the integration of *Striga* resistance genes.

This method will build multigenic resistance that could be sustainable over time and effective for the control of the parasitic weed (Badu-Apraku et al. 2012; Menkir and Kling 2007). Recurrent selection has been used to develop the first experimental pearl millet *Striga*-resistant variety (Kounche et al. 2013). In maize breeding, *Striga* damage symptoms and counts were reduced by 3% and 10% per cycle of recurrent selection, and grain yield increased by 16% (Menkir et al. 2004). The half-sib as well as full-sib selection schemes are ways to develop composite populations with moderate resistance to *S. hermonthica* by allowing few *Striga* attachments compared to susceptible genotypes (Hallauer 1992; John and Sleeper 1995; Menkir et al. 2004). Conversely, the availability of donor parents with *Striga* resistance could facilitate the introgression of a favourable gene using backcrossing (Badu-Apraku et al. 2017).

1.7.2. Marker-Assisted Selection

Molecular marker techniques are powerful tools in plant breeding and genetic analysis. Marker-assisted selection (MAS) is an indirect selection procedure to identify a trait of interest (e.g., *Striga* resistance) based on a marker linked to the trait rather than on the phenotypic trait *per se* (Ribaut et al. 2001), allowing the performance of a selected phenotype to be predicted at early generation (Yacoubou et al. 2021). Using simple sequence repeats (SSRs) and single nucleotide polymorphisms (SNPs) markers, some elite genotypes for the breeding of *Striga* resistance were selected, and new markers have been identified, which significantly contributed to the differentiation of *Striga* tolerant and susceptible genotypes (Bawa et al. 2015; Shayanowako et al. 2018). Quantitative trait locus (QTL) for *S. hermonthica* resistance from local populations have been successfully transferred through backcross breeding into adaptable maize populations using MAS (Rich and Ejeta 2008). *Striga* resistance QTL were discovered in sorghum and rice (Atera et al. 2015; Yasir and Abdalla 2013; Yohannes et al. 2016; Ali et al. 2016) while SNPs markers associated with *Striga* emergence count were reported by Dawud et al. (2018) in pearl millet. Haussmann et al. (2004) identified and mapped QTL associated with *Striga*-resistance in the sorghum variety, N13, where a mechanical barrier is the suggested mechanism of *Striga* resistance. The identification of *Striga*-resistance QTL for pearl millet will ease the transfer of candidate genes into adaptable pearl millet varieties.

Developing a marker-assisted selection scheme for enhancing quantitative *Striga* resistance in pearl millet shortens the breeding cycle. Due to low genotyping costs (Elshire et al. 2011), more significant numbers of entries could be screened for markers linked to resistance alleles, followed by field phenotyping of a selected subset of the entries with an increased selection intensity. When the field phenotyping method successfully differentiates the tested entries, the results can be re-calibrated to have the marker-based selection index (Kountche et al. 2013).

1.8. Genetic Resources of Pearl Millet for *Striga* Resistance and Economic Traits

1.8.1. Landraces

Landraces are novel sources of genetic variation for breeding based on their desirable genetic compositions for agronomic and quality attributes. Many accessions of pearl millet are curated in limited gene banks and databases globally (Table 1.1). There is a need to screen for large numbers of memberships to identify the required and desirable germplasm and genes for breeding. The first selfed generation (S_1) gene pool is more efficient for utilising landraces when limited genetic information is available. The S_1 gene pools are mixtures of selfed individuals from a more significant number of accessions, allowing for a more efficient evaluation of germplasm (Burton 1978, Hanna 1990). Furthermore, the S_1 gene pools allow to assess large populations and select the desired trait (s) more readily. Genetic diversity studies in landrace germplasm offer possibilities for their use in improving pearl millet open-pollinated and hybrids varieties (Langridge 2005; Varshney and Tuberosa 2007). In pearl millet (Wilson et al. 2004) and maize (Rich and Ejeta 2008), wild relative genotypes have been used as *Striga* resistance sources for variety development.

Table 1.1. Number of accessions curated and important gene banks and databases of pearl millet

Number of accessions	Institution/ country	References
3,082	Southern African Development Community (SADC)/Matopos, Zimbabwe	Monyo 1998 Upadhyaya et al. 2012
24,663	International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)/Patancheru, India	Mathur 2012,
3,968	Institute of Research for Development (IRD)/France	www.genebank.icrisat.org
3,821	Canadian Genetic Resources (CGR)/Saskatoon, Canada	
1,283	Germplasm Resource Information Network (GRIN)/Beltsville, USA	Yadav et al. 2007

1.8.2. Mutation Breeding

Kiruki et al. (2006) reported the first *Striga*-resistant mutant maize varieties (K9908, K9910 and K9911). The varieties had stable performances in *Striga*-infested fields in western Kenya. A mutation at LGS1 locus causes quantitative and qualitative alterations in the SL content of root exudates, significantly reducing the germination stimulant's action without negatively impacting productivity (Gobena et al. 2017). Nikièma et al. (2020) identified seven *Striga*-resistant mutants (SA38M5, SA188M6, GK715M4, GK225M5, IC47M5, IC83M5 and IC17M6) among sorghum mutants generated from gamma irradiation. For the performance and estimation of the genetic variability study, M3 population of pearl millet treated with different doses of gamma rays showed high heritability for panicle diameter, number of nodes per plant and stem diameter (Maryono et al. 2020).

Induced mutation is a powerful tool in pre-breeding in pearl millet to generate new breeding populations to identify *Striga*-resistant mutants and cultivar development.

1.8.3. Hybrid Varieties

Hybrid varieties are produced through controlled crosses between parental lines with known heterotic patterns and high heterotic responses. They represent the first generation (F_1) originating from the cross. In pearl millet, hybrids are developed as follows: i) development of inbred lines in the various original populations, ii) test crosses between the different inbred lines to find the best hybrids, and iii) production of hybrid seed for the market (Arncken and Dierauer 2006). Hybrid seed production requires efficient cross-pollination methods to keep production costs low (Duvick 2009). Hybrids outyielded local varieties by 10-15% in pearl millet (Yadav and Rai 2013). However, the new hybrids could not be adopted because of the lack of efficient seed production programs and their limited genetic superiority (Yadav et al. 2021). Although hybrids are known and desirable for their high productivity and quality, they have shown reduced disease resistance compared to the open-pollinated varieties (OPVs) with innate defence traits (Schroeder et al. 2013). It is, therefore, vital to understand the genetic make-up of the parents used to develop hybrids with enhanced resistance to *S. hermonthica* (Yacoubou et al. 2021). Pearl millet hybrid derived from crosses between *S. hermonthica* resistant and susceptible parents were reported to be susceptible due to the recessive genes conditioning resistance which were masked by dominant genes (Haussmann et al. 2000; Rouamba et al. 2022). Haussmann et al. (2000) reported that both parents of a hybrid should be selected for *Striga* resistance. Hess and Ejeta (1992) and Kling et al. (2000) reported that hybrid vigour can provide a degree of tolerance to *Striga* in sorghum and maize, which is reflected in reduced yield depression under conditions of *Striga* infestation. Maize hybrids varieties with *Striga* resistance have been reported by Menkir et al. (2004) and Karaya et al. (2012). This suggested that hybrid breeding can offer *Striga* resistance which can also be exploited in pearl millet breeding.

1.8.4. Synthetic Varieties

Lonnquist (1949) defined a synthetic variety as an open-pollinated population formed by inter-crossing selfed plants or lines that are subsequently maintained by mass selection. The term synthetic variety has been used to designate a range kept from open-pollinated seed following its synthesis by hybridising all possible combinations among several selected genotypes subjected to a combining ability test. The components of a synthetic variety could be inbred or mass-selected populations (Mandal 2014). The merit of synthetics has been observed in sorghum cultivars and demonstrated average superiority of 18% for grain yield under *Striga* infestation (Haussmann et al. 2000). Host plant damage was significantly reduced in synthetic maize populations resistant to *Striga* (Kim et al. 1998). Synthetic varieties partially utilise

heterosis because some inbreeding occurs to open pollination in later generations (Abdaluh and Ali 2013). Being cross-pollinated crop, developing pearl millet synthetic variety with *Striga* resistance may contribute to *Striga*-resistance stability over time.

1.9. Genomic-Assisted Breeding

1.9.1. Quantitative Trait Loci (QTL) Analysis

Quantitative traits are useful to plant breeders. Most of the economic traits have quantitative inheritance. A QTL is a region on the genome that may comprise one or more functional genes. In maize, the resistance to *S. hermonthica* is regulated by many genes or QTL with small additive genetic effects (Rodenburg et al. 2006; Shayanowako et al. 2020). QTL related to *Striga* damage rating and *Striga* emergence count have been identified in maize by Badu-Apraku et al. (2020), including *qepp-3, qepp-8.1, qsd-5.1, and qsc-3.1*. The identification of QTL associated with *Striga*-resistance/tolerance would facilitate rapid development of *Striga*-resistant/tolerant pearl millet genotypes using MAS, due to the polygenic nature of host–parasite relationship and its interaction with environmental factors after validation (Gedil and Menkir 2019). In SSA, little progress has been reported on the detection of QTLs or genes for *Striga* resistance (Yacoubou et al. 2021). MAS used in maize may serve as a model tool in pearl millet *Striga* resistance breeding programs.

1.9.2. Next-Generation Sequencing (NGS)

Next-generation and conventional sequencing technology have been used to elucidate the molecular events underlying *Striga* resistance (Yoshida et al. 2010). *Striga* genomes have a typical complex angiosperm genome with a size of 615 Mb for *S. asiatica,*1425 Mb for *S. hermonthica* and 2460 Mb for *S. forbesii*, suggesting several polyploidization events (Schneeweiss et al. 2004). Next-generation sequencing technology has increased available transcriptional data for *S. hermonthica* and related species (Spallek et al. 2013).

Genomics-assisted breeding is one of the most promising developments that have implications for imparting genetic gains in pearl millet breeding. Genomic selection improves the breeding program's precision and efficiency (Yadav et al. 2021). The whole-genome resequencing of Pearl Millet Inbred Germplasm Association Panel, mapping population parents, and elite hybrid parental lines helped develop >32 million repositories of genome-wide SNPs (Varshney et al. 2017). These developments offer opportunities to map and deploy genes of agronomic importance rapidly and also to resequence lines to mine and map genes of interest in pearl millet (Yadav et al. 2021). NGS based on the repository of genome-wide SNPs could substantially accelerate knowledge in *Striga*-resistance breeding to deliver pearl millet varieties with *Striga* resistance and farmers' preferred traits. The inherent biases and ambiguous alignment of repetitive genetic and nongenetic elements

lead to highly fragmented draft genome assemblies that may hinder the use of NGS and complicate studies of hidden indels and structural variants (Sedlazeck et al. 2018). Ramu et al. (2023) reported the following three genomes: Tift, ICMR 06777 and 843 B assembled using PacBio HiFi sequencing, de novo contig assembly, and hybrid scaffolding , in that order, with Bionano optical maps, which are more contiguous and larger in size than Tift-2017.

1.10. Genetic Engineering and Genome Editing

1.10.1. Genetic Engineering

Genetic engineering involves integrating genetic material through transformation followed by selection. Genetic engineering permits the transfer of resistance genes from any organism into a chosen crop. Genetic engineering can be used to enhance resistance against *Striga* by improving the strigolactone content of the host plant. Genetic resistance can either be adopted autonomously or as part of an integrated management system (Jamil et al. 2021; Kavuluko et al. 2021; Muchira et al. 2021; Mallu et al. 2022). In the case of *Striga* resistance, the main limitation to employing genetic engineering is the lack of well-defined resistance genes (Haussmann et al. 2000). The RNA interference (RNAi) technology has been explored as a genetic tool for engineering host resistance against parasitic weeds. This was to transform host plants with a plasmid encoding a double-stranded hairpin RNA (hpRNA) targeted against one or more genes of *Striga* (Runo et al. 2011; Yoder et al. 2009).

1.10.2. Genome Editing

Genome editing (also referred to as gene editing) is a set of tools enabling editing genes to enhance the genetic expression of an organism. It manipulates the specific gene loci to gain genome modifications, such as insertions, deletions or point mutations. Genome editing techniques were developed in the late 1990s with the discovery of homing and zinc-finger endonucleases, which direct DNA cleavage to particular sites within a genome. The three main genome editing tools currently used are ZFNs, TALENs, and CRISPR/Cas9 (ASSAf 2016). CRISPR-Cas9 is the most accurate and efficient genome editing technique (Barrangou 2015). Butt et al. (2018) reported that CRISPR/Cas9 system in translational research can be used for target improvement of plant architectural trait. The study showed that targeted engineering of CCD7 could improve crop yield and lower the risk of *Striga* infestation by increasing the number of tillers while significantly reducing *Striga* germination in rice.

1.11. Conclusions and Outlook

Pearl millet yield in SSA is low due to various biotic and abiotic factors. *Striga* causes yield loss of up to 100% in heavily infested fields. Cultural practices, chemical and biocontrol agent control measures are recommended for *Striga* management. However, the methods were not widely adopted by smallholder farmers because of their unavailability or high cost and *Striga*'s complex life cycle and prolonged seed dormancy in farmlands. *Striga* resistance varieties are cost-effective, environmentally friendly and affordable for smallholder farmers to control and reduce *Striga* infestations and improve pearl millet yields. Furthermore, integrated *Striga* management involving pearl millet genotypes with *Striga*-resistance and *FOS* compatibility is the most cost-effective, and environmentally friendly and can quickly be adopted by smallholder pearl millet farmers. Information presented in this review, including genetic resources, new breeding technologies, and innovations, assists in the precision and speed breeding of *Striga*-resistant cultivars. Overall, the review will guide the use of the best breeding strategies and accelerate the development of new pearl millet cultivars that are high yielding and resistant to *S. hermonthica* to reduce damage incurred by *Striga* infestations on farmers' fields in Burkina Faso and similar agro-ecologies.

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Chapter 2. Constraints to pearl millet (*Pennisetum glaucum* [L.] R. Br.) production and farmers' approaches to *Striga hermonthica* (Del.) Benth management in Burkina Faso

Abstract

Pearl millet (*Pennisetum glaucum*) is a staple food crop in Burkina Faso that is widely grown in the Sahelian and Sudano-Sahelian zones, characterised by poor soil conditions and erratic rainfall, and high temperatures. The objective of this study was to document farmers' perceptions of the prevailing constraints affecting pearl millet production and related approaches to manage the parasitic weeds *S. hermonthica*. The study was conducted in the Sahel, Sudano-Sahelian zones in the North, North Central, West Central, Central Plateau, and South Central of Burkina Faso. Data were collected through a structured questionnaire and focus group discussions involving 492 participant farmers. Recurrent drought, *S. hermonthica* infestation, shortage of labour, lack of fertilisers, lack of cash, and the use of low-yielding varieties were the main challenges hindering pearl millet production in the study areas. The majority of the respondents (40%) ranked *S. hermonthica* infestation as the primary constraint affecting pearl millet production. Respondent farmers reported yield losses of up to 80% due to *S. hermonthica* infestation. 61.4% of the respondents in the study areas had achieved a mean pearl millet yields of <1 t/ha. Poor access and the high cost of improved seed, and a lack of farmers preferred traits in the existing improved pearl millet varieties were the main reasons for their low adoption, as reported by 32% of respondents. *S. hermonthica* management options in pearl millet production fields included moisture conservation using terraces, manual hoeing, hand weeding, use of microplots locally referred to as *'zaï'*, crop rotation and mulching. These management techniques were ineffective because they do not suppress the below ground *S. hermonthica* seed, and they are difficult to implement. Integrated management practices employing breeding for *S. hermonthica* resistant varieties with the aforementioned control measures could offer a sustainable solution for *S. hermonthica* management and improved pearl millet productivity in Burkina Faso.

Keywords: agro-ecology; plant breeding; integrated pest management; pearl millet; production constraints; *Striga hermonthica*

2.1. Introduction

Pearl millet (*Pennisetum glaucum* [L.] R. Br., 2n = 2x = 14) is the sixth most important cereal crop in the world after wheat, rice, maize, barley, and sorghum [1]. The crop is adapted to arid and semi-arid environments and grows relatively well under low soil fertility conditions, outperforming other common cereal crops such as maize and wheat [2]. Approximately 22 million hectares of land in Africa are under pearl millet production with mean productivity of 1 ton ha^{-1} [3]. In Burkina Faso, the mean yield under the smallholder production system is estimated at 0.85 tons ha^{-1} compared to a potential yield of 3.00 tons ha^{-1} achievable under research conditions [3]. This yield gap can be attributed to biotic and abiotic constraints and socio-economic challenges. The key biotic constraints to pearl millet production are parasitic weeds (*Striga* species), bird damage, downy mildew, head miner, and the use of low-yielding landraces [4].

Drought stress and low soil fertility are among the major abiotic constraints affecting pearl millet production [4]. In Burkina Faso, pearl millet is mainly grown in the semiarid Sahelian and Sudano-Sahelian zones that are characterized by poor soils, low and erratic rainfall, and high temperatures. The intensity and frequency of biotic and abiotic stresses intensified by climate change have increased in sub-Saharan Africa (SSA), including Burkina Faso, which has increased the need for resilient crop cultivars [5].

Striga species are notorious parasitic weeds affecting pearl millet production in the Sahel and Sudano-Sahel regions [6]. There are 13 *Striga* species reported in Burkina Faso, with *Striga hermonthica* (Del.) Bentham and *S. gesneroïdes* (Willd) Vatke being the most devastating weeds of cereal and legume crops, respectively [7]. Yield losses due to *S. hermonthica* vary between 7 and 41% in the central zones, while up to 55% losses have been reported in the eastern zones of Burkina Faso [8,9]. The parasitic weed has a wide range of hosts, including rice (*Oryza glaberrima* Steudel and *O. Sativa* L.), maize (*Zea mays* L.), sorghum (*Sorghum bicolour* [L.] Moench), pearl millet, and fonio (*Digitaria exilis* (Kippist) Stapf) [7,10]. The wide host range, the easy dispersal of *S. hermonthica* seeds by animals and wind, and the seeds' ability to stay viable in the soil for about 14 years make it difficult to control the weed [6].

Farmers employ hand weeding, crop rotation, and botanicals such as a concoction powder prepared from pods of the African locust bean (*Parkia biglobosa* (Jacq.) R. Br. ex G. Don) and almonds of the shea tree (*Vitellaria paradoxa* C.F. Gaertn.) to control *S. hermonthica* [7]. These methods reduce the amount of *S. hermonthica* seed in the soil and improve soil fertility, but they have high labour requirements that limit their implementation and use. The use of chemical herbicides is not widely reported among smallholder farmers due to their high cost, limited access, and potential environmental hazards. In addition, the use of host plant resistance against *S. hermonthica* is limited by poor access to or the

unavailability of resistant varieties. A combination of effective *S. hermonthica* control methods is required to reduce *S. hermonthica* on pearl millet production in SSA.

The active participation of farmers in developing strategies to control *S. Hermonthica* is important to ensure high adoption of the developed strategies. It is also imperative to understand the important traits of a pearl millet variety that the farmers require to design and breed farmer-preferred pearl millet varieties. Participatory rural appraisal (PRA) is a multi-disciplinary research tool used to gain information from farmers through their participation in the initial stages of technology development. The tool helps to understand the farmers' knowledge, experiences, perceived and encountered production constraints, preferred traits, and their agricultural needs [10,11]. It emphasizes incorporating local knowledge in developing new interventions [12], which provides opportunities for local people to define their circumstances, conduct a situational analysis, and draft suitable plans for intervention. The PRA approach has been used to identify farmers' production constraints, preferred crop varieties, understand their agricultural environment, and develop suitable intervention strategies [13,14]. DeVries and Toenniessen [15] emphasized the need for farmers' involvement in all stages of cultivar development, including prioritizing target traits, selecting early breeding generations, and varietal evaluations to accommodate and promote their input in the breeding value chain.

Omanya et al. [16] lamented the low adoption rates of "improved" cultivars of pearl millet in Senegal, which was attributed to poor information dissemination among farmers and a disregard of farmers' opinions by the plant breeders during cultivar development. Farmers in Nigeria were involved in a PRA study and identified *S. hermonthica* infestation as the most important constraint of pearl millet production, and consequently, *S. hermonthica* resistance was the most preferred trait in pearl millet [17]. In Burkina Faso, PRA was employed to collect information on production constraints and farmers' preferred traits to guide pearl millet breeding programs and design new varieties that meet farmer needs and preferences [4]. However, the study area was limited to only three districts, and there were a few respondents. Therefore, the objective of the current study was to include more sites and more respondents to have a broader data set to document farmers' perceptions on the prevailing constraints affecting pearl millet production. Special emphasis was placed on their approaches to managing *S. hermonthica* to guide the future development and release of improved and locally acceptable varieties to farmers in Burkina Faso.

2.2. Materials and Methods

2.2.1. Description of the Study Sites

Burkina a tropical climate consisting of a long dry season (November to May) and a short rainy season (June to October). Pearl millet is cultivated in the short rainy season.

The study was conducted in the Sahelian and Sudano-Sahelian agro-ecological zones of Burkina Faso, where much of the pearl millet is produced (Figure 2.1). The Sahelian zone receives less than 600 mm of rainfall with monthly mean temperatures between 24 and 35.3 °C during the short rainy season between 2 and 3 months. The Sudano-Sahelian zone receives rainfall between 600–900 mm over 4 to 5 months, with mean temperatures between 25 and 33.5 °C [18]. The predominant soils are deficient in nitrogen and phosphorus due to soil erosion and high temperatures experienced in these regions [19].

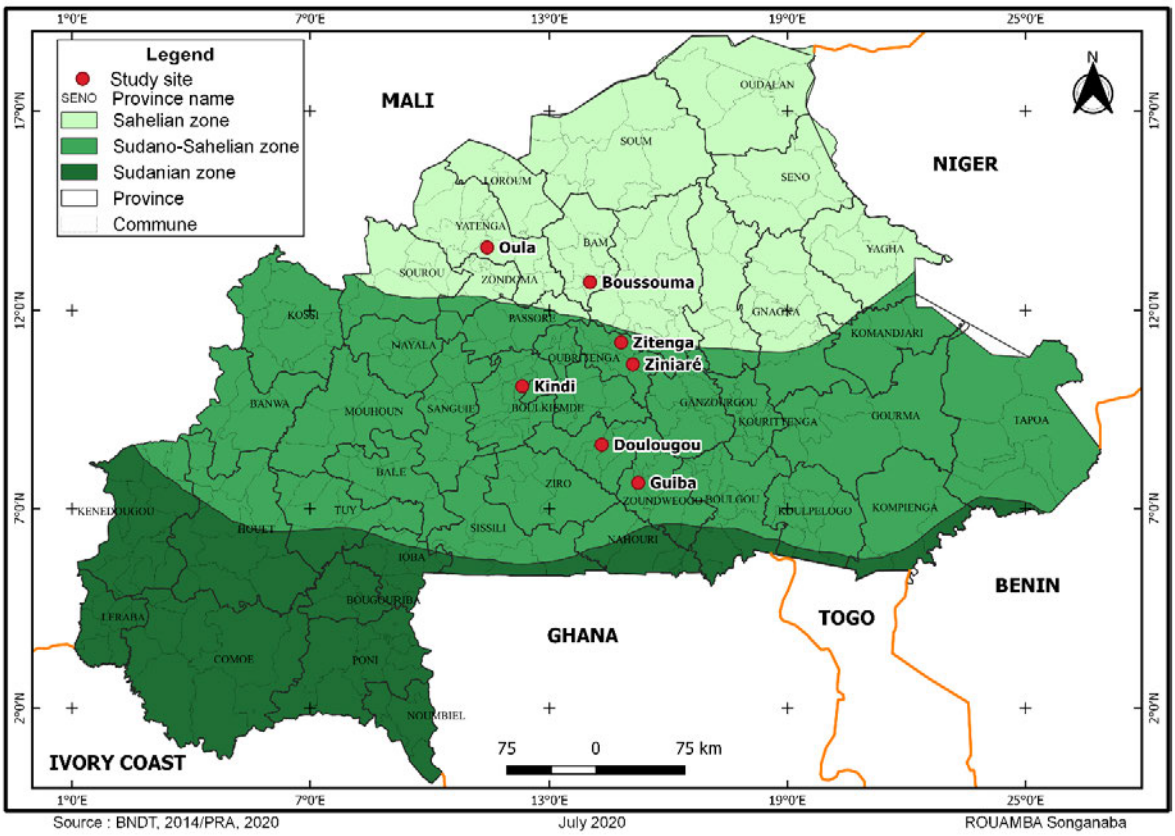

Figure 2.1. Map of Burkina Faso showing the common agro-ecological zones and the study sites.

2.2.2. Sampling Method

A hierarchical sampling method based on pearl millet production, *S. hermonthica* infestation, and the regions' administrative organisation was used to select the study sites (Figure 2.2). Secondary data on pearl millet production and *S. hermonthica* infestation were obtained from the Agriculture Department [20]. Two agro-ecological zones involved in large-scale pearl millet production were selected. Subsequently, five regions were identified based on *S. hermonthica* infestation, and accessibility. Three regions, namely Central Plateau, South Central, and West Central, were identified in the Sudano-Sahelian agro-ecological zone, while two regions, namely North and North Central, were selected in the Sahelian zone. Six provinces were selected where *S. hermonthica* regularly occurs in farmers' pearl millet production fields.

Additionally, the selected villages were known for their pearl millet production and *Striga* infestations. Farmers who experienced high *S. hermonthica* infestation in their fields were chosen after a preliminary survey. The sampling process was facilitated by a social scientist, breeders, key informants, and agricultural extension agents. A total of 492 respondents participated in the study. Three hundred farmers were interviewed using a structured questionnaire, and 192 farmers were part of the focus group discussion. Focus group discussions (FGD) were used to record farmers' perceptions, the main constraints in pearl millet production, and their strategies to coping with *S. hermonthica* infestations in the surveyed areas. The questionnaires were administered to farmers in the North, North Central, and South Central regions, while the FGD was conducted in Central Plateau and West Central regions in January and February 2020.

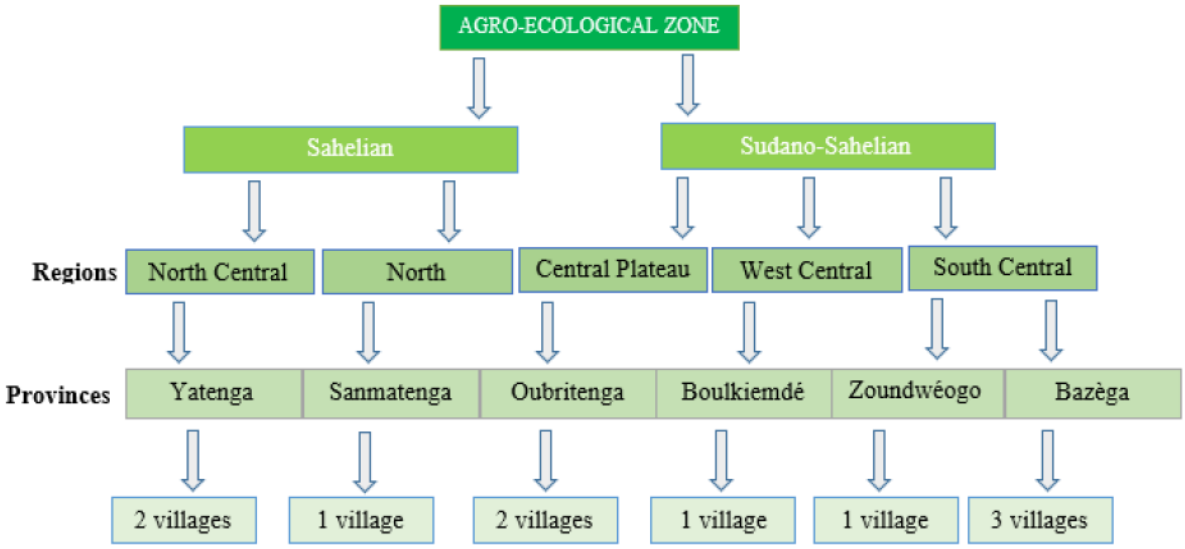

Figure 2.2. Sampling method cascading the selected zones, regions, provinces, and villages for the study.

2.2.3. Data Collection and Analyses

Data were collected through interviews using a structured open- and closed-ended questions and focus group discussions (Figure 2.3). Leaders of farmers' organisations in each village were involved in facilitating focus group discussions and administering the questionnaires. The questionnaires were pre-tested before conducting the actual data collection from farmers. The pre-test was undertaken to streamline the questionnaire and avoid ambiguous questions and improve the clarity of questions. The focus group discussions included an exhibition of photos with *S. hermonthica* and its associated damage, transect walks, and the discussions were recorded in writing and audio formats.

The constraints identified in the questionnaires were further explored in more detail and ranked using a pair-wise matrix technique during the focus group discussions.

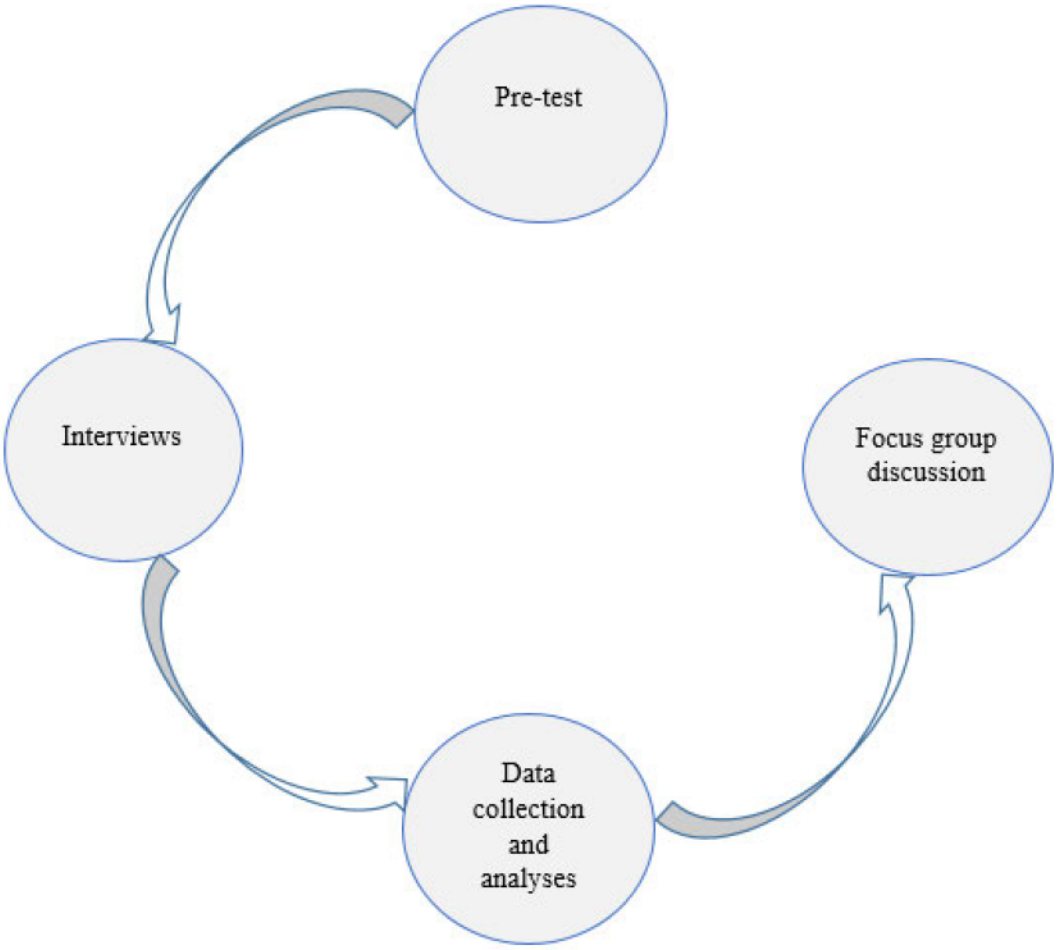

Figure 2.3. The interface of data collection and analysis during the study.

Qualitative data sets collected through the questionnaire were coded into district categories and subjected to statistical analyses using the 2005 version of the Statistical Package for Social Sciences software (SPSS Inc. Chicago, IL, USA). Cross-tabulations were computed, tables were constructed, and descriptive statistics were performed to summarise data from the questionnaires and FGDs. The pair-wise ranking method was used to prioritize the constraints raised during FGDs. To make statistical inferences, contingency Chi-Square tests were conducted to determine relationships among the different variables.

2.3. Results

2.3.1. Sociodemographic Description of Respondent Farmers

Three hundred smallholder farmers were interviewed individually using structured questionnaires, while 192 farmers were involved in focus group discussions. The demographic characteristics of participants are presented in Table 2.1. The number of male or female respondents varied significantly between the

regions (X^2 = 18.349; p < 0.000) across the different zones. The North zone had the least male respondents (36%), while South Central had 65% male representation (n = 100 per surveyed region). About 80% of the non-disabled population are involved in the agriculture sector in Burkina Faso.

Fifty-three percent of the farmers were above 50 years old, while 34% were between 30 and 50 (n = 300). The low number of individuals below 30 years indicates the rural to urban migration of youths in pursuit of urban livelihoods. The distribution of farmers in the different age groups showed similarities across the different zones. The majority (51%) of households had a family size of 1 to 10 individuals, while close to 40% had up to 20 individuals (n = 300) suggesting the high population growth rate in addition to the practice of polygamy in the rural areas. The trend was similar across the zones. Relatively few of the respondents (8.3%) had attended primary school, secondary school (1.3%), and college (0.4%) and were able to read and write. The remaining 90% did not attend formal schools and experienced difficulties in reading and writing (n = 300).

Table 2.1. Social and demographic information of respondent farmers during the study in three regions in Burkina Faso.

		Regions						
Variable	**Class**	**North Central**	**South Central**	**North**	**Mean**	**df**	**Chi-square**	***p*-value**
Gender	Male	43	65	36	48	2	18.349	0.000
	Female	57	35	64	52			
Family size	1-10	49	62	43	51.3	4	65.370	0.183
	11-20	45	32	42	39.7			
	> 20	6	6	15	9			
Age (years)	< 30	16	10	12	12.7	4	136.094	0.060
	30-50	43	61	55	53			
	> 50	41	29	33	34.3			
Marital status	Married	97	85	94	92	4	11.048	0.026
	Single	0	3	1	1.3			
	Widowed	3	12	5	6.7			
Education level	Literate	96	88	86	90	6	11.242	0.081
	Primary school	3	11	11	8.3			
	Secondary school	1	0	3	1.3			
	Graduate	0	1	0	0.4			

df, degrees of freedom, (%; n = 300).

