Title: Functionally dissimilar neighbors increase tree water use efficiency through enhancement in leaf phosphorus concentration

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Running title: Diversity increase water use efficiency and foliar P

The type of article: Letter

Keywords: Carbon isotope composition, neighborhood competition, neighborhood complementarity, stomatal conductance, stress gradient hypothesis.

The number of words in the abstract: 149

The number of words in the main text: 4390

The number of references: 43

The number of figures: 5

The number of tables: 1

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Statement of authorship: ZH designed the research, SR collected data, YF analyzed data, XW collected data, XS analyzed isotopic data, YC performed phylogenetic and trait dissimilarities analyses, ZY conducted field work. ZH wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Data accessibility statement: We confirm that, should the manuscript be accepted, the data supporting the results will be archived in Dryad and the data DOI will be included at the end of the article. If no new data were used, please mention it in the data statement.

Abstract

Water use efficiency (WUE) is central to the global cycles of water and carbon. However, whether increasing tree diversity in plantation can increase WUE remain poorly understood. Here, we conduct a forest biodiversity experiment with 32 tree species spread in 14 ha in subtropical China to assess the effects of neighboring tree diversity on foliar WUE of *Cunninghamia lanceolata*, a widespread tree plantation species in China. We measure foliar δ13C as the proxies of changes in intrinsic WUE. Folia P concentrations of focal trees increase with trait dissimilarities between focal trees and neighbors, and the increased foliar P concentrations improve foliar WUE of focal trees. This neighborhood complementarity effect on WUE is stronger under more shaded neighborhood. However, neighborhood biodiversity did not significantly affect foliar δ18O, a surrogate for stomatal conductance. These findings suggest that tree biodiversity increases WUE through the complementary usages of soil P between neighboring tree species.

Keywords

Carbon isotope composition, neighborhood competition, neighborhood complementarity, stomatal conductance, stress gradient hypothesis.

INTRODUCTION

The accelerating loss of biodiversity is often associated with decreases in ecosystem functions, such as productivity (Isbell *et al.* 2011; Reich *et al.* 2012; Huang *et al.* 2018). Terrestrial plants take in CO2 from the atmosphere through photosynthesis, a process in the company of the loss of water through transpiration from leaves. The ratio of carbon (C) uptake via assimilation per unit H2O loss from transpiration, or water-use efficiency(WUE), is a key characteristic of ecosystem function that is central to the global cycles of water, energy and C. A few studies have shown that tree diversity enhances soil water availability and the transpiration of trees through the complementarity effect, which arises from niche differentiation or facilitation, and decreases WUE of individual trees and communities (Guevara *et al.* 2010; Chaves *et al.* 2020); however, results remain controversial (Grossiord *et al.* 2014; Gonzalez *et al.* 2018) and studies on the mechanisms that regulate the WUE in forest mixtures are entirely lacking (Jansen *et al.* 2021).

In forests, the potential for niche complementarity is often restricted to interactions among near neighbors (Weiner 1990; Uriarte *et al.* 2004). Exploring species interactions at the local neighborhood level is, therefore, a key starting step to understand the mechanisms underlying the tree diversity and ecosystem function relationships in tree communities (Potvin & Gotelli 2008; Fichtner *et al.* 2018). The effect of species mixing on tree WUE depends on how leaf physiological processes such as stomatal conductance (gs) and C assimilation rates (A) respond to the variations of neighborhood tree species richness. As a consequence, changes in water, light and nutrient availability, resulting from varied levels of local neighborhood conditions, can affect the WUE of trees because gs in the leaf is controlled by the availability of water in the soil, the foliar N and P concentrations are significantly correlated with A. Light availability may significantly change both A and gs.

