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Contrasting responses to prolonged drought stress and mitigation effects of manure application on plant growth of two tropical forage legumes

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Glycine and siratro are tropical forage legumes that especially thrive in regions with low precipitation such as sub-Saharan Africa. This study investigated legume responses to drought stress and cattle manure application in a greenhouse pot experiment aiming to contribute to their cultivation. Glycine was affected by drought stress-reducing plant physiology and growth expressed by leaf relative water content, stomatal conductance, leaflet number and area, and shoot biomass could maintain leaf-to-shoot ratio and leaf nitrogen content. Manure application mitigated or compensated the effects of drought regardless of plant growth duration, except for nitrogen contents. Siratro responded faster to drought decreasing stomatal conductance. When the drought was prolonged, other traits also decreased. When manure was applied at the same time as the drought, the nutrient was used more for dry matter and nitrogen accumulation in roots, not in leaves. However, siratro increased plant biomass only during drought stress for 25 days and the stomatal conductance was the highest only during manure application. Based on the results, it was concluded that glycine showed advantages in forage cultivation in sub-Saharan Africa due to its drought tolerance and manure application effectiveness, while further study is required for siratro's potential for cultivation in this region.

Key words: Cattle manure, drought, forage legumes, glycine, siratro.

INTRODUCTION

Forage legume cultivation is increasing its importance to meet growing food security problems and develop smallholder economies in most of sub-Saharan Africa (SSA). In SSA, the current population will be twice as large in 2050 (UN, 2022) and even major crops have their yield gaps (Mueller et al., 2012) because of the low fertile soil distribution with low precipitation (Morris et al., 2007; Zingore et al., 2015). Forage legumes can contribute to soil fertility through nitrogen (N) fixation by root nodules, promote other crops and vegetation growth, minimize

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nutritive values loss during maturity (Bedoussac et al., 2015; Kocira et al., 2020; Paul et al., 2020), and enhance animal performance due to their high-protein content and digestibility (Thomas and Sumberg, 1995). Livestock is widely grazed on native grasslands, but production is constrained by the levels and distribution of available soil nutrients and water, which limit the nutrient value based on the protein content and digestibility of most grass species (Tothill et al., 1990). This feed management scheme cannot meet the livestock's nutritional requirements, especially during the dry season, and intensive management requires fencing and/or housing which is an added cost for smallholders (Thomas and Sumberg, 1995). Therefore, relay cropping, forage legume intercropping with food crops, or propagating in natural grassland are recommended to ensure higher productivity and sustainability (Nalivata et al., 2017; Paul et al., 2020). Thus, despite forage legumes' potential benefits and the availability of species adapted to a wide range of environments, actual use in the livestock sector has been limited (Thomas and Sumberg, 1995).

Fertilization is recommended in SSA (Morris et al., 2007; Zingore et al., 2015). However, smallholders struggle to balance their incomes to purchase chemical fertilizers (Kaizzi et al., 2017; Wortmann et al., 2019) and its price has been increasing since 2021 (World Bank, 2022). This makes it necessary to use fertilizer alternatives, such as manure or cattle dung, compost, etc., as a fundamental crop-livestock integration element. Manure is used as an organic fertilizer in plant cultivation and its nutrient sources, such as N, phosphorus, potassium, and other essential nutrients can increase crop growth and production, as well as soil health and nutrient status (Cooperband et al., 2002; Farhad et al., 2011; Turhan and Ozmen, 2021), producing favorable effects on soil microbial biomass carbon and N (Belay et al., 2001; Bedoussac et al., 2015).

Glycine (*Neonotonia wightii*) (native to tropical Africa) and siratro (*Macroptilium atropurpureum*), (Central and South America origin and Caribbean Islands belonging to Fabaceae), are perennial plants and are often used as tropical forage legumes in low precipitation areas globally (Gimenes et al., 2017; Thomas and Sumberg, 1995). Both legumes produce high dry matter yields compared to other tropical forage legumes, such as dolichos (*Lablab purpureus*), velvet bean (*Mucuna pruriens*), and shrubby stylo (*Stylosanthes scabra*) (Macharia et al., 2010). Glycine and siratro have a water deficit tolerance, e.g., siratro, is more tolerant to water deficits than soybean (*Glycine max* [L.] Merr.) (Ohashi et al., 1999, 2000) and other tropical forage crops, such as *Cenchrus ciliaris* and *Panicum maximum*, by maintaining high levelsof leaf water potential, and is thus able to grow without experiencing changes in its root dry weight (DW) (Ohashi et al., 1999; Tokita et al., 2006). Siratro can be regrown following rainfalls after periods of drought, being able to be cultivated during the dry season. It is successfully grown in a wide range of climatic conditions (Timberlake and Dionisio, 1984). Thus, siratro was selected to be introduced for the smallholder system in SSA together with glycine (Baijukya and Giller, 2011) for further testing under different farming systems (Nyoka et al., 2004).

Climate change is a global problem, creating a hotter, drier world, thus affecting plant productivity across both managed and unmanaged ecosystems (Franklin et al., 2016). SSA is considered to be the most vulnerable and susceptible to its effects (Connolly-Boutin et al., 2016). Water shortage is driven by increased drought and low rainfall, and these are predicted to increase in this century (Cattivelli et al., 2008). Soil droughts form and intensity are changing and prolonged drought stress at various times has brought a tremendous impact on agricultural production and livestock (Rust and Rust, 2013). Drought stress constrains crop productivity and growth by affecting photosynthesis, respiration, ion uptake, and sugar and nutrient metabolic processes (Farooq et al., 2009). Ludlow (1980) reviewed that among the legumes, siratro was the most prolific responder to drought stress, that is, rooting ability or root elongation, sensitive stomata control by humidity and leaf water potential, transpiration by dropping older, larger leaves, etc. Additionally, also including forage grasses, drought stress is generally attributed to carbon transfer to roots, which is used for their growth. Similar drought effects have been reported for other legumes and cereal crops, such as a reduction of leaf relative water content (RWC) of alfalfa cultivars, a decrease of stomatal conductance and photosynthetic rate in perennial legumes such as lucerne, siratro, *Cullen* spp., and soybean and kidney bean; DW reduction in lucerne (*Medicago sativa L.*) and siratro; and roots development and increasing root-to-shoot ratio (R/S) of turf-type tall fescue (*Festuca arundinacea* Schreb.) (Liu et al., 2003; Miyashita et al., 2005; Karcher et al., 2008; Suriyagoda et al., 2010; Lugojan and Ciulca, 2011; Pang et al., 2011; Nakagawa et al., 2018). Furthermore, drought stress negatively affected plant growth and decreased N accumulation in rice, maize, soybean, and siratro (Ohashi et al., 2000; Tanguilig et al., 1977).

