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Effects of drought stress on the functional traits and rhizosphere microbial community structure of Cyperus esculentus

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Abstract

Drought is a major factor limiting plant growth. Plants cope with stress via morphophysiological responses. However, it is unclear whether plant root-microbe interactions improve plant stress tolerance. We conducted a pot experiment on *Cyperus esculentus* wherein we subjected it to various drought levels and analyzed the functional traits of its aboveground and belowground organs. High-throughput sequencing was used to study the structure and diversity of the microbial community in the rhizosphere. Drought stress substantially lowered the densities of the leaves, stems, roots, and seeds relative to the untreated control. Drought stress inhibited the growth and reduced the yield of *C. esculentus*. The leaves and seeds have higher water content and are more sensitive to drought stress than the roots. Change in shoot height was the most evident response of *C. esculentus* to drought stress. Plants under drought stress reduced their leaf area and assumed a specific leaf weight to maintain photosynthetic performance. Rhizosphere fungi were more sensitive to drought stress than rhizosphere bacteria. Drought-stressed *C. esculentus* maintained their photosynthetic performance by reducing shoot height and leaf area while assuming a stable specific leaf weight. Drought stress exerted a significantly stronger negative impact on rhizosphere fungi than rhizosphere bacteria.

1. Introduction

Drought has a considerable influence on plant growth and development. Arid and semi-arid regions account for ~ 50% of the global cultivated land area. The arid and semi-arid regions in China comprise ~ 52.5% of the national land area (Wang et al. 2021). Plant functional traits are measurable species-specific characteristics that have clear relationships with individual performance, reflect the ecological strategies of plants, and are the principal indices of ecosystem responses to global climate change (Guittar et al. 2016; Enquist et al. 2015). Leaves and roots are vital plant organs that acquire aboveground and belowground resources, respectively. In response to drought stress, plants mitigate water loss by increasing leaf thickness and stomatal density while decreasing specific leaf area and stomatal size (Wright et al. 2004). Plants adapt to water stress by regulating changes in their functional traits such as root nitrogen content, diameter, and specific length (Zhou et al. 2018). Synergistic changes in plant aboveground and belowground traits occur in response to drought stress (Tjoelker et al. 2005). Evaluating the changes in leaf and root structure and physiology and their correlations will help clarify the relationships among plant adaptation strategies and environmental change.

High-throughput sequencing technology has elucidated rhizosphere microorganism community structure and demonstrated that bacteria, fungi, and other microorganisms are more active in this environment than other soil locations (Caporaso et al. 2012). Rhizosphere microorganisms form secure community structures through cooperation and competition and are essential for plant growth as well as disease and stress resistance (Berendsen et al. 2012). Abiotic stress alters rhizosphere microbial community abundance, composition, and diversity (Santos-Medellin et al. 2017). Changes in microbial community composition and plant metabolism protect plants against various stressors. Plants can establish mutualistic associations with certain rhizosphere microorganisms and these interactions may also attenuate the negative effects of stress (Toju et al. 2018).

Cyperus esculentus is a sedge plant of the Cyperaceae (Roselló-Soto 2018). It is an emerging crop with high commercial value and development potential (Wang et al. 2019). It has strong natural insect pest and pathogen resistance and its root system can help mitigate soil erosion. Hence, it is an ideal plant for improving the ecological environment. Recent research has focused primarily on the planting density (Asare et al. 2020), physicochemical properties (Adekiya et al. 2020), active ingredients (Kizzie-Hayford et al. 2021), and other aspects of *C. esculentus.* However, few studies have investigated its functional traits in response to drought stress. Therefore, the present

study used *C. esculentus* as the research object and endeavored to determine (1) the changes that occur in the functional traits of the leaves and roots of *C. esculentus* under drought treatment, and (2) the responses of the abundance, composition, diversity, and structure of the rhizosphere microbial community of *C. esculentus* under drought stress. It is hoped that the results of the present work will define a theoretical basis for rational cultivation of *C. esculentus* and the phytoremediation of arid and water-deficient areas.

2. Materials And Methods

2.1 Experimental materials and handling

A pot experiment was used in this experiment and conducted in the greenhouse of Jilin Jianzhu University, Changchun, China. Changes in soil water content were controlled by the weighing method. The research object was *C. esculentus* (Cyperaceae). Seeds were harvested from crops planted in the Songyuan region in 2020. At the end of April 2021, *C. esculentus* seeds were germinated in a laboratory incubator. Seedlings with equal growth were randomly selected and five of them were transplanted per pot (25 cm height × 11 cm diameter; PVC pipe) containing chestnut soil (44°56'N, 124°260'E) characteristic of local Songnen grassland. After 30 d, the plants were submitted to drought stress treatments. The soil moisture conditions were designated the control (70% field capacity), moderate drought (50% field capacity), and severe drought (25% field capacity). There were five replicates per treatment, and the experiment was run for 60 d. During the drought stress period, the weighing method was used to control the soil water content. Weights were measured every 2 d.

2.2 Plant collection and measurements

At the end of the drought stress treatments, the plants were excavated and removed their loose soil on root systems. The remaining intact rhizosphere soil was collected with a sterile brush, placed in a sterile test tube, labeled, and transported in a liquid nitrogen tank to Arrive Biomarker Technologies Corp. (Beijing, China) where it was subjected to high-throughput sequencing. The aboveground and belowground organs were excised, placed separately in envelopes, heated in an oven at 105°C for 30 min, dried at 65°C to constant weight, and weighed separately. The leaves were scanned and analyzed with ImageJ (NIH, Bethesda, MD, USA) to obtain the leaf area.