Neighborhood diversity may increase the availability of soil water and nutrients by means of niche differentiation and facilitation. For example, some tree species used soil water from top 30 cm, whereas others took up most of their water from deeper layers during the dry season, which, in turn, contributes to increasing foliar gs and transpiration in ecosystem (Amin *et al.* 2019). A more diverse community has a greater likelihood of including deep-rooted species which may redistribute water from deep and denuded areas to surface soil through hydraulic lift and increase water availability to plants with shallow roots, as observed in some xeric ecosystems (Cardon *et al.* 2013). The more soil water available under diverse plant mixtures lead to increasing leaf gs, but decrease foliar WUE in species mixtures, which can act at both the community and neighborhood scale. Findings from tree biodiversity experiments provided evidence that soil nitrate and phosphate availabilities increased with tree species richness, particularly in the surface soil (Chaves *et al.* 2020). Soil organic matter and the availability of limiting nutrients are regulated by many biological processes such as the root and microbial soil respiration, which are positively affected by diversity (Chen *et al.* 2019). The facilitation of soil nutrient cycling due to neighborhood diversity may improve the foliar nutrient concentrations, A and therefore increase tree WUE.

Here, we used tree communities in subtropical China, which were planted in 2019, to establish a more mechanistic basis for biodiversity-WUE relationships in forest plantation. We chose Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook) as a target tree species because it is the most important plantation species in China and its monoculture covers 10 million hectares (Huang *et al.* 2013). The established tree communities cover a wide range of diversity gradient, varying from monocultures to 32-species mixtures. It was often suggested that Chinese fir can experience higher rate of growth when growing in mixture with other tree species compared with growing in its monoculture (Ma *et al.* 1998). However, the mechanisms are lacking. We focus on leaf physiological responses of young Chinese fir trees to varying levels of local neighborhood conditions by experimentally manipulating a gradient of neighborhood species richness with a maximum of eight heterospecific neighbors. It was reported that soil water is seldom the limiting factor for Chinese fir plantation in south China (Ouyang *et al.* 2018), while soil nutrient availabilities, especially phosphate availabilities, are often limiting and hence significantly related to the C assimilation rates in subtropical forests (Huang *et al.* 2016). We expect that:

1. the WUE of Chinese fir increases with greater tree species richness, trait and phylogenetic dissimilarities to its neighbors due to a positive neighborhood complementarity effect on soil nutrient availabilities, foliar nutrients and the C assimilation rates of Chinese fir. We used δ13C in leaves as the proxies of long-term changes in intrinsic WUE (Farquar *et al.* 1982).
2. the responses of foliar gs in Chinese fir to greater neighborhood species richness, trait and phylogenetic dissimilarities are insignificant because the availability of soil water in subtropical China is a less limiting factor. We use the δ18O in leaves to separate the responses of gs to neighborhood species richness because the *δ*18O signature in leaves is dependent on foliar gs, but not on A (Farquar *et al.* 2007).
3. increasing shading from neighbors will decrease the foliar WUE of Chinese fir due to intensified competition for light and nutrients, which leads to lower C assimilation rates (A).

MATERIALS AND METHODS

**Study site and experimental design**

The experimental platform is located in Baisha Forest Farm, Fujian Province, China (25°05′N, 116°42′E). Climate at the site is subtropical, with mean annual temperature and precipitation of 19.8 °C and 1637 mm, respectively (averaged from 1971-2020). The region is covered by subtropical broad-leaved forest and plantations of two commercially important coniferous species, *Pinus massoniana* and Chinese fir*.* We established a large-scale tree biodiversity experiment in March 2019 of approximately 14 ha. The site was previously used as Chinese fir plantation. After the trees were harvested and site was slash-burnt, we planted a total of 76,544 individual trees on 299 plots. Each plot was 12 × 12 m in size and planted with 256 tree individuals arranged in a rectangular with 0.75 m spacing between rows and columns (Figure S1 and S2).

