A global meta-analysis of the effects of plant diversity on biomass partitioning in grasslands

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Abstract

The partitioning of belowground biomass (BGB) to aboveground biomass (AGB) is commonly described as the root-to-shoot ratio (R/S). Although a number of studies have shown that biodiversity can influence AGB and BGB in grasslands at the local and global scale, the global-scale patterns reflecting how plant diversity affects R/S and the factors controlling such effects remain unclear. In this study, we explored the global patterns and associated drivers of biomass partitioning responding to plant diversity by conducting a meta-analysis of 333 observations from 30 studies in grasslands worldwide. Overall, plant diversity significantly increased AGB, BGB, and total biomass, whereas significantly decreased R/S. The effects of plant diversity on biomass partitioning varied with experimental types. The effect size for AGB and BGB in the field was larger than in greenhouse experiments, but the effect size for R/S did not significantly differ between field and greenhouse experiments. Moreover, there was no significant relationship between R/S and species richness and experimental duration in greenhouse experiments. However, the effect size for AGB, BGB, and R/S increased logarithmically with species richness and experimental duration in the field experiments. Specifically, the effect size for R/S in the field experiments switched from negative to neutral as the species richness and experimental duration increased. Furthermore, the effect size for R/S was positively correlated with complementary effects of BGB, and it increased logarithmically with mean annual temperature (MAT) and precipitation. Structural equation models showed that species richness, experimental duration, and MAT impact R/S indirectly by changing the BGB. Overall, our findings suggest that plant mixtures invest less in BGB than monocultures, and highlight that low investment in BGB will disappear gradually over time as species richness increases.

1. Introduction

The root-to-shoot ratio (R/S) is a key parameter for estimating root biomass from shoot biomass, and is therefore an important input for terrestrial ecosystem carbon modelling (Jackson et al. 1996, Hui and Jackson 2005). Increasing plant diversity has been shown to have positive effects on above- (AGB) (Tilman et al. 2001, Ravenek et al. 2014, Prieto et al. 2015, Oram et al. 2018) and belowground biomass (BGB) (Kreyling et al. 2017, Peng and Chen 2020). Accordingly, decreases in grassland plant diversity through grazing mismanagement, land conversion, and climate change will likely change the biomass partitioning of grassland ecosystems (Poorter et al. 2012, Reich et al. 2012, Isbell et al. 2013, Hautier et al. 2018). Grasslands, which are among the most widespread vegetation types in the world, play a critical role in global carbon cycles (Scurlock and Hall 1998, Suttie et al. 2005). Therefore, quantifying the effects of plant diversity on biomass partitioning in grasslands is critical to predicting global carbon cycles in terrestrial ecosystems (Hui and Jackson 2005, Mokany et al. 2006).

Biomass partitioning reflects a strategy of plants in response to environmental and resources stress...
(Mokany et al. 2006, Poorter et al. 2012), and a major mechanism by which resources in plant mixtures is partitioned through allocation to different species tissues as they exploit resources differently, which leads to a greater overall exploitation of resources (Bazzaz 1996, Grime 2001). Plant diversity has been reported to have a positive effect on AGB and BGB, leading to ‘overyielding’ in plant mixtures compared with monocultures (Tilman et al. 2001, Hector et al. 2010, Craven et al. 2016). Complementary effects have been proposed to explain such overyielding (Yachi and Loreau 1999, Loreau and Hector 2001, Cardinale et al. 2007, Prieto et al. 2015). For example, increased AGB with species richness was found to be induced by the improved light use efficiency through niche differentiation (Hooper 1998, Demelah et al. 2017). Additionally, increased BGB with increased species richness was shown to be a result of improved resources use efficiency (e.g. nitrogen and water) through root depth differentiation (Wardle and Peltzer 2003, Oram et al. 2018). The functional balance hypothesis suggested that plant photosynthetic products will be preferentially distributed to parts that alleviate environmental stress (Brouwer 1962). Hence, plant diversity may increase R/S by alleviating light stress (Ma et al. 2019) and decrease R/S through alleviation of soil nutrient stress (Bessler et al. 2009, Martin-Guay et al. 2019). However, little is known about the dynamics of biomass partitioning along plant diversity gradients at the global scale.

