

Suppressive abilities of legume fodder plants against the invasive weed *Parthenium hysterophorus* (Asteraceae)

Fredrick Ojija^{a,b,*}, Christopher Ngimba^b

^a Department of Sustainable Agriculture, Biodiversity and Ecosystem Management, School of Life Sciences and Bio-Engineering, The Nelson Mandela African Institution of Science and Technology, P.O. Box 447, Arusha, Tanzania

^b Department of Applied Sciences, Mbeya University of Science and Technology, P.O. Box 131, Mbeya, Tanzania



ARTICLE INFO

Keywords:

Biological invasions
Desmodium intortum
Famine weed
Invasive species
Lablab purpureus

ABSTRACT

The alien invasive plant *Parthenium hysterophorus* (Asteraceae) has been reported to impend smallholder farmers' livelihood, and biodiversity conservation in sub-Saharan Africa. While earlier studies reported that the invasion may be suppressed if plant density in invaded habitats is sufficiently maintained, only a few quantitative experiments on competition between legume (Fabaceae) fodder plants and invasive plant species have been conducted. We determined whether three selected test legume fodder species, *Desmodium intortum* (greenleaf desmodium), *Lablab purpureus* (hyacinth bean) and *Medicago sativa* (lucerne), can suppress *P. hysterophorus* growth. These legumes were selected because they have been used to suppress various weeds in sub-Saharan Africa owing to their rapid growth, strong root systems, bigger leaf canopy, high biomass production and capacity to form many branches. Also, they are used by livestock as forage when other fodders are dry and become limited. The legume fodder plant species and *P. hysterophorus* were grown as mono- and mixed cultures in pot experiments. Fifty-day-old *P. hysterophorus* seedlings were harvested to determine any suppressive abilities of the legume species against the invasive. We found that the growth of *P. hysterophorus* was negatively impacted when grown with two or three test legume species compared with monoculture. Respectively, stem height, total fresh biomass and leaf chlorophyll content of *P. hysterophorus* seedling were reduced by >60%, >59%, and >70% when grown in combination with all three legume fodder species compared with sole cropping or in mixture with just *D. intortum* or *M. sativa*. The results suggest that the selected legume fodder plants have the ability to suppress growth of *P. hysterophorus*. Further, this study demonstrates the potential importance of using legume fodder plant species in the management of alien invasive plants.

1. Introduction

Alien plant species introduced to new geographical areas in some cases become invasive and cause deleterious effects on recipient ecosystem (Pyšek et al., 2004). Traits that may contribute towards invasiveness in a newly introduced range include capacity to produce abundant seeds, rapid dispersal of seeds or propagules, rapid germination, high growth and survival rate (Axmacher and Sang, 2013), long seed dormancy and ability to form persistent seed banks (Gioria et al., 2019). Also, alien invasive species often become free from biotic constraints outside their native range as they lack effective natural enemies such as bacteria, fungi, insects, mites, viruses, and larger grazing animals (Perkins et al., 2011). Therefore, following establishment of alien

invasive species in new habitats, they crowd out native species via allelopathy and/or competition for light, nutrients, space, and water (Tracy et al., 2004; Tanveer et al., 2015). Furthermore, invasive species can deplete native plant seedbanks to the point that native species cannot re-establish following their removal (Schuster et al., 2018).

The invasive plant *Parthenium hysterophorus* L. (Asteraceae), commonly known as "parthenium weed", is indigenous to North and South America, and is widely distributed as an invasive in many countries (Ojija et al., 2019a, 2019b, 2021). *Parthenium hysterophorus* constitutes a significant threats to biodiversity, agriculture and the delivery of ecosystem services in recipient environments (Terblanche et al., 2016). Apart from altering vegetation community structure into monospecific stands of parthenium weed, *P. hysterophorus* also reduces the quantity

* Corresponding author. Department of Sustainable Agriculture, Biodiversity and Ecosystem Management, School of Life Sciences and Bio-Engineering, The Nelson Mandela African Institution of Science and Technology, P.O. Box 447, Arusha, Tanzania.

E-mail address: fojija@mustnet.ac.tz (F. Ojija).

<https://doi.org/10.1016/j.indic.2021.100111>

Received 11 July 2020; Received in revised form 9 March 2021; Accepted 11 March 2021

Available online 13 March 2021

2665-9727/© 2021 The Author(s). Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

and quality of palatable forages, and crop production (Ojija et al., 2019a, 2019b). Parthenium weed can grow up to 2 m high under suitable agro-climatic conditions (Khan et al., 2013; Shabbir et al., 2013). It produces abundant seeds (ca. 10,000–25,000 per plant) which are dispersed by wind, water and human activities (Ojija and Manyanza, 2021; Ojija et al., 2019a). The seeds spread easily and establish in disturbed habitats as well as along waterways and road networks (Khan et al., 2013; Shabbir et al., 2013). If *P. hysterophorus* invasion is not controlled, it may suppress natural flora, increase management costs, and affect biodiversity and ecosystem function (Pratt et al., 2017).

Despite the growing knowledge about the negative impacts of *P. hysterophorus*, little information regarding effective management methods is available for sub-Saharan Africa (Ojija et al., 2019b). Even the most common control methods, e.g. synthetic herbicides, physical management, biological control and metabolites from fungal species available in other invaded countries such as Australia, India, Pakistan, South Africa, and Sri Lanka have limited effects when used alone (Khan et al., 2013; Shabbir et al., 2013). However, earlier studies have shown that a feasible way to control invasives in cultivated land is to maintain diverse assemblages of suppressive plant species (Knops et al., 1999; Tracy et al., 2004; Ammond and Litton, 2012; Shabbir et al., 2013; Schuster et al., 2018). These species are able to outcompete alien invasive plants for water, growth space, light, and impede their germination and growth (Khan et al., 2013; Schuster et al., 2018; Shabbir et al., 2013). Vilà and Weiner (2004) claimed that suppressive plant species at high density suppressed invasive plants. Also, Li et al. (2015) showed that growth of the invasive plant *Ipomoea cairica* L. was suppressed when grown together with the suppressive plants *Pueraria lobata* (Willd.) Ohwi or *Paederia scandens* (Lour.) Merr.

