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Short-term canopy and understory nitrogen addition differ in their effects on seedlings of dominant woody species in a subtropical evergreen broadleaved forest

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ABSTRACT

As atmospheric nitrogen (N) deposition continues to increase, information on how N deposition affects seedling performance of tree species is critical for predicting forest regeneration. In this study, we examined the effects of canopy N addition at 25 and 50 kg ha⁻¹ year⁻¹ of N (CAN25 and CAN50), and understory N addition at 25 and 50 kg ha⁻¹ year⁻¹ of N (UAN25 and UAN50) on the survival, physiology, and growth of seedlings of two dominant woody species (*Schima superba* and *Ardisia quinquegona*) that were transplanted into a subtropical evergreen broadleaved forest. At two years after transplanting, understory N addition greatly decreased seedling height and biomass production for both species, especially at 50 kg ha⁻¹ year⁻¹ of N. N-addition treatments, however, had only minor effects on seedling survival and biomass allocation. UAN50 decreased leaf light-saturated photosynthesis (A_{sat}) in the dry season and increased stem N concentration; UAN25 increased intrinsic water-use efficiency (WUE_i); and CAN50 increased concentrations of N and P in the roots and stems of *S. superba* seedlings. Both UAN25 and UAN50 generally increased stem and leaf N concentrations and the leaf N/P ratio in *A. quinquegona* seedlings. UAN50 decreased whole-plant N-use efficiency of both species, and CAN50 reduced whole-plant N- and P-use efficiencies of *S. superba* seedlings. Overall, *S. superba* seedlings performed better than *A. quinquegona* seedlings in terms of height, biomass, A_{sat} , and WUE_i. Our results indicate that N deposition can profoundly influence the seedling growth of woody species, and that seedling height, basal diameter and biomass are more sensitive to the understory addition of N than to the canopy addition of N, i.e., the traditional use of understory addition of N to simulate atmospheric N deposition may overestimate the effects of N deposition on seedling performance.

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1. Introduction

With the impact of anthropogenic activities, atmospheric nitrogen (N) deposition has greatly increased in the past decades and will reach $50 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N in some regions by 2050 (Galloway et al., 2008). Many studies have therefore focused on the influences of elevated N deposition on the growth and composition of forests, which are the main components of terrestrial ecosystems and which play important roles in biodiversity conservation and climate regulation (Zaccherio and Finzi, 2007; Lu et al., 2010; Mao et al., 2017; Payne et al., 2017). During plant recruitment, the seedling stage is vulnerable and sensitive to changes in environmental conditions (Tripathi and Raghubanshi, 2014; Wang et al., 2019). Seedling establishment and growth are crucial for plant community regeneration (Gómez-Aparicio et al., 2008; Patterson et al., 2012). As atmospheric N deposition continues to increase, information on how N deposition affects the performance of seedlings of woody species is critical for predicting forest regeneration (Tanentzap et al., 2013; Förster et al., 2017).

Nitrogen can greatly influence seedling performance including survival, biomass production, physiology and nutrient uptake (Guo et al., 2010; BassiriRad et al., 2015. Sahoo et al., 2021). In field studies, the effects of elevated N deposition on seedling survival and growth of forest species sometimes varied. For instance, experimental N addition significantly increased the survival of tree seedlings in a northern temperate forest (Sefcik et al., 2007) and in a tropical dry forests (Ceccon et al., 2003), but declined the survival of most understory tree seedlings in a mixed temperate forest (Catovsky and Bazzaz, 2002). In general, seedling growth responds positively to N addition in N-limited forests but not in N-sufficient forests (Santiago et al., 2012; Yi et al., 2015; Wang et al., 2019). However, Mo et al. (2008) found that seedling growth was increased by an N application rate of 100 or $150 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N, but was significantly inhibited by an N application rate of $300 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N, suggesting that the effects of simulated N deposition on tree seedlings depend on the N deposition rate in tropical forests where N is not limited. The response of seedlings to N addition also often varies among species. In a temperate forest, N addition greatly increased seedling growth of early-successional tree species but not of late-successional tree species (Catovsky et al., 2002). Based on the results of a long-term N-addition field experiment, Cárdate-Tandalla et al. (2018) concluded that the responses of different tropical forest tree seedlings to N addition are not constant. Therefore, the effects of increased N deposition on seedling establishment and growth require further investigated.

To simulate atmospheric N deposition in forest ecosystems, researches have traditionally applied N solutions to the understory or the forest floor (e.g., Mao et al., 2017; Lu et al., 2018; Mo et al., 2020). The effects of N inputs from atmospheric N deposition, however, can be influenced by the forest canopy, which can intercept and retain a substantial portion of the N deposited from the atmosphere (Sparks, 2009; Gaige et al., 2007; Wang et al., 2021). These results indicate that understory N addition does not realistically reveal the effects of atmospheric N deposition on forest ecosystems (Zhang et al., 2015). For example, Hu et al. (2019) demonstrated that canopy N addition but not understory N addition greatly increases plant intrinsic water-use efficiency. In another study, the species richness of the shrub layer was more sensitive to canopy N addition than to understory N addition (Tian et al., 2019). It follows that, experiments that include canopy vs. understory addition of N will improve our understanding of the effects of elevated N deposition on the seedling performance of woody species in forests.