2.3.2. Main Socio-Economic Activities in the Study Provinces

Crop production was the single most common source of income among the respondent farmers, with 36.7% affirming that they derived income from crop production (Table 2.2). The second most important income source was a combination of crop and livestock production, as indicated by 21.0% of the farmers. In comparison, about 18.0% of the respondents earned income from either livestock production alone or businesses such as in small shops (n = 300).

Most of the respondents derived their livelihood from agriculture in one form or the other. Farmers practice mixed farming—a combination of livestock rearing and crop production to pursue food security and livelihoods.

2.3.3. Pearl Millet Varieties Grown in the Study Areas

Several different crops were grown in the study area, as confirmed by the respondent farmers and observation made during transect walks (Table 2.3). The majority of the farmers used local varieties of pearl millet, while 32% adopted improved varieties. However, there were significant variations among the different regions. For instance, almost all of the farmers (93%) in the North Central region cultivated improved pearl millet varieties owing to the support given by the local non-governmental organisations NGOs. In contrast, in the South Central and North regions, 80 and 97% of respondents, respectively, cultivated local varieties. This is due to the limited research support to pearl millet when compared with other major crops such as maize and rice (n = 100 in each region).

Table 2.2. Income source according to the regions.

	Regions						
Income source	**North Central**	**South Central**	**North**	**Mean**	**df**	**Chi-square**	***p*-value**
Crop production	43	7	60	36.7			
Livestock production	4	41	11	18.7			
Crop and livestock production	49	0	14	21.0			
Tuckshop	3	45	5	17.7			
Crop production and tuckshop	0	0	8	2.7	16	2.326	0.000
Craftmanship	0	3	1	1.3			
Gardening	0	3	1	1.3			
Livestock production and tuckshop	0	1	0	0.3			
Processing of crop products	1	0	0	0.3			

df, degrees of freedom, (%; n = 300).

Table 2.3. Proportion of farmers using different crop varieties in the study area.

		Regions						
Crop	**Varieties**	**North Central**	**South Central**	**North**	**Mean**	**df**	**Chi-square**	***p*-value**
Pearl millet	Local	6	80	97	61	2	2,876	0.000
	Improved	93	0	3	32			
Sorghum	Local	14	79	43	45.3	2	106.840	0.000
	Improved	25	0	3	9.3			
Cowpea	Local	5	56	40	33.7	2	169.769	0.000
	Improved	81	12	6	33			
Maize	Local	0	50	23	24.3	2	166.425	0.000
	Improved	1	37	6	14.7			
Groundnut	Local	4	30	44	26	2	101.267	0.000
	Improved	34	0	0	11.3			
Sesame	Local	0	2	6	2.7	2	13.090	0.011
	Improved	3	0	0	1			
Bambara nut	Local	4	1	4	3	2	72.177	0.000
	Improved	31	0	0	10.3			
Rice	Local	0	5	0	16.7	2	18.557	0.001
	Improved	0	4	0	1.3			

df, degrees of freedom, (%; n = 300).

2.3.4. Status of Pearl Millet Production

Table 2.4 represents the mean area allocated to pearl millet production in the study sites between 2015 and 2019. About 23% of the interviewed farmers allocated less than one hectare (ha) of land to pearl millet production, while 62.6% have less than two hectares (n = 300). Ancestral or family land ownership was confirmed by 87% of the respondents (n = 300). The mean yield produced and reported is presented in Table 2.5. Most of the respondents (61.4%) harvest grain yields less than 1 ton ha^{-1}, while the mean yield achieved in *S. hermonthica*-free pearl millet fields was between 0.5 and 2.0 ton ha^{-1} (n = 300). Globally, pearl millet production is estimated with a mean yield of 0.89 ton ha^{-1} [21]. The trend of pearl millet production area during the last five years is the same across the study area. This is mainly attributed to a lack of agricultural lands leading to monoculture systems and lowering soil fertility and enhancing *Striga* infestation and development. In Burkina Faso a blanket recommendation of 100 kg nitrogen, phosphorus, and potassium (NPK) and 50 kg of urea fertilizers and 5 kg crop seed per hectare are used for pearl millet production.

Table 2.4. Trends of pearl millet production area in the study areas from 2015-2019.

		Production areas (ha) and number of respondents							df	Chi-Square	*p*-value
Year	**Regions**	**[0-1]**	**[1-2]**	**[2-3]**	**[3-4]**	**[4-5]**	**[5-6]**	**[6-7]**			
2015	South Central	26	10	0	0	0	0	0			
	North	15	43	25	8	1	1	0	12	119.895	0.000
	North Central	10	27	24	19	3	0	1			
Total		51	80	49	27	4	1	1			
2016	South Central	23	13	1	0	0	0	0			
	North	14	42	26	8	1	1	0	12	102.140	0.000
	North Central	11	27	25	20	2	0	1			
Total		48	82	52	28	3	1	1			
2017	South Central	27	25	4	1	0	0	0			
	North	16	44	28	8	1	1	0	12	91.024	0.000
	North Central	11	28	29	19	3	0	1			
Total		54	97	61	28	4	1	1			
2018	South Central	31	29	3	1	0	0	0			
	North	16	46	28	8	1	1	0	12	101.618	0.000
	North Central	12	30	29	21	2	0	1			
Total		59	105	60	30	3	1	1			
2019	South Central	49	26	4	1	0	0	0			
	North	14	48	26	8	1	1	0	12	113.365	0.000
	North Central	14	31	31	20	2	1	1			
Total		77	105	61	29	3	2	1			

df, degrees of freedom.

2.3.5. Constraints to Pearl Millet Production in Burkina Faso

Farmers mentioned that bird damage, drought, downy mildew, *Psalydolytta* spp, *S. hermonthica*, a lack of access to improved varieties, lack of fertilisers, labour unavailability, shortage of cash, lack of farm equipment, and poor soil fertility were the major challenges affecting pearl millet production (Table 2.6). Forty percent of the respondents ranked *S. hermonthica* infestation as the most important challenge

of pearl millet production (n = 300). *S. hermonthica* infestation is estimated to cause up to 80% yield losses in pearl millet production according to the respondents during FGDs. Yield loss accompanied by *Striga* damage that lead to poor seed germination, leaf chlorosis, stunted pearl millet growth and development and plant death under heavy infestation. A lack of access to fertilisers was ranked by 34.7% of the farmers as the most important constraint due to the high costs of inorganic fertilizers, which are prohibitive for most small farmers (n = 300).

Table 2.5. Mean grain yield of pearl millet and percentage of participants in the study areas.

	Regions						
Yield (kg/ha)	**North Central**	**South Central**	**North**	**Mean**	**df**	**Chi-square**	***p*-value**
[0-500]	8	69	15	30.7			
[500-1000]	51	5	36	30.7			
[1000-1500]	14	0	17	10.3			
[1500-2000]	8	0	22	6.7			
[2000-2500]	5	0	6	3.7			
[2500-3000]	8	0	2	3.3	20	3.199	0.000
[3000-3500]	2	0	2	1.3			
[3500-4000]	0	0	0	0			
[4000-4500]	0	0	0	0			
[4500-5000]	2	0	0	0.7			
[5000-5500]	1	0	0	0.3			

df, degrees of freedom, (%; n = 300).

Table 2.6. Number of participant farmers who ranked the constraints to pearl millet production in three regions of Burkina Faso.

		Regions						
Constraints	**Rank**	**North Central**	**South Central**	**North**	**Mean**	**df**	**Chi-square**	***p*-value**
Striga hermonthica	1rst	26	64	30	40			
	2nd	48	17	7	24	6	43.524	0.000
	3rd	24	15	4	14.3			
	4th	2	1	0	1			
Lack of fertilisers	1rst	47	16	41	34.7			
	2nd	47	36	32	38.3	6	41.471	0.000
	3rd	4	15	6	8.3			
	4th	0	8	0	2.7			
Lack of cash	1rst	25	3	16	14.7			
	2nd	3	4	22	9.7	6	37.008	0.000
	3rd	21	5	15	13.7			
	4th	26	12	5	14.3			
Drought	1rst	2	10	5	5.7			
	2nd	2	33	8	14.3	6	64.906	0.000
	3rd	26	9	10	15			
	4th	22	2	1	8.3			
Lack of improved varieties	1rst	0	3	1	1.3			
	2nd	0	4	3	2.3	6	8.876	0.181
	3rd	2	23	4	9.7			
	4th	3	24	1	9.3			
Shortage of labour	1rst	0	0	3	1			
	2nd	0	1	12	4.3	6	23.185	0.001
	3rd	4	18	5	9			
	4th	0	1	1	0.7			

Df, degrees of freedom, (%; n = 300).

2.3.6. *S. hermonthica* Infestation and Control Strategies

Almost all of the farmers (99%) recognized the negative impact of *S. hermonthica* on pearl millet growth and yield (n = 300). They understood the need for weed management for yield improvement. Hand-weeding of *S. hermonthica* plant and fertilizer application was the main *S. hermonthica* control measures reported by 90% of the respondents (Table 2.7) (n = 300). These methods are believed to reduce the *S. hermonthica* seed bank in the soil. Hand weeding was practiced by 34.7% of the farmers, while a combination of weeding by hand and hoe was the next most common method used by 31.0% of the farmers. Very few farmers used crop rotation and herbicides due to the lack of arable land (n = 300).

Table 2.7. *S. hermonthica* control measures used by farmers.

***S. hermonthica* control measures**	**Regions**						
	North Central	**South Central**	**North**	**Mean**	**df**	**Chi-square**	***p*-value**
Hand weeding	57	47	0	34.7	26	3.063	0.000
Hand weeding and hoeing	0	21	72	31.0			
Crop rotation, intercropping, and hand weeding	26	0	0	8.7			
Use of organic manure and hoeing	0	8	0	2.7			
Intercropping with cowpea and hand weeding	5	0	0	1.7			
Intercropping, hand weeding	5	0	0	1.7			
Hoeing	0	0	4	1.3			
Crop rotation and hand weeding	3	0	0	1.0			
Crop rotation and intercropping	2	0	0	0.7			
Micro plots, crop rotation, hand weeding	1	0	0	0.3			
Crop rotation and hand weeding	1	1	0	0.7			
Hand weeding and use of herbicides	0	0	1	0.3			
Hand weeding and use of inorganic fertilisers	0	1	0	0.3			
Use of inorganic Fertilisers	0	1	0	0.3			

df, degrees of freedom, (%, n = 300).

The farmers used various soil moisture conservation methods (Figure 2.4, Table 2.8), as a tool to control *S. hermonthica*. Terraces, mulching, the use of micro plots or planting holes (locally referred to as *zai*), ridges, and grass strips were some of the techniques used for moisture conservation and to suppress the impact of *S. hermonthica* (Figure 2.4, Table 2.8) (n = 300). Terraces, mulching, ridges, and grass strips are used to reduce ran off during the raining season, allowing water to be conserved and infiltrate into the soil. Micro plots or planting holes is a traditional technique used to conserve moisture and increase soil fertility to favour pearl millet production.

Table 2.8. Percentages of participant farmers who reported the use of moisture conservation methods in the study areas.

	Regions						
Moisture conservation method	**North Central**	**South Central**	**North**	**Mean**	**df**	**Chi-square**	***p*-value**
Terraces	99	77	89	88.3			
Mulches	0	13	0	4.3			
Ridges	0	5	0	1.7	8	42.885	0.000
Micro plots/planting holes	0	2	3	1.7			
Grass stripes	0	1	0	0.3			

df, degrees of freedom, (n = 300).

(A)

(B)

(C)

(D)

(E)

Figure 2.4. The common soil moisture conservation methods in pearl millet production fields in Burkina Faso to suppress *S. hermonthica* infestation. Note: (**A**) = terrace, (**B**) = ridge, (**C**) = grass strips, (**D**) = micro plots or planting holes (zaï), and **E**: field/crop of pearl millet (Photo by Rouamba 2020 (**A**, **B**, **E**); Botoni et Reij, 2001 (**D**), GIZ 2012 (**C**). *S. hermonthica* infestation. Note: (**A**) = terrace, (**B**) = ridge, (**C**) = grass strips, (**D**) = micro plots or planting holes (zaï), and (**E**): field/crop of pearl millet (Photo by Rouamba 2020 (**A**, **B**, **E**); Botoni et Reij, 2001 (**D**), GIZ 2012 (**C**).

2.4. Discussion

2.4.1. Social and Demographical Description of Respondent Farmers

The study found an almost equal representation of female (52%) and male (48%) respondent farmers involved in pearl millet cultivation in the study areas (Table 2.1). The active participation of women pearl millet farmers is critical in pursuing food security in the country. Women play important roles in crop production and strengthening social networks [22]. The participation of women in this study was important to facilitate discussions and capture women farmers' perspectives because they are often underrepresented in agricultural interventions. It is also important because the lessons will cascade down to family and households, given women's multiple roles in providing household welfare. Previously, more female farmers were reported to be involved in producing crops such as Bambara groundnut in Ghana and improved agricultural technologies and practices in sub-Saharan Africa compared to male farmers [23,24].

Most participants were between 30 and 50 years of age and married (Table 2.1), an appropriate and active demographic group for decision-making, farm operations, and participation in the local economy. In African tradition, age and marital status are highly influential traits for making decisions such as the type of crop and variety to cultivate and land allocation that an individual can make in a household, directly impacting pearl millet production. Thus, having the majority of the participants in this demographic group was important to obtain relevant information, since most respondents were experienced in pearl millet production and encountered the constraints they perceived to be important, know some management options, and influence decisions made in the household. For instance, youths and widowed female farmers are usually at the bottom of the decision-making pyramid as they usually take directives from an older and male household head. In addition, household dynamics are also determined by family size, especially for farming operations. Most subsistence farming operations are carried out by family members [25]. Households with many family members can carry out diverse farming operations, particularly during the harvesting and processing season when labour is scarce [26]. This gives such households with large families the advantage of being able to farm on larger areas. There were no significant differences among the different zones in terms of family sizes because, in Burkina Faso, families are large, often with over eight people per household, due to the extended family system prevalent across the country [27]. Despite the large families, the farmers owned small landholdings, which negatively impacted their ability to expand their production, leading to inefficient labour practices. The small landholdings are traditionally owned along ancestral lineage and controlled by the most senior male of the family [28].

Most farmers had no formal education (Table 2.1), which will complicate communication processes, such as extension services, adoption of improved technologies, and access to information. Farmers with limited formal education are often unwilling to adopt new technologies and have shown a strong

tendency to rely on traditional knowledge and experience. Therefore, intervention strategies that include a change in farmer behaviour will likely be well-received as the level of education increases among the farmers. Literate farmers usually take the initiative and participate in developmental projects to improve agricultural practices. In contrast, farmers with little or no education are usually passive, depend on receiving information and are not proactive in participatory approaches to find solutions [29]. The low literacy rate among farmers found in this study corroborated earlier findings reported by PNDES [30]. The education level among farmers has strong implications for devising intervention strategies to improve agricultural productivity in developing countries. Farmers with strong educational backgrounds could be useful as agents to gather information regarding new interventions and play important roles as leaders in technology adoption [26].

2.4.2. Main Socio-Economic Activities in the Study Provinces

Many of the respondents derived their livelihood from agriculture in one form or the other (Table 2.2), as is typical in most developing countries. Sorgho [31] estimated that agriculture accounted for 76.3% of Burkina Faso's economy, showing that it was integral to sustaining livelihoods. However, agriculture faces several challenges, including low mechanization levels for intensifying production, poor sustainability, and a lack of agricultural credit access that impede agricultural expansion [30]. These challenges limit agricultural productivity and make farming communities vulnerable to natural disasters such as severe droughts. The farmers in the study sites are highly vulnerable because they have no alternative sources of food or money if there is a crop failure or their livestock dies. It is crucial to build a resilience in their systems against unexpected stresses notably from climate change. One method might be to increase the participation of the local farmers in value addition on their agricultural products. Some of the respondents (17.7%) generated some income by selling household wares such as groceries and toiletries in small shops. Still, they alluded to the fact that such enterprises' viability and profitability depended on a good harvest in the area, which creates disposable income for the region (Table 2.2). During drought years, leading to crop failure and livestock deaths, other enterprises suffer significantly because most clients are farmers who depend on crop sales for disposable income to spend on household goods [32].

2.4.3. Pearl Millet Varieties Grown in the Study Areas

The farmers were cultivating a range of crops dominated by local varieties, common among subsistence farmers who often lack resources to buy seeds of improved varieties (Table 2.3). However, there were significant differences between the zones in terms of the pearl millet varieties cultivated. Varietal choices can vary due to localized challenges or opportunities. Farmers who have access to extension

services, agricultural inputs, and novel information usually cultivate more improved cultivars than farmers who live in inaccessible areas, farther away from agro-dealers. The majority of farmers in the North Central zone cultivated improved cultivars (Table 2.3). The widespread adoption of improved cultivars in North Central could be attributed to several agricultural and livelihood projects established with the support of various non-governmental organisations (NGOs) working with farmers and more active extension services in this region than in the other regions.

Many farmers used local varieties by retaining seeds for the next cycle of planting. For example, superior panicles of local pearl millet varieties would be selected and conserved for seed for the next season at harvest time. The use of retained seed is common among smallholder farmers in Africa, as reported in Uganda, where 92% of farmers used local varieties [33], and in Nigeria, where 80% of farmers used farm-retained seed [17]. However, the cultivation of local varieties is one factor contributing to the low yields attained by most farmers in the study areas (Table 2.5).

Local varieties are often highly adapted to their agroecology, perform relatively well in marginal environments, with minimal inputs, and have been selected for cooking qualities appropriate for preparing traditional foods [34]. However, many have low yield potential and lack uniformity compared to improved cultivars bred for yield. The adoption of improved varieties is limited by seed costs and a lack of access to seed by the local farmers. In addition, the improved varieties often do not meet cooking quality criteria [16].

In Burkina Faso, the commercial seed industry for traditional crops such as sorghum and pearl millet is not well developed. This limits seed distribution to distant communities in rural areas. Low adoption rates of improved cultivars may also be related to scepticism among the farmers for varieties that they are not familiar with, and sometimes the susceptibility to pest/disease of some improved varieties, which do not have essential farmer preferred traits [22]. Local pearl millet varieties were mainly used in the North, South Central, West Central, and Central Plateau regions. The predominance of local varieties in these regions is due to a poorly developed seed system, especially for neglected crops such as pearl millet, and a poor extension service in these regions. Farmers in these regions have little access to information, extension services, and seed supply, which leaves them entirely dependent upon farm-saved seeds of local varieties.

Improved varieties such as IKMP 5 and MISARI, which are medium maturing and have a high yield potential of above 2.00 tons ha^{-1}, were widely cultivated in the North Central region, where access to seed and to extension services was better established. The farmer-preferred traits in pearl millet in Burkina Faso have been documented by Drabo et al. [4]. They include large-sized panicles that are

compact and non-bristled, large grain size, medium plant height, early maturity, medium panicle length, and wide panicle diameter. In any breeding program, it would be vital to integrate these traits during cultivar development to ensure a high adoption rate for newly improved varieties of pearl millet in the study areas. It has been noted that involving farmers and other stakeholders during variety design and development increases adoption rates of improved cultivars [33]. A PRA provides an opportunity to bridge the gap between farmers' expectations and breeders' objectives for cultivar development. Previously plant breeders were more focused on developing modern varieties with high productivity in optimal and intensively managed environments. In reality, most farmers operate in sub-optimal environments and select varieties specifically adapted for production under marginal growing environments, with particular quality traits [22]. Breeders must understand farmers' conditions and expectations to breed suitable cultivars with high adoption rates.

2.4.4. Pearl Millet Production

This study showed that farmers allocated between one and three hectares of land for pearl millet production (Table 2.4), which is common for subsistence farmers who have small landholdings passed on from a previous generation under the traditional ownership system of inheritance. The land tenure system is a major challenge for agricultural development in smallholder communities. The landholdings are too small for substantial production, and there is no formal security of tenure, limiting the incentives for capital investments. In Africa, small farms of less than 2 ha represent 80% of all farms [35], contributing to non-commercialization and little or no mechanization of farm operations.

The farmers continue to use traditional and often inefficient agricultural practices because there is no incentive to improve methods because yields are often too low to offset investment costs on smallholdings (Table 2.5). The majority of farmers (87%) use ancestral land, while the female farmers were cultivating land belonging to their marital family. The lack of land ownership rights among women is also a challenge for agricultural development. Single or widowed female farmers are the most disadvantaged in land ownership because they cannot own land and may be removed from the lands that they are farming if the husband/male figure dies [28]. This takes away their decision-making powers in terms of cropping practices and contribution to agricultural development. In terms of variety design and development, female farmers' preferences are often overridden by the dominant male farmers, who are the landowners. This also affects cultivar adoption because cultivars that male farmers prefer are adopted to a larger extent than those cultivars that incorporate traits preferred by female farmers.
For instance, the adoption of improved maize varieties in Malawi by females was about 12% lower than their male counterparts [36], showing that women are often sidelined in varietal adoption.

2.4.5. Constraints to Pearl Millet Production

The farmers mentioned that damage from birds, drought stress, downy mildew disease, cantharid beetles, *S. hermonthica*, lack of improved varieties, lack of fertilisers, a shortage of labour at critical stages, a shortage of cash, a lack of equipment, and soil infertility were the most important challenges affecting pearl millet production in their environments. *S. hermonthica* infestation was ranked as the most important challenge to pearl millet production (Table 2.6). Almost all the farmers mentioned that they experience *S. hermonthica* infestation in their fields. A transact walk across the farms showed that *S. hermonthica* infestation was widespread. The lack of resources for *S. hermonthica* control, poor soil fertility, and drought contributed to the proliferation of the weed in this area. The abundance of *S. hermonthica* is attributed to its ability to produce many seeds that remain viable for many years, even under harsh conditions [37]. The *S. hermonthica* weed is prevalent in most semi-arid regions of sub-Saharan Africa, north of central Tanzania.

Ouedraogo et al. [38] found that *S. hermonthica* was a devastating weed in sorghum, while Dawud et al. [17] also reported that *S. hermonthica* was the main constraint affecting pearl millet production in Nigeria. According to the respondents, *S. hermonthica* infestation can cause up to 80% yield loss in pearl millet, making it the most important constraint of pearl millet production. In some places, farmers ended up abandoning *S. hermonthica* infested pearl millet fields or replaced the pearl millet with sorghum, which is more tolerant to *S. hermonthica* [4,33]. The other important constraint to pearl millet production is that most farmers have limited access to fertilizers. The soils in the study area are sandy with low fertility levels, which increase *S. hermonthica* infestation and result in poor crop yields. The Sahel and Sudano-Sahel regions account for some of the most degraded and infertile soils in sub-Sahara Africa [7,9]. As a result, most soils require supplemental fertilizers to increase plant-available nutrients. Although pearl millet is relatively resilient and has a dense root system, the highly degraded nature of the soils provides minimal nutrients to support proper plant growth, which significantly reduces achievable yields.

The lack of access to financial resources, land tenure policies, and high fertilizer costs exacerbate the shortage and lack of fertilizer inputs. Suboptimal fertilizer use among farmers in marginal environments has also been reported across Africa [33]. Land shortages, a lack of access to extension services, a lack of land tenure resulting in a lack of access to financial credit, and high labour costs have been reported previously as constraints to pearl millet production [17,33]. These challenges will affect even improved cultivars of pearl millet. Therefore, it is essential to develop the agricultural support system parallel to cultivar design and development. It will be futile to deploy improved cultivars into a poorly developed agriculture system where farmers lack ancillary support to boost their agricultural potential. For instance, the lack of adoption of improved cultivars has been attributed partially to the non-performance

of some improved cultivars [39]. However, the inadequate support systems could be partly responsible for the poor performance of the improved cultivars. Thus, it is essential to improve the agricultural environment concurrently with variety design and development for the highest impact on crop productivity, food security, and rural farmer development.

2.4.6. *S. hermonthica* Infestation and Control Strategies

The farmers recognized that *S. hermonthica* was detrimental to plant growth and reduced yield potential. Therefore, they employed various measures to control the weed. The control measures included hand-weeding of *S. hermonthica* plant, weeding, and fertiliser application (Tables 2.7 and 2.8), which had varying success rates, depending on the extent of infestation and time of intervention. To a large extent, these methods helped reduce the *S. hermonthica* seed bank in the soil and conserve soil moisture, which increased yield potential. The methods were readily available to the farmers since they depend on family labour for these operations. Most farmers lack resources such as equipment or financial means to acquire pesticides, which leaves them with minimal options but to use hand weeding and hoeing. Crop rotations are not feasible due to limitations in the size of their landholdings and given the long life of *S. hermonthica* seeds. Most farmers own less than 3 ha of land, which is too small to allow effective crop rotation in controlling *S. hermonthica*. Previously, in Nigeria, 79% of farmers confirmed using hand weeding in *S. hermonthica* management, while only the remainder used hoeing and inorganic fertiliser application [17]. Inorganic fertilisers enhance pearl millet growth and development and its competitive ability against *Striga* infestation. Although these methods have been encouraged for many years, crop losses are still high due to a wide host range for *S. hermonthica* and the persistence of its seed in the soil for long periods [40]. Furthermore, these methods have many limitations, including being labour intensive and not managing underground *S. hermonthica* infestation of pearl millet roots before the parasitic plants emerge. Therefore, integrating breeding for *S. hermonthica* host resistance with other control measures, such as biological control, may offer a more viable solution to control *S. hermonthica* infestation [40].

2.5. Conclusions

Pearl millet is an important cereal crop adapted to arid and semi-arid environments. In Burkina Faso, pearl millet production is primarily constrained by *S. hermonthica* infestation, which is estimated to cause up to 80% yield losses. Many respondent farmers (68%) used local varieties with low yield potential, which are also highly susceptible to *S. hermonthica* infestation. Hand weeding and hoeing were the most commonly used methods to control *S. hermonthica*, although they are not very effective. The farmers lack resources such as labour, inorganic fertilizer, and finance to implement more effective

strategies against *S. hermonthica* and boost agricultural productivity. Therefore, an integrated management approach, which would involve breeding for *S. hermonthica* host resistance combined with other control measures, may offer a better option for managing *S. hermonthica* infestation in Burkina Faso. It is also recommended that variety design and development for *S. hermonthica* resistance be coupled with agricultural development such as improved extension services, increased access to information, access to micro-finance, and developing functional agro-input systems. The provision of an enabling environment would draw maximum benefits from improved varieties of pearl millet. Local farmers perceived that landrace varieties have good eating quality and adaptation to adverse effects.

2.6. References

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Chapter 3. Screening of pearl millet genotypes for resistance to *Striga hermonthica* and compatibility to a biocontrol agent, *Fusarium oxysporum* f.sp. *Strigae,* in the Sahel

Abstract

Pearl millet (*Pennisetum glaucum* [L.] R. Br., 2n = 2x = 14) is a nutritionally rich and climate-resilient food crop cultivated globally. It is a crucial staple crop in Burkina Faso and the dry Sahel region, encompassing Niger, Mali, and Senegal. However, the yield of pearl millet is relatively low in the region (< 0.85 tons ha^{-1}) due to *Striga hermonthica* (Del.) Bentham (*Sh*) infestation, bird damage, insect pests, diseases, and low-yielding open-pollinated landrace varieties. The objective of this study was to screen genetically diverse pearl millet accessions for *Sh* resistance and compatibility to a *Striga* bio-control agent, *Fusarium oxysporum* f.sp. *Strigae* (*FOS*), to select contrasting and promising parents for resistance breeding and production. One hundred and fifty genotypes were evaluated in *Sh* hotspot fields in the rain-fed and greenhouse conditions using an alpha lattice design and two replications in Burkina Faso. Significant differences were recorded among the tested pearl millet genotypes for the assessed agro-morphological and *Striga* resistance. Days to flowering was significantly delayed in the assessed genotypes due to *Sh* infestation. Applying *FOS* on pearl millet seed significantly reduced the mean *Striga* number in *Sh*-infested conditions. The following genotypes: IP-3098, IP-6112, IP-9242, IP-10579, and IP-11358 were identified as exhibiting *Sh* resistance and were compatible to *FOS*. The pearl millet genotypes supported few to none *Sh* emerged plants and had relatively low values under the *Striga* number progress curve. The selected genotypes are useful parents for breeding and integrated *Striga* management in Burkina Faso and related agro-ecologies.

Keywords: Biocontrol agent; Burkina Faso; *Fusarium oxysporum* f.sp. *Strigae;* Integrated *Striga* Management; pearl millet; resistance breeding; *S. hermonthica.*

3.1. Introduction

Pearl millet (*Pennisetum glaucum* [L.] R. Br., 2n = 2x = 14) is protein rich and valuable staple crop in the semi-arid regions of the world, including Burkina Faso (Bationo and Ntare 2000). Globally, pearl millet is grown for food, feed, and bioenergy on an estimated area of 32.1 million ha, with a total annual grain production of 30.5 million tons. Nearly 97% of the global pearl millet grain outputs are from sub-Saharan Africa (SSA) and Asia. In SSA, pearl millet is produced from an estimated area of 19.7 million hectares, of which 13.8 million ha is in West Africa, with a mean productivity of < 0.74 tons ha^{-1} (FAOSTAT 2022).

Pearl millet is widely cultivated in the semi-arid areas in Burkina Faso by small-scale farmers for household uses and the local market. In the country, an estimated area of 4.38 million ha is allocated for cereal crop production, of which 1.2 million ha is under pearl millet cultivation (FAOSTAT 2022). Grain productivity of the crop is < 0.81 tons ha^{-1} in Burkina Faso, which is considerably below the mean yield of 1.4 tons ha^{-1} reported in Asia under smallholder farmers' production conditions (FAOSTAT 2022). The low yields of pear millet in Burkina Faso are attributable to both biotic factors (e.g., infestation by *Striga hermonthica* (Del.) Benth (*Sh*), bird damage, insect pests, diseases, and the use of low-yielding landraces), abiotic stresses (e.g., poor soil fertility and recurrent drought), and socio-economic factors (e.g., lack of pre-and post-harvest technologies and poor access to finance and markets) (Rouamba et al. 2021).

Among the biotic stresses of pearl millet production, *Sh* stands out first, causing severe yield losses varying from 7 to 41% in the central (Zombré and Nikiéma 1992) and 28 to 55% in the eastern (Traoré and Yonli 2001) zones of Burkina Faso. *Striga hermonthica* affected areas are situated in the semi-arid regions of the Sahel and Sudano-Sahel zones. The zones are known for their poor soil fertility, low and erratic rainfall, and high temperatures, making them conducive environments to severe *Striga* infestation. Also, *S. hermonthica* decimates other cereal crops, including rice (*Oryza glaberrima* Steudel and *O. sativa* L.), maize (*Zea mays* L.), sorghum (*Sorghum bicolour* [L.] Moench), and fonio (*Digitaria exilis* [Kippist] Stapf) (Boussim et al. 2011; Mrema et al. 2016). However, the magnitude of yield losses due to *Sh* depends on the varieties grown, the level of the infestation, the prevailing climatic conditions, and the control measures (Mrema et al. 2016).

Striga is widely distributed in most agricultural fields due to the production of millions of seeds per plant and its quick dispersal via animals, crop seeds, water runoff, wind, and farming tools. The seeds can remain viable in the soils for more than 14 years (Emechebe et al. 2004). Damages caused by *Sh* on its host were about 75% before its emergence (Parker and Riches 1993). Reportedly, flowering time was delayed by two weeks in 40% of *Sh*-susceptible sorghum genotypes (Van Ast 2006).

Several control strategies have been recommended to reduce *Striga* infestations and yield loss. These include resistant varieties, biological agents, cultural practices and chemical control methods (Hearne 2009). Hand weeding, crop rotation, soil amendments using botanicals such as pods of the African locust bean (*Parkia biglobosa* (Jacq.) R. Br. ex G. Don) and almonds of the shea tree (*Vitellaria paradoxa* C.F. Gaertn.), inorganic and organic fertilizers application, and soil moisture management are the common cultural practices in *Sh* management (Boussim et al. 2011). Cultural practices help improve the soil structure and fertility, stimulate host plant growth and development and retard the germination of *Sh* seeds and the growth of *Sh* plants (Reda and Verkleij 2004). However, implementing these measures is not affordable for most smallholder farmers. Some herbicides, such as 2, 4-D, were reported to be effective in reducing the build-up of *Striga* (De Groote et al. 2008). But they are less effective in controlling the effect of the parasite before emergence (Haussmann et al. 2000; Hearne 2009). The post-emergent herbicide has little impact on crop growth and yield and the cost of herbicides and spray units makes this approach unaffordable for smallholder farmers.

Host resistance is an economical and environmentally friendly *Striga* management option for smallholders. *Striga*-resistant cultivars can reduce new seed production and causes suicidal germination of *Striga* seed held in the soil seed bank. *Striga*-resistant cultivars supported significantly fewer *Striga* plants and yielded better than susceptible genotypes (Doggett 1988; Ejeta et al. 1992). Several *Striga*-resistance mechanisms have been reported such as low production of germination stimulants, mechanical barriers, inhibition of germ tube exoenzymes by root exudates, phytoalexin synthesis, incompatibility, antibiosis, insensitivity to *Striga* toxin, avoidance through root growth habit (Ejeta et al. 1992).

The presence of unique and major genes conferring *Striga* resistance may be examined in the laboratory. In contrast, complex resistance must be assessed under field and hotspot conditions (Haussmann et al. 2000). Integrated *Striga* management (ISM) options involving host resistance and biological control are the best strategies for controlling *Striga*. ISM may involve the use of fungal microbes such as *Fusarium oxysporum* f.sp. *Strigae* (*FOS*) that destroy *Striga*, use of resistant cultivars, cultural practices and crop protection chemicals (Mrema et al. 2017). The application of *FOS* on sorghum seed reduced *Striga* number and improved grain yield (Rebeka et al. 2013; Mrema et al. 2017; Shayanowako et al. 2020). The fungus kills *Striga* seedlings before it penetrates the roots of the host plants (Rebeka et al. 2007). *FOS* is reported to be host-specific, highly aggressive against *Striga*, easy to mass-produce, and genetically diverse (Ciotola et al. 2000).