Significant negative impacts of parthenium weed have been reported in rangelands (i.e. natural grasslands) of Tanzania where its invasion reduces forage species needed by livestock and threaten wildlife conservation. It has also invaded crop lands where it lessens crop productivity and increases the cost of controlling the weed to small holder farmers. Thus, we hypothesized that increased numbers of suppressive legume fodder plant species in croplands can suppress *P. hysterophorus* growth. Based on this, we conducted a pot experiment to investigate the suppressive ability of legume (Fabaceae) fodder plant species *Desmodium intortum* L., *Lablab purpureus* L., and *Medicago sativa* L. against *P. hysterophorus*.

2. Materials and methods

2.1. Characteristics of test plant species

Lablab purpureus (hyacinth bean) is a fast growing herbaceous legume that can reach 6 m high (Madzonga and Mogotsi, 2014). It grows in a diverse range of environmental conditions in bushland, grassland, and forest because it is drought resistant and highly adaptable (Maass et al., 2010). *Lablab purpureus* is a multi-purpose perennial food and forage crop grown in the tropics (Maass et al., 2010). In the dry season it remains green, making it attractive to cattle when other fodders are dry and scarce. The annual tropical forage legume *Desmodium intortum* of up to 7.5 m height grows in areas with annual rainfall of 900–3000 mm, and temperatures between 25 and 30 °C (USDA NRCS, 2012).

Desmodium intortum (greenleaf desmodium) is grazed as a long-term pasture and used as a conservation cover crop because its leaf materials decay mildly in the soil (USDA NRCS, 2012). *Desmodium intortum* takes about four months to cover the soil and prevents weeds from establishing (Maina et al., 2006).

Medicago sativa (lucerne) is relatively tolerant to drought and can live for several years within its ideal temperature range of 15–25 °C and rainfall of 200–2500 mm (Lei et al., 2018). Its erect stems can reach up to 1 m tall with numerous branches (Radovic et al., 2009). It is often grown as cover crop, for hay and green manure.

Due to their high protein content, high biomass production and

adaptability, these three legume species are widely used to outcompete weeds (Maina et al., 2006; Madzonga and Mogotsi, 2014). The ability of test plants to grow relatively tall, form many branches and strong root systems, make them potentially suitable for suppression of *P. hysterophorus*. For instance, the deep (4–7 m) root system of *M. sativa* increases its resilience in droughts (Radovic et al., 2009). However, future climate change may affect the interaction of suppressive plants and *P. hysterophorus*, particularly when CO₂ concentration rises. For instance, a study by Shabbir et al. (2019) showed that when *P. hysterophorus* was grown under a high CO₂ concentration (550 μmol mol⁻¹), it produced more branches (35%), greater dry biomass (38%), and more seeds per plants (37%) than when it was grown in ambient CO₂ concentration (380 μmol mol⁻¹). Nevertheless, since our test plants are tolerant to a broad range of temperature and habitat conditions, they may not in the short term be affected by climate change or rise of CO₂ concentration. In general, we selected these legume fodder plants because they have rapid growth, strong root systems, relatively large leaf canopy and form many branches (Debela et al., 2012).

2.2. Competition experiment and seedling growth parameters

Parthenium hysterophorus seeds were obtained from the Agricultural Division, Tropical Pesticide Research Institute (TPRI), Tanzania. *Desmodium intortum* and *Medicago sativa* seeds were sourced from Kibo Seed Company Ltd., Arusha, Tanzania, and *L. purpureus* seeds were obtained from the Department of Sustainable Agriculture, Biodiversity and Ecosystem Management, Nelson Mandela African Institution of Science and Technology (NM-AIST). We investigated the suppressive ability of *D. intortum*, *M. sativa*, and *L. purpureus* on *P. hysterophorus* seedling growth under pot experiment established at NM-AIST (3° 24.149' S and 36° 47.790' E, 1197 m a.s.l.). Pots were equally filled with black clay soil from an uninvaded field plot. Twenty-five (25) seeds of *P. hysterophorus* and test plant species each were sown in five pots at varying combinations in monoculture as a control, and mixtures. Plant seedlings were allowed to grow at a density of four *P. hysterophorus*/six test plants per pot (Table 1). A total of 11 planting combinations were replicated five times to make 55 pot trials (Table 1). Pots were kept in a naturally illuminated screen-house at NM-AIST.

Each pot was irrigated daily in the morning with 0.5 l of water. Positions of the pots were randomised twice per week to ensure uniform distribution of sunlight. Any other emerging germinating seedlings were removed in the pots. The fifty (50)-day-old seedlings of *P. hysterophorus* were harvested from each pot without destroying the roots to assess legume plant suppressive abilities on invasive growth. We washed the roots carefully to remove soils by placing them on top of a steel mesh tray. Any other remaining debris were then removed carefully by forceps. Harvesting time was within the critical competition period of *P. hysterophorus* with different plant species which ranges from seven to 60 days (Rana et al., 2008; Safdar et al., 2016). During this time, an increase in

Table 1

Experimental planting design diagram with *P. hysterophorus* (P) and suppressive plant species (S). P = *Parthenium hysterophorus*, M = *Medicago sativa*, D = *Desmodium intortum*, and L = *Lablab purpureus*. S₀, S₁, S₂, and S₃ refer to levels of suppressive species richness, respectively, i.e., S₀ = no suppressive plant species added, S₁ = one species (M, D or L) added, S₂ = two species, S₃ = three species added. We used five replicates per treatment.

