Community Ecology (2023) 24:333–342
https://doi.org/10.1007/s42974-023-00165-3

ORIGINAL ARTICLE

Inter-specific competition between seeds and seedlings of two confamilial tropical trees

Serajis Salekin[1] · Md. Nazmul Hossain[2,3] · Md Azharul Alam[4] · Sharif Hasan Limon[3] · Md. Saidur Rahman[3]

Received: 23 May 2023 / Accepted: 10 September 2023 / Published online: 3 October 2023

Abstract

Inter-specific competition among species in a mixed species plantation is inevitable, and the degree of competition for available resources determines the success of species co-existence. Different species compete and interact for resources at different physiological and developmental stages. However, most research has investigated inter-specific competition at the mature stage. We examined seed germination and seedling growth of two confamilial species, *Albizia saman* and *Albizia lebbeck,* and explored inter-specific competition at their early life stages, grown in a mixture of different proportions of seeds and seedlings through a series of replacement experiment. The experiment included germination and height growth tests for each species on its own, as well as three mixtures of species with ratios of 25:75, 50:50 and 75:25. We found that the germination speed and percentage, the probability of seedling emergence, and the seedling height were significantly higher in *A. saman* than in *A. lebbeck*. Moreover, in mixtures, we observed that *A. saman* exhibits higher germination speed and percentages compared to *A. lebbeck*. The increase in seedling height did not vary significantly among treatments when the seedlings of the studied species were mixed in different proportions. However, both species showed an apparent benefit when growing together, which was significantly influenced by *A. saman* in terms of inter-specific competition indexes. The knowledge of the early growth performance of these species and their inter-specific competition presented in this study may influence recruitment success and will be useful in understanding the population dynamics in the case of a mixed species plantation. Furthermore, our study suggests that there could be an impact of species mixture on the regeneration or recruitment process, even when the species are confamilial. Therefore, this information could be useful for selecting suitable species mixtures in any afforestation and reforestation activities.

Keywords Inter-specific competition · *Albizia saman* · *Albizia lebbeck* · Seed germination · Replacement series · Mixed-species plantation

Introduction

Globally, planting trees is considered one of the most efficient strategies to combat climate change due to their ability to rapidly capture atmospheric carbon dioxide (CO_2) through both afforestation and reforestation (Bastin et al., 2019; Griscom et al., 2017). Hence, the selection of suitable species is critical in any plantation and the suitability of plantation types such as mono- or mixed-culture for different ecosystems is still under scrutiny (Lewis et al., 2019). While monoculture plantations dominate (Evans, 2009), mixed species plantations are frequently recommended due to their multiple functional benefits compared to timber production from monoculture (Lamb et al., 2005; Li et al., 2022; Paquette & Messier, 2010). In particular, in countries with low per capita land mass and high climate vulnerability, such as Bangladesh, mixed species plantations are encouraged through various forms of plantation activities like social forestry and agroforestry (Iftekhar, 2006).

Despite their multiple benefits, the success of mixed species plantations is challenging because the intra- and

✉ Serajis Salekin
serajis.salekin@scionresearch.com

[1] Scion (New Zealand Forest Research Institute), Rotorua, New Zealand

[2] Bangladesh Forest Department, Agargaon, Dhaka 1207, Bangladesh

[3] Forestry and Wood Technology Discipline, Khulna University, Khulna 9208, Bangladesh

[4] Department of Pest-Management and Conservation, Lincoln University, Lincoln 7647, New Zealand

inter-specific competition among species strongly influences individual fitness and the ways these species co-exist in communities (Antonovics & Levin, 1980). At the very early stage of plant growth, competition outcomes are driven and defined by resource capture and the rapid occupation of available spaces (Aschehoug et al., 2016; Trinder et al., 2013). Broadly, plant competitive ability consists of two components: (i) the ability to suppress a neighbour, known as a competitive effect, and (ii) the ability to tolerate a neighbour's competitive effect, known as a competitive response (Goldberg & Barton, 1992). When two plant species interact, the ability of both competitors to respond determines the competitions outcome, which is usually measured as the overall performance of each individual species (Tilman et al., 2014). So far, studies on plant competition have predominantly focused on either individuals and the direct negative effects of competition, such as community assembly theory (Gotzenberger et al., 2012; Weiher & Keddy, 2001), or on co-occurring plant species, where both species mutually affect each other, influencing the structure, dynamics, and evolution of plant communities (Mathias & Chesson, 2013; Silvertown, 2004; Tilman, 2004). Nevertheless, there is still debate and scope to further address inter-specific competitive phenomena (Connolly et al., 2001; Silvertown, 2004), particularly by focusing on mutualistic interactions of species from the same family or taxa (Jones et al., 2012).