Thus far, no single control measure was reported effective in managing *Striga*. The combined use of host resistance and *FOS* have shown promise as an economically sustainable integrated *Striga* control option in cereal crops. The approach is effective when compatibility and synergy exist between the host plant and *FOS*. *Striga*-resistant host should enable *FOS* to proliferate, whereas the fungus should inhibit

the *S. haustoria* from infecting the host. Changes in biotic and abiotic conditions due to microbes surrounding the rhizosphere have been reported to retard the parasite (Shayanowako et al. 2020).

In an attempt to develop and deploy *Sh*-resistant pearl millet genotypes, the Environmental Institute for Agricultural Research (INERA) introduced genetically diverse open-pollinated varieties and accessions adapted to the local environments. Consequently, the extent of *Sh* resistance and agronomic performance of the newly acquired lines must be determined for breeding or production. Breeding pearl millet varieties resistant to *Sh* and compatible with *FOS* will significantly increase pearl millet production in Burkina Faso. In light of the above background, the objective of this study was to screen genetically diverse pearl millet accessions for *Sh* resistance and compatibility with a *Striga* bio-control agent, *Fusarium oxysporum* f.sp. *Strigae* (*FOS*), to select contrasting and promising parents for resistance breeding and direct production.

3.2. Materials and Methods

3.2.1. Study Sites and Plant Materials

A field experiment was conducted in the 2019/20 main growing season in a naturally *Striga*-infested hotspot field at the Didri site in Burkina Faso. Also, a screenhouse evaluation was conducted at the main station of INERA in the offseason of 2020/21. The Didri site is located at 12° 12' 15" N and 1° 14' 13" W and was identified as being highly infested by *Sh*. The site received an annual rainfall of 748.5 mm for 46 days during the rainy season and has a leached tropical ferruginous soil, a coarse silty-clay texture and ferro-manganic gravels. The INERA site is located at 12°28/27 N and 1°33/31W. In both studies, 150 genetically diverse pearl millet accessions were used. The 148 genotypes were acquired from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)/Niger, and the two lines were locally adapted entries obtained from INERA. The descriptions of the test genotypes are summarised in Table 3.1.

Table 3.1. Description of the pearl millet genotypes used in the study.

E.N.	Genotype code	Pedigree or name	Source	Presumed *Striga* resistance	E.N.	Genotype code	Pedigree	Source	Presumed *Striga* resistance
1	IP-2058	Z 42	ICRISAT	S	39	IP-7633	S 195	ICRISAT	S
2	IP-3098	-	ICRISAT	R	40	IP-7886		ICRISAT	S
3	IP-3110	-	ICRISAT	S	41	IP-7910	D 89 C-1-1	ICRISAT	S
4	IP-3122	-	ICRISAT	S	42	IP-7922	IP 5238-2; D 175 C-2-2	ICRISAT	S
5	IP-3125	-	ICRISAT	S	43	IP-7942	IP 5452-1; P 2742-1	ICRISAT	S
6	IP-3175	-	ICRISAT	S	44	IP-7952	IP 6578-1; Kolala local 7-1	ICRISAT	S
7	IP-3389	-	ICRISAT	S	45	IP-7953	IP 6191-1; P 87-1	ICRISAT	S
8	IP-3564	-	ICRISAT	S	46	IP-7967	IP 6342-1; P 337-2	ICRISAT	S
9	IP-3593	-	ICRISAT	S	47	IP-8002	37 K-1-1	ICRISAT	S
10	IP-3732	-	ICRISAT	S	48	IP-8129	GS 112	ICRISAT	S
11	IP-3757	-	ICRISAT	S	49	IP-8166	GS 148	ICRISAT	S
12	IP-3865	-	ICRISAT	S	50	IP-8172	GS 154	ICRISAT	S
13	IP-3890	-	ICRISAT	S	51	IP-8174	GS 156	ICRISAT	S
14	IP-4378	-	ICRISAT	S	52	IP-8181	IP 338-1	ICRISAT	S
15	IP-4927	Souna D2	ICRISAT	S	53	IP-8182	IP 406-B-1	ICRISAT	S
16	IP-4974	700111	ICRISAT	S	54	IP-8187	IP 2695-1	ICRISAT	S
17	IP-5031	700482	ICRISAT	S	55	IP-8210	IP 1739 L-1	ICRISAT	S
18	IP-5131	D 235	ICRISAT	S	56	IP-8276	IP 2130-1/CG 51	ICRISAT	S
19	IP-5272	D 258	ICRISAT	S	57	IP-8280	Souna 57-1	ICRISAT	S
20	IP-5438	P 2727	ICRISAT	S	58	IP-8294	IP 6132-1; P 24-2	ICRISAT	S
21	IP-5695	45-327	ICRISAT	S	59	IP-8426	SDN 496-1	ICRISAT	S
22	IP-5713	45-349	ICRISAT	S	60	IP-8761	-	ICRISAT	S
23	IP-5816	P 1407/S1.45	ICRISAT	S	61	IP-8767	-	ICRISAT	S
24	IP-5900	P 1505/S1.228	ICRISAT	S	62	IP-8786	-	ICRISAT	S
25	IP-5923	P 1531-1/S1.293	ICRISAT	S	63	IP-8863	-	ICRISAT	S
26	IP-6099	P 932	ICRISAT	S	64	IP-8949	P 3254; PL 73	ICRISAT	S
27	IP-6103	P 939	ICRISAT	S	65	IP-9242	Sanio 35	ICRISAT	R
28	IP-6111	P 947	ICRISAT	S	66	IP-9347	-	ICRISAT	S
29	IP-6112	P 949	ICRISAT	R	67	IP-9651	PI 286865	ICRISAT	S
30	IP-6584	-	ICRISAT	S	68	IP-9692	PI 286979	ICRISAT	S
31	IP-6682	-	ICRISAT	S	69	IP-9710	PI 287043	ICRISAT	S
32	IP-6745	-	ICRISAT	S	70	IP-9854	Acc 50-1	ICRISAT	S
33	IP-6769	-	ICRISAT	S	71	IP-9969	1769	ICRISAT	S
34	IP-6882	Acc 124	ICRISAT	S	72	IP-10085	P 5439	ICRISAT	S
35	IP-6891	Acc 144	ICRISAT	S	73	IP-10339	-	ICRISAT	S
36	IP-6892	Acc 147	ICRISAT	S	74	P-10471	-	ICRISAT	S
37	IP-7470	-	ICRISAT	S	75	IP-10486	-	ICRISAT	S
38	IP-7536	K 46	ICRISAT	S	76	IP-10488	-	ICRISAT	S

Table 3.1. Continued

E.N.	Genotype code	Pedigree	Source	Presumed *Striga* resistance	E.N.	Genotype codes	Pedigree	Source	Presumed *Striga* resistance
77	IP-10579	CMM 410	ICRISAT	R	115	IP-15872	P 15	ICRISAT	S
78	IP-10705	CMM 540	ICRISAT	S	116	IP-15917	NPT 1	ICRISAT	S
79	IP-10820	Acc 615	ICRISAT	S	117	IP-16289	-	ICRISAT	S
80	IP-10953	BM 8	ICRISAT	S	118	IP-16403	-	ICRISAT	S
81	IP-10964	-	ICRISAT	S	119	IP-17099	-	ICRISAT	S
82	IP-11310	CVP 152	ICRISAT	S	120	IP-17150	-	ICRISAT	S
83	IP-11346	CVP 278	ICRISAT	S	121	IP-17554	-	ICRISAT	S
84	IP-11353	CVP 298	ICRISAT	S	122	IP-17611	-	ICRISAT	S
85	IP-11358	CVP 311	ICRISAT	R	123	IP-17690	-	ICRISAT	S
86	IP-11577	P 6041	ICRISAT	S	124	IP-18062	-	ICRISAT	S
87	IP-11593	P 6062	ICRISAT	S	125	IP-18147	-	ICRISAT	S
88	IP-11670	Millet 199	ICRISAT	S	126	IP-18246	-	ICRISAT	S
89	IP-11677	100	ICRISAT	S	127	IP-18293	BLP 1	ICRISAT	S
90	IP-11763	Arnold 2131	ICRISAT	S	128	IP-18500	-	ICRISAT	S
91	IP-11765	Arnold 2141	ICRISAT	S	129	IP-18621	-	ICRISAT	S
92	IP-12128	-	ICRISAT	S	130	IP-19334	-	ICRISAT	S
93	IP-12138	-	ICRISAT	S	131	IP-19361	-	ICRISAT	S
94	IP-12298	-	ICRISAT	S	132	IP-19386	-	ICRISAT	S
95	IP-12322	-	ICRISAT	S	133	IP-19388	-	ICRISAT	S
96	IP-12364	-	ICRISAT	S	134	IP-19612	C 90-119	ICRISAT	S
97	IP-12395	JM 4615	ICRISAT	S	135	IP-19613	C 90-120	ICRISAT	S
98	IP-12840	-	ICRISAT	S	136	IP-19626	C 90-133	ICRISAT	S
99	IP-12967	-	ICRISAT	S	137	IP-21020	-	ICRISAT	S
100	IP-13016	P 565-1	ICRISAT	S	138	IP-21169	P 1449-3	ICRISAT	S
101	IP-13154	Maiwa local 2-1	ICRISAT	S	139	IP-21206	D 332/1/2-2	ICRISAT	S
102	IP-13180	No. 2-1	ICRISAT	T	140	IP-21517	-	ICRISAT	S
103	IP-13324	Acc 9-1	ICRISAT	S	141	IP-22419	ICML 1; ICMPE 13-6-27	ICRISAT	S
104	IP-13344	Acc 736-1	ICRISAT	S	142	IP-22420	ICML 2; ICMPE 13-6-30	ICRISAT	S
105	IP-13363	-	ICRISAT	S	143	IP-22423	ICML 5; SSC FS 252-S-4	ICRISAT	S
106	IP-13459	-	ICRISAT	S	144	IP-22424	ICML 6; ICI 7517-S-1	ICRISAT	S
107	IP-13817	CVP 230	ICRISAT	S	145	IP-22455	ICMP 85410	ICRISAT	S
108	IP-13964	-	ICRISAT	S	146	IP-22494	ARD 282 (133)	ICRISAT	S
109	IP-13971	-	ICRISAT	S	147	IP-21142	Tifton 186	ICRISAT	S
110	IP-14210	-	ICRISAT	S	148	SOSAT-C88		ICRISAT	C
111	IP-14624	-	ICRISAT	S	149	IKMP5-S4-41	IKMP5	INERA	S
112	IP-15320	-	ICRISAT	S	150	MISARI 1-S4-27	MISARI 1	INERA	S
113	IP-15533	139	ICRISAT	S					
114	IP-15857	-	ICRISAT	C					

E.N. = entry number; ICRISAT = International Crop Research Institute for the Semi-Arid Tropics/Niger; INERA = Institut de l'Environnement et de Recherches Agricoles/Burkina Faso; C = check; R = denotes resistance; T = denotes tolerance; S = susceptible.

3.2.2. *Fusarium oxysporum* Inoculum Preparation and Inoculation

A pathogenic strain of *FOS*, isolated initially from sorghum fields infested with *Striga* in the northeastern lowlands of Ethiopia, was used (Rebeka et al. 2013). The Phytomedicine Department of Humboldt University made the taxonomic identification of *FOS* in Berlin, Germany. Rebeka (2007) confirmed the pathogenicity and host specificity of the *FOS* isolate to *Striga* in sorghum accessions. The isolate was maintained on a special nutrient agar (SNA) (Rebeka et al. 2013) medium at -40°C. The *FOS* strain grown in toothpicks and conserved in drinking straws was obtained from Plant Health Products (Pty) Ltd, Kwazulu-Natal, South Africa. *FOS* was mass-produced on 1250 g pearled rice soaked in distilled water for one hour and then autoclaved at 121°C for 15 minutes in a tightly sealed autoclavable plastic bag. The rice bag was then left to cool for 24 hrs at room temperature. It was re-autoclaved for the same time and left to cool for one hr, and the media was then inoculated with *FOS* on agar disks under a laminar airflow. The plastic bags containing the inoculated rice was then sealed and incubated at 25°C for one week. Four grams of *FOS* inoculated rice was applied in each pot.

3.2.3. Experimental Design and Trial Management

The field and greenhouse experiments were laid out using a 10 × 15 alpha lattice design in two replicates with and without *FOS*. The experiment was conducted once in the greenhouse and twice in the field. Data from the second evaluation in the field were discarded due to recurrent drought that affected *Striga* germination and plant growth. In the greenhouse, pots of 5L capacity were filled with a soil media composed of clay, sand, and organic manure in a ratio of 2:1:1, respectively. Two weeks before planting, each pot was infested with a scoop of sand mixed with 0.05 g of 1-year-old *Sh* seed collected from farmers' fields in Burkina Faso. In the naturally infested field, pearl millet seeds were sown in 4.2 m long in one row with an inter-row spacing of 160 cm and intra-row spacing of 60 cm, providing a total plot size of 6.72 m^2 per genotype. Four seeds were initially sown per hill and later thinned to one plant two weeks after planting. A total of 10 plants were selected randomly from the middle of the experimental unit and tagged for data collection. Standard agronomic practices recommended for pearl millet production were followed; first hoeing fifteen days after planting, followed by fertilization using nitrogen, phosphorus and potassium (NPK) at 14:23:14, in that order, applied as a microdose of 3 g per hill. Hand weeding was routinely done to remove all other weeds except *Striga* after the first hoeing.

3.2.4. Laboratory Experiments

Preliminarily selected pearl millet genotypes with *Sh* resistance, including IP-3098, IP-6112, IP-9242, IP-10579, and IP-11358 and the two checks were evaluated in an agar gel assay. The goal was to assess their *Striga* germination stimulant production (SGSP) using an agar-gel assay proposed by Hess et al. (1992)

using a completely randomized design replicated three times. The SGSP is an indicator of *Sh* resistance mechanism. Prior to planting, the one-year-old *Striga* seeds collected from farmers' fields and pearl millet seeds were surfaces sterilized by soaking in a 1% sodium hypochlorite solution for 30 min and then washing with double distilled water using a filter paper on a funnel until the chlorine odour disappeared.

Two layers of circular filter paper were placed in a Petri dish (9 cm diameter) base and wetted with distilled water. Sterilized and dried *Striga* seeds were sprinkled onto the discs, and the Petri dishes were covered with a lid and kept under dark conditions by covering them with aluminium foil. The *Striga* seeds were then incubated at 25°C for 14 days (Mrema et al. 2017).

Following the completion of *Sh* seeds preconditioning, pearl millet seeds were primed to germinate on filter papers. Six sterilized seeds from each pearl millet genotype were selected randomly. They were then transferred into 9 cm diameter Petri dishes with moist Whatman filter papers and incubated in the dark at 28°C for 3 days. Germinated seeds with about 2 cm root length were used to test *Striga* germination stimulant activity. The amount of *Striga* germination stimulant was assessed using the procedure proposed by Mohamed et al. (2010). Fifty µl of distilled water containing the preconditioned *Striga* seeds were pipetted into 9 cm diameter Petri dishes. Water agar solution (1.05 mg of agar) with 500 ml of double distilled water was autoclaved for 15 min, then cooled and poured into the Petri dish containing the conditioned *Sh* seeds and swirled gently to ensure an even distribution of the seeds. Germinated seeds were gently submerged in solidifying agar near the Petri dish's edge, with the root tip pointing across the Petri dish. All Petri dishes were placed into the incubator for 48 hours before observing *Striga* seeds germination under a dissection microscope.

3.2.5. Test of Haustorium Fixation on Pearl Millet Roots

Haustorium fixation test was conducted using the above five genotypes, which showed no germinated *Striga* under field and greenhouse conditions. The genotypes were grown in disposable cups of 200 millilitres capacity to observe the emergence of *Striga* seedlings. The genotypes planted in disposable cups were grown in a mixture of sand and soil (1:1). Then 0.05 gram of 14 days preconditioned *Striga* seeds were added to each cup to record the amount of production of germination stimulant. This allowed observing the emergence of *Sh* to indicate the low production of germination stimulant. After planting, the cups were watered until the emergence of *Striga* was observed, showing the attachment of haustorium to the host's roots. Haustorium connection to host root was observed in a microscope after withdrawing the cup and thoroughly cleaning genotypes roots attached with emerged *Striga* plants.

3.2.6. Field and Screenhouse Data Collections

The following agronomic parameters were collected from pearl millet: days to 50% flowering (DTF) by recording the day when 50% of the plants in each plot had intruded stigma. Plant height (PH) was measured from the base of the plant (expressed in cm) to the top of the panicle of the main tiller. Number of tillers per plant (NT) was recorded by counting the number of tillers with panicles for the tagged plant. Panicle length (PCL) was measured (cm) from the base to the top of the main tiller panicle. Panicle weight (PWT) was recorded (g) by weighing the harvested panicles for each entry after 14 days of sun-dry, and thousand grains weight (TGW) was determined (g) by weighing a thousand grains for each of the entries. Grain weight per plant (GW) was determined (g) by weighing the grain after threshing and dividing by the number of harvested plants for each plot.

The data collected on *Striga* parameters are: the number of emerged *Sh* plants in each plot that was estimated at 70, and 96 days after sowing in the naturally infested field for each row, excluding the borders, and 116 and 144 days after sowing in the greenhouse for each pot. The area under the *Striga* Number Progress Curve (ASNPC) (Haussmann et al. 2000) was computed using the successive *Striga* counts as follows:

$$ASNPC = \sum_{i=0}^{n-1} \left[\frac{Y_i + Y_{(i+1)}}{2}\right](t_{i+1} - t_i)$$

where n is the number of *Striga* assessment dates, Y_i is the *Striga* count at the i^{th} assessment date, $Y_{(i+1)}$ is the *Striga* count at the i^{th} plus 1 assessment date, t_i is the number of days after planting (DAP) at the i^{th} assessment date, $t_{(i+1)}$ is DAP at the i^{th} plus 1 assessment date.

3.2.7. Data Analysis

Both the crop and *Striga* data were subjected to analysis of variance using GenStat 19th Edition (http://www.genstat.co.uk). Homogeneity of variance test was done for each site using the Bartlett procedure before combined analyses. Boxplots were drawn using R software to elucidate treatment differences. The treatment, genotype, and genotype × treatment interaction and their significance of effects were computed using GenStat. The Best Linear Unbiased Prediction (BLUP) was calculated according to (Haslett and Puntanen 2014) to predict the accuracy and to enhance the efficiency of selection. The area under the *Striga* number progress curve was drawn using R.

ASReml-R Version 4 was used to fit the linear mixed models using Residual Maximum Likelihood (REML) in the R environment (Butler et al. 2017).

3.3. Results

3.3.1. Effects of *Striga hermonthica* on Agronomic Performance of Pearl Millet

Table 3.2 summarises the analysis of variance (ANOVA) when evaluating diverse pearl millet genotypes with and without *Sh* under the field and screenhouse conditions. Pearl millet genotypes differed significantly ($P < 0.001$) for days to 50% flowering (DTF), plant height (PH), number of tillers per plant (NT), panicle length (PCL), panicle weight (PWT), thousand grains weight (TGW), and grain yield (GW), under *Sh* infestation. Genotypes differed significantly ($P < 0.001$) for the area under the *Striga* number progress curve (ASNPC). The genotype by *Striga* interaction was non-significant for the NT and ASNPC (Table 3.2).

Table 3.2. Mean squares and significant tests for pearl millet and *Striga* parameters when evaluating 137 genotypes with and without *Striga* infestation under the field and screenhouse environments.

Source of variation	DF	DTF	PH	NT	PCL
Replication	1	66.53^{ns}	3203.50***	20.93***	26.98^{ns}
Genotype	136	317.00***	2394.50***	4.12***	114.63***
Striga	1	389.51***	37599.60***	156.73***	556.95***
Environment	1	5113.06***	84488.00***	490.35***	2353.17***
Genotype × *Striga*	136	33.18***	526.60***	0.85^{ns}	12.13*
Genotype × Environment	136	65.94***	686.20***	1.24***	16.286***
Residual	416	21.80	341.70	0.78	8.94
Total	827				
Source of variation	**DF**	**PWT**	**TGW**	**GW**	**ASNPC**
Replication	1	131169.00***	0.43^{ns}	11016.00***	349.40^{ns}
Genotype	136	16218.00***	14.04***	4953.00***	1627***
Striga	1	2511363.00***	73.23***	1037689.00***	120730.90***
Environment	1	7181785.00***	250.04***	2859964.00***	88892.80***
Genotype × *Striga*	136	4095.00^{ns}	4.03***	2375.00***	813.00^{ns}
Genotype × Environment	136	12991.00***	3.74***	6013.00***	1688.70***
Residual	416	4421.00	2.46	1183.00	785.40
Total	827				

* and *** = denote significant differences at 0.05, and 0.001 probability levels, respectively; ns = not significant; DF = degree of freedom; DTF= days to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers; PCL = panicle length (cm); PWT = panicle weight (g); TGW = thousand grains weight (g); GW = grains weight per plant (g); ASNPC = area under the *Striga* number progress curve.

Table 3.3 shows the mean performances of pearl millet genotypes evaluated with and without *Striga* in the naturally *Striga*-infested field and screenhouse conditions. Table 3.3 displayed the top 10 and bottom five performing genotypes ranked by the area under the *Striga* number progress curve. The best

genotypes showed less *Sh* germination in the naturally infested field and the screenhouse environments. Based on high agronomic trait performance and a low number of emerged *Striga* plants, five *Sh* pearl millet-resistant genotypes were selected (i.e., IP-3098, IP-6112, IP-9242, IP-10579, IP-11358). The genotypes had low values for ASNPC in the infested field and the screenhouse environments.

Table 3.3. Mean values for agronomic traits of the top 10 and bottom five performing pearl millet genotypes evaluated with and without *Striga* in the naturally infested field and screen house conditions.

Genotype	DTF	PH	NT	PCL	PWT	TGW	GW	ASNPC
Top 10								
IP-3098	53.50	133.90	2.00	21.93	58.77	7.90	36.03	0.00
IP-6112	65.00	164.25	1.00	10.25	160.06	5.50	7.00	0.00
IP-9242	55.50	127.20	2.22	24.68	128.30	10.17	58.14	0.00
IP-10579	74.94	177.10	1.72	24.75	48.60	6.31	2.54	0.00
IP-11358	70.75	182.05	2.00	29.00	134.80	5.75	85.43	0.00
IP-11353	61.17	127.80	1.50	20.50	38.18	7.88	7.71	2.16
IP-18293	60.33	155.30	1.56	17.50	70.63	6.85	45.09	2.16
IP-19613	66.67	142.20	1.94	18.80	86.33	6.45	4.96	2.16
IP-22455	65.67	144.30	1.14	22.58	58.65	7.92	45.59	2.16
IP-7952	62.00	150.20	1.33	23.37	115.96	9.20	44.31	2.16
Bottom five								
IP-10964	61.00	140.30	2.22	15.99	103.94	7.87	47.68	57.83
IP-13459	72.17	136.40	1.72	14.80	42.96	6.40	24.38	61.11
IP-17150	67.17	184.80	1.56	20.64	198.37	9.47	89.65	68.27
IP-17099	78.67	160.80	1.17	30.42	107.65	6.86	43.19	79.69
IP-8863	87.83	115.90	2.22	21.33	36.41	5.09	2.68	103.55
Grand Mean	62.95	148.54	1.70	20.90	97.36	8.50	56.55	17.08
F Test	***	***	***	***	***	***	***	***
SED (Genotype)	2.34	9.24	0.44	1.50	33.25	0.78	17.20	14.01
SED (*Striga)*	0.34	1.36	0.07	0.22	4.90	0.12	2.54	2.07
SED (Environment)	0.40	1.57	0.08	0.25	5.66	0.13	2.93	2.39
SED (Gen x *Striga*)	3.69	14.61	0.70	2.36	52.57	1.24	27.20	28.03
SED (Gen x Env)	4.04	16.01	0.76	2.59	57.58	1.36	29.79	30.98
LSD (5%) (Gen)	4.59	18.17	0.87	2.94	65.36	1.54	33.82	27.54
LSD (5%) (*Striga*)	0.68	2.68	0.13	0.43	9.64	0.23	4.99	4.06
LSD (5%) (Environment)	0.78	3.09	0.15	0.50	11.13	0.26	5.76	4.69
LSD (5%) (Gen x *Striga*)	7.26	28.73	1.37	4.65	103.34	2.44	53.47	43.55
LSD (5%) (Gen x Env)	7.95	31.47	1.50	5.09	113.20	2.67	58.58	47.71
CV (%)	7.40	12.40	51.80	14.30	68.30	18.40	60.80	18.20

*** = denotes significant difference at 0.001 probability level; DTF= days to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers; PCL = panicle length (cm); PWT = panicle weight (g); TGW = thousand grains weight (g); GW = grains weight per plant (g); ASNPC = area under the *Striga* number progress curve; SED = standard error of the mean difference; LSD = least significant difference; CV = coefficient of variation; Gen = genotype; Env = environment.

Table 3.4 summarises the mean response of the top 10 and bottom five pearl millet genotypes ranked based on the ASNPC values in the naturally *Sh*-infested field. Compared to the control treatments, DTF was delayed for three days in pearl millet genotypes infested with *Striga*. Traits that showed low mean

values included plant height (with a mean of 156.20 cm), panicle length (19.28 cm), and the number of tillers (1.07) in genotypes infested with *Striga* compared to the control. The ASNPC values were markedly higher in pearl millet genotypes infested with *Sh* than the control.

Table 3.4. Mean values for agronomic traits and *Striga* parameter for the top 10 and bottom five pearl millet genotypes ranked by ASNPC values in naturally *Sh*-infested field.

Genotype	DTF			PH			NT			PCL		
	GenStr	GenInf	Gen	GenStr	GenInf	Gen	GenStr	GenInf	Gen	GenStr	GenInf	Gen
Top 10												
IP-11358	57.40	84.00	55.00	163.07	190.29	153.50	1.00	2.00	1.00	24.13	33.97	21.00
IP-3098	55.00	51.00	54.50	148.00	128.10	125.50	1.50	4.00	0.50	23.00	23.30	19.50
IP-9242	59.00	56.50	51.00	137.00	123.00	121.50	2.00	2.66	2.00	22.50	26.53	25.00
IP-6112	60.90	69.12	50.00	177.35	146.13	167.00	1.00	1.00	1.00	10.65	10.19	11.00
IP-10579	81.50	73.91	69.00	198.50	137.40	196.50	1.50	2.33	1.50	24.50	25.91	24.00
IP-11353	63.00	57.00	63.50	137.50	102.50	143.50	1.00	2.00	1.50	24.00	20.50	17.00
IP-18293	62.00	60.00	59.00	171.50	122.40	172.00	0.50	2.66	1.50	17.00	20.00	15.50
IP-19613	62.00	75.00	63.00	147.50	125.60	153.50	2.00	1.83	2.00	17.50	21.41	17.50
IP-22455	70.50	56.00	70.50	162.00	110.50	160.50	0.50	2.41	0.50	22.00	23.73	22.00
IP-5272	63.00	57.50	66.50	144.00	154.10	151.50	1.50	2.00	1.00	21.50	36.37	27.00
Bottom five												
IP-3122	73.00	57.00	67.00	171.00	105.80	178.50	2.00	4.50	1.50	21.50	24.93	26.50
IP-13459	79.00	66.50	71.00	154.00	96.60	158.50	1.50	2.66	1.00	14.50	14.91	15.00
IP-18246	58.00	63.00	63.00	144.50	120.10	160.50	1.00	2.83	1.50	17.50	18.86	17.50
IP-17150	70.50	57.50	73.50	176.00	148.80	229.50	1.00	3.16	0.50	18.50	24.43	19.00
IP-8863	90.50	89.00	84.00	122.00	97.10	128.50	2.00	3.16	1.50	21.00	22.50	20.50
Grand Mean	65.51	59.42	63.92	156.20	131.39	158.06	1.07	2.95	1.08	19.28	23.48	19.61
F Test	***	***	***	***	***	***	***	***	***	***	***	***
SED	4.28	3.33	4.41	17.75	13.79	16.27	0.60	1.01	0.57	2.79	2.29	2.67
LSD (5%)	8.46	6.58	8.72	35.11	27.26	32.18	1.18	1.99	1.13	5.52	4.52	5.28
CV (%)	7.50	6.50	8.00	1.00	12.10	11.90	3.10	39.30	60.70	16.70	11.20	15.70

Table 3.4. Continued

Genotype	PWT			TGW			GW			ASNPC	
	GenStr	GenInf	Gen	GenStr	GenInf	Gen	GenStr	GenInf	Gen	GenStr	GenInf
Top 10											
IP-11358	19.59	264.20	16.10	-	11.62	18.40	7.07	119.70	7.43	-0.38	-3.27
IP-3098	15.48	149.70	11.00	6.10	7.95	9.65	4.93	99.90	3.23	-0.92	-0.01
IP-9242	25.28	274.70	29.58	9.80	8.40	12.30	13.14	149.90	11.35	0.40	-0.01
IP-6112	11.73	-	4.88	7.60	-	4.60	2.22	-	0.29	-0.75	0.00
IP-10579	17.52	135.00	15.96	6.65	3.51	8.65	2.01	153.40	3.05	0.40	1.42
IP-11353	21.18	74.70	18.53	8.35	6.25	9.05	8.17	153.40	7.25	0.95	6.49
IP-18293	21.08	174.70	15.98	7.25	7.25	6.05	7.71	124.90	2.62	-0.99	6.49
IP-19613	17.82	224.70	16.35	8.40	4.15	6.80	6.30	153.40	3.62	-0.71	6.49
IP-22455	13.03	149.70	13.10	9.10	5.65	9.00	6.40	124.90	5.42	0.40	6.49
IP-5272	22.71	149.70	15.49	10.10	8.95	8.94	9.05	124.90	6.88	7.19	6.49
Bottom five											
IP-3122	18.51	224.70	14.46	6.70	6.10	8.60	5.05	149.90	4.15	1.28	116.34
IP-13459	15.83	99.70	13.24	6.45	4.70	8.05	4.32	111.00	4.50	63.00	120.33
IP-18246	21.47	199.70	22.70	8.50	7.10	6.80	9.04	124.90	8.50	14.00	150.14
IP-17150	26.01	549.70	19.29	9.20	9.30	9.90	11.90	249.90	7.13	42.00	162.81
IP-8863	12.03	74.70	4.37	4.86	7.65	8.94	1.86	153.40	0.18	70.00	240.64
Grand mean	22.05	250.70	19.53	8.99	7.65	8.94	9.55	153.40	6.51	12.90	38.30
F Test	***	***	***	***	***	***	***	***	***	**	***
SED	9.90	93.33	3.85	1.38	1.12	1.54	4.14	52.85	2.51	28.92	30.63
LSD (5%)	19.57	184.61	7.62	2.74	2.21	3.05	8.18	104.67	4.96	57.18	60.57
CV (%)	6.10	43.00	22.80	17.80	16.90	19.90	6.70	39.80	44.60	6.00	92.30

** and *** = denote significant differences at 0.01, and 0.001 probability levels, respectively; DTF = days to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers; PCL = panicle length (cm); PWT = panicle weight (g); TGW = thousand grains weight (g); GW = grains weight (g); ASNPC = area under the *Striga* number progress curve; GenStr = genotype with *Striga* in the screenhouse; GenInf = genotype in *Striga* naturally infested field; Gen = genotype; SED = standard error of the mean difference; LSD = least significant difference; CV = coefficient of variation; - = denote missing value.

The box plots in Figure 3.1 summarised the data summary of plant height across all the tested pearl millet genotypes when compared as follows: without *Striga* (pearl millet genotypes evaluated without infestation, designated as Gen), genotypes evaluated with *Striga* infestation (GenStr) and genotypes grown with *Striga* with *FOS* (GenStrF). Figure 3.1 showed that *Sh* significantly reduced the height of pearl millet genotypes without *FOS* applications. The plant heights of all *FOS*-inoculated pearl millet genotypes were relatively tall, varying from 88 to 235 cm, which could contribute to crop performance and productivity (Figure 3.1).

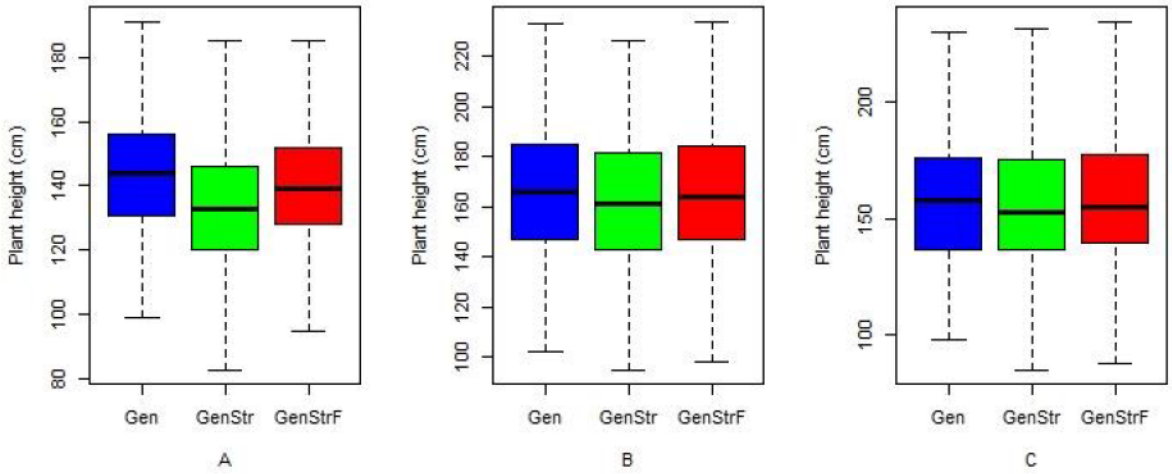

Figure 3.1. Box plots depicting plant height of 150 pearl millet genotypes compared as follows: without *Striga* (pearl millet genotypes gown without infestation, designated as Gen), genotypes grown with *Striga* infestation (GenStr) and genotypes cultivated with *Striga* with *FOS* (GenStrF). The three plots are pearl millet plant heights measured eight weeks after planting (A), 11 weeks after planting (B) and at crop maturity (C).

Figure 3.2 shows the data summary and indicates the effect of *Striga* infestation and *FOS* application on DTF among pearl millet genotypes. It was noted that the test genotypes flowered earlier with *FOS* application. This result was confirmed with delayed DTF observed in pots with *Striga* and without *FOS* and their respective control.