Specific leaf weight (mg/cm^2) = leaf DW / leaf area (1)

Root shoot ratio = underground biomass / aboveground biomass (2)

Organ water content (%) = (organ FW - organ DW) / organ FW (3)

where FW = fresh weight and DW = dry weight

2.3 DNA extraction and sequencing

Bacterial and fungal profiling was performed by Biomarker Technologies Corp. (Beijing, China) to determine the compositions of the bacterial and fungal communities in the various rhizosphere samples. Microbial DNA was extracted from each sample with a Soil DNA Isolation Kit. The 16S full-length primers were 27F (5'-AGRGTTTGATYNTGGCTCAG-3') and 1492R (5'-TASGGHTACCTTGTTASGACTT-3'. The ITS full-length primers were ITS1F (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3'). After the PCR products were assessed, a genomic library was built using the extracted DNA and the latter was sequenced on a single-molecule real-time sequencing platform (Pacific Bioscience, Menlo Park, CA, USA).

2.4 Data processing and analysis

The total circular consensus sequences were exported by Smrt Link v. 8.0, identified and filtering with Lima v. 1.7.0, and checked for chimeras with UCHIME v. 4.2 (Edgar et al. 2011). The sequences were clustered at 97% similarity level with USEARCH v. 10.0. QIIME2 was used to classify the bacteria and fungi based on the Silva v. 132 and Unite v. 8.0 databases (Assainar et al. 2020). The alpha-diversity indices including ACE, Chao1, Simpson, Shannon, and PD-whole-tree were calculated using Mothur v. 1.30 (Schloss et al. 2011). Sample dilution and grade relative abundance curves were plotted. Further analyses were conducted on the BMKCloud platform. Duncan's multiple range test was used for multiple comparisons among functional traits. Independent-samples Student's *t*-tests were performed in SPSS v. 19.0. Data were graphed with Origin v. 8.5.

3. Results

3.1 Effects of drought stress on the growth and functional traits of C. esculentus

Drought stress had significant effects on organ density in *C. esculentus* (Fig. 1). The leaf density was significantly higher under CK than the other two treatments ($P < 0.05$) and lowest under the DS treatment (Fig. 1A). The stem density was consistent with the leaf density (Fig. 1B). The root density significantly decreased with increasing drought stress ($P < 0.05$) (Fig. 1C). The minimum seed densities under the DS, DM, and CK treatments were 95.5 ind/m^2, 530.8 ind/m^2, and 636.9 ind/m^2, respectively, and they significantly differed ($P < 0.05$) (Fig. 1D).

Drought stress had evident effects on organ water content in *C. esculentus* (Fig. 2). The leaf water content was significantly greater under the CK treatment than the other two treatments ($P < 0.05$). However, there was no statistical difference between the DM and DS treatments in terms of their leaf water content ($P > 0.05$) (Fig. 2A). There was not any obvious difference between the CK and DM treatments in terms of their root water content ($P > 0.05$). However, their root water content was significantly greater than that of the DS treatment ($P < 0.05$) (Fig. 2B). The variation in seed water content was consistent with that for the leaf water content. There was not any statistical difference between the DM and DS treatments in terms of seed water content ($P > 0.05$) (Fig. 2C).

Drought stress significantly affected the plant heights, leaf areas, and root:shoot ratios (Fig. 3). The plant height was significantly greater under the CK treatment than the other two treatments ($P < 0.05$) (Fig. 3A). The leaf areas were significantly larger than that for the DS treatment ($P < 0.05$) (Fig. 3B). With worsening drought stress, there were no statistical differences among treatments of specific leaf weight ($P > 0.05$) (Fig. 3C). The root:shoot ratio of the CK treatment was significantly smaller than those of the other two treatments ($P < 0.05$) (Fig. 3D).

3.2 Effects of drought stress on bacterial and fungal community structure and diversity in C. esculentus *rhizosphere*

Table 1 showed that under drought stress, there were no significant differences among treatment groups in terms of the numbers of OTUs or the Chao, ACE, Shannon, and Simpson indices for their rhizosphere bacterial communities ($P > 0.05$). The PD_whole_tree index sequence was DS > CK > DM, and this parameter significantly differed between the DS and DM treatments ($P < 0.05$).

Table 1
Alpha-diversity indices of *Cyperus esculentus* rhizosphere samples

Microorganisms	ID	OTU	ACE	Chao1	Simpson	Shannon	PD_whole_tree	Coverage
Bacteria	CK	786 ± 26.73^{a}	1,063.83 ± 44.14^{a}	1,048.82 ± 42.06^{a}	0.9923 ± 0.002^{a}	8.33 ± 0.035^{a}	53.38 ± 6.73^{ab}	0.9355 ± 0.001^{a}
	DM	767 ± 29.63^{a}	1,066.33 ± 16.56^{a}	1,012.27 ± 14.46^{a}	0.9941 ± 0.001^{a}	8.50 ± 0.027^{a}	50.74 ± 3.31^{b}	0.9199 ± 0.001^{a}
	DS	783 ± 25.25^{a}	1,062.04 ± 41.56^{a}	1,017.77 ± 40.79^{a}	0.9940 ± 0.002^{a}	8.49 ± 0.019^{a}	55.29 ± 5.17^{a}	0.9266 ± 0.001^{a}
Fungi	CK	150 ± 4.27^{a}	152.26 ± 5.37^{a}	154.67 ± 5.63^{a}	0.9516 ± 0.017^{a}	5.44 ± 0.07^{a}	28.88 ± 1.63^{a}	0.9988 ± 0.001^{a}
	DM	109 ± 3.03^{c}	120.79 ± 5.72^{b}	117.00 ± 3.71^{b}	0.8670 ± 0.028^{b}	3.92 ± 0.07^{c}	18.79 ± 0.97^{b}	0.9977 ± 0.001^{a}
	DS	135 ± 5.39^{b}	140.92 ± 3.29^{a}	143.07 ± 6.33^{a}	0.8681 ± 0.0017^{b}	4.30 ± 0.10^{b}	27.57 ± 1.73^{a}	0.9976 ± 0.001^{a}

Note: Different letters indicate significant difference among treatments ($P < 0.05$). Values are means ± SE of three replicates per treatment.

