



Responses of biomass allocation to multi-factor global change: A global synthesis



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ABSTRACT

Knowledge of plant aboveground and belowground biomass (AGB and BGB) allocation is fundamental for our understanding of terrestrial carbon sequestration in a changing climate. However, how multiple global change factors interactively affect biomass allocation in terrestrial ecosystems remains unclear. We used meta-analysis to synthesize main and interactive effects of global change factors on AGB, BGB, and root/shoot based on 129 multiple-factor studies. Elevated CO₂ (E), nitrogen addition (N), warming (W), irrigation (I) and their combinations (EN, EW, NW, ENW, IE, IN, IW, IEN, INW and IENW) significantly increased AGB. However only half of the treatments (i.e., E, N, W, EN, EW, NW, IE and IW) stimulated BGB, leading to significant declines of root/shoot in treatments with I and/or N. Drought (D) significantly decreased both total biomass (14%) and AGB (47%), but increased root/shoot by 21% as well as DE and DW. Additive interactions between global change factors exhibited a predominance on both plant biomass (69.0%) and biomass allocation (64.8%). The proportion of synergistic interaction in AGB's responses to multiple global change factors was greater relative to that in BGB. Response correlation between AGB and root/shoot was observed in woody plants, while, in herbaceous ones, we found the correlation between BGB and root/shoot. Our findings highlight the importance of the interactive effects among global change factors on biomass allocation. Incorporating these interactions into global vegetation models may improve predictions of future global carbon storage and could inform sustainable strategies for grassland and plantation management in a future climate.

1. Introduction

Since the industrial revolution, human activities have markedly increased atmospheric CO₂ concentrations, inducing simultaneous changes in multiple environmental factors (e.g., climate warming, altered precipitation; IPCC 2013). Such changes likely have substantial impacts on ecosystem production and carbon (C) storage. Plant biomass, as the third largest C pool in terrestrial ecosystem, is a critical link of C from atmosphere to soil (Schimel, 1995). Biomass allocation has great impacts on plant competition, ecosystem succession, health and productivity (Agathokleous et al., 2019). It is also an important ecological parameter in dynamic global vegetation models (Mokany et al., 2006), as it is used to estimate the belowground plant biomass from aboveground biomass data (Litton et al., 2007). Thus, understanding how plant biomass and its allocation respond to climate change will

improve our ability to predict climate-C cycle feedbacks in terrestrial ecosystem in a changing climate.

Previous meta-analyses had examined the responses of plant biomass to single global change factors extensively. For example, elevated CO₂ (De Graaff et al., 2006; Luo et al., 2006; Nie et al., 2013), nitrogen addition (Lu et al., 2011; Li et al., 2016; Peng and Yang, 2016), warming (Luo et al., 2009; Lin et al., 2010; Lu et al., 2013), and increased precipitation (Zhou et al., 2016b) all significantly increased plant biomass in terrestrial ecosystems, while drought decreased it (Zhou et al., 2016b; Zhou et al., 2018). Although the central tendency of plant biomass to single global change factors is relatively well-understood (Yue et al., 2017), the response of biomass allocation remains elusive. According to the optimal partitioning theory, plants allocate more photosynthates to the organs acquiring the most limiting resources (McCarthy and Enquist, 2007). Thus, climate change could

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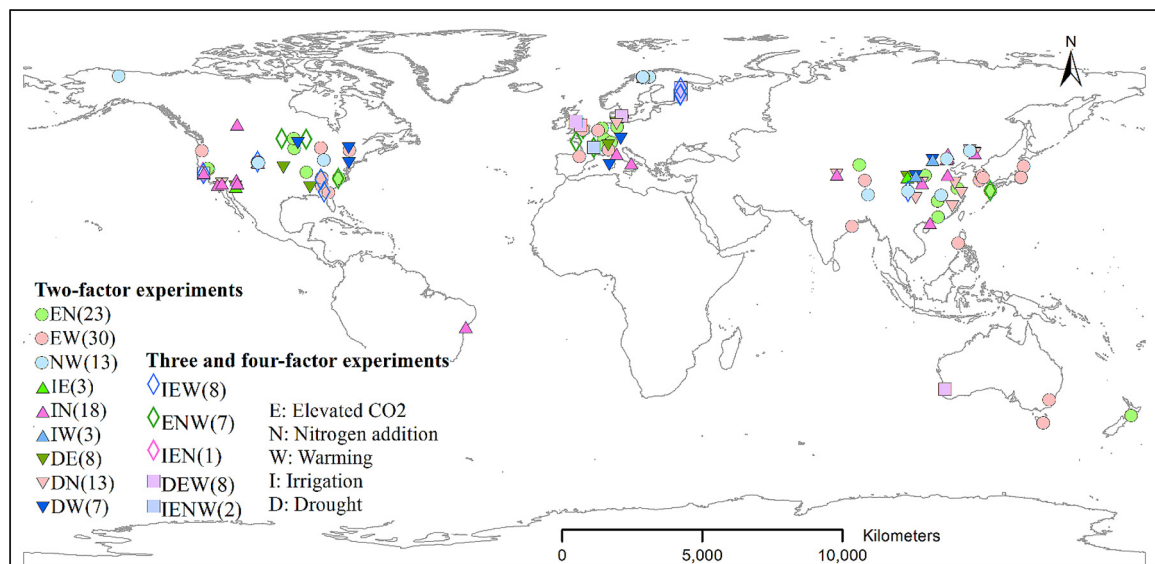


Fig. 1. Global distribution of 129 multifactor studies with two, three and four-factor treatments selected in this meta-analysis. Numbers in parentheses indicate the actual number of 119 sites with different factorial designs. Letters E, N, W, I and D indicated treatments of elevated CO₂, nitrogen addition, warming, irrigation and drought, respectively.

affect the pattern of biomass allocation between shoot and root to maximize individual supportive capacity of resources and increase chance of survival (Dodd, 2005). For instance, increased precipitation and nitrogen addition generally decrease root biomass and increase root/shoot, while decreased precipitation and elevated CO₂ have the opposite effect (Song et al., 2019). Furthermore, plants in different growth forms (e.g., woody and herbaceous) displayed distinct responses of root/shoot to increased precipitation and/or nitrogen addition, due to their differences in structural investment in xylem (Dodd, 2005; Kramer-Walter and Laughlin, 2017). Thus, plant growth form should be considered in evaluating response of biomass allocation to global change factors due to the difference of resource transport through the xylem or phloem between internal ‘sources’ and ‘sinks’ in plants (Tegeder and Masclaux-Daubresse, 2018).