Evergreen broadleaved forests are broadly distributed worldwide and greatly contribute to global carbon sequestration (Yu et al., 2014). In subtropical China, the evergreen broadleaved forest is the zonal vegetation type and has numerous ecological functions such as biodiversity conservation and climate regulation (Wang et al., 2005; Wu et al., 2019). Because of intensified industrial and agricultural activities in recent decades, large amounts of reactive N have been emitted in the region, and the forests are experiencing pressure from elevated N deposition (Liu et al., 2013; Tian et al., 2019). To better understand the dynamics in plant recruitment and forest regeneration, we need additional information on how tree seedlings respond to increases in N deposition. However, knowledge of the effects of simulated N deposition on the seedling performance (e.g., survival, growth, photosynthesis, nutrient status and nutrient use strategy) of dominant woody species in the subtropical evergreen broadleaved forest is still insufficient.

In this study, we investigated the effects of canopy and understory N addition (at 0 , 25 , and $50 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N) on the establishment and growth of seedling of two dominant woody species (*Schima superba* and *Ardisia quinquegona*) in a subtropical evergreen broadleaved forest. Our primary objective was to evaluate the influence of elevated N deposition on the seedling performance of subtropical woody species and the potential forest regeneration. Considering the background atmospheric N deposition rate was relatively high in the level of approximately $34.1 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N (Zhang et al., 2015), we tested the following hypotheses: (1) N addition would exert negative effect on the survival rate, height growth, and biomass production of dominant woody plant seedlings; (2) Seedling performances would differ in their response to canopy and understory N additions. Result of our study would have important implications for plant recruitment and regeneration in the evergreen broadleaved forest under the projected increase in atmospheric N deposition.

2. Materials and methods

2.1. Study site and plant species

The current study was carried out at the Shimentai National Nature Reserve ($24^{\circ}22'-24^{\circ}31' \text{ N}$, $113^{\circ}05'-113^{\circ}31' \text{ E}$), located at Guangdong Province, South China. This area has a subtropical monsoon climate, with a natural N deposition rate of about $34.1 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N (Zhang et al., 2015). The mean annual temperature is about 20.8°C , and the average is 11.0°C in the coldest month (January) and 28.9°C in the hottest month (July). The average annual rainfall is 1882.8 mm , and the average annual relative humidity is 78% (Zhang et al., 2015). Our experiment was conducted in the evergreen broadleaved forest within this Nature Reserve. The experimental evergreen broad-leaved forest is about 60 years old, with a canopy height of approximately 26 m. Currently, the

dominant woody species are *Schima superba*, *Ardisia quinquegona*, *Castanea henryi* and *Schefflera octophylla*, and the understory is mainly dominated by shrubs such as *Psychotria rubra* and *Blastus cochinchinensis* (Liu et al., 2020a).

Our study focused on the establishment and growth of seedlings of the two dominant woody species (*Schima superba* and *Ardisia quinquegona*) in the experimental forest. The important values of these two species were high among the woody plants in the plant community. *S. superba*, belongs to the Theaceae family and is shade-tolerant. It grows well on acidic soil to heights ranging from 5 to 25 m. *A. quinquegona* belongs to the Myrsinaceae family. It is also shade-tolerant and can reach a height of 6 m. The two species selected for this study are native and commonly distributed in the subtropical evergreen broadleaved forests in southern China.

2.2. Experimental design

A field experiment was conducted using a random block design with four blocks with five N-addition treatment plots. Each block contained five circular plots (radius = 17 m; area = 907 m²) to which the following five N-addition treatments were randomly assigned: canopy addition of N at 50 kg ha⁻¹ year⁻¹ of N (CAN50) and at 25 kg ha⁻¹ year⁻¹ of N (CAN25), understory addition of N at 50 kg ha⁻¹ year⁻¹ of N (UAN50) and at 25 kg ha⁻¹ year⁻¹ of N (UAN25), and no addition of N as a control (CT). The N-addition plots were treated with an NH₄NO₃ solution. Within each block, there was at least a 20 m buffer zone between adjacent plots, and polyvinylchloride boards were inserted in the buffer zone to prevent contamination by N solution from the neighboring plots.

In each CAN plot, a 35 m high tower was built to support the equipment that sprayed the NH₄NO₃ solution onto the forest canopy. A set of sprinklers (with a spraying radius of 17 m) were installed on each tower's top, which was approximately 5 m higher than the forest canopy. Each sprinkler could rotate 360° to ensure the uniform spraying of the NH₄NO₃ solution. The spray was also controlled by adjusting the water supply pressure, which was monitored with a water meter at the base of tower. In each UAN plot, a pump and sprinkler system were deployed in the understory. Five 1.5 m-high sprinklers (with a 360° rotation and a spray radius of 5 m) were evenly installed to spray the N solution. In the CAN and UAN plots, N solution was applied at the end of each month between April and October each year. The N solution applied each time was approximately equal to 3 mm of precipitation, with a total of 21 mm each year. The total applied solution accounted for approximately 1% of the total annual rainfall in the study region. We therefore assumed that the quantity of water added with the N solution was negligible, and no water was sprayed onto CT plots. All N-addition treatments were initiated in April 2013.