We selected 32 native tree species according to their life-history. The experiment employed a randomized factorial design of life-history diversity based on shade and drought tolerance and a level of species richness from 32 to 16, 8, 4 and 1 species was applied into these 299 plots. There were different life-history combinations (e.g., diversity of life-history) under a given tree species richness. The premise of these combined designs was to assume that the saplings with the same life-history traits appeared with the same probability. Species names and abbreviations together with major characteristics and initial size at planting are provided in Table S1 and S2. For the present study we used 34 plots, in which Chinese fir was planted in mixture with other tree species at a level of species richness from 32 to 16, 8, 4 species and Chinese fir monocultures as reference (Table S3).

**Foliar sampling, nutrient concentrations,** δ **13C, and**δ **18O stable isotope analyses**

In each of these 34 plots, eight average Chinese fir individuals were selected. Across all 34 plots, the targeted trees measured on average 1.87 ± 0.57 meters in height and 2.8 cm ± 0.95 in diameter at the ground when sampling. One south-facing branch in the middle of the canopy was randomly selected from the targeted trees following the standard collection procedure in May 2021. Twenty mature leaves were collected from the branch and pooled to make one sample per tree. All leaves were oven dried at 60 °C and entirely ground to a fine powder with a mortar and pestle before analyses.

Foliar N concentrations were determined on sub-samples using a LECO EPS-2000 CNS thermal combustion furnace (LECO Corp., St Jose, MI). The analysis of foliar total P concentration was performed as outlined in Huang *et al.* (2016). Briefly, 0.5g ground samples were digested with heated concentrated nitric acid followed by concentrated per chloric acid in 50 mL porcelain crucibles. Samples were then quantitatively transferred into 100 mL volumetric flasks and diluted with distilled water. The concentration of P in samples was read at 660 nm with a visible spectrophotometer.

Isotopic analyses for C were conducted at the Stable Isotope Mass Spectrometry Laboratory at Fujian Normal University with an isotope ratio mass spectrometer (Finnigan MAT-253, Thermo Electron, San Jose, CA) coupled to an automatic, online elemental analyzer (Flash EA1112, Thermofinnigan, San Jose, CA). The δ13C is expressed (‰) relative to the standard of Pee Dee Belemnite (PDB). Accuracy, as determined by comparing measured values to the known value of an internal laboratory standard, was better than 0.12‰ for δ13C across all samples.

We extracted cellulose from well-homogenized leaves for δ18O analysis following the Brendel procedure modified by the addition of a 17% NAOH step (wash) to remove hemicellulose (Gaudinski *et al.* 2005). Cellulose samples were weighed into silver capsules and pyrolyzed at 1100°C in a Costech Elemental analyzer (Costech Analytical Technologies, Valencia, CA, USA). The isotopic composition of the evolved CO gas was determined on a Thermo-Finnigan Delta Plus isotope ratio mass spectrometer (Thermo-Finnigan, Bremen, Germany), which had a measurement precision of < 0.23‰ on a standard reference cellulose powder. All samples were run in triplicate and data were reported on the Standard Mean Ocean Water scale.

**Relationship between plant δ13C and iWUE**

Foliar δ13C data were used to calculate changes in C isotopic discrimination (∆):

(1)

where δ13Ca and δ13Cp are the δ13C values of air and plant tissue, respectively. The δ13Ca was obtained from direct measurements at Mauna Loa, Hawaii (https://gml.noaa.gov/). Assuming that integrated and instantaneous discrimination values can be substituted for these plant species, the ratio of the CO2 concentration inside the leaf (ci) to that of ambient air (ca) can be derived from ∆13C based on:

(2)

where *a* is the fraction from diffusion through stomata (4.4‰) and *b* is the fraction from carboxylation by ribulose-1,5-bisphosphate carboxylase/oxygenase (27‰) (Farquhar *et al.* 1982). The ci/ca ratio can then be used to calculate intrinsic water use efficiency (iWUE) of the plants:

(3)

where 1.6 is the ratio of gaseous diffusivity of CO2 to water vapor.

