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Replacement control of *Mikania micrantha* in orchards and its eco-physiological mechanism

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Mikania micrantha is one of the most notorious invasive weeds in south China, especially in orchard habitats. Based on the principle of niche competition, screening plants with strong competitiveness and managing vacant niches through natural alternative methods (replacement control) were expected to achieve sustainable ecological management of invasive species. To this end, two legumes, *Desmodium heterocarpon* and *Senna tora*, were selected to conduct field competition experiments with *M. micrantha* to investigate the interspecific competitiveness of these two legumes and *M. micrantha* from the aspects of adaptability to low light and response to drought stress. We found that the relative interaction indexes of *D. heterocarpon* and *S. tora* to *M. micrantha* were both negative and the competitive inhibition of *S. tora* on *M. micrantha* was higher than that of *D. heterocarpon*. Compared with *M. micrantha*, *D. heterocarpon* and *S. tora* have higher photosynthetic efficiency and lower dark respiration efficiency under low-light conditions, thus maintaining positive plant carbon balance capacity in the low-light understory and becoming more shade-tolerant. Besides, the water stress experiment found that *M. micrantha* had the lowest tolerance to drought stress, followed by *S. tora*, and *D. heterocarpon* was the most drought tolerant. These results showed that *D. heterocarpon* and *S. tora* can effectively prevent and control *M. micrantha*, mainly due to their higher competitiveness, shade tolerance, and drought tolerance. The control effect of *D. heterocarpon* is better than that of *S. tora* which is an alien species. Therefore, we believed that the replacement control of the invasive weed *M. micrantha* by *D. heterocarpon* is expected to be a sustainable ecological management strategy for *M. micrantha* biocontrol in the dryland orchard habitat. These findings provide a theoretical basis for the selection of species for alternative control in the future and provide new ideas for solving the problem of repeated regeneration in the existing *M. micrantha* control process.

KEYWORDS

plant invasion, *Mikania micrantha*, *Desmodium heterocarpon*, replacement control, resource competition

1. Introduction

Due to the rapid development of economic globalization and international transportation, more and more species have been introduced, intentionally or unintentionally, into new environments previously isolated by natural barriers (Chen et al., 2016; Courchamp et al., 2017). These alien species are often highly adaptable and able to survive, reproduce, and spread in new environments, resulting in severe alien species invasions (Theoharides and Dukes, 2007). Biological invasions pose an enormous threat to ecosystems and public health by replacing native species, reducing biodiversity, altering community structure, and impairing ecosystem function (Slingenberg et al., 2009), resulting in huge economic losses (Pimentel et al., 2001). Therefore, how to effectively control invasive alien species, especially the control of alien weeds, is a hot spot in the field of invasive ecology research.

Mikania micrantha (mile-a-minute weed) is native to tropical regions of Central and South America and the Caribbean and is a fast-growing perennial vine belonging to the *Asteraceae* family (Choudhury et al., 2016). Due to natural and anthropogenic factors, *M. micrantha* is widely distributed in tropical and subtropical regions of Asia and the Pacific, and is one of the 100 worst invasive alien species announced by the International Union for Conservation of Nature (IUCN; Day et al., 2016). *M. micrantha* germinates early in the growing season, has a fast growth rate (up to 20 cm per day), and can reproduce vegetatively by forming roots and branches at each node, resulting in new individuals (Kaur et al., 2012). Therefore, if not controlled, it may rapidly spread to new habitats, covering the forest or plantation canopy (Day et al., 2012), causing the covered plants to suffocate and die due to lack of sunlight, so *M. micrantha* is also known as “plant killer” (Zhang et al., 2004). The rapid spread of *M. micrantha* not only destabilized the ecosystems in which it invaded, but also caused great economic losses (Day et al., 2016). For example, due to the invasion of *M. micrantha* every year in Neilingding Island in Shenzhen, China, the average annual economic loss amounts to CNY 4.5–10.13 million for the whole island (Zhong et al., 2004). Most notably, *M. micrantha* is responsible for the reduction of the production in many orchards by climbing up the orchard canopy and blocking the sunlight (Macanawai et al., 2012; Shen et al., 2015). It is thus essential to seek an effective method for controlling *M. micrantha* in orchards.

The serious invasion of *M. micrantha* in tropical and subtropical regions has attracted more and more attention around the world. In order to remove *M. micrantha* from the invasion area, different control methods have been developed, mainly divided into physical control, chemical control, and biological control (Li M. et al., 2012, 2015). Physical control, usually harvesting the above-ground part of the *M. micrantha*, can only control the invasion in a short term and does not completely eradicate *M. micrantha*, but may increase the potential threat of further spread (Swamy and Ramakrishnan, 1987). Herbicide is the main method of chemical control to remove *M. micrantha*. However, it

can lead to drug resistance and chemical contamination of the local environment (Islam et al., 2018; Mohanty and Jena, 2019). At present, the most successful method for *M. micrantha* is biological control. It has been found that the rust fungus *Puccinia spegazzinii* and the butterfly *Actinote antea*s (natural enemy insect of *M. micrantha*) have good pathogenicity and encroach on *M. micrantha*, and can control *M. micrantha* to a certain extent (Barreto and Evans, 1995; Li et al., 2004; Day et al., 2013). Previous studies found that the parasitic field dodder *Cuscuta campestris* parasitized *M. micrantha*, which could cause *M. micrantha* to die (Li F. L. et al., 2012). However, due to the safety and limitations of biological control, there is no precedent for biological control of *M. micrantha* in orchards. The growth of fruit trees and the formation of orchard habitats have their unique characteristics. With the fruit trees bearing from young age to mature, the stand space appeared obvious differentiation, which was manifested as distinct differences in plant composition, spatial distance, and microclimate between canopy and understory. However, the long-term periodic reclamation and weeding operations of understory make understory vegetation dwarf, sparse, or even lose, and the ecological niche is finally vacant, resulting in ecosystem loopholes, which leads to the invasion of notorious weeds led by *M. micrantha*. If we choose native or valuable species with high competitiveness to cover the orchard ground based on replacement control technology, the growth of *M. micrantha* could be suppressed or its establishment can be prevented.

The current control methods for *M. micrantha* cannot solve the problem of regeneration and proliferation of *M. micrantha*, the main reason is that the management of the vacant ecological niche after the control is neglected. If we can use the principle of niche competition, select plants with strong competitiveness, and fill vacant niches progressively through natural succession, it will be possible to achieve ecological sustainability in the management of invasive species, which can be regarded as replacement control (Piemeisel and Carsner, 1951; Piemeisel, 1954; Li et al., 2015; Shen et al., 2015, 2016). Compared with chemical or mechanical control methods, replacement control is generally considered more economical, safe, eco-friendly, and sustainable. Regarding the replacement control of *M. micrantha*, the reported replacement plants are mainly herbs, shrubs, and fast-growing trees, such as grass species tall fescue *Festuca arundinacea* (Xu et al., 2011), *Mosla chinensis* (Song et al., 2020), perennial Italian ryegrass *Lolium multiflorum* (Xu et al., 2011), annual wormwood *Artemisia annua* (Xu et al., 2011) and sweet potato *Ipomoea batatas* (Shen et al., 2016), leguminous shrub *Stylosanthes guianensis* (Song et al., 2020), southeast Asian pioneer tree *Macaranga tanarius* (Li M. et al., 2012), and kesseru plant *Heteropanax fragrans* (Li M. et al., 2012), etc. Among them, the replacement effect of sweet potato was better, and field experiments have been done. The results showed that when sweet potato was mixed with *M. micrantha*, it can accumulate more biomass and absorb more soil nutrients, so it has a stronger competitive advantage (Shen et al., 2015), and can inhibit the reproductive ability of *M. micrantha* (Shen et al., 2016). However,

the reported replacement plants and *M. micrantha* belong to different life forms and occupy different ecological niches. Although sweet potatoes can disperse by crawling, they cannot climb upward. According to the limiting similarity theory, species with similar niches tend to be more competitive, so whether they have a similar niche to invasive species is an important determinant for replacement plants to resist invasive species (Price and Partel, 2013; Kimball et al., 2014). Different species with the same ecological niche strive to suppress each other in order to compete for limited resources and space, which directly leads to interspecific competition (MacArthur and Levins, 1964). Replacement control research has recently focused on screening valuable or native species for competitiveness, mechanisms of competition, and native ecosystem restoration effects. Therefore, screening native species in similar ecological niches to control invasive species is beneficial to the sustainable ecological management of invasive species.

The principle of replacement control is to use the mutual competition between plant species to control harmful weeds, especially invasive weeds, with one or more plants with competitive advantage. Plant competition plays an important role in shaping individual plant morphology, physiology, and life history and in determining plant community structure and succession (Grace, 2012), thus plant competition is one of the areas that ecologists focus on. The maximum growth rate theory proposed by Grime (1979) and the minimum resource requirement theory by Tilman (1980) are two classic competition theories. Grime's theory is based on the life strategies and traits of plants, and believes that the species with the greatest resource capture potential will be the competition winner (Grime, 1977, 1979). Tilman's theory proposes a numerical model of plant individual populations with resource capture rates as a function of plant traits, which believes that the species with the smallest resource requirements will be the winner of the competition (Tilman, 1988). In recent years, many studies have carried out researches on the competition between indigenous plants and forages and invasive alien plants, and found that some indigenous plants and forages have a strong competitive effect on invasive alien plants, which can better control the growth, development, and spread of alien plants (Scasta et al., 2015). Our preliminary work found that using native legumes can be a better option for the replacement control of invasive weeds (Li et al., 2015). Therefore, in order to elucidate which theory can explain such phenomenon, we selected a variety of plants for trial to screen replacement plants in the orchard, and finally screened out two forage legumes with the potential to control *M. micrantha*, and explored the ecological processes and mechanisms of replacement control of *M. micrantha* under low-light and drought-stressed treatments in two legumes to provide a theoretical basis for the selection of replacement species in the future. The results obtained in this study are of great significance for ensuring ecological security and promoting sustainable prevention and control of invasive species and ecological restoration.