To assess the effect of canopy and understory addition of N on seedling performance of the two dominant woody species, two subplots (1 m × 1 m each) were randomly designated in each plots. In late April 2018, 12 seedlings of *S. superba* were transplanted into

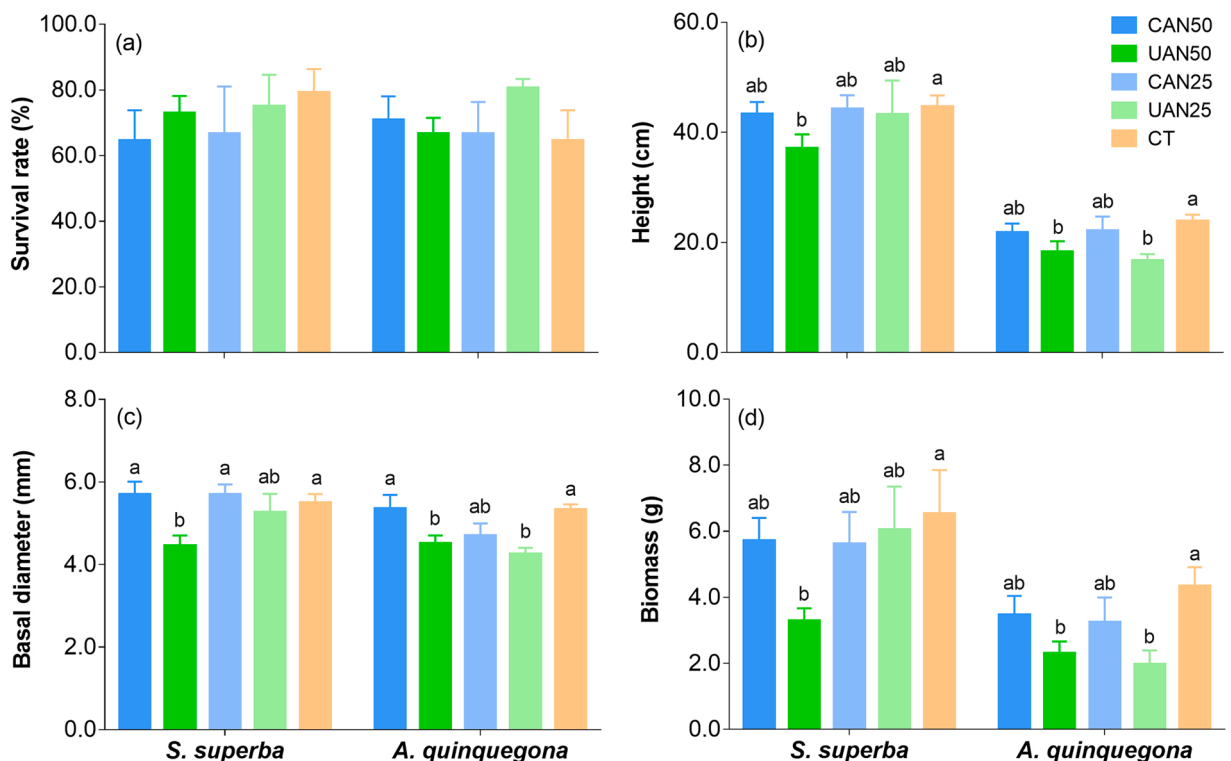


Fig. 1. Survival rate (a), height (b), basal diameter (c), and biomass (d) of *S. superba* and *A. quinquegona* seedlings as affected by canopy nitrogen-addition treatments (CAN25 and CAN50; with 25 or 50 indicating 25 or 50 kg ha⁻¹ year⁻¹ of N), understory nitrogen-addition treatments (UAN25 and UAN50), and a control (CT; 0 kg ha⁻¹ year⁻¹ of N). Values are means ± SE. For each species in each panel, means with different letters are significantly different.

one subplot, and 12 seedlings of *A. quinquegona* were transplanted into the other subplot. The seedlings were evenly spaced and were watered shortly after transplanting. Each seedling was marked by a plastic ring at the stem base. The transplanted seedlings were about 1-year old and were similar in the size for both species. The field experiment lasted 2 years and ended in April 2020.

2.3. Data collection and statistical analysis

During the experiment, leaf gas exchange was measured in July (the wet season) and December (the dry season) of 2019. On the sunny days, leaf light-saturated photosynthesis (A_{sat} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance (G_s , $\text{mol m}^{-2} \text{s}^{-1}$) and transpiration rate (T_r , $\text{mmol m}^{-2} \text{s}^{-1}$) of seedlings were measured between 09:30 and 14:00 with a LI-6800 portable photosynthesis analyzer (LI-COR, Lincoln, NE, USA) equipped with a fluorometer leaf chamber (6800–01 A). In each subplot, four or five healthy leaves of the seedlings of each species were measured. During the measurement, the photosynthetic photon flux density was set at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, and the CO_2 flux of the reference chamber was $400 \mu\text{mol mol}^{-1}$. The data were recorded after the measurement was stable. Leaf intrinsic water-use efficiency (WUE_i , $\mu\text{mol mol}^{-1}$) was determined as A_{sat}/T_r .