**Local neighborhood conditions**

Local neighborhood conditions were characterized by neighborhood tree species richness (NSR), neighborhood height index (NHI), neighborhood phylogenetic and trait dissimilarities in March 2021. NSR was calculated as the number of species in the neighborhood containing the 8 neighbors closet to a focal tree. NHI is the average height difference between neighbors and focal trees and used to account for shading effects (Jansen *et al.* 2021). Low levels of NHI mean that neighboring trees are on average smaller than the focal tree. We determined the average neighborhood phylogenetic dissimilarity (P\_diss) by weighting pairwise phylogenetic distance by neighbor tree basal area and inversely by spatial distance because larger and spatially closer neighbors were expected to have a greater influence (Uriarte *et al.* 2010). A phylogeny for the 32 species was produced using Phylomatic V3 software web client (http://phylodiversity.net/phylomatic/) and the cophenetic package in R statistical software (Parker *et al.* 2015). We generated a dissimilarity matrix for the study species where maximum dissimilarity was set to 1 and maximum similarity (i.e. neighbor of the same species as the focal tree) to 0.

We used the weighted average trait dissimilarity from a focal individual to its neighbors as our measure of functional niche. Six functional traits were initially included in the analysis: maximum tree height, leaf mass per area, leaf nitrogen content, wood density, specific root length, leaf dry matter content. These traits are thought to be closely related to resource acquisition (Westbrook *et al.* 2011). We removed collinearity among these traits by sequentially deleting the trait variable with the largest variance inflation factor until all remaining variables had variance inflation factors < 2. Wood density and leaf dry matter content were removed in this process, leaving four traits in the subsequent analyses. We estimate average neighborhood trait and phylogenetic dissimilarities between a focal tree and its neighbors using the following equation (Chen *et al.* 2016):

(4.1)

(4.2)

where is the weighted mean of neighborhood trait or phylogenetic dissimilarity for the *i*th focal tree with neighbors; is the phylogenetic distance or absolute trait distance between focal tree *i* and neighbor tree *j*; is a weight function of neighbor tree *j*’s basal area and the inverse of spatial distance between focal tree *i* and neighbor tree *j*.

**STATISTICAL ANALYSES**

We used linear mixed-effects models to determine the role of neighborhood conditions on iWUE of focal trees. First, we fitted several candidate models that included all predictors, two-way interactions between NSR, NHI and neighborhood phylogenetic or trait dissimilarities. The candidate models had the basic form:

(5)

where log(iWUEij) is the natural logarithm of iWUE for the *i*th tree, within the *j*th plot; DIAij is the diameter at the ground for the *i*th focal tree within the *j*th plot. NSRij, NHIij, P\_dissij, are neighborhood species richness, neighborhood height index, phylogenetic dissimilarity for the *i*th tree, within the *j*th plot; and, and are random intercept terms representing the effects of plots and neighborhood species composition. To investigate individual iWUE response to neighborhood trait dissimilarity, we replaced P\_diss term in eqn (5) with the individual neighborhood trait dissimilarities (T\_diss). To determine the role of neighborhood conditions on foliar nutrient concentrations or the δ18O in the leaves of focal trees, we replaced Y term in eqn (5) with foliar N, P or δ18O.

Second, we identified significant predictors (i.e. optimal fixed structure) using likelihood ratio tests based on maximum likelihood estimation. We refitted the best-fitting model with the restricted maximum likelihood method. All predictors were standardized (mean = 0, s.d. = 1) prior to analysis. Model residuals were checked for normality, independence and homoscedasticity, and the correlation between covariates did not indicate serious collinearity (variance inflation factors less than 2).