2. Materials and methods

2.1. Screening of replacement plants in the field

We selected an orchard with severe invasion of *M. micrantha* to carry out the replacement control experiment of *M. micrantha*. The orchard was located at Huaguo village in the northeast of Xinxu Town, Huiyang District, Huizhou City, Guangdong Province (22°52'24"N, 114°21'21"E, at the altitude of 93 meters), with a total area of 24 square kilometers and a subtropical monsoon climate. The village has sufficient water resources, and the fruit trees mainly include bananas and wampees. Due to its proximity to Shenzhen, most of the orchards in the village were invaded by *M. micrantha*. In June 2016, clean tillage was carried out in an orchard of Huaguo Village with mowing of natural weed flora in case of weeds emerged. We also applied herbicide with a hand pump sprayer backpack to make the plot weed-free. After the clean tillage was completed, we established 16 plots, including 3 plots of *Desmodium heterocarpon* monoculture, 3 plots of *Senna tora* monoculture, 4 plots of *Spermacoce latifolia* monoculture, 3 plots of *Ageratum conyzoides* monoculture, and 3 plots of *M. micrantha* monoculture. Each plot was 3 m × 3 m. After the experimental plot was constructed, photographs were taken once a month to record the control effects of the four test plants on *M. micrantha*.

2.2. Interspecific competition experiment in the field

The experimental materials were *D. heterocarpon*, *S. tora*, and *M. micrantha*, and the seeds were collected from the replacement control experimental site in Huaguo village, Huizhou city from November to December 2016. The experimental design was as follows: *M. micrantha*, *D. heterocarpon*, and *S. tora* were planted individually; *D. heterocarpon* and *S. tora* were planted with *M. micrantha* together with a ratio of 1:1, respectively. There were five treatments in total, and each plot was 1.5 m × 1.5 m. Three months after transplanting, the coverage and plant height of *D. heterocarpon*, *S. tora* and *M. micrantha* was measured. The number of leaves per plant was counted, and the area of leaves with medium size was measured with a leaf planimeter (LI-3100, LI-COR, USA). At the end of the experiment, the medium-sized plants in each treatment were harvested. The shoots and roots were separated from each plant and dried to constant weight for at least 72 h at 60°C and then weighed to get the total biomass of shoots and roots.

Relative interaction index (RII) was calculated as: $RII = (Bw - Bo) / (Bw + Bo)$, where *Bw* was the observed biomass of the target plant when growing with other species and *Bo* was the biomass of the target plant when growing individually. A negative value indicates that other species compete with the target plant and

therefore inhibit the growth of target plants. A positive value indicates that other species promote the growth of the target plant.

2.3. Low-light treatment of *Desmodium heterocarpon*, *Senna tora*, and *Mikania micrantha*

2.3.1. Plant materials and seedling cultivation

The seeds of *M. micrantha*, *D. heterocarpon*, and *S. tora* were collected from the replacement control experimental field and germinated in Petri dishes. After germination, the seedlings were transferred to a float tray with nutrition soil and we watered them to keep the soil moist. After about 30 days of growth, healthy seedlings were selected and transplanted into a pot (plastic flowerpot 13 cm in diameter and 12 cm in height filled with mixed soil up to 2/3 of the height of the pot to ensure that the soil weight of each pot was basically the same) in the greenhouse on the top floor of the School of Life Science, South China Normal University. The mixed soil is composed of garden soil, which was collected from the topsoil of the Botanical Garden of South China Normal University, and nutrition soil in a ratio of 1:1.

2.3.2. Low-light treatment establishment

Three light conditions (light 100%, light 42%, and light 17%) were established. After 2 weeks of adaptive cultivation, the transplanted seedlings were shaded under three light conditions. There were 8 replicates per treatment for *M. micrantha*, *D. heterocarpon*, and *S. tora* (72 pots in total). All pots were positioned randomly and the experiment lasted for 60 days. At the end of the experiment, the plants in each treatment were harvested. The above-ground and below-ground parts were separated from each plant and dried to a constant weight for at least 72 h at 60°C and then weighed. The total biomass was the sum of above-ground and below-ground parts.

2.3.3. Measurements of chlorophyll fluorescence parameters

Chlorophyll fluorescence parameters were determined on a sunny day with a portable PAM-2100 fluorometer (Waltz, Germany) once a week. All fluorescence measurements were started after an additional 20 min dark adaptation. Minimal fluorescence (F_0) and maximal fluorescence (F_m) were recorded and the maximal photochemical efficiency (F_v/F_m) is calculated as: $F_v/F_m = (F_m - F_0)/F_m$. After the plant leaves were adapted to the light intensity of $200 \mu\text{mol m}^{-2} \text{s}^{-1}$, steady-state fluorescence yield (F_s), maximal fluorescence yield (F_m), electron transfer rate (ETR), and quantum yield of photosystem II (Yield) were recorded once per week.

2.3.4. Measurements of the light response curve

The light response curve was determined on a clear sunny day with a Li-6,400 portable photosynthesis analyzer (LiCor

Inc., United States). The measurement time was 9:00–11:00 a.m. and 3:00–5:00 p.m. The chamber flow rate was adjusted to $500 \mu\text{mol s}^{-1}$. Before measuring the curve, the light intensity of $1,600 \mu\text{mol m}^{-2} \text{s}^{-1}$ was set to induce the leaves to reach a stable state. The light intensity gradient was set to 1,600, 1,400, 1,200, 1,000, 800, 600, 400, 200, 100, 40, 20, and $0 \mu\text{mol m}^{-2} \text{s}^{-1}$. After reaching the maximum stabilization time, we recorded the parameters of the instrument at each light intensity and measured continuously for 2 days until all data were obtained. Next, we took the light intensity as the x-axis and the net photosynthetic rate as the y-axis to draw a scatter plot of the light response curve. According to the method of Feng et al. (2004), we fitted the light response curve equation to calculate the maximum net photosynthetic rate (P_{max}), light compensation point (LCP), light saturation point (LSP), dark respiration rate (Rd), and apparent quantum yield (AQY). AQY was represented by the initial slope of the light response curve when the light intensity was less than $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ and was fitted by the standard form of linear regression.

2.4. Drought-stressed treatment of *Desmodium heterocarpon*, *Senna tora*, and *Mikania micrantha*

After 1 week of adaptive cultivation of the seedlings, drought stress experiment was carried out. All experimental groups were subjected to drought treatment after fully absorbing water. The method of drought stress was carried out by natural drought without water. The control group was normally watered. The experimental group was treated with drought stress for 10 days and rehydrated for 3 days from the 11th day. There were 12 replicates per treatment for *M. micrantha*, *D. heterocarpon*, and *S. tora* (108 pots in total). All pots were placed randomly. At the end of the experiment, the plants in each treatment were harvested. The above-ground and below-ground parts were separated from each plant and dried to a constant weight for at least 72 h at 60°C and then weighed. The total biomass was the sum of above-ground and below-ground parts.

2.4.1. Measurements of gas exchange parameters in the drought stress experiment

Gas exchange parameters were determined using the Li-6,400 portable photosynthesis analyzer (LiCor Inc., United States) at 9:00 a.m. and were completed within 2 h on a sunny day. The photosynthetic photon flux density (PPFD) of the natural light was set to $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ under daily ambient temperatures varied from 28 to 30°C. CO_2 concentration inside the leaf chamber was maintained at $380 \mu\text{mol m}^{-3}$ through the CO_2 -controlling system of the Li-6,400 attached to a portable CO_2 cylinder. The PPFD of $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ on the cuvette surface was provided by an

LED source. Before taking measurements, the leaves were equilibrated under artificial light conditions in the leaf chamber for at least 10 min. Net photosynthetic rate (Pn), intercellular CO₂ concentration (Ci), stomatal conductance (Gs), and transpiration rate (Tr) were recorded.

2.4.2. Measurements of proline content in the drought stress experiment

Proline was extracted by sulfosalicylic acid and the proline content was determined by ninhydrin colorimetry. 0.1 g fresh weight leaves of each plant in the control group (well-watered treatment) and the experiment group on the 10th day of drought treatment and the 3rd day of rehydration were placed in a centrifuge tube, respectively. 2.5 ml 3% sulfosalicylic acid solution was added to each tube and then all tubes were treated in the boiling water bath for 10 min. After filtering and cooling, 1 ml filtrate was absorbed into another centrifuge tube and then 1 ml glacial acetic acid and 1 ml 2.5% acid ninhydrin reagent were added. The mixture was heated in the boiling water bath for 30 min and turned red. After the mixture was cooled, 2 ml toluene was added. After 30 s of oscillation, the supernatant was transferred into a 10 ml centrifuge tube and centrifuged at 3000 rpm for 5 min. The red proline toluene supernatant was absorbed into a colorimetric cup. The toluene solution was used as blank control and the absorbance value was determined at A₅₂₀. The standard curve of proline was prepared and the content of proline was calculated according to the regression equation of the standard curve.

2.4.3. Measurements of soluble sugar content in the drought stress experiment

The soluble sugar content was determined by thiobarbituric acid method. 0.1 g plant leaves were placed in a pre-cooled mortar and 1 ml pre-cooled 10% acetic acid (TCA) was added. After the leaves were grounded on ice homogeneously, the homogenate was transferred to the centrifuge tube, and then the mortar was washed with 1 ml 10% TCA. The washing liquid was also transferred to the centrifuge tube and centrifuged at the speed of 4,000 rpm for 10 min. 1 ml supernatant (1 ml sterile water in blank control) and 1 ml 0.6% thiobarbituric acid solution (TBA) were added into a new centrifuge tube and thoroughly mixed. The mixture was heated in a boiling water bath for 15 min and centrifuged at the speed of 4,000 rpm for 10 min after cooling down at room temperature. The supernatant of the mixture was taken to determine the absorbance value at A₄₅₀.