At the end of the experiment, the surviving individuals were counted, and their height and basal diameter were measured. After that, all seedlings were individually removed from the soil with a shovel and transported to the laboratory. Seedlings were separated into leaves, stems, and roots, which were washed and oven-dried to a constant mass and weighed. The plant tissues were then milled to a fine powder and analyzed for total nitrogen (N) and phosphorus (P). The following parameters were calculated for the seedlings: root:shoot ratio (R/S, root dry weight/shoot dry weight; g g^{-1}), leaf weight to total biomass ratio (LWR; g g^{-1}), stem weight to total biomass ratio (SWR; g g^{-1}), root weight to total biomass ratio (RWR; g g^{-1}), and N:P ratios in the leaves, stems, and roots. N- and P-use efficiencies of the entire seedlings were calculated as seedling biomass (g) divided by seedling N and P contents (mg) (Zhang et al., 2013).

Analysis of variance (ANOVA) was performed to assess the effects of N addition, and plant species on seedling survival, growth, morphological and photosynthetic parameters, nutrient concentration, and whole-plant nutrient-use efficiency. Least significance difference (LSD) were used for multiple comparison when a significant effect was detected at $\alpha = 0.05$. All analyses were performed using SPSS 20.0 for Windows (IBM Inc., 2011).

3. Results

3.1. Seedling survival, growth and morphological parameters

By the end of experiment, seedling survival rate ranged from 64.6% to 79.2% for *S. superba*, and from 64.6% to 80.6% for *A. quinquegona*. Seedling survival rates for each species did not differ significantly among the N treatments (Fig. 1a). For *S. superba*, the height and biomass of seedlings were lower in the UAN50 plots than in the CT plots, and basal diameter of seedlings was lower in the UAN50 plots than in the CAN50, CAN25, or CT plots. For *A. quinquegona*, the UAN50 and UAN25 significantly decreased seedling height and reduced biomass (Fig. 1b and d). Seedling basal diameter of *A. quinquegona* was higher in the CAN50 and CT plots than in the UAN50 and UAN25 plots (Fig. 1c). Averaged across all treatments, height and biomass production were greater for *S. superba* than for *A. quinquegona* ($p < 0.05$).

In general, N addition had minor influence on seedling biomass partitioning (Table 1). For *S. superba*, RWR was significantly higher in the CAN50 plots than in the UAN50 treatment ($p = 0.024$), and R/S was much higher in the CAN50 plots than in the UAN50, CAN25, or CT plots ($p < 0.05$).

Treatments are described in Fig. 1 and in the text. LWR: leaf dry weight/total dry weight; SWR: stem dry weight/total dry weight; RWR: root dry weight/total dry weight; R/S: ratio of biomass in root and shoot. Values are means \pm SE. Means in a row followed by different letters (a, b) are significantly different ($p < 0.05$).

