Drought impacts on plants and microbes are moderated by leaf litter via species specific shifts in plant and soil biotic interactions

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Abstract

Prolonged drought affects plant–soil interactions, with cascading impacts on ecosystems. We conducted a pot experiment with soils from a seven-year Australian grassland rainfall manipulation to test how litter mediates drought effects on plant growth, nutrient cycling, and microbial communities. Two common pasture species (*Plantago lanceolata*, forb; *Microlaena stipoides*, grass) were grown for three months in soil maintained at 70% or 40% water holding capacity, reflecting field manipulations, with or without leaf litter of the same species. Litter increased shoot, but not total, biomass of both species. Further, litter increased *M. stipoides* root biomass under drought but decreased root biomass under ambient watering. Litter increased microbial biomass carbon, and drought reduced microbial biomass carbon and nitrogen, consistently across both species. Further, in *M. stipoides*, litter increased most microbial biomarkers (e.g. PLFA, NLFA), while drought increased Gram-positive and Actinobacteria. By contrast, in *P. lanceolata*, litter reduced biomarker contents under ambient conditions for Gram-positive and Actinobacteria and under drought conditions for Gram-negative, Protozoa and Arbuscular Mycorrhizae. Litter and drought further moderated plant-soil biotic relationships, particularly in *M. stipoides*, where biomass was negatively related to several microbial biomarkers under ambient conditions without litter, indicative of resource competition. Litter mass loss was positively correlated with *M. stipoides* root biomass and an arbuscular mycorrhizal biomarker under drought conditions, indicating an important plant–soil biotic feedback. Our findings suggest that drought moderate plant community dynamics via species-specific changes in plant-soil biotic interactions, including feedbacks mediated by litter decomposition.

1. Introduction

Global climate changes have resulted in reduced precipitation in many ecosystems (Clair & Lynch, 2010). In addition, seasonal rainfall patterns are changing (Padrón et al., 2020), with dry periods becoming more pronounced (Chou et al., 2013). Drought imposes significant stress on plants, negatively affecting physiological, morphological, and molecular processes and ultimately limiting plant growth (Farooq et al., 2009). Drought also reduces plant nutrient uptake by reducing nutrient diffusion and mass flow in the soil (Lambers et al., 2008), and negatively affects microbial activity, biomass production, and community composition (Touchette et al., 2007; Puijalon et al., 2011; De Leonardis et al., 2012), which impacts biochemical process such as mineralization and decomposition (Gholz et al., 2000; Borken & Matzner, 2009; Delgado-Baquerizo et al., 2013). Altogether, these changes can have profound and irreversible impacts on ecosystem structure and function in part mediated by shifts in plant-soil biotic interactions (Nielsen & Ball, 2015; Kaisermann et al., 2017; Rasmussen et al., 2020).

Plants can allocate more resources belowground to acquire water and nutrients from the soil under drought stress (Bloom et al., 1985; Poorter et al., 2012). This, however, will generally result in lower litter quality, for example through increased carbon:nitrogen (C:N) ratios of leaves, which impact decomposition processes and soil nutrient cycling (García-Palacios et al., 2016). Furthermore, to minimize effects of drought, some plants form mutualistic relationships with certain fungi, including

arbuscular mycorrhizal fungi (Smith et al., 2010; Jiang et al., 2021), increasing the accessibility of nutrients to the host plant (Van Der Heijden et al., 2008; Jiang et al., 2021). Similarly, microbes can reduce drought induced stress via morphological changes in cells or expanding hyphal networks (Oren & Steinberger, 2008; García, 2011), while other microbes become increasingly dependent on plants, for example through increased reliance on plant root exudates (Walker et al., 2003) or mycorrhizal associations (Smith et al., 2010). Additionally, many bacteria, such as Gram-negative bacteria, can release complex compounds (e.g. polysaccharides) that positively influence soil structure in the rhizosphere (Milošević et al., 2012), which improves acquisition of soil water and nutrients such as N (Grandy et al., 2008). However, plant and microbes can respond differentially to drought resulting in altered plant-microbe interactions (Hartmann et al., 2013; Deng et al., 2021). Although studies show that plants tend to rely more on mutualistic relationships with microbes under stress conditions (Pavithra & Yapa, 2018; Mathur et al., 2019), some microbes compete with plants for nutrients under severe water conditions (Collins et al., 2008; Fry et al., 2018), immobilizing inorganic N during decomposition and reducing N availability (Downs et al., 1996; Fitzpatrick et al., 2019). This suggests that plant-microbial interactions will differ under drought with the impacts strongly dependent on nutrient availability.

Plant leaf litter is an important source of both C and nutrient to the soil (Ekberg et al., 2007). Litter-derived C and nutrients are released via decomposition processes principally mediated by microbes; however, drought-associated reductions in water availability can negativity impact microbial driven decomposition of organic matter (Gholz et al., 2000; Hättenschwiler et al., 2005). It has been observed that arbuscular mycorrhizae are more resilient to drought conditions than bacteria and can accelerate decomposition processes, thereby improving plant access to nutrients stored in litter (Mariotte et al., 2015; Elumeeva et al., 2018). However, microbes can compete with plants for nutrients particularly when nutrients or other resources are scarce (Johnson et al., 1997). Hence, leaf litter can moderate nutrient pools and potentially the effects of drought via altered plant-soil biotic interactions. However, few studies have assessed whether drought impacts are moderated by litter and associated shifts in plant-soil biotic interactions (Gulis & Suberkropp, 2003; Kaisermann et al., 2017), although some studies suggests potential beneficial impacts of nutrient addition during drought (Gavito & Olsson, 2003; Zhang et al., 2016).

To provide further insight into the effects of prolonged drought on plant biomass production and allocation, microbial assemblages and nutrient cycling, including effects mediated by the decomposition pathway, we conducted an *ex-situ* study in a growth chamber using soil collected from an Australian grassland where rainfall had been manipulated for seven years (ambient versus a 50% reduction in rainfall, henceforth drought). We focussed on two common pasture species, the grass *Microlaena stipoides* and the forb *Plantago lanceolata*, with strong differences in functional attributes including leaf C:N ratio (Chapin et al., 1996; Wardle et al., 1997) and rooting depth (Reiter et al., 2002; Nie et al., 2008), that have previously shown contrasting drought-induced shifts in plant-microbe interactions (Hassan et al., 2021). We grew the two species under well-watered (70% of water holding capacity) and drought conditions (40% of water holding capacity) in soils with a legacy of ambient and prolonged drought treatment, respectively, with or without litter addition as a resource to assess how litter mediates plant-

soil biotic interactions. A previous study showed that a legacy of reduced rainfall had significant impacts on soil soluble nutrient pools (Szejgis et al., 2024b). We hypothesised that i) Drought will negatively impact plant and microbial biomass. However, the addition of litter will, at least partly, ameliorate the effect of drought by acting as a C and nutrient source. ii) Litter addition will stimulate positive plant–microbe interactions by providing additional nutrients, particularly under drought, enhancing rhizosphere development, plant growth, and microbial biomass, while drought will constrain plant–soil microbial interactions driving litter decomposition.