Finally, we assessed potential correlations between foliar iWUE and foliar N, P and δ18O using linear regression. Significance was determined using a *P* value of 0.05. To examine the pathways (stomatal conductance or C assimilation rates or both) by which WUE is affected by significant predictors (neighborhood conditions and neighborhood phylogenetic and trait dissimilarities), we conducted structural equation models with plots and neighborhood tree species composition as random effects. Foliar δ13C here reflected a time-integral estimate of the iWUE over a period of time for focal trees, which is a more useful measurement than instantaneous A/gs values, determined by gas exchange. On that account, the δ18O in the leaves was used as a surrogate for the mean gs in the focal trees and many studies have provided experimental evidences indicating that it is a potential time integrated approach to determine the variability in transpiration and gs of plants (Guerrieri *et al*., 2019). We used foliar nutrient concentration to indicate time-integrated C assimilation rates (A) because foliar CO2 assimilation rate (A) and nutrient content (N and P) are tightly correlated across growth forms and biomes (Wright *et al.*, 2005). We assumed that neighborhood phylogenetic and trait dissimilarities had a positive impact on A if foliar N or P concentration increased or the other way around, lower foliar nutrient concentrations mean a negative effect. All statistical analyses were performed with R-3.5.0 (R Core Team, 2016).

RESULTS

The neighborhood dissimilarities of specific root length (SRL\_diss) and leaf nitrogen content (LNC\_diss) have positive and significant impacts on foliar iWUE (Figure 1). The best fitting model for foliar iWUE included the effects of neighborhood height index(NHI), specific root length dissimilarity (SRL\_diss) and the interaction between NHI and SRL\_diss (Tables 1 and S4). Neighborhood tree species richness (NSR) (*p* = 0.37) did not significantly affect the variation of foliar iWUE. NHI explained the largest amount of variation in the model, followed by the interaction between NHI and SRL\_diss, and the main effect of SRL\_diss. Overall the model accounted for 24% of variation in the data of foliar iWUE from the fixed effects and 56% of variation in the data from fixed and random effects. On average, foliar iWUE decreased strongly as neighborhood height index (neighborhood shading) increased from -2 to 1 meters (Figure 2a), with a magnitude of 21.6 µmol mol-1. Foliar iWUE increased with increasing neighborhood SRL\_diss (Figure 2b). The neighborhood complementarity, or positive foliar iWUE and SRL\_diss relationship, depended on NHI, with mean net effects became stronger with increasing NHI (Figure 2c).

NHI significantly decreased the foliar P concentrations of focal trees (Figure S3). However, neighborhood trait dissimilarities significantly increased the foliar P concentrations of focal trees (Figure 3a), with best predictor for SRL\_diss (*p* = 0.0016) (Figure 3b). Interestingly, the three-way interaction between NSR, NHI and SRL\_diss was significant (Table S5), showing that the enhancement of the positive effect of neighborhood specific root length dissimilarity (SRL\_diss) on foliar P concentration by increasing NHI (neighborhood shading) was increased by neighborhood tree species richness. Foliar N concentration mainly depended on the size of focal trees. NHI had no significant impact on the foliar N concentrations of focal trees. Neither NSR, neighborhood trait nor phylogenetic dissimilarities significantly affected the variation of foliar N concentrations in focal trees (data not shown).

NHI significantly increased the δ18O in the leaves of focal trees (*p* = 0.013). On average, target trees with higher NHI (greater neighborhood shading) showed higher δ18O values in the leaves (Figure S4). Neither NSR nor neighborhood trait and phylogenetic dissimilarities significantly affected the variation of foliar δ18O values in the leaves of focal trees (data not shown).

Foliar δ18O values, N and P concentration had significant and positive correlation with iWUE (Figure 4). Final SEM models provided satisfactory fit to the data (Fisher C=11.9, df=18, P=0.851). Standardized coefficients, unstandardized coefficients, and *t* test results are presented in Table S6. NHI could directly decrease foliar iWUE. Alternatively, NHI had an indirect impact on foliar iWUE mediated by a reduction in foliar P concentrations. The indirect effect of neighborhood trait dissimilarities on foliar iWUE was initiated through a positive effect of SRL\_diss on foliar P concentrations (Figure 5).