2.5. Statistics analysis

We used one-way ANOVA analysis and Duncan's test ($p < 0.05$) to test for differences between treatments using SPSS 18.0 (SPSS Inc., United States). SigmaPlot 12.0 and Origin 8.5 software were used for data visualization.

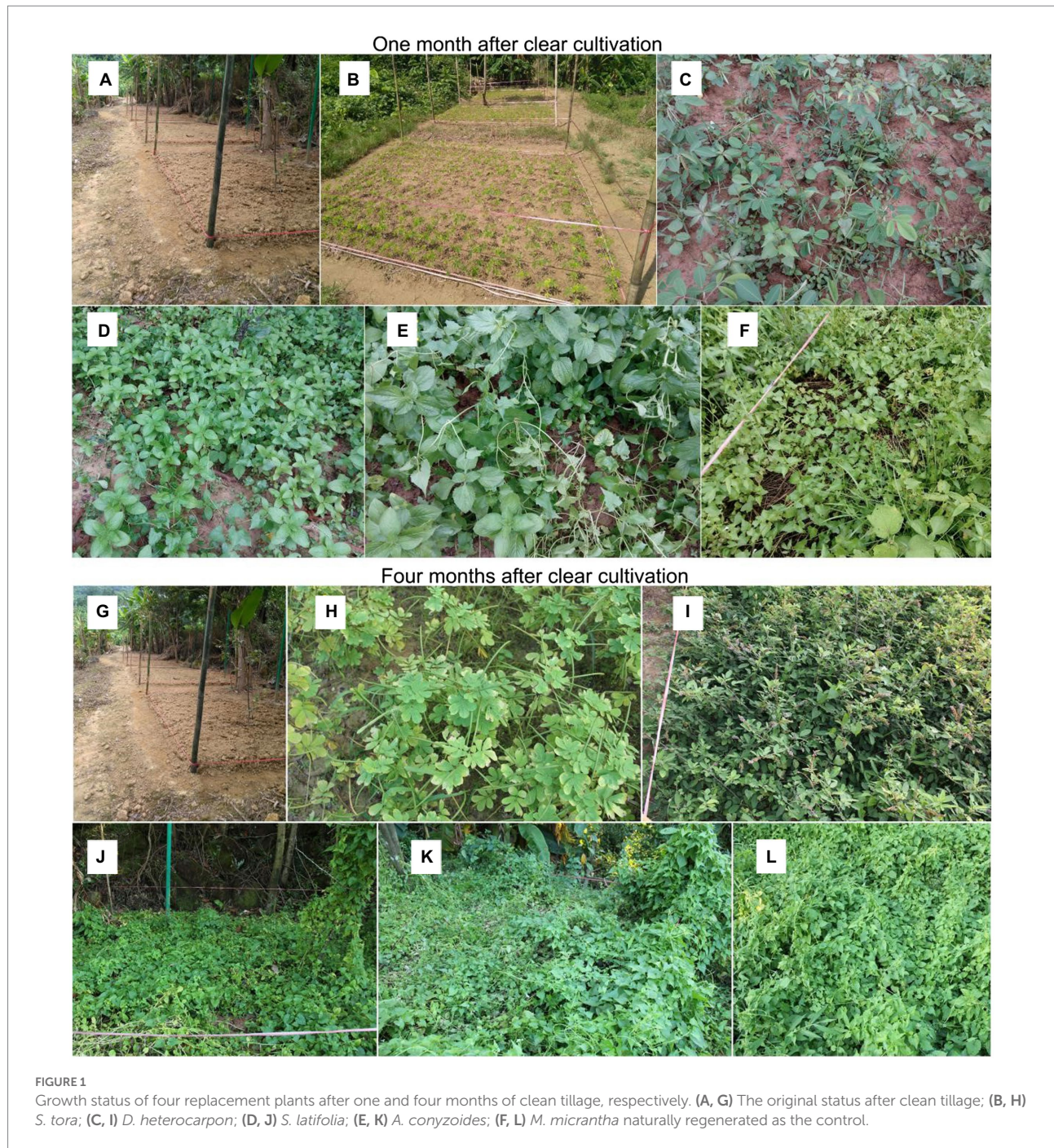
3. Results

3.1. The preliminary selection of replacement plants in the field

One month after clean tillage (Figure 1A), the seedlings of *S. tora* successfully established with a survival rate of over 95% (Figure 1B). The seedlings of *D. heterocarpon* successfully established with a survival rate of over 90% (Figure 1C). A large number of *S. latifolia* and a few *M. micrantha* individuals regenerated in the quadrats gap (Figure 1D). A few seedlings of *A. conyzoides* but a large number of *M. micrantha* individuals regenerated in the quadrats (Figure 1E). Four months after clean tillage (Figure 1G), *S. tora* entered into reproductive growth, some of the leaves aged and turned yellow, and lots of pods grew. Few *M. micrantha* was found in the plot, but weeds appeared in the lower layer (Figure 1H). *D. heterocarpon* also entered into reproductive growth, bearing a lot of pods, but the leaves remain green, with a small amount of *M. micrantha* (Figure 1I). When *S. latifolia* entered the aging stage, its stem lodging occurred and leaves withered and turned yellow, and a large amount of *M. micrantha* occupied the quadrats (Figure 1J). *A. conyzoides* entered the aging stage, while *M. micrantha* grew vigorously, occupying most of the quadrats (Figure 1K). Therefore, we did not involve *S. latifolia* and *A. conyzoides* in the following experiments. We observed that compared with the natural growth of *M. micrantha* (Figure 1F, L), *D. heterocarpon* and *S. tora* had obvious replacement control effect on *M. micrantha*, which can inhibit the growth and regeneration of *M. micrantha* in the orchards. Next, we used these two plants as replacement plants to study the interspecific competition effects between two legumes and *M. micrantha* in the field.

3.2. Interspecific competition between two legumes and *Mikania micrantha* in the field

When *M. micrantha* was planted with *S. tora* or *D. heterocarpon*, its coverage was significantly decreased compared with that of *M. micrantha* monoculture, which was 77% or 73.9%, respectively. Compared to *D. heterocarpon* monoculture, the coverage of *D. heterocarpon* decreased significantly by 17.3% when it was planted with *M. micrantha*, while the coverage of *S. tora* was not significantly different between monoculture and polyculture with *M. micrantha* (Figure 2A). Due to the competition of *S. tora* and *D. heterocarpon*, the leaf area of *M. micrantha* per plant decreased significantly by 30.9 and 36.3%, respectively. On the contrary, the leaf area of *S. tora* and *D. heterocarpon* per plant increased significantly by 7.1 and 25%, respectively, when they were planted with *M. micrantha*, compared to the monoculture (Figure 2B). The total biomass of *M. micrantha* decreased by 23.5 and 58.3%, respectively, when *M. micrantha* was planted with *S. tora* and *D. heterocarpon*, compared to the monoculture. There was no significant difference between the total biomass of *D. heterocarpon* when it was planted with *M. micrantha*