The impacts of plant diversity impacts on biomass partitioning observed in experiments may be sensitive to experimental types (e.g. field versus greenhouse) (Roscher et al. 2004, Thompson et al. 2005, Kreyling et al. 2017) and experimental duration (Chen and Chen 2019, Chen et al. 2020). Moreover, biomass partitioning has been shown to vary with environmental conditions (Malchair et al. 2010, Poorter et al. 2012). Compared with greenhouse experiments, the range of mean annual temperature (MAT) and precipitation (MAP) was larger in the field, and the increase in biomass with biodiversity in the field was stronger than the experiments with controlling for environmental covariates (Duffy et al. 2017). As a result, this may cause differences in biomass partitioning between greenhouse and field experiments. Moreover, recent meta-analysis showed that the effects of plant diversity on soil nitrogen become progressively stronger in the long term (Chen et al. 2020), which may cause the effects of diversity on R/S to decrease with experimental duration through the alleviation of soil nitrogen stress. However, synthesis studies of these diversity experiments have not explored the interactive effects of plant diversity and experimental types (field and greenhouse experiments) and duration on biomass partitioning.

Here, we compiled data from 30 studies examining the effects of plant diversity on biomass partitioning in grasslands (figure S1) based on the ratios between AGB, BGB, total biomass (TB), R/S, the shoot-to-total biomass ratio (S/T), and root-to-total biomass ratio (R/T) in plant mixtures to those in monocultures. Our specific objectives were to: (a) elucidate the effects of plant mixtures on biomass partitioning, (b) investigate how biomass partitioning responses to plant diversity change with experimental variables; and (c) identify how biotic (e.g. MAT and MAP) and abiotic (e.g. species richness and BGB) factors regulate the effects of plant diversity on biomass partitioning on a global scale.

2. Materials and methods

2.1. Data collection

We searched for all peer-reviewed publications that investigated the effects of plant diversity on biomass allocation in grasslands from 1980 to 2019 using the ISI Web of Science (isiknowledge.com) and China National Knowledge Infrastructure (CNKI, www.cnki.net) databases. The keywords and terms used were (biomass OR productivity OR allocation OR partitioning OR ratio AND diversity OR richness OR mixture OR pure OR polyculture OR monoculture OR overyielding AND grassland). The following criteria were applied to select studies: (a) experiments had at least one pair of data comparing monocultures vs. mixtures, (b) experiments had at least one pair of data comparing AGB vs. BGB, aboveground vs. total biomass, or belowground vs. total biomass, (c) the species in monocultures were included in the mixtures at the same temporal and spatial scale, (d) response variables (means, measures of variance, and sample size) were reported, and (e) the diversity levels (species richness), experimental durations, and experimental types (field or greenhouse) were clearly described. When necessary, means, standard deviations/errors and sample sizes were extracted from digitized graphs using GetData Graph Digitizer (ver. 2.24, www.getdata-graph-digitizer.com/). The Worldclim database at http://worldclim.org/ was used to extract MAP and MAT using the location information (latitude and longitude). Overall, 30 studies and 333 observations about the effects of plant diversity on biomass partitioning were selected in our meta-analysis (table S1 and figure S1 (available online at stacks.iop.org/ERL/16/064083/mmedia)).

For each study, we extracted the data on species richness, AGB, BGB, TB, complementary effects, selection effects, and experimental duration and types from the original papers. We derived the sample size corresponding to each observation based on the number of independent experimental units. In addition, we divided the experimental types into two groups: greenhouse and field experiments.
Figure 1. Comparison of biomass partitioning between plant mixtures and monocultures in grasslands. Values are the means ±95% confidence intervals of the percentage changes between plant mixtures and monocultures. The number of observations for each attribute is displayed in parentheses. AGB, aboveground biomass; BGB, belowground biomass; TB, total biomass; R/S, root-to-shoot ratio; R/T, root-to-total biomass ratio; S/T, shoot-to-total biomass ratio.