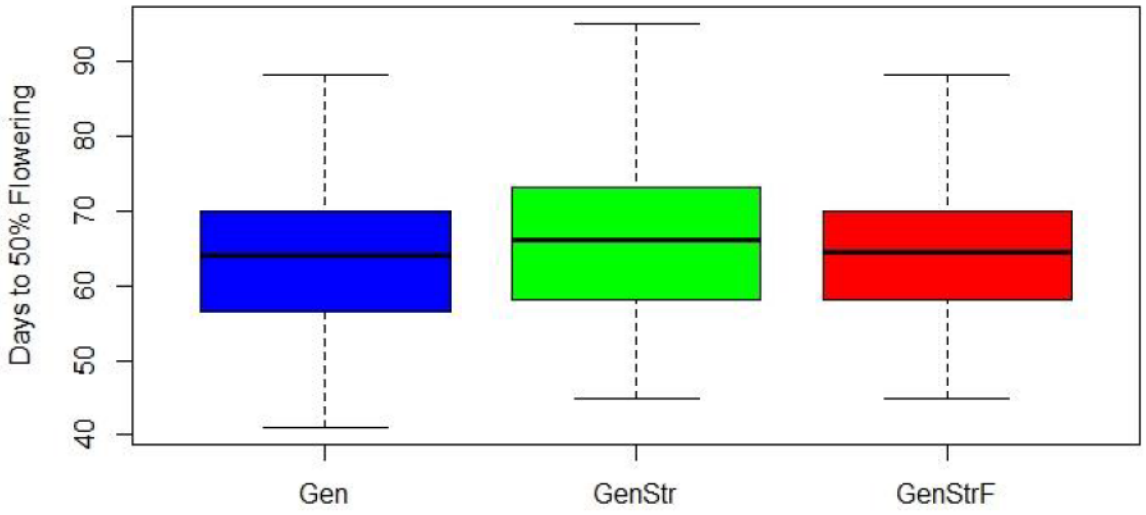

Figure 3.2. Box plots depicting the mean days to 50% flowering of 150 pearl millet genotypes compared as follows: without *Striga* (pearl millet genotypes gown without infestation, designated as Gen), genotypes grown with *Striga* infestation (GenStr) and genotypes cultivated with *Striga* with *FOS* (GenStrF).

3.3.2. *Striga* Seed Germination Induction and Haustorium Fixation

Figure 3.3 depicts *S. hermonthica* seed germination under a stimulus exudated by pearl millet seedling roots of the genotype SOSAT-C88 in an agar gel medium. The number of germinated *Striga* seeds varied considerably among the best-performing pearl millet genotypes compared with the resistant check. The number of germinated *Striga* seed was the highest (2 to 8) in susceptible genotypes (e. g., IP-10964 and SOSAT-C88) compared with the resistant checks (1 to 2) (e.g., IP-15857 and IP-10579). From Figure 3.3 it can be deduced that genotypes IP-3098, IP-6112, IP-9242, IP-10579, and IP-11358 exhibited low production of germination stimulants which is a vital *Striga* resistance mechanism. These are the most ideal genotypes for *Striga* resistance breeding.

Figure 3.3. Photo depicting the number of *Striga hermonthica* seeds germinated on the agar-gel assay. Note: the plate shows *Striga* seed germination 48 hrs after incubation in the dark at 28°C.

Figure 3.4 A and B illustrate the germination response of pearl millet genotypes using disposable cups. Figure 3. 4 A shows the appearance of *Sh* emergence in the genotype IP-10579, which was similar to all other assessed genotypes. The attachment of the haustorium confirmed the germination of *Striga* seeds to the host roots under a microscope observation (Figure 3.4. A and B).

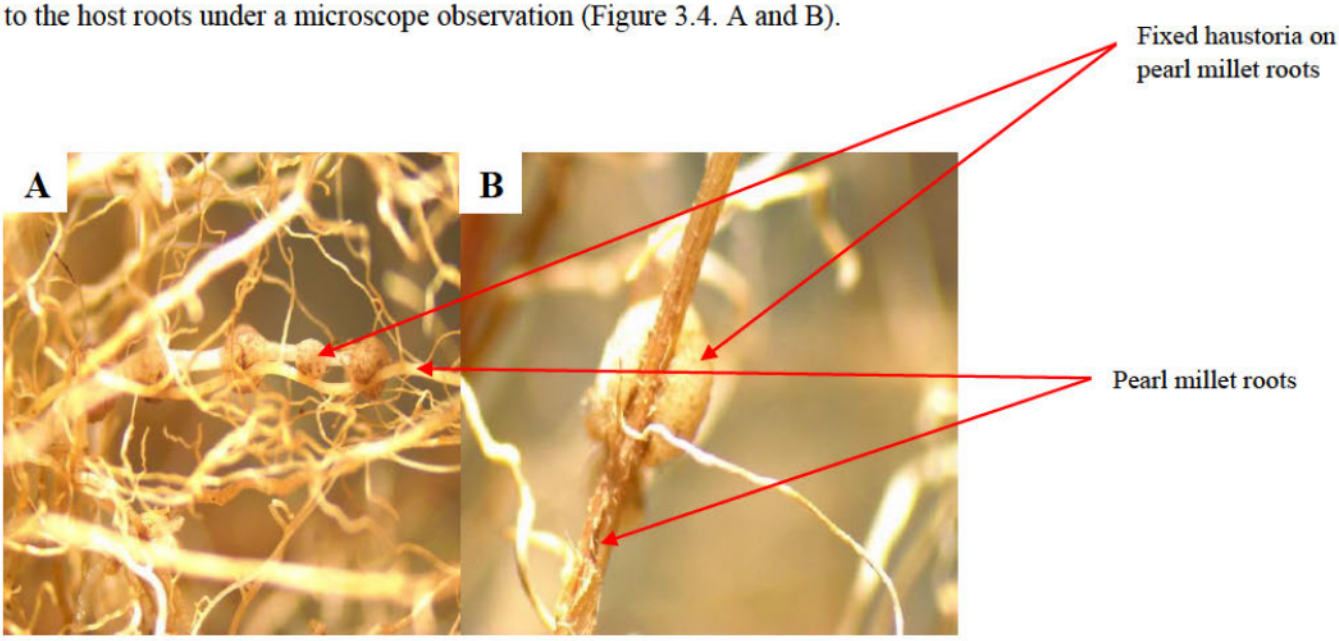

Figure 3.4. Photo depicting the attachment of the haustorium of *Striga hermonthica* seedlings on the pearl millet plant roots of the genotype IP-10579. Note: photo A presents several attachments of the haustorium on the host root, and B, a single root attachment.

3.3.3. Effect of *FOS* on *Sh* and its Compatibility With Pearl Millet Roots

Root samples of pearl millet genotypes inoculated with *FOS* showed the successful establishment of *FOS* on the root surface of pearl millet observed seven days after incubation (Figure 3.5 A and B). A mass of *FOS* colonizing the root was observed on compatible pearl millet genotype IP-9242 after 45 (Figure 3.5A) and 60 days (Figure 3.5B).

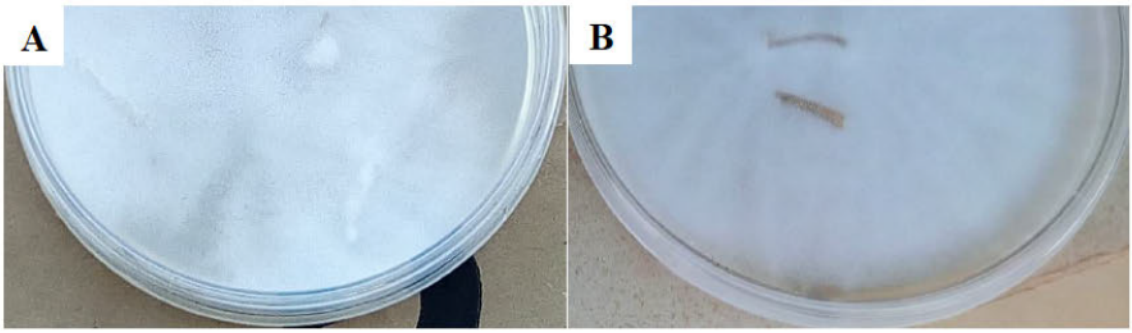

Figure 3.5. Growth of *FOS* on pearl millet genotype IP-9242 after 45 and 60 days of inoculation. Note: plate A shows pearl millet genotype IP-9242 root colonised with *FOS* 45 days after inoculation, and plate B, the same genotype 60 days after inoculation.

Figure 3.6 summarises the trend of the ASNPC values across genotypes with *Striga* infestation and pearl millet seed treated and untreated with *FOS* in the screenhouse. Pearl millet genotypes grown with *Sh* infestation, and the seed treated with *FOS* had lower ASNPC values. Untreated control showed a relatively high number of *Striga*. The mean value of ASNPC of the untreated genotypes was relatively high compared to *FOS*-treated genotypes' mean value (Figure 3.6).

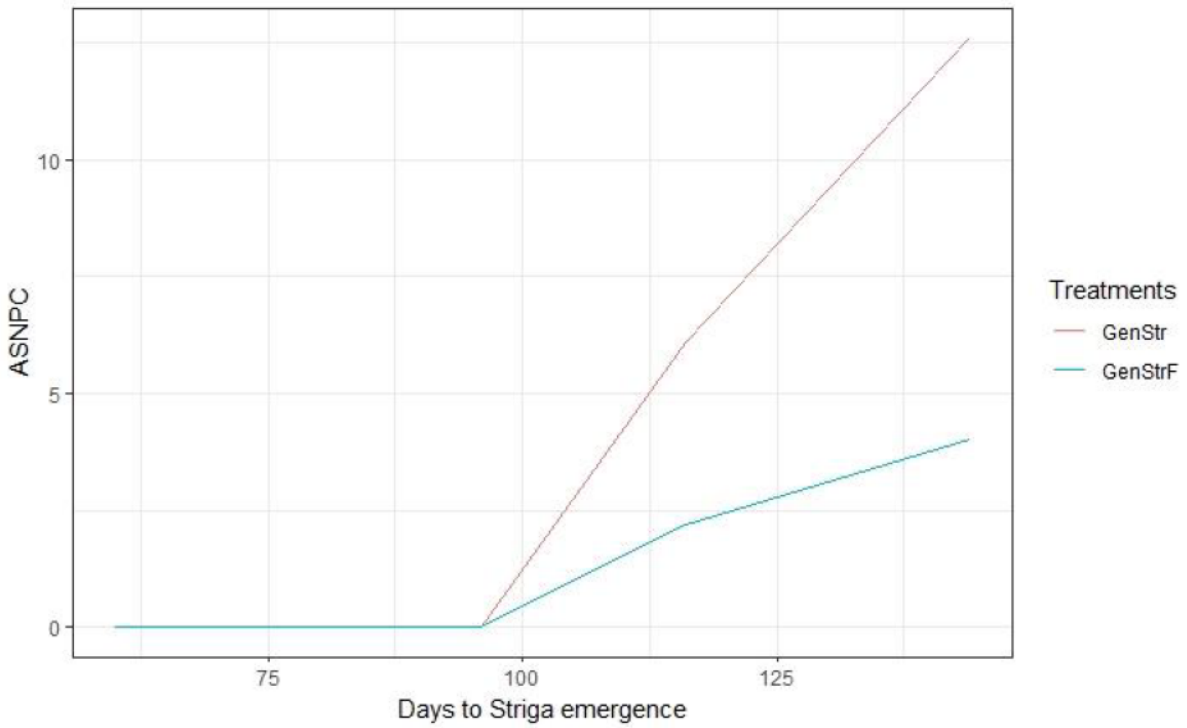

Figure 3.6. The area under the *Striga* number progress curve (ASNPC) after 75, 100 and 125 days to *Striga* emergence when evaluating 150 pearl millet genotypes infested with *Striga hermonthica*, treated and untreated with *FOS* under screenhouse condition. Note: GenStr denotes pearl millet genotypes evaluated with *Striga* infestation; GenStrF, genotypes evaluated with *Striga* and *FOS* application.

3.4. Discussion

The currently assessed pearl millet genotypes differed significantly ($P < 0.001$) for days to 50% flowering, plant height, panicle length, panicle weight, thousand-grain weight, and grain yield (Table 3.2). Also, using comparative evaluations, genotypes differed for the number of *Striga* count and the area under the *Striga* number progress curve (Table 3.2). The difference sought in this study was mainly attributed to the genetic variation among the assessed pearl millet genetic pool for grain yield, yield components, and resistance to *S. hermonthica*. High genetic variation among the test genotypes is reported to increase the probability of developing new and superior *Striga*-resistant varieties (Shayanowako et al. 2018; Lobulu et al. 2021). Delayed DTF and reduced PH were recorded for some pearl millet genotypes when evaluated with *Sh* infestation and *FOS* inoculation compared to their uninoculated control, indicating the adverse effect of *Striga* on pearl millet growth and reproduction (Figure 3.1). The impact of *S. hermonthica* to the host before seedling emergence was reported by Oswald (2005).

Variations in the number of *Sh* and ASNPC values in *FOS* inoculated genotypes indicated the difference in *FOS* compatibility among the assessed pearl millet genetic resources. Rodenburg et al. (2005) reported the potential of ASNPC in determining the duration of infestation and genotype discrimination. The low and high values of ASNPC denoted resistance and susceptibility of to the pearl millet genotypes to *Sh* infestation, respectively. These findings were confirmed by the trend of the ASNPC values where few *Sh* were counted in resistant genotypes compared to susceptible types (Haussmann et al. 2000). A control method that directly affects the germination of the parasitic seeds and their attachment to the host root is more effective than control measures applied at later stages of plant development (Kountche et al. 2016). Among *Striga* control methods, host-plant resistance has been the most effective and sustainable control option. Host resistance is accessible and affordable to farmers (Ejeta 2007; Hearne 2009; Yoder and Scholes 2010).

Poor stimulation of *Sh* seed germination and haustorium attachment (Figure 3.4) suggested the low production of germination stimulants as a resistance mechanism of the selected genotypes. This agrees with the results of Shayanowako et al. (2018), who reported low induction of germination of *Striga* seed in resistant maize genotypes. *Striga* resistance genotypes are endowed with varied mechanisms, including low germination stimulants, mechanical root barriers, post-attachment hypersensitive reactions, and insensitivity to *Striga* toxins, all dependent on the genetic variation of the host (Ejeta 2005; Haussmann et al. 2001). The paper roll assay and rhizotron techniques permit the observations of the early stages of haustorium attachment to the host roots as an effective tool for identifying early post-infection resistance mechanisms (Ejeta et al. 2000; Haussmann et al. 2000; Cissoko et al. 2011; Rodenburg et al. 2017). The fungal growth observed in *FOS*-treated pearl millet roots during the 45th and 60th days after incubation in the agar gel assay indicated the compatibility of *FOS* to some pearl millet genotypes (Figure 3.5).

The compatibility of *FOS* with the roots of some cereal crops was reported in maize (Shayanowako et al. 2020; Lobulu et al. 2021) and sorghum (Rebeka et al. 2013; Mrema et al. 2017). In these crops, *FOS* was found to be host-specific and highly aggressive against *Striga* (Abbasher et al. 1998; Ciotola et al. 2000). The roots of sorghum plants grown with *FOS* inoculations were fully colonized in their rhizosphere, and few or no *Sh*-emerged plants were recorded (Rebeka et al. 2013). The reduction of *Sh* in *FOS* inoculated genotypes indicated the ability of the biocontrol to suppress *Striga* attachment and its development in compatible pearl millet genotypes (Figure 3.6). The ability of *FOS* to reduce *Striga* emergence and increase shoot biomass and grain yield in sorghum and maize was reported in Ethiopia (Rebecca et al. 2013), Tanzania (Mrema et al. 2017), and South Africa (Shayanowako et al. 2020).

A low number of *Sh* plants were counted in *FOS*-treated genotypes at different plant growth stages (Figure 3.6), agreeing with Lobulu et al. (2021). *FOS* has a mycoherbicidal property and attacks *Striga*

spp. before the parasite emergence and flowering. In this study there were none or a few emerged *Striga* plants in some *FOS*-treated pearl millet genotypes (Figure 3.6), indicating the effectiveness of *FOS* in suppressing *Sh* (Fen et al. 2007; Lobulu et al. 2021). *FOS* was observed to surround the rhizosphere of the host, retarding the efficacy of *Sh* parasitism (Mrema et al. 2017). Relatively taller plant height was recorded for some pearl millet genotypes (Figure 3.1) with *Striga* infestation and *FOS* inoculation, suggesting the positive effect of the biocontrol on promoting plant growth and suppressing *Sh,* which may translate into yield gains. Lobulu et al. (2021) reported the effectiveness of *FOS* in improving plant biomass and productivity under *Sh* infestation in maize. Thus, the use of *FOS* as a mycoherbicide will be an effective approach for *Sh* management and improve pearl millet yield and yield components in *Striga*-infested zones of Burkina Faso and similar agro-ecologies.

3.5. Conclusions

Pearl millet is a food staple in Burkina Faso and the Sahel region. However, the grain yield of the crop in these environments is lower (<0.85 tons ha^{-1}) than the average yield, reaching up to 3 tons ha^{-1}. The low productivity is due to several biotic and abiotic constraints of which *Sh* is the leading factor causing yield loss of up to 100%. Therefore, breeding for *Striga* resistance and *FOS*-compatible genotypes is the most affordable and sustainable approach. Resistance breeding requires screening of genetically diverse pearl millet genotypes for *Striga* resistance and economic traits. Also, complementary biocontrol methods such as host-compatible *FOS* will bolster host resistance and crop performance. The current study selected the following pearl millet genotypes: IP-3098, IP-6112, IP-9242, IP-10579, and IP-11358, exhibiting *Sh* resistance and were compatible with *FOS*. The pearl millet genotypes supported few to none *Sh* emerged plants and had relatively low values under the *Striga* number progress curve. The selected genotypes are useful parents for breeding and integrated *Striga* management in Burkina Faso and similar agro-ecologies.

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Chapter 4. Genome-wide association analyses of agronomic traits and *Striga hermonthica* resistance in pearl millet

Abstract

Pearl millet (*Pennisetum glaucum* [L.] R. Br.) is a nutrient-dense, relatively drought-tolerant cereal crop cultivated in dry regions worldwide. The crop is under-researched, and its grain yield is low (< 0.8 tons ha^{-1}) and stagnant in the major production regions, including Burkina Faso. The low productivity of pearl millet is mainly attributable to a lack of improved varieties, *Striga hermonthica* [*Sh*] infestation, downy mildew infection, and recurrent heat and drought stress. Developing high-yielding and *Striga*-resistant pearl millet varieties that satisfy the farmers' and market needs requires the identification of yield-promoting genes linked to economic traits to facilitate marker-assisted selection and gene pyramiding. The objective of this study was to undertake genome-wide association analyses of agronomic traits and *Sh* resistance among 150 pearl millet genotypes to identify genetic markers for marker-assisted breeding and trait introgression. The pearl millet genotypes were phenotyped in *Sh* hotspot fields and screenhouse conditions. Twenty-nine million single nucleotide polymorphisms (SNPs) initially generated from 345 pearl millet genotypes were filtered, and 256 K SNPs were selected and used in the present study. Phenotypic data were collected on days to flowering, plant height, number of tillers, panicle length, panicle weight, thousand-grain weight, grain weight, number of emerged *Striga* and area under the *Striga* number progress curve (ASNPC). Agronomic and *Sh* parameters were subjected to combined analysis of variance, while genome-wide association analysis was performed on phenotypic and SNPs data. Significant differences ($P < 0.001$) were detected among the assessed pearl millet genotypes for *Sh* parameters and agronomic traits. Further, there were significant genotype by *Sh* interaction for the number of *Sh* and ASNPC. Twenty-eight SNPs were significantly associated with a low number of emerged *Sh* located on chromosomes 1, 2, 3, 4, 6, and 7. Four SNPs were associated with days-to-50%-flowering on chromosomes 3, 5, 6, and 7, while five were associated with panicle length on chromosomes 2, 3, and 4. Seven SNPs were linked to thousand-grain weight on chromosomes 2, 3, and 6. The putative SNP markers associated with a low number of emerged *Sh* and agronomic traits in the assessed genotypes are valuable genomic resources for accelerated breeding and variety deployment of pearl millet with *Sh* resistance and farmer- and market-preferred agronomic traits.

Keywords: Marker-trait association, pearl millet, resistance breeding, SNPs, *Striga hermonthica*.

4.1. Introduction

Pearl millet (*Pennisetum glaucum* [L.] R. Br., 2n = 2x = 14) is a highly nutritious and a key staple food crop in dry regions worldwide. It is the major crop of the Sahel region, including Burkina Faso (Bationo and Ntare 2000). In Africa, pearl millet is cultivated on an estimated area of 13.8 million hectares (ha), with an average yield of 0.7 tons ha^{-1} (FAOSTAT 2022). In Burkina Faso, an estimated area of 1.2 million ha is devoted to pearl millet production. However, the mean yield of the crop in the country is low (< 0.81 tons ha^{-1}), lesser than the global average of 0.9 tons ha^{-1} (FAOSTAT 2022). The low grain yield in the farmers' fields is attributable to various biotic and abiotic constraints, including the use of low-yielding landraces, *Striga hermonthica* (*Sh*) infestation, bird damage, insect pests, diseases, heat and drought stresses (Drabo et al. 2018; Rouamba et al. 2021).

Striga hermonthica (Del.) Benth infestation accounts for more than 40 to 55% yield losses and is the most significant biotic constraint to pearl millet production and productivity in Burkina Faso (Zombré and Nikiéma 1992; Traoré and Yonli 2001). The parasite infests several other major cereal crops, including rice (*Oryza glaberrima* Steudel and *O. Sativa* L.), maize (*Zea mays* L.), sorghum (*Sorghum bicolour* [L.] Moench), and fonio (*Digitaria exilis* [Kippist] Stapf) (Boussim et al. 2011; Mrema et al. 2016). Farmers often abandon *Sh*-infested fields and switch from pearl millet to other non-host crops, reducing the crop's overall production and economic value (Atera et al. 2012). *Striga* is a highly prolific parasite in Burkina Faso attributed to the host crop being mostly grown in semi-arid parts of the Sahelian and Sudano-Sahelian zones, which are dominated by poor soil fertility, low and erratic rainfall, and high temperatures that favour germination, growth and spread of the weed (Drabo et al. 2018).

Striga control is difficult because each parasitic plant can quickly disperse and deposit thousands of seeds into the soil seedbank. Furthermore, *Striga* seeds can remain viable in the soils for more than 14 years (Emechebe et al. 2004). *Striga hermonthica* is a major threat to food security, exacerbating hunger and poverty in many African countries (Pennisi 2010; Khan et al. 2014). Monetary losses ranging from 7 to 10 billion US$ is incurred annually due to crop damage and affecting the livelihoods of more than 300 million people in Africa (Emechebe et al. 2004; Gressel et al. 2004; Ejeta 2007; Scholes and Press 2008; Rodenburg et al. 2010).

Several *Striga* control strategies are recommended, including hand weeding, mulching crop fields with biomass of the shea tree (*Vitellaria paradoxa* C.F. Gaertn.) as a bio-control agent, optimal fertilizer application, and soil moisture management (Boussim et al. 2011; Tesso and Ejeta 2011). These strategies improve the soil properties, promote crop growth and development, and retard germination and growth of *Striga* (Reda and Verkleij 2004). Herbicides are less effective in controlling the effect of the parasite after emergence, and they are unaffordable for smallholder farmers.

The use of *Striga*-resistant pearl millet varieties is the most sustainable and environmentally friendly management option for smallholder farmers in semi-arid regions. Resistant cultivars support fewer *Striga* plants and yield higher (Doggett 1988; Ejeta et al. 1992). However, with the paucity of locally adapted and *Sh*-resistant donor sources, breeding for *Striga* resistance in pearl millet is still challenging compared to other cereals (Wilson et al. 2000; Wilson et al. 2004; Kountche et al. 2013; Sattler et al. 2018). In the past decade, intensive research on the interaction of *Striga* with the host at the molecular level has opened opportunities to develop new management strategies (Jamil et al. 2021). For instance, 154 candidate genes associated with *Sh* resistance traits were identified in maize (Badu-Apraku et al. 2020). Adwale et al. (2020) reported 13 associated markers with the *Sh* resistance trait in early maturing tropical white maize inbred lines.

Genome-wide association studies (GWAS) has been used in pearl millet for the identification of putative genes related to flowering time (Diack et al. 2020), iron, zinc and protein content (Pujar et al. 2020), downy mildew resistance (Drabo 2016) and *Sh* resistance (Dawud 2018). Also, GWAS has been used in finger millet for the identification of genes associated with *Striga* resistance (Nyongesa 2017) and grain nutritional contents (Puranik et al. 2020) and for genetic diversity analysis (Backiyalakshmi et al. 2021). GWAS is a valuable genomic tool to identify quantitative trait loci (QTLs) linked to *Striga* resistance for marker-assisted selection. GWAS results depend on the genetic marker and its density, genetic composition and diversity of the test populations.

Genetic markers are landmarks on chromosomes that help pinpoint the location of genes of interest (Acquaah 2012). They can be detected through morphological and molecular markers. Genetic markers such as GRMZM2G077208, GRMZM2G164502, GRMZM2G018508, and GRMZM2G171986, located in chromosomes 3, 5, 7, and 9 were reportedly significantly associated with *Sh* count in tropical maize germplasm (Gowda et al. 2021). SNP markers are instrumental in the dissection of complex traits such as *Striga* resistance, and their association with the trait can be revealed through GWAS. Identification of genomic regions linked to *Striga* resistance in pearl millet breeding would speed up the development of *Striga*-resistant varieties. Genetic markers improve the efficiency of novel *Striga*-resistant genes introgression and pyramiding into high-yielding elite varieties. Therefore, the objective of this study was to undertake genome-wide association analyses of agronomic traits and *Sh* resistance among 150 pearl millet genotypes to identify genetic markers for marker-assisted breeding and trait introgression.

4.2. Materials and Methods

4.2.1. Study Sites

A field experiment was conducted in the 2019/20 main growing season in a naturally infested *Striga* hotspot field at the Didri site in Burkina Faso, and a screenhouse evaluation was conducted at the main station of the Institute of Environment and Agricultural Research (INERA) in the offseason of 2020/21. The Didri site is located at 12° 12' 15" N and 1° 14' 13" W and is a hotspot site for *Sh* affecting pearl millet, maize and sorghum crops. The site received an annual rainfall of 748.5 mm for 46 days during the 2020/21 rainy season and has sandy soils. The INERA site is located at 12°28/27 N and 1°33/31W.

4.2.2. Plant Materials

The study used 148 pearl millet genotypes collected from the International Crop Research Institute for the Semi-arid Tropics (ICRISAT) in Niger and two elite breeding lines from INERA/Burkina Faso. The descriptions of the test genotypes are summarised in Table 4.1. The pearl millet genotypes acquired from ICRISAT are part of the pearl millet germplasm association panel (PMiGAP) comprising 250 inbred lines representing cultivated germplasm from Africa and Asia. They are included in the present study to identify unique genetic resources with unique agronomic and farmers' preferred traits, and because of their wide genetic diversity.

Table 4.1. Description of the pearl millet genotypes used in the study.

E.N.	Genotype code	Pedigree or name	Source	Presumed *Striga* resistance	E.N.	Genotype code	Pedigree	Source	Presumed *Striga* resistance
1	IP-2058	Z 42	ICRISAT	S	39	IP-7633	S 195	ICRISAT	S
2	IP-3098	-	ICRISAT	R	40	IP-7886		ICRISAT	S
3	IP-3110	-	ICRISAT	S	41	IP-7910	D 89 C-1-1	ICRISAT	S
4	IP-3122	-	ICRISAT	S	42	IP-7922	IP 5238-2; D 175 C-2-2	ICRISAT	S
5	IP-3125	-	ICRISAT	S	43	IP-7942	IP 5452-1; P 2742-1	ICRISAT	S
6	IP-3175	-	ICRISAT	S	44	IP-7952	IP 6578-1; Kolala local 7-1	ICRISAT	S
7	IP-3389	-	ICRISAT	S	45	IP-7953	IP 6191-1; P 87-1	ICRISAT	S
8	IP-3564	-	ICRISAT	S	46	IP-7967	IP 6342-1; P 337-2	ICRISAT	S
9	IP-3593	-	ICRISAT	S	47	IP-8002	37 K-1-1	ICRISAT	S
10	IP-3732	-	ICRISAT	S	48	IP-8129	GS 112	ICRISAT	S
11	IP-3757	-	ICRISAT	S	49	IP-8166	GS 148	ICRISAT	S
12	IP-3865	-	ICRISAT	S	50	IP-8172	GS 154	ICRISAT	S
13	IP-3890	-	ICRISAT	S	51	IP-8174	GS 156	ICRISAT	S
14	IP-4378	-	ICRISAT	S	52	IP-8181	IP 338-1	ICRISAT	S
15	IP-4927	Souna D2	ICRISAT	S	53	IP-8182	IP 406-B-1	ICRISAT	S
16	IP-4974	700111	ICRISAT	S	54	IP-8187	IP 2695-1	ICRISAT	S
17	IP-5031	700482	ICRISAT	S	55	IP-8210	IP 1739 L-1	ICRISAT	S
18	IP-5131	D 235	ICRISAT	S	56	IP-8276	IP 2130-1/CG 51	ICRISAT	S
19	IP-5272	D 258	ICRISAT	S	57	IP-8280	Souna 57-1	ICRISAT	S
20	IP-5438	P 2727	ICRISAT	S	58	IP-8294	IP 6132-1; P 24-2	ICRISAT	S
21	IP-5695	45-327	ICRISAT	S	59	IP-8426	SDN 496-1	ICRISAT	S
22	IP-5713	45-349	ICRISAT	S	60	IP-8761	-	ICRISAT	S
23	IP-5816	P 1407/S1.45	ICRISAT	S	61	IP-8767	-	ICRISAT	S
24	IP-5900	P 1505/S1.228	ICRISAT	S	62	IP-8786	-	ICRISAT	S
25	IP-5923	P 1531-1/S1.293	ICRISAT	S	63	IP-8863	-	ICRISAT	S
26	IP-6099	P 932	ICRISAT	S	64	IP-8949	P 3254; PL 73	ICRISAT	S
27	IP-6103	P 939	ICRISAT	S	65	IP-9242	Sanio 35	ICRISAT	R
28	IP-6111	P 947	ICRISAT	S	66	IP-9347	-	ICRISAT	S
29	IP-6112	P 949	ICRISAT	R	67	IP-9651	PI 286865	ICRISAT	S
30	IP-6584	-	ICRISAT	S	68	IP-9692	PI 286979	ICRISAT	S
31	IP-6682	-	ICRISAT	S	69	IP-9710	PI 287043	ICRISAT	S
32	IP-6745	-	ICRISAT	S	70	IP-9854	Acc 50-1	ICRISAT	S
33	IP-6769	-	ICRISAT	S	71	IP-9969	1769	ICRISAT	S
34	IP-6882	Acc 124	ICRISAT	S	72	IP-10085	P 5439	ICRISAT	S
35	IP-6891	Acc 144	ICRISAT	S	73	IP-10339	-	ICRISAT	S
36	IP-6892	Acc 147	ICRISAT	S	74	P-10471	-	ICRISAT	S
37	IP-7470	-	ICRISAT	S	75	IP-10486	-	ICRISAT	S
38	IP-7536	K 46	ICRISAT	S	76	IP-10488	-	ICRISAT	S

Table 4.1. Continued

E.N.	Genotype code	Pedigree	Source	Presumed *Striga* resistance	E.N.	Genotype codes	Pedigree	Source	Presumed *Striga* resistance
77	IP-10579	CMM 410	ICRISAT	R	115	IP-15872	P 15	ICRISAT	S
78	IP-10705	CMM 540	ICRISAT	S	116	IP-15917	NPT 1	ICRISAT	S
79	IP-10820	Acc 615	ICRISAT	S	117	IP-16289	-	ICRISAT	S
80	IP-10953	BM 8	ICRISAT	S	118	IP-16403	-	ICRISAT	S
81	IP-10964	-	ICRISAT	S	119	IP-17099	-	ICRISAT	S
82	IP-11310	CVP 152	ICRISAT	S	120	IP-17150	-	ICRISAT	S
83	IP-11346	CVP 278	ICRISAT	S	121	IP-17554	-	ICRISAT	S
84	IP-11353	CVP 298	ICRISAT	S	122	IP-17611	-	ICRISAT	S
85	IP-11358	CVP 311	ICRISAT	R	123	IP-17690	-	ICRISAT	S
86	IP-11577	P 6041	ICRISAT	S	124	IP-18062	-	ICRISAT	S
87	IP-11593	P 6062	ICRISAT	S	125	IP-18147	-	ICRISAT	S
88	IP-11670	Millet 199	ICRISAT	S	126	IP-18246	-	ICRISAT	S
89	IP-11677	100	ICRISAT	S	127	IP-18293	BLP 1	ICRISAT	S
90	IP-11763	Arnold 2131	ICRISAT	S	128	IP-18500	-	ICRISAT	S
91	IP-11765	Arnold 2141	ICRISAT	S	129	IP-18621	-	ICRISAT	S
92	IP-12128	-	ICRISAT	S	130	IP-19334	-	ICRISAT	S
93	IP-12138	-	ICRISAT	S	131	IP-19361	-	ICRISAT	S
94	IP-12298	-	ICRISAT	S	132	IP-19386	-	ICRISAT	S
95	IP-12322	-	ICRISAT	S	133	IP-19388	-	ICRISAT	S
96	IP-12364	-	ICRISAT	S	134	IP-19612	C 90-119	ICRISAT	S
97	IP-12395	JM 4615	ICRISAT	S	135	IP-19613	C 90-120	ICRISAT	S
98	IP-12840	-	ICRISAT	S	136	IP-19626	C 90-133	ICRISAT	S
99	IP-12967	-	ICRISAT	S	137	IP-21020	-	ICRISAT	S
100	IP-13016	P 565-1	ICRISAT	S	138	IP-21169	P 1449-3	ICRISAT	S
101	IP-13154	Maiwa local 2-1	ICRISAT	S	139	IP-21206	D 332/1/2-2	ICRISAT	S
102	IP-13180	No. 2-1	ICRISAT	T	140	IP-21517	-	ICRISAT	S
103	IP-13324	Acc 9-1	ICRISAT	S	141	IP-22419	ICML 1; ICMPE 13-6-27	ICRISAT	S
104	IP-13344	Acc 736-1	ICRISAT	S	142	IP-22420	ICML 2; ICMPE 13-6-30	ICRISAT	S
105	IP-13363	-	ICRISAT	S	143	IP-22423	ICML 5; SSC FS 252-S-4	ICRISAT	S
106	IP-13459	-	ICRISAT	S	144	IP-22424	ICML 6; ICI 7517-S-1	ICRISAT	S
107	IP-13817	CVP 230	ICRISAT	S	145	IP-22455	ICMP 85410	ICRISAT	S
108	IP-13964	-	ICRISAT	S	146	IP-22494	ARD 282 (133)	ICRISAT	S
109	IP-13971	-	ICRISAT	S	147	IP-21142	Tifton 186	ICRISAT	S
110	IP-14210	-	ICRISAT	S	148	SOSAT-C88		ICRISAT	C
111	IP-14624	-	ICRISAT	S	149	IKMP5-S4-41	IKMP5	INERA	S
112	IP-15320	-	ICRISAT	S	150	MISARI 1-S4-27	MISARI 1	INERA	S
113	IP-15533	139	ICRISAT	S					
114	IP-15857	-	ICRISAT	C					

E.N. = entry number; ICRISAT = International Crop Research Institute for the Semi-Arid Tropics; INERA = Institute of Environment and Agricultural Research/Burkina Faso; C = check; R = resistance; T = tolerance; S = susceptible, - = denote data not available.