Drought stress significantly affected rhizosphere fungal community diversity. The order of the OTU number was CK > DS > DM ($P < 0.05$). The orders of the Chao and ACE indices were the same. The values for the CK and DS treatments were significantly larger than those for the DM treatment ($P < 0.05$). The CK treatment had the largest Simpson index. The order of the Shannon index was CK > DS > DM and the differences among treatments were significant for this parameter ($P < 0.05$). The PD_whole_tree index was the largest for the CK treatment ($P < 0.05$).

A Venn diagram (Fig. 4) disclosed a total of 375 bacterial OTUs under the three treatments. The DS treatment had a maximum of 211 OTUs. There were differences among treatments in terms of their phylum-level bacterial abundances. The relative abundances of Bacteroidetes, Proteobacteria, and Acidobacteria were > 10% under all 3 treatment groups. The relative abundance of each genus significantly differed among the three treatments.

A Venn diagram (Fig. 5) revealed a total of 31 fungal OTUs under all three treatments. The CK treatment had a maximum of 70 OTUs, whereas the DM group had a minimum of 31 OTUs. There were statistical differences among treatments in terms of fungal colony structure distribution and phylum-level fungal abundance. The relative abundances of Ascomycota under the CK, DM, and DS treatments were 59.39%, 73.5%, and 83.68%, respectively. The relative abundance of Basidiomycota was obviously higher under the CK and DM treatments than the DS treatment ($P < 0.05$). There were substantial differences among treatments in terms of the compositions of their fungal genera. The relative abundance of *Schizothecium* was highest under the CK treatment (15.4%). The relative abundance of *Conocybe* was highest under the DM treatment (25.62%). The relative abundance of *Chaetomium* was highest under the DS treatment (29.29%).

Heat maps were plotted to compare relative phylum-level soil bacterial and fungal abundance under different drought stress treatment (Fig. 6). The bacterial compositions of CK and DM were similar and clustered together. Nevertheless, the bacterial community composition of DS significantly differed from those of CK and DM (Fig. 6A). EBP, Entotheonellaeota, and Armatimonadetes were relatively similar in composition, had close genetic relationships,

and clustered together. Deinococcus-Thermus and Nitrospirae, BRC1 and Actinobacteria, Patescibacteria and Bacteroidetes, Cyanobacteria and Dependentiae, Deferribacteres and Chloroflexi, and Spirochaetes and Firmicutes were similar in composition. The composition of rhizosphere bacteria under drought stress significantly differed from those under the other treatments ($P < 0.05$). The fungal communities of the DS and DM treatments were similar in composition and clustered together but obviously differed from that of the CK treatment (Fig. 6B). Glomeromycota and Blastocladiomycota, Rozellomycota, and Mortierellomycota were relatively similar in composition, had close genetic relationships, and clustered together. The composition of the rhizosphere fungi under the CK treatment significantly differed from those under the other treatments.

A network analysis showed the genus-level correlations among bacterial and fungal species in the rhizosphere of *C. esculentus* under various degrees of drought stress. The top 50 genera with the highest correlations are indicated (Fig. 7). At the bacterial genus level, there were 62 pairwise correlations among the species of which 33 were positive and 29 were negative (Fig. 7A). *RB41* and *Terrimonas* had the highest average species abundance and were negatively correlated. There were 18, 14, 12, 11, and six species positively correlated to *Dongia*, *Opitutus*, *Flaviaesturariibacter*, *Mesorhizobium*, and *Povalibacter*, respectively. At the fungal genus level, there were 71 pairwise correlations among the species of which 46 were positive and 25 were negative (Fig. 7B). *Chaetomium* had the highest average abundance and was negatively correlated with *Schizothecium*. There were 12, 10, 10, 10, 5, and five species positively correlated with *Curvularia, Thermoascus*, *Periconia*, *Monosporascus*, *Subulicystidium*, and *Scutellinia*, respectively.

4. Discussion

4.1 Responses of growth and functional traits of C. esculentus *to drought stress*

Plant functional traits intuitively indicate the extent to which drought stress has damaged plants (Wang et al. 2017). The leaf has the most contact with the atmosphere and acquires and utilizes plant resources (Zirbel et al. 2017). The root is a vital belowground vegetative organ hidden that is formed by long-term evolution. The configuration of the root system directly reflects the efficiency of material transfer and utilization of soil resources. It also affects plant growth and adaptive capacity (Bardhan et al. 2021; Pausch and Kuzyakov 2018). The seed determines seedling establishment, community succession, and plant regeneration (Grundy and Burston 2003). The present study showed that drought stress significantly reduced leaf, stem, root, and seed density per unit area. Under severe drought stress, the seed density was 96 ind/m^2 which was only 0.18-fold that for seeds under moderate drought stress. Drought stress inhibited the growth and limited the key ecological factors influencing the yield of *C. esculentus*. In *C. esculentus*, the leaf was the vital organ of photosynthesis and respiration, whereas the root system was the essential organ of water and mineral nutrient absorption. Changes in the functional traits of these organs directly determine the ability of *C. esculentus* to obtain its resources under drought stress (Zhou et al. 2018).