Competition takes place not only within and between species, but also varies across growth stages, especially when plants progress through different life history phases, like seed germination, seedling growth dynamics, or even initial development of root and shoot structures (Bergelson & Perry, 1989; Cameron et al., 2007; Navarro-Cerrillo et al., 2020; Soliveres et al., 2010). Nonetheless, competition between seeds or the continuation of competition from seed to seedling growth stage is rarely studied, as most studies have focused on competition among mature stages (Silvertown, 2004; Trinder et al., 2013). This ongoing debate and the existing knowledge gap emphasize the need for studying species competition at different life history stages to better understand and execute diverse plantation strategies.

Albizia lebbeck (L. Benth.) and *Albizia saman* (Jacq.) Merr. are large deciduous trees, native to tropical America, which have now become widespread throughout humid and subhumid tropics (NRC, 1979). They belong to the Fabaceae family and have multiple uses beyond wood production. They serve as pasture trees, shade trees in agroforestry, and have medicinal applications (Nair et al., 1984). Besides, due to their nitrogen-fixing capabilities, they are often recommended for afforestation and reforestation activities (Durr, 2001; Mishra et al., 2010). They are commonly found in roadsides, agroforestry and social forestry plantations, often in combination with other species, such as *Swietenia macrophylla* in Bangladesh (Azad et al., 2006). *A. saman* has been identified to have an allelopathic effect on other species when grown alongside with them. All plant parts (i.e., seed, stem and leaf) of this species contain and leach considerable amounts of allelochemicals, including tannins, flavonoids, steroids, glycosides and terpenoids (Ghosh et al., 2013; Noor & Khan, 1994). On the other hand, there is limited information on the allelopathic effects of *A. lebbeck*.

A significant amount of research exists on the individual germination and growth of these species using various seed treatment strategies (Khurana & Singh, 2004; Kumar et al., 2018). However, there is a lack of research on their inter-specific interactions, especially from the perspective of community organisation, when they share the same space and time. Understanding the competitive and mutualistic interactions between these two important species at different developmental stages is critical for evaluating their successful natural germination and establishment in any mixed species plantation.

Therefore, we investigated the germination and growth performance of *A. lebbeck* and *A. saman* at seed germination and seedling growth stages, and their inter-specific competition with a replacement series (RS) experiment, in which variable mixtures of these species were grown alongside a monospecific treatment. More specifically, we addressed the following research questions: 1) Do interactions between seeds of the two species influence the probabilities and timing of their emergence? 2) What is the degree of inter-specific competition between these two confamilial species grown in a mixture of variable proportions, and 3) How do the effects of inter-specific competition influence seedling height growth?

Materials and methods

Study location and climate

We conducted this experiment at the forest nursery of Khulna University, Khulna, Bangladesh (22.81°N 89.53°E). The climate of the area is influenced by tropical monsoon and is mostly characterized by hot summers (March–May), monsoonal rainy seasons (June–October) and mild winters (November–February) (Sultana et al., 2021). Based on 55 years of climate data between 1960 and 2015, Khulna has experienced an average annual temperature of 26.4 °C and an average annual rainfall of 1630 mm (Mondal et al., 2017).

Seed tree, seed collection and preparation

Both *A. saman* and *A. lebbeck* are large broadleaf trees belonging to the Fabaceae family. *A. saman* typically reaches a height of 25 m and a diameter of 300 cm, with a wide canopy. The leaves are large, 6–25 mm long and

10–25 mm wide, with unequal leaflets. The trees bear thousands of small flowers with loose umbelliform heads in groups of 2–5 axils. The fruits are broadly linear with compressed pods measuring 10–22 cm long, 1.5–2.2 cm wide and 0.5–1 cm thick. When mature, the pods contain 5–10 seeds, 8–11.5 mm long and 5–7.5 mm wide (Bawa & Buckley, 1989). *A. lebbeck,* on the other hand, grows up to 30 m in height and 100 cm in diameter, with a canopy shape similar to that of *A. saman*. The compound leaves are bipinnate, globous and slightly hairy, ranging from 15 to 65 mm long and 5–35 mm wide, closely stalked in groups. The inflorescence consists of fragrant pedunculate clustered flower heads, measuring 5–7.5 cm wide, on 5–10 mm long stalks. The pods are pale, narrow elliptical, swollen over the seeds, and indehiscent. The seeds are brown, orbicular or elliptical, measuring 7.5–9 mm in length and 5–7 mm in width, transversely placed within each pod (Mariod et al., 2017; Troup & Joshi, 1983). Interestingly, both species contain orthodox seeds and, by comparison, *A. saman* has heavier individual seeds (0.2 g) compared to those of *A. lebbeck* (0.129 g) (Khan et al., 2017). In both species, flowering occurs during the dry-season in their native range, mainly from March to May, and fruits grow to their full size from August to October in South East Asia (Bawa & Buckley, 1989; Lowry et al., 1994). Pods can persist nearly a year after flowering in the mid-dry season (Janzen, 1982).

