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Assessing the competitive ability of the invader *Senna obtusifolia* with coexisting natives species under different water stress regimes

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Competitive ability

Invasive species

Sensitivity index

Greenhouse

ABSTRACT

Invasive species tend to pose a threat to ecosystem biodiversity, functioning, and ecosystem service provision. This study was conducted in Burkina Faso to assess the competitiveness of an invasive species *Senna obtusifolia* that is a less palatable legume plant in West African Sahelian rangelands. To address the research hypothesis that the recurrent drought in the Sahel results in *S. obtusifolia* being more competitive in the land invasion, we conducted an interspecific competition involving *S. obtusifolia* and 3 herbaceous species (*Andropogon gayanus*, *Chamaecrista mimosoides*, and *Pennisetum pedicellatum*) in a greenhouse experiment under four water stress regimes using a replacement series design. The height and biomass of each species were measured throughout four months experiment. In the severe water regime, *S. obtusifolia* was the most sensitive to water deficit while the 3 other species were found to be resistant. In addition, in all water regimes, the aggressivity index revealed that *S. obtusifolia* was less competitive than the grass species *A. gayanus* and *P. pedicellatum*. Further, the study discovered that drought in the Sahel made *S. obtusifolia* more vulnerable than the other species. Hence the invasion of Sahelian rangelands by *S. obtusifolia* could be favored by overgrazing that reduces fodder species' dominance and competitiveness. Good management of sahelian rangelands by controlling grazing could help to reduce *S. obtusifolia* invasion and provide more fodder for livestock.

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1 Introduction

Invasive plant species represent a major threat to biodiversity and the ecosystem (Vilà et al. 2011; Shackleton et al. 2019; Bogale and Tolossa 2021). They directly affect native plant communities by causing biodiversity loss, ecosystem change, and reduction in ecosystem services (Wardle et al. 2011; Barros et al. 2020). Previous studies showed that the success of these species depends on several abiotic and biotic factors (Martin and Coetzee 2014; Leal et al. 2022) as well as on biological traits related to their ability to spread such as copious seed production, high germination, survival rates, efficient dispersal and good competitive ability (Wickert et al. 2017; Yu et al. 2018; El-Barougy et al. 2020).

In general, abiotic factors such as water, light, and nutrients for which plants compete in the process of growth and development (Wang et al. 2012; Gao et al. 2021) may also influence the intensity of competition (Yu et al. 2018) when these resources are present in limited quantity between nearby individuals with a common requirement (Bastiani et al. 2016; Zhou et al. 2018). With ongoing climate change impacts, water availability could decrease in severe drought conditions and this may also facilitate the competitive ability and success of invasive species (Diez et al. 2012; Paudel et al. 2018; Barros et al. 2020). For example, in West African Sahel rangeland, the arid climate characterized by severe drought (Issaharou-Matchi et al. 2016) has favoured the proliferation of invasive plant species due to their high physiological performance (Oliveira et al. 2014; Duell et al. 2021). In this situation, the species with functional traits that are consistent with high resource acquisition may overcome the congener and become invasive (Funk et al. 2016; Broadbent et al. 2018; Kumar and Garkoti 2021). These species often become a disturbance or even harm to their environment. During the last decades, many species have been listed in the national biodiversity report of Burkina Faso as invasive species and their proliferation contributes to the degradation of ecosystems (SP/CONEDD 2010, 2014). This list includes *S. obtusifolia* Linn, a herbaceous legume species belonging to the Fabaceae family commonly known as sicklepod. This species, with a 1.5–2.5 m height size (Holm et al. 1997), represent a serious threat to fields and rangelands in many tropical and subtropical regions (Palmer and Pullen 2001; Sosnoskie et al. 2021). *S. obtusifolia* has copious seed production and can germinate and grow under a wide range of environmental conditions (Retzinger 1984; Chaves Neto et al. 2020). Under favorable conditions of its development, *S. obtusifolia* can displace coexisting native species and form dense monospecific stands. This situation can lead to significant ecological changes (Mackey et al. 1997).

It is widespread in the Sahelian zone of Burkina Faso (Kiema et al. 2008, 2012; Kadeba et al. 2015) where rainfall (around 300 to 600 mm annually) is irregular and limited to only three or four months followed by a long drought period (Kiema et al. 2014).

In fact, *S. obtusifolia* has become an invader of rangelands and can completely dominate grass species, eradicate rangeland growth, and exclude livestock leading to unproductive monoculture in semi-arid rangelands (Palmer and Pullen 2001; Gebreyesus 2017). It is also known as “bush pasture” due to the damage it causes to rangelands (Chaves et al. 2002). Moreover, owing to the presence of toxic substances in its green leaves (Peres et al. 2010; Augustine et al. 2020) livestock do not graze this species in its green stage (Kiema et al. 2012). Therefore, the invasion of *S. obtusifolia* constitutes a threat to rangelands as well as to livestock which is the main source of household income in rural areas and contributes 18% of Burkina Faso’s Gross Domestic Product (MRA 2010).

Despite its high proliferation in Burkina Faso, *S.obtusifolia* has been the subject of very few studies. These studies are mainly focused on its nutritional and medicinal potential (Nacambo et al. 2021, Zare et al. 2022) and its impact on fodder species availability (Ouedraogo et al. 2021). No studies on the invasive performance of the species at the national level have been carried out yet.

To assess the competitive ability of *S. obtusifolia* and its sensitivity to water deficit in a controlled environment, three palatable species including *Chamaecrista mimosoides* L. (an annual legume), *Andropogon gayanus* Kunth (perennial grass) and *Pennisetum pedicellatum* Trin (annual grass) were used each in a mixture with *S. obtusifolia* in a greenhouse experiment under water deficit conditions. *Chamaecrista mimosoides* L. is a prostrate leguminous herb in open grasslands along roads and paths (Bargali and Bargali 2016; Li et al. 2022). It is an erect annual herb up to a meter long, sometimes woody at the base with many slender, pubescent branches. It is not very common and grows widely on grassy hills slopes in the wild form. It is spread over the entire climatic range of Burkina Faso and is considered as highly palatable for livestock (Schmidt-Groh et al. 2019). *A. gayanus* kunth and *P. pedicellatum* Trin particularly have become abundant in some areas. They are regarded among the important abundant grasses in Burkina Faso because they have high reproductive output and high dispersal ability (Grice et al. 2013; dos Santos et al. 2022; Ojo et al. 2022). Moreover, *A. Gayanus* is a C_4 perennial tufted or bunch grass that grows up to 3 m high (Baruch 1994) and possesses several positive characteristics: It exhibits higher photosynthetic efficiency and nutrient uptake (Setterfield et al. 2010; Zhang et al. 2022)owing to its ease of establishment, fast growth rate, high productivity, resilience and long growing season (Adams and Setterfield 2013). Also, *P. pedicellatum,* a fodder species widely spread in the Sudan and Sahel, is a herbaceous annual C_4 grass that grows upright up to 40-150cm in height depending on the environmental conditions where it grows. It produces high biomass that greatly improves ground cover which in turn reduces soil erosion by controlling runoff and soil loss (Issaharou-Matchi et al. 2016; Beyene 2021). These characteristics may suggest that these species may be good competitors in a low-pressure grazing system. These plants (grasses and legumes) commonly co-occur in many habitats to improve forage yield and quality (Eisenhauer and Scheu 2008). They also represent important variations in photosynthetic and growth rate physiology, morphology, and canopy architecture that may contribute to the difference in competitive ability (Roush and Radosevich 1985; Petruzzelli's et al. 2021). Furthermore, the competitive ability between legumes and non-legumes (grasses) for resources has already been tested by several authors (DeBoer et al. 2020; Grüner et al. 2020; Khatiwada et al. 2020). To achieve the purpose of the study, single container experiments were conducted to determine (i) the effect of water deficit on above-ground biomass and height of each species; (ii) the effect (in terms of biomass loss) and the nature (intra-interspecific competition) of the competition among the focus species underwater different regimes; (iii) the intensity of the competition under different water regimes.

2 Materials and Methods

2.1 Study area

Seeds of the two annual legumes (*S. obtusifolia* and *C. mimosoides*) and two grass species *A.gayanus* (perennial grass) and *P.pedicellatum* (annual grass) were collected from the rangelands of the Sahelian zone of Burkina Faso, particularly in the Séno province whose capital town is Dori (figure 1). The province, with an estimated population of 385,900 inhabitants (INSD 2019), is cohabited by several ethnic groups including Fulani, Fulcé, Mossi, Gourmantché, Bella, Rimaïbé, etc. (Kiema et al. 2012). Agriculture and husbandry are the main socio-economic activities of the study area (Ayantunde et al. 2020). The province falls within the Sahelian zone of Burkina Faso which is characterized by average rainfall between 400 and 600 mm/year and average annual temperature ranges between 22°C to 37°C. Vegetation in this zone is dominated by desert grasslands and scrub (Kiema et al. 2014). The woody layer is dominated by *Combretum glutinosum* Perr. ex DC., *Balanites aegyptiaea* (L.) Del., *Acacia tortilis* subsp. *Acacia tortilis* (Forssk.) Hayn,