2. Materials and methods

2.1 Site description and experimental design

The study was conducted using soil collected in 2021 from a long-term rainfall manipulation experiment established in 2014 in eastern Australia (33.9 °S, 150.7 °E). The site is characterized as a grassland with a mean maximum temperature of 30.3°C in January and a mean minimum temperature of 4.1°C in June and 676 mm mean annual precipitation (Canarini et al., 2018). Rainfall manipulation was imposed using a standard 2 × 2 m plot rainfall shelter design (Canarini et al., 2016), to create two treatments with four replicates at each site: drought (50% rainfall reduction relative to ambient) using rainfall-exclusion roofs to reduce incoming rainfall and ambient. Approximately 10 L of soil was collected from each of the four prolonged drought and ambient rainfall plots by excavating soil from a 30 × 30 cm quadrat to a depth of 15 cm, placed in plastic crates and transported to the Hawkesbury Institute for the Environment (HIE), Western Sydney University. The soils were sieved through a 3 mm mesh to remove stones and plant materials. Soil from each field plot was mixed thoroughly and kept separate to maintain the field replication, thus avoiding pseudo-replication Reinhart & Rinella (2016). The soils were then kept at 4°C until starting the experiment. Two sets of pots were maintained, one for litter preparation and another for the main experiment.

2.2 Litter preparation

To produce leaf litter for the experiment, P. lanceolata and M. stipoides were grown under ambient and drought conditions using a portion of the soils collected from the experimental plots. Seeds of *P. lanceolata* and *M. stipoides* were obtained from Royston Petrie Seeds Pty Ltd. Seeds, sterilized with 1% bleach solution for 5 min and washed with milli-Q water and air dried prior to sowing. Seedlings of *P. lanceolata* and *M. stipoides* were grown in sterile potting mixture in a Kwik Pot Cell Tray. Two weeks old seedling were transplanted directly into the pots. The plants were grown for 12 weeks in a growth cabinet with the following environmental conditions: 22 ± 1°C, 70 ± 5% relative humidity, and a day-light cycle of 16:8 L:D. After 3 months of incubation, the leaf litter was harvested and dried at 70°C for 5 days prior to preparation of litter bags, with approximately 1 g of leaf litter in each bag. The litter bags (10 × 6 cm) were made using glass fibre screen with a mesh size of 2 mm (Model; Permastik Fly Screen Mesh, Bunnings, Australia) and sealed with a 300 HI impulse sealer.

2.3 Plant, watering and litter treatments

The experimental units comprised 500 mL pots filled with soils from one of the four drought or four ambient rainfall plots to create true replicates. To establish the plant treatments, we transplanted two-week-old seedlings (one seedling per pot) directly into pots, with one individual of *P. lanceolata* in each of 16 pots and one *M. stipoides* in another 16 pots. Pots with soil from the long-term ambient plots (henceforth 'ambient') were kept at 70% water holding capacity (WHC) while the pots with soil from the prolonged drought plots (henceforth 'drought)' were kept at 40% WHC. One litter bag was added to four of the pots for each plant species x watering treatments while the other four pots received no litter (i.e. n = 4 for each treatment combination). Litter bags with litter from the target species were buried vertically into soil (approximately 10–15 cm), near the seedling in designated pots, immediately after litter preparation. Because litter on top of the soil may not fully reflect altered soil water contents by the treatments, we buried the litter bags to ensure exposure to soil microbial decomposers in the contrasting watering treatments (Hewins et al., 2017; Su et al., 2021). The experiment was continued for 12 weeks in a growth cabinet with the following environmental conditions: 22 ± 1°C, 70 ± 5% relative humidity, and a day-light cycle of 16:8 L:D.

2.4 Soil sampling and laboratory analyses

Soil sampling was conducted after 12 weeks by randomly inserting a 50 ml plastic tube 10 cm into the topsoil limiting impacts on the plant for each of the 32 pots. Soil samples were sieved through a 3 mm sieve to remove rocks and plant materials. The homogenized soil was then subsampled for individual analyses. After soil collection, the plants were harvested, oven-dried for 5 days at 70°C and weighed separately for root and shoot biomass.

Litter bags were removed after 12 weeks coinciding with harvesting plants and emptied into a weigh boat before gently removing all non-plant material and oven drying the remaining matter for 5 days at 70°C. Litter decomposition is presented as litter mass loss (in %) relative to the original weight.

Soluble and microbial biomass C and N were obtained using the chloroform fumigation extraction method. Unfumigated extracts were used to determine available C and N while microbial biomass C and N were estimated from the difference between the unfumigated and fumigated samples (Vance et al., 1987). C and N was extracted from 5 g fresh soil after, 4 days of chloroform fumigation, using 0.5 M K_2SO_4 solution. After shaking for 2 hours, extracts were filtered using ashless Grade 42 quantitative filter circles (125mm diameter). Both fumigated and unfumigated samples were then analysed for total C and N using a TOC-L analyser (Shimadzu, Kyoto, Japan). Data were corrected to account for moisture content and divided by an extraction efficiency of 0.54 (Brookes et al., 1985). All data are reported in mg kg^{-1} (Table S1).

Microbial phospholipid fatty acids (PLFAs) and neutral lipid fatty acids (NLFAs) were analysed based on the protocol by Buyer & Sasser, (2012), with PLFAs and NLFA extracted from ~ 3 g freeze-dried soil. NLFA was used to assess arbuscular mycorrhizae abundance (Frostegård et al., 2011). Extractions were completed using 4 ml of Bligh-Dyer extract (consisting of 200 ml 50 mM K_2HPO_4 in H_2O, 500 ml methanol, and 250 ml chloroform). Fatty acids were summed into the following biomarker groups: Gram-

positive bacteria (15:0 anteiso, 15:0 iso, 16:0 anteiso, 16:0 iso, 17:0 anteiso, 17:0 iso), Gram-negative bacteria (17:0 cyclo ω7c, 18:1 ω7c, 18:1 ω9c, 19:0 cyclo ω7c), Actinobacteria (16:0 10-methyl, 17:0 10-methyl, 18:0 10-methyl), Protozoa (20:2 ω6c, 20:3 ω6c, 20:4 ω6c, 20:5 ω3c) and fungi (18:2 ω6c). Neutral lipid 16:1 ω5c was used as the arbuscular mycorrhizae biomarker. PLFA and NLFA data are reported in μg g^{-1} (Table S2).