Both *A. saman* and *A. lebbeck* produce seeds in pods, which mature during the subsequent dry season. In Bangladesh, the dry season generally spans from November to March with temperature ranges from 21 to 36 °C, and average rainfall during this period is about 195 mm/month (Shahid, 2010). The seeds typically have hard impermeable testa. In February 2016, we first handpicked mature seed pods from 10 selected mature and healthy mother trees of each species with straight, well-formed bole, and spreading crowns situated on the Khulna University campus. We then carefully extracted the seeds from the pods, rinsed them under running tap water, dried them, and subsequently stored them at room temperature until sowing.

Nursery bed preparation, seed sowing and the experiment

We prepared a 6 m × 3.7 m nursery bed exposed to full sun throughout day. The bed was divided into three blocks, each of which were later subdivided into five subplots (1.2 m × 0.6 m). These subplots were then randomly allocated to each treatment for seed germination and seedling competition experiments, respectively. The stored seeds were soaked in water for 24 hours before being randomly scattered onto the allocated subplots. We chose this procedure to mimic natural regeneration in any mixed species plantation. Every afternoon, the whole bed was watered by sprinkling to keep it moist.

The experiment was conducted through a randomised complete block design (RCBD) to assess the effect of species mixture on germination and growth of *A. lebbeck* and *A. Saman* at the seedling stage. A total of four treatments were executed, including controls (Table 1). Three replications were applied for each treatment.

Theoretical framework

The replacement series (RS) experiment was first proposed by de Wit (1960) to measure the overlap in the use of resources between competing species. Since its inception, it has been widely used to provide insight into the relative magnitude of the effects of competition between two or more species (Connolly et al., 2001). In the design of an RS experiment, plants of two species are grown together at the same overall density, but in varying proportional mixes. Each species is also grown in pure stands, as, without it, the interpretation of a replacement series experiment can be difficult (Snaydon, 1991). With time, a large number of indices have been developed for the RS experimental method of plant competition studies purporting to measure various facets of species interactions, such as aggressiveness, enhancement, suppression and competitiveness (Bi & Turvey, 1994; Fetene, 2003; Gibson et al., 1999).

In the interpretation of this study's results, two indices were calculated: the relative crowding coefficient (K), and

Table 1 Description of the experimental design

Abbreviation	Treatment	Description
AS100	100% *A. saman*	100 seeds for seed germination and 30 seedlings per block
AL100	100% *A. lebbeck*	100 seeds for seed germination and 30 seedlings per block
AS50:AL50	50% *A. saman* and 50% *A. lebbeck*	50 seeds per species for germination and 15 seedlings per species
AS75:AL25	75% *A. saman* and 25% *A. lebbeck*	75 seeds of *A. saman* and 25 seeds for *A. lebbeck* per block. 22 seedlings for *A. saman* and 8 seedlings for *A. lebbeck* per block
AS25:AL75	25% *A. saman* and 75% *A. lebbeck*	25 seeds of *A. saman* and 75 seeds for *A. lebbeck* per block. 8 seedlings for *A. saman* and 22 seedlings for *A. lebbeck* per block

the relative yield total (RYT), in terms of height yield (Bi & Turvey, 1994; Fetene, 2003; Firbank & Watkinson, 1985). The relative crowding coefficient is a formal measure of the aggressiveness of one species towards another. It can be calculated by Eq. 1.

$$K_{ij} = Y_{ij}F_j/\left(Y_{ii} - Y_{ij}\right)F_i \tag{1}$$

where K_{ij} is the relative crowding coefficient of species i towards species j, Y_{ii} is the yield of species i in its monoculture, and Y_{ij} is the yield of species i in a mixture with species j, the relative frequencies of the species being F_i and F_j. Lower or negative values of K indicates less aggressiveness towards the next species or surrounding, whereas the higher values indicate higher aggressiveness. The relative yield total (RYT) estimates whether the two species are demanding on the same resources, i.e., the degree of overlap in the use of resources (Eq. 2):

$$RYT = \frac{Y_{ij}}{Y_{ii}} + \frac{Y_{ji}}{Y_{jj}} \tag{2}$$

where Y_{ji} is the yield of species J in a mixture with species i, and Y_{jj} is the yield of species j in its monoculture. A value of RYT of 1 implies that the two species are making equal demands on the same limited resources of the environment. Values of RYT > 1 suggest that, although the species may still be competing for the same resources, they also make demands on different resources. Values of RYT < 1 indicate a mutual antagonism.