Figure 2. Effects of plant diversity on biomass partitioning between field and greenhouse experiments in grasslands. Values are the mean ±95% confidence intervals of the percentage changes between the plant mixtures and monocultures. The number of observations for each attribute is displayed in parentheses. Points with different colors represent different experimental types. AGB, aboveground biomass; BGB, belowground biomass; R/S, root-to-shoot ratio.
2.2. Data analysis

We used the methods described by Hedges et al (1999) and Gurevitch et al (2018) to evaluate the changes in biomass and its partitioning in plant mixtures. The log response ratio for biomass (equation (1)) and partitioning (equation (2)) were calculated as follows:

\[
\ln RR = \ln \left( \frac{\bar{x}_t}{\bar{x}_c} \right) = \ln (\bar{x}_t) - \ln (\bar{x}_c) \tag{1}
\]

\[
\ln RR = \ln \left( \frac{\bar{x}_{ta}/\bar{x}_{tb}}{\bar{x}_{ca}/\bar{x}_{cb}} \right) = \ln (\bar{x}_{ta}/\bar{x}_{tb}) - \ln (\bar{x}_{ca}/\bar{x}_{cb}) \tag{2}
\]

where \( \bar{x}_t \) and \( \bar{x}_c \) are the means of the biomass in all mixtures and monocultures plots respectively, and \( a \) and \( b \) are the means of AGB and BGB. Random-effects models were used to estimate the weighted average response ratio via the rma function in the metafor package (Cooper et al 2009) in R 3.5.1 (R Core Team 2018). Weights for studies were estimated by sample size (Hedges et al 1999) and between-sample variability:

\[
w_r = \left( \frac{N_t \times N_c}{N_t + N_c + \tau^2} \right)^{-1} \tag{3}
\]

where \( N_t \) and \( N_c \) are the sample sizes for the mixtures and monocultures, respectively, and \( \tau^2 \) is the total amount of heterogeneity. For ease of interpretation, \( \ln RR \) and the corresponding 95% confidence intervals (CIs) were transformed to a percentage change between monocultures and mixtures using the following equation: \((e^{\ln RR} - 1) \times 100\%\).

We also examined the potential influence of publication bias on our results with Egger’s test using the metabias function in R 3.5.1 (R Core Team 2018). We conducted univariate meta-regression to examine the relationships between effect size and moderator variables (e.g. MAP and MAT). Statistical results reported included the heterogeneity in effect size associated with each moderator variable (\( Q_M \)), the residual error (\( Q_E \)), and total heterogeneity (\( Q_T \)).

\[\text{Figure 3. Relationship between species richness (a), experimental duration (b), mean annual temperature (c), mean annual precipitation, (d) and the response ratio of the root-to-shoot ratio (R/S) in field experiments. The size of the circles represent the relative weights of the corresponding sample size. Solid lines represent significant relationships (} \ \rho < 0.05\text{), and shaded areas show 95% confidence intervals of the fit.}\]
among all observations. A significant Qₘ indicates significant effects of moderator variable on the effect size (Hedges et al 1999). We also used random-effects meta-regression to evaluate the relationships between biomass, R/S, species richness, experimental duration, complementary effects, selection effects, and climate conditions. Furthermore, to combine causal hypotheses about direct and indirect effects of biotic and abiotic factors on R/S, we incorporated them into structural equation models (SEM) and displayed their results with path-analysis graphs using the sem package of R 3.5.1 (R Core Team 2018). Model-fit statistics such as χ²-tests and the goodness-of-fit index (GFI) were used to assess the models.

3. Results

3.1. Average changes in biomass partitioning in plant mixtures

Across all the studies, we observed a significant increase in biomass partitioning relative to monocultures for biomass in grasslands including AGB (67.4%), BGB (45.8%), and TB (98.6%) (figure 1(a)), but a significant decrease in R/S (−7.09%) (figure 1(b)). Conversely, plant diversity had minor effects on S/T and R/T, as indicated by the changes, and 95% CIs for the effects of plant diversity on S/T and R/T are −3.31% (−13.3% to 6.63%) and −5.91% (−21.3% to 9.47%), respectively (figure 1(b)).

3.2. Effect sizes varied with experimental types and duration

Subgroup meta-analysis indicated that the effects of plant diversity on biomass partitioning differed between experimental types (figure 2). Generally, the positive effects of plant diversity on AGB and BGB in the field were larger than in the greenhouse experiments, while the effects of plant diversity on R/S did not differ significantly between field and greenhouse experiments (figure 2). Moreover, random-effects meta-regression revealed that there was no significant relationship between species richness, experimental duration, and R/S in the greenhouse experiments (figure S4). However, AGB, BGB, and R/S increased logarithmically with species richness and experimental duration in the field experiments (figures S5 and 3). Specifically, plant diversity led to a significant decrease in R/S at low species richness but had minor effects on R/S at high species richness (figure 3(a)). Plant diversity significantly decreased R/S in the short term but had minor effects on R/S in long term experiments (figure 3(b)).