4.2.3. Experimental Design and Trial Management

The field and greenhouse experiments were laid out using a 10 × 15 alpha lattice design with two replicates. In the greenhouse, 5L plastic pots were used and filled with a soil media composed of clay, sand, and organic manure at a ratio of 2:1:1 respectively. Two weeks before planting, each pot was infested with a scoop of sand mixed with 0.05 g of 1-year-old *Sh* seed collected from farmers' fields in Burkina Faso. Pearl millet seeds in the naturally *Striga*-infested field (hereafter designated as GenInf), were sown during the main crop growing season from Jun to October 2019. Genotypes were established in 4.2 m long rows spaced at an inter-row spacing of 160 cm and intra-row spacing of 60 cm, providing a total plot size of 6.72 m^2 per genotype. Four seeds were initially sown per hill and later thinned to one plant two weeks after planting. A total of three plants were selected randomly from the middle of the experimental unit and tagged for agronomic data collection. In the greenhouse, one healthy and vigorous plant was grown per pot for the test genotypes with *Sh* (hereafter denoted as GenStr), and genotypes without *Sh* (hereafter referred to as control) treatments. Standard agronomic practices recommended for pearl millet production were followed. Experimental units were fertilized using nitrogen, phosphorus and potassium (NPK: 14:23:14) and applied as a microdose of 3 g per hill 15 days after planting. Hand weeding was routinely done after the first hoeing to remove all other weeds except *Striga*.

4.2.4. Data Collection

4.2.4.1. Phenotypic Data

The following agronomic parameters were collected from pearl millet: days-to-50%-flowering (DTF) were recorded as the days when 50% of the plants in each plot had intruded stigma. Plant height (PH) was measured in cm from the base to the top of the panicle of the main tiller. The number of tillers per plant (NT) was recorded by counting the number of tillers with panicles for the tagged plants. Panicle length (PCL) was measured in cm from the base to the top of the main tiller panicle. Panicle weight (PWT) was recorded in grams by weighing the harvested panicles for each entry after 14 days of sun-dry, and thousand grains weight (TGW) was determined in grams by weighing one thousand grains for each of the entries. Grain weight per plant (GW) was determined in grams by weighing the grain after threshing and dividing it by the number of harvested plants for each plot.

For *Striga* parameters, the number of emerged *Sh* plants per plot were recorded at 70 and 96 days after sowing in the naturally infested field for each row, excluding the borders. The number of emerged *Sh* plants were counted per pot 116 and 144 days after sowing in the greenhouse. The area under the *Striga* Number Progress Curve (ASNPC) was computed using the successive *Striga* counts according to Haussmann et al. (2000) as follows:

$$ASNPC = \sum_{i=0}^{n-1} \left[\frac{Y_i + Y_{(i+1)}}{2}\right](t_{i+1} - t_i)$$

where n is the number of *Striga* assessment dates, Y_i is the *Striga* count at the i^{th} assessment date, $Y_{(i+1)}$ is the *Striga* count at the i^{th} plus 1 assessment date, t_i is the number of days after planting (DAP) at the i^{th} assessment date, $t_{(i+1)}$ is DAP at the i^{th} plus 1 assessment date.

4.2.4.2. Phenotypic Data Analysis

Both the crop and *Striga* data were subjected to analysis of variance using GenStat 19th Edition (http://www.genstat.co.uk). Homogeneity of variance test was done for each site using the Bartlett (1937) procedure before combined analyses. The treatment, genotype, and genotype × treatment interaction significance tests were computed using GenStat. The Best Linear Unbiased Prediction (BLUP) was calculated according to Haslett and Puntanen (2014) to predict the accuracy and to aid selection. The area under the *Striga* number progress curve was drawn using R. ASReml-R Version 4 was used to fit the linear mixed models using Residual Maximum Likelihood (REML) in R (Butler et al. 2017).

4.2.4.3. Genotyping and GWAS Analysis

To assemble the pearl millet genome, whole genome shotgun (WGS) and bacterial artificial chromosome (BAC) sequencing were used. Ten small inserts (of ~170, 250, 500 and 800 bp) and 13 large inserts (of ~2, 5, 10, 20 and 40 kb) WGS libraries were constructed using Tift 23D2B1-P1-P510 genotype. These libraries were sequenced on the Illumina HiSeq 2000, and 520 Gb of sequence data, representing 296 × genome coverage. Two BAC libraries, with an average insert size of ~120 kb, were constructed from Tift 23D2B1-P1-P5 using EcoRI and HindIII. Nine hundred seventy-two Gb of sequence data were generated from 100,608 BAC clones at ~80 × genome coverage. In brief, 1.49 Tb of sequence data, after stringent filtering and correction steps, were assembled into 1.58 Gb of contigs and 1.82 Gb of scaffolds (https://doi.org/10.1038/nbt.3943). A raw marker set consisting of 29 million SNPs generated from 345 pearl millet genotypes was sourced from the Nature Paper Pearl Millet (https://doi.org/10.1038/nbt.3943) and filtered using Tassel v4.2 for site coverage of 90%, minor allele frequency of 0.1, taxa coverage of 30% and maximum heterozygosity of 50%. The resulting final set of variants contained 256 K SNPs was used for the current analysis. Phenotypic data collected from 150 genotypes were available for marker-trait association analysis. Principal component analysis (PCA) was calculated, and the resulting eigenvalue (7) was used for genome-wide association analysis (GWAS) following multiple methods procedures generated from GAPIT

v3.0 (Lipka et al. 2012). The Bayesian-information and linkage-disequilibrium iteratively nested keyway (BLINK) software was used to determine the significant variations among pearl millet and *Sh* traits.

4.3. Results

4.3.1. Phenotypic Variations

Pearl millet genotypes differed significantly ($P < 0.001$) for days to 50% flowering (DTF), plant height (PH), number of tillers per plant (NT), panicle length (PCL), panicle weight (PWT), thousand grains weight (TGW), and grain weight (GW) under *Sh* infestation. Genotypes differed significantly ($P < 0.001$) for the area under the *Striga* number progress curve (ASNPC). The genotype by *Striga* interaction was non-significant for the NT and ASNPC (Table 4.2). Genotypes with missing data were excluded from the analysis.

Table 4.2. Mean squares and significant tests for pearl millet and *Striga* parameters when evaluating 150 genotypes with and without *Striga* infestation under the field and screenhouse environments in Burkina Faso.

Source of variation	**DF**	**DTF**	**PH**	**NT**	**PCL**
Replication	1	66.53^{ns}	3203.50***	20.93***	26.98^{ns}
Genotype	136	317.00***	2394.50***	4.12***	114.63***
Striga	1	389.51***	37599.60***	156.73***	556.95***
Environment	1	5113.06***	84488.00***	490.35***	2353.17***
Genotype × *Striga*	136	33.18***	526.60***	0.85^{ns}	12.13*
Genotype × Environment	136	65.94***	686.20***	1.24***	16.286***
Residual	416	21.80	341.70	0.78	8.94
Total	827				
Source of variation	**DF**	**PWT**	**TGW**	**GW**	**ASNPC**
Replication	1	131169.00***	0.43^{ns}	11016.00***	349.40^{ns}
Genotype	136	16218.00***	14.04***	4953.00***	1627.00***
Striga	1	2511363.00***	73.23***	1037689.00***	120730.90***
Environment	1	7181785.00***	250.04***	2859964.00***	88892.80***
Genotype × *Striga*	136	4095.00^{ns}	4.03***	2375.00***	813.00^{ns}
Genotype × Environment	136	12991.00***	3.74***	6013.00***	1688.70***
Residual	416	4421.00	2.46	1183.00	785.40
Total	827				

* and *** = denote significant differences at 0.05, and 0.001 probability levels, respectively; ns = not significant; DF = degree of freedom; DTF= days to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers; PCL = panicle length (cm); PWT = panicle weight (g); TGW = thousand grains weight (g); GW = grain weight per plant (g); ASNPC = area under the *Striga* number progress curve.

Table 4.3 presented the best linear unbiased prediction means for the response of pearl millet genotypes evaluated under *Sh* infestation. The DTF and PH ranged from 60.13 to 64.95 days and 132.57 to 159.74 cm in the naturally-infested field and the greenhouse conditions, respectively. The TGW ranged from 7.60 to 9.03 grams under *Striga* infestation in field and in screenhouse. Several emerged *Striga* were recorded during the second counting, particularly in the plastic pots (Figure 4.1A) and the hotspot field

(Figure 4.1B) conditions compared to *Striga*-free field condition (Figure 4.1C). Thousand grain weight markedly reduced due to high *Striga* infestations compared to *Striga*-free field (Table 4.3).

A low broad-sense heritability value was computed for the number of emerged *Sh* (18.17 and 28.61%), while high heritability values ranging from 75.07 to 92.42% were recorded for the DTF, PCL, TGW, and PH (Table 4.3).

Table 4.3. Best linear unbiased prediction means and standard error for 150 pearl millet genotypes evaluated in naturally *Sh* infested field and their genetic parameters.

	Predicted Value					
Trt/Trait	**DTF**	**PH**	**PCL**	**TGW**	**SN1**	**SN2**
GenInf	60.13	132.57	23.61	7.60	1.10	1.43
GenStr	64.95	153.06	19.42	8.97	0.87	0.88
Genotype	63.66	159.74	19.70	9.03		
Trial statistics						
SED (GenInf)	0.82	2.93	0.42	0.19	0.03	0.04
SED (GenStr)	0.84	2.99	0.41	0.21	0.03	0.03
SED (Genotype)	0.84	2.98	0.41	0.22		
H^2 (bs)	87.48	84.46	92.42	75.07	28.61	18.17
LSD (5%)	ns	21.20	ns	1.92	ns	0.21
CV (%)	6.93	8.66	15.22	18.88	38.29	44.82

Trt = treatment; DTF = days to 50% flowering; PH = plant height at maturity (cm); PCL = panicle length (cm); TGW = thousand-grain weight (g); SN1 = the number of *Striga* counted 70 days after sowing in the *Striga*-infested field and 116 days after planting in the screenhouse; SN2 = *Striga* number counted 96 days after sowing in the *Striga*-infested field and 144 days after sowing in the screenhouse; GenInf = genotypes in naturally *Striga* infested field; GenStr = genotypes with *Striga* infestation in the screenhouse; SED = standard error of the mean difference; H^2 (bs) = broad sense heritability; LSD = least significant difference; CV = coefficient of variation; ns = non-significant.

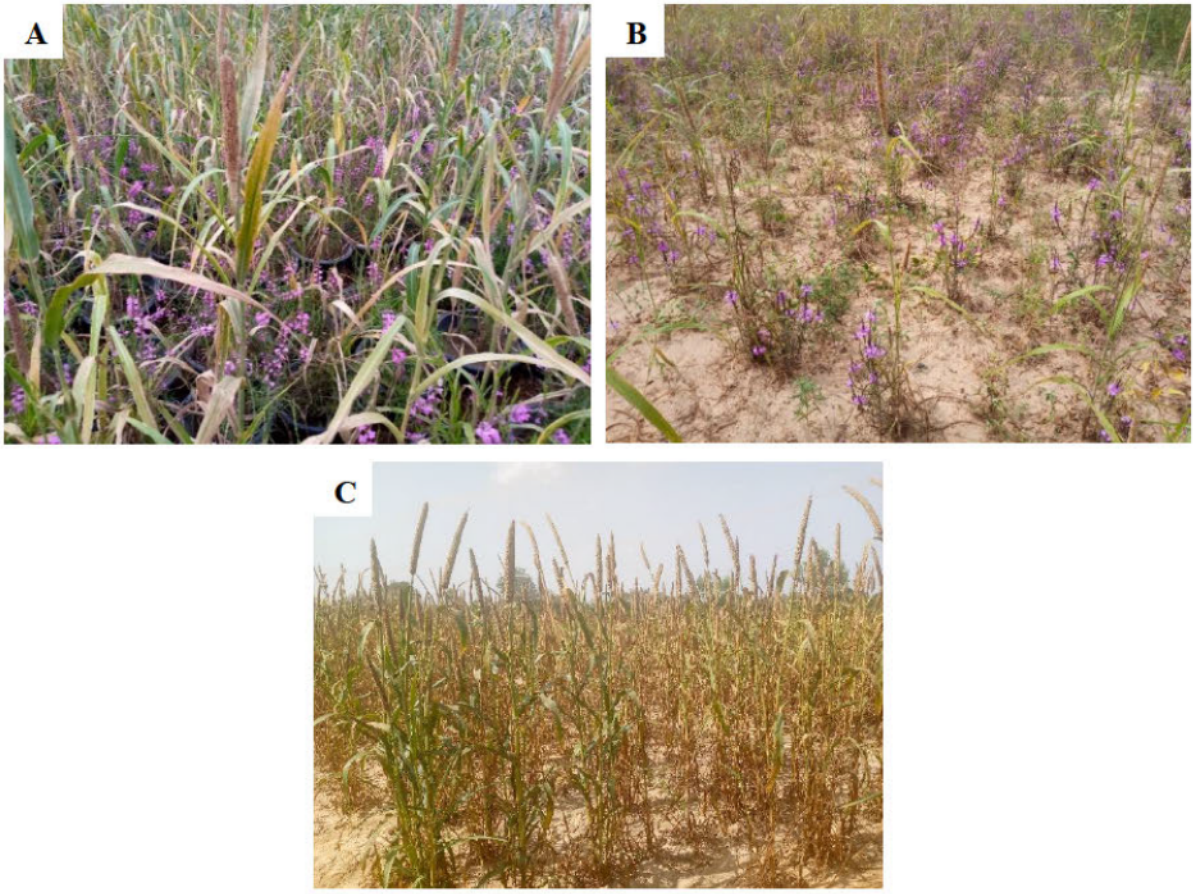

Figure 4.1. Pearl millet crop and *Striga* infestation in Burkina Faso. Note: *Striga hermonthica* infestation under screenhouse (A) and field (B) conditions. Photo C denotes *Striga* free field at the Didri site in Burkina Faso. (Photos supplied by Armel Rouamba).

4.3.2. Genome-Wide Association Mapping

The number of emerged *Sh* counted on the Manhattan plot is presented in Figure 4.2. BLINK model analysis for *Sh* traits led to identifying candidate genetic regions associated with *Striga* resistance. Twenty-eight SNPs were significantly associated with *Sh* emergence on chromosomes 1, 2, 3, 4, 6, and 7 (Table 4.4).

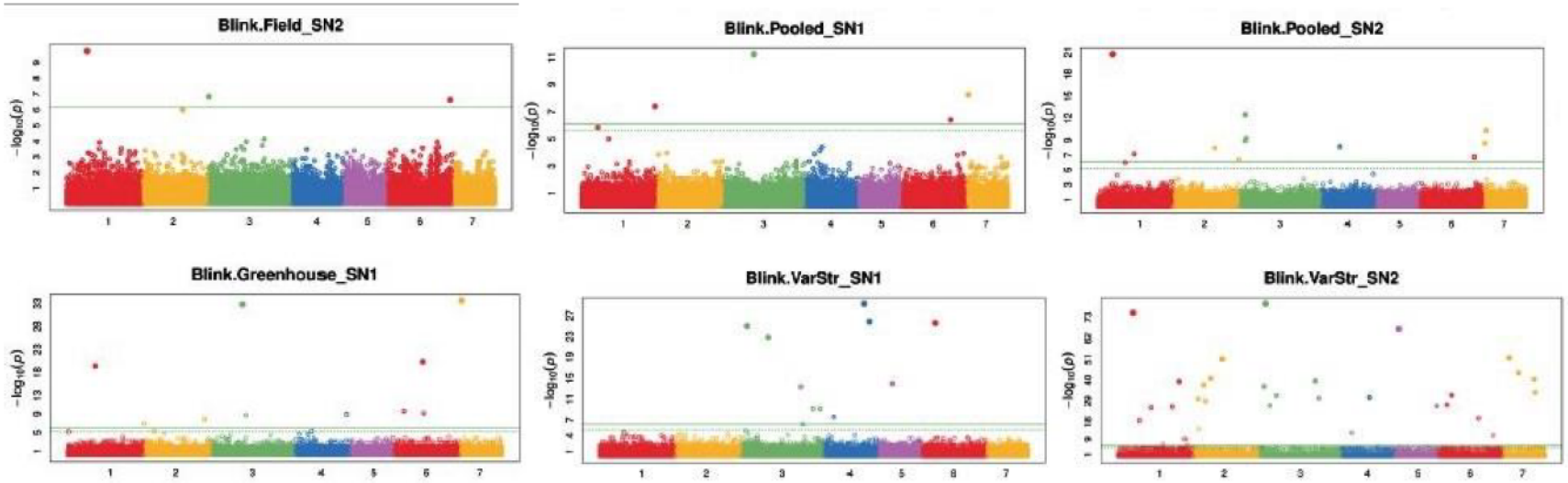

Figure 4.2. Manhattan plots showing associations between single nucleotide polymorphisms and *Sh*-related traits in naturally *Striga*-infested fields and greenhouse conditions. Single nucleotide polymorphisms were plotted on the x-axis according to their positions on each chromosome against association with *Sh*-related traits on the y-axis (-log 10 p-value). The top line indicates genome-wide significant threshold.

Twenty-eight SNPs markers were significantly (P < 0,001) associated with *Sh* resistance located at chromosomes 1, 2, 3, 4, 6, and 7. Two SNPs, S3_113184999 and S3_113184999, were located at the same position and were associated with the number of *Sh* counted (Table 4.4). Three significant (P < 0,001) SNP markers, S1_75620319, S3_1159738, and S6_231436300, were associated with *Striga* resistance in the naturally *Striga*-infested field on chromosomes 1, 3, and 6. In the greenhouse, 10 significant SNPs were associated with *Sh*-resistance, while 15 SNPs were associated with *Sh*-resistance on chromosomes 1, 2, 3, 4, 6, and 7.

Table 4.4. Markers significantly associated with *Striga* resistance traits in 150 pearl millet genotypes assessed in naturally infested fields and greenhouse conditions in Burkina Faso.

Trait	SNP	Chr.	Position	P. value	MAF	AdjP	Annotation	Gene
Field_SN2	S1_75620319	1	75620319	1.80E-10	0.01369863	1.23E-05	intergenic_region	GENE_CDS_1_75476337_75476480-GENE_CDS_1_75717949_75717961
Field_SN2	S3_1159738	3	1159738	1.41E-07	0.034246575	0.00480715	intron_variant	Pgl_GLEAN_10031109
Field_SN2	S6_231436300	6	231436300	2.34E-07	0.020547945	0.005295382	intergenic_region	GENE_CDS_6_231423518_231423673-GENE_CDS_6_231543192_231543410
Greenhouse_SN1	**S7_7890799**	7	**7890799**	2.13E-34	0.02739726	1.45E-29	intergenic_region	GENE_CDS_7_7862940_7862984-GENE_CDS_7_7993524_7994057
Greenhouse_SN1	**S3_113184999**	3	**113184999**	1.37E-33	0.020547945	4.67E-29	intergenic_region	GENE_CDS_3_113129296_113129642-GENE_CDS_3_113377327_113377432
Greenhouse_SN1	S6_108023970	6	108023970	4.21E-21	0.01369863	9.55E-17	downstream_gene_variant	Pgl_GLEAN_10009280
Greenhouse_SN1	S1_99630014	1	99630014	3.61E-20	0.034246575	6.14E-16	intergenic_region	GENE_CDS_1_99187249_99187566-GENE_CDS_1_99759745_99759760
Greenhouse_SN1	S6_39394185	6	39394185	2.43E-10	0.02739726	3.30E-06	intergenic_region	GENE_CDS_6_39351328_39351639-GENE_CDS_6_39440122_39440890
Greenhouse_SN1	S6_111447163	6	111447163	7.07E-10	0.04109589	8.01E-06	intergenic_region	GENE_CDS_6_111439201_111439539-GENE_CDS_6_111452367_111453077
Greenhouse_SN1	S4_182636703	4	182636703	1.24E-09	0.01369863	1.21E-05	intron_variant	Pgl_GLEAN_10034091
Greenhouse_SN1	S3_126337466	3	126337466	2.16E-09	0.02739726	1.83E-05	intergenic_region	GENE_CDS_3_126225889_126226120-GENE_CDS_3_126476234_126476446
Greenhouse_SN1	S2_218400344	2	218400344	1.35E-08	0.034246575	0.000101769	intergenic_region	GENE_CDS_2_218366655_218366812-GENE_CDS_2_218413717_218413989
Greenhouse_SN1	S2_803192	2	803192	1.10E-07	0.01369863	0.000748906	synonymous_variant	Pgl_GLEAN_10017839
Pooled_SN1	**S3_113184999**	3	**113184999**	5.70E-12	0.020547945	3.88E-07	intergenic_region	GENE_CDS_3_113129296_113129642-GENE_CDS_3_113377327_113377432
Pooled_SN1	**S7_7890799**	7	**7890799**	5.54E-09	0.02739726	0.000188415	intergenic_region	GENE_CDS_7_7862940_7862984-GENE_CDS_7_7993524_7994057
Pooled_SN1	S1_270246408	1	270246408	4.10E-08	0.034246575	0.000929872	upstream_gene_variant	Pgl_GLEAN_10038191
Pooled_SN1	S6_184283909	6	184283909	3.95E-07	0.020547945	0.006717724	intergenic_region	GENE_CDS_6_184262794_184263538-GENE_CDS_6_184291509_184291562
Pooled_SN2	S1_54412075	1	54412075	1.86E-21	0.01369863	1.27E-16	upstream_gene_variant	Pgl_GLEAN_10003483
Pooled_SN2	S3_22414758	3	22414758	3.15E-13	0.01369863	1.07E-08	missense_variant	Pgl_GLEAN_10034999
Pooled_SN2	**S7_7890799**	7	**7890799**	4.50E-11	0.02739726	1.02E-06	intergenic_region	GENE_CDS_7_7862940_7862984-GENE_CDS_7_7993524_7994057
Pooled_SN2	S3_26238337	3	26238337	4.89E-10	0.01369863	8.31E-06	intergenic_region	GENE_CDS_3_26144223_26144501-GENE_CDS_3_26273998_26275158
Pooled_SN2	S3_22104285	3	22104285	1.24E-09	0.01369863	1.69E-05	upstream_gene_variant	Pgl_GLEAN_10034978
Pooled_SN2	S7_2011566	7	2011566	2.33E-09	0.034246575	2.64E-05	synonymous_variant	Pgl_GLEAN_10022900
Pooled_SN2	S4_68863333	4	68863333	7.15E-09	0.01369863	6.95E-05	downstream_gene_variant	Pgl_GLEAN_10029552
Pooled_SN2	S2_152870927	2	152870927	1.09E-08	0.01369863	9.25E-05	intergenic_region	GENE_CDS_2_152669342_152669906-GENE_CDS_2_153313889_153313993
Pooled_SN2	S1_133683128	1	133683128	6.95E-08	0.04109589	0.000525221	intergenic_region	GENE_CDS_1_133517524_133517793-GENE_CDS_1_134364799_134365161
Pooled_SN2	S6_204391395	6	204391395	1.79E-07	0.01369863	0.001214075	intergenic_region	GENE_CDS_6_204203637_204204055-GENE_CDS_6_204398055_204398642
Pooled_SN2	S2_242049249	2	242049249	3.82E-07	0.123287671	0.002360813	upstream_gene_variant	Pgl_GLEAN_10018078

SNP = single nucleotide polymorphism, Chr. = chromosome, MAF = minor allele frequency, AdjP = false discovery rate adjusted P-values.

Agronomic Traits

BLINK model analysis of pearl millet agronomic traits under *Sh* infestation identified candidate genetic regions associated with DTF, PCL, and TGW (Figure 4.3). Eleven SNP markers were associated with the assessed pearl millet phenotypic traits. Four SNPs were associated with DTF on chromosomes 3, 5, 6, and 7; six with PCL on chromosomes 2, 3, and 4; and two with TGW on chromosome 6 (Table 4.5).

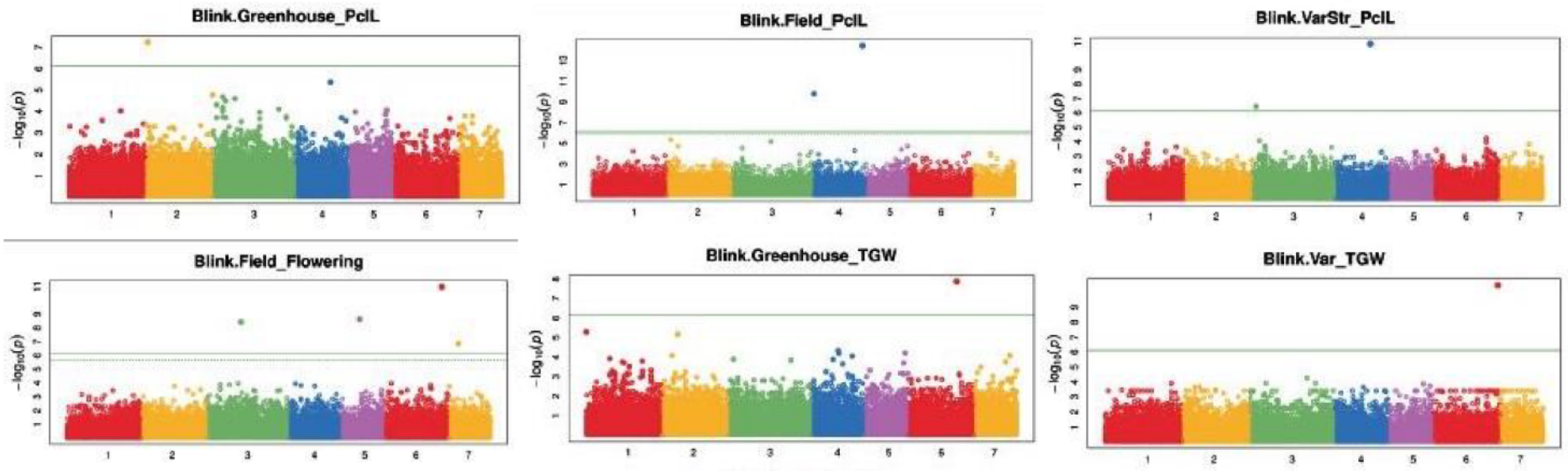

Figure 4.3. Manhattan plots showing associations between single nucleotide polymorphisms and pearl millet-related agronomic traits under *Sh* conditions in naturally *Striga* infested field and greenhouse. Single nucleotide polymorphisms were plotted on the x-axis according to their positions on each chromosome against association with pearl millet-related traits on the y-axis (-log 10 p-value). The top line indicates genome-wide significant threshold.

Table 4.5. Markers significantly associated with agronomic traits in 150 pearl millet genotypes assessed in naturally *Striga*-infested fields and screenhouse conditions in Burkina Faso.

Trait	SNP	Chr.	Position	P. value	MAF	AdjP	Annotation	Gene
Field_Flowering	S6_214124725	6	214124725	1.05E-11	0.02739726	7.13E-07	intergenic_region	GENE_CDS_6_214064703_214065150-GENE_CDS_6_214144811_214144961
Field_Flowering	S5_70437618	5	70437618	2.36E-09	0.04109589	8.03E-05	intron_variant	Pgl_GLEAN_10010062
Field_Flowering	S3_124462289	3	124462289	3.65E-09	0.01369863	8.26E-05	intergenic_region	GENE_CDS_3_124448276_124448524-GENE_CDS_3_124546255_124546494
Field_Flowering	S7_34887211	7	34887211	1.34E-07	0.034246575	0.002276945	intron_variant	Pgl_GLEAN_10030410
Field_PclL	S4_178741335	4	178741335	3.80E-15	0.02739726	2.58E-10	synonymous_variant	Pgl_GLEAN_10011399
Field_PclL	S4_4389968	4	4389968	1.65E-10	0.01369863	5.61E-06	downstream_gene_variant	Pgl_GLEAN_10014324
Greenhouse_PclL	S2_9048490	2	9048490	5.77E-08	0.047945205	0.003923655	intron_variant	Pgl_GLEAN_10013735
Greenhouse_TGW	S6_176707138	6	176707138	1.36E-08	0.02739726	0.000922491	intergenic_region	GENE_CDS_6_176509156_176509570-GENE_CDS_6_176832456_176832571
VarStr_PclL	S4_125228939	4	125228939	1.61E-11	0.01369863	1.10E-06	downstream_gene_variant	Pgl_GLEAN_10035535
VarStr_PclL	S3_14571318	3	14571318	3.65E-07	0.205479452	0.012407417	upstream_gene_variant	Pgl_GLEAN_10018534
Var_TGW	S6_232020017	6	232020017	3.26E-11	0.020547945	2.22E-06	downstream_gene_variant	Pgl_GLEAN_10024656

SNP = single nucleotide polymorphism, Chr. = chromosome, MAF = minor allele frequency, AdjP = false discovery rate adjusted P-values.

4.4. Discussion

The assessed genotypes exhibited significant differences in agronomic traits and *Sh* parameters (Table 4.2), suggesting substantial genetic variation for selection. The results allowed marker-trait association analysis valuable for current and future selection and new variety design and commercialisation. A significant genotype by *Sh* interaction effect existed (Table 4.2), revealing the potential existence of genes controlling *Sh* resistance among the populations. This concurs with the deductions made by Mrema et al. (2017) and Shayanowako et al. (2020), who reported significant variation and differential genotypic responses to *Sh* infestation among sorghum and maize genotypes, in that order. Thus, the set of population evaluated in the current study was suitable for marker-trait association analyses for *Sh* resistance and economic traits.

Reduced DTF and PH were recorded on pearl millet genotypes under *Striga* infestation (Table 4.3), indicating the negative impact of the parasite on the measured traits. These findings concur with reports by Ransom and Odhiambo (1995). Wilson et al. (2000) reported a negative correlation between the number of emerged *Sh* and DTF in pearl millet. Similarly, a reduction of PH by 28% under *Sh* infestation was reported in pearl millet by Graves et al. (1990). Badu-Apraku (2007) reported a negative correlation between *Striga* damage rating and DTF in maize in Sub-Saharan. Poor crop growth and subsequent low productivity is because of the *Striga* plant attachment and siphoning of nutrients from the host plant's roots.

The recorded TGW of 7.60 to 9.03 g in the present study (Table 4.3) is in line with the 6.9 to 12.9 g reported by Kanatti et al. (2014). The relatively high ranges of values in the current results are probably attributed to the large grain size, which increased the yield of pearl millet (Kanatti et al. 2014; Jukanti et al. 2016). The broad-sense heritability (H^2) for agronomic traits ranged from 75.07 to 92.42% and 18.17 to 28.61% for emerged *Sh* count (Table 4.3). The high broad-sense heritability estimates of 75.07 to 92.42% computed for DTF, PH, PCL, and TGW indicated that the traits are mainly governed by genes with limited influence by the test environment (Afolayan et al. 2020). Traits with high heritability are easy to select and improve using marker-assisted selections and pyramiding and stacking in a desirable genetic background. The lower broad-sense heritability estimates of 18.17 to 28.61% for the number of emerged *Striga* (Table 4.3) suggests that the traits are mainly under the influence of the environment, indicating the possibility of a strong genotype by environment interaction due to the role polygenes with minor genetic effect (Afolayan et al. 2020). Robert (2011) and Kaewchumnong and Price (2008) reported a low heritability estimate for *Striga* resistance-related traits in sorghum and rice, respectively.

The ability of BLINK to produce fewer false positives and more true positives than the GWAS method, FarmCPU, was also reported by Huang et al. (2019). Liu et al. (2016) reported the power of BLINK to outperform FarmCPU relative to statistical capabilities vs False Discovery Rate (FDR) and statistical

power vs type I error. The seven pearl millet chromosomes harbour several genes (Table 4.5) conditioning *Striga* resistance and agronomic traits. Each chromosome had at least two significant marker-trait associations in the present study. After successful validation, the 28 significant SNP markers associated with *Sh* emergence on chromosomes 1, 2, 3, 4, 6, and 7 (Table 4.4) can be used for marker-assisted selection and trait introgression to improve *Sh* resistance in pearl millet. Dawud (2018) identified 16 SNP markers associated with the area under the *Striga* number progress curve on chromosomes 2, 3, 4, 5, and 7 in pearl millet. The findings confirm that the chromosomes harbour some beneficial alleles influencing *Sh* resistance. Dawud (2018) reported significant gene markers related to *Striga* resistance on chromosomes 1, 2, 3, and 5 in pearl millet. Markers associated with *Striga* resistance traits have also been reported in sorghum and maize (Khangura 2019; Pfunye et al. 2021). The two SNP makers located adjacent to each other and associated with the low number of *Sh* count could be tightly linked and co-segregating. Hence the respective candidate genes can be selected for and introgressed simultaneously (Adewale et al. 2020). Identifying genetic markers associated with agronomic traits will facilitate marker-assisted breeding in pearl millet (Figure 4.3). In *Striga*-free conditions, Kannan et al. (2014), using SSR markers, detected significant markers associated with pearl millet panicle length and thousand-grain weight. In maize, some quantitative traits loci associated with grain yield and ear aspect have been reported by Stanley et al. (2021) and Badu-Apraku et al. (2020). Significant SNPs markers related to the number of tillers were also reported in pearl millet by Dawud (2018). In this study, 28 SNP markers associated with low *Sh* emergence were identified on chromosomes 1, 2, 3, 4, 6, and 7 involving genetic analysis of 150 genetically diverse pearl millet genotypes in Burkina Faso (Figure 4.3). The candidate markers and genotypes are novel genomic and genetic resources for *Striga* resistance breeding programs in the country and elsewhere.