The water content of plant organs directly reflects their water status (Cornelissen et al. 2003). Here, the leaves and seeds of *C. esculentus* had relatively high water content and sensitivity to drought stress. The water content of the CK treatment was significantly taller than those of the DM and DS treatments. However, severe drought stress significantly reduced the root water content. Hence, *C. esculentus* could maintain stable root water content and soil water absorption under moderate drought stress. Wheat root systems perceived the arrival of drought and rapidly produced chemical signals that were transmitted acropetally, promoted stomatal closure, and reduced water loss (Jia and Zhang 2008). Here, the water content of *C. esculentus* leaves significantly decreased under moderate drought and the photosynthetic and respiration rates were reduced. Wang and Bader (2018) proposed that the moisture and photosynthetic light-responsive and water-responsive traits of mosses are interrelated. Seed size, traits, quantities,

and other factors are closely related to the traits of the seedlings they produce (Moles and Westoby 2006). There was not any significant difference between *C. esculentus* under moderate and severe drought stress ($P > 0.05$) in terms of its water content. The plant maintained this survival strategy by generating only small numbers of large seeds. In stressful or highly competitive environments, large seeds are relatively more likely to establish seedlings as they provide comparatively more storage material for early seedling growth (Westoby et al. 1996).

Reseach data shows that plants adapt to changes in environment stress by altering their functional traits including leaf area, shoot height, leaf quality (Lienin and Kleyer 2012). In the present study, drought stress significantly affected plant height but did not significantly alter specific leaf weight. The leaf areas were significantly higher in the CK and DM groups than the DS group. The root:shoot ratios were obviously lower in the CK than the DM and DS. Adaptive changes occur in the cell structure, physiology, biochemistry, and morphology of plants under drought stress. The most evident response of grasses to drought stress was a change in shoot height (Han and Wang 2005). A recent study used perennial forage grasses as the research objects and found that the inhibition of shoot elongation increased with the degree of drought stress. This finding was consistent with those of the present study (Ji et al. 2021). The specific leaf weight reflects the photosynthetic performance of plants and their ability to return the resources they acquire (Cornelissen et al. 2003). Under drought stress, plants conserve water by efficiently utilizing limited water resources and/or by avoiding drought. Drought-tolerant plants have small, narrow leaves and high specific leaf weight and xylem density. The observed changes in the drought tolerance-related functional traits of *C. esculentus* were consistent with results reported for wheat, camel thorn, and oat (Markesteijn and Poorter 2009). In response to changes in the ambient environment, plants allocate biomass to various organs to obtain the water, nutrients, and light required for growth (McCarthy and Enquist 2007). In the present experiment, *C. esculentus* adapted to drought stress by increasing its biomass investment in the belowground organs. An earlier study showed that neither gymnosperms nor angiosperms increased their root:shoot ratios under extreme drought stress (Huang et al. 2018). Hence, there is a soil moisture threshold for plant biomass allocation under water stress.

4.2 Responses of rhizosphere bacterial and fungal community structure and diversity in C. esculentus *under drought stress*

Rhizosphere microorganisms convert soil nutrients into forms that plants can absorb and assimilate through their metabolic activity. Thus, rhizosphere microorganisms play main roles in plant growth and stress resistance (Chamkhi et al. 2022). The abundance and diversity of the fungal community in the CK treatment were greater than those in the DS treatment which, in turn, were greater than those in the DM group. There were also phylum-level differences among groups in terms of the abundances of their rhizobacteria. The relative abundances of Bacteroidetes, Proteobacteria, and Acidobacteria were > 10% in all three treatments. Drought stress increased the relative abundances of Bacteroidetes, Verrucomicrobia, Patescibacteria, Actinobacteria, and Nitrospirae. Bacteroidetes was considered relatively less common and important than the other phyla (Schreiter et al. 2014). However, the results of the present study contradicted this viewpoint. Ascomycota and Basidiomycota were the principal fungal phyla in the rhizosphere of *C. esculentus*. Under drought stress, the relative abundance of Ascomycota significantly increased to 59.39–83.68%. By contrast, the relative abundance of Basidiomycota significantly decreased under severe drought stress. Ascomycota and Basidiomycota are the two main branches of soil fungi. In general, fungi are more severely affected by drought than other soil microorganisms (Coleman-Derr et al. 2016). The relative abundances of Ascomycetes in the semi-arid area of the Loess Plateau were in the range of 43.23–69.38% This fungal phylum predominates in arid soils (de Boer et al. 2005). A related study on Basidiomycota showed that these symbiotic microorganisms significantly promote plant growth even under drought conditions (Ghimire et al. 2009). Severe drought stress significantly increased the relative abundance of *Chaetomium* spp. which produce metabolites that inhibit the growth of other soil fungi (Nelson 2018).