However, there is limited information on the plants' responses to drought stress and duration, with/without manure application. Therefore, a greenhouse pot trial was conducted using the two vegetative growth stage species, which were susceptible to terminal drought, grown with minimal nutrition, assuming low-fertility soils, the effects of drought stress and manure application with the different duration on traits related to moisture, photosynthesis and respiration, growth, and N content and quantity, which determines its value as a forage crop, were examined. The results between the two species were compared and based on this, the objective of this study is to gather information about the responses of these forage species during drought conditions and how manure application could mitigate it for further field trial.

MATERIALS AND METHODS

Experimental design

The experiment started with glycine and siratro seeding conducted on July 8, 2020, in a greenhouse (28/23°C day/night; average temperature and humidity: 27.2°C and 77.3%; Thermo Recorder TR-72wb, T&D Corporation, Nagano, Japan), which were located at the Japan International Research for Agricultural Sciences (JIRCAS, 36°03'14"N, 140°05'12"E). The three treatment groups were: drought treatment (D), manure application (M), manure application with drought treatment (MD), and no treatment group (control, C) were set up with four pots replication each, and each pot with one plant. The two forage legumes' single and interactive responses, glycine var. Tinaroo and siratro var. Aztec of vegetative growth stage, to the treatments were examined.

A total of 80 long pots (30.5 cm in height and 15 cm in diameter), with an equal number of pots per species (two) and treatments (four), and two sampling days (25 and 45 days after treatment started) were assigned and distributed randomly. Before sowing, the pots were filled with vermiculite for measurement of the manure application effect that excluded interference of individual soil types with different agroecological zones. The 5 t/ha of cattle manure (N, 1.5%; phosphorous, 1.6%; potassium, 2.2%; carbon-to-N ratio; 19, Tamura Farm, Tochigi, Japan), or 8.83 g pot^{-1}, was added to the manure treatment groups (M and MD) which were assumed to be the amount available for cattle holders in SSA (Abebe et al., 2005; Vanlauwe et al., 2015), while no manure was applied to C and D. The crude ash content was measured at 43.9% DW. At 10 days after sowing, seedlings were thinned to obtain one plant per pot. Since the plants were grown in vermiculite, from 25 days after sowing until the experiment's end, a 10 mL pot^{-1} time^{-1} of 100% Hoagland's solution (H2395, Salt Mixture Hoagland's solution Sigma and Aldric) was applied to all pots three times a week, according to the procedures described in McElroy et al. (2017). The drought treatment started 60 days after sowing and continued for 45 days by completely ceasing to water the plants to simulate terminal drought conditions.

Measurement

All pots were weighed every 2 or 3 days after drought treatment started. The weight of the pots at 0 days after drought treatment initiation (DAT) was taken as 100%, and the relative weight thereafter expressed as %, was defined as the pot water content (PWC). Soil samples were taken at a depth of 15 cm in the pots at 25 and 45 DAT (the mid and end point days, respectively), air-dried at 80°C for 48 h in an oven, and soil water content (SWC, %) was determined from the fresh and DW. The RWC (%) of leaflets at the same sampling days was calculated according to Ishibashi et al. (2011), as the ratio of leaflet water content measured from the uppermost fully expanded trifoliate leaf, drying for 48 h at 80°C to the turgid leaflet water content after water saturation for 24 h at 4°C. An AP4 Porometer (Delta-T Devices Ltd, Cambridge, UK) was used to measure the stomatal conductance twice a week on the uppermost fully expanded trifoliate leaf of the plant with four replications for each treatment between 10:00 and 12:00 h starting 0 DAT.

Plant growth on leaf expansion (that is, total leaflet number and area which express photosynthetic capacity) were measured based on all the leaves photos with scale taken with a digital camera (Tough TG-6, Olympus, Tokyo, Japan) on the sampling days, using ImageJ software (version 1.53a, National Institutes of Health, http://rsb.info.nih.gov/ij/). Four plant samples for each treatment were also taken at the same time and they were separated into leaves, stems and petioles, and roots. Each sample was air-dried at 80°C and measured DW. After grinding each sample using a high-speed vibration mill, the N content was determined by dry combustion method using an NC analyzer (Sumigraph NC 220F, Sumika, Japan). Then, N contents expressed per leaf unit area (g m^{-2}) and N amount by parts and whole plant (gDW plant^{-1}) were calculated.

Statistical analysis

Statistical analyses were conducted using SPSS 27 (IBM, Japan). The drought stress and manure application single effects and their interactions were analyzed on the measured and analyzed variables on PWC, SWC, RWC, stomatal conductance, leaf expansion, plant growth, dry matter allocation, and N contents and allocation of each species at each measurement and sampling time by General Linear Model of a two-way analysis of variance (ANOVA) with repetition. The replicate (n = 4) was treated as a random factor. The treatment means were subjected to one-way ANOVA to determine the differences at the 5% probability level when significant interactions among the factors were found for a parameter. Tukey's honestly significant difference (HSD) test was used for multiple comparisons of the means at the 5% probability level.