Ecosystems around the world currently exposed to multiple global change factors simultaneously (Norby et al., 2005; Luo et al., 2008). However, our knowledge of multi-factor effects on biomass allocation is far from adequate for predicting biomass distribution under climate change. Due to high costs and technological challenges, experiments with full-factorial designs are rare. Thus simple addition of single-factor effects are often used to estimate combined effects when the specific interaction (e.g., additive, antagonistic, or synergistic interactions, Crain et al., 2008) between two or more factors is unclear. Indeed, several syntheses suggest that additive effects between global change factors on terrestrial C processes and storage are common (e.g., Zhou et al., 2016a; Yue et al., 2017; Song et al., 2019). However, antagonistic and synergistic interactions were also reported among global change factors on plant biomass (e.g., elevated CO₂, warming, nitrogen deposition, Kim et al., 2008; Dieleman et al., 2012). Moreover, possible tradeoffs (or competition) between plant above- and below-ground compartments with multiple global changes introduce additional uncertainty (Shipley and Meziane, 2002; Kiær et al., 2013). Response of biomass allocation to multiple global change factors might not be predictable from single factors (Reich, 2009; Thakur et al., 2019).

Here, we conducted a comprehensive meta-analysis to elucidate main and interactive effects of multiple global change factors, including warming, elevated CO₂, nitrogen deposition, and increased or decreased precipitation on plant biomass and biomass allocation. We then quantified and classified the multi-factorial interactions on above-ground biomass (AGB, also shoot biomass), belowground biomass (BGB, also root biomass), total biomass, and root/shoot for woody and

herbaceous plants into three types interactions (i.e., additive, antagonistic, or synergistic interactions, see Fig. A1 from Zhou et al., 2016a, in Appendix B). Our objectives were to: (i) examine the individual and combined effects of multiple global change factors on plant biomass; (ii) explore the central tendencies of the interactive effects between these global change factors on root/shoot; and (iii) compare the central tendency of root/shoot for woody and herbaceous plants in response to multiple global change factors.

2. Materials and methods

2.1. Data sources

We searched Web of Science (1900–2019) for papers reporting changes in plant root/shoot, total biomass, aboveground biomass (AGB), and belowground biomass (BGB) in response to experimental manipulations of elevated CO₂ (E), nitrogen addition (N), warming (W), drought (D), or irrigation (I). Papers met the following six criteria were included in our database (Appendix A): (i) studies with manipulative experiments included at least two global change factors of E, N, W, D, and/or I; (ii) studies included a fully factorial design of global change factors; (iii) at least one plant variable was reported with the mean and standard deviation/error and sample size in both control and treatment groups; (iv) initial environmental conditions and plant species composition were the same in all treatments; (v) the duration of each treatment was equal to or longer than one growing season; and (vi) methods to apply each global change treatment were clearly indicated (see Table S5–S7 in Appendix C). Methods of elevated CO₂ included free-air CO₂ enrichment (FACE), CO₂ temperature gradient chamber (CTGC), and open top chamber (OTC). Warming experiments contained CTGC, OTC, infrared heater, soil heating cable, and greenhouse. For nitrogen addition, we considered various forms of N fertilizer (i.e., NH₄⁺, NO₃⁻, NH₄NO₃, and urea). Similarly, the methods for root measurements included direct harvest, indirect soil core, and ingrowth mesh bags. In total, we found 129 published papers including 572 multi-factor experiments (Appendix A and D). Note that there were no DEN and DNW treatments reported (Fig. 1). Among the selected 129 multi-factor studies, there were 20 treatment types, including single factors and their combinations with 696 one-factor, 515 two-factor, 48 three-factor, and 9 four-factor treatments. In each treatment, at least one variable of interest (i.e. AGB or BGB or total biomass or root/shoot) was observed

Table 1

Number of observations in one-factor, two-factor, three-factor and four-factor treatments meeting the criterion listed in the text. Letters E, N, W, I and D are the abbreviations for elevated CO₂, nitrogen addition, warming, irrigation and drought, respectively.

	One-factor					Two-factor					Three-factor					Four-factor				
	E	N	W	I	D	EN	EW	NW	IE	IN	IW	DE	EN	DW	ENW	IEN	IEW	INW	DEW	IENW
Total biomass	134	150	98	39	48	92	64	33	17	36	14	17	92	30	11	6	8	6	1	6
Aboveground biomass	89	137	96	58	43	42	67	36	18	64	20	21	42	32	11	8	11	6	19	8
Belowground biomass	73	95	60	28	33	49	40	29	17	25	14	13	49	19	11	8	8	6	0	6
Root/shoot	71	86	59	26	31	41	42	25	15	23	14	13	41	17	8	6	8	6	0	6

(Table 1, Appendix D). The sites of studies we searched out from Web of Science were mainly distributed in Eastern Asia, North America, and Europe (Fig. 1), reflecting current biogeographical hotspots of global change researches around the world.

Environmental variables, including latitude (42°42'S~68°38'N, Fig. 1), mean annual temperature (MAT, -7 °C~27.7 °C) and precipitation (MAP, 0.55 mm~2061 mm, Table S1 in Appendix C), were obtained directly from the papers or works cited therein, or extracted from the WorldClim dataset (<http://www.worldclim.org/>) using the location information (Fick & Hijmans, 2017). The duration of these studies ranged from one growing season (e.g., 6-week warming and elevated CO₂ in Hovenden et al., 2008) to 15 years (e.g., warming and fertilization in Rinnan et al., 2007). In order to simplify the types of treatment, we reclassified the total 20 treatment types: 5 one-factor (E, N, W, D, I), 9 two-factor (EN, EW, NW, IE, IN, IW, DE, DN, DW), 5 three-factor (ENW, IEN, IEW, INW, DEW) and one four-factor (IENW) into the following climate scenarios. Scenario I: Drought and drought with warming; Scenario II: Drought with elevated CO₂ and/or nitrogen addition; Scenario III: Elevated CO₂ and/or warming; Scenario IV: Irrigation and I with E and/or W; Scenario V: nitrogen addition and N with E and/or W; Scenario VI: Irrigation and N, with E and/or W. The types of biomes (wetland, forest, cropland, grassland, Fig. S3), plant growth stages (seedlings vs. mature trees), life history (annual vs. perennial), and function types (e.g., trees vs. shrubs, grasses vs. forbs, and deciduous vs. evergreen trees) were also differentiated in some analysis (see Table S2 and S8 in Appendix C).