3.3. Factors influencing biomass partitioning in field experiments

Univariate meta-regression indicated that species richness, experimental duration, MAP, and MAT significantly regulated the effects of plant diversity on AGB, BGB, and R/S (table S2). Specifically, the effect size for R/S logarithmically increased with MAT and MAP (figures 3(c) and (d)), while the rma analysis showed that the effects of plant diversity on AGB, BGB, and R/S did not interact with the effects of experimental duration (table S3). Investigation of factors closely correlated with biomass partitioning were revealed that the effects of plant diversity on AGB and BGB were positively correlated with the complementary effects (figures S6(a) and (c)), and the complementary effects increased linearly with species richness (figures S7(a) and (c)). A significant positive relationship between R/S and BGB was also found in our study (figure S3(b)). Additionally, R/S was positively correlated with complementary effects of BGB (figure 4(c)), but negatively correlated with selection effects of BGB (figure 4(d)).

The results of SEM analysis showed that MAT and BGB jointly explained 72% of the variation in the response of R/S to plant diversity in grasslands (figure 5). Specifically, MAT affected R/S directly, as well as directly through its positive effect on BGB (figure 5). Finally, we found that species richness and experimental duration affected R/S indirectly via changes in the BGB (figure 5).

4. Discussion

Many studies have explored the responses of AGB and BGB and productivity to increasing plant diversity from based on both experiments and meta-analysis (Tilman et al 2001, Roscher et al 2004, Ma and Chen 2016, Chen and Chen 2019, Chen et al 2020, Wang et al 2020b). Three aspects of our study distinguish it from previous synthesis studies. Specifically, our study is the first to investigate the effects of plant diversity on biomass partitioning in grasslands at the global scale. Additionally, our study attempts to reconcile the effects of experimental types by exploring the differences between field and greenhouse experiments. Finally, the SEM analyses in the field experiments indicated that species richness, experimental duration, and MAT regulate the effects of plant diversity on R/S mainly through changes in BGB.

4.1. Biomass partitioning varied with plant diversity

Our results showed that more diverse plant mixtures had significantly higher increased biomass above- and belowground. Overyielding in AGB and BGB in plant mixtures has commonly been observed as a result of due to complementary plant interactions (Tilman et al 1997, Ma and Chen 2016, Wang et al 2020b), and the strong general effects of diversity found in the present study indicate that these mechanisms are important in grassland ecosystems. Plant species with different architectures in plant mixtures capture of more incoming light, resulting in an increase in AGB (Naeem et al 1994). In addition, species producing
roots at differing depths in the soil profile results in greater overall nutrient uptake, resulting in a larger BGB for plant mixtures (Köchy and Wilson 2000). The increase in complementary effects of AGB and BGB have been shown to induce an increase of TB in plant mixtures (Cowles et al 2016, Wang et al 2020b).

However, we observed that R/S decreased significantly in plant mixtures, which have been caused by the balance of competition and resource partitioning between AGB and BGB (Poorter et al 2012). A previous study showed that higher overyielding in the aboveground organs in plant mixtures reduced biomass partitioning to belowground organs (Bessler et al 2009), resulting in a significant decrease in R/S. Additionally, soil available nitrogen was found to significantly increase in plant mixtures (Oelmann et al 2011, Wolf et al 2017) and alleviate nitrogen stress belowground. This may lead to greater allocation of plant photosynthetic products to aboveground areas to capture light (Brouwer 1962, Zeng et al 2020), resulting in roots being less affected by resource partitioning than shoots, and therefore a lower R/S. However, as species richness increases, the effects of plant diversity on R/S tend to become neutral. Indeed, previous studies showed that soil available nitrogen did not change with increasing species richness (Oelmann et al 2011, Mueller et al 2013), but belowground overyielding increased with species richness (figure S7) owing to root depth differentiation. As a result, plants needed to allocate more photosynthetic products belowground to absorb nutrients to maintain plant growth (Brouwer 1962), positive relationship between R/S and belowground complementary effects leading to increases in R/S with increased species richness. Therefore, belowground resource partitioning regulates the effects of diversity on R/S.