2.5 Statistical analysis

All data were checked for normality using the Shapiro-Wilk normality test (Royston, 1982). Most of the data, except microbial C and N and litter mass loss, showed a non-normal distribution and were square-root transformed for further statistical analysis. Effects of litter presence, watering treatments and plant species identity, and their interactions, were tested for using three-way ANOVA (Chambers et al., 2017). Significant treatment interactions were analysed using Tukey's Honest Significant Different (HSD) post-hoc test using the package "emmeans" in R. Regression analyses were used to investigate relationships among microbial biomass (C, N, PLFAs, NLFA) with plant shoot and root biomass, and litter mass loss across both plant species and watering treatment. All statistical analyses were conducted using R (R Foundation for Statistical Computing) ver. 4.4.2 (2024-10-31) with R-Studio 2024.09.01 Build 394 "Cranberry Hibiscus" Release (a1fe401f, 2024-11-03) for Windows.

3. Results

3.1 Effects of watering and litter treatments on plant biomass and nutrient pools

Watering treatments had no main effects on total plant biomass of either species (Table S1, S3). The addition of litter increased shoot biomass (Fig. 1A) and marginally increased total plant biomass ($p < 0.1$, Table S3, Fig. S1), for both species. A three-way interaction showed that *M. stipoides* had higher root biomass without litter under ambient watering, whereas root biomass was higher with litter under drought conditions (Fig. 1B). A similar, significant pattern was observed for root:shoot ratio (Fig. 1C). In addition, litter mass loss was significantly different between plant species with *P. lanceolata* showing higher litter mass loss ($F_{1,12}=8.73$, $p < 0.05$, Table S1 and S3) and watering treatments influenced decomposition with greater litter mass loss under drought conditions ($F_{1,12}=20.66$, $p < 0.05$, Table S1 and S3).

Watering and litter addition had no main effects on soluble C, but we observed a significant two-way interaction for litter addition and plant species with higher soluble C for *P. lanceolate* with litter addition (Fig. S2A, Table S1). Watering and litter addition had no effect on soluble N or soluble C:N ratios (Table S3, Fig. S2). Microbial biomass C and N was significantly affected by watering treatments with reduced content in drought treatments for both plant species (Fig. 2A, B; Table S5). Litter addition significantly increased microbial biomass C content in well-watered treatments across both plant species (Fig. 2A). No significant effects of were recorded for microbial C:N ratio (Fig. 2C).

3.2 Effects of watering and litter treatments on microbial biomarkers

Microbial PLFA and NLFA biomarkers generally increased significantly with litter addition but showed more variable responses to watering treatments between plant species (Table S3). Gram-positive bacteria and Actinobacteria showed higher biomarker contents, specifically for *M. stipoides*, with litter addition for both watering treatments while, without litter, higher microbial biomarker content was observed under drought compered to ambient watering (Fig. 3A, B). Additionally, higher microbial biomarker contents were observed with litter addition for *P. lanceolata* under ambient watering compered to ambient watering without litter. Arbuscular mycorrhizae biomarker content was higher with litter addition under drought conditions in pots with *M. stipoides*, while in pots with *P. lanceolata* arbuscular mycorrhizae fungal biomarker content was higher without litter addition under drought conditions (Fig. 3C). Gram-negative bacteria, Protozoa and fungal biomarker contents increased in response to litter addition for *M. stipoides* (Fig. S3). Additionally, Gram-negative bacteria and Protozoa biomarker content was higher without litter under drought conditions for *P. lanceolata* (Fig. S3A, B).

3.3 Relationships among plant biomass, microbial biomarkers and litter decomposition

Shoot biomass was positively related to microbial C and N for *P. lanceolata* under ambient watering, whereas shoot biomass in *M. stipoides* was negatively related to microbial C under ambient watering (Fig. 4A, B). A significant negative relationship was observed between shoot biomass, and Gram-positive and Gram-negative bacteria in *P. lanceolata* under drought conditions (Fig. 4C, D). Shoot biomass was not related to Actinobacteria, Protozoa, fungi or arbuscular mycorrhizae for either species (Fig. S4A-D).

Root biomass was positively related to microbial C and N for *P. lanceolata* under ambient watering (Fig. 5A, B). In contrast, root biomass was negatively related to Gram-positive bacteria, Gram-negative bacteria, Actinobacteria and arbuscular mycorrhizae for *M. stipoides* under ambient watering (Fig. 5C-F). Root biomass was not related to protozoa or fungi for either species (Fig. S5A, B).

Litter mass loss was significantly different between plant species ($F_{1,12}$=8.73, $p < 0.05$), with *P. lanceolata* showing higher litter mass loss (Table S1). In addition, watering influenced decomposition, with greater litter mass loss under drought conditions ($F_{1,12}$=20.66, $p < 0.05$). Root biomass and arbuscular mycorrhizae were positively related to litter mass loss for *M. stipoides* (Fig. 6A, C), whereas microbial C was negatively related to litter mass loss for *P. lanceolata* (Fig. 6B). Litter mass loss was not related to Gram-positive bacteria, Actinobacteria, fungi, microbial N, Gram-negative bacteria or Protozoa (Fig. S6A-G).

4. Discussion

4.1 Effects of reduced water availability and litter addition on plant biomass and microbial biomarkers

We hypothesised that drought would negatively impact plant and microbial biomass but that this effect would, at least partly, be ameliorated by litter addition acting as a C and nutrient resource. Contrary to expectations, watering had limited main effects on plant biomass or microbial biomarkers, although drought consistently negatively impacted microbial biomass C and N. Litter addition, however, mediated plant biomass and biomarker responses as hypothesized, with plant species specific influences. Litter consistently increased shoot biomass (and marginally total plant biomass) in both species. However, the effect of litter on plant root biomass and root:shoot ratio differed between the two species and watering treatments. Specifically, litter increased root biomass and root:shoot ratio under drought but had the opposite effect under ambient condition for *M. stipoides*. By contrast, litter increased root biomass in *P. lanceolata* under ambient treatment only. Previous studies have reported inconclusive impacts of litter addition, with some reporting both negative and positive effects of litter on plant biomass (Ostonen et al., 2007; Lopez-Iglesias et al., 2014; Chen et al., 2018), suggesting that the response is highly species and context dependent. The observed drought effect on microbial biomass C and N pools is in alignment with previous studies that have observed decreased activity of microbes involved in nutrient cycling in response to water stress (Van Meeteren et al., 2008; Muhr et al., 2010). Overall, we observed a significant positive effect of litter addition on microbial biomass C and microbial biomarkers, particularly in association with *M. stipoides.* Similar increases in microbial biomass in response to nutrient addition in litter form have previously been observed in other studies (Brant et al., 2006; Sanaullah et al., 2016). These results partially support our first hypothesis with microbial C and N decreasing under drought conditions, while litter addition greatly enhanced most of the microbial biomass biomarkers under reduced water availability. Below, we discuss potential mechanisms underlying these results.