2.2. Data analysis

Response of a variable to a single-factor or multi-factor treatment was defined as an individual effect (Crain et al., 2008), and calculated as the response ratio (RR, the natural log-transformed ratio of the mean value in treatment plots ($\bar{X}_t$) to that in control ($\bar{X}_c$), Eq.1) according to Hedges et al. (1999) and Luo et al. (2006).

$$RR = \ln\left(\frac{\bar{X}_t}{\bar{X}_c}\right) = \ln(\bar{X}_t) - \ln(\bar{X}_c) \quad (1)$$

We calculated weighted mean response ratio (RR_{++}) using individual effects (RR_{ij}) and their respective weights (W_{ij}), which are the reciprocals of the variances (V_{ij} , Eq.2).

$$RR_{++} = \frac{\sum_{i=1}^m \sum_{j=1}^k W_{ij} RR_{ij}}{\sum_{i=1}^m \sum_{j=1}^k W_{ij}} = \frac{1}{V_{ij}} V_{ij} = v + \frac{Q - df}{C} \quad (2)$$

where m is the number of groups, and k is the number of RR in the i th group ($i = 1, 2, \dots, m; j = 1, 2, \dots, k$), $df = mk - 1$, and the Q (i.e., total variance) and C (a scaling factor) are calculated using Eq. 3 and 4, respectively.

$$Q = \sum_{i=1}^m \sum_{j=1}^k w_{ij} RR_{ij}^2 - \frac{\left(\sum_{i=1}^m \sum_{j=1}^k w_{ij} RR_{ij}\right)^2}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}} \quad (3)$$

$$C = \sum_{i=1}^m \sum_{j=1}^k w_{ij} - \frac{\sum_{i=1}^m \sum_{j=1}^k w_{ij}^2}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}} = \frac{1}{v} = \frac{S_t^2}{n_t \bar{X}_t^2} + \frac{S_c^2}{n_c \bar{X}_c^2} \quad (4)$$

where n_t , n_c , S_t and S_c are the number of replications and standard deviations for the concerned variable in the treatment and control groups, respectively. We used bootstrapping method (with 999 iterations) to obtain the lowest and highest 2.5% values and the 95% confidence interval (CI) in MetaWin software ver. 2.1 (Rosenberg et al., 2000). We considered the treatment effect was significant only when the 95% CI did not overlap with zero.

Main effect of a global change factor indicates the difference of its net effect between the presence and absence of a second factor (Crain et al., 2008). The definitions and calculations of interactive effects (additive, antagonistic, or synergistic interaction) of global change factors in this study followed the method in Zhou et al. (2016a) using Hedge's d (Appendix B). If the 95% CI of the interaction overlapped with zero, we considered it as additive interaction. If not, we classified it as following: i) if the main effects of two factors were both negative, their interaction was considered as synergistic when it was less than zero and antagonistic when it greater than zero; ii) if the main effects of factors were both positive, the interaction was synergistic when it was greater than zero and antagonistic when less than zero; and iii) if the main effects of two factors were opposite, the sum of them was positive, the interaction was synergistic when it was positive, and antagonistic when it was negative, and vice versa (Zhou et al., 2016a). In addition, we examined differences between sub-groups in MetaWin software using the between-group heterogeneity (Q_b) at the $p < 0.05$ level (Table S3). The effects of treatment (E, N, W, D, and I, and their combinations), plant types (woody and herbaceous plants) on the responses of a concerned variable were examined by analysis of variance (ANOVA).

3. Results

3.1. Individual effects of single and multiple factors on biomass allocation

Most of single and two-factor treatments with elevated CO₂ (E), nitrogen addition (N) and warming (W) stimulated plant biomass (i.e., total biomass, above- and below-ground biomass, AGB and BGB, $p < 0.05$) but didn't change root/shoot (including E, W, EW and NW, $p > 0.05$) except for N- and EN-induced declines in root/shoot (-11% and -9.8%, respectively, Fig. 2). Drought (D) dampened both total biomass (-14%) and AGB (-47%) but enhanced root/shoot by 21%. Treatment DE decreased AGB by 13.6% (CI: -42.3~-6.1%) but increased BGB by 5.9% (CI: 3.6~25.6%). Treatments DE and DW increased root/shoot by 101% (CI: 61.6~118%) and 98% (CI: 66~122%), respectively. Irrigation (I) increased AGB by 33.5% but decreased root/shoot by 15%. Treatments IE and IW increased plant biomass but did not change root/shoot, while IN increased total biomass and AGB by 34.5% and 36.3%, respectively, but decreased root/shoot by 34.1%. Three- and four- factor treatments (ENW, IEN, IEW, INW and IENW) all increased AGB, but caused negative or non-significant effects on BGB, inducing negative effects on root/shoot (Fig. 2).

Treatment effects on plant biomass differed between woody and herbaceous plants. Specifically, total biomass of woody plants displayed

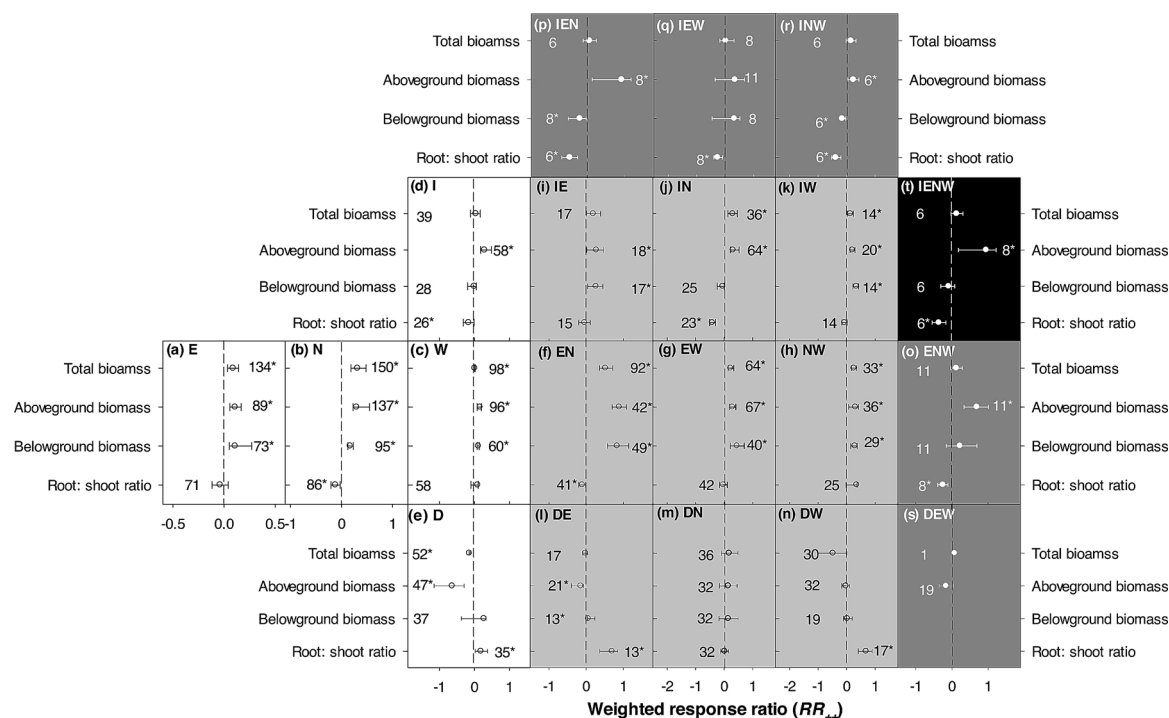


Fig. 2. Weighted response ratio (RR_{+}) of total biomass, above- and below-ground biomass and root: shoot ratio to 5 one-factor (white plots, a-e), 9 two-factor (light grey plots, i-n), 5 three-factor (dark grey plots, o-s) and one four-factor (t) treatments. Letters E, N, W, I, and D were the abbreviations for elevated CO_2 , nitrogen addition, warming, irrigation and drought, respectively. The error bars indicated the 95% confidence interval (CI). Numbers in each plots were the sample sizes, and symbol * indicated statistical significance ($p < 0.05$)

a greater positive response to IEW but a lower one to EN than that in herbs. Woody plants increased more AGB than herbs under I, IN and EN conditions. Treatment IEW induced a negative effect on BGB for herbs, but a positive one for woody plants. Root/shoot displayed a positive and negative response to IE for woody plants and herbs, respectively. Herbs declined R/S greater than woody plants in response to IN (Figs. 3, 4, and Table S3).