4.5. Conclusions

The current study detected significant genetic variability and markers for *Sh* resistance and agronomic traits through GWAS involving 150 pearl millet genotypes in Burkina Faso. There were significant genotypes by *Sh* interaction for assessed agronomic traits, the number of *Sh* and ASNPC. Twenty-eight SNPs were associated with *Sh* traits on chromosomes 1, 2, 3, 4, 6, and 7. SNPs markers associated with DTF, PCL, and TGW were located on chromosomes 2, 5, 6, and 7; chromosomes 2, 3, and 4; and chromosome 6, respectively. After successful validation, the new markers would be deployed for marker-assisted breeding emphasising the above agronomic traits and *Sh* resistance in pearl millet in Burkina Faso or related agro-ecologies.

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Chapter 5. Generation mean analysis of *Striga hermonthica* resistance in pearl millet (*Pennisetum glaucum* [L.] R. Br.)

Abstract

Striga hermonthica [Del.] Benth. (*Sh*) is a noxious parasitic weed causing substantial yield loss in sub-Saharan Africa's pearl millet. The objective of this study was to determine the gene action and inheritance of *Sh* resistance in newly developed pearl millet populations to guide selection and genetic advancement. Bi-parental crosses were derived from pairs of pearl millet lines by contrasting reactions to *Striga* infestations. The two sets of parental lines, F_1s, F_2s, and backcrosses, were evaluated using a randomized complete block design with three replications. Data on the number of *Striga* counted at 60 and 80 days after planting were collected. The analysis of the variance showed significant ($P < 0.001$) differences among the generations across sets for *Sh* parameters. Duplicate gene action controlled the inheritance of the number of emerged *Sh*. Unique F_2 individuals with *Sh* resistance were selected from the two sets for genetic advancement through recurrent selection methods for pearl millet variety development by integrating desirable agronomic and farmer-preferred traits.

Keywords: Gene action; generation mean analysis; pearl millet; *Striga hermonthica*; trait inheritance

5.1. Introduction

Pearl millet (*Pennisetum glaucum* [L.] R. Br., 2n=2x=14) is one of the most important cereal crops cultivated in the semi-arid tropics of sub-Saharan Africa (SSA) and India, serving millions of households and local and regional markets. Pearl millet is a highly cross-pollinated crop due to variable stigma receptivity and anther dehiscence. In SSA, pearl millet is used as a staple food, livestock feed, fuelwood, and construction material (Burgarella et al. 2018). In West Africa, pearl millet ranked first in total area under cultivation and fourth in total production after maize, rice, and sorghum in cereal (FAOSTAT 2021). In Burkina Faso, it is the third major cereal crop after maize and sorghum. Burkina Faso accounted for 18.48% of the global pearl millet production (5179104 tons) in 2020 (INSD 2021). Pearl millet is adapted to relatively hot and dry agro-ecologies with low annual rainfall (300–500 mm) and poor soil fertility conditions where other cereal crops fail (Burton, Wallance, and Radice 1972; Vadez et al. 2012). Despite the economic value of pearl millet, the average grain yield of the crop in Burkina Faso is 0.90 tons per hectare (INSD 2021).

The low productivity of pearl millet in SSA is attributable to several biotic and abiotic stresses (Khan et al. 2014). Among the biotic constraints, *Striga hermonthica* (*Sh*) is a significant threat to pearl millet production and productivity, leading to food insecurity and poor household income in many African countries (Parker and Riches 1993; Khan et al. 2014). Complete crop losses have been recorded under heavy *Striga* infestation (Unachukwu et al. 2020; Rodenburg et al. 2016).

The wide adaptability and varied host range of *Sh* have contributed to its successful parasitism. *Striga* attacks staple cereal crops such as Sorghum (*Sorghum bicolor* [L.] Moench), maize (*Zea mays* L.), and rice (*Oriza* spp.) (Mohamed et al. 2006). Several control measures have been recommended for reducing *Sh* infestation (Mrema, Shimelis, and Laing 2017). These include the use of resistant varieties, cultural practices, and chemical and biological agent control methods (Hearne 2009). Some of the most effective cultural control practices are hand weeding, crop rotation, trap-cropping, intercropping, soil-fertility improvement, and soil-moisture management (Hess and Dodo 2004; Samake et al. 2006; Hooper et al. 2015; Rouamba et al. 2021). These methods reduced *Striga* seed bank in the soil, improved soil structure and fertility, promoted growth and development of the host plant, and retarded the growth and development of juvenile *Striga* plants (Mrema, Shimelis, and Laing 2017). The herbicide 2,4-D can reduce *Striga* emergence (Kanampiu et al. 2003). Biocontrol agents, such as the pathogenic fungus *Fusarium oxysporum* f.sp. *Strigae*, are promising mycoherbicides against *Striga* (Eltayb et al. 2013; Zarafi et al. 2015; Watson 2013; Rebeka et al. 2013; Mrema, Shimelis, and Laing 2017; Shayanowako et al. 2020). The above approaches could offer little protection when used individually due to the diversity of the host crops and variable environmental conditions favoring the parasite (Kountche, Al-Babili, and Haussmann 2016). This suggests that no single control method can effectively solve the

Striga problem (Joel 2000; Oswald 2005). However, host resistance is considered the most economical, practical, and sustainable long-term approach for controlling *Sh*, notably under resource-poor farming systems (Hearne 2009; Mandumbu et al. 2019).

The development of improved varieties with *Sh* resistance depends on the availability of genetic variation for resistance and desirable agronomic traits (Kountche, Al-Babili, and Haussmann 2016). *Striga* resistance is the ability of the host genotype to forestall *Striga* attachment, growth, and development while producing higher yield than the susceptible genotypes (Ramaiah 1987; Ejeta and Butler 1993). Tolerance, on the other hand, is the ability of the host plant to maintain high biomass and yield compared to susceptible genotypes under the same level of *Striga* parasitism (Haussmann et al. 2000; Rodenburg et al. 2005a; Hearne 2009).

Few studies are available to elucidate the mechanisms and inheritance of *Striga* resistance in pearl millet. In other major cereal crops, such as sorghum, both qualitative and quantitative *Striga* resistances have been reported (Mrema, Shimelis, and Laing 2017; Akaogu et al. 2019). Haussmann et al. (2001) reported a major gene and several minor genes conditioning *Striga* seed germination in sorghum. Stable and broad-based *Striga* resistance is achieved when additive genes are involved (Badu-Apraku et al. 2009; Mrema, Shimelis, and Laing 2017). Genetic information such as the mode of gene action governing the inheritance of *Striga* resistance and agronomic traits will facilitate the introgression of candidate genes and the deployment of resistant genotypes in pearl millet improvement programs (Akanvou and Doku 1998).

Only a few pearl millet cultivars are reportedly partially resistant or tolerant to *Striga* (Ramaiah 1987). Partial quantitative *Sh* resistance in wild pearl millet was reported in Africa (Wilson, Hess, and Hanna 2000; Wilson et al. 2004). *Striga* resistance based on the number of emerged *Striga* plants, counted 56 days and 70 days after planting, suggested the presence of polygenes governing resistance (Akaogu et al. 2019). Kountche et al. (2013) reported the presence of multiple genes providing *Sh* resistance among diverse gene pools of the cultivated pearl millet under field conditions.

Various mating designs have been used to partition the genetic effects into additive and non-additive components and postulate the mode of trait inheritance. The generation mean analysis (GMA) is one of the genetic designs used to determine the type of gene effects conditioning quantitative traits (Mather and Jinks 1982a). The GMA allows the computation of various genetic parameters based on six genetic generations P_1, P_2, F_1, F_2, BC_{11}, and BC_{12} (Singh and Singh 1992). Partitioning the genetic effects into distinct components provides valuable information for gene introgression and deployment in *Striga* resistance breeding programs (Akaogu et al. 2019).

Host plant resistance against *Sh* has been identified for sorghum (Tesso and Ejeta 2011; Akaogu et al. 2019), maize (Badu-Apraku et al. 2019; Menkir and Meseka 2019), rice (Cissoko et al. 2011), and pearl millet (Dawud 2018; Kountche et al. 2013). *Striga*-resistant pearl millet cultivars are yet to be developed and deployed in SSA, including Burkina Faso. Only cultural practices are routinely used to control *Striga* in pearl millet production in the region. This is due to a lack of agronomically suitable, locally adapted and *Striga*-resistant genotypes. There is a dire need for a concerted breeding effort and complementary genetic and genomic resources to develop and deploy *Striga*-resistant pearl millet varieties (Kountche et al. 2013; Sattler et al. 2018). Several studies have characterized the mechanisms and inheritance of resistance to *Striga* in the major cereal crops (Amusanm et al. 2008; Cissoko et al. 2011; Jamil et al. 2011; Satish et al. 2012). Knowledge of *Striga* resistance and its inheritance is required in pearl millet (Jamil, Kountche, and AL-Babili 2021). Therefore, the objective of this study was to determine the gene action and inheritance of *Sh* resistance in selected parents and derived pearl millet populations with variable responses to *Sh* infestation through GMA to guide selection, genetic advancement and variety development.

5.2. Materials and Methods

5.2.1. Study Sites

The study was conducted in Burkina Faso in a *Sh* hotspot field at the Tanghin Dassouri site and under artificial infestation in a screenhouse at the "Institut de l'Environnement et de Recherches Agricoles" (INERA) during the main cropping season of 2021–2022. Tanghin Dassouri and INERA are located at 12° 16′ 10″ N; 1° 42′ 55″ W and 12°28/27 N; 1°33/31 W, respectively. They receive an annual rainfall of 600 to 900 mm per year, and the temperatures range from 25 to 33.5 °C (Pieyns 2017). Tanghin Dassouri has a leached tropical ferruginous soil, a coarse loamy-sandy texture and ferro-manganic gravels. These sites represent the semi-arid areas of Burkina Faso, known for high levels of pearl millet production and heavy *Sh* infestations.

5.2.2. Genetic Material and Crosses

Two sets (A and B) of first-filial generation (F_1) crosses were developed using a bi-parental mating design. In set A, F_1 crosses were developed using *Sh*-resistant parent IP-10579 (designated as P_1) and a susceptible parent IP-8129 (P_3), whereas in Set B, the cross involved IP-3098 (P_2, resistant) and IP-8786 (P_4, susceptible). The F_1 generations were selfed to produce the second-filial generation (F_2) and backcrossed to the respective resistant and susceptible parents. The Set A consisted of P_1, P_3, F_1, F_2, and BC_{11} and BC_{13} and Set B contained P_2, P_4, F_1, F_2, BC_{12}, and BC_{14}. The two *Striga*-resistant pearl millet

genotypes, IP-10579 and IP-3098, are inbred lines acquired from ICRISAT and selected after screening for resistance to *Striga*, whereas entries IP-8129 and IP-8786, also inbred lines obtained from ICRISAT, were selected for their susceptibility to *Striga*. The reasons for developing the two sets of crosses were to develop unique populations for selection and reliably estimate the nature and mode of inheritance of the candidate genes present in the two parents to guide current and future selection and genetic advancement. Crosses and backcrosses were performed following the procedure of Akaogu et al. (2019). Pearl millet is a highly cross-pollinated crop with protogynous and hermaphroditic flowers. Briefly, the panicles of both parents were bagged before anthesis, with pollen bags. At anthesis, viable pollen grains (Figure 5.1B) were collected from each resistant parent in a pollen bag and panicles of the susceptible female parents (Figure 5.1A) were pollinated. Pollination was carried out by gently shaking the pollen bag and dusting the pollen grains onto the panicles to allow the transfer of pollen grains to the stigma. After pollination, the panicle was bagged and labelled until the F_1 seed had matured. The F_1 seed was planted along with resistant and susceptible parents. The panicles of the F_1 plants were either bagged and selfed to provide the F_2 seed or crossed with either parent to generate the backcrosses.

Figure 5.1. Pearl millet panicles showing maternal (A) and paternal (B) inflorescences for pollination. Note the protruding and active pollen grain in panicle B. (Photo by Armel Rouamba).

5.2.3. Experimental Design and Establishment

The six generations were planted simultaneously using a randomized complete block design (RCBD) with three replicates in both sets. At INERA, a mixture of clay and sandy soil was prepared and five-liter capacity plastic pots were filled with it. Each pot received a scoop of *Sh* seeds that weighed 0.05 g prior to planting the pearl millet seed. The pots were then watered twice a week to precondition *Striga* seed, and pearl millet seeds were planted 11 days after preconditioning *Striga* seed. Each replication consisted of 10 plants for parents and the F_1 generations, 20 and 60 plants for backcrosses, and F_2, respectively. In the *Striga*-infested field, parents and F_1 were planted in one row of 10 hills, backcrosses in two rows (20 hills), and the F_2 in six rows (60 hills), with an inter-row and intra-row spacing of 1.6 m and 0.6 m, respectively. At both locations, management of the trials followed the standard pearl millet production practices, and weeds other than *Sh* were hand-pulled when necessary.

5.2.4. Data Collection and Analysis

Data were collected based on *Striga* parameters, including the number of emerged *Striga* at 60 days and 80 days after sowing, and the area under the *Striga* number progress curve (ASNPC) was computed. Data were recorded on 10 plants for non-segregating populations (P_1, P_2, P_3, P_4, and F_1), 20 plants for the backcrosses (BC_{11}, BC_{12}, BC_{13}, and BC_{14}), and 60 plants for the F_2 populations. The data for Set B from the infested field were discarded due to non-uniform germination of *Striga* seeds and poor infestation levels. The ASNPC was computed using the successive count of the *Striga* emergence as follows:

$$ASNPC = \sum_{i=0}^{n-1} \left[\frac{Y_i + Y_{(i+1)}}{2}\right](t_{i+1} - t_i)$$

where n is the number of *Striga* assessment dates, Y_i is the *Striga* count at the i^{th} assessment date, $Y_{(i+1)}$ is the *Striga* count at the i^{th} plus 1 assessment date, t_i is the number of days after planting (DAP) at the i^{th} assessment date, $t_{(i+1)}$ is DAP at the i^{th} plus 1 assessment date (Haussmann et al. 2000).
Striga count data were transformed using square root and subjected to the mixed model's analysis procedure using GenStat 20th Edition (http://www. genstat.co.uk) to assess the significant differences among generations for the assessed traits. The blocks were treated as random, whereas genotypes were considered fixed factors. The model used was:

$$Y_{ijk} = \mu + g_i + b_j + p_{ij} + e_{ijk}$$

where Y_{ijk} is the *Striga* count for the i^{th} genotype in the j^{th} block, for the k^{th} tested plant in the ij^{th} plot, μ is the overall mean, g_i is the effect of the i^{th} genotype, b_j is the effect of the j^{th} block, p_{ij} is the effect of the ij^{th} plot on the i^{th} genotype and the j^{th} block, and e_{ijk} is the residual effect. The errors for plots (p_{ij}), genotypes (g_i), blocks (b_j), and plants (k^{th}) were considered normally distributed with a mean of zero and phenotypic variance (σ^2_p) and error variance (σ^2_e) (Piepho and Möhring 2010).

A scaling test was used to determine the existence of non-allelic interaction (Mather and Jinks 1949; Hayman and Mather 1955). The scales A, B, C, and D were computed as follows:

$$A = 2BC_{11}\text{-}P_1\text{-}F_1;$$

$$B = 2BC_{12}\text{-}P_2\text{-}F_1;$$

$$C = 4F_2\text{-}2F_1\text{-}P_1\text{-}P_2;$$

$$D = 2F_2\text{-}BC_{11}\text{-}BC_{12};$$

where P_1, P_2, F_1, F_2, BC_{11}, and BC_{12} are the mean values of the respective generations of pearl millet populations for *Striga* parameters.

The adequacy of the genetic model was tested using the joint-scaling test, as proposed by Cavalli (1952). The linear genetic model used was as follows:

$$Y = m + \alpha a + \beta d + \alpha^2 aa + 2\alpha\beta ad + \beta^2 dd.$$

where Y is the observed generation mean; m, mean of the F_2 generation as the base population and intercept value; *a*, additive genetic effect; α, coefficient of *a; d*, dominance genetic effect; *aa*, additive × additive gene interaction effect; *ad*, additive × dominance gene interaction effect; *dd*, dominance × dominance gene interaction effect; β, coefficient of *d*. The variance components were estimated, as described by Mather and Jinks (1982b), using the OPSTAT software (http://14.139.232.166/opstat/) (Sheoran et al. 1998).

The narrow-sense heritability (h^2) was determined using the following formula (Acquaah 2012):

$$h^2(ns) = V_A/V_P,$$

where V_A is the additive genetic variance and V_P, the phenotypic variance representing the sum of the genetic variance, environmental variance, and variance associated with the genetic and environmental interaction.

5.3. Results and Discussion

5.3.1. Mixed Model Analysis

A mixed model for *Striga* resistance traits among pearl millet families derived from the two crosses is presented in Table 5.1. Pearl millet genotypes (that represented the resistant and susceptible parents, the first and second filial generations) were significantly ($P < 0.001$) different for all variables in both crosses in the screenhouse and in the field for Set A.

The present study examined two sets of pearl millet populations obtained by crossing selected *Sh* resistant and susceptible parents in Burkina Faso.

Table 5.1. Mixed model analysis and significant tests for the number of emerged *Striga* plants, for two sets of crosses, under screenhouse and field tests.

Variables	Wald statistic	F statistic	N.D.F.	Estimate	D.D.F.	S.E.	*p-value*
Set A Screenhouse							
ASNPC	51.68	10.34	5	724.40	382.00	1.55	<0.001
SN60	55.76	11.15	5	1.92	382.00	0.08	<0.001
SN80	44.68	8.94	5	1.85	382.00	0.08	<0.001
Field							
ASNPC	129.85	25.97	5	453.40	382.00	8.10	<0.001
SN60	95.90	19.18	5	1.05	382.00	0.39	<0.001
SN80	127.20	25.44	5	1.63	382.00	0.43	<0.001
Set B Screenhouse							
ASNPC	28.22	5.64	5	1019.00	382.00	5.47	<0.001
SN60	31.33	6.27	5	3.38	382.00	0.26	<0.001
SN80	18.98	3.80	5	2.52	382.00	0.29	0.002

ASNPC = Area under the *Striga* number progress curve, SN60 = *Striga* count 60 days after planting, SN80 = *Striga* count 80 days after planting, N.D.F. = Numerator degrees of freedom, D.D. F. = Denominator degrees of freedom, S.E. = Standard error of the mean difference.

The resistant and susceptible parents, the first and second filial generations (P_1, P_3, F_1, F_2, and BC_{11} and BC_{13} in Set A, and P_2, P_4, F_1, F_2, BC_{12}, and BC_{14} in Set B.) were assessed in the screenhouse and field (Set A) conditions with *Sh* infestations to determine gene action conditioning *Sh* resistance in pearl millet and to select desirable F_2 individuals for recombination through recurrent selection. The mixed model analysis showed significant differences for *Striga* parameters, such as SN60, SN80, and ASNPC, among the assessed genotypes and environments. A considerable level of genetic variation for *Sh* resistance existed among the assessed generations for selection and to deduce genetic parameters. Significant differences among generations and environments for all *Striga* traits in the study were detected by generation mean analysis for *Sh* resistance in pearl millet by Dawud (2018).

5.3.2. The Effect of *Striga* Test Environments on Pearl Millet Populations Derived From the Cross IP-10579 × IP-8129

The combined analysis of variance indicates significant differences ($P < 0.001$) for the assessed *Striga* traits among pearl millet genotypes and environments (Table 5.2). Variation attributable to genotypes, environments, and the genotypes × environments interaction was significant ($P < 0.001$) for *Striga* count and the area under the *Striga* number progress curve, indicating that the environment affected the *Sh* emergence, as also reported by Dawud (2018).

Table 5.2. Combined mixed model analysis and significant tests for *Striga* count and the area under the *Striga* number progress curve values among pearl millet populations derived from the cross of IP-10579 × IP-8129 (Set A), under screenhouse and field tests.

Variables	Wald statistic	F statistic	N.D.F.	Estimate	D.D.F.	S.E.	*p-value*
Set A Combined							
ASNPC	135.20	27.04	5	31.81	771.00	2.58	<0.001
SN60	109.89	21.98	5	1.61	771.00	0.85	<0.001
SN80	127.39	25.48	5	1.89	771.00	0.42	<0.001

ASNPC = Area under the *Striga* number progress curve, SN60 = *Striga* count 60 days after planting, SN80 = *Striga* count 80 days after planting, N.D.F. = Numerator degrees of freedom, D.D. F. = Denominator degrees of freedom, S.E. = Standard error of the mean difference.

Table 5.3. Mean response of six pearl millet generations for the number of *Sh*, the area under the *Striga* number progress curve, and narrow sense heritability values for two sets of crosses in the screenhouse and field evaluations for Set A.

Set A: IP-10579 × IP-8129						
	Screenhouse evaluation			**Field evaluation**		
Generations	**SN60**	**SN80**	**ASNPC**	**SN60**	**SN80**	**ASNPC**
P_1	2.800	3.330	61.330	0.070	0.300	4.000
P_3	6.100	7.330	134.330	1.470	3.800	52.670
F_1	11.800	11.900	237.000	4.930	12.230	171.670
F_2	12.040	11.770	238.110	2.920	6.990	98.440
BC_{11}	7.900	8.580	164.830	1.070	3.880	49.500
BC_{13}	9.550	8.680	182.330	5.080	10.200	152.830
h^2 (ns)	-1.444	-2.749	-1.952	-1.264	-4.442	-1.988
Set B: 1P-3098 × IP-8786						
	Screenhouse evaluation					
Generations	**SN60**	**SN80**	**ASNPC**			
P_2	7.630	12.200	198.300			
P_4	12.370	13.570	259.300			
F_1	15.530	16.030	315.700			
F_2	17.780	18.330	361.100			
BC_{12}	18.800	21.480	402.800			
BC_{14}	20.780	20.920	417.000			
h^2 (ns)	-1.439	-1.432	-1.324			

P_1 and P_2 are resistant parents, P_3 and P_4 are susceptible parents, F_1 = First filial generation, F_2 = Second filial generation, BC_{11} and BC_{12} denote backcross generation 1 derived from the crosses of the F_1 with the resistant parents P_1 and P_2, in that order, BC_{13}, and BC_{14} refer to backcross generation 1 derived from the crosses of the F_1 with the susceptible parents P_3 and P_4, respectively, h^2 (ns) = narrow sense heritability, SN60 = *Striga* count 60 days after planting, SN80 = *Striga* count 80 days after planting, ASNPC = Area under the *Striga* number progress curve.

5.3.3. Mean Response of the Six Generations for *Striga* Parameters

The mean response of the six pearl millet generations for the number of emerged *Sh* is presented in Table 5.3. The number of emerged *Sh* showed that the resistant parents 1 and 2 (P_1 and P_2) supported fewer emerged *Striga* plants in both environments. However, the susceptible parents 3 and 4 (P_3 and P_4)

had many emerged *Striga* plants in the two test environments. A relatively few *Sh* plants (3.33 to 12.20) emerged in the experimental units consisting of resistant pearl millet parents (P_1 and P_2), whereas many parasitic plants were counted in the susceptible parents P_3 and P_4, (Table 5.3). These findings suggest the existence of *Sh* resistance genes in the donor parents to be used to develop and select new pearl millet populations with *Striga* resistance. The current findings are in line with Akaogu et al. (2019), who reported fewer *Striga* plants in maize genotypes possessing *Striga* resistance derived from a cross between *Striga* resistant and susceptible inbred lines. In the present study, ASNPC showed low values (61.33 to 198.30) for resistant parents (P_1 and P_2) (Table 5.3; Figures 5.2 A, B, C). Kountche et al. (2013) reported a low ASNPC in areas with low *Sh* counts in pearl millet. The increased number of *Sh* in F_1 was similar to the sorghum (Obilana 1984), maize (Akaogu et al. 2019), and pearl millet (Dawud 2018) hybrid developed from a cross between resistant and susceptible parents.

The existence of partial and/or complete dominance for *Sh* susceptibility was reported by Haussmann et al. (2000). A lower *Striga* count in BC_{11}, BC_{12} than in BC_{13}, BC_{14} for both crosses and environment indicated that the *Striga* resistance is quantitatively inherited and controlled by several genes (Dawud 2018; Akaogu et al. 2019). Backcrossing to the susceptible parent increased the frequency of the allele for susceptibility. In contrast, allele frequency for resistance increased with backcrossing to the resistant parent (Akaogu et al. 2019). Dawud (2018) reported that fewer *Striga* plants were found in F_1 families backcrossed to resistant parents than when backcrossed to the susceptible parents. These results indicate that the *Striga* resistance genes were integrated in the offsprings during the crosses (Dawud 2018), allowing the selection of 25 individual plants supporting less than two *Sh* plants in the segregating populations (F_2 and backcross) to be advanced through the recurrent selection method. Breeding for *Sh* resistance using recurrent phenotypic selection has been shown to result in a significant improvement in *Sh* resistance in cultivated pearl millet and the development of the first pearl millet *Sh* resistant experimental varieties (Kountche et al. 2013a). The use of genetically heterogeneous *Striga*-resistant open-pollinated cultivars, in which different plants carry different resistance alleles, has been reported to be a practical alternative for ensuring the stability of resistance to *Sh* across time (Kountche et al. 2013a). The expression of the additive variance as a proportion of the phenotypic variance is the narrow sense heritability which is a measure of the genetic relationship between parent and progeny (Badu-Apraku 2007). According to Moore and Shenk (2017), heritability explains the variation in a trait due to genetic differences among individuals. The study found negative narrow sense heritability for SN60, SN80, and ASNPC in screenhouse for sets A and B and in field evaluation for Set A, describing the traits' discordant tendency among the genotypes, corroborating the findings of Steinsaltz, Dahl, and Wachter (2020). Hallauer and Miranda (1988) argued that the epistatic effect will influence the estimates of additive genetic variance, hence narrow-sense heritability.

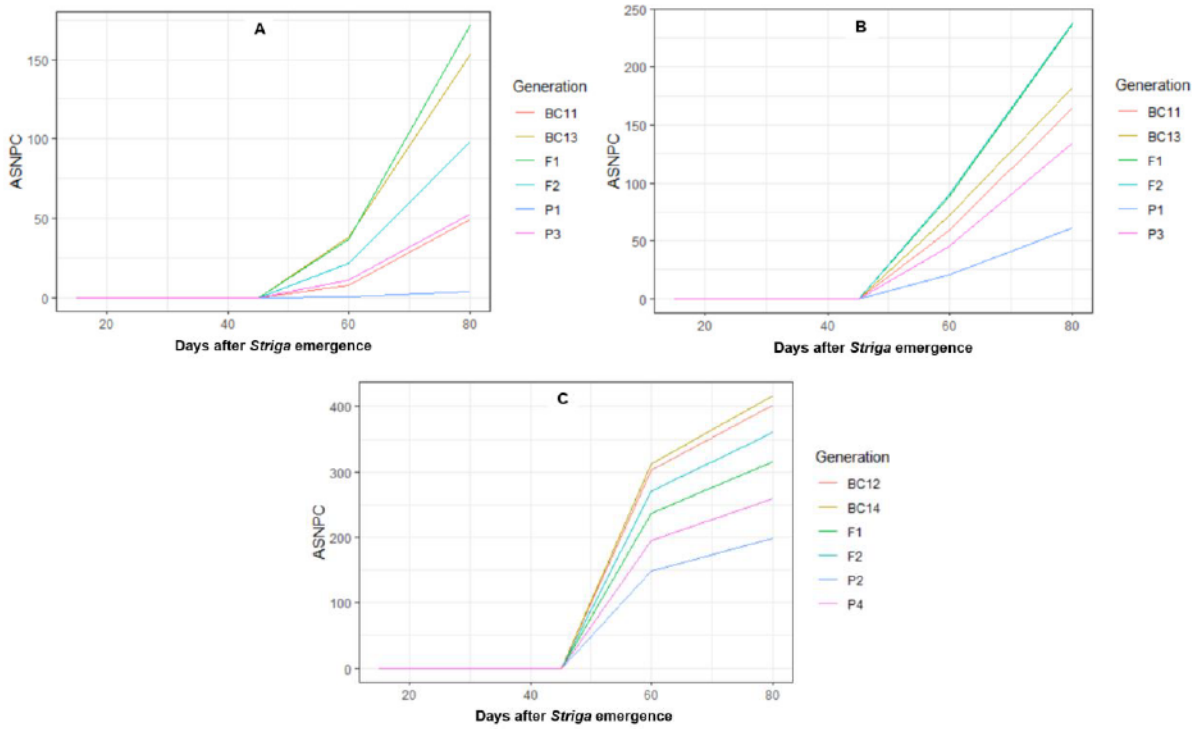

Figure 5.2. The area under *Striga* number progress curve (ASNPC): (A), Set A genotypes in naturally *Sh* infested field condition; (B) Set A genotypes in screenhouse condition; (C), Set B genotypes in the screenhouse environment.

5.3.4. Variance Components

The scaling test revealed significant effects for one or more A, B, C, and D scales. The χ^2 value of the joint-scaling test for all the traits under study also had significant effects in the two environments for Set A and Set B (Table 5.4). This suggests the inadequacy of the simple additive-dominance genetic model and the presence of non-allelic gene interaction to explain the inheritance of the genes governing *Sh* resistance in pearl millet. The mean effects (*m*) for all measured characters were highly significant, indicating that the traits were quantitatively inherited. This is in concordance with reports by Dawud (2018) and Fouad (2020) on pearl millet and faba bean, respectively. The significant negative additive gene effects (*a*) for SN60, SN80, and ASNPC in the *Sh*-infested field indicated that these traits were controlled by the dominant genes. This was confirmed by the significant dominance genetic effects (*d*) for the number of emerged *Sh* count and larger mean values of dominance than additive effects. Mbogo, Dida, and Owuor (2015) and Akaogu et al. (2019) reported the significant contribution of the dominance effects over additive gene effects for the number of emerged *Striga* plants in maize. Conversely, Gethi and Smith (2004) showed that additive gene effects played a more critical role than dominance effects in the inheritance of *Striga* resistance. Furthermore, Mrema, Shimelis, and Laing (2017) and Dawud (2018) reported the preponderance of additive gene effects for *Striga* resistance in sorghum and pearl

millet, respectively. The differences in the expression of the *Striga* emerged count in the screenhouse and infested field suggested the presence of genotype × environment interactions (Badu- Apraku et al. 2015; Akaogu et al. 2019). Martin and Hallauer (1976) reported an interaction between epistatic effects and the environment in maize.

The negative and significant additive-additive gene effects (*aa*) observed for SN60 and SN80, and ASNPC in the screenhouse for IP-10579 × IP- 8129 implied that breeding for *Striga* resistance is a useful approach to pearl millet selection. The dominance gene effects (*d*) and dominance–dominance gene effects (*dd*) revealed opposite signs for *Striga* emerged, indicating a duplicate gene interaction (Azizi, Rezaei, and Saeidi 2006; Dawud 2018; Akaogu et al. 2019). A complementary gene interaction has been reported for plant height in maize and faba bean (Mbogo et al. 2015; Fouad 2020). The occurrence of a duplicate mode of gene interactions confirmed the involvement of epistatic effects in the inheritance of *Striga* resistance genes (Akaogu et al. 2019). Crosses between promising lines may be necessary for accumulating favorable genes, as suggested by Samad, Sarker, and Deb (2016) and Azizi, Rezaei, and Saeidi (2006).

Table 5.4. Scaling and joint scaling test, variance components, and significance tests for *Striga* count, and the area under the *Striga* number progress curve in the screenhouse and field evaluations.

	IP-10579 × IP-8129						IP-3098 × IP-8786		
	Screenhouse			Field			Screenhouse		
Variable	**SN60**	**SN80**	**ASNPC**	**SN60**	**SN80**	**ASNPC**	**SN60**	**SN80**	**ASNPC**
A	-1.20^{ns}	-1.93^{ns}	-31.33^{ns}	2.87*	4.77*	76.67*	-14.43*	-14.73*	-452.08*
B	-1.20^{ns}	1.87^{ns}	6.67^{ns}	-3.77*	-4.37^{ns}	-81.33^{ns}	-13.67**	-12.23**	-401.45**
C	-15.66***	-12.62**	-282.78**	-0.27^{ns}	0.86^{ns}	6.22^{ns}	-20.07**	-15.48*	-550.94**
D	6.63**	6.28**	129.06**	-0.317^{ns}	-0.23^{ns}	-5.44^{ns}	-4.02^{ns}	-5.74^{ns}	-151.30^{ns}
m	12.04***	11.77***	238.11***	2.92***	6.93***	98.44***	17.78***	18.33***	559.72***
a	-1.65^{ns}	-0.10^{ns}	-17.50^{ns}	-4.02***	-6.32***	-103.33***	-1.98^{ns}	0.57^{ns}	-21.94^{ns}
d	-5.91^{ns}	-5.99^{ns}	-118.95^{ns}	4.80*	10.64**	154.22*	13.57^{ns}	14.64^{ns}	437.19^{ns}
aa	-13.26**	-12.56**	-258.11**	0.63^{ns}	0.46^{ns}	10.89^{ns}	8.03^{ns}	11.49^{ns}	302.59^{ns}
ad	-0.00^{ns}	3.80^{ns}	38.00^{ns}	-6.63***	-9.13***	-158.00***	0.77^{ns}	2.50^{ns}	50.63^{ns}
dd	10.86^{ns}	12.49^{ns}	233.45^{ns}	-1.53^{ns}	-0.06^{ns}	-15.56^{ns}	-36.13*	-38.46**	-1156.13**
χ^2	14.17**	14.27**	14.14**	19.97***	12.95**	16.44***	14.85**	15.42**	17.08***

*, **, *** and ns = Significant at $p < 0.05$; $p < 0.01$; $p < 0.001$ and non-significant, respectively. A, B, C and D denote the scales where A = $2BC_{11}$-P_1-F_1; B = $2BC_{12}$-P_2-F_1; C=$4F_2$-$2F_1$-P_1-P_2; D=$2F_2$-BC_{11}-BC_{12}, respectively, *m* = Mean effect, *a* = Pooled additive effect, *d* = Pooled dominance effect, *aa* = Pooled additive-additive interaction effect, *ad* = Pooled additive-dominance interaction effect, *dd* = Pooled dominance-dominance interaction effect, χ^2 = Chi-square. SN60 = *Striga* count 60 days after planting, SN80 = *Striga* count 80 days after planting, ASNPC = Area under the *Striga* number progress curve.