Besides the above indices, an inter-specific competition index was calculated by following Jolliffe et al. (1984) through Eq. 3.

$$R_{ji} = \left(Y_{ii} - Y_{ij}\right)/Y_{ii} \tag{3}$$

where R_{ji} is the relative effect of inter-specific competition from species J on the yield of species I. Y_{ii} is the ''projected yield'' of species I, which is the expected yield of that species at a given density in the absence of intra- and inter-specific competition. Y_{ij} is calculated as the product of the density of the species and the yield of the species

when grown as single plants. A general increase in R indicates pronounced competition between species, while a decrease resembles the reverse. All the described indices were calculated based on seedling height in this study.

Measurements

We observed and recorded daily seed germination for 45 days. The germination percentage was then calculated from the difference between the number of sprouting seeds and the total number of seeds in each treatment per species (Sultana et al., 2021), and germination speed was calculated by following Eq. 4 (Gairola et al., 2011).

$$\mathrm{Ger}_{\mathrm{speed}} = \frac{n_1}{d_1} + \frac{n_2}{d_2} + \frac{n_3}{d_3} + - - - \tag{4}$$

where $\mathrm{Ger}_{\mathrm{speed}}$ is the germination speed per day, n indicates the number of germinated seeds, and d stands for the number of days.

Besides, soon after seed germination, we measured the height of a subset of individual seedling using a linear scale in centimetres (cm) fortnightly for 90 days (6 periods in total). The height of individual seedlings was used in different competition indices mentioned above.

Statistical analyses

Data normality and homoscedasticity were checked graphically and by using Shapiro–Wilk tests. In case of non-normality, data were appropriately transformed to meet the assumptions of normality and equal variances, and then subsequently back transformed to present graphically.

The cumulative seed germination percentages (%) were compared by a two-way analysis of variance (ANOVA at $P < 0.05$), followed by a Tukey's post-hoc analysis for different species and treatments. The probability of seedling emergence was modelled by fitting and evaluating a logistic regression model. The best model was chosen based on the Akaike information criterion (AIC) (Akaike, 1974): it began with a full model, including all possible explanatory variables, and then was reduced to the simplest model by deleting all non-significant variables and their interactions, which could adequately explain the data.

As the height measurements were collected periodically, a two-way repeated measure ANOVA using Satterthwaite's approximated degrees of freedom (DF) was used to test species and treatment-wise changes in height yield and their height-related competition indices. The final model was constructed by putting an interaction between species and treatment as a fixed term and measurement periods were considered as the random term. Similar to germination percentage, Tukey's post-hoc analysis was applied by following a Kenward-Roger approximation in all statistically significant situations.

All statistical analyses were carried out in R statistical environment (v4.1.3 for Windows) (R core team, 2022) through RStudio as an integrated development environment (IDE) (RStudio team, 2021). "Anova" functions from the "rstatix" package (Kassambra, 2021), "emmeans" function from the "emmeans" package (Lenth, 2021), and "cld" from "multcomp" (Hothorn et al., 2008) were consequently used to do ANOVA and post-hoc analyses. The logistic regression was fitted through a "glm" function from the base package by assuming a binomial distribution with “logit” link. Finally, all models were diagnosed with a “performance” package (Lüdecke et al., 2021), and data organisation and graphical operations were done through “tidyverse” (Wickham et al., 2019).

Results

Germination performance

The cumulative germination percentages were significantly different between the two species ($F_{1,18} = 85.20$, $P < 0.05$), and *A. saman* had a higher seed germination percentage than *A. lebbeck* (Fig. 1). Significant variations were also observed within and between different proportional mixtures for the two species ($F_{4,18} = 4.51$, $P < 0.05$). However, none of the different species mixtures showed significant difference in their post-hoc comparisons when compared to their pure (100% conspecific) treatments. Interestingly, the highest percentages of *A. lebbeck* seed germination occurred when grown in a pure stand, while *A. saman* had the highest germination percentages in moderate to dominant mixtures (AS75 and AS50).

Status of seedling emergence

The seedling emergence analysis showed that all species and treatments significantly differed from each other (Table S1). Both species and treatments exhibited similar timing for initial seedling emergence. However, the treatment with 100% *A. saman* (control) had the highest probability of seedling emergence throughout the experimental period. Pure *A. lebbeck* exhibited the highest seedling emergence among all treatments. Overall *A. saman* demonstrated a higher probability of seedling emergence and faster seedling emergence compared to *A. lebbeck* (Fig. 2, Table 2).