Shoot biomass of both species significantly increased with litter addition, indicating increased nutrient availability mediated by root associated or free-living microbial mineralisation of nutrients (Nikièma et al., 2011). Moreover, the reduction in root:shoot ratio in *M. stipoides* under ambient watering with litter addition may indicate a greater reliance on symbiotic microbes for nutrient acquisition (Verlinden et al., 2018). However, this pattern was not observed under drought conditions, indicating that beneficial plant-microbe interactions may not occur under water stress. By contrast, we found no changes in root biomass or root:shoot ratio in *P. lanceolata* across watering treatments.

Contrary to our expectation, we observed a significantly greater content of two microbial PLFA biomass markers (Gram-positive bacteria, Actinobacteria) under drought conditions compared to ambient without litter addition, particularly in *M. stipoides*. This suggests that some microbes can be quite resistant to drought as previously observed in other studies (Cruz-Martínez et al., 2009; Landesman & Dighton, 2010; Szejgis et al., 2024a). However, we found a higher content of most microbial biomarkers for *M. stipoides* in both watering treatments with litter addition compared to *P. lanceolata*, indicating that the former may allocate more C to the rhizosphere resulting in greater microbial biomass growth (Bengtson et al., 2012;

Finzi et al., 2015). Increased rhizosphere C can result in a positive feedback induced by microbes (Abdelaal et al., 2021), particularly with litter as a source of additional nutrients (Rinnan et al., 2008). Moreover, drought increased the NLFA biomarker for arbuscular mycorrhizae in *M. stipoides* when litter was added and in *P. lanceolata* without litter addition, indicating species-specific shifts in plant-mycorrhizal associations. This contrasts to previous studies where a reduction in mycorrhizal markers under drought condition was reported (Sheteiwy et al., 2021; Zhang et al., 2024). Hence, drought-induced shifts in plant-soil biotic interactions and plant biomass allocation are species-specific.

While it is plausible that microbial markers increased under drought conditions, particularly given the limited impact on plants, environmental conditions can induce changes in microbial fatty acid composition and nutrient allocation, allowing microbes to better adapt to altered conditions (Norris et al., 2023). Hence, the perceived increase in certain biomarkers may be associated with differential allocation of resources of the same microbes. In contrast, the observed higher mycorrhizae content in P. lanceolata under drought without litter was likely due to a shift toward greater energy storage in stable lipids, reflecting a response to nutrient limitation (Holmstrup et al., 2002).

4.2 Relationships among plant biomass, microbial biomarkers and litter decomposition

We hypothesised that litter addition would stimulate positive plant–microbe interactions by providing additional nutrients, particularly under drought, enhancing both plant growth and microbial biomass. In partial support of our second hypothesis, we observed positive relationships for microbial C and microbial N with shoot and root biomass for *P. lanceolata* but only under ambient watering. These positive relationships are likely associated with microbial mediated nutrient cycling, especially when litter is present as a resource. Similarly, previous studies have reported that *P. lanceolata* can influence processes such as mineralization or nitrification via enzymatic changes in soil (Dietz et al., 2013; Pijlman et al., 2020). However, under drought conditions, we found negative relationships for Gram-positive bacteria and Gram-negative bacteria with shoot biomass in *P. lanceolata*, partly mediated by reduced biomarker contents when litter was present. This suggests potential competition for nutrients between plants and microbes, indicating a negative microbes-plant interaction under drought conditions, with similar results observed previously (Fry et al., 2018). Furthermore, *M. stipoides* root biomass was negatively associated with most microbial biomass markers under ambient watering, with the relationship moderated by lower microbial biomarker contents when litter was not present. This suggests that microbes may compete with *M. stipoides* for nutrients, with *M. stipoides* allocating more resources to root biomass to prioritize nutrient uptake over microbial associations, particularly under favourable but resource limited conditions. This partially aligns with a previous study, suggesting that *M. stipoides* compete for nutrients with microbes when in short supply but can stimulate microbial activity when more nutrients are available (Chieppa et al., 2019).

Litter decomposition was influenced by the watering treatment and differed significantly between the two plant species, with *P. lanceolata* showing greater litter mass loss overall (Table S1). We suspect that

the higher litter mass loss under *P. lanceolata* is related to its litter being richer in N and easier to decompose compared to *M. stipoides* (Wardle et al., 1997; Shaw & Harte, 2001). The positive relationship between litter mass loss and root biomass in *M. stipoides* is likely driven by the increased root biomass under drought conditions and decreased root biomass under ambient conditions with litter addition. Importantly, this relationship can also be linked to the positive association between litter mass loss and arbuscular mycorrhizae in *M. stipoides*, suggesting that root biomass may mediate the observed effect of arbuscular mycorrhizae on litter decomposition, which is consistent with our second hypothesis. While no positive relationship was observed between arbuscular mycorrhizae and *M. stipoides* biomass, arbuscular mycorrhizae can still play a significant role for *M. stipoides* in nutrient acquisition process stored in litter, compensating for the observed reduction in root biomass under ambient conditions. This aligns with increasing evidence that arbuscular mycorrhizae are important in the litter decomposition process, owing to their ability to penetrate litter material through a well-developed hyphal network (Hodge et al., 2001; Leigh et al., 2009; Liu et al., 2010). In contrast to our expectation, microbial C was negatively related to litter mass loss for *P. lanceolata*, with a similar trend found for *M. stipoides*. Moreover, the observed negative relationship corresponded with lower microbial biomass C and higher litter mass loss under drought conditions. This is likely because microbes have sufficient access to nutrients for growth in the ambient watering treatment, whereas under drought stress, microbes invest more resources in accessing nutrients stored in litter, contributing to litter decomposition to acquire C.