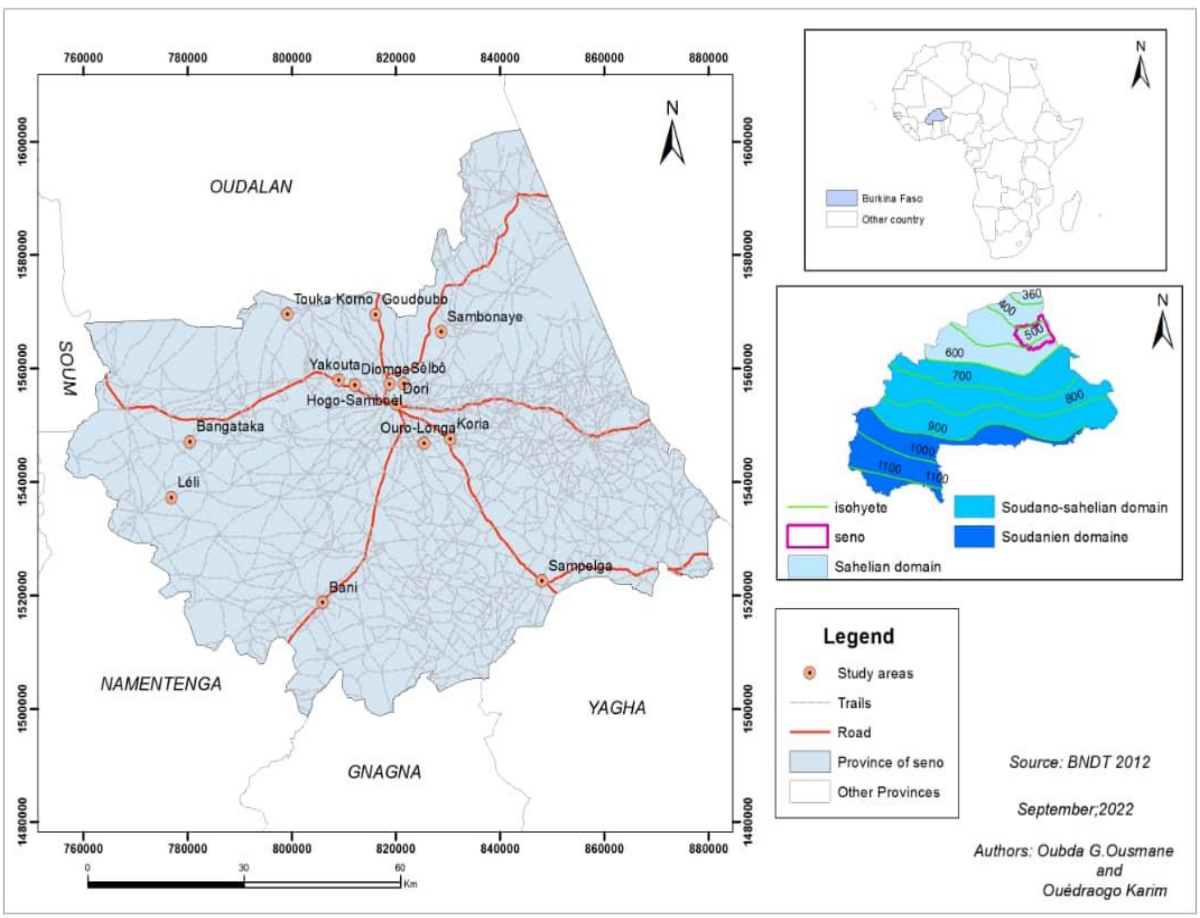


Figure 1 Geographical situation of the study area

Faidherbia albida (Delile) A. Chev., (Fontes and Guinko 1995). The vegetation of the herbaceous layer remains mainly dominated by annual grasses and characteristic pasture grasses such as *Pennisetum pedicellatum* Trin., *Loudetia togoensis* (Pilg.) Hubb., *Triumfetta pentandra* A. Rich, *Achyranthes aspera* L., *Andropogon gayanus*, *Andropogon pseudapricus* Stapf, *Aristida mutabilis* Trin, *Senna obtusifolia* (L.) H.S. Irwin & Barneby, *Tephrosia pedicellata* Bak, *Acanthospermum hispidum* DC, *Schoenefeldia gracilis* Kunth; *Zornia glochidiata* C.Rchb. ex DC. (Kiema et al. 2014; Nacoulma et al. 2019). The pods containing seeds were harvested at maturity in mid-November directly from standing individuals to avoid infestation with soil and put into envelopes. The harvested seeds were stored in the laboratory at ambient temperature (25 to 30°C) for seven months from November 2018 to June 2019.

2.2 Experimental conditions

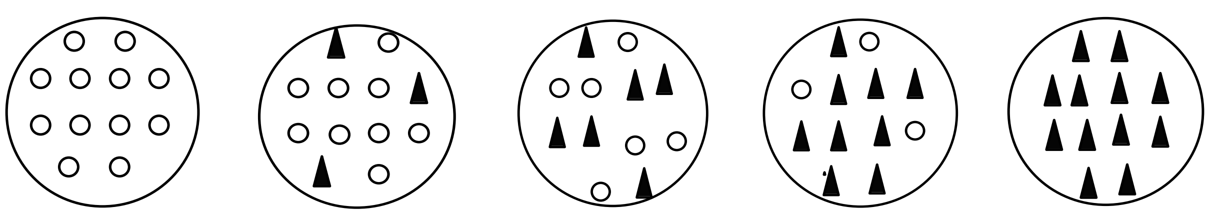
The experiment was conducted under greenhouse conditions at the National Forest Seed Center (12°24'-31°78'N and 01°28'-59°33'W) in Ouagadougou Burkina Faso. The average minimum and maximum temperatures within the greenhouse are 28.13°C and 36.3°C respectively while those in the open environment are 27.32°C and 34.76°C. The experiment (from laboratory to greenhouse) started on 22 June 2019 corresponding to the beginning of the rainy season in Burkina Faso and was completed on 07 September 2019 when the leaves of *S. obtusifolia* were almost yellowing. First of all, a substrate was prepared and it is composed of soil, sand, and manure in a ratio of 3:2:1. This was prepared by mixing 3-wheel barrows of soil, 2-wheel barrows of sand, and 1 wheelbarrow of manure. The complete substrate mixture was sterilized and from this 30 kg of the substrate was filled in a container with a 50 cm diameter and 25cm depth. The bottom of each container was carefully perforated to allow the excess water to drain after watering. To ensure that planting density would be enough to result in competition, laboratory studies were conducted before sowing. These studies consisted in lifting the tegumentary dormancy of the seeds by pre-treating them with acid and water. The first pre-treatment consisted of soaking the seeds of *P. pedicellatum* and *A. gayanus* in tap water for 24 hours. The second pre-treatment was immersion of seeds in 96% concentrated sulfuric acid (H_2SO_4), in this, *S. obtusifolia* seeds were treated for 5 minutes and *Chamaecrista mimosoides* seeds for 3 minutes. The acid-pretreated seeds were then washed with water for 15 minutes.

The germination rate was about 90% for all species. After two weeks of sowing in the greenhouse, an adjustment was carried out to obtain seedlings with similar sizes which 3; 6; 9, and 12 individuals in monoculture and 12 individuals per container in the appropriate proportions in a mixture (figure 2).

2.3 Experimental design

Among methods to investigate the competitive relationships between plants, the experiments in replacement series have been widely used since its introduction by De Wit (1960) where one species gradually replaces another in a mixture at constant overall density (in this study constant overall density was 12). This method allows the understanding of the competitive process between plants. In particular, its application includes an aspect of inter-and intraspecific interactions between wild plants (Solbrig et al. 1988; Savić et al. 2021). In order to assess the competitive ability of *S. obtusifolia*, this method was used to assess how one species growing in a mixture with another species can affect the performance of this one. The focus was to determine how *S. obtusifolia* responds in terms of biomass production when it competes with *A. gayanus*, *C. mimosoides*, and *P. pedicellatum*. Also, the variation of water regimes in the experiment aimed at understanding how differences in water availability may change the competitive relationship between *S. obtusifolia* and the target species. Each of the species in this experiment was grown in monoculture with 3:0; 6:0; 9.0 and 12:0 densities on one side. On the other side, *S. obtusifolia* was grown in a mixture with the other species in the proportion of 9:3; 6:6; 3:9 as shown in figure 2. A total of 25 containers/pots were used in the experiment, among these, 16 containers are in monoculture, and 9 containers are in mixed species planting. Each container was replicated five times giving a total of 80 containers in monoculture and 45 containers in mixed culture i.e. 125 pots per block. Further, the total plant density was twelve plants per container (60 plants m^{-2}). The appropriate combined proportion of *S. obtusifolia* would reflect the level of invasion of *S. obtusifolia* in the field.

For the water regime, a split-plot approach was used in a randomized complete block design to avoid the microclimatic



12:0 9:3 6:6 3:9 0:12

Figure 2 Schematic diagram of the replacement series (O circles represent *S.obtusifolia* and ▲triangular represent one of the 3 other species) effect. Four (04) blocks corresponding to four watering regimes were applied. The watering regime consisted of watering plants in each container every two days with a determined amount of water from the germination to the mature phenology stage. This quantity of water or volume of water (VW) varied progressively from one block to another according to the predefined level of stress. The applicable volume of water was determined by calculating the field capacity which is the mass of water remaining in the soil after a rapid drainage of 1 to 2 days. It is expressed as a percentage of the dry weight of the soil. A sample of dry soil placed in a container was first weighed to determine the dry weight (DWs) and then soaked in water to saturation. After 48 hours, the water infiltrated through the perforated bottom of the container. The soil was weighed again to determine its wet weight (WWs). Then the field capacity (FC) was determined in grams of water per gram of dry soil using the following formula (Veihmeyer and Hendrickson 1931):

$$\mathrm{FC} = \frac{\mathrm{WWs} - \mathrm{DWs}}{\mathrm{DWs}}$$

Where FC is the field capacity, WWs is the wet weight expressed in kg and DWs is the volume of dry soil which is expressed in kg.

The volume of water (VWs) for each regime is determined from the following formula VWs=VS*FC *X% with VWs being the volume of water. VS represents the volume of dry soil, FC is the field capacity, and X the portion corresponding to the level of water stress applied. This portion varies progressively from 25%; 50%; 75% and 100%. Thus 100% FC is the proportion of water irrigation in the control regime and the other three are considered stressed regimes depending on the amount of water irrigation. All blocks were under a plastic-covered greenhouse preventing rainwater infiltration. The water stress application at the end of germination consisted of watering all the plants regularly every two days in the water regimes until the end of the experiment.

2.4 Measured parameters

To characterize the effects of water regime and competition on the plants, the height and above-ground biomass of each plant species were measured. Generally, plant biomass and height have been used to provide information on the size and aggressiveness of a species which may determine its competitive ability (Radosevich 1987; Reeves et al. 2021). The height (cm) for each species was measured using a tape measure. Because of the difficulty of accurately separating the roots of individual plants in each pot for analysis and in particular for perennial grasses, only above-ground biomass was examined (Meekins and McCarthy 1999; Bolinder et al. 2002). When plants were in a vegetative state (50 days after planting), above-ground plant materials were cut at soil level and above-ground dry biomass of the plants was determined after drying in an oven at 65°C for 72 h using a precision balance (0.01g). These parameters provide a better understanding of the mechanism adopted by each species under conditions of water deficit combined with competition and thus help to evaluate species adaptation potential (Kagambèga et al. 2019).

2.4.1 Sensitivity index

To characterize and compare the degrees of tolerance of the different species to water deficit, the stress sensitivity index (SSI) was calculated at the end of the experiment following the different regimes. In this study, the stress sensitivity index developed by Fischer and Maurer (1978) was used because it is successfully applied in many studies (Nana et al. 2009; Kagambèga et al. 2019) and was determined from the height of the plant species using the formula below:

$$\mathrm{SSI}(\%) = 100\ \mathrm{x}\frac{\mathrm{H1} - \mathrm{H2}}{\mathrm{H1}}$$

Where H_1 is the value of the plant's height in the control plants and H_2 is the value of the plant's height in the stressed plants. Thus stress sensitivity index based on plant height (SSI-H) was determined for each species following the different regimes and the species with the higher sensitivity value is the most sensitive.

2.4.2 Competition Index

Weigelt and Jolliffe (2003)have grouped the competition index into three categories to quantify the effect and outcome of the competition. In this study, three indices were calculated notably the Relative Yield (RY), Relative Yield Total (RYT) to quantify the effect of competition, and the Agressivity (A) to quantify the intensity of the competition. All of these indices were calculated using the weight of the average above-ground dry biomass per species in each container.

2.4.3 Relative competitive ability

Relative values are used to compensate for absolute differences in biomass between different species and to allow interspecies comparisons to be made (Fowler 1982). The Relative Yield (RY) value indicates the type of competition experienced by the species. If RY is greater than 1.0, the interspecific competition is less than the intraspecific competition. If RY is less than 1.0, the interspecific competition is more than the intraspecific competition. When RY is equal to 1.0, it indicates that the degree of competition of the species in mixture and monoculture is the same. The RY values were obtained according to the following equation:

$\mathrm{RYA} = \frac{\mathrm{MA}}{\mathrm{PA}}$ and $\mathrm{RYB} = \frac{\mathrm{MB}}{\mathrm{PB}}$ (De Wit and Van den Bergh 1965)

PA & PB = mean yield of species `A' and `B' in monoculture; Ma & Mb = mean yield of species `A' and `B' in the mixture.