RESULTS

Physiological status

The PWC of both plants exposed to water deficit treatment (D and MD) showed a significant ($p < 0.05$) reduction in most measurement days after 10 DAT, as a result of the interaction effect of both treatments (Figure 1). The reduction rate with only drought stress (D) at 41 DAT was 38.2 and 42.5% for glycine and siratro, respectively, while C and M only showed a 2 to 12% reduction. MD resulted in a higher reduction, down to 48.1 and 61.1% for each species. Only the single effect of drought was found on SWC on both days for glycine ($p < 0.05$, Figure 2A). The D and MD contents declined with prolonged treatment duration, but the mean MD value (32.2%) was lower than that of D (43.6%) at the end (45 DAT). For siratro, only single effects by each treatment were detected at both measurement days (Figure 2B). Hence, at the midpoint (25 DAT), D was decreased compared to C and M, and MD was even lower when compared to D ($p < 0.05$). However, the mid-to-end changed, thus only the MD (26.2%) amount was even lower ($p < 0.05$) and the D (49.2%) content remained unchanged.

The RWC in glycine was maintained above 90% when plants were not subjected to drought stress. Only drought stress significantly reduced the content on both sampling

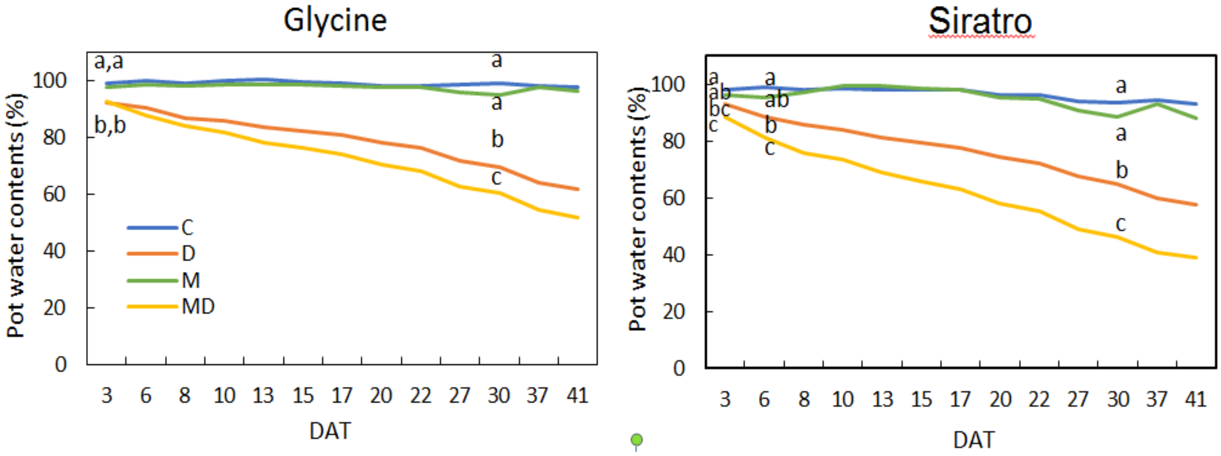

Figure 1. Effects of drought stress and manure application on pot water content (PWC, %) of glycine and siratro plants. PWC was calculated by assuming control and manure treatments in pot weight containing vermiculite, plants, and water at 0 day after drought treatment initiation (0 DAT) was considered as 100% and the relative weight thereafter expressed as %, was measured. C, control; D, drought treatment; M, manure application; and MD, manure application with drought treatment. Interaction of the effects of drought stress and manure application by two-way ANOVA was found from 10 DAT until the end of the experiment except for 30 DAT ($p < 0.1$). The drought stress and manure application single effects were shown from the 3 and 6 DAT, respectively ($p < 0.1$), in glycine. In siratro, the interaction was found from 8 DAT until the end, except 30 and 41 DAT ($p < 0.1$), and single effects by both treatments were detected from 3 DAT. Different alphabets for each measurement day indicate significant differences in means by Tukey's HSD test ($p < 0.05$), and alphabets in squares indicate identical results during the period. The error bar represents standard deviation.
Source: Authors

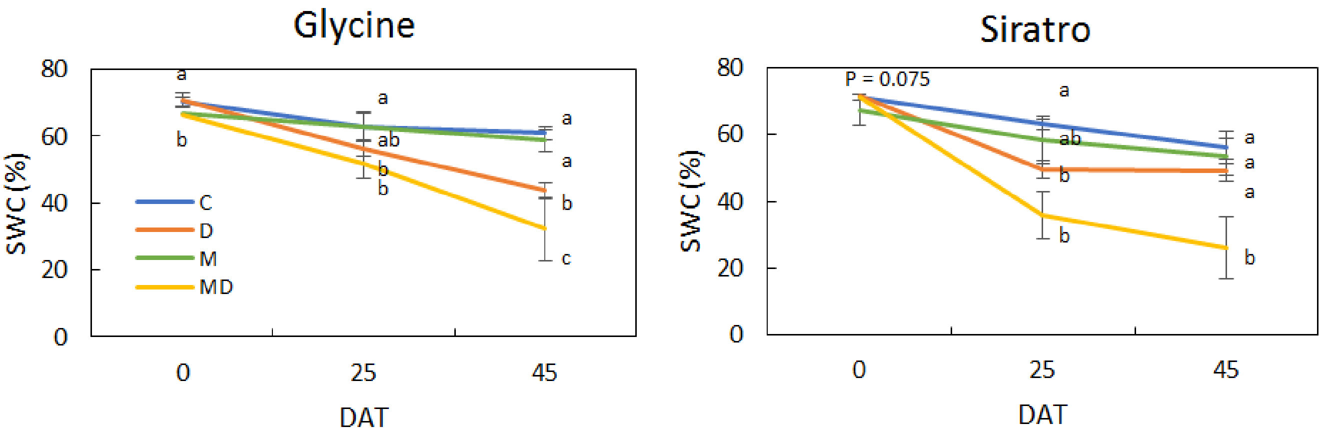

Figure 2. Drought stress and manure application effects on soil water content (SWC, %) of glycine and siratro plants. SWC was measured using the samples taken at a depth of 15 cm in the pots and then air-dried. C, control; D, drought treatment; M, manure application; and MD, manure application with drought treatment (n = 4). The single effect of drought was shown at both measurement days ($p < 0.05$), and the effect of manure application and interaction was not found in glycine by two-way ANOVA ($p > 0.05$). In siratro, single effects were detected by each treatment at both measurement days and no interaction was found. Different alphabets for each day indicate significant differences in the means by Tukey's HSD test ($p < 0.05$). The error bar represents standard deviation.
Source: Authors