3.2. Main and interactive effects of global change factors on biomass allocation

The main effects of E, N, and W on total biomass, N and I on AGB, and W on BGB were positive. Warming exhibited positive ones on root/shoot for NW, IW and DW, but showed negative for EW. Nitrogen addition displayed negative effects on root/shoot for EN, IN and DN, but positive for NW. The main effects of E on root/shoot were positive for EN and EW but negative for DE. Irrigation had negative main effects on root/shoot for IN and IW, while drought induced positive main effects for DE and DN (Fig. 5).

Across all studies, the proportion of additive, synergistic and antagonistic interactions between global change factors was 69.0%, 21.2%, 9.8% for plant biomass, and 64.8%, 18.8%, 16.4% for root/shoot, respectively. Synergistic interactions were found on total biomass for EN, EW, NW, IN and IW, on AGB for EN, EW, IE, IN and DE, on BGB for EN and DN, and on root/shoot for EW, NW and IW. We observed antagonistic interactions on AGB for NW and DN, on BGB for DW, and on root/shoot for DN and DW (Fig. 5). The combined effects of two factors were greater than the sum of their single effects (summed effects), performing with the significant difference of slope in correlation of combined vs. summed effects from 1 (Fig. 6).

3.3. Regulation of experimental and environmental variables

Plant types (i.e., woody vs. herbaceous plants) significantly affected responses of total biomass ($p = 0.010$), BGB ($p = 0.000$), and root/

shoot ($p = 0.017$) to global change factors, but not for AGB ($p = 0.947$). Treatment type ($p < 0.0001$) and its interactions with plant forms ($p = 0.000$, 0.005, 0.003, and 0.031, respectively) all significantly regulated the responses of total biomass, AGB, BGB and root/shoot (Table 2).

Mean annual precipitation (MAP) exhibited a weaker impact on the initial biomass allocation (initial root/shoot, $R^2 = 0.04$, $p < 0.0001$, Fig. S1). The initial root/shoot was positively correlated with root/shoot after treatments for both woody and herbaceous plants (Fig. S2). Treatment effects on AGB were correlated positively with mean annual temperature (MAT) in sites with $MAT \leq 10^\circ C$, but were correlated negatively with MAT in sites with $MAT > 10^\circ C$ (Fig. S1).

4. Discussion

4.1. Single and combined effect of global change factors on biomass allocation

In natural ecosystems, plant biomass closely links with resource availability, so that global change factors would affect biomass accumulation due to changes in temperature, precipitation, CO_2 , and nutrients (Luo et al., 1994; Luo and Weng, 2011). Our analysis indicated that plant biomass was significantly stimulated by warming, elevated CO_2 , nitrogen addition, and its combined treatments (Fig. 2), which was similar to results from several previous studies (e.g., Gough et al., 2000; Rustad et al., 2001; Norby et al., 2005; Lin et al., 2010; Zhou et al., 2016b; Song et al., 2019). Among the single-factor impacts on biomass accumulation, the effects of nitrogen addition were larger than effects of increased precipitation and elevated CO_2 . These results are consistent with a previous meta-analysis of global change impacts on grasslands (Lee et al., 2010).

Plants allocated more newly accumulated biomass to aboveground than belowground under treatments with nitrogen and irrigation (i.e., N, EN, ENW, I, IN, IEN, IEW, INW, and IENW, Fig. 2), and reduced root/shoot due to improved soil water and nitrogen supply (Litton et al.,

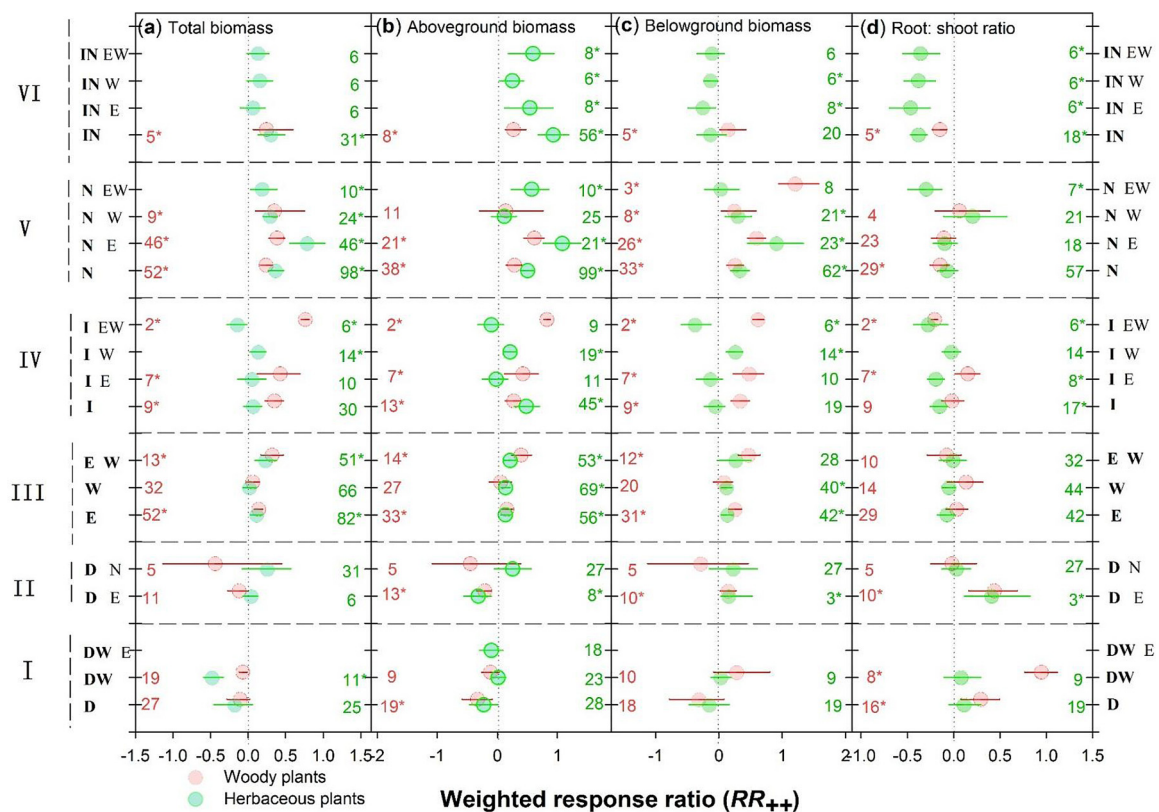


Fig. 3. Weighted response ratio (RR_{++}) of total biomass (a), above- (b) and below-ground biomass (c) and root: shoot ratio (d) to different treatments for woody and herbaceous plants. Letters E, N, W, I, and D were the abbreviations for elevated CO_2 , nitrogen addition, warming, irrigation and drought, respectively. I, II, III, IV, V, and VI were Scenario I: Drought (D) or D with warming; Scenario II: Drought with elevated CO_2 (E) and/or nitrogen addition (N); Scenario III: Elevated CO_2 and/or warming (W); Scenario IV: Irrigation (I) and I with E and/or W; Scenario V: Nitrogen addition (N) and N with E and/or W; Scenario VI: Irrigation and N, with E and/or W. The error bars indicated the 95% confidence interval (CI). Numbers in each plots were the sample sizes, and symbol * indicated statistical significance ($p < 0.05$).