Parthenium hysterophorus (P) and suppressive plant species (S)				Suppressive plant species grown alone
PS ₀	PS ₁	PS ₂	PS ₃	
4P	4P/ 6M	4P/6L/6D	4P/6M/6L/ 6D	6M
	4P/6D	4P/6M/ 6L		6L
	4P/6L	4P/6M/ 6D		6D

the legume plants' biomass might be able to suppress the growth of parthenium weed (Safdar et al., 2016). Growth parameters measured were stem height, shoot diameter, root length, above- and belowground fresh biomass (AFB and BFB, respectively), above- and belowground dry biomass (ADB and BDB, respectively), and total fresh biomass of *P. hysterophorus*. Harvested seedlings were washed in water to remove soil materials and separated into below- and aboveground biomass components. Each component was dried in separate paper bags in an oven at 70 °C for 48 h (Khan et al., 2014). Stem height (from soil level to the tip of the tallest plant part) and root length were measured using a metric ruler. Shoot diameter (above the first two seedling leaves) and biomass were measured using digital callipers and an analytical balance, respectively.

2.3. Measurement of leaf chlorophyll content

Four young fresh leaves from three 50-day-old seedlings of *P. hysterophorus* were selected randomly per pot for analysis of total leaf chlorophyll content ("total Chl") as an index of seedling health in response to competition effects of legume plant(s). It was extracted according to Hiscox and Israelstam (1979) with some modification, i.e. 70 mg of *P. hysterophorus* leaves were immersed in 6 ml of dimethyl sulfoxide (DMSO) in a test-tube, and incubated at 65 °C for 12 h. Afterwards, the extract was made up to a total volume of 10 ml with DMSO. 3 ml of *P. hysterophorus* leaf chlorophyll extract was transferred into a microplate to determine absorbance or optical density (OD) of the sample. The OD of the blank liquid (DMSO) and samples was determined in a Synergy HTX Multi-Mode Microplate Reader at 663 nm and 645 nm. Prior to calculating total Chl, the OD of the blank was deducted from the OD readings of every sample. The equation (1) was used to calculate total Chl contents

(Hiscox and Israelstam, 1979). Respectively, A_{663} and A_{645} are absorbance readings at 663 nm and 645 nm.

$$Total\ Chl = 0.0202A_{663} + 0.00802A_{645} \tag{equation1}$$

2.4. Statistical data analysis

Stem height, shoot diameter, root length, total fresh biomass, AFB, ADB, BFB, BDB and total Chl of *P. hysterophorus* were compared across the test legume species planting combinations using one-way ANOVA. We verified normality and homogeneity of variance using a Shapiro-Wilk test and Levene's test respectively. The post-hoc Tukey-Kramer HSD test was used to separate the means at $p \leq 0.05$. The statistical software used was Origin (2013) version 9.0 SR1 at a significance level of $\alpha = 0.05$.

3. Results

Parthenium hysterophorus growth was more reduced when it was grown with *L. purpureus* in all combinations compared with the two other legume species. *Parthenium hysterophorus* seedlings had lower stem height, root length, shoot diameter, and biomass in mixtures than when grown in monoculture. The stem height ($F_{(7, 32)} = 9.41, p < 0.0001$), root length ($F_{(7, 32)} = 2.78, p = 0.0224$), and shoot diameter ($F_{(7, 32)} = 20.01, p < 0.0001$) of *P. hysterophorus* seedlings grown with legume plants differed significantly between the number of intercropped legume species (Fig. 1). The stem height of *P. hysterophorus* seedlings was 77% shorter when grown in combination with three legume species than when grown with one or two species, and in monoculture. Also, the stem height was >60% shorter when grown with one (*L. purpureus*) or two