days ($p < 0.05$), but in the end, those with manure added (M; 91.3% or MD; 80.4%) were significantly lower than those with no manure (C; 95.1% or D; 85.9%), respectively ($p < 0.05$, Figure 3A). The siratro content was also significantly lower in the drought-stressed groups (D or MD) than in the unstressed groups (C or M)

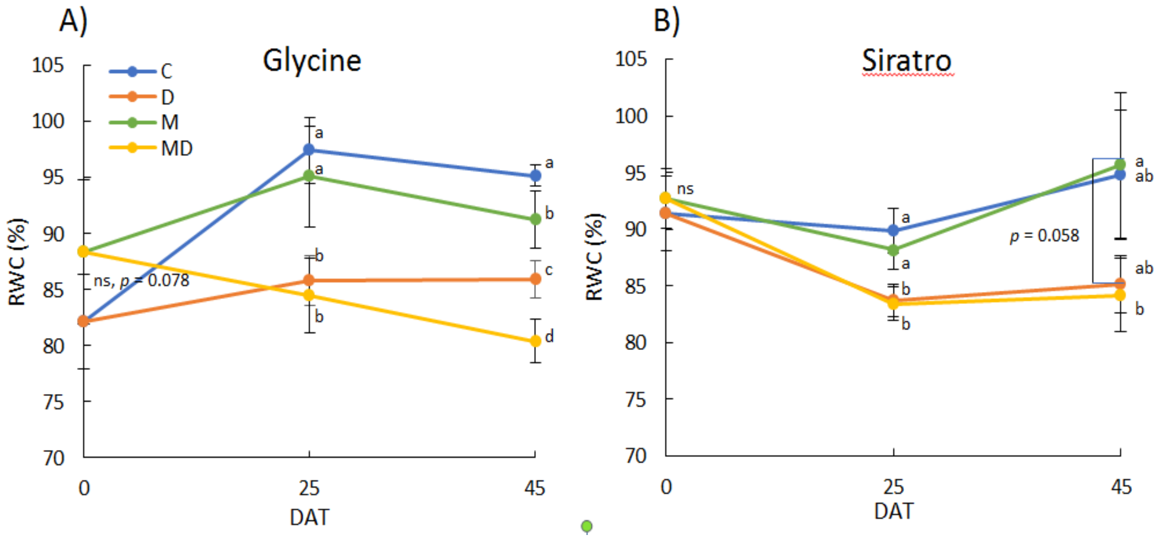

Figure 3. Drought stress and manure application effects on leaf relative water content (RWC, %) of glycine and siratro plants. RWC of leaflets at the same sampling days was calculated according to Ishibashi et al. (2011). C, control; D, drought treatment; M, manure application; and MD, manure application with drought treatment (n = 4). In glycine, drought or manure application single effect was detected on both measurement days ($p < 0.001$) or on the second measurement day, respectively. No interaction was found by two-way ANOVA ($p > 0.05$). In siratro, a single effect of drought treatment was found at both measurement days ($p < 0.05$) and no other single effect nor interaction was found ($p > 0.05$). Different alphabets for each day indicate significant differences in the means by Tukey's HSD test ($p < 0.05$). The error bar represents standard deviation.
Source: Authors

at the mid ($p < 0.05$, Figure 3B). The trend continued but was not affected by manure application and the D (85.1%) and MD (84.2%) contents were almost similar until the end.

No significant differences among the treatment groups were found on glycine stomatal conductance until 22 DAT ($p > 0.05$, e.g., ranged 112-357 mmol m^2 s^{-1} in D and MD during 4 and 22 DAT), but from 28 DAT, it decreased significantly due to drought stress regardless of manure application ($p < 0.05$, e.g., ranged 56-123 mmol m^2 s^{-1} in D and MD after 28 DAT, Figure 4A). In siratro, the interaction effect was detected only three days in the early to medium timing (8, 15, and 22 DAT) (Figure 4B). Drought stress had an effect and the values in D were significantly low ($p < 0.05$) compared with those in C almost all the time after 18 DAT. The value of M (ranged 369-1424 mmol m^2 s^{-1} after 8 DAT) was higher than that in C during almost all the experiment time ($p < 0.05$). Manure application also mitigated the drought stress several times as seen in the MD value (523 mmol m^2 s^{-1}) was significantly higher than that of D (117 mmol $m^{-2}s^{-1}$) at 37 DAT ($p < 0.05$).

Plant growth and dry matter allocation

The treatment effects on plant growth, including leaf expansion and dry matter allocation, are shown in Table 1. Results are presented only from the single effect, as no interaction effect was found on all variances for each sampling day ($p > 0.05$). For glycine leaf expansion on the leaflet number and area, drought stress had no effect at mid ($p > 0.05$ for both traits) and significantly affected ($p < 0.01$) and decreased at the end, whereas manure application significantly increased at each sampling day ($p < 0.001$-0.01). In siratro, the drought forced it to be greater at mid ($p < 0.05$ for leaflet number and $p < 0.001$ for the area), but after that, the affected severely became lower than those of the non-drought treatment groups ($p < 0.001$).