2007; Song et al., 2019). For example, under treatment IN, AGB in both woody and herbaceous plants displayed greater increments than BGB (Figs. 2–4, Gong et al., 2015). These effects would induce a lower relative proportion of carbon allocation to root and its symbionts, causing a lower root/shoot (Khalili et al., 2016), which agreed with the effects of nitrogen addition on root/shoot in Peng & Yang (2016).

Negative responses of root/shoot to nitrogen addition and irrigation reflected the allometric growth between root and shoot when plant biomass also increased (Askari et al., 2017). However, the root/shoot did not always decline with increasing biomass accumulation under global change. For example, elevated CO_2 and/or warming, and warming with I and N (i.e., IW and NW) did not affect root/shoot, although they significantly increased total biomass (Fig. 2). The beneficial impacts of irrigation and nitrogen addition on soil water content and nutrients might regulate biomass investments between above- and belowground compartments (Figs. 2 and 3, Zhou et al., 2012), which could disrupt the conventionally negative relationship of root/shoot with plant biomass (Weiner, 2004). In addition, under treatments with combination of irrigation and elevated CO_2 (IE), the responses of root/shoot were opposite between woody (positive) and herbaceous plants (negative, Fig. 3). Herbaceous plants did not increase total plant biomass in response to IE, being consistent with that in Hovenden et al. (2019), but reduced their root/shoot. Thus, herbaceous plants would allocate more biomass into aboveground to enhance competition strength (e.g., for light) in facing more precipitation and nitrogen supply in the future (increasing AGB significantly by ENW, IEN, INW and IENW, in Figs. 2–4, Yang et al., 2011). For woody plants, IE stimulated both AGB and BGB but with a greater increment for BGB, causing an increase in root/shoot (Fig. 3). In this study, most treatments

with drought induced positive effects on root/shoot except for DN (Fig. 2), under which nitrogen addition offset the negative impact of drought on belowground biomass accumulation, causing insignificant variation of root/shoot (Khalili et al., 2016). It was important to note that the treatments ENW, IEN, INW and IEN mainly focused on herbaceous plants and relatively scarce because of the technological difficulties in experiments with full-factorial design of three to four global change factors (Fig. 3, Song et al., 2019).

4.2. Interactions of multiple global change factors on biomass allocation

Given the sensitivity of global carbon budget estimation to biomass allocation, understanding the multi-factor interactions on root/shoot is important to predict global carbon stock under climate change (Mokany et al., 2006). In line with previous analyses (Fig. 5, Zhou et al., 2016a; Yue et al., 2017), we found that additive interaction between global change factors was predominant for both total biomass and root/shoot. For total biomass, the proportion of synergistic interactions (21.2%, EN, EW, NW, IN and IW) was greater than that of antagonistic interactions (9.8%, Fig. 5). The synergy between elevated CO_2 and nitrogen addition, irrigation and nitrogen addition, and elevated CO_2 and warming were agreed with that for land carbon uptake in Churkina et al. (2009), temperate steppe carbon sequestration in Niu et al. (2009), and root biomass in Fenner et al. (2007), respectively.

The proportion of synergistic interactions for BGB (EN and DN) was relatively low compared to that for AGB (EN, EW, IE, IN and DE, Fig. 5), resulting in incongruous responses between AGB and BGB (0.74 slope vs. 1, $p < 0.0001$). In addition, relationships of the response ratio (RR) between AGB and BGB were $RR(BGB) = 0.14 + 0.65 RR(AGB)$ for

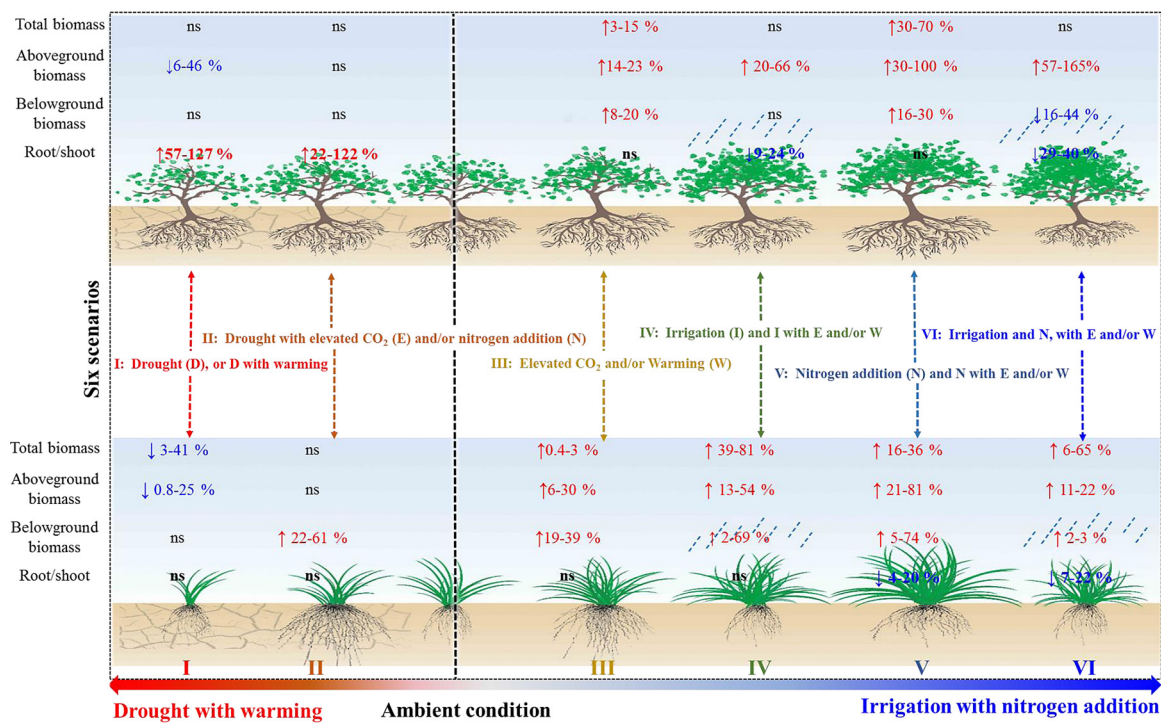


Fig. 4. Sketch of the responses of plant total biomass, above- and below-ground biomass, and root/shoot for woody and herbaceous plants to six scenarios from conditions of drought with warming to irrigation with nitrogen addition (red to blue color). I, II, III, IV, V, and VI were Scenario I: Drought (D) or D with warming; Scenario II: Drought with elevated CO₂ (E) and/or nitrogen addition (N); Scenario III: Elevated CO₂ and/or warming (W); Scenario IV: Irrigation (I) and I with E and/or W; Scenario V: Nitrogen addition (N) and N with E and/or W; Scenario VI: Irrigation and N, with E and/or W. The arrows and “ns” indicated increase or decrease, and no significant changes, respectively.

woody plants, while $RR(BGB) = -0.05 + 0.78 RR(AGB)$ for herbaceous ones (Fig. 7, Table S4).