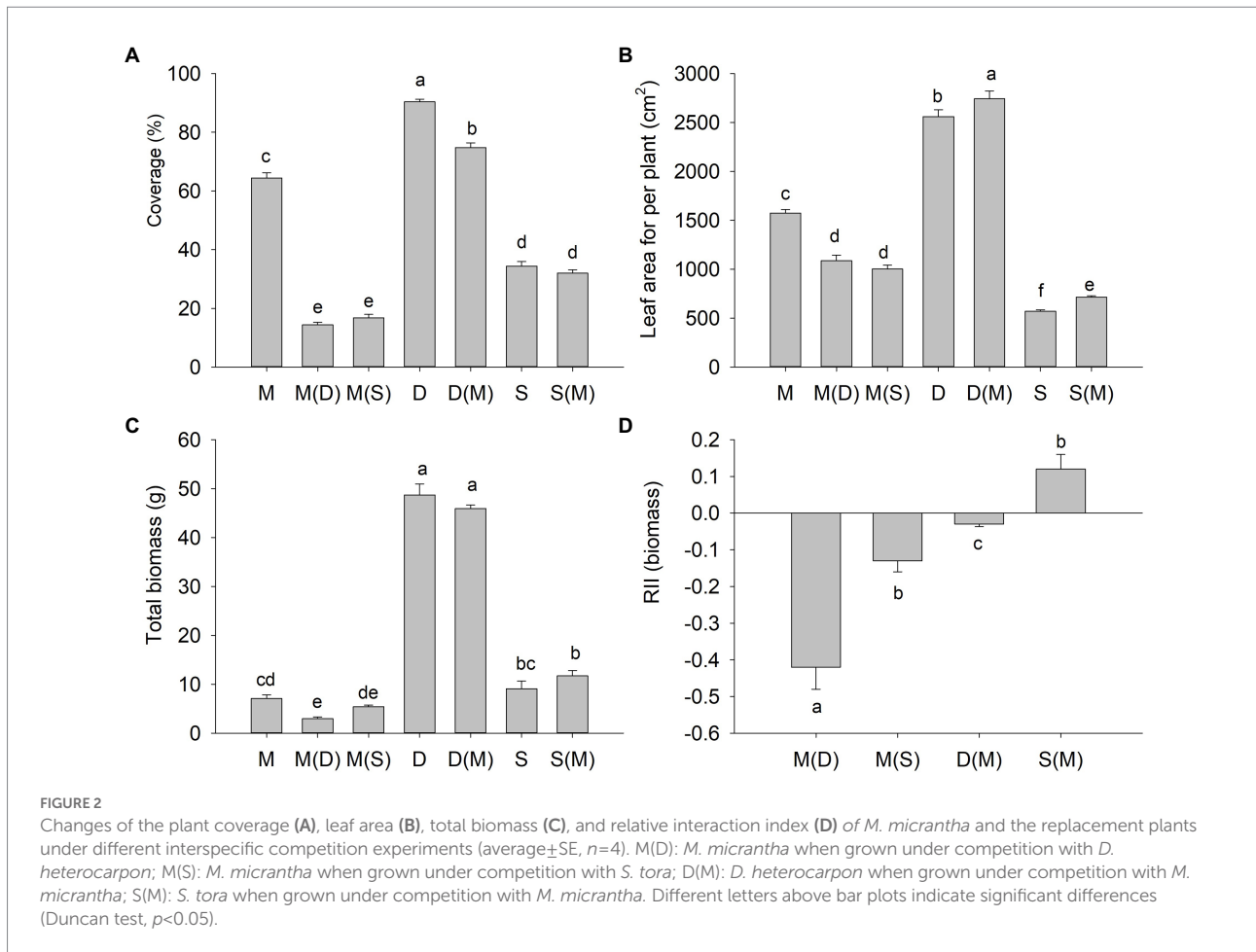


and the monoculture, so as *S. tora* (Figure 2C). The RII can indicate the interaction between plants. A negative value indicates competition and a positive value indicates facilitation. The RII of *M. micrantha* in the presence of *D. heterocarpon* and *S. tora* were both negative ($RII_{Mm(Dh)} = -0.42$, $RII_{Mm(Si)} = -0.13$, respectively), indicating that two replacement species competed well with *M. micrantha*, and that the strength of the negative effect of *D. heterocarpon* on *M. micrantha* was larger than that of *S. tora* on *M. micrantha* (Figure 2D). On the other hand, the effect of *M. micrantha* on *D. heterocarpon* was negative [$RII_{Dh(Mm)} = -0.03$], close to zero, while the effect of

M. micrantha on *S. tora* was positive [$RII_{St(Mm)} = 0.12$, Figure 2D], indicating that *M. micrantha* could promote the growth of *S. tora*.

3.3. The adaptability of two replacement forage legumes and *Mikania micrantha* to low-light stress

Under light 100%, *M. micrantha* had more branches and leaves, but the leaves turned yellow. As the light intensity



decreased, the number of branches and leaves of *M. micrantha* decreased significantly and the greenness of the leaves deepened. *M. micrantha* was the smallest and grew the worst under light 17% (Figure 3A). Under light 100% and light 42%, *D. heterocarpon* had more branches and leaves. The number of branches and leaves decreased under light 17%. As the light intensity decreased, the greenness of *D. heterocarpon* leaves deepened (Figure 3B). Under light 100%, *S. tora* grew low and stout with yellowish leaves and branches; with the decrease in light intensity, the plants became thinner and taller, and the greenness of leaves deepened. *S. tora* was the highest under light 42% (Figure 3C).

From the perspective of root phenotype changes, *M. micrantha* had the most developed roots and the largest number of roots under light 100%. With the decrease in light intensity, the number of roots decreased significantly. Under light 17%, the growth of roots was greatly affected and the number of roots was the least (Figure 3D). Under light 100%, the roots of *D. heterocarpon* were the most developed. With the decrease in light intensity, the number of roots gradually decreased, and the number of roots was the least under light 17% (Figure 3E). Under light 100%, the number of *S. tora* roots was the largest, and with the decrease in light intensity, the number of roots decreased dramatically. Under light 17%,

the growth of *S. tora* roots was greatly inhibited and the number was the least (Figure 3F).

Compared with light 100%, the above-ground biomass of *M. micrantha* decreased significantly by 32.8 and 78.8% under light 42% and light 17%, respectively (Figure 3G). The above-ground biomass of *D. heterocarpon* and *S. tora* decreased by 55 and 63.6% under light 17% compared with that under light 100%. The root biomass of *M. micrantha* decreased significantly by 63 and 91.3% under light 42% and light 17%, respectively, compared with that under light 100%. The root biomass of *D. heterocarpon* significantly decreased by 81% under light 17% compared with light 100%, while there was no significant difference between the root biomass of *D. heterocarpon* under light 42% and light 100%. The root biomass of *S. tora* was significantly decreased by 31.3 and 79.7% under 42% and light 17% compared with light 100%, respectively. Under light 42% and light 17%, the total biomass of *M. micrantha* decreased significantly by 38.5 and 86.5%, respectively. The total biomass of *D. heterocarpon* decreased significantly by 60.2% under light 17% compared with light 100% and the total biomass of *S. tora* decreased by 66.1% under light 17% compared with light 100%. It can be seen that under the low-light treatment the biomass of *M. micrantha*

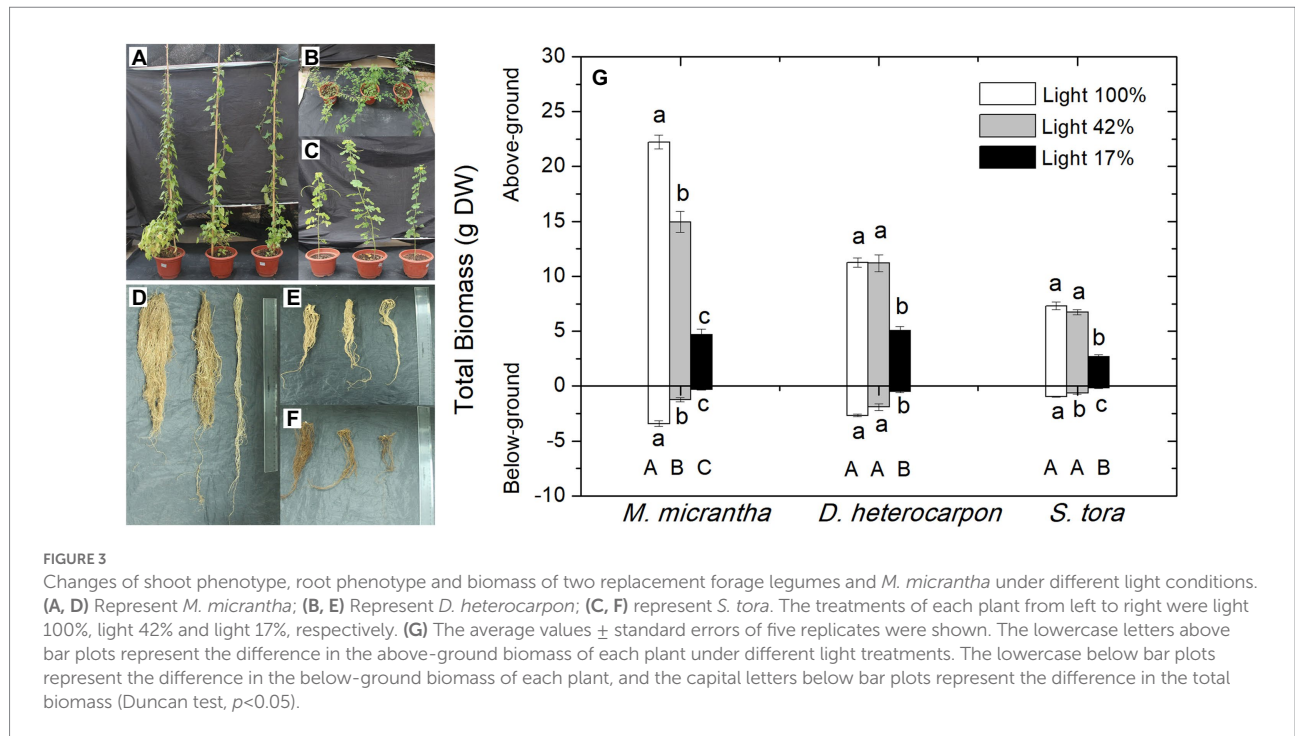


TABLE 1 Changes of photosynthetic parameters under different light conditions (average \pm SE, $n = 4$).

Treatments	P_{max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	LSP ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	LCP ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	AQY ($\text{CO}_2 \text{ photon}^{-1}$)	Rd ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
<i>M. micrantha</i>					
Light 100%	14.77 \pm 1.08a	1247.1 \pm 126.3a	22.42 \pm 1.24a	0.085 \pm 0.008a	1.87 \pm 0.15a
Light 42%	11.32 \pm 0.92b	840.5 \pm 69.5b	19.21 \pm 1.45ab	0.066 \pm 0.002b	1.48 \pm 0.12a
Light 17%	9.19 \pm 0.31b	724.2 \pm 55.4b	16.98 \pm 1.29b	0.061 \pm 0.011b	1.47 \pm 0.28a
<i>D. heterocarpon</i>					
Light 100%	13.61 \pm 0.25a	979.2 \pm 134.80a	22.24 \pm 2.37a	0.065 \pm 0.006a	1.47 \pm 0.06a
Light 42%	13.63 \pm 1.53a	873.8 \pm 146.5a	16.79 \pm 1.61ab	0.061 \pm 0.002a	1.03 \pm 0.15b
Light 17%	12.16 \pm 0.61a	633.4 \pm 102.9a	11.02 \pm 0.42b	0.060 \pm 0.001a	0.90 \pm 0.11b
<i>S. tora</i>					
Light 100%	16.44 \pm 0.89a	1498.6 \pm 309.5a	22.00 \pm 0.90a	0.067 \pm 0.002a	1.62 \pm 0.19a
Light 42%	16.06 \pm 1.25a	991.5 \pm 163.4a	21.45 \pm 2.19a	0.061 \pm 0.002a	1.43 \pm 0.3ab
Light 17%	14.70 \pm 1.46a	825 \pm 115.5a	16.36 \pm 1.23b	0.062 \pm 0.002a	1.09 \pm 0.21b

P_{max} , maximum net photosynthetic rate; LSP, light saturation point; LCP, light compensation point; AQY, apparent quantum yield; Rd, dark respiration rate. Data with different letters for each plant in the column indicate significant differences (Duncan test, $p < 0.05$).

decreased the most, followed by *S. tora*, and the biomass of *D. heterocarpon* was the smallest, and it was also the least affected by low light.