Where, RY expresses the relationship between the mean yield of species A (Ma) when grown in a mixture containing species B with the mean yield of species A (Ma) when grown in monoculture and conversely for species B. In this study, A represents *S.obtusifolia* and B was represented by each of the 3 other target species.

Furthermore, the method of graphical analysis of the relative yield can be used (Radosevich 1987; Galon et al. 2022). This model can also involve the construction of a diagram based on the relative yield (RY) and also the relative total yield (RYT) for the studied plant proportions (0; 3; 6; 9 and 12). Equal competition between species would be represented by lines with constant slopes across all proportions resulting in an intersection point of the two curves at the 50:50 proportions.

Expected RY (straight line) for a species occurs when plants of a given species grow equally well in mixture and monoculture. That means there is no effect of one species over the other or the ability of the species to interfere with one another is equivalent. Comparisons of the actual RY of each species with their expected RY (diagonal dashed line in replacement diagrams) indicate competition if the actual RY curve of one species is concave and that of the second convex. When the RY of A is a convex curve, it indicates that the growth of A in the mixture was positively affected whereas the growth of B with a concave curve was negatively affected. However, niche differentiation occurs if the actual RY curves of both species are convex and there is mutual antagonism when the actual RY curves of both species are concave.

Relative Yield Total (RYT) is a measure of resource complementarities (Kumar et al. 2017). The RYT data were represented by the ½ sum of the relative yield of A and B (McGilchrist and Trenbath 1971). RYT equal to 1.0 (straight line) means that there was competition for the same resources. However, a value greater than 1.0 (convex line) means that there was no competition either because the supply of resources exceeds the demand or because the demands for the resources are different for each species. Finally, a value of RYT less than 1 (concave line) indicates the occurrence of antagonism that harmed the growth of both species (Bastiani et al. 2016).

2.4.4 Intensity of competition

Aggressivity (A) is an index that has been proposed to measure the strength of competition (Willey and Rao 1980). RY can be used to determine the agressivity index (McGilchrist and Trenbath 1971; Roush and Radosevich 1985). It is obtained according to the following formula.

$$A_A = \frac{1}{2}(RY_A - RY_B)$$

$$A_B = \frac{1}{2}(RY_B - RY_A)$$

Where RY_A is the relative yield of species A and RY_B is the relative yield of species B. An aggressivity value of zero indicates that component plants are equally competitive with the sign of the dominant species being positive and that of the dominated species being negative (Connolly et al. 2001). When two species are grown together in a pot, the more aggressive species will have the higher A value. The plant with the higher aggressivity value is assumed to be the stronger competitor (Meekins and McCarthy 1999).

2.5 Statistical Analysis

To assess the differences between water regimes at each species level, data obtained from the measured parameters (height and biomass) were subjected to a one-way ANOVA analysis of variance. A two-factor analysis of variance (ANOVA) was used to assess differences in performance (SSI) between species in response to the water regime. The interactive effects were evaluated with the two-way ANOVA procedure. Means were separated and ranked using the Tukey HSD (Honestly Significant Difference) test at the 5% threshold. Index data were analyzed by performing a three-way GLM ANOVA procedure. The effects of species, proportions, and water regime on plant above-ground biomass were examined using relative yield, and aggressivity index as the dependent variables. Species combination and water regime represent the fixed factors. RY and RYT from each mixed culture were compared to the value of 1.0 using t-tests (P=0.05). The aggressivity value from each mixed culture was compared to the zero value using t-tests (P=0.05). All analyses were performed using software version 4.1.0 (RCore Team 2021).

3 Results

3.1 Effect of water deficit condition on height and above-ground biomass

Water deficiency significantly reduced the vegetative growth of the four herbaceous species. Regarding the morphological parameters, height and biomass values were negatively influenced by water regimes i.e. control (100% FC); sufficient water supply (75% FC); moderate water stress (50% FC), and severe water stress (25% FC)for all species (Figures 3 and 4). Height was higher in the control block containers and progressively reduced until severely water-stressed blocks. A similar trend was observed for above-ground biomass (Figures 3 and 4) indicating a positive correlation (r=0. 69) between these two parameters.

Concerning the plant height, the sensitivity stress index (SSI-H), increased progressively from the water regime of 100% FC to the most stressed one 25% FC (Figure 5). Significant variability in stress sensitivity stress index (SSI-H) was observed for each species under different water regimes (Figure 5). The stress sensitivity index varied significantly with the water stress regime and with the combination of species (Table1). However, the sensitivity stress index did not vary significantly between species in the regime 75% FC and 50% FC. In opposite, in the regime 25% FC there is a highly significant variation of the SSI-H (dl = 3; F =26.72 and p < 7.81 e-14) (Figure 5).With its highest sensitive index, *S. obtusifolia* was the most sensitive species to water deficit compared respectively to the other three species, i.e. *C. mimosoides*, *P. pedicellatum*, and *A. gayanus* (Figure 6).

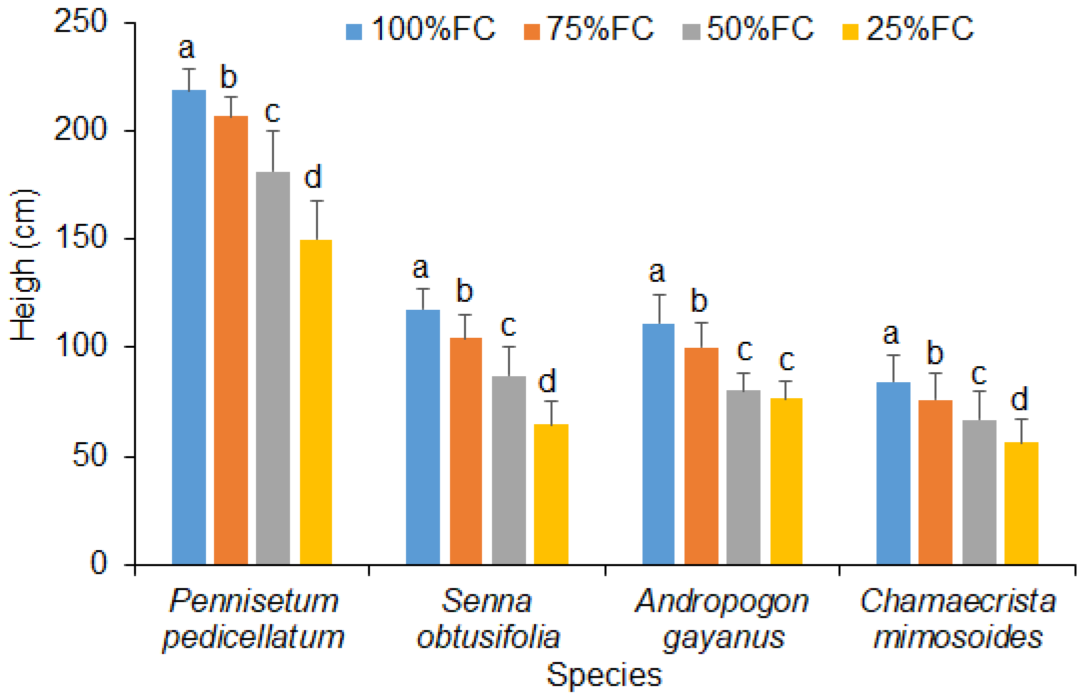


Figure 3 Variation in species height under different water regimes (Values without common letter differ significantly at P ≤ 0.05 as per Tukey HSD test); error bars represent standard deviation

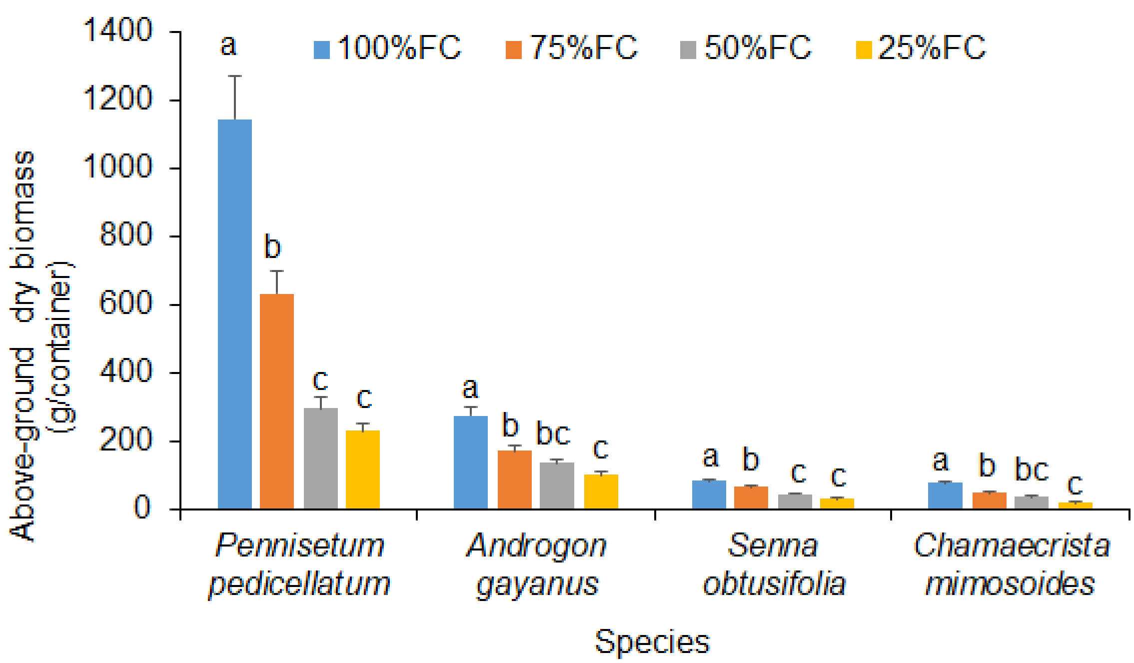


Figure 4 Variation in species biomass under different water regimes (Values without common letter differ significantly at P ≤ 0.05 as per Tukey HSD test); error bars represent standard deviation

Table1 Effect of species combination and water regime on the stress sensitivity index (SSI-H)

Source of variation	SSI-H		
	df	F value	Pr(>F)
Species	3	23.244	0.006*
Water regime	3	689.092	<0.002*
Species x water regime	9	7.907	0.007*