Biomass (gDW $plant^{-1}$) of each glycine part was not affected by drought stress until the mid ($p > 0.05$), but was reduced only on the leaves at the end ($p < 0.01$). It increased significantly after manure application on both days ($p < 0.001$-0.05). The results for siratro biomass were similar to those for glycine in which leaf biomass was reduced by drought stress regardless of manure application at the end of treatment; roots were elongated under manure effect regardless of drought. A difference was also detected in drought stress which caused a significant increase in leaf, stem, and petioles ($p < 0.05$) and root ($p < 0.001$) at mid, and significantly decreased at the end ($p < 0.001$ for leaf; $p < 0.05$ for stem and petioles, and root). Then, the glycine biomass of the whole plant

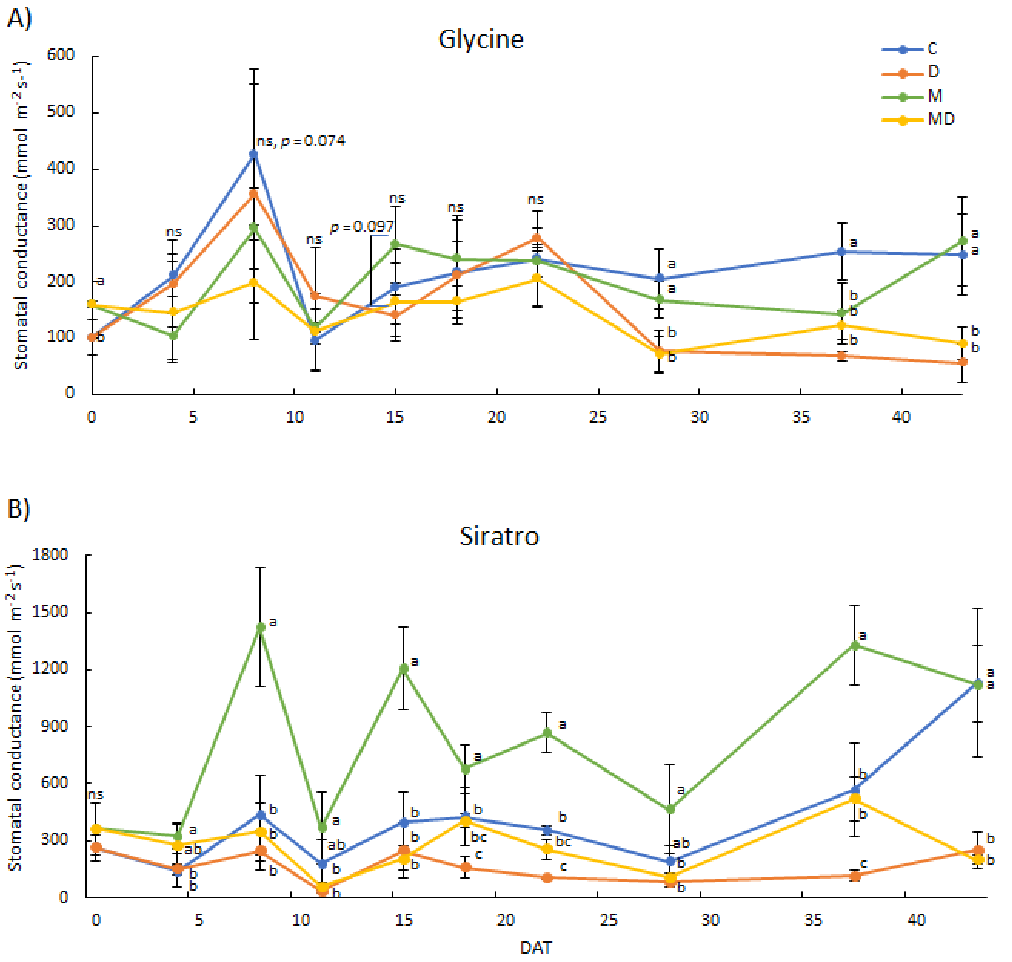

Figure 4. Drought stress and manure application effects on leaf stomatal conductance of glycine and siratro plants. Stomatal conductance was measured on the uppermost fully expanded trifoliate leaf of the plant every 2 or 3 days from 0 days after drought treatment initiation (0 DAT). C, control; D, drought treatment; M, manure application; and MD, manure application with drought treatment (n = 4). In glycine, drought treatment single effect was seen at 15, 28, and 43 DAT ($p < 0.001 - 0.05$). No interaction effect of the two treatments was found ($p > 0.05$). In siratro, an interaction effect of the two treatments was detected in 8, 15, and 22 DAT ($p < 0.001 - 0.01$). On the other measurement days, the single effect of the dry treatment appeared after days 11, 18, 37 and 43, and the effect of manure application on four, 18, 28 and 37 DAT ($p < 0.001 - 0.01$). Different alphabets for each measurement day indicate significant differences in the means by Tukey's HSD test ($p < 0.05$). The error bar represents standard deviation.
Source: Authors

was decreased by the prolonged drought (45 DAT), but increased by manure application, whereas that of siratro increased at mid and decreased at the end because of the drought.

The L/S of glycine on each day was not affected by the treatments ($p > 0.05$), whereas R/S increased because of the prolonged drought effect ($p < 0.05$) as seen in the mean R/S of D (0.34) which was significantly the highest in the treatment groups at the end ($p < 0.05$). The drought stress affected siratro and reduced L/S at the end and increased R/S at mid ($p < 0.001$ for both). Siratro was a bigger plant than glycine compared with the mean number of leaflets (glycine ≤64.3 and siratro ≤111.8) and with the whole plant average weight (glycine ≤3.72 gDW and siratro; ≤7.98 gDW). Glycine allocated more dry matter to the leaves than siratro from the L/S at 45 DAT (glycine >0.45 and siratro <0.37).