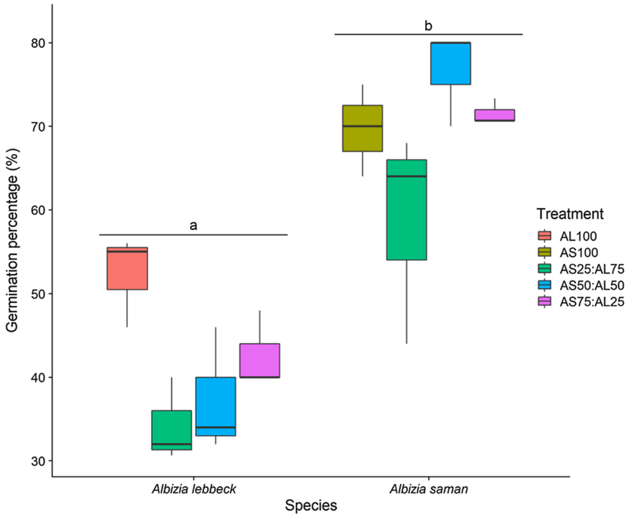

Fig. 1 Cumulative germination percentages (%) of two different species with different treatments. Different letters indicate their significant differences at $P < 0.05$

Height growth

The seedling heights of the two studied species were significantly different from each other, based on the two-way repeated measures ANOVA ($P < 0.05$) followed by Tukey’s post-hoc analysis. Nevertheless, none of the treatments was significantly different for height growth (Fig. 3). All the treatments, for both species, showed more consistent height increment over the experimental period.

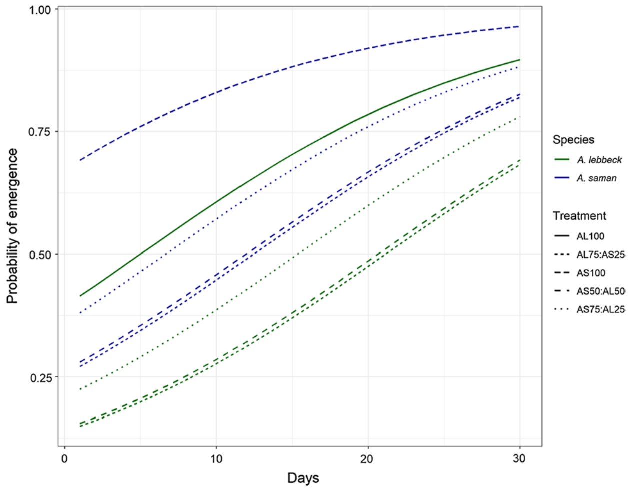

Fig. 2 Probability of emergence by days for two different species at different treatment levels

Table 2 Germination speed of *A. lebbeck* and *A. Saman* at different level of mixtures. $\text{Ger}_{\text{speed}}$ indicates the germination speed of each species for different treatments

Species	Treatment	$\text{Ger}_{\text{speed}}$ (seeds/day)
A. saman	AS100	7.201
	AS75:AL25	5.650
	AS50:AL50	3.095
	AS25:AL75	1.803
A. lebbeck	AL100	3.854
	AS75:AL25	0.974
	AS50:AL50	1.927
	AS25:AL75	1.846

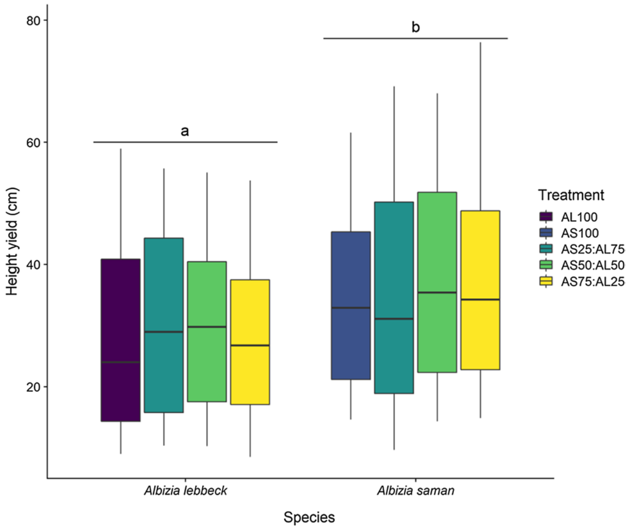

Fig. 3 Height yield (cm) of two different species with different treatments. Different letters indicate significant differences at $P < 0.05$

Inter-specific competition

Among the three different inter-specific competition indices, the crowding coefficient (K) was found to be non-significant between the species and even within treatments. However, the relative yield total (RYT) significantly varied between species and within treatments, particularly the AS50:AL50 treatment, which was statistically different from other treatments (Table 3). The RYT values (RYT > 1) indicated the demand of both species for resources other than competing resources. This was further consolidated from a significant relative inter-specific competition index (R), where *A. lebbeck* showed strong competition and was subsequently surpassed by *A. saman*, particularly when it was the dominant species (AS75) (Table 3 and Fig. 4).