*means significantly different

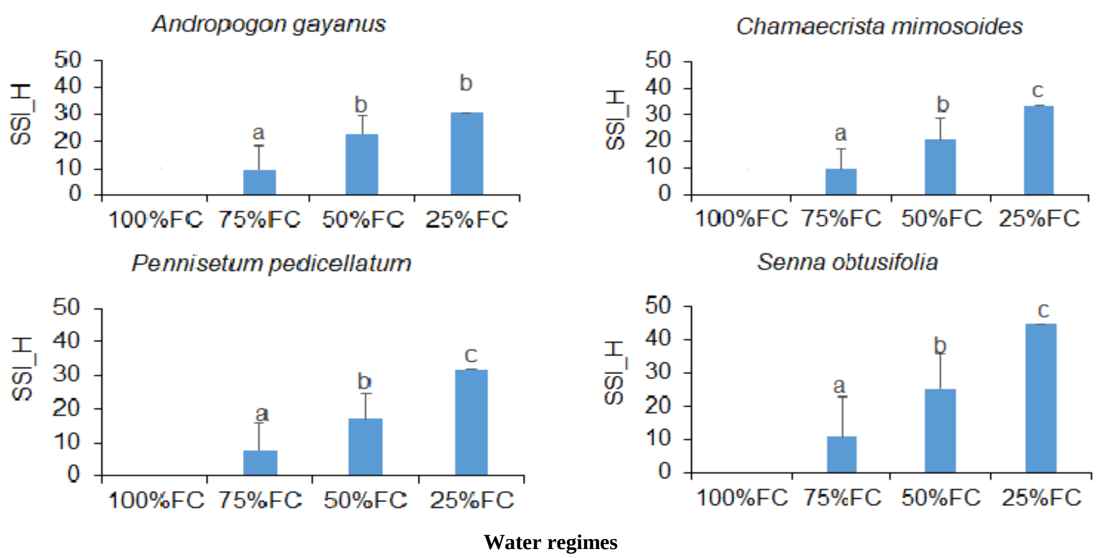


Figure 5 Variations in species sensitivity index to different water stress regimes (Values without common letter differ significantly at P ≤ 0.05 as per Tukey HSD test); error bars represent standard deviation; SSI-H: stress sensitivity index based on plant height

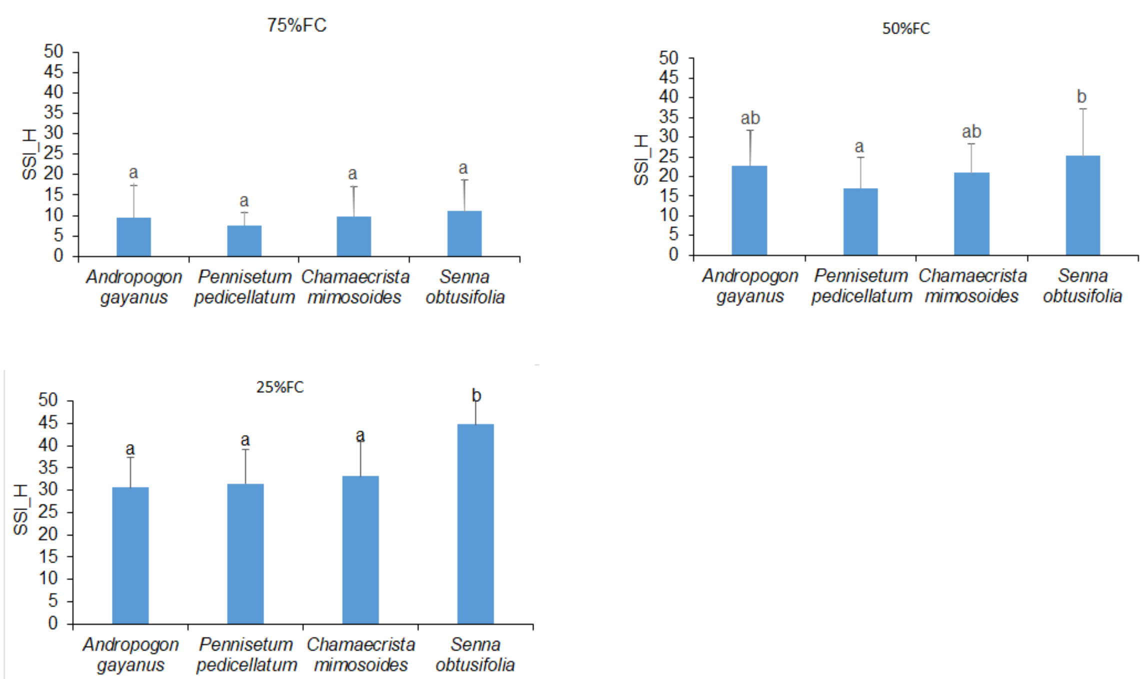


Figure 6 Sensitivity of the four species in severe water stress; (Values without common letter differ significantly at P ≤ 0.05 as per Tukey HSD test); error bars represent standard deviation; SSI-H: stress sensitivity index based on plant height

Table 2 Dry above-ground biomass (g) of plant species in monoculture and mixed culture under different water regimes

	Monoculture		Mixed culture			
Water regime	Species	Mean	Species	Mean	F	P
Control (100%FC)	*S. obtusifolia*	90.98 ± 35.97	SA	59.97 ± 2.10	-2.77	0.037*
			SC	86.97 ± 28.23	-0.36	0.984ns
			S P	60.17 ± 29.41	-2.75	0.039*
	A. gayanus	385.57 ± 108.85	AS	376.21 ± 103.88	0.06	0.81ns
	C. mimosoides	93.77 ± 36.71	CS	53.97 ± 28.77	10.92	0.002***
	P. pedicellatum	1490.83 ±688.03	PS	1476.42 ± 68.55	0.003	0.950ns
	S. obtusifolia	74.54 ± 32.25	SA	43.06 ± 21.21	-3.28	0.001***
			SC	68.55 ± 28.98	-0.62	0.924ns
			SP	41.66 ± 20.78	-3.42	0.001*
Sufficient water supply (75%FC)	*A. gayanus*	237.94 ± 93.96	AS	226.39 ± 81.47	0.13	0.72ns
	C. mimosoides	64.71 ± 22.74	CS	32.73 ± 14.91	20.75	0.001***
	P. pedicellatum	830.75 ± 377.76	PS	818.33 ± 382.69	0.008	0.93ns
	S. obtusifolia	47.82 ± 23.34	SA	27.83 ± 15.09	-3.29	0.001***
			SC	43.94 ± 13.72	-0.64	0.91ns
			SP	24.96 ± 12.03	-3.77	0.002***
Moderate water stress (50% FC)	*A. gayanus*	187.05 ± 66.30	AS	177.85 ± 54.96	0.17	0.68ns
	C. mimosoides	47.97 ± 15.21	CS	25.01 ± 13.43	19.19	0.001***
	P. pedicellatum	342.63 ± 130.87	PS	330.98 ± 128.90	0.06	0.80ns
	S. obtusifolia	38.86 ± 19.92	SA	17.21 ± 5.60	-4.90	0.001***
			SC	22.25 ± 6.03	-3.75	0.002***
			SP	14.66 ± 11.02	-5.47	0.001***
Severe water stress (25%FC)	*A. gayanus*	147.10 ± 43.18	AS	131.00 ± 23.38	1.61	0.21
	C. mimosoides	25.27 ± 3.33	CS	13.66 ± 3.18	95.14	0.001*
	P. pedicellatum	290.05 ± 115.70	PS	286.11 ± 115.81	0.009	0.92ns

The values used are averages and (*) indicate significance at the 5% threshold according to the Tukey HSD test; *** Highly significant; ns not significant; ± standard error Here SA: *Senna obtusifolia* in mixture with *Andropogon gayanus*; SC: *Senna obtusifolia* in mixture with *Chamaecrista mimosoides*; SP: *Senna obtusifolia* in mixture with *Pennisetum pedicelatum*; AS: *Andropogon gayanus* in mixture with *Senna obtusifolia*; CS: *Chamaecrista mimosoides* in mixture with *Senna obtusifolia*; PS: *Pennisetum pedicellatum* in mixture with *Senna obtusifolia*

3.2 Effect of competition under the water regime

3.2.1 Biomass production

The above-ground dry biomass of *S. obtusifolia* was negatively influenced in combination with *A. gayanus* and *P. pedicellatum* under the four water regimes. In contrast, the above-ground biomass of *S. obtusifolia* was not influenced in combination with *C. mimosoides*. Indeed, a significant difference ($P<0.05$) was found between *A. gayanus* and *P. pedicellatum* under the four water regimes (table 2). In contrast to this, no significant difference ($P> 0.05$) was reported between the biomass of *S. obtusifolia* in monoculture from its production in mixed culture with *C. mimosoides* under a water regime of 100% FC; 75% FC, and 50% FC. While in the case of 25% FC water regime a significant difference ($P<0.05$) was found between the biomass of *S. obtusifolia* in monoculture from its production in mixed culture with *C. mimosoides*. Biomass of *A. Gayanus* and *P. pedicellatum* in monoculture was not significantly different ($P> 0.05$) from their biomass production in mixed culture with *S. obtusifolia* in all regimes (table 2). Further, the biomass of *C. Mimosoides* in monoculture under severe water stress (regimes of 25% FC) was significantly different from its biomass in mixed culture with *S. obtusifolia*.

3.2.2 Relative Yield and Relative Yield Total

Relative Yield (RY) and Relative Yield Total (RYT) based on the shape of the curves differed significantly among regimes, proportions, and species (P<0.05). Under all water regimes regarding *S.obtusifolia* and *C. mimosoides*, RY of *S.obtusifolia* over-yielded the expected (diagonal dashed line) and had always convex curves except for proportions 6:6; 9:3, and 12:0 under