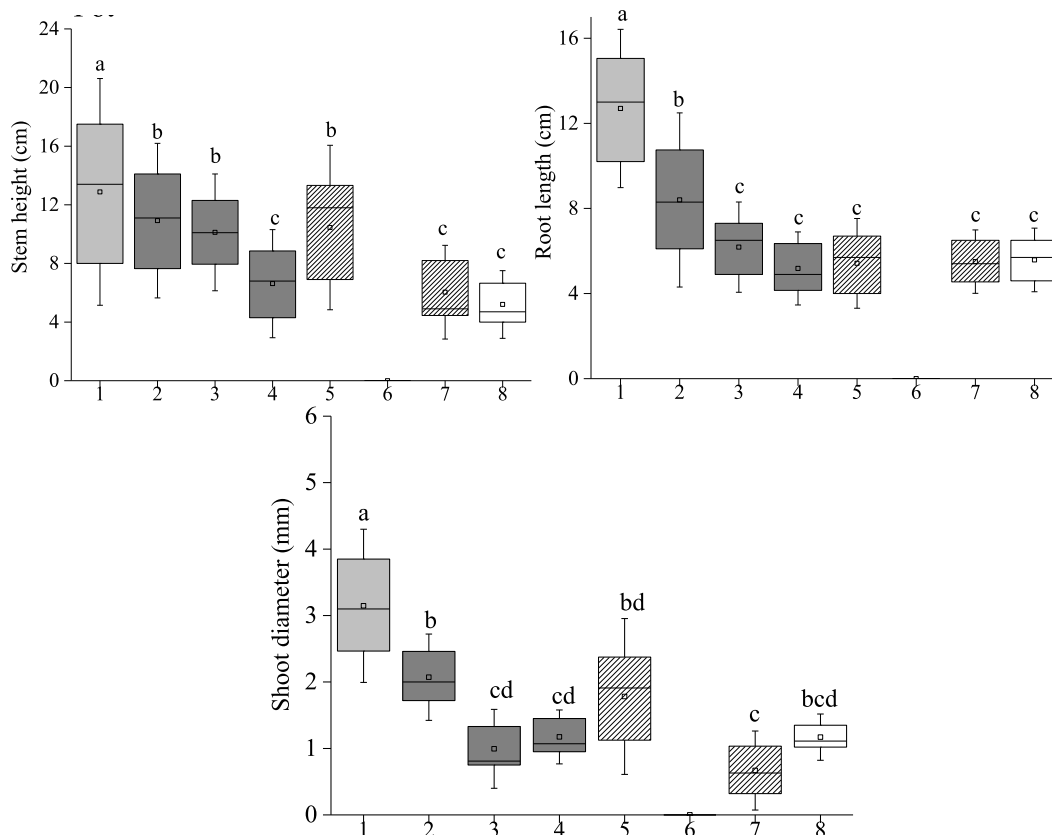


Fig. 1. Mean (\pm SE) stem height, root length, and shoot diameter of *Parthenium hysterophorus* seedlings when grown alone (light grey box), and with one (dark grey boxes), two (dashed boxes) or three (white box) suppressive plant species. Boxplots show the mean (square within boxes), 25% and 75% quartile ranges, and whiskers show standard deviations. Boxes with dissimilar letters are significantly different based on Tukey's HSD test at $p \leq 0.05$. Numbers 1–8 represent P, PM, PD, PL, PMD, PML, PLD, PMDL, where P = *Parthenium hysterophorus*, M = *Medicago sativa*, D = *Desmodium intortum*, and L = *Lablab purpureus*. *Parthenium hysterophorus* seedlings in planting mixture PML did not grow.

(*L. purpureus* and *D. intortum*) legume species than when grown alone or with *M. sativa* (Fig. 1). *Parthenium hysterophorus* had >50% shorter root length when grown with *L. purpureus* and/or *D. intortum* than when grown in monoculture or with *M. sativa* (Fig. 1). When grown with all three legume plant species (*L. purpureus*, *D. intortum*, and *M. sativa*), *P. hysterophorus* root length was 64% shorter than when grown with one or two species, and in monoculture. Further, when *P. hysterophorus* seedlings were grown with *L. purpureus* in any combination the shoot diameter was reduced by >62% compared with other legume plant species and in monoculture.

Mean AFB and ADB of *P. hysterophorus* seedlings differed significantly between planting diversity (AFB: $F_{(7, 32)} = 13.99, p < 0.0001$, ADB: $F_{(7, 32)} = 10.33, p < 0.0001$, Fig. 2). Also, mean BFB and BDB was significantly different between different planting diversity (BFB: $F_{(7, 32)} = 22.78, p < 0.0001$, BDB: $F_{(7, 32)} = 15.94, p < 0.0001$, Fig. 3). *Parthenium hysterophorus* AFB and ADB were >53% lower when grown with legume species in either combination than when it was grown alone or with *M. sativa* only. Moreover, *P. hysterophorus* BFB was >55% lower when grown with legume species in planting mixtures except when grown with *M. sativa* alone (Fig. 3). Additionally, BDB was >55% lower when the invasive was grown in mixture with *L. purpureus* than when it was grown with other species.

Total leaf chlorophyll content (Chl) of *P. hysterophorus* differed

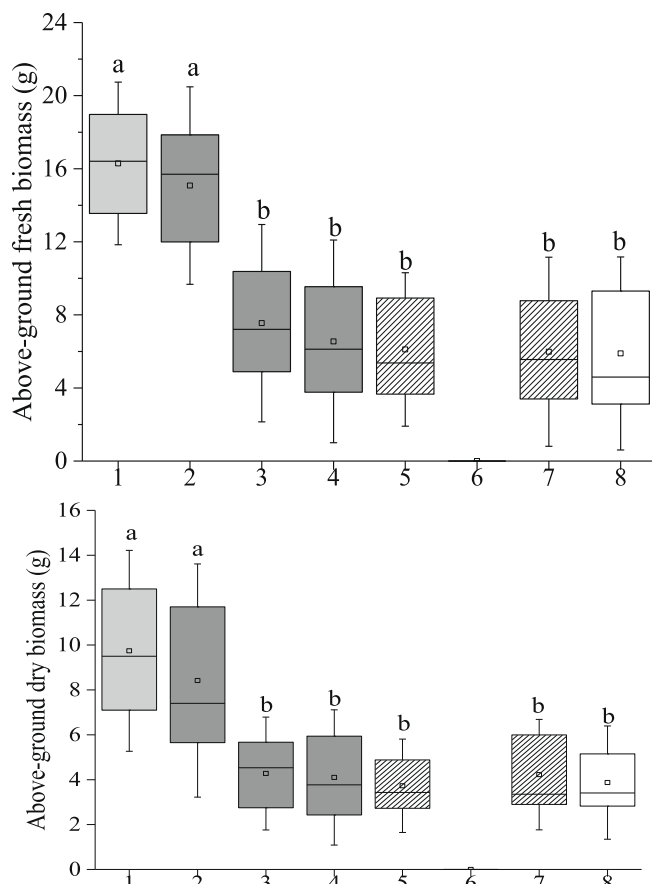


Fig. 2. Mean (\pm SE) above-ground fresh and dry biomass of *Parthenium hysterophorus* seedlings when grown alone (light grey box), and with one (grey boxes), two (dashed boxes) or three (white box) suppressive plant species. Boxplots show the mean (square within boxes), 25% and 75% quartile ranges, and whiskers show standard deviations. Boxes with dissimilar letters are significantly different based on Tukey's HSD test at $p \leq 0.05$. Numbers 1–8 represent P, PM, PD, PL, PMD, PML, PLD, PMDL, where P = *Parthenium hysterophorus*, M = *Medicago sativa*, D = *Desmodium intortum*, and L = *Lablab purpureus*. *Parthenium hysterophorus* seedlings in planting mixture PML did not grow.

significantly across legume plant species planting mixture ($F_{(4, 20)} = 26.87, p < 0.0001$, Fig. 4). Test plant species affected *P. hysterophorus* Chl negatively when grown with one (except *M. sativa*), two or three legume plant species. *Parthenium hysterophorus* Chl was reduced by > 75% when grown with three legume species than when it was grown in other mixtures. However, *P. hysterophorus* Chl was 84% lower when grown with *L. purpureus* alone than when it was grown in monoculture, with *M. sativa* or *D. intortum* alone.