The species abundance heat map for soil bacterial and fungal phyla showed that the rhizobacteria were similar in composition and clustered together for CK and DM. However, the compositions of the rhizosphere bacterial phyla under severe drought significantly differed from those for the other two groups. The rhizosphere fungi under DS and DM were similar in composition, clustered together, and significantly differed from those under CK. The results indicated that fungi were relatively more sensitive to drought stress than bacteria and that the fungal community groups under moderate drought stress significantly differed from those under severe drought stress. These findings were consistent with the results inferred from the Shannon and Simpson indices and the OTUs. Drought stress had a significant effect on the rhizobacteria of *C. esculentus*. Previous studies showed that certain rhizosphere fungi can reduce the adverse effects of stress on host plants (Miransari 2014; Zhang et al. 2019). Plants can cope with stress through their morphophysiological responses. Nevertheless, the root-microorganism system more substantially improves stress tolerance in host plants (Santos-Medellin et al. 2017). We used a network analysis to determine the correlations among the bacterial genera and fungal species in rhizosphere soil under drought stress. At the genus level, there were 62 pairwise correlations among bacterial species. *RB41* and *Terrimonas* had the largest average abundance and were negatively correlated. At the genus level, there were 71 pairwise correlations among fungal species. *Chaetomium* had the highest average abundance and it was negatively correlated with *Schizothecium*. Acosta-Martínez et al. (2014) found that the relative abundance of *Terrimonas* increased after drought stress in a manner independent of soil C, N, or P content. Thus, *Terrimonas* might serve as a bioindicator of drought stress. Fungi may persist during drought and respond faster than bacteria to increases in soil water content (Davinic et al. 2013). As a rule, mycorrhizal fungi are more tolerant to drought stress than bacteria and facilitate host plant nutrient and water uptake (Schwarze et al. 2004).

5. Conclusion

Drought stress had significant impacts on the growth, functional traits, and biomass distribution of *C. esculentus* organs. The leaves and seeds had higher water content and were more sensitive to drought stress than the roots. Under drought stress, the specific leaf weight did not significantly change whereas the root:shoot ratio increased and the shoot height and leaf area decreased. *C. esculentus* adapted to drought stress by increasing its biomass investment in the belowground parts. Drought stress had a significantly greater impact on the fungi than the bacteria in the rhizosphere of *C. esculentus*. The rhizosphere fungi of *C. esculentus* were relatively more sensitive to drought stress. However, mycorrhizal fungi had comparatively higher tolerance to drought stress. *C. esculentus* adapted to drought stress through the mutual regulation of plant biomass accumulation, functional traits, and nutrient distribution and modulation of the abundance, composition, and diversity of its rhizosphere microbial communities.

Abbreviations

CCS, circular consensus sequence; OTU, operational taxonomic unit

Declarations

Ethics approval and consent to participate

All authors confirmed that experimental research on *Cyperus esculentus*, including receiving the seeds, complied with relevant institutional, national, and international guidelines and legislation. Furthermore, methods were conducted according to the relevant guidelines and regulations. We have permission to use the plant material for experimental purposes.

Consent for publication

Not applicable.

Availability of data and materials

The relevant data in this study are included in this article. The soil bacteria and fungi data have been deposited in the Genome Sequence Archive under accession number of CRA008944 (https://ngdc.cncb.ac.cn/gsa/s/02q2GNY3).

Competing interests

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

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Authors' contributions

Binshuo Liu: Conceptualization and Methodology. Yunhang Hu: Investigation. Honghai Xue: Writing - review & editing. Ming Li: Data analysis. Ying Wang: Writing - original draft. Zhonghe Li: Investigation.

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Figures

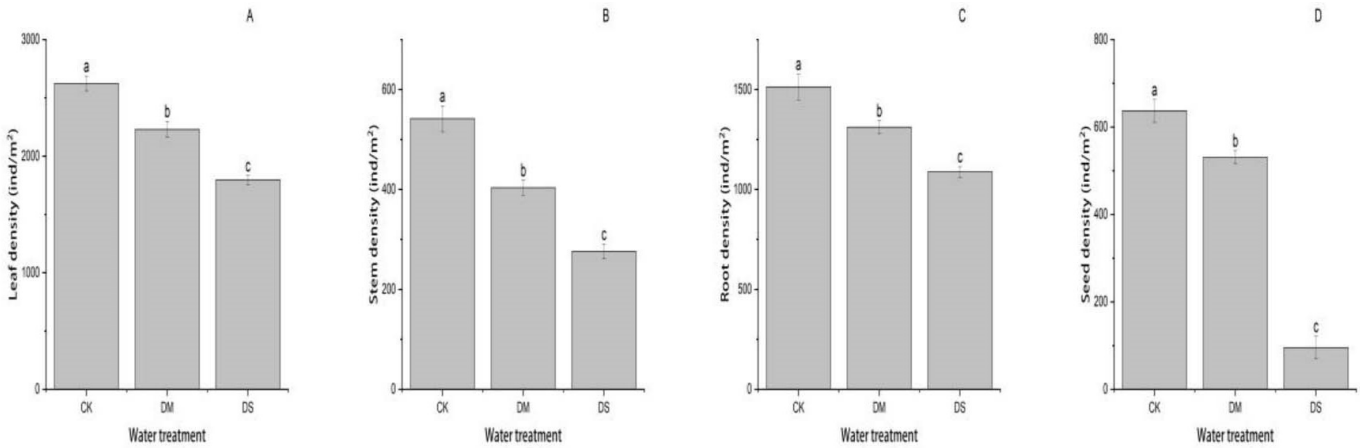


Figure 1

Relative changes in organ density of *Cyperus esculentus* under drought stress A: Leaf density, B: Stem density, C: Root density, D: Seed density