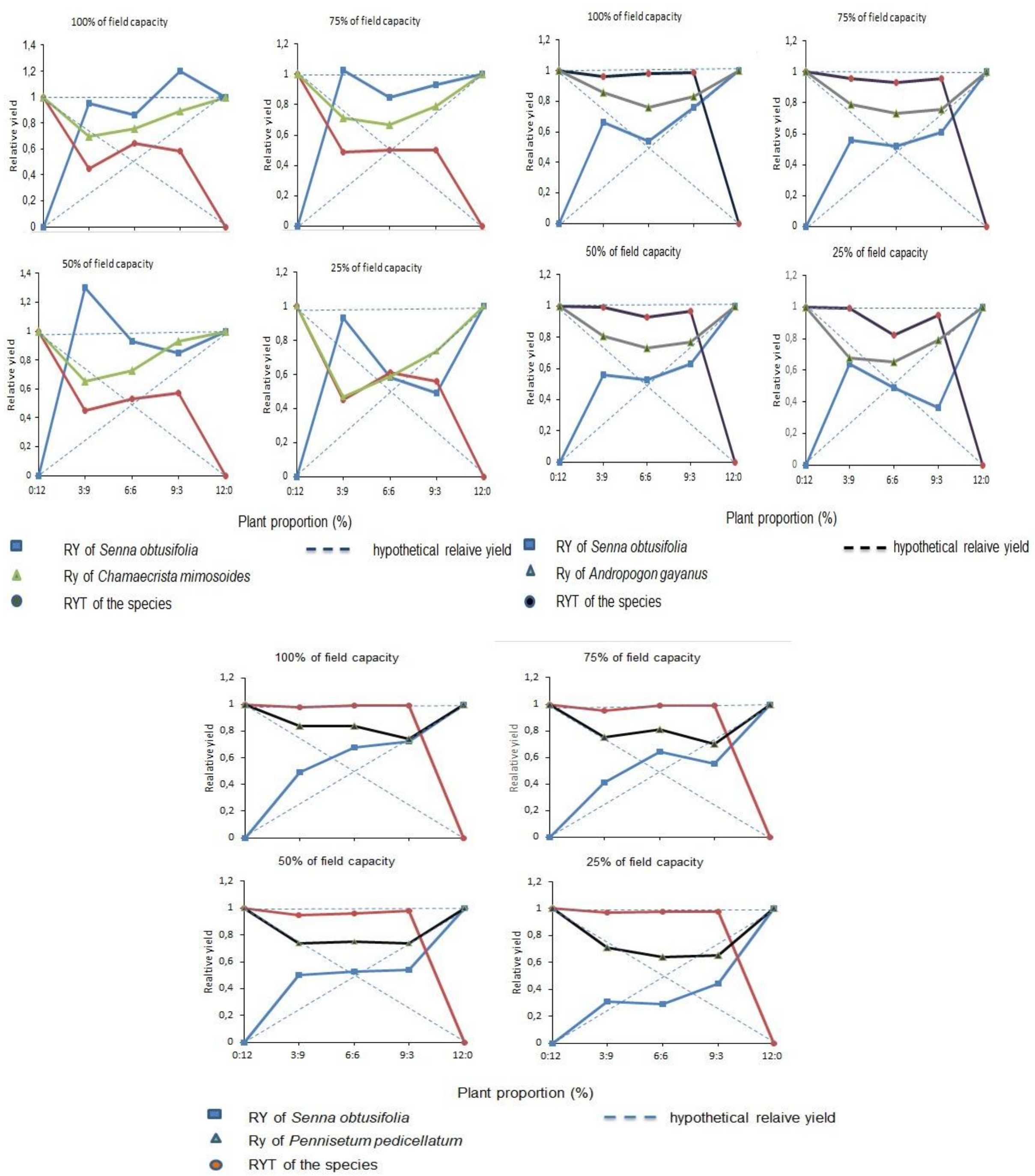


Figure 7 Replacement series diagrams illustrating mean ± sd relative yield of *S. obtusifolia* (□), *C. mimosoides*(Δ), *A. gayanus* (Δ), *P. pedicellatum* (Δ) and relative yield total (●) as a function of species proportion. Dashed lines represent the expected values in the absence of competition and solid lines represent the observed values when the species competed in different plant proportions. Proportions 100%, 75%, 50%and 25% represented different water regimes.

water deficit (25%FC) where it under-yielded the expected and had a concave curve (figure 6). Whereas, the curve of *C. mimosoides* was concave for 0:12 to 6:6 proportion and became convex until proportion 12:0.

RY of *S. obtusifolia* and *A. gayanus*, when grown together were significantly different from expected values in each mixture proportion under all water regimes. *S. obtusifolia* over-yielded the expected and had a convex curve for 0:12 to 6:6 proportions and later on these curves became progressively concave for the proportion 12:0 whereas *A.gayanus* over-yielded the expected in all proportions under all regimes (figure 6).

RY of *S. obtusifolia* and *P. pedicellatum* were significantly different from expected values in each mixture proportion under all water regimes. RY of *S. obtusifolia* was significantly higher than expected and had convex curves from proportions 0:12 to 6:6. These curves became progressively concave after proportion 6:6, whereas *P.pedicellatum* over-yielded the expected in all proportions under all regimes. Mixtures were under-yield i.e. RYT and RY of the four species in the mixture at all regimes were each other less than 1.0 as represented by the dashed line in figure 7.

3.2.3 Intensity of competition

The aggressivity index (A) differed significantly between species and proportions of species combination in pairs but not for the regime (Table 3). *S. obtusifolia* had a positive aggressivity value while *C. mimosoides* had negative aggressivity across all proportions at almost all water regimes. In contrast, when *S.obtusifolia* was grown in a mixture with *A. gayanus* and *P. pedicellatum*, the aggressivity value of *S.obtusifolia* was negative whereas the aggressivity of *A.gayanus and P.pedicellatum* were positive (table 3). Water regime, species combination, and interactions of species significantly affected the aggressivity index (A). However, the Relative yield total (RYT) was not affected by the interaction between the water regime and species combination (table 4).

Table 3 Effect of different water regimes on the Aggressivity of selected species

Water regimes	Proportions	Mean ± sd *S. obtusifolia* X *C. mimosoides*	Mean ± sd *S. obtusifolia* X *A. gayanus*	Mean ± sd *S. obtusifolia* X *P. pedicellatum*
Control	75 :25	0.25 ± 0.06*	-0.09 ± 0.02*	-0.12 ± 0.04*
	50 :50	0.1 ± 0.09	-0.21 ± 0.03*	-0.15 ± 0.03*
	25 :75	0.31 ± 0.11*	-0.16 ± 0.09*	-0.25 ± 0.04*
Stand mean		0.22 ± 0.08	-0.15 ± 0.05	-0.17 ± 0.04
Sufficient water supply	75 :25	0.22 ± 0.04*	-0.17 ± 0.04*	-0.19 ± 0.3
	50 :50	0.17 ± 0.09*	-0.21 ± 0.05*	-0.18 ± 0.3*
	25 :75	0.25 ± 0.10*	-0.2 ± 0.04*	-0.29± 0.3
Stand mean		0.21 ± 0.07	-0.19 ± 0.04	-0.22 ± 0.3
Moderate water stress	75 :25	0.2 ± 0.06*	-0.18 ± 0.03*	-0.2 ± 0.04
	50 :50	0.19 ± 0.25	-0.2 ± 0.05*	-0.21 ± 0.03*
	25 :75	0.36 ± 0.17*	-0.2 ± 0.03*	-0.23 ± 0.03
Stand mean		0.25 ± 0.09	-0.19 ± 0.04	-0.13 ± 0.03
Severe water stress	75 :25	0.01 ± 0.01	-0.31 ± 0.01*	-0.26 ± 0.03*
	50 :50	-0.01 ± 0.07	-0.16 ± 0.09*	-0.34 ± 0.04*
	25 :75	0.18 ± 0.06*	-0.16 ± 0.05*	-0.34 ± 0.05*
Stand mean		0.18 ± 0.09	-0.21 ± 0.05	-0.31 ± 0.04

Aggressivity value (mean± sd) of *C. mimosoides*, *A. gayanus*, *P. pedicellatum* when grown with *S. obtusifolia* at different combinations under different water regimes control (100% FC); sufficient water supply (75% FC); moderate water stress (50%FC) and severe water stress (25% FC); here the proportion is the ratio of the percentage of *S. obtusifolia* plants to the target species in a container; A: t-test being considered significant (*) when differing ($p \leq 0.05$) from 0.

Table 4 The effects of species combination and water regime on the Aggressivity (A) and Relative yield total (RYT)

Sources of variation		A		RYT	
	DF	F-value	P-value	F-value	P-value
Species	3	30.36	0.001***	15.26	0.001***
Proportion	2	8.23	0.001***	28.71	0.001* **
Regime	3	1.40	0.25ns	3.16	0.031 *
Species-proportion	4	9.05	0.001***	1.47	0.212ns
Species-regime	6	2.44	0.03*	2.03	0.061ns
Proportion-regime	6	1.29	0.03*	1.50	0.182ns
Species-proportion-regime	12	1.55	0.11ns	1.19	0.291ns

The values used are averages and (*) indicate significance at the 5% threshold according to the Tukey HSD test examined with three-way of Anova.. (***) Highly significant; (ns) not significant.

4 Discussion

4.1 Effect of water stress on plant's height and above-ground biomass

In this study, all four species' height and above-ground biomass were negatively affected by water stress. This could be explained by the juvenile state of the plants (16-day-old plants) during the induction of water deficiency and duration of stress. Indeed, the response of a plant to water deficit is complex and depends on the stage of development of the plant, the intensity of the deficit, the duration of the stress, the genotype of the plant, and the state the plant was in when the stress occurred (Sawadogo et al. 2006; Aziadekey et al. 2014; Peng et al. 2022). In addition, when the plants are subjected to long-term severe water stress during the vegetative growth stage, the stress may be great enough to cause substantial yield losses (Wijewardana et al. 2019).

Plants subjected to soil moisture deficit conditions experienced a decrease in the performance of their parameters (height and biomass) compared to plants of the control regime. This reduction in growth following a water deficiency is considered a regulatory mechanism allowing the adaptation of plants to water restrictions by a reduction in the transpiration surface (Chaves et al. 2002; Yang et al. 2021; Wu et al. 2022).

Furthermore, the sensitivity index (SSI-H) varies significantly for each species under different water regimes. The differences observed between species showing their degree of sensitivity to water stress would be due to the intrinsic characteristics of each species as reflected in the sensitivity index. Grasses are empirically considered "tolerant" to drought (Baruch 1994; Pardo and VanBuren 2021). Hence *A. gayanus* was one of these grasses relatively more tolerant and less affected by drought due to a slowing down of the growth of the aerial organs in favour of root development which preferentially glues the layers of the substrate with residual humidity (Buldgen 1997). In the severe stress regime, *S. obtusifolia* was the most sensitive species to water deficit (having the highest sensitive index) compared respectively to the other species i.e. *C. mimosoides*, *P. pedicellatum*, and *A. Gayanus*.

However, a plant is tolerant when it can maintain its metabolic activity under low water potentials (Kagambèga et al. 2019). The species with the lowest sensitivity index to water stress, in decreasing order, were *A. Gayanus*, *P. pedicellatum*, and *C. Mimosoides* suggest that these species are the most tolerant to water deficits. Previous studies (Bargali and Bargali 2016; de Moura et al. 2020) have reported that *A. Gayanus* and *P. pedicellatum* are drought-tolerant species. In addition, it is argued that *C.mimosoides* can withstand low water deficit (Bargali and Bargali 2016). On the contrary, *S. obtusifolia*, characterized by the highest sensitivity index, is the least tolerant to water deficit in soil. This shows that *S.obtusifolia* prefers well-drained soils (DAF 2016). This situation could suggest that *S.obtusifolia* used less water under water deficit than the other species. Similarly, Moreshet et al. (1996) reported that *S.obtusifolia*tends to use less water than *Arachis hypogea* when grown together in a mixture with Arachis hypogea (peanut) under water deficit.

4.2 Effect of competition

4.2.1 Biomass production

The biomass of *S. obtusifolia* is significantly reduced when grown in a mixture with *A.gayanus* or *P.pedicellatum*as compared to its biomass in monoculture under all regimes except C. *mimosoides.* In contrast to this, the biomass of *A. gayanus* and *P. pedicellatum* are not significantly influenced when comparing their performance in mixtures versus monocultures. According to Hartvigsen (2000), the growth of some species is restrained when grown in mixtures. Furthermore, the combination of *S. obtusifolia* and *C. mimosoides* revealed that in the three least stressed regimes, the biomass of *S. obtusifolia* was not influenced while the biomass of *C. Mimosoides* decreased as compared to its biomass in monoculture. However, the biomass of *S. obtusifolia* decreased when grown in a mixture with *C. mimosoides* under the severe water regime. Our results are in line with the evidence showing that invasive plant species often produced more biomass than competing plant species under high water conditions while the opposite pattern has been found under drought as the invaders became less competitive than competing species (Kelso et al. 2020).