4. Discussion

Our results show that the tested legume plant species demonstrate strong suppressive abilities against *P. hysterophorus* growth. The growth of *Parthenium hysterophorus* seedlings was negatively impacted by these legume forage species, particularly when the latter were in mixtures. This corroborates well with the findings of Khan et al. (2013), Shabbir et al. (2013), and Zheng et al. (2015). Further, the study reveals that *L. purpureus* was the primary species responsible for suppression of *P. hysterophorus* growth because the invasive growth parameters were lower across planting mixtures with *L. purpureus*. This could be due to *L. purpureus*'s ability of forming an extensive ground cover, broad leaves, and many branches which might have prevented *P. hysterophorus* seedlings from obtaining enough sunlight for photosynthesis and other nutrients for growth and development. In contrast, in mixtures that did not contain this species, little or no significant suppressive effect was observed. For instance, in planting combinations PMDL, PML, PDB, and PL, *Parthenium* weed seedlings displayed a lower biomass, stem height and root length. This finding is similar to that of Khan et al. (2013) which concluded that *L. purpureus* suppressed *P. hysterophorus*'s growth in field plots.

In our experiment, the dense ground cover and/or broad leaves of *L. purpureus* and *D. intortum* shaded the juvenile seedlings of *P. hysterophorus* and likely reduced their growth due to their structural features. In addition to forming an extensive ground cover, *L. purpureus* and *D. intortum* also exhibited rapid growth, higher stem height, strong root systems and biomass which may have enhanced their suppressive effects. Thus, we suggest that management approaches to control *Parthenium* weed using suppressive forage species should target the seedling growth stage which is the most vulnerable. While *D. intortum* has been recommended for conservation as ground cover and pasture (Maina et al., 2006), we showed that it can also be used to control *P. hysterophorus*, particularly when mixed with legume fodder plant species with strong suppressive abilities. Further, we highlight that in croplands biological control through suppressive plants is an approach with potential for managing *P. hysterophorus* (Khan et al., 2013).

Furthermore, our results showed that with increasing density of the test species *D. intortum*, *L. purpureus*, and *M. sativa* in pots, growth suppression of test species was increased against *Parthenium* weed. *Parthenium hysterophorus* stem height, root length, shoot diameter, biomass and leaf chlorophyll content decreased accordingly. This decrease followed a gradient of effectiveness, i.e. the most effective plant species were *L. purpureus* > *D. intortum* > *M. sativa*, with little evidence that *M. sativa* alone exerted a suppressive effect against *P. hysterophorus*. However, in order to increase the suppressive effect of these legume fodder plants, both the more and less suppressive legume species can be used in a mixture as rehabilitative species in suppressing *P. hysterophorus*. Their combinations can further increase croplands resilience against invasions of *P. hysterophorus* (Christina et al., 2015; Cummings et al., 2012). Moreover, our findings highlight the importance of keeping cultivated lands from becoming impoverished by maintaining the density of suppressive plant species in our habitats.

Our results suggested that suppressive plant species seeded together with *P. hysterophorus* in communities of high species diversity may suppress the invasive, which is in accordance with studies that found higher plant diversity suppressed invasive plant species in cultivated pastures (Khan et al., 2013; Knops et al., 1999; Shabbir et al., 2013; Tracy et al.,