Discussion

This study explored the seed germination and height growth responses of two confamilial species and their inter-specific competition at three different levels of competitive mixtures. The results from the study highlighted that both germination and height growth significantly varied between species. Different species and treatments followed significantly different patterns of emergence, and the magnitude of inter-specific competition varied between the species.

At the germination stage, this study demonstrated that *A. saman* outperformed *A. lebbeck* in terms of cumulative seed germination percentage as well as for seed germination speed, which may be due to the relative abundance of food storage within the seed, triggering the onset of metabolism and completing the seed germination process (Ali & Elozeiri, 2017; Bewley, 2001). *A. saman* has a normal, oval shaped, thick and heavy seed compared to the seed of *A. lebbeck* which is concave in the centre and lighter. This indicates its higher relative food abundance for embryos which may have accelerated its seed germination (Harper et al., 1970; Mariod et al., 2017; NRC, 1979). Moreover, the thickness of the seed coat could influence germination speed, as it is often reported to affect the germination success of different species (Boesewinkel & Bouman, 1995). The thicker seed coat of *A. lebbeck* compared to the seed of *A. saman* was confirmed by the requirements of rigorous pre-sowing treatments to improve the germination success of *A. lebbeck* (Azad et al., 2006; Khurana & Singh, 2004; Missanjo et al., 2013), which may have ultimately resulted in lower germination of this species. However, it is interesting to note that both of the species are confamilial and, having an orthodox type of seed, their seed can be viable for a long period and may germinate over time. Unfortunately, investigating this phenomenon and the condition of ungerminated seeds or the overall germination success was out of the capacity of this experiment (Solberg et al., 2020).

Table 3 Inter-specific competition indices in replacement series for height yield of *A. lebbeck* and *A. saman*

Species	Treatment	K_{NS}			RYT***			R***		
		Mean	SD	Sig	Mean	SD	Sig	Mean	SD	Sig
A. lebbeck	AS25:AL75	− 3.020	1.229	*NS*	2.085	0.042	*a*	0.141	0.028	*a*
	AS50:AL50	− 1.555	6.126	*NS*	2.6078	3.421	*b*	0.144	0.026	*a*
	AS75:AL25	− 23.388	46.152	*NS*	2.144	0.040	*a*	0.204	0.026	*b*
A. saman	AS25:AL75	− 31.517	41.534	*NS*	0.320	1.395	*a*	− 0.203	0.029	*a*
	AS50:AL50	− 30.268	16.652	*NS*	2.250	0.039	*b*	− 0.399	0.044	*a*
	AS75:AL25	3.944	7.307	*NS*	2.554	0.395	*a*	− 0.378	0.056	*b*

AS A. saman, *AL A. lebbeck*, *K* crowding coefficient, *RYT* relative yield total, *R* inter-specific competition index, *SD* standard deviation of values, *Sig.* statistical significance status (Note: "NS" and "***" in heading indicate their species level statistical significance, where NS = no significance, *** = significant at 0.05)