5. Conclusions

Our study showed that the effects of reduced water availability and litter addition on plants and microbes are species-specific and contribute to contrasting shifts in plant-soil biotic interactions. Overall, microbial biomass C and N, and microbial biomarkers (i.e. PLFAs), were negatively impacted by drought but increased with litter addition. These patterns were particularly pronounced in *M. stipoides*. We found no changes in plant–microbe relationships under drought, but under ambient water conditions these relationships were strongly shaped by litter addition, indicating a decomposition-mediated shift in plant–soil biotic interactions. Further, changes in litter decomposition (litter mass loss) were moderated by the watering treatments. Both litter decomposition and arbuscular mycorrhizae increased under drought conditions for *M. stipoides*, likely because of an increased reliance on root symbionts for nutrient acquisition from the litter. Moreover, drought stimulated microbial biomass C, as microbes decomposed more litter to access nutrients compared with ambient conditions. Our results suggest that prolonged drought will moderate plant community dynamics via species specific changes plant-soil biotic interactions, including feedbacks mediated by litter decomposition.

Declarations

Data Availability Statement

Data are archived in the figshare repository: https://doi.org/10.6084/m9.figshare.30244795.v2

Ethics statement

Not applicable.

Consent to publish

Not applicable.

Consent to participate

Not applicable.

Clinical Trail

Not applicable.

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Figures

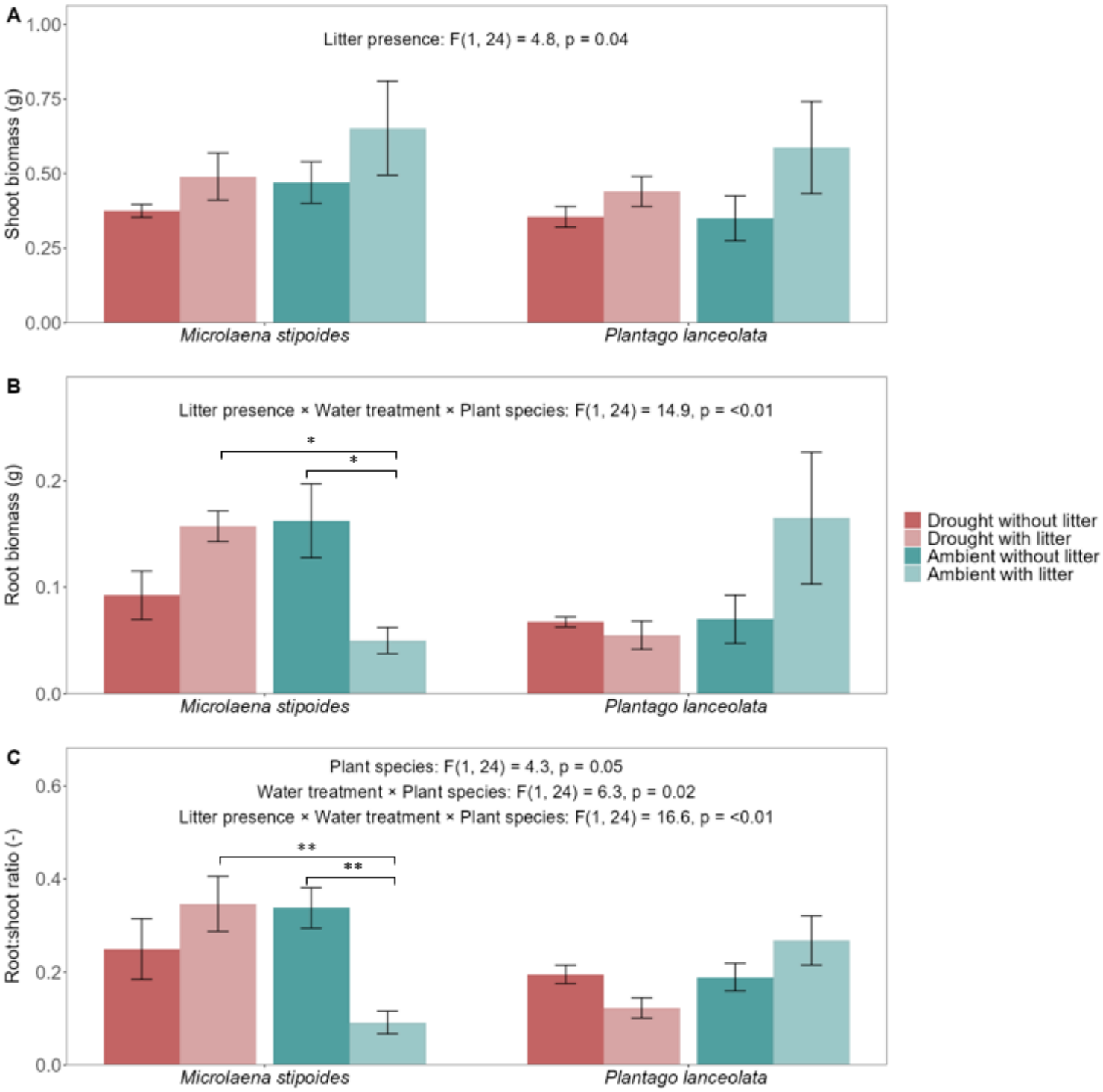

Figure 1

Average shoot (A) and root (B) biomass, and root:shoot ratio (C), across water treatments, plant species and litter addition. Bars represent standard error. Test statistics are shown for significant differences three-way ANOVA. Brackets above bars indicate significant differences among litter presence and watering treatment using Tukey's HSD test. Asterix * indicates significant relationships strength with *** p<=0.001, ** p<=0.01, * p<=0.05.