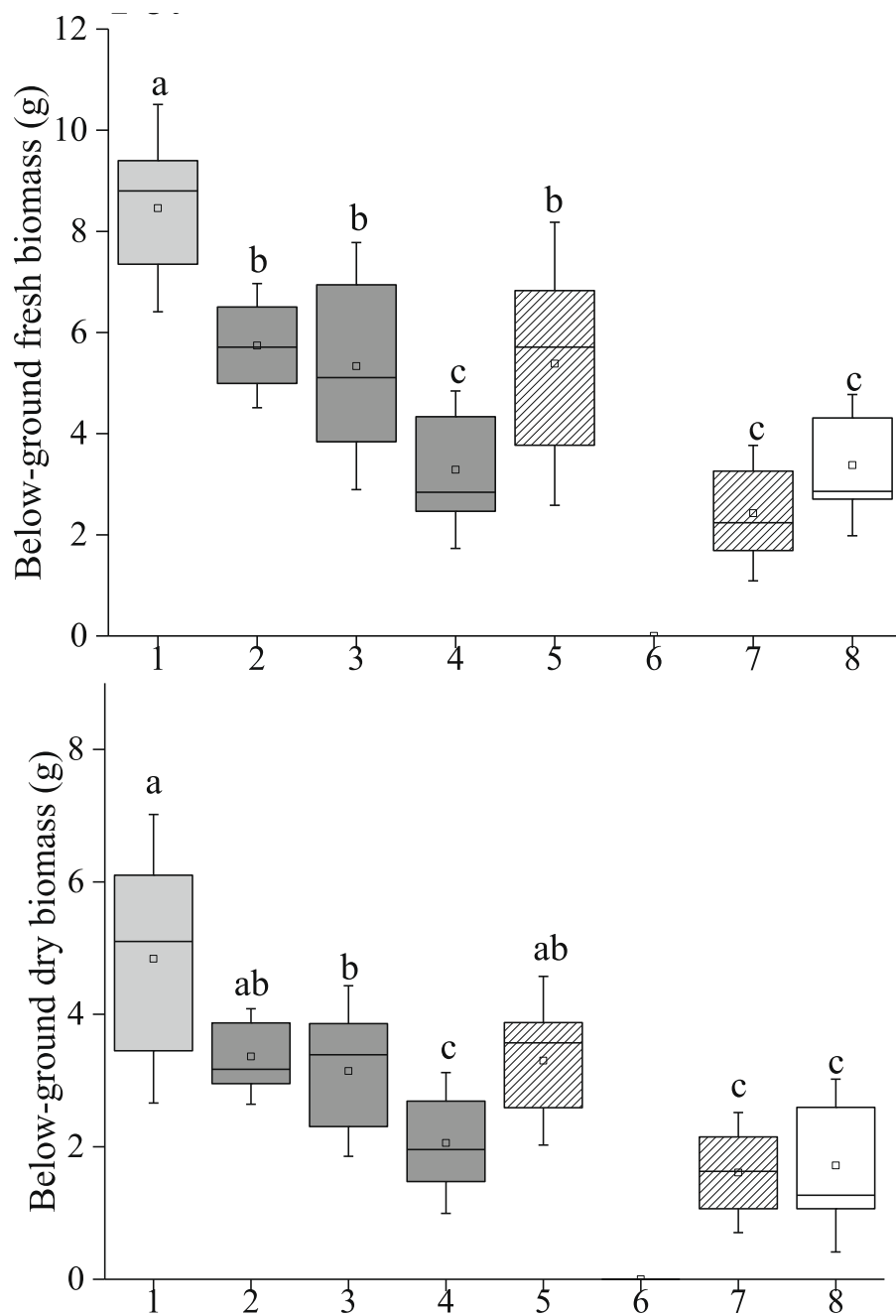


Fig. 3. Mean (\pm SE) below-ground fresh and dry biomass of *P. hysterophorus* seedlings when grown alone (light grey box), and with one (grey boxes), two (dashed boxes) or three (white box) suppressive plant species. Boxplots show the mean (square within boxes), 25% and 75% quartile ranges, and whiskers show standard deviations. Boxes with dissimilar letters are significantly different based on Tukey's HSD test at $p \leq 0.05$. Numbers 1–8 represent P, PM, PD, PL, PMD, PML, PLD, PMDL, where P = *P. hysterophorus*, M = *M. sativa*, D = *D. intortum*, and L = *L. purpureus*. *Parthenium hysterophorus* seedlings in planting mixture PML did not grow.

2004). For instance, Khan et al. (2013) found that *Setaria incrassata* (Hochst.) Hack. cv. Inverell, *Cenchrus ciliaris* L. cv. Gayndah, *Panicum maximum* Jacq., and *Eulalia aurea* (Bory) Kunth at higher abundance suppressed *P. hysterophorus* growth. Also, Ammond and Litton (2012) showed that the invasive grass *Megathyrsus maximus* Jacq. stem height and biomass were reduced when planted with the suppressive species *Myoporum sandwicense* (A.DC) Grey, *Dodonaea viscosa* (L.) Jacq., and *Plumbago zeylanica* L. So, management of *P. hysterophorus* by increasing density of suppressive legume fodder plant species might ensure "ecosystem" health and stability in a planted pasture.

Moreover, since *P. hysterophorus* causes allergic reactions in humans and animals in cases of skin contact during manual weeding or livestock handling, controlling the invasive using suppressive legume fodder plants would not require touching or uprooting it. This approach reduces health risks to humans, livestock or wildlife. In sub-Saharan Africa where

people and animals are threatened by *P. hysterophorus* this represents a low-cost and sustainable management method for controlling the invasive tendencies of this plant species. While suppressive plants have been used in other countries in Asia to suppress *P. hysterophorus* (Khan et al., 2013; Shabbir et al., 2013; Adkins and Shabbir, 2014) they have never previously been tested in most of sub-Saharan Africa. Our selected legume plant species, which are weed competitor and drought tolerant could enhance their suppressive fitness in mixture over *P. hysterophorus* (Amole et al., 2013; Maina et al., 2006). Their non-target impacts on the environment are also less severe compared with other biological control agents such as insects or microorganisms. Nonetheless, this technique must be complemented with other management methods because parthenium weed cannot be controlled easily by a single method *per se* (Shabbir et al., 2013; Ojja et al., 2019b). Besides, selection of suppressive legume plant species must consider the benefits and traits, which

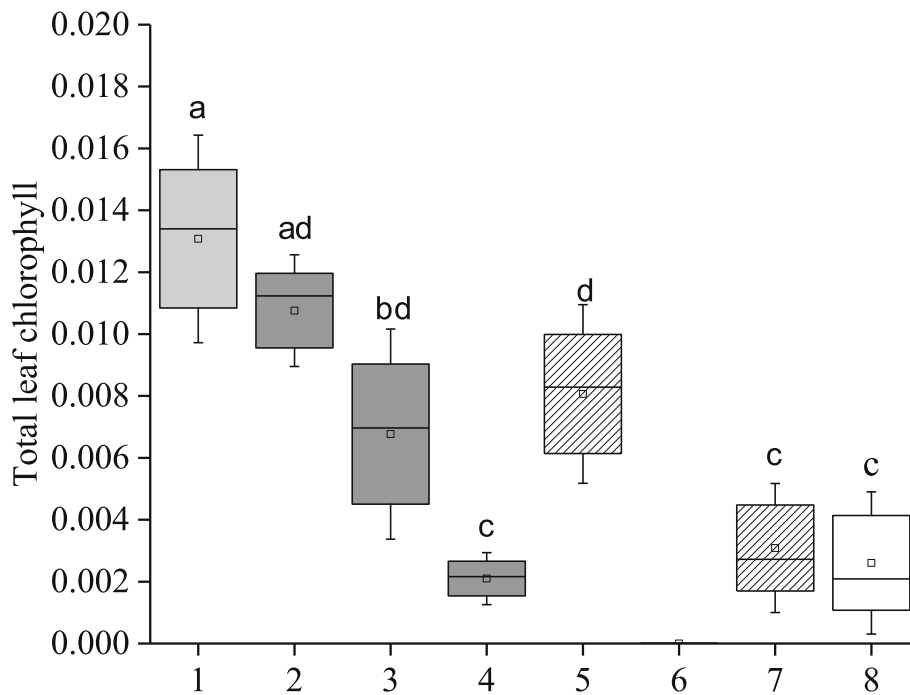


Fig. 4. Mean (\pm SD) total chlorophyll content of *Parthenium hysterophorus* seedlings when grown alone (light grey box), and with one (grey boxes), two (dashed boxes) or three (white box) suppressive plant species. Boxplots show the mean (square within boxes), 25% and 75% quartile ranges, and whiskers show standard deviations. Boxes with dissimilar letters are significantly different based on Tukey's HSD test at $p \leq 0.05$. Numbers 1–8 represent P, PM, PD, PL, PMD, PML, PLD, PMDL, where P = *Parthenium hysterophorus*, M = *Medicago sativa*, D = *Desmodium intortum*, and L = *Lablab purpureus*. *Parthenium hysterophorus* seedlings in planting mixture PML did not grow.

enhance an ecosystem's resilience to invasion. However, the use of non-native plant species is not advised for protected areas or intact natural vegetation to control alien invasions.