DISSCUSION

Our results provide evidence that the positive effect of niche complementarity on the WUE of individual tree at leaf level, which partially supported our first hypothesis. Furthermore, the positive effects of niche complementarity on iWUE enhanced with neighborhood height index. For individuals experiencing relatively high intensity of shading from neighbors, promotion of neighbors with dissimilar functional traits could reduce the negative effects of shading on foliar iWUE. Our study disentangled the key role of photosynthesis and foliar P concentrations on rising foliar iWUE in Chinese fir, which resulted from neighborhood trait dissimilarities in a large-scale subtropical forest experiment.

Interestingly, we found that neighborhood trait dissimilarities increased foliar P concentration in Chinese fir, but had no significant impact on foliar N. The greater responses of foliar P, compared with foliar N, to the variation of local neighborhood conditions could be attributed to the low P availability in this forest. High foliar N:P ratios (on average 19.6) was found in this site and a relatively shallower relationship between maximal Rubisco carboxylation rate and foliar N had been reported in many other subtropical forests (Hou *et al.* 2012; Huang *et al.* 2016), which suggests P limitation of productivity.

The higher foliar P concentration of focal trees significantly linked to greater neighborhood trait dissimilarities, but not to tree species richness. This finding is consistent with the results from Firn *et al.* (2007) who suggested that plant diversity effect on P cycling was not determined simply by the number of species, but more likely depended on specific traits of the species present. Three trait dissimilarity indices (maximum tree height, MTH; specific root length, SRL; and leaf nitrogen content, LNC) had significant positive effects on foliar P concentrations (Figure 3), suggesting multiple processes contribute to neighborhood complementarities. SRL is closely related to plant species’ P-mobilization and acquisition strategies. A high SRL leads to a greater soil volume to be explored for P per unit C invested (Laliberté et al., 2015) and greater release of roots exudates which mobilize poorly-soluble inorganic and organic P, while a low SRL was characterized by a high acid phosphatase activity in the rhizosphere (Nobile et al., 2019). Therefore, a neighborhood community with greater SRL\_diss may enhance overall foliar P concentration because of complementarities in P-mobilization and -acquisition. MTH and LNC are closely related to plant species’ strategies with respect to competition for resources (Maracahipes et al., 2018). Greater MTH and LNC, suggesting a resource‐acquisitive strategy, identify species that adapt resource-rich conditions; the opposite resource-conservative strategy identify species that tolerate resource-poor conditions. As a result, a neighborhood community with greater MTH\_diss and LNC\_diss may have an overall greater P acquisition as facilitated by niche differentiation in space and time.

By identifying the indirect pathways by which neighborhood trait dissimilarities acts on the foliar iWUE of focal tree through foliar P concentration, rather than through foliar δ18O (Figure 5), we can identify potential mechanism regulating the foliar iWUE of focal trees. Our results reveal an increase in foliar iWUE due to neighborhood trait dissimilarities has been likely associated with the enhancement of foliar C assimilation rates (A) which leads to a decrease in ci. Indeed, phosphorus is of the essence for many compounds including sugar phosphates, nucleic acids, nucleotides, coenzymes, phospholipids, nucleic acids and triphosphonucleotides, which are associated with metabolism, energy transfer and genetic material in plants (Rao & Norman 1989). Given these key roles foliar P plays, it is not surprising that many studies have demonstrated that an adequate supply of inorganic P is essential to C assimilation and therefore plant WUE (Thomas *et al.* 2006) (Figure 4). If a reduction in the foliar gs of target trees because of greater neighborhood trait dissimilarities occurs, this should be reflected in a reduction in leaf transpiration, which in turn leads to less dilution of the enriched (in the heavy isotope 18O) water at the evaporative site by the unenriched water coming from the soil via xylem, thus increasing the δ18O in foliar cellulose (Guerrieri, *et al.* 2019).