From the perspective of photosynthetic parameters, P_{max} of *M. micrantha* significantly decreased by 23.4 and 37.8% respectively, under light 42% and light 17%, compared with light 100% (Table 1). There was no significant difference in P_{max} between *D. heterocarpon* and *S. tora* under three light conditions, indicating that *D. heterocarpon* and *S. tora* have higher photosynthetic efficiency under medium-light and low-light conditions. Under the conditions of light 100% and light 17%, the LSPs of *M. micrantha* and *S. tora* were greater than those of

D. heterocarpon, indicating that *D. heterocarpon* has stronger photosynthetic utilization ability under low-light conditions. The LCPs of *M. micrantha* and *D. heterocarpon* both decreased with the decrease in light intensity, and the LCP of *D. heterocarpon* was lower than that of *M. micrantha* and *S. tora* under light 42% and light 17%, indicating that *D. heterocarpon* was more tolerant to low-light condition. There was no significant difference in the AQY of *D. heterocarpon* and *S. tora* under different light conditions, while the AQY of *M. micrantha* significantly decreased by 22.4 and 28.2% under light 42% and light 17%, respectively, compared with light 100%, which indicated that the two forage legumes were more efficient for low light. The Rd. of *M. micrantha*

under light 42% and light 17% was not significantly different from that under light 100%. Under light 42% and light 17%, the Rd. of *D. heterocarpon* decreased significantly by 29.9 and 38.8% compared with light 100%, respectively, and that of *S. tora* decreased significantly by 32.7% under light 17% compared with light 100%, which indicated that under low-light conditions, *D. heterocarpon* and *S. tora* can adapt to the low-light environment by reducing their own energy consumption.

With the increase of treatment time, the Fv/Fm of *M. micrantha* continued to decrease under the three light conditions (Figure 4A), while that of *D. heterocarpon* was not significant under different light conditions and showed an upward trend (Figure 4B). Similar to *M. micrantha*, the Fv/Fm of *S. tora* also continued to decrease under three light conditions (Figure 4C). Under light 100%, the ETR and Yield of *M. micrantha* remained stable, showed a downward trend under light 42% and light 17%, and decreased dramatically under light 17% (Figures 4D, G). The ETR and Yield of *D. heterocarpon* showed an upward trend under all light conditions (Figures 4E, H), showing good adaptability to the low-light environment. The ETR and Yield of *S. tora* increased gradually with the increase of treatment time, and there was little difference among different treatments (Figures 4F, I). After light 42% and light 17% treatment for 49 days, the photochemical quenching (qp) of *M. micrantha* decreased significantly compared with light 100% (Figure 4J), while that of *D. heterocarpon* and *S. tora* both increased with the increase of treatment time (Figures 4K, L).

3.4. The response of two replacement forage legumes and *Mikania micrantha* to drought stress

After 7 days of drought treatment, the leaves of *M. micrantha* began to wilt and the leaves of *S. tora* wilted on the 10th day, while the leaves of *D. heterocarpon* did not change significantly (Figure 5). After 10 days of drought treatment, the phenotypes of two replacement forage legumes and *M. micrantha* showed obvious differences. The leaves of *D. heterocarpon* were still green without visible changes, while the leaves of *M. micrantha* shrunk due to water loss, and the stem tips were dry and withered. The leaves of *S. tora* also lost water and wilted, and the leaves were closed, but the degree of wilting was significantly lower than that of *M. micrantha*. From the observation of phenotype, the tolerance to drought stress of *D. heterocarpon* was higher than that of *S. tora* and *M. micrantha*, among which *M. micrantha* has the deepest degree of wilting. After rehydration, the leaves of *M. micrantha* were still wilted, the wilting symptoms of *S. tora* leaves disappeared, and the leaves of *D. heterocarpon* did not change significantly and remained green.

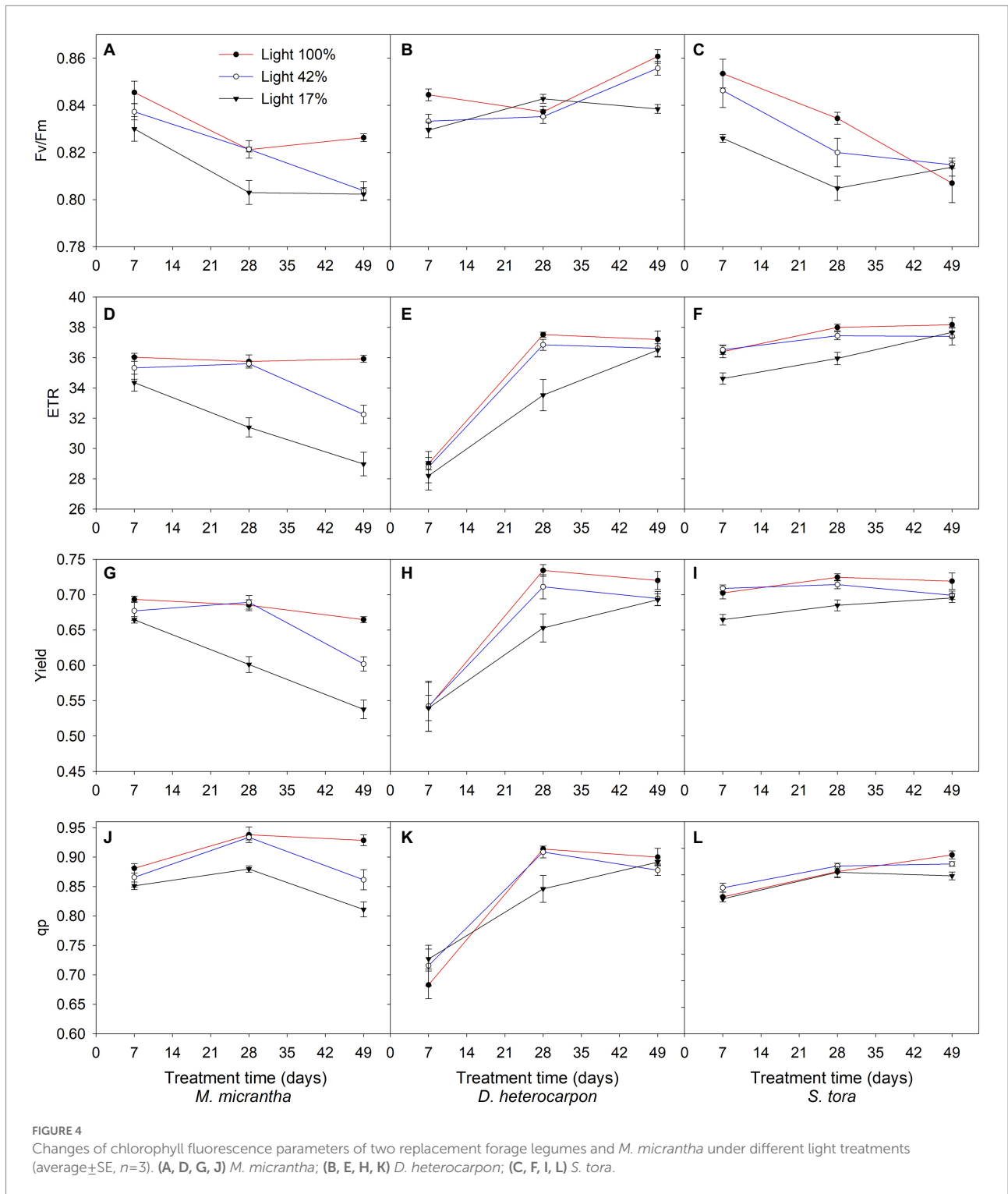
Under drought stress, the total biomass of *M. micrantha* and *S. tora* decreased significantly by 65 and 14.9%, respectively, while *D. heterocarpon* was not affected by drought stress (Figure 6A). The root biomass of *M. micrantha* was significantly reduced under

drought stress, while neither *D. heterocarpon* nor *S. tora* was affected by drought stress (Figure 6C). Under the drought treatment, the plant height and root length of *M. micrantha* decreased significantly by 38.7 and 32%, respectively, compared with the well-watered group (Figures 6B, D). There were no significant differences in plant height and root length between the well-watered group and drought stress group for *D. heterocarpon* and *S. tora* (Figures 6B, D).

Drought stress had a significant effect on the P_n of *M. micrantha* and *S. tora*. With the increase of drought treatment time, P_n of *M. micrantha* and *S. tora* showed a continuous downward trend, and *M. micrantha* had the largest decrease (96.71%), followed by *S. tora*, with a decrease of 92.4%, while the P_n of *D. heterocarpon* remained at a relatively high level after 10 days of drought treatment, only decreased by 2.4%. After rehydration, the P_n of *M. micrantha* remained at a low level and could not be recovered, and that of *S. tora* recovered to a level comparable to the well-watered group, while that of *D. heterocarpon* increased slightly (Figure 7A). The G_s and T_r of *M. micrantha* and *S. tora* showed similar changing patterns, both of which continued to decline with the increase of drought treatment time. After rehydration, the G_s and T_r of *M. micrantha* could not recover to a level comparable to the well-watered group, while that of *S. tora* could basically recover (Figures 7B, D). During the drought treatment, G_s , C_i , and T_r of *D. heterocarpon* remained at a stable level with little change (Figures 7B–D).