5. Conclusions

This study has indicated that *P. hysterophorus* can be suppressed by legume forage species at high density, thus, we recommend that local communities should be empowered with knowledge about the suppressive potential of legume plants and on how to facilitate the planting of these fodder species in croplands or heavily disturbed rangelands. However, a coordinated national strategy and policy to mitigate *P. hysterophorus* is essential to ensure effective management of the invasive in sub-Saharan Africa, particularly in Tanzania. Since our study is limited to germination and early growth stage of *P. hysterophorus*, future studies should test suppressive abilities of these legume species in already established invasive stands. Additionally, as this study was conducted under controlled environments, we advise further studies to be conducted under field conditions. Moreover, if ecologists or invasion biologists aim to control any invasive using alien plant species, they should first assess and quantify their impacts at different levels of ecological complexity to ensure that they will not become invasive in the future.

Declaration of interest statement

The author declares that there is no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

This work is all original research carried out by the author. No part of the research has been published in any form elsewhere. The manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The author thanks Prof Anna C Treydte, Dr Sarah J Arnold and Dr Kafula Chisanga for providing input to improve the manuscript. We also, thank R. Kilewa from Agricultural Division at Tropical Pesticide Research Institute for providing *P. hysterophorus* seeds, Dr P. Venkataramana in the Department of Sustainable Agriculture, Biodiversity and Ecosystem Management at NM-IST for providing *L. purpureus* seeds, and NM-AIST community for their support. This study was funded by the World Bank through its African Centre of Excellence, "Centre for Research, Agricultural advancement, Teaching Excellence and Sustainability in Food and Nutritional Security (CREATES)", in the School of Life Sciences and Bioengineering at the Nelson Mandela Institution of Science and Technology (NM - AIST), Arusha, Tanzania. The Idea Wild supported us with research equipment.

References

- Ammond, S.A., Litton, C.M., 2012. Competition between native Hawaiian plants and the invasive grass *Megathyrsus maximus*: implications of functional diversity for ecological restoration. *Restor. Ecol.* 20, 638–646. <https://doi.org/10.1111/j.1526-100X.2011.00806.x>.
- Amole, T.A., Oduguwa, B.O., Shittu, O., Famakinde, A., Okwelum, N., Ojo, V.O.A., Dele, P.A., Idowu, O.J., Ogunlolu, B., Adebisi, A.O., 2013. Herbage yield and quality of *Lablab purpureus* during the late dry season in western Nigeria. *Slovak J. Anim. Sci.* 46, 22–30.
- Axmacher, J.C., Sang, W., 2013. Plant invasions in China – challenges and chances. *PLoS One* 8, e64173. <https://doi.org/10.1371/journal.pone.0064173>.
- Christina, M., Rouifed, S., Puijalón, S., Vallier, F., Meiffren, G., Bellvert, F., Piola, F., 2015. Allelopathic effect of a native species on a major plant invader in Europe. *Sci. Nat.* 102 <https://doi.org/10.1007/s00114-015-1263-x>.