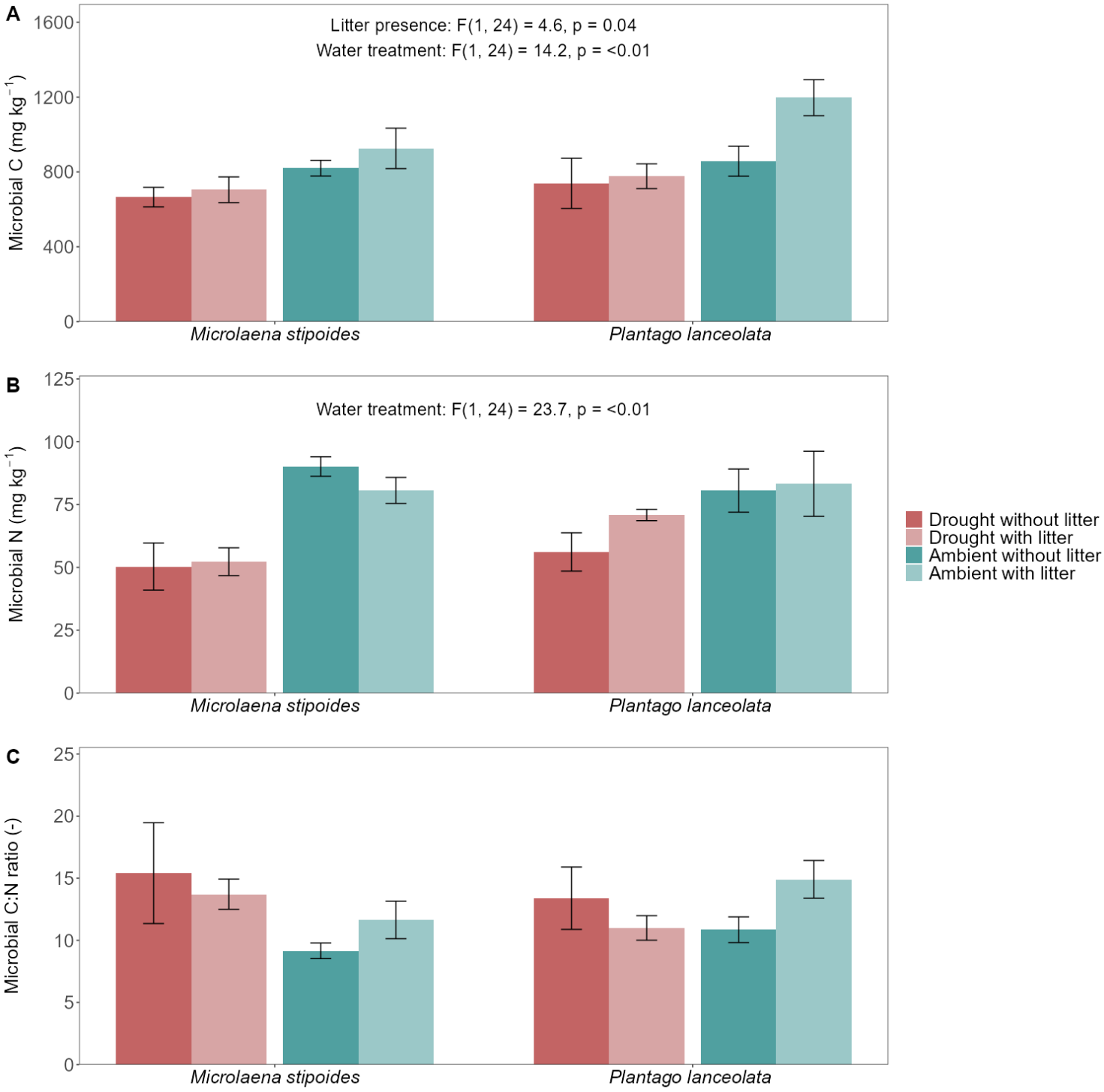

Figure 2

Average soil chloroform fumigation derived microbial biomass C (A), N (B) and microbial C:N ratio (C) content across watering treatments, plant species and litter addition. Bars represent standard error. Test statistics are shown for significant differences three-way ANOVA.

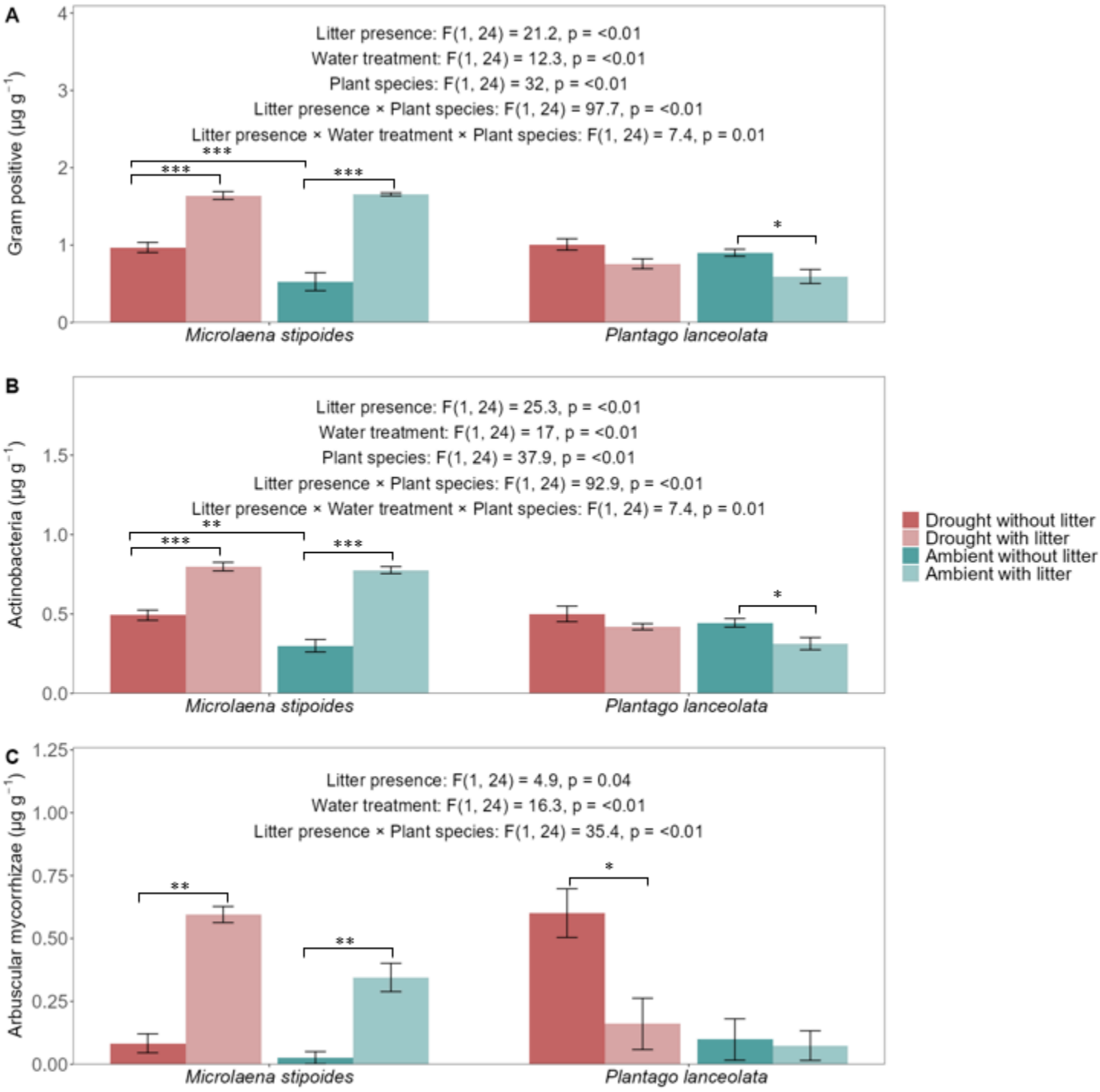

Figure 3

Average PLFA content for Gram-positive bacteria (A), Actinobacteria (B), and NLFA content for arbuscular mycorrhizae (C), across water treatments, plant species and litter addition. Bars represent standard error. Test statistics are shown for significant differences three-way ANOVA. Brackets above bars indicate significant differences among litter presence and watering treatment using Tukey's HSD test. Asterix * indicates significant relationships strength with *** p<=0.001, ** p<=0.01, * p<=0.05.