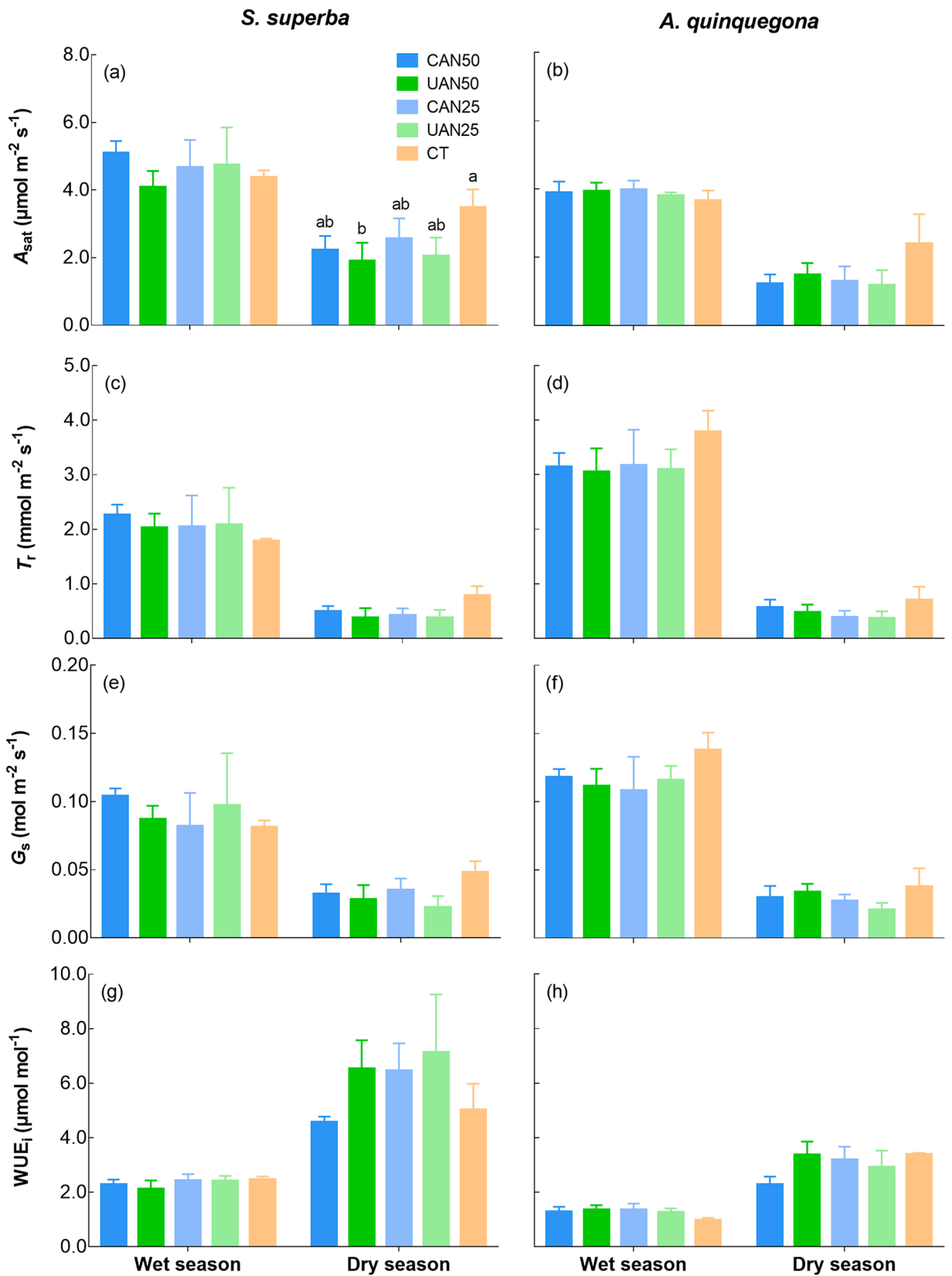
3.2. Seedling photosynthetic properties

In the wet season, N addition did not significantly affect leaf light-saturated photosynthesis (A_{sat}), stomatal conductance (G_s), transpiration rate (T_r), or intrinsic water-use efficiency (WUE_i) of either species (Fig. 2a–h). In the dry season, A_{sat} of *S. superba* seedlings was lower in the UAN50 plots than in the CT plots (Fig. 2a, $p = 0.043$). A_{sat} and WUE_i of seedlings were much higher for *S. superba* than *A. quinquegona* in both dry and wet seasons ($p < 0.05$). In the wet season, G_s and T_r were lower for *S. superba* seedlings

Table 1

Morphological characteristics of *S. superba* and *A. quinquegona* seedlings as affected by canopy and understory nitrogen-addition treatments.

		CAN50	UAN50	CAN25	UAN25	CT
<i>S. superba</i>	RWR (g/g)	0.37 \pm 0.04 ^a	0.25 \pm 0.03 ^b	0.26 \pm 0.03 ^{ab}	0.29 \pm 0.05 ^{ab}	0.29 \pm 0.04 ^{ab}
	SWR (g/g)	0.45 \pm 0.02	0.48 \pm 0.01	0.49 \pm 0.03	0.43 \pm 0.03	0.47 \pm 0.04
	LWR (g/g)	0.18 \pm 0.04	0.28 \pm 0.03	0.25 \pm 0.01	0.29 \pm 0.07	0.24 \pm 0.07
	R/S (g/g)	0.69 \pm 0.14 ^a	0.34 \pm 0.04 ^b	0.36 \pm 0.06 ^b	0.43 \pm 0.11 ^{ab}	0.42 \pm 0.07 ^b
<i>A. quinquegona</i>	RWR (g/g)	0.35 \pm 0.04	0.32 \pm 0.02	0.33 \pm 0.04	0.37 \pm 0.02	0.32 \pm 0.01
	SWR (g/g)	0.43 \pm 0.05	0.45 \pm 0.04	0.42 \pm 0.01	0.41 \pm 0.01	0.40 \pm 0.01
	LWR (g/g)	0.22 \pm 0.02	0.23 \pm 0.03	0.25 \pm 0.03	0.21 \pm 0.03	0.29 \pm 0.01
	R/S (g/g)	0.63 \pm 0.13	0.52 \pm 0.06	0.53 \pm 0.09	0.67 \pm 0.07	0.48 \pm 0.02



(caption on next page)

Fig. 2. Leaf light-saturated photosynthesis (A_{sat}), transpiration rate (T_r), stomatal conductance (G_s), and intrinsic water-use efficiency (WUE_i) of *S. superba* and *A. quinquegona* seedlings as affected by season and nitrogen addition treatments. Treatments are described in Fig. 1 and in the text. Values are means \pm SE. For each season in each panel, means with different letters are significantly different ($p < 0.05$).

than for *A. quinquegona* seedlings ($p < 0.05$). For both species, A_{sat} , G_s , and T_r of seedlings were much higher in the wet season than in the dry season ($p < 0.05$), while WUE_i showed the opposite trend (Fig. 2, $p < 0.05$).

3.3. N and P concentrations and N- and P-use efficiencies of seedlings

In general, N addition significantly increased N and P concentrations in roots, and N concentration in stems of both species ($p < 0.05$). For *S. superba*, CAN50 increased N and P concentrations in the roots and stems, and UAN50 increased N concentration in