- Cummings, J.A., Parker, I.M., Gilbert, G.S., 2012. Allelopathy: a tool for weed management in forest restoration. *Plant Ecol.* 213, 1975–1989. <https://doi.org/10.1007/s11258-012-0154-x>.
- Debela, E., Tolera, A., Eik, L.O., Salte, R., 2012. Condensed tannins from *Sesbania sesban* and *Desmodium intortum* as a means of *Haemonchus contortus* control in goats. *Trop. Anim. Health Prod.* 44, 1939–1944. <https://doi.org/10.1007/s11250-012-0160-y>.
- Gioria, M., Le Roux, J.J., Hirsch, H., Moravcová, L., Pyšek, P., 2019. Characteristics of the soil seed bank of invasive and non-invasive plants in their native and alien distribution range. *Biol. Invasions* 21, 2313–2332. <https://doi.org/10.1007/s10530-019-01978-y>.
- Hiscox, J.T., Israelstam, G.F., 1979. A method for the extraction of chlorophyll from leaf tissue without maceration. *Can. J. Bot.* 57, 1332–1334.
- Khan, N., O'Donnell, C., George, D., Adkins, S.W., 2013. Suppressive ability of selected fodder plants on the growth of *Parthenium hysterophorus*. *Weed Res.* 53, 61–68. <https://doi.org/10.1111/j.1365-3180.2012.00953.x>.
- Khan, N., Shabbir, A., George, D., Hassan, G., Adkins, S.W., 2014. Suppressive fodder plants as part of an integrated management program for *Parthenium hysterophorus* L. *Field Crop. Res.* 156, 172–179. <https://doi.org/10.1016/j.fcr.2013.11.003>.
- Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E., Groth, J., 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol. Lett.* 2, 286–293. <https://doi.org/10.1046/j.1461-0248.1999.00083.x>.
- Lei, Y., Xu, Y., Hettenhausen, C., Lu, C., Shen, G., Zhang, C., Li, J., Song, J., Lin, H., Wu, J., 2018. Comparative analysis of alfalfa (*Medicago sativa* L.) leaf transcriptomes reveals genotype-specific salt tolerance mechanisms. *BMC Plant Biol.* 18, 1–14. <https://doi.org/10.1186/s12870-018-1250-4>.
- Li, W., Luo, J., Tian, X., Soon Chow, W., Sun, Z., Zhang, T., Peng, S., Peng, C., 2015. A new strategy for controlling invasive weeds: selecting valuable native plants to defeat them. *Sci. Rep.* 5, 1–11. <https://doi.org/10.1038/srep11004>.
- Maass, B.L., Knox, M.R., Venkatesha, S.C., Angessa, T.T., Ramme, S., Pengelly, B.C., 2010. *Lablab purpureus*—a crop lost for Africa? *Trop. Plant Biol.* 3, 123–135. <https://doi.org/10.1007/s12042-010-9046-1>.
- Madzonga, Z., Mogotsi, K., 2014. Production, harvest and conservation of *Lablab purpureus* (L) sweet forage in semi arid livestock regions: the case of east central Botswana. *J. Anim. Plant Sci.* 24, 1085–1090.
- Maina, J.M., Mburu, M.W.K., Mureithi, J.G., Gachene, C.K.K., Mburu, J.N., Ngugi, J.N., Kimemia, J.K., Kabete, K., 2006. Evaluation of legumes as cover crops for soil and weed management in smallholder coffee cropping systems in central Kenya. In: *Proc. 10th KARI Bien. Sci. Conf.*, “Responding to Demands and Opportunities through Innovative Agricultural Technologies, Knowledge and Approaches.” Presented at the 10th KARI Bien. Sci. Conf., 2 - 17 November 2006, Nairobi, Kenya, p. 8.
- Ojija, F., Manyanza, N.M., 2021. Distribution and impact of invasive *Parthenium hysterophorus* on soil around Arusha national park. *Ecol. Evol. Biol.* 6, 21–27. <https://doi.org/10.11648/j.eeb.20210601.13>.
- Ojija, F., Arnold, S.E.J., Treydte, A.C., 2021. Plant competition as an ecosystem-based management tool for suppressing *Parthenium hysterophorus* in rangelands. *Rangelands* 41, 239–243. <https://doi.org/10.1016/j.rala.2020.12.004>.
- Ojija, F., Arnold, S.E.J., Treydte, A.C., 2019a. Impacts of alien invasive *Parthenium hysterophorus* on flower visitation by insects to co-flowering plants. *Arthropod-Plant Interact.* 13, 719–734. <https://doi.org/10.1007/s11829-019-09701-3>.
- Ojija, F., Arnold, S.E.J., Treydte, A.C., 2019b. Bio-herbicide potential of naturalised *Desmodium uncinatum* crude leaf extract against the invasive plant species *Parthenium hysterophorus*. *Biol. Invasions* 21, 3641–3653. <https://doi.org/10.1007/s10530-019-02075-w>.
- Perkins, L.B., Leger, E.A., Nowak, R.S., 2011. Invasion triangle: an organizational framework for species invasion. *Ecol. Evol.* 1, 610–625. <https://doi.org/10.1002/ece3.47>.
- Pratt, C.F., Constantine, K.L., Murphy, S.T., 2017. Economic impacts of invasive alien species on African smallholder livelihoods. *Glob. Food Secur.* 14, 31–37. <https://doi.org/10.1016/j.gfs.2017.01.011>.
- Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M., Kirschner, J., 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53, 131–143. <https://doi.org/10.2307/4135498>.
- Safdar, M.E., Tanveer, A., Khaliq, A., Maqbool, R., 2016. Critical competition period of parthenium weed (*Parthenium hysterophorus* L.) in maize. *Crop Protect.* 80, 101–107. <https://doi.org/10.1016/j.cropro.2015.11.002>.
- Schuster, M.J., Wragg, P.D., Reich, P.B., 2018. Using revegetation to suppress invasive plants in grasslands and forests. *J. Appl. Ecol.* 55, 2362–2373. <https://doi.org/10.1111/1365-2664.13195>.
- Shabbir, A., Dhileepan, K., O'Donnell, C., Adkins, S.W., 2013. Complementing biological control with plant suppression: implications for improved management of Parthenium weed (*Parthenium hysterophorus* L.). *Biol. Contr.* 64, 270–275. <https://doi.org/10.1016/j.biocontrol.2012.11.014>.
- Shabbir, A., Dhileepan, K., Zalucki, M.P., Adkins, S.W., 2019. Biological control under a changing climate: the efficacy of the parthenium weed stem-galling moth under an atmosphere enriched with CO₂. *Biol. Contr.* 139, 1–19. <https://doi.org/10.1016/j.biocontrol.2019.104077>.
- Tanveer, A., Khaliq, A., Ali, H.H., Mahajan, G., Chauhan, B.S., 2015. Interference and management of parthenium: the world's most important invasive weed. *Crop Protect.* 68, 49–59. <https://doi.org/10.1016/j.cropro.2014.11.005>.
- Terblanche, C., Nänni, I., Kaplan, H., Strathie, L.W., McConnachie, A.J., Goodall, J., Van wilgen, B., 2016. An approach to the development of a national strategy for controlling invasive alien plant species: the case of *Parthenium hysterophorus* in South Africa. *Bothalia* 46, 1–11. <https://doi.org/10.4102/abc.v46i1.2053>.
- Tracy, B.F., Renne, L.J., Gerrish, J., Sanderson, M.A., 2004. Effects of plant diversity on invasion of weed species in experimental pasture communities. *Basic Appl. Ecol.* 5, 543–550. <https://doi.org/10.1016/j.baae.2004.08.007>.
- USDA, N.R.C.S., 2012. *Kuiaha' Desmodium Intortum* (Mil.) Urb. USDA natural resource conservation service, Hoolehua plant materials center, Hoolehua, Hawaii.
- Vilà, M., Weiner, J., 2004. Are invasive plant species better competitors than native plant species? - evidence from pair-wise experiments. *Oikos* 105, 229–238. <https://doi.org/10.1111/j.0030-1299.2004.12682.x>.