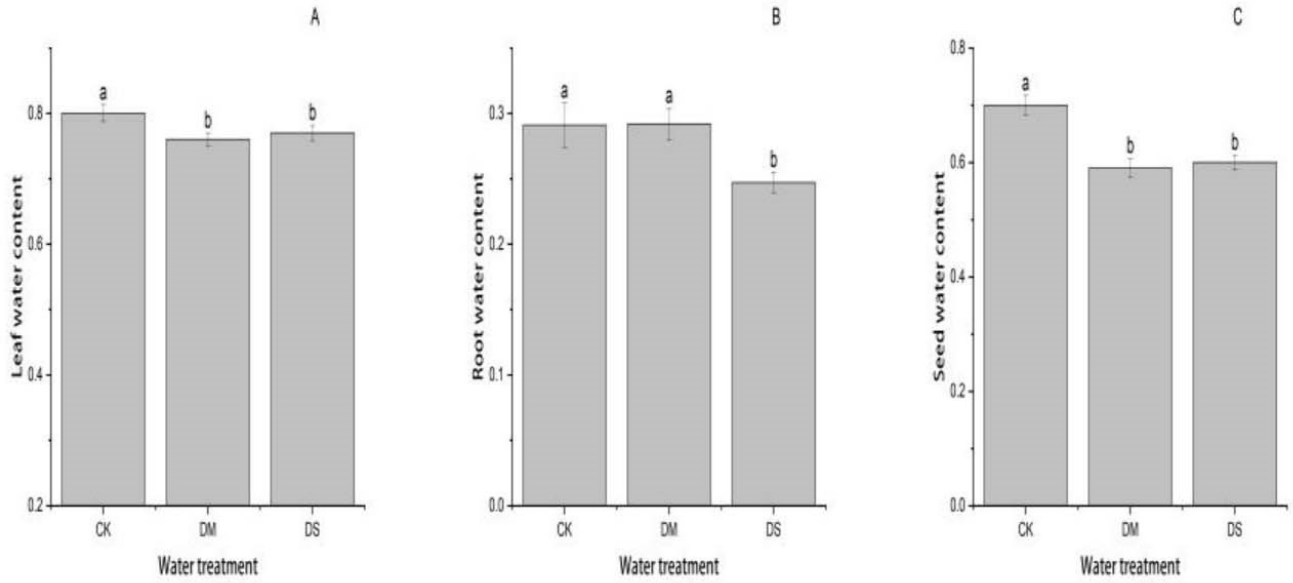


Figure 2

Relative changes in organ water content of *Cyperus esculentus* under drought stress A: Leaf water content, B: Root water content, C: Seed water content

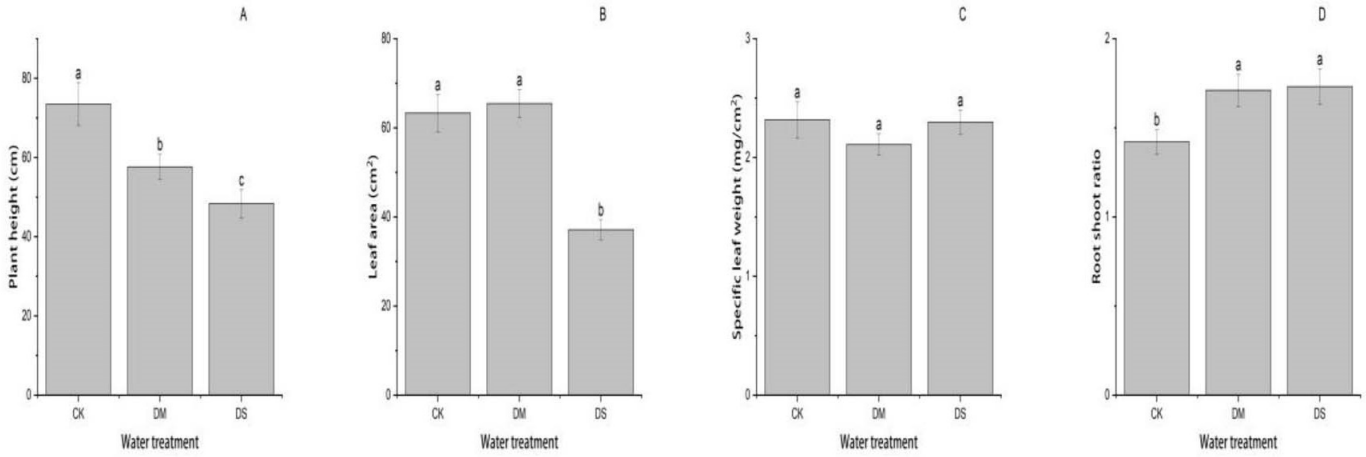


Figure 3

Relative changes in functional traits of *Cyperus esculentus* under drought stress A: Plant height, B: Leaf area, C: Specific leaf weight, D: Root shoot ratio