The Fv/Fm of *M. micrantha* and *S. tora* showed a downward trend under drought treatment, which could not be recovered after rehydration, but continued to decline, while that of *D. heterocarpon* did not change and slightly increased after rehydration (Figure 8A). As drought treatment continued, ETR of *M. micrantha* decreased by 16%, and that of *S. tora* decreased by 26.6%, while ETR of *D. heterocarpon* increased by 6.5% (Figure 8B). After rehydration, the ETR of *M. micrantha* was unable to recover, while that of *S. tora* was partially recovered (Figure 8B). On the 10th day of drought treatment, the Yield of *M. micrantha* and *S. tora* decreased by 30.6 and 21.9%, respectively. After rehydration, the Yield of *S. tora* partially recovered, while that of *M. micrantha* could not recover to a level comparable to the well-watered group (Figure 8C). During the drought treatment, the Yield of *D. heterocarpon* was at a high level (Figure 8C). With the increase of drought treatment time, the qp of *M. micrantha* and *S. tora* decreased by 11.6 and 20.7%, respectively, on the 10th day and could be recovered to a level comparable to the untreated group after rehydration, while that of *D. heterocarpon* remained basically unchanged under all conditions (Figure 8D).

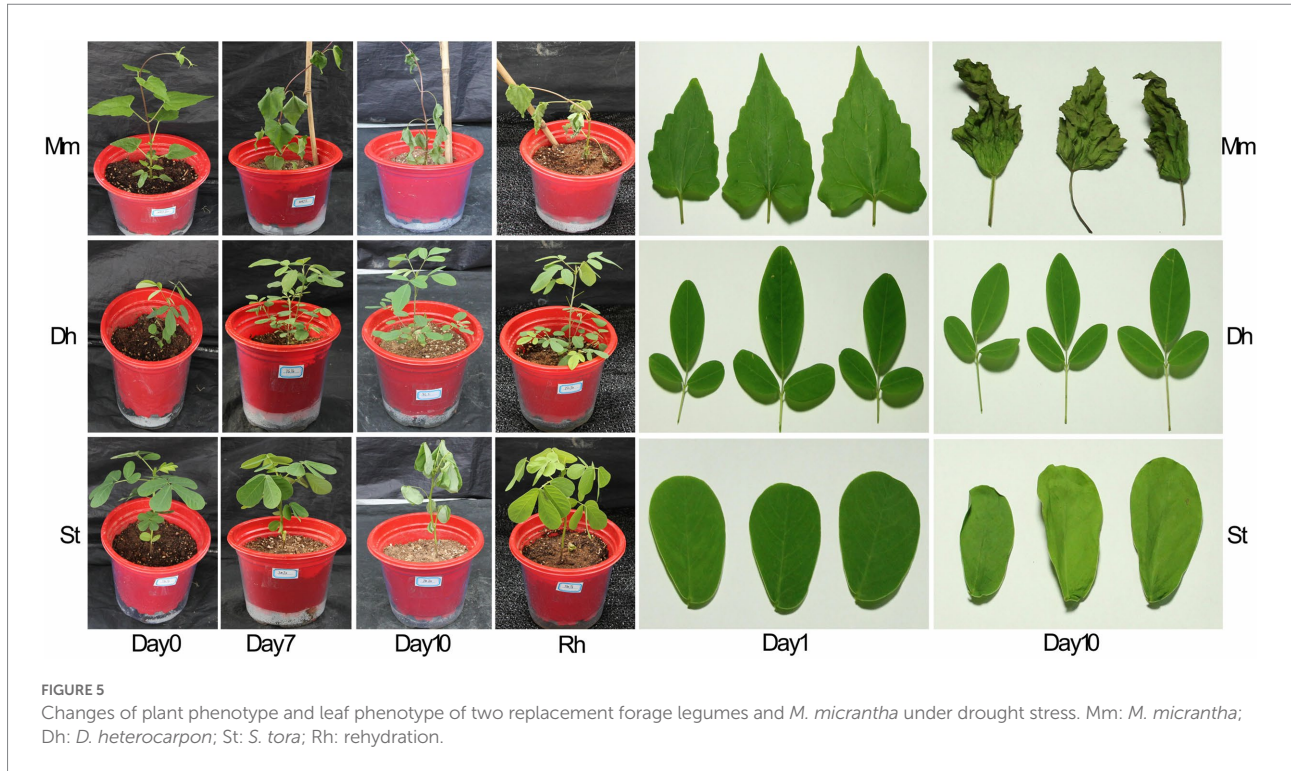
Under the drought treatment, the proline content of *M. micrantha*, *D. heterocarpon*, and *S. tora* increased to varying degrees, and were significantly increased by 229.3, 0.96 and 47.7 times, respectively, compared with well-watered treatment (Figure 9A). After rehydration, the proline content of *M. micrantha* remained at a high level and both *D. heterocarpon* and *S. tora* recovered to a level comparable to the well-watered group



(Figure 9A). Under drought treatment, the soluble sugar content of *M. micrantha*, *D. heterocarpon*, and *S. tora* increased significantly by 72.4, 28.9, and 31% respectively, compared with the well-watered treatment. The soluble sugar content of all three plants recovered to a level comparable to the well-watered group after rehydration (Figure 9B).

4. Discussion

Much work so far has focused on the ecological mechanism of why biological invasion could be successful (Hengeveld, 1988; van der Putten et al., 2007; Rejmánek, 2014; Olenin et al., 2017). However, rather than understanding the mechanism of the



invasion, it might be more important to apply the mechanism to the actual restoration and management of invaded sites. We provided experimental evidence that replacement control of invasive plants, through selecting and cultivating suitable native plants, is effective. In the field experiment, we selected 4 replacement plants that commonly appear in orchard habitats (i.e., *D. heterocarpon*, *S. tora*, *S. latifolia*, and *A. conyzoides*) and screened out two potentially effective plants among these four plants, *D. heterocarpon* and *S. tora*, for further experiments to investigate the potential in controlling *M. micrantha*. One of the most important reasons for the successful replacement of invasive plants by replacement plants is the interspecific competitive advantage of replacement plants (Gaudent and Keddy, 1988; Keddy et al., 2002). Species with greater competitiveness can inhibit the growth of invasive plants and replace them, thereby enabling sustainable restoration of damaged soil ecosystems (Chen et al., 2017). We investigated the effect of interspecific competition on the replacement effect of two forage legumes, *D. heterocarpon* and *S. tora* in mixed cultivation with *M. micrantha*. Both *D. heterocarpon* and *S. tora* significantly reduced the coverage of *M. micrantha* and suppress the growth of *M. micrantha*. At the same time, the total leaf area per plant and the total biomass of *M. micrantha* were also significantly reduced when mixed cultivation, indicating that *D. heterocarpon* and *S. tora* had great potential in controlling the expansion of *M. micrantha*. RII is one of the important indicators to measure the competition strength of plants (Ulrich and Perkins, 2014). RII of *M. micrantha* grown in the presence of *D. heterocarpon* [$RII_{Mm(Dh)}$] was -0.42 , while that of *M. micrantha* grown in the

presence of *S. tora* [$RII_{Mm(St)}$] was -0.13 , indicating that these two species have a more competitive advantage compared to the alien species. In addition, we observed that $RII_{Mm(Dh)}$ was significantly smaller than $RII_{Mm(St)}$, indicating that *D. heterocarpon* was more effective in controlling *M. micrantha* than *S. tora*. The question we were trying to answer in this study is why *D. heterocarpon* and *S. tora* are so effective in suppressing the expansion of *M. micrantha* in the field experiment. The field competition experiment was carried out in an orchard habitat with low soil moisture content and some degree of light blocking. Therefore, we simulated low-light and drought-stressed environmental conditions and compared the growth and photosynthetic characteristics of these two plants with *M. micrantha* in order to study the physiological and ecological mechanism of the success replacement controlling effect.

M. micrantha is a tropical heliophytic plant (Han et al., 2017; Sheam et al., 2020), and the biomass of *M. micrantha* decreased significantly with the decrease in light intensity after low-light treatment. On one hand, the AQY of the *M. micrantha* significantly decreased under low-light condition, illustrating that the amount of the light-harvesting pigment-protein complexes which absorbs sunlight and transforms light energy into chemical energy might be reduced, resulting in a decrease of photosynthetic rate and a consequent weakening of the ability to utilize weak light (Richardson and Berlyn, 2002). On the other hand, the dark respiration rate of *M. micrantha* was maintained at a high level, while the photosynthetic rate decreased, leading to a proportional reduction in biomass accumulation. However, under low-light treatment, the dark respiration rate of *D. heterocarpon* and *S. tora*