According to the theory of resource translocation between sources and sinks in plants, sink strengths of growing meristems controlled resources (e.g., carbohydrates and nutrients) translocation between the organs of plant (Fatichi et al., 2014). One of major benefits for a plant to

invest root system is to increase its ability to absorb water and mineral nutrients. The improved environments induced by global change (e.g., warming, irrigation, or nitrogen addition) might increase the carbohydrate fluxes into the root sink (Mueller et al., 2018). However, in terms of biomass allocation, roots appeared to be at an apparent lower priority level as a C “sink” relative to aboveground parts (e.g., leaves

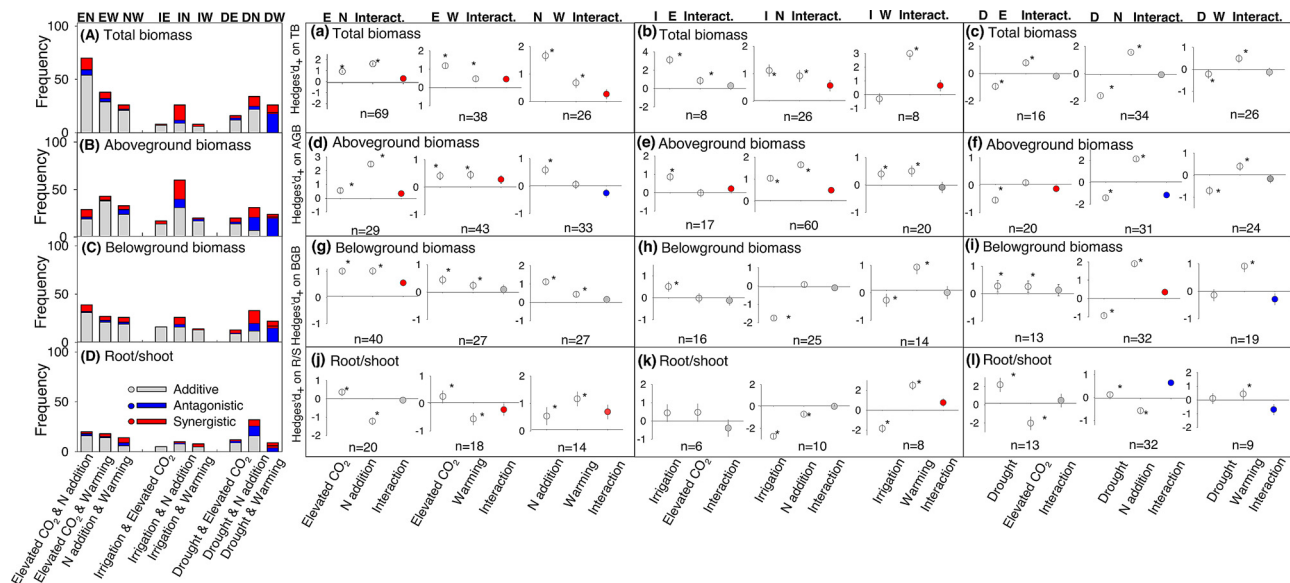


Fig. 5. Frequency distribution of interaction types in individual studies with two factorial designs for total biomass (A), above- (B), below-ground biomass (C), and root/shoot (D), and the weighted main effects (Hedge's d_+) of two factors and interactions on total biomass (a, b and c), above- (d, e and f) and below-ground biomass (g, h and i), and root/shoot (j, k and l) respectively. E, N, W, I, D and Interact. indicated the main effects of elevated CO₂, nitrogen addition, warming, irrigation, drought, and the interactions between corresponding two factors, respectively. The symbol “n =” and the following numbers indicated the sample sizes. Asterisks in plots a-l indicated statistical significance ($p < 0.05$).