Plant N contents and allocation

For glycine, leaf N content (%DW) was significantly decreased by the single effect of drought stress ($p < 0.05$) or manure application ($p < 0.001$-0.01), in which the mean content was highest in C, intermediate in D, and significantly lower in M and MD ($p < 0.05$). The results were similar on the stem and petiole at mid and treatment interaction was observed at the end ($p < 0.01$). Root N content decreased at the end only when manure was applied ($p < 0.05$). Hence, dry matter allocation was also involved in the interaction effect ($p < 0.05$) at the end that significantly reduced total N contents and the amount of leaf N per unit area (g m^{-2}). The leaf N (gDW $plant^{-1}$) amount decreased under the influence of drought stress at the end ($p < 0.05$) and increased with manure application at the mid ($p < 0.05$), which tended to continue until the end. The stem and petioles, and root N amount increased significantly only with manure application ($p < 0.001$-0.05). Therefore, total N significantly or tended to decrease with drought stress ($p < 0.05$ at 25 DAT and $p = 0.054$ at 45 DAT) and increased with manure application ($p < 0.01$ and 0.05, respectively). No significant difference ($p > 0.05$) was found between the means of N amounts in C and MD, and M and MD at the end.

In siratro, drought stress decreased shoot N contents only at the mid (leaf, $p < 0.001$ and stem and petioles, $p < 0.05$) and increase root N contents at the end ($p < 0.05$). Manure application did not affect N contents of any part at each sampling time except in stems and petioles at mid. The total N content was then decreased at the mid and increased at the end because of the interaction effect. Leaf N content per unit area was decreased only by drought at the end ($p < 0.05$). Initially, drought stress did not affect the amount of leaf N and increased root, but strongly affected ($p < 0.001$) the leaf at the end of the experiment. Manure application when compared with no application maintained or increased the amount of all parts in the prolonged drought stress. Mean plant N content was significantly lower in MD at the end compared to C and M in leaves ($p < 0.05$). However, the D and MD comparison showed that MD content in roots was significant and was almost six times higher, therefore, three times higher than in the total N content ($p < 0.05$).

DISCUSSION

Influence of drought stress on plant physiology and growth

Glycine and siratro exposed to drought and manure fertilization showed similar responses at some points which are in agreement with previous studies (Nakagawa et al., 2018; Ohashi et al., 2000; Suriyagoda et al., 2010), that is, decrease of RWC, leaf stomatal conductance, DW, especially of shoot, an increase of R/S through root development, and decrease of N accumulation especially in shoot. With adequate water supply, as in C and M, PWC hardly decreased, SWC decreased only enough to support plant body maintenance and growth, and RWC was in the normal range (Figures 1 to 3). The drought stress treatment reduced PWC and SWC. Under unfavorable conditions, in general, tissue water potential and water contents were maintained close to unstressed levels, increasing water uptake as a stress avoidance and tolerance mechanism (Versules et al., 2006). Reduction of leaf RWC, leaf number, and area (Table 1) caused by drought stress may be associated with a decrease in leaf turgor due to reduction of leaf water potential and photosynthetic activity (Ohashi et al., 2000). It means that these phenomena are interrelated, that is, decrease in stomatal conductance due to drought stress (Figure 4); simultaneously decreasing photosynthesis and green cell respiration by stomatal closure; and resulting in reduced organic matter and plant growth production, including N accumulation (Tanguilig et al., 1977), that is, leaflet number and area reduction, slowing down photosynthesis, and accelerate shoot biomass decrease (Table 1). The effect becomes more obvious as the stress is prolonged. An R/S increment as shown in the present study is a medium- to long-term change adopted to keep plant water loss balance and uptake during drought conditions when it cannot be achieved by short-term mechanisms such as stomatal closure, to maximize plant water uptake (Versules et al., 2006).

A greater PWC and SWC reduction in the manure applied than in non-applied showed an increased moisture necessity in soils for plants when manure was applied at sowing. A direct supply of the available nutrients, such as N (Cooperband et al., 2002; Farhad et al., 2011) provides more nutrients for plant growth and the larger the biomass of a species or individual plant, the greater the demand for water and the greater the decrease in the indicator of water contents.

Drought stress mitigation by manure application

Manure application alone increased biomass and plant N amount and mitigated or compensated damage even under drought stress based on a comparison between drought treatments (D and MD at the end for both plants; Tables 1 and 2). N supply mitigated and enhanced plant resistance to drought stress by enhanced photosynthetic capacity through increased nitrate accumulation and nitrate reductase activity in maize seedlings (Li et al., 2020). Manure application provided more N and other nutrients essential for plant growth than non-application, by fast-acting of ash portion and slow acting by the remaining organic matter portion. Therefore, manure application increases biomass by inducing plant growth while mitigating drought-induced reduction in N and other nutrients in the whole plant.

Table 1. Effect of drought treatment and manure application on plant growth expressed by leaf expansion and dry matter allocation in glycine and siratro plants on different days after treatment.