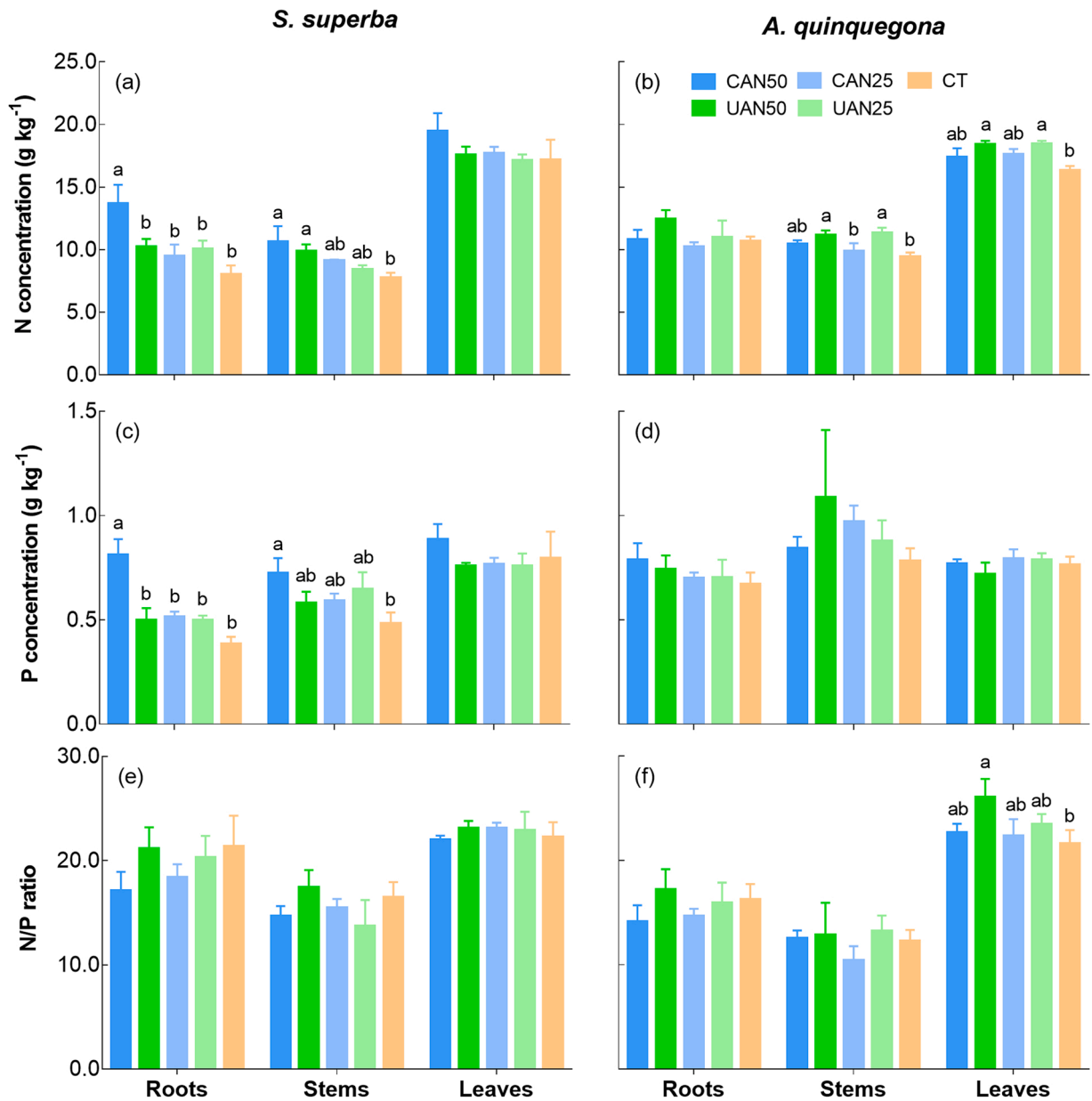


Fig. 3. N and P concentrations and N/P ratios in roots, stems, and leaves of *S. superba* and *A. quinquegona* seedlings as affected by nitrogen addition treatments, which are described in Fig. 1 and in the text. Values are means \pm SE. For each tissue type in each panel, means with different letters are significantly different ($p < 0.05$).

the stems (Fig. 3a and c). For *A. quinquegona* seedlings, both UAN50 and UAN25 increased N concentration in stems and leaves (Fig. 3b). The leaf N/P ratio was much higher in the UAN50 plots than in the CT plots (Fig. 3f).

The leaf N/P ratio ranged from 22.0 to 23.1 for *S. superba* seedlings, and from 21.6 to 26.0 for *A. quinquegona* seedlings (Fig. 3e and f). Averaged across all five treatments together, the P concentration in roots, the N and P concentrations in stems were lower, while the N/P ratio in roots and stems were higher in *S. superba* seedlings than in *A. quinquegona* seedlings ($p < 0.05$).

Nitrogen addition significantly affected whole-plant N- and P-use efficiencies of *S. superba* seedlings. CAN50 and UAN50 significantly decreased whole-plant N-use efficiency, and CAN50 decreased whole-plant P-use efficiency of *S. superba* seedlings (Fig. 4, $p < 0.05$). Whole-plant N-use efficiency of *A. quinquegona* seedlings was lower in UAN50 plots than in CT plots (Fig. 4a). Overall, differences in the whole-plant N-use efficiency between the two species were insignificant ($p > 0.05$), but the whole-plant P-use efficiency was much higher for *S. superba* than *A. quinquegona* ($p < 0.05$).