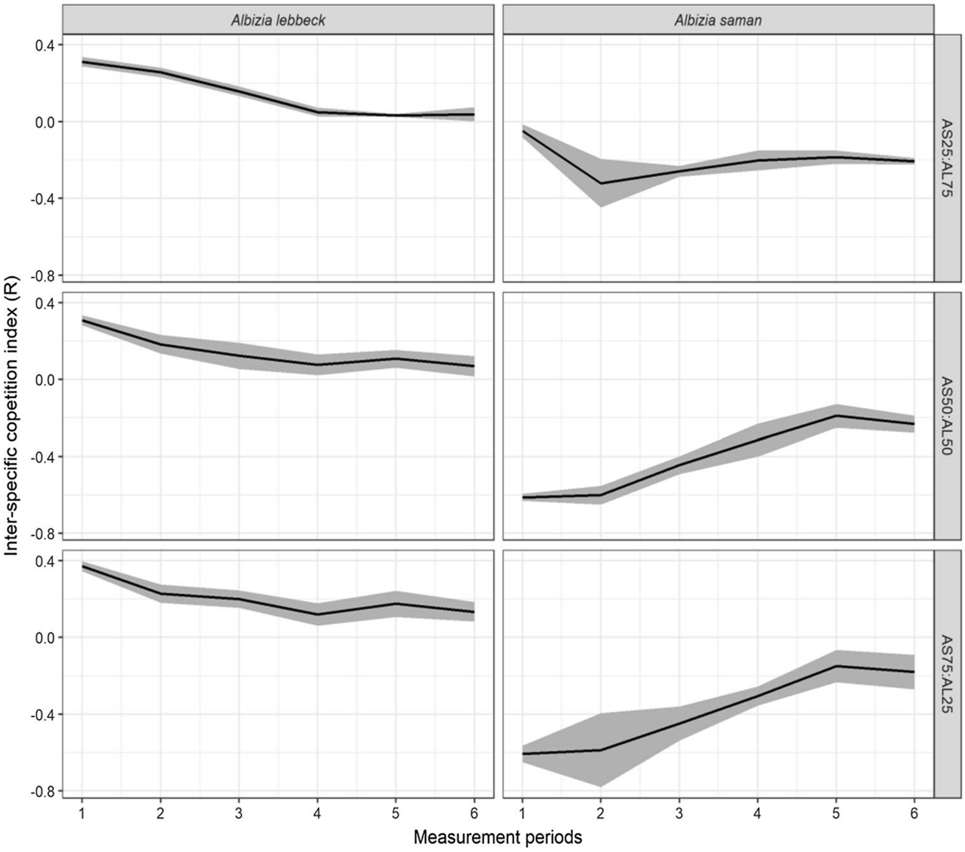

Fig. 4 Relative inter-specific competition index (R) by height for two studied species at different treatments. Grey shaded areas indicate confidence intervals at alpha level of 0.05

The probability of seedling emergence in a competitive environment can be driven by two main mechanisms (Bergelson & Perry, 1989): firstly, by altering the chemical environment of the soil through the passive release of CO_2 and other diffusing chemicals or by diminishing the available pool of nutrients; secondly, by changing the soil physical environment during sprouting. By facilitating these processes, each species can alter the germination microsites, as well as the environmental cues for subsequent germination of other seeds, thus taking advantage of the competitive environment (Towers et al., 2022). Our findings of a higher probability of seedling emergence of *A. saman* than of *A. lebbeck* in the mixture is in line with the mechanisms stated above, where *A. saman* has exploited the surrounding physical and chemical environment and suppressed the seedling emergence of *A. lebbeck*. The inhibitory allelopathic effects of *A. saman* on seed germination and seedling growth of other species are well documented (Ghosh et al., 2013; Noor & Khan, 1994), especially in mixed species plantations. However, the mechanisms of seeds as allelopathic agents for different species are not well studied (Friedman & Waller, 1983). The allelopathic influence of *A. saman* seeds on *A. lebbeck* during germination in the mixture or even associated mechanisms needs further investigation. One possible mechanism is the higher amount of phytochemicals that are found in the seeds of *A. saman,* which may produce a noticeable amount of phytotoxic chemicals such as tannin, phytic acid, and saponin during the decomposition of their seed coat (Mariod et al., 2017; Mishra et al., 2010; NRC, 1979) and prevent seed germination of *A. lebbeck* in mixtures (Lawan et al., 2017). Furthermore, the physical movement of soil caused by each germinating seed may also influence germination of subsequent seeds. Seed mixtures were sown randomly without any prior spatial organisation and the early emergence of *A. saman* seeds may have changed the physical condition of the soil to become more unfavourable for the germination of *A. lebbeck* seeds.

Seedling height growth exhibited a similar trend to seed germination, and *A. saman* grew significantly taller. This may have resulted from earlier germination, as the early bloomer may be better acclimatised and may make the growing conditions less favourable for the later germinating species (Monaghan, 2008). The growth of *A. lebbeck* may also be influenced by slower germination speed.

Among the three different competition indices, the non-significant difference in the crowding coefficient (K) indicates a mutualistic or weak relationship as both species belonging the same family. On the other hand, the significant differences in relative yield total (RYT) and inter-specific competition (R) indicates that the species were actively seeking and consuming resources other than from their local competitive pools, which is common in the mixture of nitrogen-fixing species, as they produce a certain level of complementarity since the competition between studied species was significant (Fetene, 2003). The R-value in our study indicated a weak negative interactive effect over the period of study from *A. saman,* which may have caused its well known allelopathic inhibitory effect (Ghosh et al., 2013; Noor & Khan, 1994) that slowed down the growth of any surrounding tree species. Paine et al. (2008) reported similar weak and complementary interactions among tropical tree species.

Overall, our findings from this study suggest that seed germination and seedling growth of these economically important tree species perform better when grown individually, and mixing them in nursery seedbeds to mimic nature or in a natural environment might negatively influence each other through inter-specific competition, allelopathy or other mechanisms. Trenbath (1976) and Xia et al. (2016) reported similar autotoxicities in mixed broadleaf and conifer plantations through below-ground chemical interactions, although, seedling height growth was not affected by mixing them, which suggests their coexistence at a later growth stage. As N-fixing species, both can be mixed with other species in afforestation or restoration plantation (Mo et al., 2016; Wang et al., 2010). However, further information about their inter-specific competition and coexistence beyond the seedling stage is essential. Furthermore, including more species in such experimentation would enhance their representation of tropical ecosystems. Several questions still remain to be answered, particularly the influence of various edaphic and climatic variables on inter-specific competition, and its impact on other morphological traits related to ontogenetic development, such as biomass partitioning, and leaf area. Moreover, following a more structured seed deployment strategy and extending the study to later stages, e.g., sapling to the competitive life history stages, would increase further understanding of this complex relationship.