4.2.2 Relative competitive ability

Interaction among *S. obtusifolia* and other species in the mixture was negative showing a frequent occurrence of interspecific competition. In general, equal competition between species would be represented by lines with constant slopes across all ratios resulting in an intersection point of the two curves at the 50:50 ratio. In this study, the curve representing the relative yield of *S.obtusifolia* and the curves of the relative yield of each species in a mixture with *S. Obtusifolia* usually do not intersect at the 6: 6 proportion. Moreover, the curve of *S. obtusifolia* is generally concave and yields less than the expected quantities while curves of *A. gayanus* and *P. pedicellatum* are convex and yield higher than the expected quantities across all regimes. These trends suggest that *S. obtusifolia* was subordinate whereas *A. gayanus* and *P. pedicellatum* were the dominant species. In contrast to *A. gayanus* and *P. pedicellatum, C. mimosoides* was negatively affected by the presence of *S. obtusifolia* under all regimes. The RY curve of *C. mimosoides* was concave and produced yields less than expected while the RY curve of *S. obtusifolia* produced a yield higher than expected.

However, in *S. obtusifolia* combinations with the other three species (*A. gayanus, C. mimosoides,* and *P. pedicellatum*), the relative yields total values were less than expected and indicated that there was intense competition between their populations. The relative yields total may be lower than expected (dashed line) if one species or both are more affected than expected when there is crowding for the same space (Baghdadi et al. 2016). When the total value of relative yield is lower than expected, it may be a case of mutual antagonism (Dekker et al. 1983). This suggests that one species may produce a toxin that reduces the growth of the other species (allelopathy) or one of the species in combination may lose its ability to grow due to the presence of its congener.

Similar studies on legume and non-legume mixtures had attributed high values of relative yields total through the use of different nitrogen sources in addition to differences in root and above-ground characteristics (Zand and Beckie 2002; Ball et al. 2020). Contrary to their study, the results of this study showed a lower value of relative yield totals through the use of water stress as the main factor in addition to above-ground biomass. Our results are in agreement with Martin and Field (1984) who found relative yields total values less than expected by using grass-legume mixtures in shallow boxes in addition to differences in root and above-ground biomass. This situation suggested that the value of relative yields total in grass-legume competition depends on the nature of the species, resources, and the measured parameters.

4.2.3 Intensity of competition

S. obtusifolia was the subordinate species and *A. Gayanus* and *P. pedicellatum* were dominant except *C. mimosoides*. The aggressivity of *S.obtusifolia* was negative and lower while the aggressivity of *A. gayanus* and *P. pedicellatum* were positive and greater when grown in all proportions under all water regimes. The highest aggressiveness value of *A. gayanus* and *P. pedicellatum* may be due to their efficient C_4 photosynthetic pathway and high nitrogen and water use efficiency. This result supports the view of Zhang et al. (2011), and Sheppard (2019) who reported that the species with the greater competitive ability is usually termed as the dominant species or superior competitor and has a greater ability to acquire resources and to occupy the superior ecological niche. *S. obtusifolia* was expected to be the best competitor in its proliferation in the Sahel rangelands. In addition, previous studies show that this species is the most troublesome or best competitor when in a mixture with soybean (*Glycine max*), tobacco (*Nicotiana tabacum* L.), peanut (*Arachis hypogaea* L.), cotton (*Gossypium hirsutum*) and vegetables (Buchanan et al. 1980; Monks and Oliver 1988; Webster and Macdonald 2001) due to its many competitive attributes such as fast-growing, deep-rooting, rapid biomass accumulating and forms a close canopy cover to recycle nutrients from the subsoil and suppress the growth of noxious weeds (Hauser et al. 1975; Holt 1995). However, the experimentation in the greenhouse under water stress revealed that this species is a poor competitor suggesting that its invasion could be favoured by other factors. These results are in agreement with Chambers et al. (2014), and Waddell et al. (2020) who report that generally invasion is facilitated by land uses or management activities that disturb native vegetation increase resource availability, and promote the establishment and spread of the species. Moreover, the degree of this disturbance may be partly due to overgrazing (Hobbs and Huenneke 1992; He et al. 2022)

Conclusion

From the results of the study, we can deduce that the predictive competitive ability of *S. obtusifolia* is not due to its biology but due to the presence of other factors. Specifically, the current invasion of *S. obtusifolia* could be favored by overgrazing in the rangeland which reduces fodder species' dominance and competitiveness. Further, good and sustainable management of sahelian rangelands by controlling grazing would help to reduce *S. obtusifolia* invasion and provide more fodder for livestock.

Author contributions

OO and AZ conceived and designed the experiments. OO, KO, PCB, and AZ performed the experiments. KO, PCB, and AZ analyzed the data. AZ wrote the paper. All authors reviewed and approved the final manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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References

Adams, V. M., & Setterfield, S. A. (2013). Estimating the financial risks of Andropogon gayanus to greenhouse gas abatement projects in northern Australia. *Environmental Research Letters*, *8*(2), 025018. http://dx.doi.org/10.1088/1748-9326/8/2/025018

Augustine, C., Khobe, D., Madugu, A. J., Babakiri, Y., et al. (2020). Productive performance and cost benefits of feeding wistar albino rats with processed tropical sickle pod (*Senna obtusifolia*) leaf meal-based diets. *Translational Animal Science*, *4*(2), 589-593.https://doi.org/10.1093/tas/txaa036

Ayantunde, A. A., Oluwatosin, B. O., Yameogo, V., & van Wijk, M. (2020). Perceived benefits, constraints and determinants of sustainable intensification of mixed crop and livestock systems in the Sahelian zone of Burkina Faso. *International Journal of Agricultural Sustainability*, *18*(1), 84-98. https://doi.org/10.1080/14735903.2019.1698494

Aziadekey, M., Atayi, A., Odah, K., & Magamana, A. E. (2014). Étude de l'influence du stress hydrique sur deux lignées de niébé. *European Scientific Journal, 10* (30), 328-338.

Baghdadi, A., Halim, R. A., Othman, R., Yusof, M. M., & Atashgahi, A. R. M. (2016). Productivity, relative yield and plant growth of forage corn intercropped with soybean under different crop combination ratio. *Legume Research*, *39*(4), 558-564. doi:10.18805/lr.v0iOF.10755

Ball, K. R., Power, S. A., Brien, C., Woodin, S., et al. (2020). High-throughput, image-based phenotyping reveals nutrient-dependent growth facilitation in a grass-legume mixture. *PloS one*, *15*(10), e0239673. https://doi.org/10.1371/journal.pone.0239673

Bargali, K., & Bargali, S. S. (2016). Germination capacity of seeds of leguminous plants under water deficit conditions: implication for restoration of degraded lands in Kumaun Himalaya. *Tropical Ecology*, *57*(3), 445-453.

Barros, V., Melo, A., Santos, M., Nogueira, L., Frosi, G., & Santos, M. G. (2020). Different resource-use strategies of invasive and native woody species from a seasonally dry tropical forest under drought stress and recovery. *Plant Physiology and Biochemistry, 147*, 181-190. https://doi.org/10.1016/j.plaphy.2019.12.018

Baruch, Z. (1994). Responses to drought and flooding in tropical forage grasses. *Plant and Soil*, *164*(1), 87-96. https://doi.org/10.1007/BF00010114

Bastiani, M. O., Lamego, F. P., Agostinetto, D., Langaro, A. C., & Silva, D. C. D. (2016). Relative competitiveness of soybean cultivars with barnyardgrass. *Bragantia*, *75*, 435-445. https://doi.org/10.1590/1678-4499.412

Beyene, M. A. (2021). *Production status, biomass yield under different management practices and nutritional values of desho grass (Pennisetum pedicellatum)* in southern Ethiopia, Doctoral dissertation submitted to the Hawassa University, Ethiopia.

Bogale, G. A., & Tolossa, T. T. (2021). Climate change intensification impacts and challenges of invasive species and adaptation measures in Eastern Ethiopia. *Sustainable Environment*, *7*(1), 1875555. https://doi.org/10.1080/23311843.2021.1875555

Bolinder, M. A., Angers, D. A., Bélanger, G., Michaud, R., & Laverdière, M. R. (2002). Root biomass and shoot to root ratios of perennial forage crops in eastern Canada. *Canadian journal of plant science*, *82*(4), 731-737. https://doi.org/10.4141/P01-139

Broadbent, A., Stevens, C. J., Peltzer, D. A., Ostle, N. J., & Orwin, K. H. (2018). Belowground competition drives invasive plant impact on native species regardless of nitrogen availability. *Oecologia*, *186*(2), 577-587. https://doi.org/10.1007/s00442-017-4039-5

Buchanan, G. A., Crowley, R. H., Street, J. E., & McGuire, J. A. (1980). Competition of sicklepod (*Cassia obtusifolia*) and redroot pigweed (*Amaranthus retroflexus*) with cotton (*Gossypium hirsutum*). *Weed Science*, *28*(3), 258-262. https://doi.org/10.1017/S0043174500055259

Buldgen, A. (1997). Croissance juvénile et comportement phydiologique d' Andropogon gayanus Kunth var. bisquamulatus en conditions de stress hydrique. *Base, Biotechnologie, Agronomie, Société et Environnement*, *1*(4), 278-294.

Chambers, J. C., Bradley, B. A., Brown, C. S., D'Antonio, C., et al. (2014). Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrub lands of western North America. *Ecosystems*, *17*(2), 360-375. https://doi.org/10.1007/s10021-013-9725-5

Chaves Neto, J. R., Mazutti, M. A., Zabot, G. L., & Tres, M. V. (2020). Bioherbicidal action of *Phoma dimorpha* fermented broth on seeds and plants of *Senna obtusifolia*. *Pesquisa Agropecuária Tropical*, *50*. https://doi.org/10.1590/1983-40632020v5056894

Chaves, M. M., Pereira, J. S., Maroco, J., Rodrigues, M. L., et al. (2002). How plants cope with water stress in the field? Photosynthesis and growth. *Annals of botany*, *89*(7), 907-916. https://doi.org/10.1093/aob/mcf105

Connolly, J., Goma, H. C., & Rahim, K. (2001). The information content of indicators in intercropping research. *Agriculture, ecosystems & environment*, *87*(2), 191-207. https://doi.org/10.1016/S0167-8809(01)00278-X

D. of A. and F. (DAF). (2016). Restricted invasive plant. The State of Queensland, Department of Agriculture and Fisheries. www.biosecurity.qld.gov.au.

De Moura, R. L., de Oliveira, M. E., de Carvalho, W. F., Rodrigues, M. M., et al. (2020). Goat performance on pure *Andropogon gayanus* pastures or associated with legumes. *Tropical Animal Health and Production*, *53*(1), 1-12. https://doi.org/10.1007/s11250-020-02434-z

De Wit, C. T. (1960). *On competition* (No. 66.8). Pudoc.

De Wit, C. T., & Van den Bergh, J. P. (1965). Competition between herbage plants. The Journal of Agricultural Science, *13*, 212 - 221.