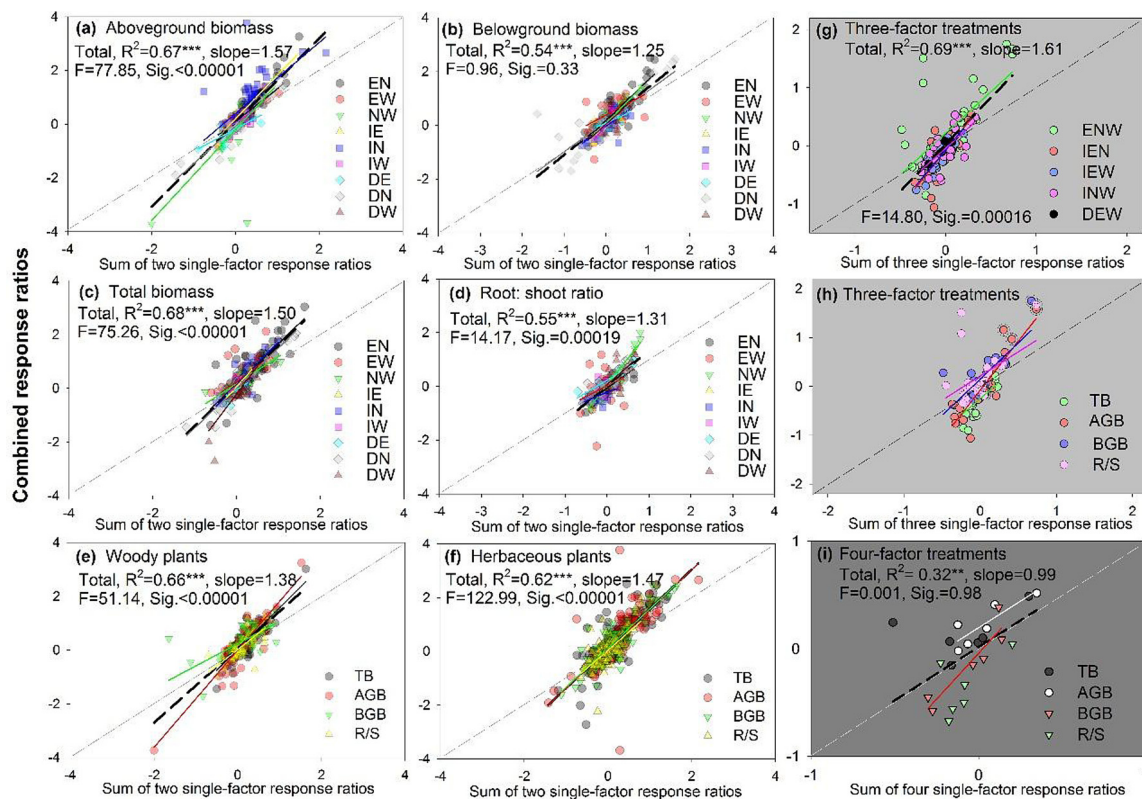


Fig. 6. Correlations of the combined response ratio for two-factor (a-f) or three-factor (g and h) or four-factor (i) treatments with the summed two or three or four single-factor response ratio of aboveground biomass (a), belowground biomass (b), total biomass (c), root/shoot (d) for woody and herbaceous plants (e and f). Letters E, N, W, I, and D were the abbreviations for elevated CO₂, nitrogen addition, warming, irrigation and drought, respectively. Values of F and Sig. in each plots indicated the difference of slopes between the regression line and 1:1 line. *** < 0.0001, ** < 0.001, and * < 0.05.

and young branches) as a C “source” (Norby and Jackson, 2000). The accelerated root growth might induce a greater root penetration resistance in soil compared to both initial soil condition and shoot growth in air, restricting root development and positive responses of BGB to multi-factor global change (Kembel and Cahill, 2005). The results of comparisons (summed vs. combined effects, Fig. 6) also demonstrated the different proportions of synergistic interactions between AGB and BGB (Fig. 5). The summed effects of global change factors had no significant difference with the combined effects for BGB (1.25 slope vs. 1, $p = 0.33$), while the combined effects of AGB were significantly higher than the summed ones (1.57 slope vs. 1, $p < 0.00001$, Fig. 6, Table S4). Therefore, under the global change, the actual relative changes in BGB were significantly lower than that of AGB; the changes of BGB would be overestimated from observed data of AGB (e.g., using remote sensing in regional scale).

For root/shoot, there were similar proportions of synergistic (EW, NW and IW, 18.8%) and antagonistic interactions (DN and DW, 16.4%, respectively). Among the insignificant effects of EW, NW and IW on root/shoot (Fig. 2), the main effects of warming were negative in EW, and positive in NW and IW (Fig. 5). As one of the most environment

factors, higher temperature generally improves aboveground productivity (Lu et al., 2011), and nitrogen and water uptake from soil (An et al., 2005), and correspondingly turnover of organic matter for plants. Due to its comprehensive co-occurrence impacts for root and shoot, warming plays a predominant role in determining the changes of root/shoot (no significant shift in short time compared with control, Fig. 2, Patel and Franklin, 2009; Zhou et al., 2012), showing opposite main effects in combination with factors improving aboveground or belowground resource supplies. The antagonistic interactions in DW mainly occurred in woody plants with a positive response of root/shoot, while the herbaceous plants displayed a non-significant response of root/shoot (Fig. 3). In combination, warming and drought increased BGB, offsetting the decline of root biomass under drought stress to avoid hydraulic failure (Fig. 4). In turn, this response leads to the unbalanced reductions in AGB and BGB, which subsequently caused an increased root/shoot (Koepke et al., 2010). In addition, opposite main effects between drought and nitrogen addition on plant investments to root caused the antagonistic interaction in DN (Fig. 2, King et al., 2003).

Table 2

ANOVA results of the effects of plant types (woody and herbaceous plants) and treatment types [treatments: elevated (CO₂), nitrogen addition, warming, drought, irrigation, and all the types of multiple-factor combinations] on the response ratio (RR) of total biomass, aboveground biomass (AGB), belowground biomass (BGB) and root/shoot.

Sources	RR (total biomass)			RR (AGB)			RR (BGB)			RR (root/shoot)		
	df	F	Sig.	df	F	Sig.	df	F	Sig.	df	F	Sig.
Plant types	1	6.589	0.0104*	1	0.004	0.947	1	14.370	0.0002**	1	5.761	0.017*
Treatments	19	7.932	< 0.0001***	19	8.299	< 0.0001***	18	4.136	< 0.0001***	18	4.518	< 0.0001***
Plant types × Treatments	14	3.098	0.0001***	16	2.635	0.0005**	14	2.382	0.0032*	14	1.838	0.0309*