Interestingly, our result showed no relationship between the foliar δ 18O of focal trees and neighborhood tree species richness or neighborhood dissimilarities, which suggests foliar gs remained constant. This finding therefore provides strong support for our second hypothesis that soil water in subtropical China is a less limiting factor, compared with soil nutrients, especially for Chinese fir plantation. Indeed, a study in a 20-year-old Chinese fir plantation showed that the total stand transpiration was 37.3% of the annual gross rainfall and daily stand transpiration had an average value of 1.43 mm day−1, which is much lower than the plantations of broadleaved species (Ouyang *et al.* 2018). Our outcome represents first and direct evidence that neighborhood complementarity effect increased foliar iWUE (decrease in foliar ci) through the enhancement of C assimilation rate. The finding, however, disagrees with several studies which reported decreasing δ13C signatures of trees (increases in foliar ci) and the improved water supply to focal trees in mixed-species communities (Metz *et al.* 2016; Jansen *et al.* 2021). Future studies examining biodiversity-WUE relationships need to ensure that they include tree species with a variety of water use strategies and experiencing a wide range of soil water availability.

Unsurprisingly, we found that neighborhood height index was the most important predictor for foliar iWUE. Increased NHI can have a negative and direct impact on foliar iWUE or decreased foliar iWUE indirectly through negative effect on foliar P concentration (Figure 5). The finding therefore supported our third hypothesis. The decrease in foliar iWUE (increased foliar ci) because of increased NHI can be attributed to lower photosynthesis (A). Trees subjected to greater shading levels might have received lower radiation and then displayed lower foliar nutrient concentrations, A and iWUE (Saur *et al.* 2000; Linares *et al.* 2009). The increased foliar ci with greater NHI could not be attributed to the gs because we found a significant and positive relationship between NHI and the δ18O values in foliar cellulose (Figure S4). The increases of foliar δ18O due to increasing NHI mean a decrease of gs, which should decrease ci (Scheidegger *et al.* 2000) and is consistent with earlier observation (Aranda *et al*. 2005).

The interaction between NHI and neighborhood SRL\_diss was the second most important predictor in the full model (Table 1). This interaction indicates that the negative effects of shading on foliar iWUE decrease with neighborhood SRL\_diss or that the positive effects of neighborhood SRL\_diss on foliar iWUE become stronger with increasing shading from neighbors. This finding lends support for the stress gradient hypothesis at the individual tree level (van Mantgem *et al.* 2009). Plant neighbors may impact physiological processes of a focal plant, mainly through competition (Fernández-de-Uña *et al.* 2016). Such impacts may depend on the neighbors’ traits and their similarity with the traits of the focal plant (McGill *et al.* 2006). Our finding also corroborates the idea that although a focal plant with dissimilar neighbors has been shown to compete less for soil nutrients and perform better in nutrient acquisition (Schwilk & Ackerly 2005), these complementarity effects are only important when light is limiting.

Niche complementarity among neighbors is a crucial driver for positive biodiversity-ecosystem function relationship at the community level. In this study, we demonstrate that the role of neighborhood dissimilarity and its key mechanisms in modulating foliar iWUE require a better understanding of species interactions at the local neighborhood level. This finding calls into question the notion that increased neighborhood tree species richness enhances gs and hence transpiration, at least for the mesic ecosystems in subtropical China, where, indeed, no significant changes in gs were observed. Moreover, the assumption that different tree species follow the same physiological strategy in response to increasing neighborhood tree species richness is probably too simplistic. Our finding suggests that niche complementarity can increase with increasing stresses, implying that the intensity of competition in the local neighborhood of a focal tree determines the strength of niche complementarity. Together, these results have important meanings in future forest management by suggesting the functional diversity of tree species at the local neighborhood level has a fundamental control on the cycles of water, nutrient and C in forest ecosystems.

ACKNOWLEDGEMENT

We thank Baisha Forest Farm, Shanghang, Fujian, China for the assistance in the establishment of biodiversity and ecosystem function experimental plots. The research was supported by the Key Project (31930077) and Excellent Young Scholar Project (31625007) from National Natural Science Foundation of China.

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