Species	DAT	Treatment	Leaflet no.	Leaf area	Leaf	Stem and petioles	Root	Total	Leaf-to-shoot ratio	Root-to-shoot ratio
				m^2	gDW $plant^{-1}$					
Glycine	25	C	34.3^{b}	0.0206^{bc}	0.61^{bc}	0.38^{b}	0.17^{b}	1.16^{b}	0.61^{a}	0.18^{a}
		D	27.5^{b}	0.0145^{c}	0.33^{c}	0.25^{b}	0.11^{b}	0.69^{b}	0.58^{a}	0.20^{a}
		M	49.8^{ab}	0.0448^{a}	1.38^{a}	1.03^{a}	0.43^{ab}	2.83^{a}	0.58^{a}	0.18^{a}
		MD	51.0^{a}	0.0392^{ab}	1.05^{ab}	1.01^{a}	0.55^{a}	2.61^{a}	0.51^{a}	0.27^{a}
	45	C	51.0^{a}	0.0238^{bc}	0.77^{bc}	0.65^{bc}	0.25^{a}	1.67^{bc}	0.54^{a}	0.18^{b}
		D	20.8^{b}	0.0104^{c}	0.38^{c}	0.34^{c}	0.26^{a}	0.98^{c}	0.54^{a}	0.34^{a}
		M	64.3^{a}	0.0634^{a}	1.68^{a}	1.46^{a}	0.58^{a}	3.72^{a}	0.53^{a}	0.18^{b}
		MD	47.4^{a}	0.0355^{b}	1.04^{ab}	1.25^{ab}	0.56^{a}	2.85^{ab}	0.45^{a}	0.26^{ab}
Siratro	25	C	49.0^{b}	0.0209^{b}	0.36^{b}	0.41^{b}	0.13^{c}	0.90^{b}	0.47^{a}	0.18^{c}
		D	61.3^{ab}	0.0332^{ab}	0.83^{ab}	1.40^{ab}	1.00^{ab}	3.27^{ab}	0.37^{a}	0.42^{ab}
		M	55.0^{b}	0.0179^{b}	1.06^{ab}	1.51^{ab}	0.71^{bc}	3.28^{ab}	0.41^{a}	0.25^{bc}
		MD	111.8^{a}	0.0589^{a}	1.54^{a}	2.49^{a}	1.80^{a}	5.82^{a}	0.38^{a}	0.45^{a}
	45	C	68.0^{a}	0.0333^{b}	1.19^{b}	2.52^{ab}	1.84^{a}	5.55^{ab}	0.32^{a}	0.49^{a}
		D	29.6^{b}	0.0096^{b}	0.21^{c}	0.64^{b}	0.42^{b}	1.27^{c}	0.24^{b}	0.47^{a}
		M	96.0^{a}	0.0550^{a}	1.89^{a}	3.29^{a}	2.80^{a}	7.98^{a}	0.37^{a}	0.55^{a}
		MD	27.4^{b}	0.0126^{bc}	0.39^{c}	2.42^{ab}	2.22^{a}	5.02^{b}	0.14^{b}	0.77^{a}
Significance										
Glycine	25	D	ns	ns	ns	ns	ns	ns	ns	ns
		M	**	***	**	**	**	**	ns	*
		M × D	ns	ns	ns	ns	ns	ns	ns	ns
	45	D	**	**	**	ns	ns	*	ns	*
		M	**	***	*	***	**	***	ns	ns
Siratro	25	D	*	**	*	*	***	**	*	***
		M	ns	ns	*	*	ns	*	ns	ns
		M × D	ns	ns	ns	ns	ns	ns	ns	ns
	45	D	***	***	***	*	*	***	***	ns
		M	ns	*	*	*	**	**	ns	ns
		M × D	ns	ns	ns	ns	ns	ns	ns	ns

DAT, Day after treatment initiation; DW, dry weight. Shoot includes leaf, stem and petioles. C, control; D, drought treatment; M, manure application; MD, manure application with drought stress. Values are the mean (n = 4). Significance: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, ns; $p > 0.05$ or not significant by two-way ANOVA. Within each column of each DAT, means with different alphabets indicate significant differences among the treatments at 5% of Tukey' HST test

Source: Authors

Contrasting responses detected between glycine and siratro

Glycine and siratro reacted differently in several aspects. Glycine responses showed that drought stress inhibits plant growth, especially if prolonged (Tables 1 and 2). However, there was no significant reduction in L/S between with/without drought stress and its duration. Manure application increased water requirement but minimized or compensated the drought stress effect regardless of duration, that is, there was no significant reduction in all traits related to plant growth, except plant

Table 2. Effect of drought treatment and manure application on nitrogen contents and allocation in glycine and siratro plants on different days after treatment.

Species	DAT	Treatment	Leaf	Stem and petioles	Root	Total	Leaf	Leaf	Stem and petioles	Root	Total
			%DW				g m^{-2}	10^{-3}g DW plant^{-1}			
Glycine	25	C	3.22^{a}	2.32^{a}	1.54^{a}	2.68^{a}	0.854^{a}	19.87^{ab}	8.75^{ab}	2.57^{b}	31.19^{ab}
		D	2.71^{ab}	1.83^{ab}	1.55^{a}	2.21^{a}	0.828^{a}	9.03^{b}	4.53^{b}	1.65^{b}	15.21^{b}
		M	1.84^{bc}	1.15^{bc}	1.49^{a}	1.54^{b}	0.582^{a}	25.15^{a}	11.34^{a}	6.37^{a}	42.86^{a}
		MD	1.74^{c}	1.01^{c}	1.42^{a}	1.39^{b}	0.527^{a}	17.47^{ab}	9.76^{ab}	7.57^{a}	34.79^{a}
	45	C	2.77^{a}	1.71^{a}	1.77^{a}	2.20^{a}	0.907^{a}	21.19^{ab}	10.79^{ab}	4.48^{ab}	36.45^{ab}
		D	2.05^{ab}	1.01^{b}	1.50^{ab}	1.55^{b}	0.554^{b}	7.68^{b}	3.29^{b}	3.84^{b}	14.81^{b}
		M	1.74^{b}	0.83^{b}	1.47^{b}	1.35^{b}	0.442^{b}	27.78^{a}	11.25^{ab}	8.41^{ab}	47.44^{a}
		MD	1.65^{b}	0.93^{b}	1.48^{b}	1.31^{b}	0.483^{b}	18.36^{ab}	11.82^{a}	8.49^{a}	38.70^{ab}
Siratro	25	C	5.43^{a}	3.17^{a}	1.42^{a}	3.81^{a}	1.662^{a}	19.56^{a}	12.59^{ab}	1.88^{b}	34.02^{b}
		D	2.87^{b}	0.99^{b}	0.96^{a}	1.48^{b}	0.731^{a}	20.99^{a}	10.89^{b}	8.93 ^{ab}	40.82^{ab}
		M	3.48^{ab}	1.15^{ab}	0.98^{a}	1.89^{b}	1.673^{a}	35.59^{a}	15.96^{ab}	7.03 ^{ab}	58.58^{ab}
		MD	2.56^{b}	0.88^{b}	0.81^{a}	1.29^{b}	0.696^{a}	38.89^{a}	20.59^{a}	16.20^{a}	75.68^{a}
	45	C	2.38^{a}	0.88^{b}	0.99^{a}	1.24^{b}	0.897^{a}	28.72^{b}	22.51^{ab}	18.58^{ab}	69.8^{b}
		D	3.45^{a}	1.57^{a}	1.21^{a}	1.76^{a}	0.898^{a}	6.78^{c}	9.54^{b}	4.83^{b}	21.15^{c}
		M	2.60^{a}	0.99^{b}	0.99^{a}	1.37^{ab}	0.800^{a}	48.83^{a}	32.86^{a}	27.42^{a}	109.11^{a}
		MD	2.94^{a}	1.07^{b}	1.27^{a}	1.31^{ab}	0.836^{a}	11.48^{c}	25.81^{ab}	27.70^{a}	65.00^{b}
Significance											
Glycine	25	D	*	*	ns	*	ns	ns	ns	ns	*
		M	***	***	ns	***	*	*	:**	:***	**
		M × D	ns	ns	ns	ns	ns	ns	ns	ns	ns
	45	D	*	*	ns	*	ns	*	ns	ns	ns (p = 0.054)
		M	**	**	*	**	*	ns	*	*	*
		M × D	ns	**	ns	*	*	ns	ns	ns	ns
Siratro	25	D	***	*	ns	***	*	ns	ns	*	ns
		M	ns	*	ns	**	ns	ns	*	ns	*
		M × D	ns	ns	ns	**	ns	ns	ns	ns	ns
	45	D	ns	ns	*	ns	ns	***	*	ns	***
		M	ns	ns	ns	ns	ns	*	**	**	***
		M × D	ns	ns	ns	*	ns	ns	ns	ns	ns