DeBoer, M. L., Grev, A. M., Sheaffer, C. C., Wells, M. S., et al. (2020). Herbage mass, botanical composition, forage nutritive value, and preference of grass–legume pastures under horse grazing. *Crop, Forage & Turfgrass Management*, *6*(1), e20032. https://doi.org/10.1002/cft2.20032

Dekker, J. H., Meggitt, W. F., & Putnam, A. R. (1983). Experimental methodologies to evaluate allelopathic plant interactions. *Journal of Chemical Ecology*, *9*(8), 945-981. https://doi.org/10.1007/BF00982204

Diez, J. M., D'Antonio, C. M., Dukes, J. S., Grosholz, E. D., et al. (2012). Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment*, *10*(5), 249-257. https://doi.org/10.1890/110137

Dos Santos, P. R. R., de Souza Carlos Mourão, D., Dalcin, M. S., Osorio, P. R. A., et al. (2022). Pathogenicity of fungi associated with Andropogon grass seeds. *Journal of Plant Pathology*, *104*(2), 565-573. https://doi.org/10.1007/s42161-022-01038-w

Duell, E. B., Londe, D. W., Hickman, K. R., Greer, M. J., et al. (2021). Superior performance of invasive grasses over native counterparts will remain problematic under warmer and drier conditions. *Plant Ecology*, *222*(9), 993-1006. https://doi.org/10.1007/s11258-021-01156-y

Eisenhauer, N., & Scheu, S. (2008). Earthworms as drivers of the competition between grasses and legumes. *Soil Biology and Biochemistry*, *40*(10), 2650-2659. https://doi.org/10.1016/j.soilbio.2008.07.010

El-Barougy, R., MacIvor, J. S., Arnillas, C. A., Nada, R. M., et al. (2020). Richness, phylogenetic diversity, and abundance all have positive effects on invader performance in an arid ecosystem. *Ecosphere*, *11*(2), e03045. https://doi.org/10.1002/ecs2.3045

Fischer, R. A., & Maurer, R. (1978). Drought resistance in spring wheat cultivars. I. Grain yield responses. *Australian Journal of Agricultural Research*, *29*(5), 897-912. https://doi.org/10.1071/AR9780897

Fontès, J., & Guinko, S. (1995). *Carte de la végétation et de l'occupation du sol du Burkina Faso*.

Fowler, N. (1982). Competition and coexistence in a North Carolina grassland: III. Mixtures of component species. *The Journal of Ecology*, *70* (1), 77-92. https://doi.org/10.2307/2259865

Funk, J. L., Standish, R. J., Stock, W. D., & Valladares, F. (2016). Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. *Ecology*, *97*(1), 75-83. https://doi.org/10.1890/15-0974.1

Galon, L., Santin, C. O., Radünz, A. L., Andres, A., et al. (2022). Competitive ability of sweet sorghum (*Sorghum bicolor* (L.) Moench) cultivars against hairy beggarticks (*Bidens pilosa* L.). *Revista de Ciencias Agrícolas*, *39*(1). https://orcid.org/0000-0002-2397-011X

Gao, F. L., He, Q. S., Zhang, Y. D., Hou, J. H., et al. (2021). Effects of soil nutrient heterogeneity on the growth and invasion success of alien plants: a multi-species study. *Frontiers in Ecology and Evolution*, *8*, 619861. https://doi.org/10.3389/fevo.2020.619861

Gebrekiros, M. G. (2017). Livestock herders' perception on the causes and effects of Senna obtusifolia L. invasion in rangelands of Northern Ethiopia. *African Journal of Agricultural Research*, *12*(42), 3081-3087. doi: 10.5897/AJAR2017.12505

Grice, A. C., Vanderduys, E. P., Perry, J. J., & Cook, G. D. (2013). Patterns and processes of invasive grass impacts on wildlife in Australia. *Wildlife Society Bulletin*, *37*(3), 478-485. https://doi.org/10.1002/wsb.314

Grüner, E., Wachendorf, M., & Astor, T. (2020). The potential of UAV-borne spectral and textural information for predicting aboveground biomass and N fixation in legume-grass mixtures. *PloS one*, *15*(6), e0234703. https://doi.org/10.1371/journal.pone.0234703

Hartvigsen, G. (2000). Competition between co-dominant plants of the Serengeti plains depends on competitor identity, water, and urine. *Plant Ecology*, *148*(1), 31-41. https://doi.org/10.1023/A:1009835424490

Hauser, E. W., Buchanan, G. A., & Ethredge, W. J. (1975). Competition of Florida beggar weed and sicklepod with peanuts I. Effects of periods of weed-free maintenance or weed competition. *Weed Science*, *23*(5), 368-372. doi:10.1017/S0043174500062688

He, Y., Liu, X., Wang, M., Sun, S., et al. (2022). Grazing alters seedling emergence number, dynamics, and diversity of herbaceous plants in a semiarid sandy grassland. *Ecological Research*. https://doi.org/10.1111/1440-1703.12355

Hobbs, R. J., & Huenneke, L. F. (1992). Disturbance, diversity, and invasion: implications for conservation. *Conservation biology*, *6*(3), 324-337. https://doi.org/10.1046/j.1523-1739.1992.06030324.x

Holm, L., Doll, J., Holm, E., Pancho, J. V., et al. (1997). *World weeds: natural histories and distribution*. John Wiley & Sons.

Holt, J. S. (1995). Plant responses to light: a potential tool for weed management. *Weed Science*, *43*(3), 474-482. doi:10.1017/S0043174500081509

INSD. (2019). Annuaire Statistique 2018. (p. 407p.). MEF (Ministère de l'Économie et des Finances).

Issaharou-Matchi, I., Barboni, D., Meunier, J. D., Saadou, M., et al. (2016). Intraspecific biogenic silica variations in the grass species *Pennisetum pedicellatum* along an evapotranspiration gradient in South Niger. *Flora-Morphology, Distribution, Functional Ecology of Plants*, *220*, 84-93. https://doi.org/10.1016/j.flora.2016.02.008

Kadeba, A., Nacoulma, B. M. I., Ouedraogo, A., Bachmann, Y., et al. (2015). Land cover change and plants diversity in the Sahel: A case study from northern Burkina Faso. *Annals of Forest Research*, *58*(1), 109-123. *DOI:10.15287/afr.2015.350*

Kagambèga, F. W., Nana, R., Bayen, P., Thiombiano, A., et al. (2019). Tolérance au déficit hydrique de cinq espèces prioritaires pour le reboisement au Burkina Faso. *Biotechnology, Agronomy and Society and Environment, 23(4), 245-256* https://doi.org/10.25518/1780-4507.18199

Kelso, M. A., Wigginton, R. D., & Grosholz, E. D. (2020). Nutrients mitigate the impacts of extreme drought on plant invasions. *Ecology*, *101*(4), e02980. https://doi.org/10.1002/ecy.2980

Khatiwada, B., Acharya, S. N., Larney, F. J., Lupwayi, N. Z., et al. (2020). Benefits of mixed grass–legume pastures and pasture rejuvenation using bloat-free legumes in western Canada: a review. *Canadian Journal of Plant Science*, *100*(5), 463-476. https://doi.org/10.1139/cjps-2019-0212

Kiema, A., Nianogo, A. I., Kabore-Zoungrana, C. Y., & Jalloh, B. (2012). Effets des demi-lunes associées au scarifiage sur les productions fourragères en région sahélienne du Burkina Faso. *International Journal of Biological and Chemical Sciences*, *6*(6), 4018-4030. doi: 10.4314/ijbcs.v6i6.13

Kiema, A., Nianogo, A. J., Somda, J., & Ouédraogo, T. (2008). Valorisation de Cassia obtusifolia L. dans l'alimentation des ovins d'embouche en région sahélienne du Burkina Faso. *Tropicultura*, *26*(2), 98-103.

Kiema, A., Tontibomma, G., & Zampaligré, N. (2014). Transhumance et gestion des ressources naturelles au Sahel: contraintes et perspectives face aux mutations des systèmes de productions pastorales. *VertigO: la revue électronique en sciences de l'environnement*, *14*(3), 16.

Kumar, M., & Garkoti, S. C. (2021). Functional traits, growth patterns, and litter dynamics of invasive alien and co-occurring native shrub species of chir pine forest in the central Himalaya, India. *Plant Ecology*, *222*(6), 723-735. https://doi.org/10.1007/s11258-021-01140-6.

Kumar, M., Singh, H., & Singh, V. (2017). Competitive Interactions between Rice and *Caesulia axillaris* or *Echinochloa crus-galli* : A Replacement Series Study. *Annals of Agricultural & Crop Sciences*, *2*(1), 1025.

Leal, R. P., Silveira, M. J., Petsch, D. K., Mormul, R. P., et al. (2022). The success of an invasive Poaceae explained by drought resilience but not by higher competitive ability. *Environmental and Experimental Botany*, *194*, 104717. https://doi.org/10.1016/j.envexpbot.2021.104717

Li, Y., Liu, G., Han, K., Sun, L., et al. (2022). Distribution and biodiversity of rhizobia nodulating *Chamaecrista mimosoides* in the Shandong peninsula of china. *Systematic and Applied Microbiology*, *45*(1), 126280. https://doi.org/10.1016/j.syapm.2021.126280

M. des R. A. (MRA) (2010). Politique nationale de développement durable de l'élevage au Burkina Faso (pp. 45).

Mackey, P. A., Miller, E. N., & Palmer, W. A. (1997). Sicklepod (*Senna obtusifolia*) in Queensland: Pest status review series–Land protection. *Department of Natural Resources, Queensland, Australia*, Retrieved from https://www.daf.qld.gov.au/__data/assets/pdf_file/0011/63875/IPA-Sicklepod-PSA.pdf.

Martin, G. D., & Coetzee, J. A. (2014). Competition between two aquatic macrophytes, *Lagarosiphon major* (Ridley) Moss (Hydrocharitaceae) and *Myriophyllum spicatum* Linnaeus (Haloragaceae) as influenced by substrate sediment and nutrients. *Aquatic botany*, *114*, 1-11. https://doi.org/10.1016/j.aquabot.2013.11.001

Martin, M. P. L. D., & Field, R. J. (1984). The nature of competition between perennial ryegrass and white clover. *Grass and Forage Science*, *39*(3), 247-253. https://doi.org/10.1111/j.1365-2494.1984.tb01689.x

McGilchrist, C. A., & Trenbath, B. R. (1971). A revised analysis of plant competition experiments. *Biometrics*, *27*(3), 659-671. https://doi.org/10.2307/2528603

Meekins, J. F., & McCarthy, B. C. (1999). Competitive ability of *Alliaria petiolata* (garlic mustard, Brassicaceae), an invasive, nonindigenous forest herb. *International Journal of Plant Sciences*, *160*(4), 743-752. https://doi.org/10.1086/314156

Monks, D. W., & Oliver, L. R. (1988). Interactions between soybean (*Glycine max*) cultivars and selected weeds. *Weed Science*, *36*(6), 770-774. doi:10.1017/S0043174500075809

Moreshet, S., Bridges, D. C., NeSmith, D. S., & Huang, B. (1996). Effects of water deficit stress on competitive interaction of peanut and sicklepod. *Agronomy Journal*, *88*(4), 636-644. https://doi.org/10.2134/agronj1996.00021962008800040023x

Nacambo, H., Nanema, K. R., Kiebre, M., Traore, R. E., Sawadogo, N., et al. (2021). Nomenclature locale et usages de *Senna obtusifolia* (L.) au Burkina Faso. *Journal of Applied Biosciences*, *160*, 16438-16453. https://doi.org/10.35759/JABs.160.1

Nacoulma, M. B. I., Ouédraogo, I., Ouédraogo, O., Dimobé, K., & Thiombiano, A. (2019). Phytodiversity of Burkina Faso in Global Biodiversity.