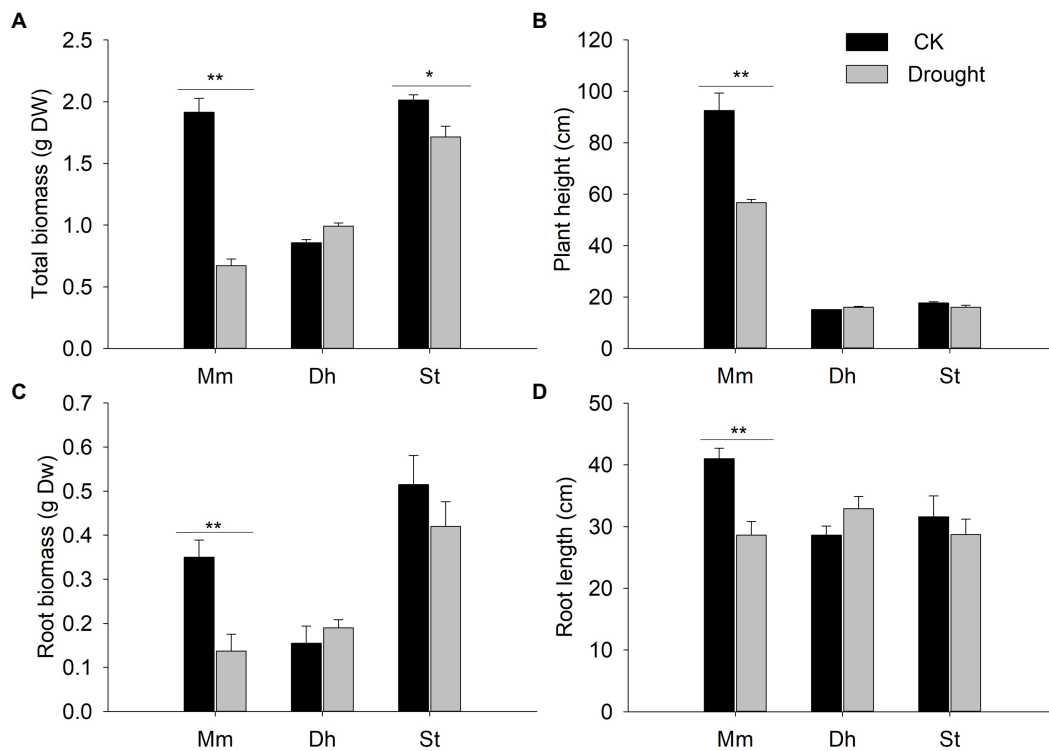


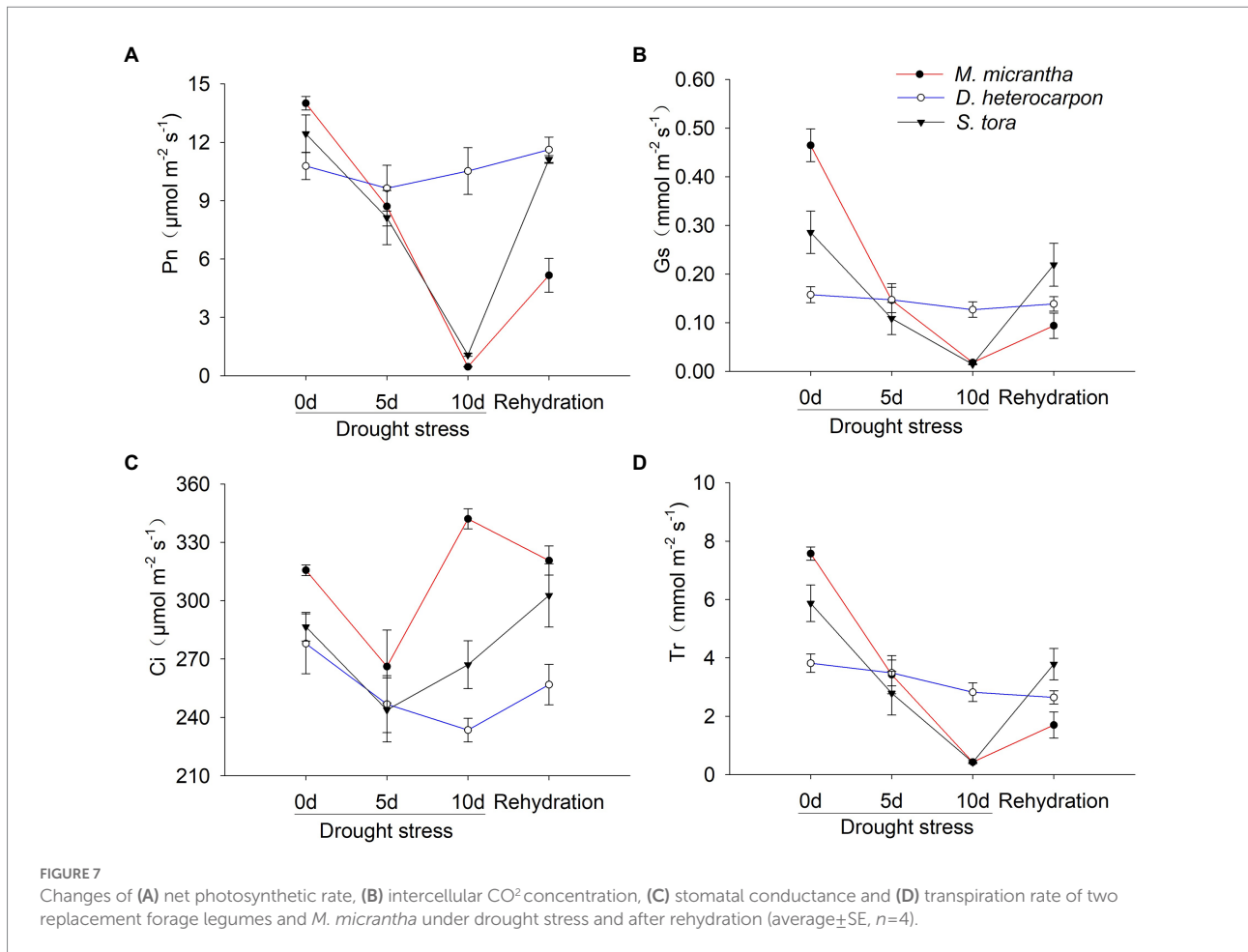
FIGURE 6

Changes of (A) total biomass, (B) plant height, (C) root biomass, and (D) root length of two replacement forage legumes and *M. micrantha* under drought stress (average \pm SE, $n = 4$). Different letters above bar plots indicate significant differences analyzed using ANOVA followed by Dunnett's test. Significance levels: ** $p < 0.01$; * $p < 0.05$.

were significantly decreased, indicating that the replacement plants were able to adapt to the low-light environment by reducing energy consumption and maintaining a higher photosynthetic rate (Gyimah and Nakao, 2007; Martínez Pastur et al., 2007). Fv/Fm reflects the maximum light energy conversion efficiency of PSII, which tends to decrease significantly when plants are stressed (Guo and Tan, 2014). ETR reflects the activity of PSII and is directly related to plant photosynthetic rate (Koblížek et al., 2001; Burda, 2007; Yamori et al., 2008), and Yield is also positively correlated with the activity of PSII (Krall and Edwards, 1992). Fv/Fm, ETR, Yield, and qp of the replacement plants under low-light treatment did not change significantly compared with those values under light 100%, while those of *M. micrantha* decreased to different degrees after low-light treatment. Therefore, *D. heterocarpon* and *S. tora* show good adaptability and strong shade tolerance under low-light environment so that they can quickly grow and cover the soil surface to rob most of the light.

Moisture is an important limiting factor during plant growth and development (Davies et al., 1990; Ghaderi and Siosemardeh, 2011). Soil moisture is a key factor in *M. micrantha* seed germination and population expansion, and determines the growth and distribution of *M. micrantha* (Yue et al., 2019). After drought treatment, we found that the biomass of *M. micrantha* decreased by 65% and the plant height and root also decreased by 38.7 and 32%, respectively, compared to the well-watered group,