5.3.5. The Area Under the *Striga* Number Progress Curve (ASNPC)

Highly significant differences ($P < 0.001$) were detected among the tested genotypes for ASNPC for both Sets in the screenhouse and in Set A in the naturally infested field evaluations (Table 5.1). Figures 5.2 A, B, and C show the ASNPC curves across screenhouse and field evaluations for the two sets of crosses. The curves show that in Set A and Set B genotypes, the resistant parents had lower values of ASNPC in each environment compared to the susceptible parents that showed a relatively high number of *Striga* after emergence. The mean value of ASNPC of the F_1 crosses with the resistant parents was low compared to F_1 crosses to the susceptible parent mean value (Figure 5.2 A, B, C).

The area under the *Striga* number progress curve was calculated using the successive *Striga* counts as proposed by Haussmann et al. (2000). Low ASNPC mean values indicate resistance, whereas high mean values indicate susceptibility to *Striga*. The trend of the curves across screenhouse and field evaluation showed low values of the resistant parents compared to susceptible parents, confirming the presence of *Striga* resistance genes and *Striga* susceptibility genes in the selected parents. This concurs with Dawud's (2018) report in which low ASNPC values were recorded for *Striga*-resistant parents in pearl millet. The F_1 progenies presented higher mean values of ASNPC than their parents, suggesting susceptibility to *Striga*. Sorghum hybrids derived from crosses between a resistant and a susceptible parent were reported to be susceptible (Rana et al. 1982; Obilana 1984), indicating partial or complete dominance of genes for susceptibility. Both parents of a hybrid should be selected for *Striga* resistance (Haussmann et al. 2000). *Sh* resistance in pearl millet is quantitatively inherited and controlled by several genes. The present study computed and postulated duplicate gene action indicating gene interactions conditioning *Striga* resistance. The recurrent selection method is adapted to develop pearl millet *Sh* resistant open-pollinated varieties.

5.4. Conclusions

The generation mean analysis is used in the current study, to design appropriate breeding approaches for pearl millet *Sh* resistant varieties development. The resistant and susceptible parents, the first and second filial generations presented significant differences in the screenhouse for Set A and Set B and in the naturally infested field for Set A for *Sh* traits. Non-allelic gene interaction explained the inheritance of the genes governing *Sh* resistance in pearl millet. The study found that duplicate gene action controlled the inheritance of the number of emerged *Sh*. Unique F_2 individuals with *Sh* resistance were selected from the two sets for genetic advancement through recurrent selection for pearl millet variety development by integrating desirable agronomic and farmer-preferred traits.

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Chapter 6. Combining ability and hybrid breeding in pearl millet (*Pennisetum glaucum* [L.] R. Br.) for agronomic traits and resistance to *Striga hermonthica*

Abstract

Pearl millet (*Pennisetum glaucum* [L.] R. Br., 2n = 2x = 14) is a nutrient-dense and climate-resilient crop widely cultivated in the dry regions of Africa and Asia. In Burkina Faso, the actual mean yield of the crop is < 1 ton/ha compared with a potential yield of 3 tons/ha. Several constraints, including cultivar susceptibility to the noxious weed *Striga hermonthica* (Del.) Bentham (*Sh*) and severe and recurrent drought stress, limit the potential productivity of the crop. Breeding and deploying high-yielding and *Striga*-resistant varieties is a cost-effective approach to enhancing yield gains and narrowing the yield gap. Therefore, the objective of this study was to determine the combining ability effects and degree of heterosis for agronomic traits and resistance to *Sh* among complementary pearl millet genotypes to select promising parental lines and hybrids to develop and deploy farmer-preferred varieties. Five *Sh*-resistant testers were crossed with three selected lines using a line × tester mating design, and 15 F_1 hybrids generated. The 15 hybrids, eight parents and three checks were evaluated using a 4 × 6 alpha lattice design with two replications under three contrasting environments in Burkina Faso. Data was collected on agronomic traits and *Sh* parameters and subjected to combining ability and heterosis analyses. Significant ($P < 0.01$) differences were recorded among hybrids, lines and testers for most assessed agronomic traits and *Sh*-resistance. The interaction effect of line × tester was significant ($P < 0.001$) for *Sh* reaction. The narrow-and broad-sense heritability were relatively higher for *Striga*-resistance (≥ 70%) and low (≤ 23%) for grain yield. The general combining ability (GCA) and specific combining ability (SCA) ratios were less than unity for agronomic traits and *Striga* reaction indicating the predominance of non-additive gene action conditioning the assessed traits. The tester IP-11358 exhibited a high positive GCA effect for grain yield and a negative GCA effect for the number of *Sh* per pot in a desirable direction. The line ICMB177111 and tester IP-6112 recorded positive GCA effects for grain yield. The best-performing experimental hybrid IP-11358 × ICMB177111 had high SCA effects and heterosis with a mean grain yield of 1128.10 kg/ha across the test environments. The new experimental hybrids such as IP-11358 × ICMB177111, IP-11358 × IKMB18002, IP-10579 × ICMB177002 and IP-9242 × ICMB177002 are recommended for multi-environment evaluation and production in *Sh*-infested pearl millet cultivation agro-ecologies in Burkina Faso or similar agro-ecologies.

Keywords: Combining ability, heterosis, hybrid breeding, pearl millet, resistance breeding

6.1. Introduction

Pearl millet (*Pennisetum glaucum* [L.] R. Br., 2n = 2x = 14) is a multi-purpose grain crop of social and economic importance in dry regions globally. In sub-Saharan Africa (SSA), pearl millet grain is processed to prepare various foods, whereas the dry stover is used for livestock feed, fuelwood, and construction material (Drabo 2016; Burgarella et al. 2018). The grain is rich in protein (i.e., 11 to 12.5%), calcium, phosphorous, iron and zinc, with a relatively high amount of vitamins, including thiamine, riboflavin and niacin (Ghatak et al. 2016; Gupta et al. 2022). It has several health benefits, including alleviating anaemia, constipation, cancer, diabetes, celiac and diarrhoea (Gupta et al. 2022). In SSA, the crop is mainly grown in arid and semi-arid environments and thrives under low moisture, high temperatures, and nutrient-deficient soil conditions (Shivhare and Lata 2017). The high phenotypic and genotypic plasticity of the crop makes it a crop of choice in harsh agroecologies of SSA with the potential to contribute to the livelihoods and nutritional well-being of the population.

Pearl millet is the third largest cereal grain crop produced in SSA. The leading producers in the region are Niger (3.5 million tons per annum), Mali (1.9 million tons), Nigeria (1.9 million tons), Senegal (1.1 million tons) and Burkina Faso (0.9 million tons) (FAOSTAT 2022). In Burkina Faso, the crop's actual yield is 0.76 ton/ha (MARAH 2022), much lower than the potential yield of 3.00 ton/ha (ECOWAS-UEMOA-CILSS 2021). Several biotic and abiotic stresses are attributed to its low productivity. Among the biotic stresses, *Sh* infestation is the leading cause of yield losses of up to 90 to 100% (Kountche et al. 2016; Kanampiu et al. 2018; Rouamba et al. 2021). In Burkina Faso, *Sh* is reported to cause yield losses of about 80% in pearl millet (Rouamba et al. 2021). *Striga* infestation is manifested in degraded environments and low-input cropping systems, especially in cereal monocropping conditions (Parker 2009; Parker 2012). The yield gap is partly attributed to farmers' lack of improved *Sh*-resistant varieties and modern crop management and inputs. Breeding and deploying *Striga*-resistant and high-yielding varieties will enhance crop productivity under low-input farming systems commonly practiced by small-scale farmers in SSA, including Burkina Faso.

Various genetic designs are widely used to develop breeding populations and determine the combining ability effects of parents for applied breeding, including for *Sh*-resistance (Nduwumuremyi et al. 2013; Sharma and Singh 2019; Yehia and El-Hashash 2019; Zebire et al. 2021; Balami et al. 2022). The line × tester mating design proposed by Kempthorne (1957) is useful for identifying the best-performing genotypes for hybrid development and performance evolution. The procedure enables to estimate of the general combining ability (GCA) of parents and the specific combining ability (SCA) effects of progenies (Barathi et al. 2020) and corresponding breeding values (Yehia and El-Hashash 2019; Barathi et al. 2020). In pearl millet, positive GCA effects have been reported for the following agronomic traits: days to 50% flowering, plant height, panicle length, thousand-grain weight and grain yield, which aided

the identification of useful parental genotypes for breeding (Santosh et al. 2018; Kumawat et al. 2019; Barathi et al. 2020; Balami et al. 2022). Also, negative GCA effects have been reported for *Sh* reaction in pearl millet, indicating the possibility of developing pearl millet genotypes with enhanced resistance to the highly noxious weed in cereal crop production (Karaya et al. 2014; Sangaré et al. 2018; Zebire et al. 2020; Balami et al. 2022; Lobulu et al. 2023). Positive SCA effects were reported for panicle length, plant height, thousand-grain weight, and grain yield in pearl millet, whereas negative SCA effects were reported for *Striga* traits, allowing the identification of the best crosses (Karaya et al. 2014; Sangaré et al. 2018; Balami et al. 2022; Lobulu et al. 2023).

In an attempt to develop pearl millet varieties with increased yield and *Sh*-resistance, the Burkina Faso pearl millet breeding programme introduced pearl millet inbred lines from the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT). Initially, 148 pearl millet inbred lines, including two other lines used in the breeding programme, were screened for *Striga*-resistance, which aided the identification of five promising *Sh*-resistant lines for breeding (Unpublished data). The identified genotypes are useful genetic resources for open-pollinated or hybrid pearl millet breeding with *Sh*-resistance and promising agronomic traits. Therefore, the objective of this study was to determine the combining ability effects and degree of heterosis for agronomic traits and resistance to *Sh* among complementary pearl millet genotypes to select promising parental lines and hybrids to develop and deploy farmer-preferred varieties.

6.2. Materials and Methods

6.2.1. Plant Materials

The study used two sets of parents consisting of three lines and five testers. The testers were selected from diverse pearl millet lines exhibiting *Sh*-resistance, while the lines are local genotypes used in the pearl millet breeding programme in Burkina Faso. The standard single cross hybrid Nafagnon and experimental *Sh*-resistant genotype IP-15857 and *Sh* susceptible line SOSAT-C88 were used as check varieties. The names, sources of origin and attributes of the lines, testers and checks are presented in Table 6.1.

Table 6.1. Names, sources of origin and genetic attributes of lines, testers and check varieties used in the study.

Parents	Genotypes	Source	Attributes
Line	ICMB177002 IKMB18002 ICMB177111	INERA	B-line
Tester	IP-6112 IP-10579 IP-9242 IP-3098 IP-11358	ICRISAT	*Striga*-resistant
Checks			
	Nafagnon	INERA	Hybrid
	IP-15857	ICRISAT	*Striga*-resistant
	SOSAT-C88	ICRISAT	*Striga*-susceptible

INERA = Institute of Environment and Agricultural Research, ICRISAT = International Crop Research Institute for the Semi-Arid Tropics.

6.2.2. Crossing Procedure

The lines and testers were crossed using a line-by-tester mating design under greenhouse conditions at the Institute of Environment and Agricultural Research (INERA) main research station (12°28/27 N; 1°33/31 W) during the 2020 offseason. A five-litre capacity plastic pots were filled with a mixture of clay and sandy soil, and organic manure in a ratio of 2:1:1. Each of the lines and testers was planted in two rows of 10 pots in the greenhouse in three successions of two-week intervals. The plants were thinned to one plant per pot and irrigated every two days. A compound fertilizer (N: P: K; 14:23:14) was supplied in microdose of 3 g/pot two weeks after planting. Weeds were continuously removed from pots. Plants were allowed to grow until the heading stage and were covered with pollen-bag before anthesis. When the panicle had produced pollen, viable pollen grains were collected from each tester in a pollen bag. Thereafter, the panicles of the lines were pollinated by gently shaking the pollen bag and dusting the pollen grains from testers onto the panicles to allow the transfer of pollen grains to the stigma. The pollinated panicles were bagged and labelled until the seed maturation. The seeds were harvested from successfully pollinated panicles and labelled and stored for later use.

6.2.3. Study Sites

Fifteen experimental F_1 hybrids, their eight parents, and three checks (Table 6.1) were evaluated at three locations in Burkina Faso. The two locations include Gampela and Fada, where agronomic performances were evaluated. The third location is the INERA main research station at Ouagadougou, and the study was conducted under greenhouse conditions to evaluate *Sh*-resistance using artificial infestation. The studies were conducted during the 2021 growing season. The Gampela and Fada sites are the principal

pearl millet evaluation sites in the country, allowing the expression of heterosis in constrained and non-constrained production areas.

Gampela and Fada are located at 12° 25'51'' N; 1°22'18'' W and 11°56'16'' N, 0°17'48'' E, respectively. The sites receive a total annual rainfall of 600 to 900 mm and 700 to 900 mm with erratic distribution. During the study period (June to October 2021), 940.8 mm and 731.56 mm of rainfall were recorded at Gampela and Fada, respectively. Gampela has a leached tropical ferruginous soil of a sandy-clay texture, while in Fada, the soil is a leached tropical ferruginous of a sandy texture.

6.2.4. Experimental Design and Trial Management

The field experiments (at Gampela and Fada) were planted using a 4 × 6 alpha lattice design with two replications. Field plots consisted of one row of 4 m in length with a spacing of 0.80 m between rows and 0.40 m spacing between plants within a row. Fifteen days after sowing, plants were thinned to one plant per hill to achieve the desired plant density of 31250 /ha. The trials received soil fertilisers of 100 kg/ha of nitrogen, phosphorus and potassium (N:P:K; 14:23:14) fifteen days after planting and 50 kg/ha N in the form of urea at the booting stage at Gampela and Fada under rain-fed conditions. All other management practices followed the standard agronomic practices recommended for pearl millet production in Burkina Faso (INERA 2000). In the greenhouse, 5-litre capacity plastic pots were filled with a soil media composed of clay and sand. The media was infested with a scoop of sand mixed with 0.05 g of 2-year-old *Sh* seed collected from farmers' fields in Burkina Faso and preconditioned for eleven days before planting. Hand weeding was routinely done to remove all other weeds except *Sh*.

6.2.5. Data Collection

The following agronomic data were collected: days to 50% flowering (DTF) recorded as the number of days when 50% of the plants in each plot had intruded stigma, plant height (PH) measured from the base of the plant (expressed in cm) to the top of the panicle of the main tiller, the number of tillers (NT) were counted per plant, panicle length (PCL) measured in cm from the base to the top of the main tiller panicle, panicle diameter (PCD) measured in mm using a vernier calliper aiming the middle section of the panicle, panicle weight (PWT, g) recorded by weighing the harvested panicles for each entry after 14 days of sun-drying, and thousand-grain weight (TGW, g) determined by weighing a thousand grains. Grain weight per plant (GW, g) was determined by weighing the grains after threshing and dividing them by the number of harvested plants for each plot. Grain yield (GY) was computed as the grain weight per plant of the total plants per plot area and extrapolated to kg per hectare (kg/ha). Under the greenhouse environment, data on *Striga* parameters were collected, including the number of emerged *Sh* plants in each pot, estimated at 60 days (SN60) and 80 days (SN80) after sowing. The area under the

Striga Number Progress Curve (ASNPC) was computed using the successive *Striga* counts according to Haussmann et al. (2000) as follows:

$$ASNPC = \sum_{i=0}^{n-1} \left[\frac{Y_i + Y_{(i+1)}}{2}\right](t_{i+1} - t_i)$$

where n is the number of *Striga* assessment dates, Y_i is the *Striga* count at the i^{th} assessment date, $Y_{(i+1)}$ is the *Striga* count at the i^{th} plus 1 assessment date, t_i is the number of days after planting (DAP) at the i^{th} assessment date, $t_{(i+1)}$ is DAP at the i^{th} plus 1 assessment date.

6.2.6. Data Analysis

6.2.6.1. Analysis of Variance

The collected data were assembled in Excel and subjected to the combined analysis of variance (ANOVA) in GenStat 20th Edition (VSN International, Hempstead, UK) after performing tests for normality and homogeneity of variances. Differences between treatment means were determined using the least significant difference (LSD) test at 5% level of significance.

6.2.6.2. Combining Ability Estimates

The GCA and SCA effects were estimated using a line-by-tester genetic analysis using the agricolae package (de Mendiburu and de Mendiburu 2019) in R software version 4.1.2 (R Core Team 2021). The GCA and SCA effects were determined for each site. The genotypes were considered fixed effects, while replications were treated as random effects. The following linear model was used to determine the combining ability effects:

$$Y_{ijk} = \mu + r_k + g_i + g_j + s_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} is the observed performance of the cross between the i^{th} line and j^{th} tester; μ is the overall trial mean; r_k is the effect of replicate k; g_i general combining ability of the lines; g_j is the general combining ability of the testers; s_{ij} is the specific combining ability of the cross between line i and tester j; ε_{ijk} is the residual. The significance of the estimated GCA effects of the lines and testers and the SCA effects of experimental hybrids were tested using the t-test procedure at the 5% significance level (Divya et al. 2014).

6.2.6.3. Estimate of Heterosis

The mid-parent heterosis (MPH) and standard heterosis (SH) were calculated according to Falconer and Mackay (1996). These were computed as a percentage increase or decrease of the cross performances over the mid-parents and the best standard check, respectively, referring to the superiority of the F_1 over mid-parents (MP) and the check variety (Cv). Mid-parent and standard heterosis were estimated using the following formula (Falconer and Mackay 1996):

$$\text{MPH (\%)} = \frac{F_1 - MP}{MP} \times 100$$

$$\text{SH (\%)} = \frac{F_1 - Cv}{Cv} \times 100$$

6.2.6.4. The Ratio of the General Combining Ability and the Specific Combining Ability Effects

The ratio of the general combining ability (GCA) and the specific combining ability (SCA) effects was determined using the general prediction ratio (GPR) according to Baker (1978) as follows:

$$GCA/SCA = 2MSGCA/(2MSGCA + MSSCA).$$

where MSGCA and MSSCA are the mean squares of GCA and SCA effects, respectively.

A Bakers' ratio close to 1.00 indicates that the GCA effects were more important in conditioning the heritability of that trait, whereas a ratio close to zero would indicate that SCA effects would be more important in controlling trait heritability.

6.2.6.5. Estimate of Heritability

The broad-sense heritability (H^2) and narrow-sense heritability (h^2) for each environment were determined using the Analysis of Genetic Designs with R (AGD-R) version 5.0 (Rodríguez et al. 2015) software according to Acquaah (2012) using the following formulae:

$$H^2 \text{ (bs)} = V_G/V_P$$
$$h^2 \text{ (ns)} = V_A/V_P$$

where Vg is the genetic variance, V_A is the additive genetic variance, and V_P is the total phenotypic variance.

6.3. Results

6.3.1. Analysis of Variance for Agronomic Traits

Table 6.2 presented the assessed agronomic traits' mean squares and significant tests. The genotype effects showed significant differences ($P < 0.001$) for all assessed agronomic traits, while the locations showed a significant effect ($P < 0.01$) on DTF and GY. Genotype-by-test site interaction effect was significant ($P < 0.01$; $P < 0.001$) for DTF and GY (Table 6.2).

Table 6.2. Mean squares and significant tests from combined analysis of variance for agronomic traits of pearl millet genotypes across two environments in Burkina Faso.

SV	DF	DTF	PH	NT	PCL	PCD	TGW	GY
Replication	1	49.18**	118.40^{ns}	0.00^{ns}	0.12^{ns}	10.70^{ns}	3.61^{ns}	5957.00^{ns}
Block	5	17.37*	1301.30**	0.91^{ns}	23.03^{ns}	15.58*	2.77^{ns}	6267.00^{ns}
Genotype (Gen)	23	29.69***	2305.10***	2.01*	112.99.***	30.07***	4.42**	194967.00***
Environment (Env)	1	1235.23***	30451.20***	0.30^{ns}	151.15**	4.30^{ns}	9.01**	3950400.00**
Gen*Env	18	29.11***	790.60^{ns}	1.23^{ns}	16.16^{ns}	3.42^{ns}	2.58^{ns}	154173.00**
Error	30	6.58	447.80	1.05	17.39	6.10	1.59	64229.00
Trial statistics								
Mean		60.33	191.70	4.81	28.96	20.88	8.40	694.00
CV (%)		4.26	11.03	21.093	14.38	11.78	15.04	36.19
SED		2.57	21.16	1.02	4.17	2.47	1.26	253.40
LSD (5%)		1.22	9.66	0.48	1.90	1.16	0.58	126.00

*, ** and *** = denote significant differences at 0.05, 0.01, and 0.001 probability levels, respectively; ns = not significant; SV = source of variation; DF = degree of freedom; DTF = day to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grain yield (kg/ha); CV = coefficient of variation; SED = standard error of the mean difference; LSD (5%) = Least significant difference at 5% probability value.

6.3.2. Mean Response of Pearl Millet Genotypes for Agronomic Traits Under Field Conditions

The mean values for crosses, lines, testers, and checks evaluated across *Sh*-non-infested environments in Burkina Faso are presented in Table 6.3. DTF varied from 56 to 64 for crosses. It ranged from 54 to 70 for testers and from 56 to 66 for lines. PH varied from 171 to 236 cm for crosses, while for lines and testers, it varied from 137 to 167 cm and 132 to 186 cm, respectively. The following crosses had longer

plant height (> 200 cm) namely: IP-11358 × IKMB18002, IP-6112 × ICMB177002, IP-11358 × ICMB177002, IP-10579 × ICMB177111, IP-10579 × ICMB177002, IP-6112 × ICMB177111, IP-11358 × ICMB177111 and IP-6112 × IKMB18002. Also, 33.33% of crosses recorded PH exceeding their parental lines and testers. Cross IP-9242 × ICMB177111 presented the maximum NT (5 tillers per plant), whereas tester IP-6112 had the lowest NT (2 tillers per plant). IP-11358 × ICMB177002 had the highest PCL (38.64 cm) and IP-6112 × ICMB177111 had the lowest (18.26 cm). PCD ranged from 19 to 31 mm, 18 to 24 mm and 13 to 21 mm for crosses, lines and testers, respectively. Crosses IP-6112 × ICMB177111 and IP-6112 × IKMB18002 recorded PCD at 31.95 mm and 25.28 mm, in that order, higher than the lines and testers. Cross IP-11358 × ICMB177002 had the highest TGW (10.72 g), followed by IP-11358 × IKMB18002 (10.07 g), whereas IP-3098 × ICMB177002 had the lowest TGW (7.17 g). The crosses, except IP-3098 × ICMB177002, IP-6112 × ICMB177002 and IP-10579 × ICMB177002 recorded higher TGW (> 8 g) than lines and testers. Crosses had mean grain yields ranging from 455.20 to 1128.10 kg/ha. Crosses IP-11358 × ICMB177111 (1128.10 kg/ha), IP-11358 × IKMB18002 (938.60 kg/ha) and IP-6112 × IKMB18002 (890.30 kg/ha) were high performers for GY than their parental lines and testers. None of the families out-performed the check variety Nafagnon which had a mean grain yield of 1506.40 kg/ha. The mean grain yield ranged between 138.30 to 744.50 kg/ha for lines, while for testers, it ranged from 202.30 to 883.50 kg/ha.

Table 6.3. Mean values for agronomic traits among pearl millet lines, testers, crosses, and checks evaluated under two environments in field conditions in Burkina Faso.

Crosses	DTF	PH	NT	PCL	PCD	TGW	GY
IP-3098 × ICMB177002	59.91	172.90	3.22	33.92	20.08	7.17	455.20
IP-10579 × ICMB177111	60.36	216.90	4.83	23.50	20.05	8.74	537.30
IP-3098 × IKMB18002	56.54	185.30	3.54	28.09	20.00	8.20	617.50
IP-10579 × IKMB18002	60.72	219.60	4.28	28.48	20.79	8.48	658.60
IP-6112 × ICMB177002	57.29	213.00	3.71	29.68	21.47	7.47	725.60
IP-10579 × ICMB177002	62.41	216.00	3.84	36.50	21.71	7.46	740.90
IP-3098 × ICMB177111	55.65	195.40	4.59	26.09	20.59	8.76	741.90
IP-9242 × ICMB177111	56.58	171.30	5.05	24.69	22.34	8.76	760.80
IP-9242 × IKMB18002	57.00	186.20	4.88	31.02	19.53	8.67	770.70
IP-11358 × ICMB177002	63.44	217.60	3.47	38.64	18.92	10.72	773.40
IP-6112 × ICMB177111	60.63	214.40	4.71	18.26	31.95	9.56	801.30
IP-9242 × ICMB177002	58.79	171.20	4.30	35.44	20.76	8.56	825.50
IP-6112 × IKMB18002	63.23	207.30	4.30	26.50	25.28	9.61	890.30
IP-11358 × IKMB18002	62.80	235.90	4.59	33.23	21.69	10.07	938.60
IP-11358 × ICMB177111	59.60	213.20	4.79	30.13	19.75	9.26	1128.10
Lines							
ICMB177002	66.04	137.50	4.00	39.00	18.00	7.56	138.30
IKMB18002	55.68	156.40	4.51	22.46	20.88	6.89	189.50
ICMB177111	60.97	166.80	3.64	22.93	23.33	6.90	744.50
Testers							
IP-10579	61.02	185.60	4.05	22.18	13.50	6.78	202.30
IP-9242	58.13	132.50	4.28	22.04	20.95	6.97	388.90
IP-3098	53.98	180.00	4.53	21.52	14.04	7.00	465.90
IP-11358	70.04	214.80	4.38	30.00	17.52	7.38	883.50
IP-6112	60.00	160.00	2.00	31.00	19.00	-	-
Checks							
Nafagnon	58.87	204.70	5.91	33.86	23.61	9.55	1506.40

DTF = day to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grains yield (kg/ha); - = denote missing value due to poor seed set.

6.3.3. Mean Response of Pearl Millet Genotypes for *Striga* Parameters Under Greenhouse Conditions

Striga parameters evaluated under greenhouse conditions are presented in Table 6.4. SN60 varied from 0 for cross IP-10579 × ICMB177002 to 31.00 *Striga* plants per pot for cross IP-3098 × ICMB177111. The following crosses, namely: IP-10579 × ICMB177002, IP-9242 × ICMB177002, IP-11358 × ICMB177111, IP-11358 × IKMB18002, IP-10579 × ICMB177111, and IP-10579 × IKMB18002, had the lowest SN60 count (< 2). The crosses IP-3098 × ICMB177111, IP-6112 × IKMB18002, IP-3098 × IKMB18002, IP-6112 × ICMB177111, and IP-9242 × IKMB18002 had the highest *Striga* count (> 10) at SN60. For lines, ICMB177002 had the lowest count (1.20) at SN60, whereas tester IP-9242 had the lowest SN60 count (0.30). At SN80, the mean *Striga* count per pot varied from 0.20 for cross IP-10579 × ICMB177002 to 25.00 for cross IP-6112 × IKMB18002. Crosses IP-10579 × ICMB177002, IP-9242 × ICMB177002, IP-11358 × ICMB177111, IP-10579 × IKMB18002, IP-10579 × ICMB177111 and IP-11358 × IKMB18002 recorded the lowest *Striga* count (< 3) at SN80, whilst IP-6112 × IKMB18002, IP-3098 × ICMB177111, IP-6112 × ICMB177111, IP-3098 × IKMB18002 and IP-9242 × IKMB18002 recorded the highest values (> 10). SN60 for lines ranged from 1.20 to 5.00 and 1 to 5.30 for SN80,

whereas SN60 and SN80 ranged from 0 to 10.20 and 0 to 8.20 for testers. ASNPC ranged from 1.80 for cross IP-10579 × ICMB177002 to 485.10 for cross IP-6112 × IKMB18002 and 21.80 for line ICMB177002 to 103.50 for line IKMB18002. ASNPC for testers ranged between 10.10 for IP-9242 to 183.50 for IP-3098. IP-15857, the *Sh*-resistant check, had low SN60 (0.80), whereas SOSAT-C88, the susceptible check, recorded high SN60 (8.00). For SN80, the *Sh*-resistant check had low count (2.50) and the susceptible check, SOSAT-C88 had high SN80 count (10.70). The ASNPC was low (33.50) and high (186.80) for *Sh*-resistant and susceptible checks, respectively.

Table 6.4. Mean values of *S. hermonthica* parameters when evaluating pearl millet lines, testers, crosses and checks under greenhouse conditions with artificial *Striga* infestation.

Crosses	SN60	SN80	ASNPC
IP-10579 × ICMB177002	0.00	0.20	1.80
IP-3098 × IKMB18002	22.20	22.20	443.50
IP-11358 × ICMB177002	3.30	3.80	71.80
IP-3098 × ICMB177002	2.70	3.30	60.10
IP-6112 × IKMB18002	23.50	25.00	485.10
IP-6112 × ICMB177002	4.50	3.00	75.10
IP-9242 × ICMB177111	6.70	5.70	123.50
IP-3098 × ICMB177111	31.00	23.50	545.10
IP-9242 × ICMB177002	0.20	0.30	5.10
IP-10579 × ICMB177111	1.70	2.20	38.50
IP-9242 × IKMB18002	12.80	12.00	248.50
IP-10579 × IKMB18002	1.70	2.00	36.80
IP-6112 × ICMB177111	18.30	23.30	416.80
IP-11358 × IKMB18002	1.20	2.20	33.50
IP-11358 × ICMB177111	0.50	0.70	11.80
Lines			
ICMB177002	1.20	1.00	21.80
ICMB177111	3.00	3.30	63.50
IKMB18002	5.00	5.30	103.50
Testers			
IP-3098	10.20	8.20	183.50
IP-6112	0.80	0.50	25.00
IP-9242	0.30	0.70	10.10
IP-10579	1.50	1.10	26.00
IP-11358	2.30	2.30	45.10
Checks			
IP-15857	0.80	2.50	33.50
SOSAT-C88	8.00	10.70	186.80

SN60 = *Striga* count 60 days after planting; SN80 = *Striga* count 80 days after planting; ASNPC = area under the *Striga* number progress curve.

6.3.4. Combining Ability Analysis for Agronomic Traits and *Striga*-Resistance

The analysis of variance for lines, testers and crosses for agronomic traits at Gampela, Fada and greenhouse conditions is presented in Tables 6.5 and 6.6. Parents differed significantly ($P \leq 0.05$) for all evaluated traits except TGW at the Gampela site, whereas there were significant ($P \leq 0.05$) differences except PH and NT at Fada. Lines showed significant ($P \leq 0.01$; $P \leq 0.001$) differences for NT at Gampela

and PCL at Fada. Testers showed significant ($P \leq 0.01$) differences for PH, PCL and TGW at Gampela and significant ($P \leq 0.05$; $P \leq 0.01$; $P \leq 0.001$) for PH, PCL and GY at Fada (Table 6.5). Line × tester showed a non-significant effect for all traits at Gampela but significant ($P \leq 0.05$) for DTF at Fada. DTF, PCD, and TGW had high narrow-sense heritability (> 58%) at both Gampela and Fada. In that order, low narrow-sense heritability was observed for PH, NT, and GY at 4.87% to 8.17%, 3.00% to 13.95%, and 23.96% to 47.07% at both locations.

Table 6.6 presented mean squares and significant tests for lines, testers, and crosses under *Striga* infestation in the greenhouse. A significant ($P < 0.001$) difference was observed for genotypes, parents vs crosses, crosses, testers and line × tester, for *Striga* parameters. SN60, SN80 and ASNPC had high broad- and-narrow-sense heritability values of > 99% and > 69%, in that order. Baker's ratio was less than unity (≤ 0.99) for all *Striga* parameters.

Table 6.5. Mean squares and significant tests for lines, testers and crosses evaluated at Gampela and Fada sites in Burkina Faso.

Gampela								
SV	**DF**	**DTF**	**PH**	**NT**	**PCL**	**PCD**	**TGW**	**GY**
Replication	1	2.73^{ns}	584.76^{ns}	1.90^{ns}	2.77^{ns}	19.93^{ns}	1.57^{ns}	172827.79^{ns}
Treatment	23	35.03***	2070.75***	2.30**	64.35***	27.92**	2.38*	132178.82**
Parents (P)	8	66.61***	2738.97***	3.47**	65.84***	31.38**	0.98^{ns}	190244.91**
P vs Cr	1	82.14**	10235.45***	1.25^{ns}	32.34^{ns}	47.65*	8.68**	436951.52**
Crosses (Cr)	14	13.62*	1105.71**	1.70^{ns}	65.78***	24.53*	36.80*	81376.30^{ns}
Line (L)	2	10.13^{ns}	250.00^{ns}	7.23**	336.43^{ns}	19.23^{ns}	2.30^{ns}	96225.40^{ns}
Tester (T)	4	25.67^{ns}	3184.58**	1.22^{ns}	48.38**	46.70^{ns}	6.00**	88683.15^{ns}
L×T	8	8.47^{ns}	280.21^{ns}	0.57^{ns}	6.81^{ns}	14.78^{ns}	1.02^{ns}	74010.60^{ns}
Error	22	6.26	351.68	0.86	10.39	9.51	1.18	51231.14
Trial statistics								
SED (L)		0.79	5.93	0.29	1.02	0.98	0.34	71.58
SED (T)		1.02	7.66	0.38	1.32	1.26	0.44	92.40
SED (L×T)		1.77	13.26	0.65	2.28	2.18	0.77	160.05
H^2 (%)		74.78	66.59	36.05	98.72	94.54	77.49	84.16
h^2 (%)		69.65	8.17	13.95	94.74	68.95	77.49	47.07
GCA/SCA		0.89	0.96	0.97	0.99	0.90	0.94	0.83
Fada								
Replication	1	7.03^{ns}	37.52^{ns}	1.03^{ns}	14.75^{ns}	12.78^{ns}	2.23^{ns}	580613.29^{ns}
Treatment	19	120.44***	1534.18*	0.54^{ns}	64.25^{ns}	22.65*	4.84^{ns}	284712.14^{ns}
Parents (P)	5	191.98***	1455.48^{ns}	0.78^{ns}	114.48*	35.02**	8.26*	1690716.65***
P vs Cr								
Crosses (Cr)	14	97.96**	1191.79^{ns}	0.42^{ns}	50.49^{ns}	18.79*	2.34^{ns}	224252.63^{ns}
Line (L)	2	91.47^{ns}	144.78^{ns}	0.68^{ns}	152.21***	11.14^{ns}	2.49^{ns}	238.49^{ns}
Tester (T)	4	155.86^{ns}	3031.90**	0.28^{ns}	84.41***	27.66^{ns}	1.88^{ns}	517614.28*
L×T	8	70.63*	533.49^{ns}	0.42^{ns}	8.09^{ns}	16.26^{ns}	2.53^{ns}	133575.34^{ns}
Error	13	21.34	621.32	0.38	30.19	6.71	2.12	135547.42
Trial statistics								
SED (L)		1.46	7.88	0.20	1.74	0.82	0.46	116.42
SED (T)		1.89	10.18	0.25	2.24	1.06	0.59	150.30
SED (L×T)		3.27	17.63	0.44	3.89	1.83	1.03	260.33
H^2 (%)		98.35	58.99	-	93.28	87.44	86.76	-
h^2 (%)		58.93	4.87	3.00	12.44	58.57	62.19	23.96
GCA/SCA		0.88	0.92	0.82	0.98	0.83	0.78	0.89

*, ** and *** = denote significant differences at 0.05, 0.01, and 0.001 probability levels, respectively; ns = not significant; SV = source of variation; DF = degree of freedom; DTF = days to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grain yield (kg/ha); P = parents; Cr = crosses; L = line; T = tester; L×T = line × tester; SED = standard error of the mean difference; H^2 (%) = broad sense heritability; h^2 (%) = narrow sense heritability; GCA = general combining ability; SCA = specific combining ability.