4.2. Biomass partitioning differed in field and greenhouse experiments

Our comparison of field and greenhouse experiments revealed that there were no significant differences in the effects of diversity on R/S, but the relationship between R/S and species richness and experimental duration differed between experimental types. Experimental duration and climate condition constraints in greenhouse experiments likely explain much of these differences. Specifically, greenhouse experiments lasted less than 3 years, while many field experiments lasted for a decade or more (figures 3 and S4), and field experiments showed a positive relationship between experimental duration and R/S. Our study found

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**Figure 4.** The relationship between response ratio of root-to-shoot ratio (R/S) and complementary and selection effects in the field experiments. Solid lines represent significant relationships ($p < 0.05$), dashed lines represent insignificant ($p > 0.05$), shaded areas show 95% confidence intervals of the fit.
Figure 5. Path-analytic representations of structural equation models relating the effects of plant diversity on biomass partitioning to biotic and abiotic factors in the field experiments. Solid red arrows represent significant positive paths ($p < 0.05$), dashed grey arrows represent insignificant paths ($p > 0.05$). All arrows are scaled relative to the strength of the relationship, with numbers alongside the arrows showing the standard path coefficients. $R^2$ values are proportions of variance explained by dependent variables in the model. The model-fit statistics are $\chi^2 = 88.0$, $d.f. = 9$, $p = 0.01$, and GFI = 0.78.

that the positive relationship between R/S and complementary effects of BGB, and thus mechanisms important in longer experiments that were not detected in greenhouses could include a faster increase in complementary effects of BGB over time (figure S3(b); Wang et al 2020b). Furthermore, we found that MAT impacts R/S indirectly through its positive effects on BGB, suggesting that the stronger complementary effects of BGB in the field were induced by the greater range of MAT, and thus a positive relationship between species richness and BGB may lead to a positive relationship between species richness and R/S.

4.3. Biomass partitioning tends to be neutral over time in the field experiments

The effects of plant diversity on R/S shifted from negative to neutral over time in the field experiments, which have been a result of the dynamics of soil available nutrients. Previous studies have shown that the allocation of plant photosynthetic products is related to the availability of resources (Brouwer 1962, Dovrat et al 2019); thus, the allocation of more biomass to aboveground portions may be closely related to the increase in soil nutrient availability that was observed in the plant mixtures. Soil available nitrogen significantly increased in the plant mixtures (Kevin et al 2013, Scalise et al 2015), which promoted plant transfer of photosynthetic products aboveground to capture light (Brouwer 1962). This, in turn, resulted in a greater increase in AGB than BGB (figure S3), and thus, R/S decreased significantly. As experimental duration increases, the effects of plant diversity on nitrogen availability in soil become progressively stronger in the long term (Kevin et al 2013, Mueller et al 2013, Cong et al 2015); however, the limiting resources may then shift from nitrogen to water or phosphorus (Aber et al 1998, Wang et al 2020a). If such shifts occur, plants must allocate more biomass belowground to absorb diverse nutrients, resulting in a higher overyielding in BGB over time (Wang et al 2020b). As a result, the effect size for R/S increased with experimental duration and shifted from negative to neutral. Therefore, changes in requirement for soil resources in belowground portions of plant mixtures regulate R/S dynamics over time.

5. Conclusions

In summary, this study quantified the effects of plant diversity on biomass partitioning in grasslands through a meta-analysis. The results revealed that plants tend to allocate more carbon to aboveground portions in plant mixtures, but this tendency gradually weaken with increasing species richness. Additionally, the effects of diversity on R/S did not differ between greenhouse and field experiments, whereas the effect size for R/S was positively correlated with species richness and experimental duration in the field, but not in the greenhouse experiments. Overall,
our findings show the importance of experimental duration and climate condition on the response of biomass partitioning to plant diversity, and highlight the need for further long term in situ field studies investigating plant diversity effects on biomass partitioning at the long-term perspective. The results presented herein greatly improve our understanding of terrestrial ecosystem and our ability to conduct carbon modeling following biodiversity loss.

Data availability statement

The data that support the findings of this study will be openly available at the IOP Publishing Figshare repository.

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.6084/m9.figshare.14727855.v1. Data will be available from 31 May 2022.

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