Nana, R., Tamini, Z., & Sawadogo, M. (2009). Effets d'un stress hydrique intervenu pendant le stade végétatif et la phase de floraison chez le gombo. *International Journal of Biological and Chemical Sciences*, *3*(5). https://doi.org/10.4314/ijbcs.v3i5.51094

Ojo, F. M., Nwokeocha, C. C., & Faluyi, J. O. (2022). Germplasm Collections and Morphological Studies of Andropogon gayanus-Andropogon tectorum Complex in Southwestern Nigeria. *bioRxiv*. doi: https://doi.org/10.1101/2022.09.10.507395

Oliveira, M.T., Matzek, V., Dias Medeiros, C., Rivas, R., Marinho Falcão, H., et al. (2014). Stress tolerance and ecophysiological ability of an invader and a native species in a seasonally dry tropical forest. *PLoS One*, *9*(8), e105514. https://doi.org/10.1371/journal.pone.0105514

Ouedraogo, K., Zaré, A., Ouedraogo, O., & Anja, L. (2021). Resilience strategies of West Africa pastoralists in reponse to scarce forage resources. *Pastoralism*, *11*(1), 1-14

Palmer, W. A., & Pullen, K. R. (2001). The phytophagous arthropods associated with Senna obtusifolia (Caesalpiniaceae) in Mexico and Honduras and their prospects for utilization for biological control. *Biological Control*, *20*(1), 76-83. https://doi.org/10.1006/bcon.2000.0879

Pardo, J., & VanBuren, R. (2021). Evolutionary innovations driving abiotic stress tolerance in C4 grasses and cereals. *The Plant Cell*, *33*(11), 3391-3401. https://doi.org/10.1093/plcell/koab205

Paudel, S., Milleville, A., & Battaglia, L. L. (2018). Responses of native and invasive floating aquatic plant communities to salinity and desiccation stress in the southeastern US coastal floodplain forests. *Estuaries and Coasts*, *41*(8), 2331-2339. https://doi.org/10.1007/s12237-018-0419-2

Peng, X., Li, J., Sun, L., Gao, Y., et al. (2022). Impacts of water deficit and post-drought irrigation on transpiration rate, root activity, and biomass yield of Festuca arundinacea during phytoextraction. *Chemosphere*, *294*, 133842. https://doi.org/10.1016/j.chemosphere.2022.133842

Peres, M. T. L. P., da Silva Cândido, A. C., Bonilla, M. B., Faccenda, O., & Hess, S. C. (2010). Phytotoxic potential of *Senna occidentalis* and *Senna obtusifolia*. *Acta Scientiarum. Biological Sciences*, *32*(3), 305-309. https://doi.org/10.4025/actascibiolsci.v32i3.5833

Petruzzellis, F., Tordoni, E., Tomasella, M., Savi, T., et al. (2021). Functional differentiation of invasive and native plants along a leaf efficiency/safety trade-off. *Environmental and Experimental Botany*, *188*, 104518. https://doi.org/10.1016/j.envexpbot.2021.104518

Radosevich, S. R. (1987). Methods to study interactions among crops and weeds. *Weed Technology*, *1*(3), 190-198. doi:10.1017/S0890037X00029523

RCore Team. (2021). A language and environment for statistical computing. R Foundation for Statistical Computing.

Reeves, E. R., Kerns, J. P., Cowger, C., & Shew, B. B. (2021). *Pythium spp*. associated with root rot and stunting of winter wheat in North Carolina. *Plant Disease*, *105*(4), 986-996. https://doi.org/10.1094/PDIS-09-20-2022-RE

Retzinger, E. J. (1984). Growth and development of sicklepod (*Cassia obtusifolia*) selections. *Weed Science*, *32*(5), 608-611. doi:10.1017/S0043174500059658

Roush, M. L., & Radosevich, S. R. (1985). Relationships between growth and competitiveness of four annual weeds. *Journal of Applied Ecology*,*22* (3), 895-905. https://doi.org/10.2307/2403238

Savić, A., Oveisi, M., Božić, D., Pavlović, D., et al. (2021). Competition between *Ambrosia artemisiifolia* and *Ambrosia trifida*: Is there a threat of a stronger competitor?. *Weed Research*, *61*(4), 298-306. https://doi.org/10.1111/wre.12479

Sawadogo, M., Zombre, G., & Balma, D. (2006). Expression de différents écotypes de gombo (*Abelmoschus esculentus* L.) au déficit hydrique intervenant pendant la boutonnisation et la floraison. *Biotechnologie, Agronomie, Société et Environnement*, *10* (1), 43–54.

Schmidt-Groh, S. E., Bernhardt-Römermann, M., Thiombiano, A., & Hahn, K. (2019). Intraspecific habitat adaptation: How the germinability of herbaceous plant seeds change due to environmental conditions in West African savannas. *Flora et Vegetatio Sudano-Sambesica*, *22*, 36-42. https://doi.org/10.21248/fvss.22.81

Setterfield, S. A., Rossiter-Rachor, N. A., Hutley, L. B., Douglas, M. M., & Williams, R. J. (2010). Biodiversity research: turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. *Diversity and distributions*, *16*(5), 854-861. https://doi.org/10.1111/j.1472-4642.2010.00688.x

Shackleton, R. T., Larson, B. M., Novoa, A., Richardson, D. M., et al. (2019). The human and social dimensions of invasion science and management. *Journal of Environmental Management*, *229*, 1-9. https://doi.org/10.1016/j.jenvman.2018.08.041

Sheppard, C. S. (2019). Relative performance of co-occurring alien plant invaders depends on traits related to competitive ability more than niche differences. *Biological Invasions*, *21*(4), 1101-1114. https://doi.org/10.1007/s10530-018-1884-z

Solbrig, O. T., Curtis, W. F., Kincaid, D. T., & Newell, S. J. (1988). Studies on the population biology of the genus Viola. VI. The demography of *V. fimbriatula* and *V. lanceolata*. *The Journal of Ecology*, *76* (2) 301-319. https://doi.org/10.2307/2260595

Sosnoskie, L. M., Steckel, S., & Steckel, L. E. (2021). Sicklepod [*Senna obtusifolia* (L.) HS Irwin &Barneby]"Getting sleepy?". *Weed Technology*, *35*(6), 1052-1058. doi:10.1017/wet.2021.70

SP/CONEDD, S. P. du C. N. pour l'Environnement et le D. D. (2010). Quatrième rapport national du Burkina Faso sur la diversité biologique (p. 119).

SP/CONEDD, S. P. du C. N. pour l'Environnement et le D. D (2014). Cinquième rapport national du Burkina Faso sur la diversité biologique (p. 104).

Veihmeyer, F. J., & Hendrickson, A. H. (1931). The moisture equivalent as a measure of the field capacity of soils. *Soil Science*, *32*(3), 181-194.

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., et al. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology letters*, *14*(7), 702-708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Waddell, E. H., Banin, L. F., Fleiss, S., Hill, J. K., et al. (2020). Land-use change and propagule pressure promote plant invasions in tropical rainforest remnants. *Landscape Ecology*, *35*(9), 1891-1906. https://doi.org/10.1007/s10980-020-01067-9

Wang, J., Fan, X., Fan, J., Zhang, C., et al. (2012). Effect of aboveground competition on biomass partitioning of understory

Korean pine (*Pinus koraiensis*). *ShengtaiXuebao/Acta EcologicaSinica*, *32*(8), 2447-2457.

Wardle, D. A., Bardgett, R. D., Callaway, R. M., & Van der Putten, W. H. (2011). Terrestrial ecosystem responses to species gains and losses. *Science*, *332*(6035), 1273-1277. DOI: 10.1126/science.1197479

Webster, T. M., & Macdonald, G. E. (2001). A survey of weeds in various crops in Georgia. *Weed Technology*, *15*(4), 771-790. doi:10.1614/0890-037X(2001)015[0771:ASOWIV]2.0.CO;2

Weigelt, A., & Jolliffe, P. (2003). Indices of Plant Competition. *Journal of Ecology*, *91*(5), 707–720. http://www.jstor.org/stable/3599697

Wickert, K. L., O'Neal, E. S., Davis, D. D., & Kasson, M. T. (2017). Seed production, viability, and reproductive limits of the invasive *Ailanthus altissima* (Tree-of-Heaven) within invaded environments. *Forests*, *8*(7), 226. https://doi.org/10.3390/f8070226

Wijewardana, C., Alsajri, F. A., Irby, J. T., Krutz, L. J., et al. (2019). Physiological assessment of water deficit in soybean using midday leaf water potential and spectral features. *Journal of Plant Interactions*, *14*(1), 533-543. https://doi.org/10.1080/17429145.2019.1662499

Willey, R. W., & Rao, M. R. (1980). A competitive ratio for quantifying competition between intercrops. *Experimental Agriculture*, *16*(2), 117-125. https://doi.org/10.1017/S0014479700010802

Wu, J., Wang, J., Hui, W., Zhao, F., et al. (2022). Physiology of Plant Responses to Water Stress and Related Genes: A Review. *Forests*, *13*(2), 324. https://doi.org/10.3390/f13020324

Yang, X., Lu, M., Wang, Y., Wang, Y., et al. (2021). Response mechanism of plants to drought stress. *Horticulturae*, *7*(3), 50. https://doi.org/10.3390/horticulturae7030050

Yu, H., Shen, N., Yu, S., Yu, D., et al. (2018). Responses of the native species *Sparganium angustifolium* and the invasive species *Egeria densa* to warming and interspecific competition. *Plos one*, *13*(6), e0199478. https://doi.org/10.1371/journal.pone.0199478

Zand, E., & Beckie, H. J. (2002). Competitive ability of hybrid and open-pollinated canola (*Brassica napus*) with wild oat (*Avena fatua*). *Canadian Journal of Plant Science*, *82*(2), 473-480. https://doi.org/10.4141/P01-149

Zare, A., Emmanuel Traore, I. C., Hien, B. S., Bonde, L., & Ouedraogo, O. (2022). Local Knowledge, Perceptions and Uses Values of *Senna obtusifolia* (L.) H.S. Irwin & Barneby, an Invasive Native Plant Species in Burkina Faso, West Africa. *European Scientific Journal, ESJ*, *18*(30), 343. https://doi.org/10.19044/esj.2022.v18n30p343

Zhang, G., Yang, Z., & Dong, S. (2011). Interspecific competitiveness affects the total biomass yield in an alfalfa and corn intercropping system. *Field crops research*, *124*(1), 66-73. https://doi.org/10.1016/j.fcr.2011.06.006

Zhang, Y., Leng, Z., Wu, Y., Jia, H., et al. (2022). Interaction between nitrogen, phosphorus, and invasive alien plants. *Sustainability*, *14*(2), 746. https://doi.org/10.3390/su14020746

Zhou, W., Cheng, X., Wu, R., Han, H., Kang, F., et al. (2018). Effect of intraspecific competition on biomass partitioning of *Larix principis-rupprechtii*. *Journal of Plant Interactions*, *13*(1), 1-8. https://doi.org/10.1080/17429145.2017.1406999