Table 6.6. Mean squares and significant tests for lines, testers, and crosses when evaluating 24 pearl millet genotypes with *Striga* infestation.

SV	DF	SN60	SN80	ASNPC
Replication	1	22.04^{ns}	1.07^{ns}	1349.92^{ns}
Treatment	23	149.27***	135.04***	55936.44***
Parents (P)	8	19.12^{ns}	18.85^{ns}	7248.96^{ns}
P vs Cr	1	347.55***	306.84***	131017.92***
Crosses (Cr)	14	209.47***	189.16***	78394.89***
Line (L)	2	322.47^{ns}	321.98^{ns}	128643.12^{ns}
Tester (T)	4	382.78*	346.94*	144557.35*
L×T	8	94.58***	77.07***	32751.60***
Error	22	8.99	10.02	3320.78
Trial statistics				
SED (L)		0.95	1.00	18.22
SED (T)		1.22	1.29	23.53
SED (L×T)		2.12	2.24	40.75
H^2 (%)		99.24	99.02	99.26
h^2 (%)		69.52	71.99	71.23
GCA/SCA		0.94	0.95	0.94

* and *** = denote significant differences at 0.05, and 0.001 probability levels, respectively; ns = not significant; SV = source of variation; DF = degree of freedom; SN60 = *Striga* count 60 days after planting; SN80 = *Striga* count 80 days after planting; ASNPC = area under the *Striga* number progress curve; P = parents; Cr = crosses; L = line; T = tester; L×T = line × tester; SED = standard error of the mean difference; H^2 (%) = broad sense heritability; h^2 (%) = narrow sense heritability; GCA = general combining ability; SCA = specific combining ability.

6.3.4.1. General Combining Ability Effects for Agronomic and *Striga* Parameters

GCA effects for agronomic traits and *Sh* parameters are presented in Tables 6.7 and 6.8, respectively. The line ICMB177002 recorded positive GCA effects for DTF (0.43), PH (2.26) and PCL (6.33). The testers IP-11358 and IP-6112 and line ICMB177111 had high positive GCA effects for GY at 158.99, 69.61 and 86.67 across locations. Negative GCA effects were computed for *Sh* parameters in a desirable direction. Testers IP-10579 and IP-11358 and line ICMB177002 had negative GCA effects for *Sh* parameters, SN60 (-7.58, -6.99, -6.55), SN80 (-7.18, -6.40, -6.49) and ASNPC (-147.45, -134.08, -130.33), whereas testers IP-6112 and IP-3098 and lines IKMB18002 and ICMB177111 had positive GCA effects for SN60 at 6.77, 9.92, 3.59 and 2.95, SN80 at 8.50, 7.72, 4.04 and 2.44 and ASNPC at 152.55, 176.43, 76.34 and 53.99 respectively.

Table 6.7. General combining ability (GCA) effects of the pearl millet lines and testers evaluated in two environments in Burkina Faso.

Genotypes	DTF	PH	NT	PCL	PCD	TGW	GY
ICMB177002	0.43^{ns}	2.26^{ns}	-0.24^{ns}	6.33**	-0.07^{ns}	-0.06^{ns}	-24.98^{ns}
ICMB177111	-0.30^{ns}	6.36^{ns}	0.32^{ns}	-3.50^{ns}	2.38^{ns}	0.21^{ns}	86.67^{ns}
IKMB18002	-1.67^{ns}	11.22^{ns}	0.14^{ns}	0.05^{ns}	0.92^{ns}	0.26^{ns}	22.15^{ns}
IP-3098	-2.76^{ns}	-0.38^{ns}	0.01^{ns}	-0.11^{ns}	-0.88^{ns}	-0.02^{ns}	-24.89^{ns}
IP-6112	-0.87^{ns}	6.24^{ns}	-0.16^{ns}	-0.17^{ns}	1.93^{ns}	0.04^{ns}	69.61^{ns}
IP-9242	-0.71^{ns}	-14.72^{ns}	0.17^{ns}	0.02^{ns}	0.21^{ns}	0.07^{ns}	9.70^{ns}
IP-10579	1.87^{ns}	23.32^{ns}	0.02^{ns}	0.05^{ns}	-0.42^{ns}	0.00^{ns}	6.51^{ns}
IP-11358	2.44^{ns}	20.96^{ns}	-0.01^{ns}	0.31*	-0.45^{ns}	0.18^{ns}	158.99^{ns}

*, and ** = denote significant differences at 0.05, and 0.01 probability levels, respectively; ns = not significant; DTF = days to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grain yield (kg/ha).

Table 6.8. General combining ability (GCA) effects of the pearl millet lines and testers evaluated in a greenhouse condition under *Striga* infestation.

Genotypes	SN60	SN80	ASNPC
ICMB177002	-6.55***	-6.49***	-130.33***
ICMB177111	2.95**	2.44*	53.99**
IKMB18002	3.59***	4.04***	76.34***
IP-3098	9.92***	7.72***	176.43***
IP-6112	6.77***	8.50***	152.55***
IP-9242	-2.13^{ns}	-2.63^{ns}	-47.45^{ns}
IP-10579	-7.58***	-7.18***	-147.45***
IP-11358	-6.99***	-6.40***	-134.08***

*, ** and *** = denote significant differences at 0.05, 0.01 and 0.001 probability levels, respectively; ns = not significant; SN60 = *Striga* count 60 days after planting; SN80 = *Striga* count 80 days after planting; ASNPC = area under the *Striga* number progress curve.

6.3.4.2. Specific Combining Ability Effects for Agronomic and *Striga* Parameters

SCA effects of agronomic traits for crosses evaluated across two environments in Burkina Faso are presented in Table 6.9. Crosses IP-9242 × ICMB177002, IP-3098 × IKMB18002, IP-10579 × IKMB18002, IP-11358 × ICMB177111 and IP-6112 × ICMB177002 had high positive SCA effects for GY at 65.33, 58.07, 39.62, 23.62 and 23.15 in that order. The hybrids IP-11358 × ICMB177002 had positive SCA effects for PCL (2.03), TGW (1.11) and GY (7.88).

Table 6.10 presented the SCA effects for crosses evaluated in the greenhouse under *Sh*-infestation. Crosses IP-3098 × ICMB177002, IP-6112 × ICMB177002 and IP-11358 × ICMB177111 had high and negative SCA for *Sh* parameters SN60 at -9.40, -4.40 and -4.14, SN80 at -6.50, -7.63 and -4.01 and ASNPC at -159.10, -120.22 and -81.21 in that order. Crosses IP-3098 × ICMB177111,

IP-11358 × ICMB177002 and IP-10579 × ICMB177002 had large and positive SCA effects for SN60 (9.45, 8.21 and 5.45), SN80 (4.72, 8.12 and 5.20) and ASNPC (141.58, 163.11 and 106.43).

Table 6.9. Specific combining ability (SCA) effects for agronomic traits among pearl millet crosses evaluated across two environments in Burkina Faso.

Hybrids	DTF	PH	NT	PCL	PCD	TGW	GY
IP-3098 × ICMB177002	0.95^{ns}	-2.28E-13^{ns}	-0.26^{ns}	-0.65^{ns}	0.36^{ns}	-0.50^{ns}	-63.77^{ns}
IP-6112 × ICMB177002	1.25^{ns}	2.49E-13^{ns}	0.04^{ns}	-2.93^{ns}	-0.33^{ns}	-0.51^{ns}	23.15^{ns}
IP-9242 × ICMB177002	-0.87^{ns}	1.13E-14^{ns}	0.07^{ns}	0.46^{ns}	0.30^{ns}	0.18^{ns}	65.33^{ns}
IP-10579 × ICMB177002	-0.74^{ns}	4.79E-14^{ns}	-0.06^{ns}	0.90^{ns}	1.28^{ns}	-0.34^{ns}	21.10^{ns}
IP-11358 × ICMB177002	-1.08^{ns}	1.35E-13^{ns}	-0.14^{ns}	2.03^{ns}	-0.47^{ns}	1.11*	7.88^{ns}
IP-3098 × ICMB177111	-1.20^{ns}	4.64E-14^{ns}	0.27^{ns}	0.80^{ns}	-0.71^{ns}	0.21^{ns}	16.81^{ns}
IP-6112 × ICMB177111	-0.06^{ns}	6.37E-14^{ns}	0.11^{ns}	-3.20^{ns}	3.56**	0.32^{ns}	-2.15^{ns}
IP-9242 × ICMB177111	0.79^{ns}	9.86E-15^{ns}	0.13^{ns}	0.51^{ns}	-1.06^{ns}	0.28^{ns}	-31.00^{ns}
IP-10579 × ICMB177111	-0.51^{ns}	1.42E-13^{ns}	0.21^{ns}	0.95^{ns}	0.15^{ns}	0.40^{ns}	-55.24^{ns}
IP-11358 × ICMB177111	-0.49^{ns}	-1.95E-13^{ns}	-0.08^{ns}	0.67^{ns}	-1.13^{ns}	-0.32^{ns}	23.62^{ns}
IP-3098 × IKMB18002	-0.07^{ns}	-5.06E-14^{ns}	-0.22^{ns}	0.17^{ns}	0.01^{ns}	0.03^{ns}	58.07^{ns}
IP-6112 × IKMB18002	-0.96^{ns}	-1.21E-13^{ns}	-0.02^{ns}	-1.36^{ns}	0.58^{ns}	0.34^{ns}	14.82^{ns}
IP-9242 × IKMB18002	0.13^{ns}	1.42E-13^{ns}	0.21^{ns}	1.10^{ns}	-0.81^{ns}	-0.16^{ns}	20.71^{ns}
IP-10579 × IKMB18002	-0.45^{ns}	2.25E-13^{ns}	-0.02^{ns}	2.16^{ns}	0.93^{ns}	0.14^{ns}	39.62^{ns}
IP-11358 × IKMB18002	-0.55^{ns}	9.66E-14^{ns}	0.11^{ns}	2.35^{ns}	-0.11^{ns}	0.48^{ns}	-28.89^{ns}

* and ** = denote significant differences at 0.05, and 0.01 probability levels, respectively; ns = denote not significant; DTF = days to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grain yield (kg/ha).

Table 6.10. Specific combining ability (SCA) effects for *Striga* parameters among pearl millet crosses evaluated under *Striga*-infestation.

Hybrids	SN60	SN80	ASNPC
IP-3098 × ICMB177002	-9.40**	-6.50*	-159.10**
IP-6112 × ICMB177002	-4.40^{ns}	-7.63**	-120.22*
IP-9242 × ICMB177002	0.14^{ns}	0.80^{ns}	9.78^{ns}
IP-10579 × ICMB177002	5.45*	5.20*	106.43*
IP-11358 × ICMB177002	8.21**	8.12**	163.11**
IP-3098 × ICMB177111	9.45**	4.72^{ns}	141.58**
IP-6112 × ICMB177111	-0.05^{ns}	3.79^{ns}	37.11^{ns}
IP-9242 × ICMB177111	-2.85^{ns}	-2.78^{ns}	-56.24^{ns}
IP-10579 × ICMB177111	-2.40^{ns}	-1.70^{ns}	-41.24^{ns}
IP-11358 × ICMB177111	-4.14^{ns}	-4.01^{ns}	-81.21^{ns}
IP-3098 × IKMB18002	-0.04^{ns}	1.77^{ns}	17.53^{ns}
IP-6112 × IKMB18002	4.45^{ns}	3.84^{ns}	83.11^{ns}
IP-9242 × IKMB18002	2.71^{ns}	1.97^{ns}	46.46^{ns}
IP-10579 × IKMB18002	-3.04^{ns}	-3.48^{ns}	-65.19^{ns}
IP-11358 × IKMB18002	-4.07^{ns}	-4.11^{ns}	-81.91^{ns}

* and ** = denote significant differences at 0.05, and 0.01 probability levels, respectively; ns = denote not significant; SN60 = *Striga* count 60 days after planting; SN80 = *Striga* count 80 days after planting; ASNPC = area under the *Striga* number progress curve.

6.3.5. Heterosis for Agronomic Traits

Mid-parent and standard heterosis for pearl millet crosses for agronomic traits evaluated across two environments in Burkina Faso are presented in Table 6.11. MPH for PH were positive and varied from 2 to 30%. The MPH for NT was positive for 53.33% of the crosses. The MPH for PCL was positive in 86.67% of crosses, such as in IP-10579 × ICMB177002, IP-3098 × IKMB18002, IP-9242 × ICMB177002 and IP-6112 × IKMB18002 at 46.58%, 28.07%, 25.43% and 21.98%, in that order. For PCD, high and positive MPH was observed for IP-10579 × ICMB177002 and IP-6112 × IKMB18002 at 64.67% and 15.96%, in that order. High MPH for TGW was recorded for IP-11358 × ICMB177002 (91.25%), IP-6112 × ICMB177111 (46.70%), IP-6112 × IKMB18002 (39.81%), IP-3098 × ICMB177111 (33.72%) and IP-10579 × ICMB177002 (25.20%). For GY, MPH was high and positive for IP-6112 × ICMB177002, IP-6112 × IKMB18002, IP-10579 × IKMB18002 and IP-9242 × IKMB18002 at 160.71%, 89.98% 38.02% and 21.07%, in that order.

The SH for PH was positive for 40% of crosses. All crosses recorded negative SH for NT and GY. For PCL, high and positive SH was observed for IP-11358 × ICMB177002 (17.33%), IP-10579 × ICMB177002 (11.70%) and IP-9242 × ICMB177002 (8.69%). Positive SH were recorded for 6.67% of crosses for PCD, whereas 53.33% had positive SH for TGW.

Table 6.11. Mid-parent and standard heterosis for agronomic traits among pearl millet crosses evaluated across two environments in Burkina Faso.

Hybrid	Mid-parent heterosis						Standard heterosis					
	PH	NT	PCL	PCD	TGW	GY	PH	NT	PCL	PCD	TGW	GY
IP-10579 × ICMB177002	29.75	-5.88	46.58	64.67	25.20	8.06	4.23	-49.94	11.70	-12.35	-14.55	-68.12
IP-3098 × ICMB177002	6.94	-3.68	2.38	2.49	-1.33	7.72	-17.75	-49.94	4.83	-19.94	-18.14	-67.45
IP-3098 × IKMB18002	28.74	-22.75	28.07	4.40	17.84	3.03	-9.87	-46.61	-14.09	-19.28	-7.85	-54.45
IP-10579 × ICMB177111	8.29	7.11	1.47	3.14	9.42	4.25	4.47	-23.27	-28.98	-20.42	0.07	-53.72
IP-11358 × ICMB177002	21.66	32.47	16.43	2.51	91.25	-1.57	6.35	-39.94	17.33	-23.65	22.99	-46.02
IP-6112 × ICMB177002	19.97	-6.25	-2.50	1.35	0.99	160.71	-1.09	-36.61	-9.09	-13.23	-13.79	-43.24
IP-10579 × IKMB18002	10.83	1.02	9.39	7.57	6.71	38.02	6.95	-29.94	-13.01	-16.16	-2.03	-41.89
IP-9242 × ICMB177111	2.57	5.96	1.65	0.60	7.74	1.33	-16.38	-13.27	-24.77	-10.52	0.41	-41.89
IP-3098 × ICMB177111	15.71	20.76	8.47	-4.10	33.72	0.47	-5.87	-6.35	-20.45	-17.08	0.19	-41.58
IP-9242 × IKMB18002	7.00	0.62	9.77	-1.03	6.71	21.07	-10.55	-23.27	-4.83	-21.55	-0.27	-38.16
IP-9242 × ICMB177002	19.98	-13.28	25.43	7.79	22.01	20.70	-9.68	-29.94	8.69	-16.08	-1.64	-37.53
IP-6112 × IKMB18002	25.82	-9.99	21.98	15.96	39.81	89.98	-1.54	-29.94	-18.98	1.06	8.98	-35.42
IP-6112 × ICMB177111	19.48	-1.74	-14.67	8.97	46.70	8.17	-1.09	-46.35	-43.86	-34.67	9.90	-35.31
IP-11358 × IKMB18002	11.85	1.68	7.05	3.25	14.18	7.63	15.22	-26.61	1.93	-12.05	15.86	-24.96
IP-11358 × ICMB177111	6.65	8.35	3.11	2.11	12.49	3.88	3.71	-16.61	-8.98	-9.74	6.73	-3.08

PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grains yield (kg/ha).

6.4. Discussion

Striga, commonly called witchweed, is a noxious parasitic weed that causes significant yield losses in cereal crops, including pearl millet. Due to *Striga* parasitism, yield losses varying from 80% to 100% have been reported in pearl millet (Kountche et al. 2016, Kanampiu et al. 2018; Rouamba et al. 2021). In Burkina Faso, the weed poses a major constraint to pearl millet production, especially under low-input production systems (Boussim et al. 2011; Drabo et al. 2018; Rouamba et al. 2021). The currently cultivated varieties are susceptible to *Striga*, and there are modest previous breeding efforts, but *Striga*-resistant pearl millet varieties are yet to be developed. There is a need to develop high-yielding and *Sh*-resistant pearl millet varieties with farmers' preferred traits. The current study determined the combining ability and heterosis for agronomic traits and *Sh*-resistance in pearl millet to select promising parental lines and testers for breeding and selection of *Sh*-resistant hybrids with farmer-preferred traits for genetic advancement and cultivar release.

The significant difference observed among the studied pearl millet genotypes for most agronomic traits suggests the presence of adequate genetic variation for breeding (Table 6.2). Significant interaction effects existed between lines, testers and crosses and the test environments for most traits. The differential response indicated that lines, testers and crosses allow the selection of the best candidates based on the target production environments. For example, crosses IP-11358 × ICMB177111, IP-11358 × IKMB18002, IP-6112 × ICMB177111 and IP-9242 × ICMB177002 with grain yields of 1128.10 kg/ha, 938.60 kg/ha, 890.30 kg/ha and 825.50 kg/ha, in that order, were the top-yielders across the test locations (Table 6.3). Therefore, they are suitable for production in the major pearl millet production zones of Burkina Faso and similar environments of SSA. The study identified crosses IP-10579 × ICMB177002, IP-9242 × ICMB177002 and IP-11358 × ICMB177111 with low levels of *Striga* damage and possessing candidate *Sh*-resistant genes as compared to the resistant check (Table 6.4). These suggest the possibility to develop *Sh*-resistant pearl millet genotypes. Also, the testers IP-9242, IP-6112, and IP-10579 were *Striga*-resistant and valuable germplasm to augment this trait into elite pearl millet genotypes (Table 6.4).

Combining ability analysis allows the selection of parents for breeding, new progenies for selection, genetic advancement and new variety release. The present study revealed that most agronomic and *Striga* parameters were conditioned by non-additive gene effects (Table 6.5), in agreement with Sanghera and Hussain (2012), Barathi et al. (2020), and Balami et al. (2022). The preponderance of non-additive gene action in the expression of pearl millet traits indicates that hybrid breeding is possible using the current gene pool to exploit heterosis. Narrow-sense heritability varied from high (94.74%) to low (3.00%) for agronomic traits and high (69.52%) for *Striga* traits suggesting the involvement of

additive and non-additive gene effects controlling their expression. Reportedly, non-additive genetic effects were found to govern the inheritance of plant height, the number of tillers per plant, and grain yield in pearl millet in India (Rattunde 1988; Jeeterwal et al. 2018).

The tester parent IP-11358 had high positive GCA effects for grain yield and negative GCA effects for the number of emerged *Sh* plants estimated at 60 days and 80 days after sowing and the area under the *Striga* number progress curve. Positive effects for grain yield and negative effects for the number of *Sh* counts are desirable traits when breeding for high-yielding and *Striga*-resistant varieties (Lobulu et al. 2023). In contrast, negative effects for days to 50% flowering and the number of *Sh* count are desirable for early maturity and *Striga*-resistance (Balami et al. 2022). As a result, the tester parent IP-11358 was identified as a good combiner for grain yield and *Sh*-resistance for future breeding. High positive SCA effects for grain yield and negative SCA effects for the number of *Sh* recorded for IP-6112 × ICMB177002 and IP-11358 × ICMB177111 indicated that their parents have greater genetic distance and combine well to produce *Sh*-resistant high-yielding progenies. High SCA effects for panicle length, thousand-grain weight, and grain yield for IP-11358 × ICMB177002 indicated the ability to develop new pearl millet varieties which combined desirable and yield-improving agronomic traits. Significant SCA effects for yield and yield components and low SCA for *Striga* tolerance were reported by Balami et al. (2022) in pearl millet. Host-plant resistance has been widely recognised as the most economical and sustainable method for the long-term control of *Striga* in farmers' fields (Yoder and Scholes 2010).

Negative and positive standard heterosis observed for the number of tillers and thousand-grain weight is in line with findings by Sumit and Wali (2016), Sumathi and Revathi (2017), Acharya et al. (2017), and Dawud (2018) in pearl millet. High standard heterosis for the grain yield was observed for some evaluated pearl millet crosses, such as IP-11358 × ICMB177111, IP-11358 × IKMB18002 and IP-6112 × ICMB177111, suggesting successful development and delivery of high-yielding pearl millet hybrids. This is in line with the findings by Chittora and Patel (2017) and Sumathi and Revathi (2017), who reported higher hybrid vigour in pearl millet. The newly bred experimental hybrids are recommended for genetic advancement and further selection to recommend for high-yielding and *Striga*-resistant pearl millet varieties.

6.5. Conclusions

The present study estimated the combining ability of selected lines and testers and the hybrid performance of their crosses for agronomic traits and resistance to *Striga* for variety development in pearl millet. The testers IP-10579, IP-6112 and IP-11358 were identified as promising genetic stocks for grain yield and *Striga*-resistance breeding. Lines such as ICMB177111 and IKMB18002 were

identified as valuable sources of genes for breeding for high-yield potential. The experimental hybrids IP-11358 × ICMB177111, IP-10579 × IKMB18002 and IP-6112 × ICMB177002 with high grain yield potential and *Striga*-resistance were identified for multi-environment evaluation, genetic advancement and production in Burkina Faso.

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An Overview of the Research Findings

Introduction and objectives of the study

Pearl millet (*Pennisetum glaucum* [L.] R. Br. 2n = 2x = 14) is an important cereal crop grown in the semi-arid tropics of Africa and India. It is adapted to growing in areas with low soil fertility, rainfall, and high temperatures where other cereals fail to produce. The mean grain yield is very low in West Africa (< 0.74 tons ha^{-1}) and in Burkina Faso (≤ 0.81 tons ha^{-1}), where it is a staple food for millions of people in rural and urban areas. Recurrent drought, *S. hermonthica* infestation, shortage of labour, lack of inorganic fertiliser, lack of cash, and the use of low-yielding varieties were the main challenges hindering pearl millet production in Burkina Faso. *S. hermonthica* infestation is the major constraint affecting pearl millet production, inducing up to 80% yield losses. Poor access, the high cost of improved seed, and a lack of farmers preferred traits in the existing improved pearl millet varieties were the main reasons for their low adoption rates, as 32% of respondents reported. *S. hermonthica* management options in pearl millet production fields included moisture conservation using terraces, manual hoeing, hand weeding, use of microplots locally referred to as 'zaï', crop rotation and mulching. These management techniques were ineffective because they do not suppress the below ground *S. hermonthica* seed and are difficult to implement. Integrated management practices employing breeding for *S. hermonthica* resistant varieties with the aforementioned control measures could offer a sustainable solution for *S. hermonthica* management and improved pearl millet productivity in Burkina Faso. This study was, therefore, executed with the following primary objectives:

The specific objectives of the study were:

a. To investigate the constraints affecting pearl millet production and farmers' approaches to *S. hermonthica* management in Burkina Faso to guide breeding and production.

b. To screen pearl millet genotypes for resistance to *S. hermonthica* and compatibility with a biocontrol agent, *FOS*, in the Sahel to select contrasting and promising parents for resistance breeding and production.

c. To determine the genome-wide association analyses of agronomic traits and *S. hermonthica* resistance in pearl millet to identify genetic markers for marker-assisted breeding and trait introgression.

d. To determine the generation mean analysis of *S. hermonthica* resistance in pearl millet to guide selection, genetic advancement and variety development.

e. To determine the combining ability effects and the response of pearl millet genotypes for agronomic traits and *S. hermonthica* resistance for selecting superior parents and hybrids.

Research findings in brief

Constraints to pearl millet production and farmers' approaches to *Striga hermonthica* management in Burkina Faso

A participatory rural appraisal (PRA) study was conducted using semi-structured interviews and focus group discussions. A hierarchical sampling method based on pearl millet production, *S. hermonthica* infestation, and the regions' administrative organisation was used to select the study sites. Two agro-ecological zones (Sahelian and Sudano-Sahelian) involved in large-scale pearl millet production were selected. Subsequently, five regions were identified based on *S. hermonthica* infestation, and accessibility. Three regions, namely Central Plateau, South Central, and West Central, were identified in the Sudano-Sahelian agro-ecological zone, while two regions, namely North and North Central, were selected in the Sahelian zone. A total of 492 respondents participated in the study. Three hundred farmers were interviewed using a structured questionnaire, and 192 farmers were part of the focus group discussion. The main outcomes of this study were:

- The majority of smallholder farmers (61%) grow local varieties of pearl millet, with crop production being the most common source of income (36.7%).
- The use of local varieties has resulted in a yield output of less than 1 ton ha^{-1} in 61.4% of smallholder farmers' fields.
- *S. hermonthica* infestation, drought, lack of cash, lack of improved varieties, shortage of labour, and lack of fertilisers, were identified as major constraints to pearl millet production and productivity in the study areas.
- *S. hermonthica* ranked first constraints by 40% of the respondents, inducing a yield loss of up to 80%.
- Terraces, micro plots (zaï), ridge, grass strips, hand weeding, crop rotation, mulching, and organic manure were farmers *S. hermonthica* management approaches.
- Integrated management practices employing breeding for *S. hermonthica* resistant varieties with the aforementioned control measures could offer a sustainable solution for *S. hermonthica* management and improved pearl millet productivity in Burkina Faso.

Screening of pearl millet genotypes for resistance to *Striga hermonthica* and compatibility to a biocontrol agent, *Fusarium oxysporum* f.sp. *Strigae*, in the Sahel

The study used a total of 150 pearl millet lines, where 148 genotypes were acquired from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)/Niger, and the two lines were locally adapted entries obtained from the Institute of Environment and Agricultural Research (INERA). In addition, a pathogenic strain of *Fusarium oxysporum* f.sp. *Strigae* was part of the study. Test genotypes were evaluated in a naturally *Striga*-infested hotspot field at Didri during the 2019/2020 main growing season, and in a screenhouse at the main station of INERA in the offseason 2020/2021. The experiment was laid out on 10 × 15 alpha lattice design in two replications.

The following major outputs were obtained:

- The following five pearl millet *S. hermonthica* resistant inbred lines were identified with *Fusarium oxysporum* f.sp. *Strigae* compatibility: IP-3098, IP-6112, IP-9242, IP-10579, and IP-11358.
- The resistant genotypes exhibited low production of *S. hermonthica* germination stimulant.
- The effect of *S. hermonthica* delayed days to flowering and reduced pearl millet plant height.
- *Fusarium oxysporum* f.sp. *Strigae* suppressed *S. hermonthica* emergence.
- The selected genotypes are useful parents for breeding and integrated *Striga* management in Burkina Faso and related agro-ecologies.

Genome-wide association analyses of agronomic traits and *Striga hermonthica* resistance in pearl millet

A set of 150 genotypes were assessed using phenotypic traits for resistance to *S. hermonthica* and agronomic traits in *S. hermonthica* hotspot field and in the screenhouse under *S. hermonthica* condition. The test genotypes were further profiled using 256 K single nucleotide polymorphisms markers to complement the phenotypic data.
The main results of this study were:

- Twenty-eight significant associated SNPs located on chromosomes 1, 2, 3, 4, and 7 were detected that were associated with *S. hermonthica* emergence count.
- Four SNPs were associated with days-to-50%-flowering on chromosomes 3, 5, 6, and 7.
- Five were associated with panicle length on chromosomes 2, 3, and 4.
- Seven SNPs were linked to thousand-grain weight on chromosomes 2, 3, and 6.
- The putative SNP markers associated with a low number of emerged *S. hermonthica* and agronomic traits in the assessed genotypes are valuable genomic resources for accelerated

breeding and variety deployment of pearl millet with *S. hermonthica* resistance and farmer-and market-preferred agronomic traits.

Generation mean analysis of *Striga hermonthica* resistance in pearl millet (*Pennisetum glaucum* [L.] R. Br.)

Bi-parental crosses were derived from contrasting pairs of pearl millet lines, including IP-10579 (*Striga* resistant)/IP-8129 (*Striga* susceptible), and IP-3098 (*Striga* resistant)/IP-8786 (*Striga* susceptible). The F_1 generations were selfed to advance to the second generation (F_2) or backcrossed to the respective resistant and susceptible parents. The two sets of parental lines, F_1s, F_2s, and backcrosses, were evaluated under greenhouse and *S. hermonthica* infested field conditions using a randomized complete block design with three replications.

The core findings of the study were:

- Non-allelic gene interaction explains the inheritance of the genes governing *S. hermonthica* resistance in pearl millet.
- *S. hermonthica* resistance in pearl millet is quantitatively inherited and controlled by several genes.
- The *S. hermonthica* resistance gene has a duplicate gene interaction.
- The recurrent selection method is suitable for breeding pearl millet against *S. hermonthica.*
- Unique F_2 individuals with *S. hermonthica* resistance were selected from the two sets for genetic advancement through recurrent selection methods for pearl millet variety development by integrating desirable agronomic and farmer-preferred traits.

Combining ability and heterosis for agronomic traits and resistance to *S. hermonthica* in pearl millet (*Pennisetum glaucum* [L.] R. Br.)

Fifteen pearl millet families were developed through controlled crosses using the Line × Tester mating design. Crosses were conducted using 5 lines possessing *Striga* resistance, and 3 testers selected for their adaptability and good agronomic traits. The F_1s, their parents and checks were evaluated in two locations (Gampela and Fada) and in greenhouse at the main station of INERA under *Striga* infestation, using a 4 × 6 alpha lattice design with two replications. Data were collected on *Striga* and pearl millet parameters.

The main findings of this study were:

- IP-11358, ICMB177111 and IP-6112 exhibited high positive general combining ability (GCA) effects for grain yield.
- IP-11358 recorded negative GCA effects for *S. hermonthica* count.
- Hybrids, IP-6112 × ICMB177111, IP-11358 × IKMB18002, and IP-11358 × ICMB177111 out-performed the best check at Gampela site.
- IP-113558, ICMB177111, and IP-6112 are identified as good general combiners for grain yield;
- IP-113558 × ICMB17711 presented 254.63 SCA effects and 24.50% standard heterosis for grain yield at Gampela location with a < 1 mean *Striga* emergence count.
- The hybrid IP-11358 × ICMB177002 had SCA effect of 2.27 and 1.10 for days to fifty per cent flowering and thousand-grain weight, in that order.
- The hybrid IP-3098 × ICMB177111 had SCA effect of 11.67 and 0.67 for plant height, and number of productive tillers, respectively.
- The new hybrids are recommended for direct production or as testers for the development of *S. hermonthica* resistant pearl millet genotypes.

Implications of the research findings for breeding pearl millet for higher yield and resistance to the witchweed, *S. hermonthica*

- The PRA study highlighted *S. hermonthica* infestation as the primary pearl millet production constraint for smallholder farmers, which is estimated to cause up to 80% yield losses in Burkina Faso.
- Many respondent farmers (68%) used local varieties with low yield potential, which are also highly susceptible to *S. hermonthica* infestation. Hand weeding and hoeing were the most commonly used methods to control *S. hermonthica*, although they are ineffective.
- An integrated management approach, which would involve breeding for *S. hermonthica* host resistance combined with other control measures, may offer a better option for managing *S. hermonthica* infestation in Burkina Faso.
- The current study selected the following pearl millet genotypes: IP-3098, IP-6112, IP-9242, IP-10579, and IP-11358, exhibiting *S. hermonthica* resistance and were compatible with *FOS*. They are useful parents for breeding and integrated *Striga* management in Burkina Faso and similar agro-ecologies.
- Non-allelic gene interaction explained the inheritance of the genes governing *S. hermonthica* resistance in pearl millet. The study found that duplicate gene action controlled the inheritance of the number of emerged *S. hermonthica*.

- Twenty-eight SNPs were associated with *S. hermonthica* traits on chromosomes 1, 2, 3, 4, 6, and 7. SNPs markers associated with DTF, PCL, and TGW were located on chromosomes 2, 5, 6, and 7; chromosomes 2, 3, and 4; and chromosome 6, respectively.
- The new markers would be deployed for marker-assisted breeding emphasising the above agronomic traits and *S. hermonthica* resistance in pearl millet in Burkina Faso or related agroecologies after successful validation.
- The study revealed IP-113558, ICMB177111, and IP-6112 as good general combiners for grain yield and IP-113558 × ICMB17711 as the best hybrid for grain yield and *S. hermonthica* resistance.
- The above genetic and genomic resources identified by this study are useful for pearl millet breeding in Burkina Faso.