*** < 0.0001, ** < 0.001, and * < 0.05.

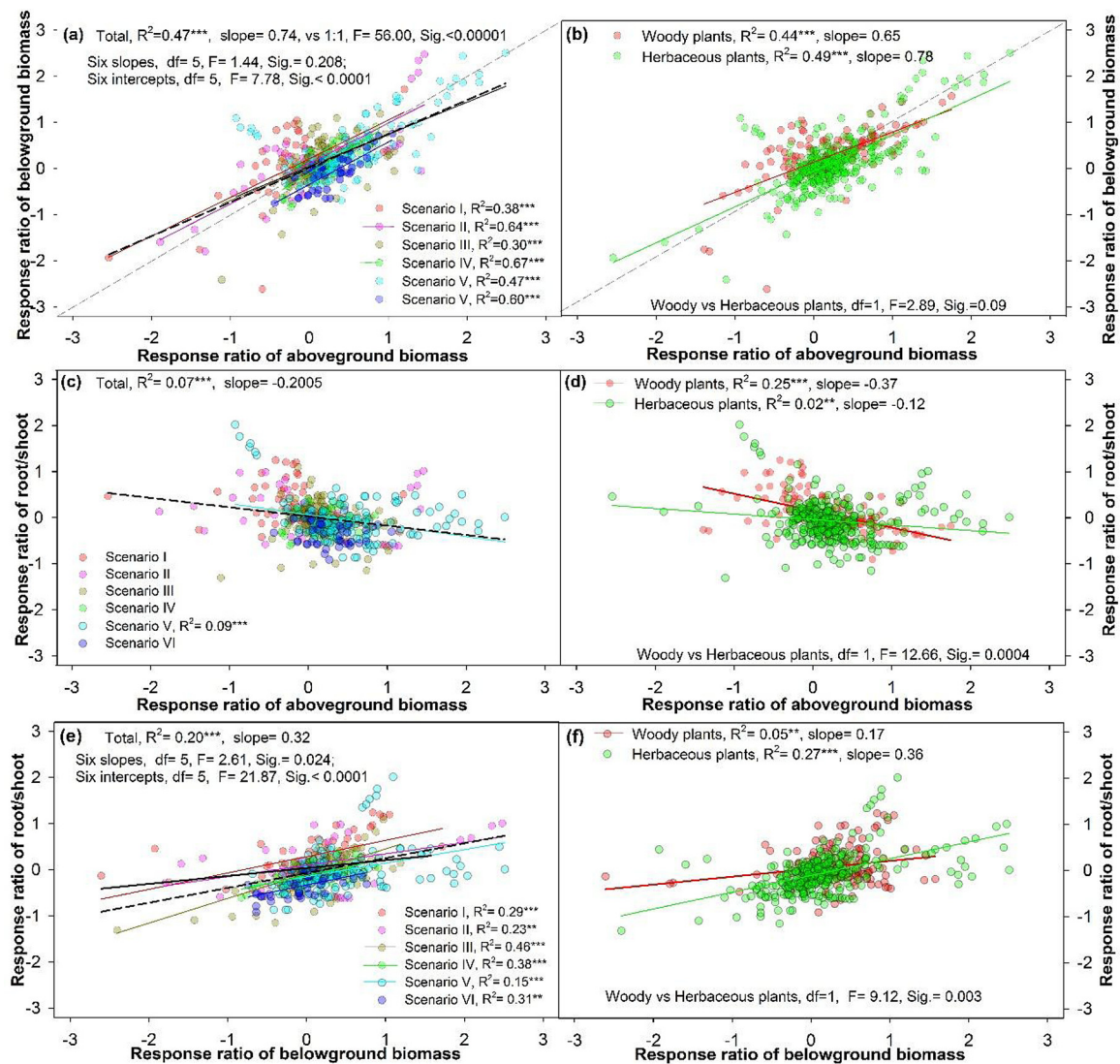


Fig. 7. The relationship between the response ratio of aboveground biomass vs. belowground biomass (a, b), response ratio of root/shoot vs. aboveground biomass (c and d) as well as belowground biomass (e and f) for woody and herbaceous plants under six scenarios. Scenario I: Drought (D) or D with warming; Scenario II: Drought with elevated CO_2 (E) and/or nitrogen addition (N); Scenario III: Elevated CO_2 and/or warming (W); Scenario IV: Irrigation (I) and I with E and/or W; Scenario V: Nitrogen addition (N) and N with E and/or W; Scenario VI: Irrigation and N, with E and/or W. $^{***} < 0.0001$, $^{**} < 0.001$, and $^* < 0.05$.

4.3. Spatial variation of biomass allocation responses to global changes

In this study, the responses of AGB in sites with lower MAT ($\leq 10^\circ\text{C}$) displayed a weakly positive correlation with MAT (Fig. S1). The positive relation between MAT and activities of photosynthesis-related enzymes could probably explain this correlation in boreal regions (Fig. S1, Larjavaara and Muller-Landau, 2012). The negative correlation between responses of AGB and MAT at higher temperatures ($> 10^\circ\text{C}$) was consistent with a global study reporting a negative correlation between root/shoot and MAT in natural biomes (e.g., grasslands and shrublands, Mokany et al., 2006).

The well-known negative correlation between MAP and root/shoot (e.g., forests, woodlands, Luo et al., 2012) was also found in this study (initial root/shoot vs MAP, $p < 0.0001$, $R^2 = 0.04$). However, warming-induced decreases in soil moisture, and elevated CO_2 -enhanced plant water use efficiency (Eamus, 1991) may potentially weaken this relationship (Fig. S1). Additionally, initial root/shoot in manipulative experiments displayed a significant positive relationship with the root/shoot after treatments, and this relation become weaker for woody plants at the site with a relative high root/shoot (4 ~ 8, e.g., cool temperate arid shrublands, Mokany et al., 2006, Fig. S2).

Therefore, we should pay more attention to the impacts of local MAT and MAP on the pattern of biomass distribution in dynamic global vegetation models (Del Grosso et al. 2009), and differentiate the initial root/shoot between woody and herbaceous plants in simulating biomass allocation under a climate scenario.

4.4. Implications for ecosystem management and future model development

The amount and distribution of plant biomass in terrestrial ecosystems are among the most important ecological issues in both theoretical and field studies on global change impact (Mokany et al., 2006; Poeplau, 2016). Our findings may inform future irrigation and fertilizer management practices and help to optimize allocation parameters for the model development. First, although our results showed the predominance of the additive effects among global change factors for root/shoot, synergistic and antagonistic interactions also occurred in a considerable proportion of the studies (e.g., 18.75 % for EW, NW, and IW and 16.4% for DN and DW, Fig. 5). Thus, assuming additive effects of single global change factors on plant biomass and its allocation to simulate the combined effects of multiple factors in dynamic global models (e.g., ED 2.1 and DAYCENT, Del Grosso et al., 2009), may cause

substantial under- or over-estimation for ecosystem and global carbon budgets. Therefore, caution should be taken when projecting climate-biosphere feedbacks in terrestrial ecosystems under simultaneous changes in multiple global change factors. Furthermore, the current multiple factor experiments mainly distributed in East Asia, North America and Europe (Fig. 1). These manipulative experiments are still scarce in other regions, especially in tropical and Africa regions, limiting a comprehensive understanding of future biomass distribution in a changing world.

Second, the responses of both biomass accumulation and biomass allocation were significantly distinct among different climate scenarios. For example, relatively more BGB would be stored in woody than herbaceous plants in ecosystems with less precipitation (i.e., under drought, Fig. 5). However, herbaceous plants would allocate more biomass in aboveground than belowground in those studies with more nitrogen deposition, while woody plants had no significant changes in root/shoot (Fig. 5). Therefore, we should consider the actual climate scenarios in a certain region in future land surface modeling to forecast the pattern of biomass allocation and carbon storage. Third, increased precipitation, nitrogen addition, and their combination significantly stimulated AGB, but decreased root/shoot (Figs. 2 and 4). When grasslands and plantations encounter drought stress to obtain the maximum aboveground harvest, irrigation and nitrogen addition might benefit their productivity and resistance (Fig. 5). For regions with high nitrogen deposition, e.g., Asia, western Russia, Europe and North America (Lamarque et al., 2005), more aboveground biomass accumulation than belowground one would support extensive livestock system, but more attention should be paid on management of drought mitigation due to lower root/shoot (Fig. 5).

5. Conclusions

Our study showed that warming (W), elevated CO₂ (E), nitrogen addition (N), and their combinations (i.e., EW, EN, NW) significantly increased both aboveground and belowground plant biomass (AGB and BGB, 8% - 100%), suggesting negative feedback of the carbon cycle to climate change. Treatments with irrigation often induced positive effects on AGB and negative one on root/shoot, and visa versa for treatments with drought, while above-mentioned effects on BGB were relatively complicated and determined by what factors were combined. The proportion of weighted synergy among E, N, W and irrigation were greater on AGB (55.6%) than BGB (22.2%), implying a decline trend of carbon stock proportion in belowground compartment relative to that in aboveground one. We found the considerable synergistic (21.2% and 18.8%) and antagonistic interactions (9.8% and 16.4%) of global change factors on plant biomass and its allocation in this study, likely being a potential uncertainty source in future model prediction if additive effects were used to simulate the combined effects of multiple factors. Therefore, incorporating these interactive effects on biomass allocation into land surface modeling could better improve the prediction of climate-carbon cycle feedbacks and develop sustainable strategies for grassland and forest management in a changing climate.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2020.107115>.

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