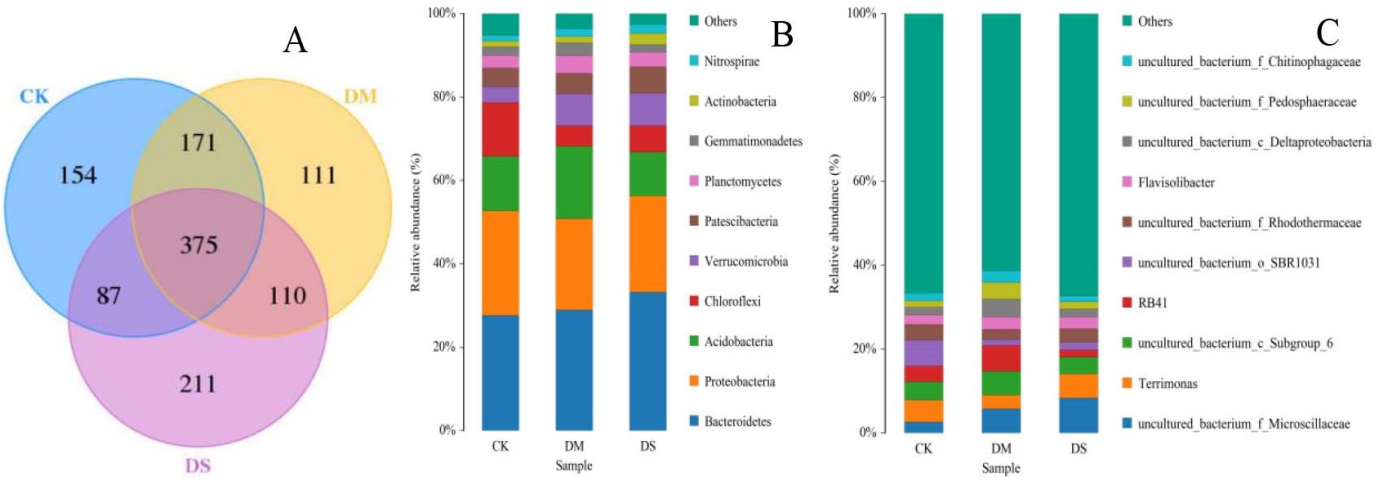


Figure 4

Venn diagram (A) and relative phylum (B) and genus (C) level abundances of rhizosphere bacteria of *Cyperus esculentus* under drought stress

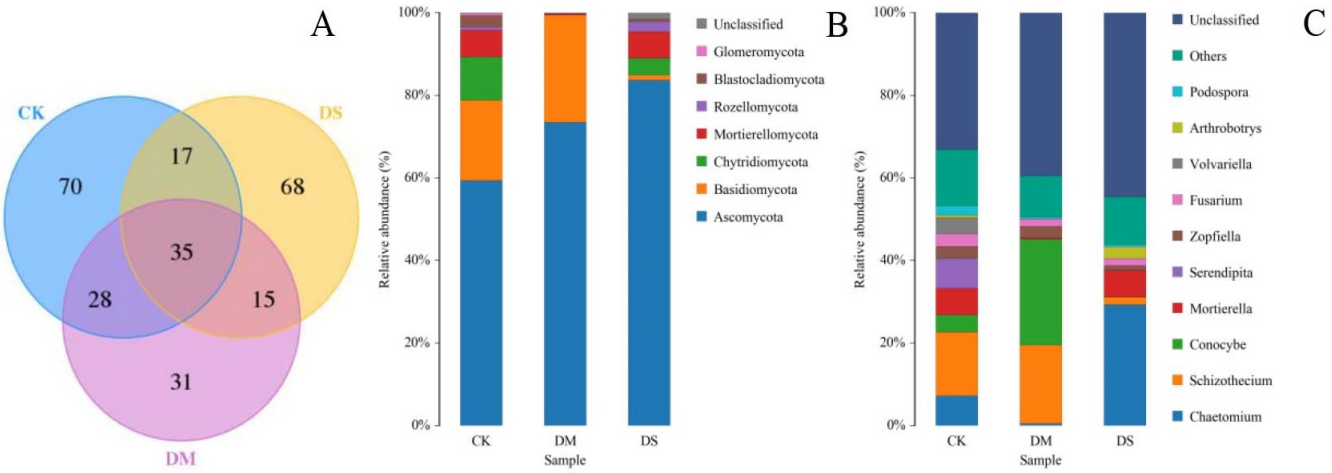


Figure 5

Venn diagram (A) and relative phylum (B) and genus (C) level abundances of rhizosphere fungi of *Cyperus esculentus* under drought stress