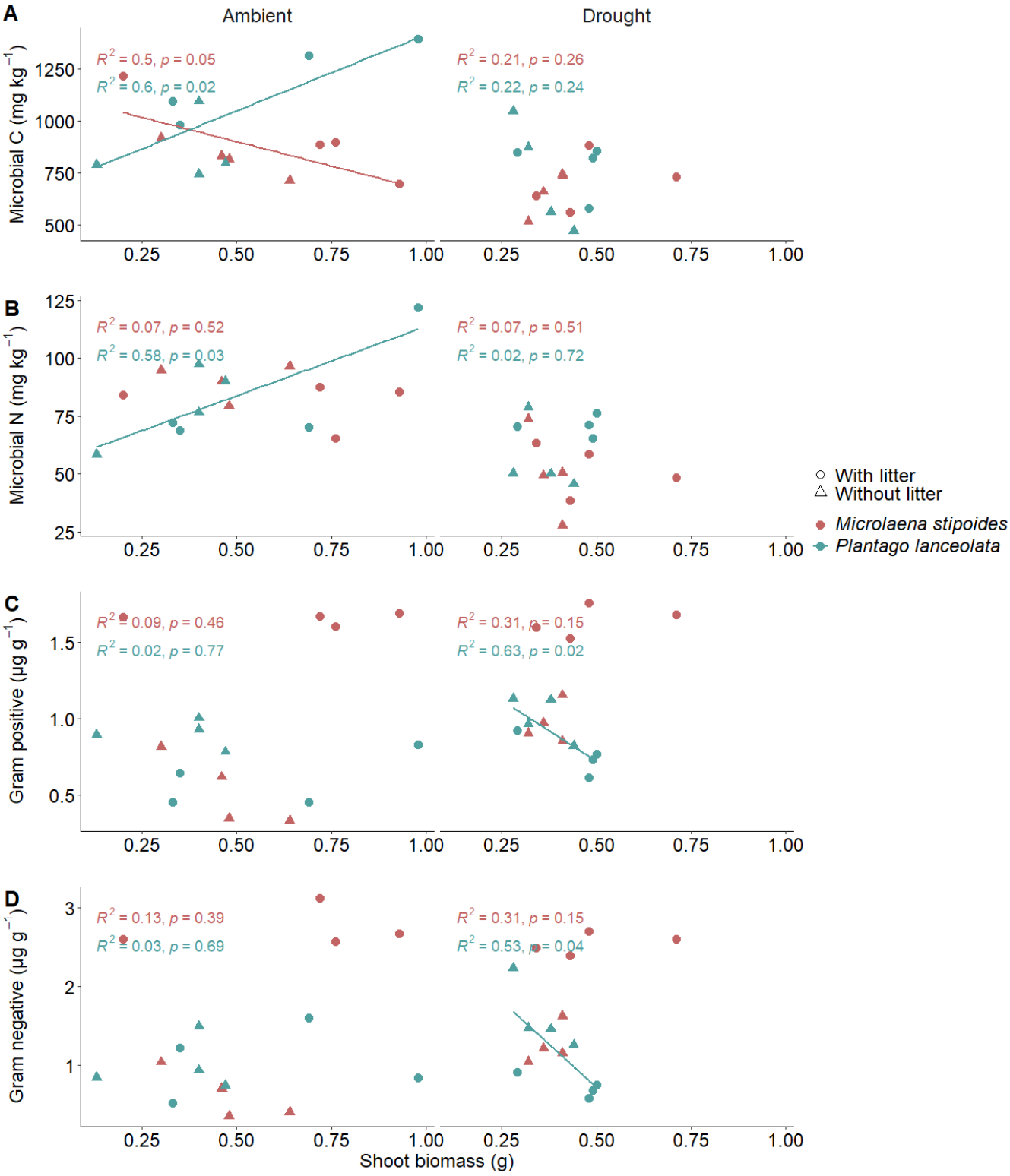

Figure 4

Shoot biomass relationships with microbial C (A), microbial N (B), Gram-positive (C) and Gram-negative (D) between plant species affected by watering or litter treatments. The fitted lines represent statistically significant linear relationships between microbial biomass and shoot biomass, under ambient or drought treatment for M. stipoides or P. lanceolata.