DAT, Day after treatment initiation; DW, dry weight. Shoot includes leaf, stem and petioles. C, control; D, drought treatment; M, manure application; MD, manure application with drought stress. Values are the mean (n = 4). Significance: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, ns; $p > 0.05$ or not significant by two-way ANOVA. Within each column of each DAT, means with different alphabets indicate significant differences among the treatments at 5% of Tukey' HST test
Source: Authors

N content. These results showed glycine’s high potential as a feed for livestock especially when manure is applied. Thus, further field experiments are expected to confirm the results in practice and provide local holders in SSA with information to improve forage yield and quality.

Compared to glycine, siratro was more sensitive to drought stress and manure application and showed a more complex phenomenon. In siratro, plants under drought stress grew as well as or better than in the non-drought-stressed plants in terms of leaf expansion and biomass traits using residual moisture up to mid. However, at the end of the treatment, particularly when drought stress-only (D), all the traits that showed excellent results on the previous measurement day were significantly decreased. Less leaf number and area and L/S ratio meant that photosynthetic capacity was reduced, and the plants wilted. Less shoot biomass means less forage. In addition, leaves have a higher N content than stems and petioles and are more digestible by being retained in the rumen for a shorter period (Mganga et al., 2021). Leaves biomass was reduced more than that of stem and petioles, resulting in a lower leaf-to-stem ratio and lower forage value. On the other hand, at mid-to-end changed N contents for each part and the whole plant tended to increase rather than decrease in drought treatment (D). Furthermore, in the end, the N content in D tended to be higher than in C in each part. These results were different from those in glycine and others reviewed but known phenomenon as an adaptive form of maintaining the N and protein content of the plant. Physiologically, as described by Sahid et al. (2020), it might be an upregulation of crude protein percentage or N content, led by overexpression of response proteins under drought.

Since plants with higher biomass, siratro compared with glycine, require more water supplies to maintain normal growth conditions, it can be argued that water deficit had a more severe effect or had a stronger adaptive response in small plants when exposed to prolonged drought. The wilting of the D plants appears to be due to a lack of water but taken together with the fact that MD plants continued to grow to the end, the wilting could be due to a lack of both water and nutrients. This suggested that siratro has its disadvantage for cultivation in regions where low-fertility soils are distributed, as is the case in SSA. However, siratro was shown to have it is superior a seen MD root elongation and increased shoot N contents (Tables 1 and 2). These results are complemented by those on the PWC and SWC results. Particularly at the end of the treatment, the SWC of D remained relatively high (Figure 2), possibly due to the wilted plant’s decreased root water absorbance, while that of MD continued to decrease. The plants were able to prevent transpiration by reducing the shoot biomass along with accumulation and similar amounts of plant N as observed at mid, but as indicated by the higher stomatal conductance value maintained by MD than by D, still actively photosynthesizing and respiration using water-promoted root growth. This is a form of adaptation for survival to avoid drought injury as Karcher et al. (2008) noted. As shown in the high productivity along with constantly high photosynthesis activity at the time of manure application, once rainfall and nutrition are favorable, it is ready to start growing again (Timberlake and Dionisio, 1984). Thus, further studies are required for the high possibility that siratro can be used in SSA after determining the conditions where it can thrive.

Conclusions

The accurate responses of the two tropical forage legumes were obtained from the greenhouse pot experiment which excluded the individual soil types’ effects with different moisture conditions. Glycine was affected by drought stress, especially if prolonged, but could avoid shoot loss by maintaining plant growth, and has shown advantages in its cultivation for foraging purposes when compared with siratro. Manure application mitigated or compensated the effects of drought stress. Thus, further field experiments are expected to confirm the results which showed drought tolerance and effectivity of manure application in practice and provide local smallholders in SSA with information to improve forage yield and quality. Siratro required more water and nutrition, manure mitigated the effect of drought stress, and further studies are required for the possibility that siratro can be cultivated in SSA after determining the conditions where it can thrive.

CONFLICT OF INTERESTS

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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