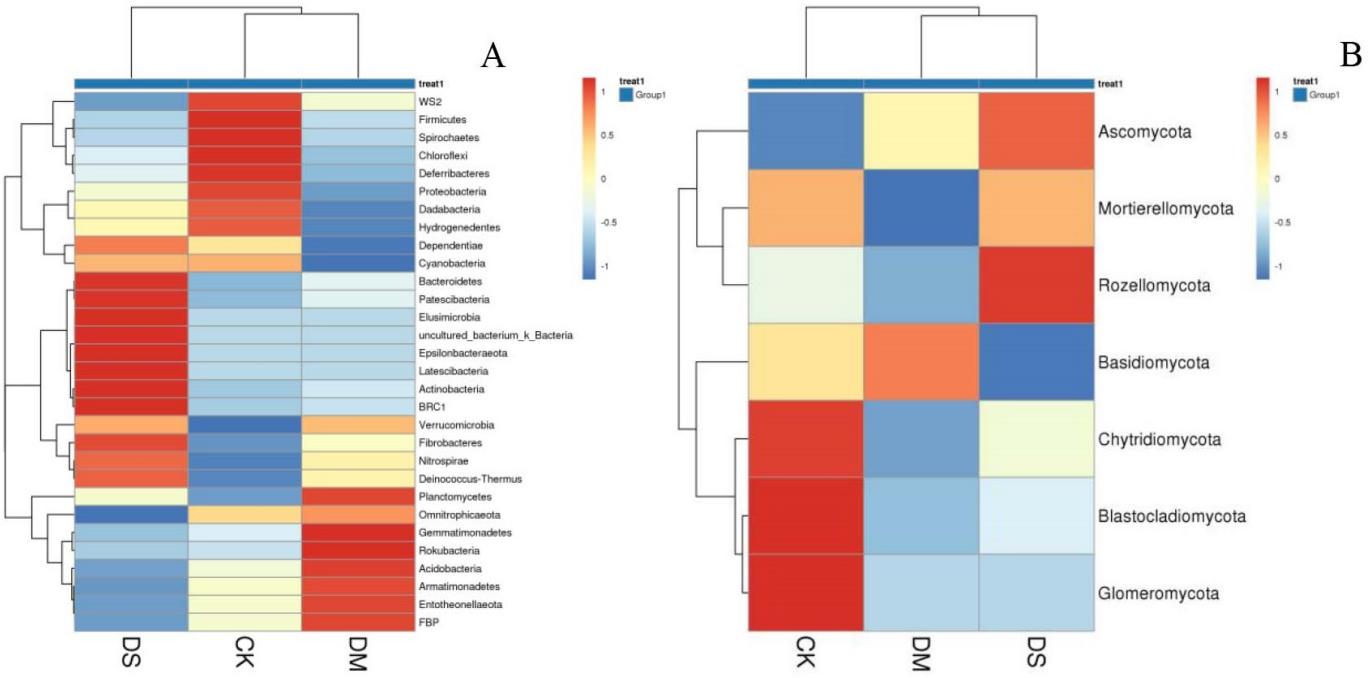
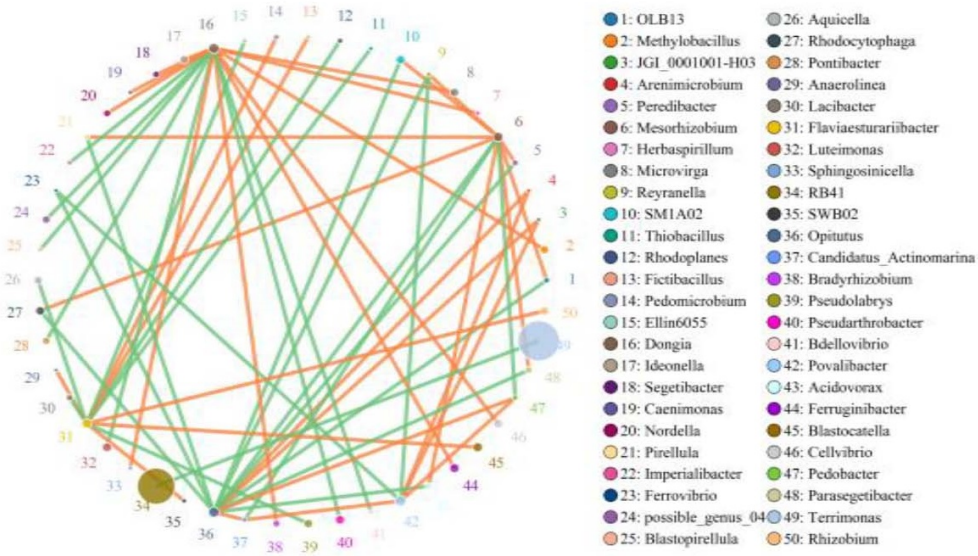


Figure 6

Heat map of relative phylum-level abundances of bacteria and fungi in rhizosphere of *Cyperus esculentus* under drought stress. Horizontal clustering = sample data. Vertical clustering = species data. Left clustering tree = species. Upper clustering tree = sample. Middle = heat map.

A



B

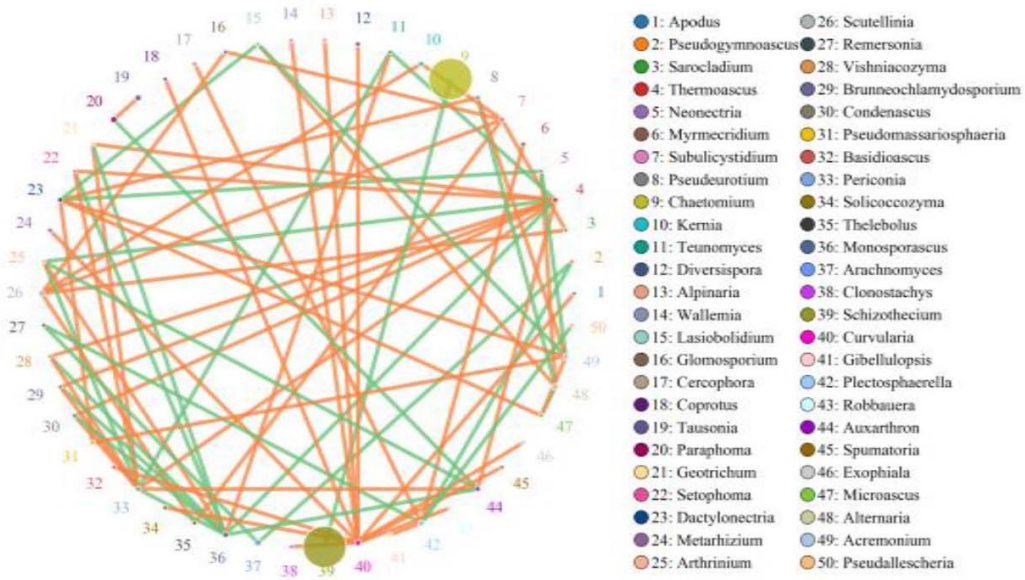


Figure 7

Network diagram of genus-level correlations among bacteria (A) and fungi (B) in rhizosphere of *Cyperus esculentus*under drought stress

Note: circle = species. Circle size is proportional to average species abundance. Line represents correlation between two species. Line thickness is proportional to correlation strength. Orange line = positive correlation. Green line = negative correlation.