4. Discussion

Previous studies have shown that external N supplies can profoundly affect seedling survival in forests (Catovsky and Bazzaz, 2002; Ceccon et al., 2003; Sefcik et al., 2007; Patterson et al., 2012). In this study, seedling survival of the two target tree species was unaffected by N-addition treatments, which was similar to the results obtained in a *Banksia* woodland (Standish et al., 2012). Nitrogen is required by plants, and plant responses to N deposition have always been related to the environmental context and the quantity of experimental N inputs (Mo et al., 2008; Guo et al., 2010; Sahoo et al., 2021). Overall, simulated N deposition in the current study tended to reduce seedling growth. Understory N addition in particular was detrimental to seedling height, basal diameter growth, and biomass production. More specifically, we found that height, basal diameter, and biomass were greatly reduced for *S. superba* seedlings in the UAN50 plots, and for *A. quinquegona* seedlings in both the UAN50 and UAN25 plots. These results were inconsistent with previous findings obtained in other subtropical forests. Liu et al. (2021), for example, found that N addition increased the height and biomass of tree seedlings in a subtropical forest. Zhang et al. (2019) also demonstrated that an increase in N input generally accelerated the growth of tree seedlings in a subtropical forest, although a very high rate of N addition ($200 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N) reduced the growth of seedling basal diameter. In the forest of the present study, the background atmospheric N deposition rate was high, i.e., approximately $34.1 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N (Zhang et al., 2015). Moreover, the addition of N solution in the plots of the current study was initiated in 2013, 5 years before seedlings were transplanted into the plots. Thus, the availability of soil N at the study site might have been sufficiently high to preclude positive responses to N addition and may have been increased to inhibitory levels in plots subjected to understory N addition.

In addition to being affected by the availability of N, the growth of terrestrial plants is substantially affected by the balance of N and

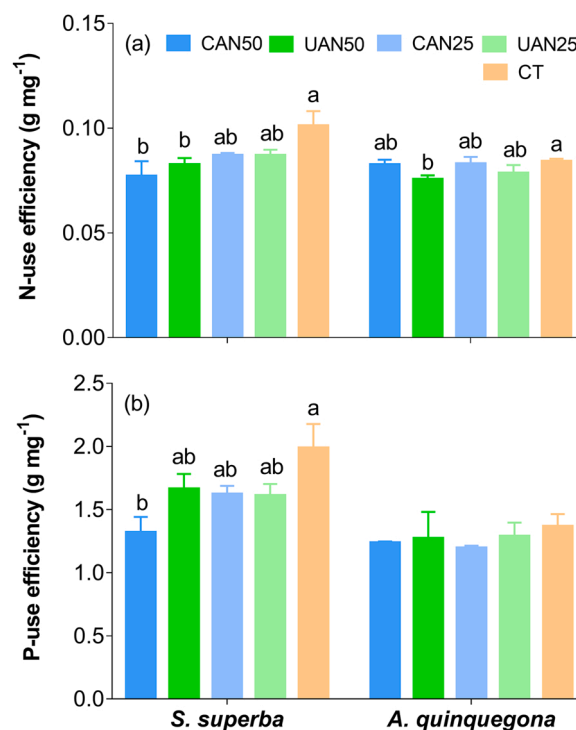


Fig. 4. N- and P-use efficiencies for the whole seedlings of *S. superba* and *A. quinquegona* as affected by nitrogen addition treatments, which are described in Fig. 1 and in the text. Values are means \pm SE. For each species in each panel, means with different letters are significantly different ($p < 0.05$).

P availability (Güsewell, 2004). In our study, the leaf N:P ratio of seedlings was high (ranging from 21.6 to 26.0), and understory addition of N, especially at $50 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N tended to increase leaf N:P ratios (Fig. 3). This nutrient imbalance may have contributed to the suppression of seedling growth (Mo et al., 2008; Santiago et al., 2012). The responses of the two study species to the UAN50 and UAN25 treatments was somewhat different. Both the UAN50 and UAN25 treatments decreased height, basal diameter and biomass of *A. quinquegona* seedlings, while these growth parameters were decreased only by UAN50 treatment for *S. superba* seedlings. This observation could be attributed to the N-requirement feature of species (Nakaji et al., 2001; Mo et al., 2008). Compared with *A. quinquegona* seedlings, *S. superba* had relatively higher N-requirement (Liu et al., 2020b). Additionally, height and biomass of *A. quinquegona* seedlings were much lower than that of *S. superba* seedlings in the control plots, indicating that *S. superba* seedlings were superior in the relative growth rate. Thus, soil N availability in the study site might already meet the N demand of *A. quinquegona* seedlings and their height, basal diameter and biomass growth could be inhibited even at the low rate of understory N addition ($25 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N).

Patterns of plant biomass allocation pattern always change with altered nutrient availability (Santiago et al., 2012; Tripathi and Raghubanshi, 2014; Umaña et al., 2021). There is a widely held view that nutrient enrichment increases the allocation of resources to leaves and favours shoot growth over root growth, and thereby reduces the root to shoot biomass ratio (Poorter et al., 2012; Varma et al., 2018; Sahoo et al., 2021). In the present study, however, N addition overall had only minor effects on seedling biomass partitioning except that CAN50 significantly increased R/S value of *S. superba*. Similar results were reported for deciduous forest hardwood seedlings (Walters and Reich, 1996) and tropical forest tree seedlings (Cárate-Tandalla et al., 2018). Plant water-use efficiency generally increases and photosynthesis decreases as leaf stomata close to reduce water loss (Standish et al., 2012). Several researches have shown that N application can increase the maximum photosynthetic rate, stomatal conductance, and transpiration rate while reducing intrinsic water-use efficiency (Wang and Liu, 2014; Su et al., 2021). In our study, however, N addition generally had no significant effect on A_{sat} , G_s , T_r , or WUE_i of *S. superba* and *A. quinquegona* seedlings, and only the UAN50 treatment significantly decreased A_{sat} of *S. superba* seedlings in the dry season. Such results are partly consistent with a previous report that chronic N addition did not alter maximum photosynthetic capacity of understory plants in a reforested pine forest (Mao et al., 2017). The overall neutral responses of leaf photosynthetic performances to N addition indicated that an excessive supply of N might not be invested in photosynthetic machinery, which was also reported by Hu and Wan (2019).