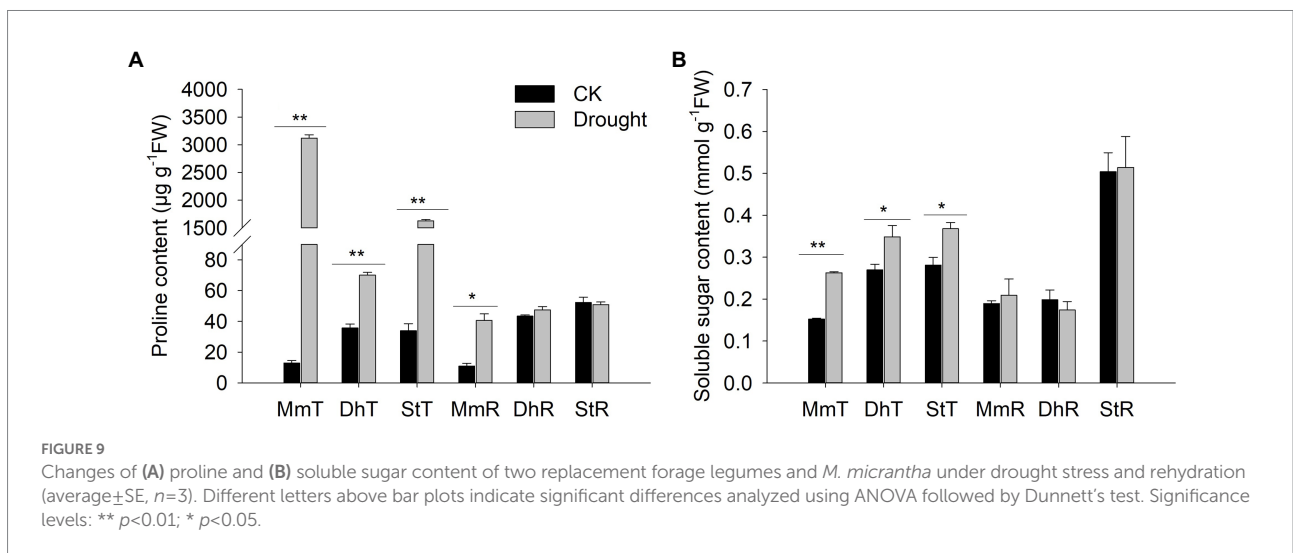
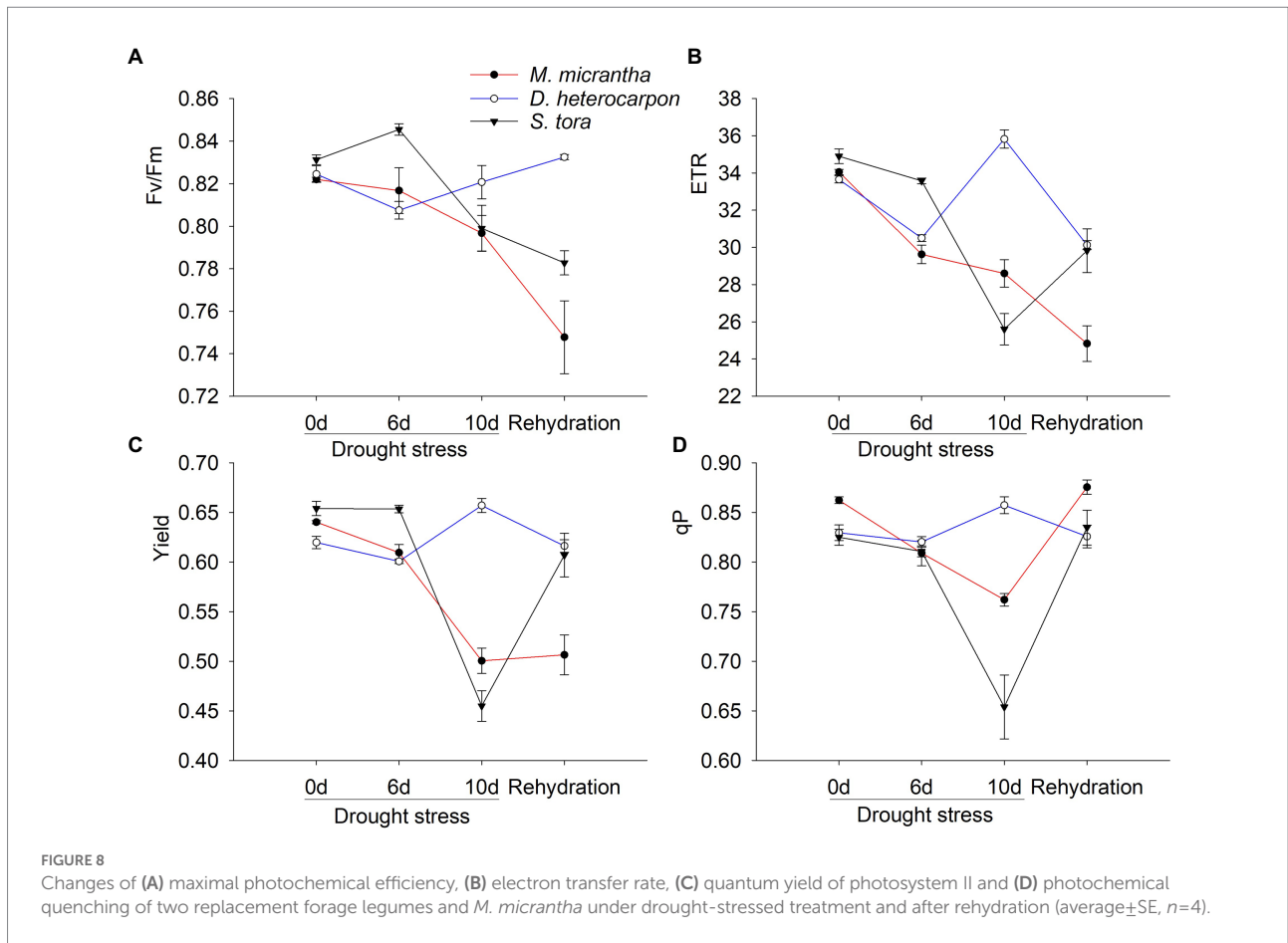
while the replacement plants outperformed *M. micrantha* in all aspects of plant growth parameters. In addition, under drought-stressed condition, phenotype change of *M. micrantha* was the most serious, and the water loss was severe, so that *M. micrantha* needed to absorb more water from the soil for supplementation, resulting in serious soil water loss and soil compaction, which was difficult to restore soil nutrient supply and return to original soil status (Demchik and Sharpe, 2000; Ober and Parry, 2011; Kilpeläinen et al., 2017). A large number of studies have shown that photosynthesis is sensitive to water stress, and the photosynthetic rate decreases with the increase of water stress (Boyer, 1970). We observed that *M. micrantha* was irreversibly damaged after 10 days of drought treatment, and all photosynthetic indexes of *M. micrantha* failed to recover after rehydration. Chlorophyll fluorescence parameters can detect the effects of drought stress on plant photosynthesis (Bi et al., 2008; Su et al., 2015). Chlorophyll fluorescence parameters of *M. micrantha* revealed that drought stress caused irreversible damage to the PSII of *M. micrantha*. However, both the photosynthetic index and chlorophyll fluorescence parameters of *S. tora* recovered after rehydration, indicating that *S. tora* had strong self-repair potential in drought stress and showed resistance to drought stress (Georgieva et al., 2006). The performance of *D. heterocarpon* was better than that of *S. tora*, and its various indicators remained stable during drought stress, reflecting excellent adaptability and



tolerance to drought stress. Among two replacement forage legumes and *M. micrantha*, *D. heterocarpon* was the most drought-resistant, while *M. micrantha* was the least drought-resistant and its growth was susceptible to water limitation. In addition, in response to drought stress, *M. micrantha* accumulated a large amount of proline, and after rehydration, the proline concentration remained high, indicating that *M. micrantha* is often difficult to recover after severe damage (Waldren and Teare, 1974; Patel and Vora, 1985; Carvalho et al., 2019). Nevertheless, the proline content of *D. heterocarpon* and *S. tora* recovered to a level comparable to the well-watered group after rehydration. The replacement plants show excellent adaptation to drought stress, suggesting that the use of *D. heterocarpon* and *S. tora* to control the spread of *M. micrantha* in dryland orchards has good application prospects.

Theoretical studies of plant interspecific competition have been the focus of research in the field of ecology, and the long-standing debate on explaining interspecific competition is between Philip Grime and David Tilman (Grime, 1977; Tilman, 1980). A series of previous studies tend to support one side (Jabot and Pottier, 2012; DeMalach et al., 2016). In our study, we found that the replacement plants can obtain sufficient nutrients to sustain themselves and grow rapidly in low-level resource environments,

accumulate more above-ground and underground biomass, and more mineral nutrition, water, and sunlight, to eventually win in the competition against invasive plants, eliminate them, and achieve the ecological restoration of the invaded sites. The invasive plants often covered the soil surface quickly through rapid growth and excluded the native plants, which severely disrupted ecological balance and threatening biodiversity (Pyšek and Richardson, 2010; Oduor, 2013). When the resource was sufficient, the plant height and above-ground biomass of *M. micrantha* were significantly higher than those of *D. heterocarpon* and *S. tora*, indicating that these two legumes are not better than *M. micrantha* in terms of growth rate during the same time period. The key to the legume's victory over *M. micrantha* in the field was not its rapid growth, which was not in line with Grime's theory. However, with the reduction of light resources and the lack of water, the difference between the plant heights of *D. heterocarpon*, *S. tora*, and *M. micrantha* has narrowed, while the above-ground biomass of *D. heterocarpon* has successfully surpassed *M. micrantha* under low light and water shortage. The above-ground biomass of *S. tora* also surpassed that of *M. micrantha* under drought stress. It can be seen that low light and drought were the environmental constraints that can significantly reduce the above-ground biomass of *M. micrantha*. When the light and water resources



were limited, the two legumes have higher resource utilization and smaller resource requirements. The limited resources can be fully utilized, thereby accumulating more above-ground biomass and ultimately winning the competition. This is consistent with the idea that “resource availability can affect competition” proposed

by Carlyle et al. (2010). Therefore, we propose that the reason why *D. heterocarpon* and *S. tora* are more competitive than *M. micrantha* may be that they have smaller resource requirements and can survive in the absence of light and water resources, which is in line with Tilman’s theory of minimum resource requirements.

Because of the rapid growth and expansion of invasive plants, environmental conditions and resources are particularly important to them and also tend to be limiting conditions. The findings of this study mean that in the future, people can control one or more resources that restrict the rapid growth of invasive plants by analyzing the environmental resources of the invaded site, and screening out the native plants that can grow rapidly and cover the soil surface under stressed conditions and eventually the invasive plants can be replaced without leaving other ecological problems. The two-phase resource dynamics hypothesis states that resources appear as pulses rather than continuously, including two stages, one is pulse periods when the available resources are high and most plants can grow and accumulate resources; the other is interpulse periods when the available resources are too low for most plants to absorb, and most plants die due to insufficient resources (Goldberg and Novoplansky, 1997). Our experimental environment is the understory habitat of the orchard, the trees have a canopy effect on light, and soil moisture content is relatively low, which means that light resources and water resources are always in interpulse periods. Therefore, we infer that in the pulse period, the resources can meet the growth of the invasive plant *M. micrantha*, and once transferred to the interpulse period, the replacement plants can survive and grow well, and *M. micrantha* was eventually eliminated because it was at a disadvantage in the competition for resources (Goldberg et al., 2017).

5. Conclusion

In this study, we selected two plants with practical application value for replacement control, which is a potential method to prevent invasive weeds *M. micrantha* from regeneration. *D. heterocarpon* and *S. tora* have strong competitive advantage over *M. micrantha*, mainly due to their strong shade tolerance and drought tolerance. However, considering that *S. tora* is an alien species, it is hoped that the sustainable ecological management of *M. micrantha* in the dryland orchard will be achieved by using *D. heterocarpon*, a native legume, as a competitive substitute for *M. micrantha*. Our study revealed the physiological and ecological mechanism of using replacement plants to control biological invasion, and provide a new method to solve the problem of alien invasive weeds. Based on Tilman's theory of minimum resource requirements, native plants with higher resource utilization and

smaller resource requirements (e.g., shade tolerance and drought tolerance) are potential species for controlling *M. micrantha* in dryland orchard habitats.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

WL designed the study. PJ, JW, HL, Z-hW, and FL performed the experiments and analyzed the data. PJ and WL wrote the first draft of the manuscript and contributed substantially to revisions. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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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