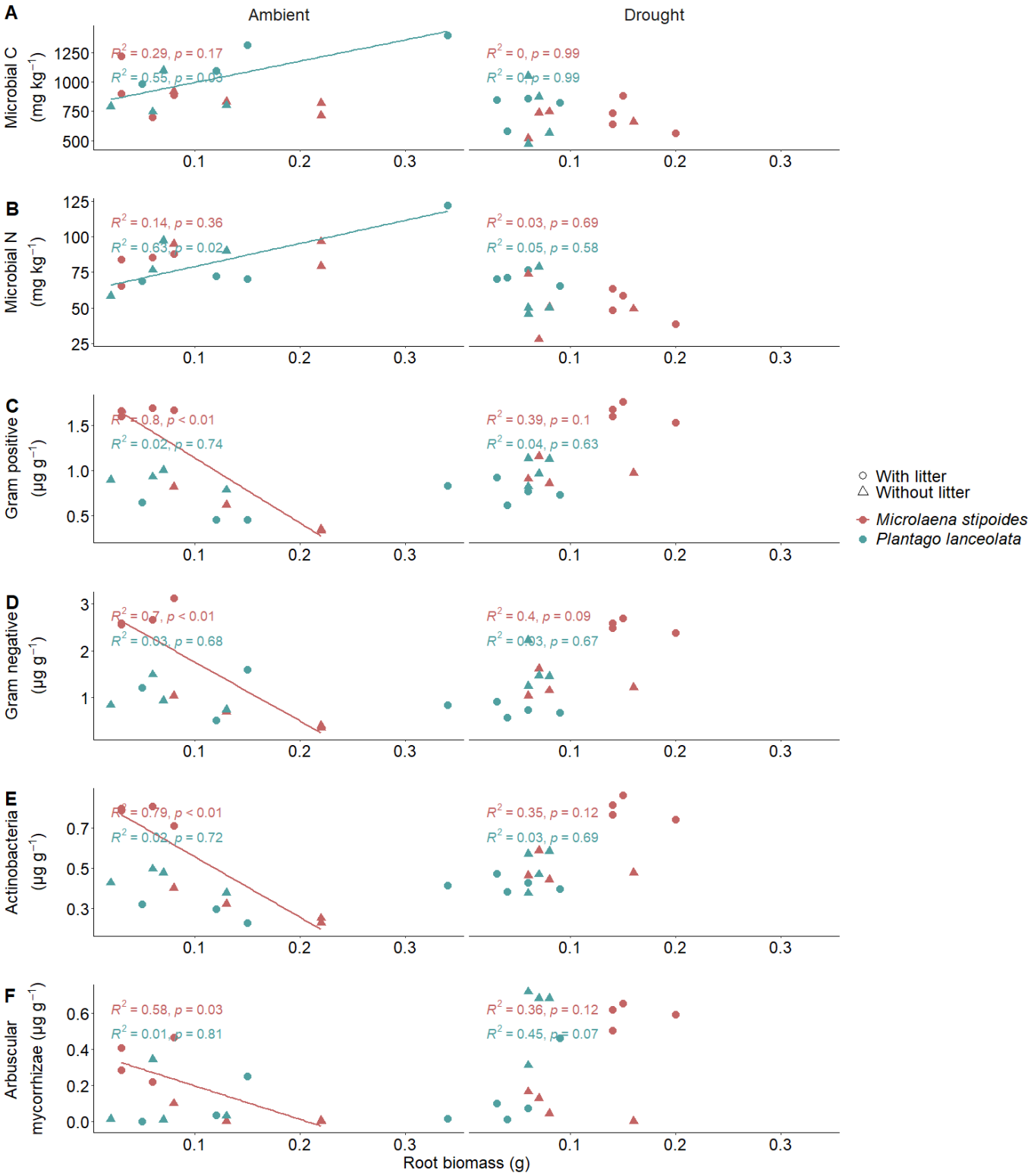

Figure 5

Root biomass relationship with microbial C (A), microbial N (B), Gram-positive (C), Gram-negative (D), Actinobacteria (E) and arbuscular mycorrhizae (F) between plant species affected by watering or litter treatments. The fitted lines represent statistically significant linear relationships between microbial biomass and root biomass, under ambient or drought treatment for M. stipoides or P. lanceolata.

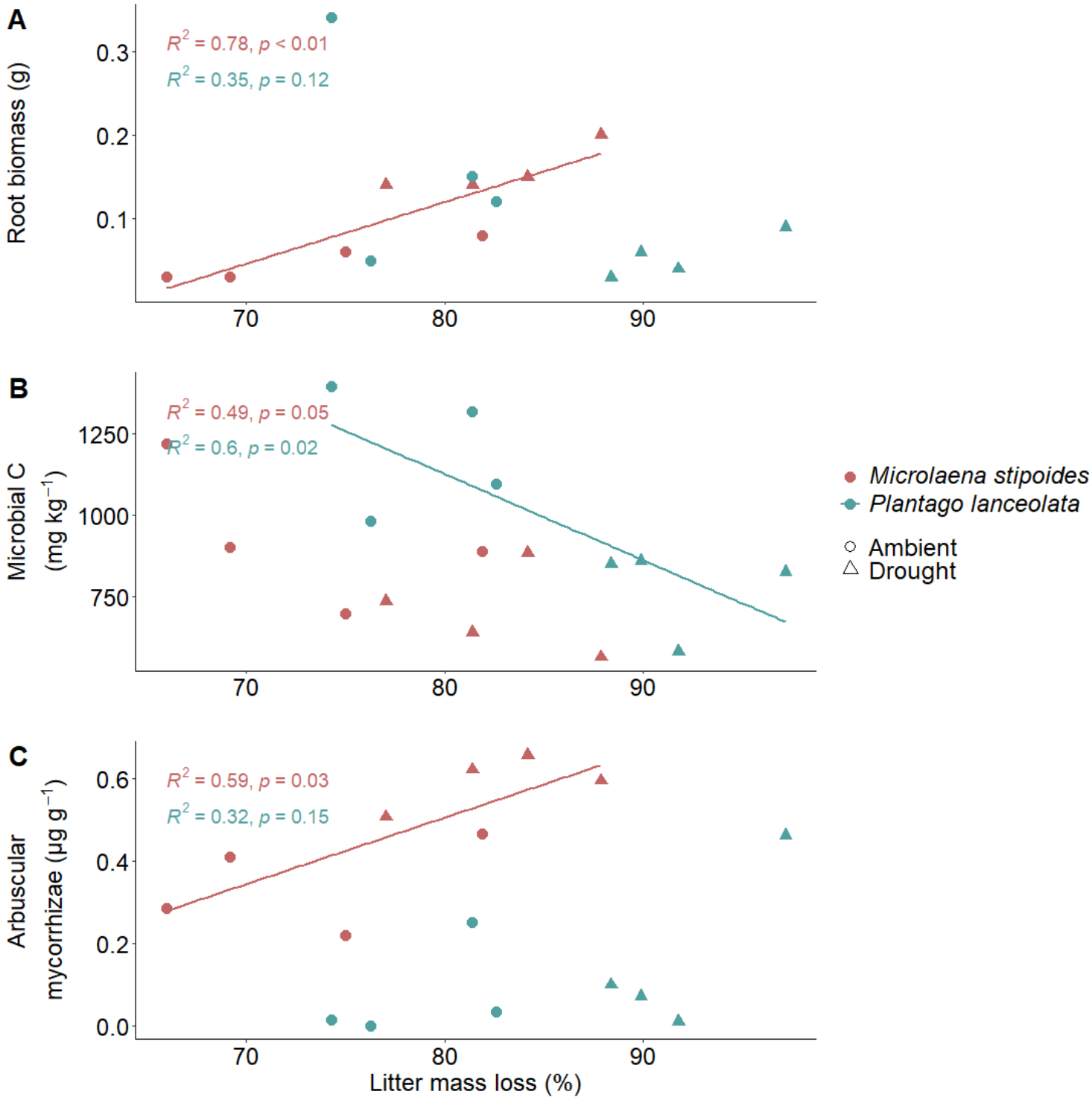

Figure 6

Litter mass loss relationship with root biomass (A), microbial C (B) and arbuscular mycorrhizae (C) between plant species affected by watering treatments. Fitted lines represent statistically significant linear relationships between microbial biomass (PLFA, NLFA, microbial C), plant biomass and litter mass loss.

Supplementary Files

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