External N inputs always increase soil N availability, which is beneficial to improves N status of plants (Duan and Chang, 2017; Wright, 2019). Consistent with previous findings that N addition increased plant tissue N and P concentrations (Bethers et al., 2009; Cárate-Tandalla et al., 2018), we found higher concentrations of N and P in the roots and stems of *S. superba* seedlings in CAN50 plots than in control plots, and higher N concentrations in leaves and stems of *A. quinquegona* seedlings in UAN50 and UAN25 plots than in control plots. N and P concentrations in stems and roots seemed to be more sensitive to changes in the external N supply than N and P concentrations in leaves. This indicated that stems and roots of plants may function as nutrient reservoirs (Mo et al., 2015). In the present study, the leaf N:P ratio of seedlings in the control plots were > 16 , indicating that seedling growth might be limited by P as suggested by Güsewell (2004). P-addition experiments are needed to clarify whether plants in the experimental forest are P limited. Increases in the N concentration in leaves generally lead to relatively high leaf photosynthesis ability (Jose et al., 2003; Hu and Wan, 2019). In the present study, however, the maximum photosynthetic rate of *A. quinquegona* seedlings was not increased by UAN25 and UAN50 treatments, which greatly increased leaf N concentrations. In adapting to nutrient-deficient conditions, plants always maintain a high nutrient-use efficiency (Lü et al., 2014; Wu et al., 2020). In the present study, the CAN50 and UAN50 treatments decreased whole-plant N-use efficiency of *S. superba* seedlings, and the UAN50 treatment decreased whole-plant N-use efficiency of *A. quinquegona* seedlings. In addition, the whole-plant P-use efficiency of *S. superba* seedlings was much lower in CAN50 plots than in control plots. In line with previous findings (Puri and Swamy, 2001; Sahoo et al., 2021), these results suggested that N- and P-use efficiencies decrease with an increase in the supply of N.

The forest canopy can influence the effects of atmospheric N deposition on forest ecosystems because the canopy retains a large proportion of the deposited N (Lindberg et al., 1986; Clark et al., 1998; Gaige et al., 2007). In the present study, the growth of *S. superba* and *A. quinquegona* seedlings was not affected by canopy N addition. Similarly, canopy addition of N at a level 50% higher than the natural N deposition level did not significantly affect the growth of *Abies balsamea* and *Picea mariana* seedlings in a boreal forest (Marty et al., 2020). In the current study, *S. superba* seedlings had lower height, basal diameter and biomass in UAN50 plots than in CT plots, and *A. quinquegona* seedlings had lower height, basal diameter and biomass in both UAN25 and UAN50 plots than in CT plots, while these measured parameters of seedlings were similar between CAN50, CAN25 and CT plots, indicating that these seedling growth parameters were more sensitive to understory N addition than to canopy N addition. Our results corroborated previous findings that, when used to simulate atmospheric N deposition, understory N addition tended to overestimate the effects of N addition on understory ecological processes (Zhang et al., 2015; Liu et al., 2020a). It is worth noting that CAN50 instead of understory N addition treatments which increased the R/S, root N and P concentrations of *S. Superba*. Thus, the inference about seedlings are more sensitive to understory N addition should be limited to growth parameters such as height, basal diameter and biomass. Although the concentrations of N and P in *S. superba* seedling roots and stems significantly differed between the CAN50 and UAN50 treatments, leaf chemistry was not influenced by the N addition method. This was partly consistent with previous findings that leaf traits of understory plants are less affected by canopy N addition than understory N addition (Tang et al., 2021).

5. Conclusions

Unlike canopy addition of N, understory addition of N, especially at $50 \text{ kg ha}^{-1} \text{ year}^{-1}$ of N, greatly decreased the height and biomass production of *S. superba* and *A. quinquegona* seedlings. Regardless of N addition method, however, N addition had only minor

effects on seedling survival, biomass allocation, and physiology. The effects of N addition on nutrient concentration in the seedlings depended on the plant tissue and the N-supply method. For *S. superba* seedlings, the CAN50 treatment increased N and P concentrations of in roots and stems, and the UAN50 treatment increased N concentration in stems. For *A. quinquegona* seedlings, the UAN50 and UAN25 treatments generally increased N concentrations in stems and leaves and the N/P ratio in leaves. The UAN50 treatment decreased the whole-plant N-use efficiency of both species, and the CAN50 treatment reduced whole-plant N- and P-use efficiencies of *S. superba* seedlings. Overall, differences in the growth of the species were obvious, with significantly higher height, biomass, A_{sat} , and WUE_i for *S. superba* seedlings than for *A. quinquegona* seedlings. In conclusion, our results indicate that elevated N deposition could be detrimental for the growth of woody species seedlings and that seedling height, basal diameter and biomass were more sensitive to the understory addition of N than canopy addition of N. The findings generated from the present study suggest that woody species recruitment in evergreen broadleaved forests could be greatly influenced by increased N deposition, and the use of understory N addition to simulate atmospheric N deposition could overestimate the effect of N deposition on seedling performance in the understory.

Declaration of Competing Interest

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

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