Conclusion

We have presented results from two confamilial species, addressing their competition and interactions strategies across two different life stages through a series of replacement experiments. Competitive interaction initiated during the seed germination stage and gradually diminished at the seedling growth stage. Germination patterns were markedly different for two species, despite being confamilial. The results suggested that they followed fundamental competition theories for seed germination and seedling height. In the case of seedling height, the relationship leaned towards competitive irrelevance and promoted a moderate complementary effect, indicating their potential coexistence.

Finally, this study highlights the importance of evaluating the effect of inter-specific competition in a mixed species plantation forest. The selection of species and understanding their underlying competitive interaction is critical for enhancing resilience, sustainability, and management efficiency of such forest plantations. This kind of continuous life stages (seed-seedling continuum) study for multipurpose tree species would enable decision-makers to select suitable species mixtures and implement appropriate management strategies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42974-023-00165-3.

Acknowledgements We thank Forestry and Wood Technology Discipline, Khulna University for granting an experimental space in the nursery and providing all other logistics. We are grateful to Dr Yvette Dickinson and Dr Alan G. Jones for useful discussions and comments during preparation of this manuscript, and Mr Walter Raymond for English language improvement. We are also thankful to the editor and reviewer for their constructive suggestions to improve the manuscript.

Authors contributions S.S., M.N.H., M.S.H.L. and M.S.R. conceptualised and designed this study. M.N.H and M.S.H.L. executed and coordinated the experiment and data collection. S.S. performed the investigation, formal analyses and drafted the manuscript. All authors contributed meaningfully to the final draft and gave final approval for publication.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. This research did not receive any financial support.

Data availability The data used in this study is available through the GitHub repository, https://github.com/serajis/seed-seedling-competition.git.

Declarations

Competing interests Authors declare no competing interests.

References

Akaike, H. (1974). The Akaike information criterion: Background, derivation, properties, application, interpretation, and refinements. *IEEE Transactions on Automatic Control, 19*, 716–723.

Ali, A. S., & Elozeiri, A. A. (2017). Metabolic processes during seed germination. In J. C. Jimenez-Lopez (Ed.), *Advances in seed biology* (pp. 167).

Antonovics, J., & Levin, D. A. (1980). The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics, 11*(1), 411–452. https://doi.org/10.1146/annurev.es.11.110180.002211

Aschehoug, E. T., Brooker, R., Atwater, D. Z., Maron, J. L., & Callaway, R. M. (2016). The mechanisms and consequences of interspecific competition among plants. *Annual Review of Ecology, Evolution, and Systematics, 47*(1), 263–281. https://doi.org/10.1146/annurev-ecolsys-121415-032123

Azad, M. S., Islam, M. W., Matin, M. A., & Bari, M. A. (2006). Effect of pre-sowing treatment on seed germination of *Albizia lebbeck* (L.) Benth. *South Asian Journal of Agriculture, 1*(2), 32–34.

Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C. M., & Crowther, T. W. (2019). The global tree restoration potential. *Science, 365*(6448), 76–79.

Bawa, K. S., & Buckley, D. (Eds.). (1989). Seed/ovule ratios and mating systems in the Leguminosae (Vol. 29). *Monograph in Systematic Botany from the Missouri Botanical Garden*. 29, 243–262.

Bergelson, J., & Perry, R. (1989). Interspecific competition between seeds: Relative planting date and density affect seedling emergence. *Ecology, 70*(6), 1639–1644.

Bewley, J. D. (2001). Seed germination and reserve mobilization. *Encyclopedia of Life Sciences*. https://doi.org/10.1038/npg.els.0002047

Bi, H., & Turvey, N. (1994). Inter-specific competition between seedlings of *Pinus radiata*, *Eucalyptus regnans* and *Acacia melanoxylon*. *Australian Journal of Botany, 42*(1), 61–70.

Boesewinkel, F. D., & Bouman, F. (1995). The seed: Structure and function. In J. Kigel & G. Gad (Eds.), *Seed development and germination* (pp. 872). Routledge.

Cameron, T. C., Wearing, H. J., Rohani, P., & Sait, S. M. (2007). Two-species asymmetric competition: Effects of age structure on intra- and interspecific interactions. *Journal of Animal Ecology, 76*(1), 83–93.

Connolly, J., Wayne, P., & Bazzaz, F. A. (2001). Interspecific competition in plants: How well do current methods answer fundamental questions? *The American Naturalist, 157*(2), 107–125. https://doi.org/10.1086/318631

de Wit, C. T. (1960). *On competition* (Vol. 66). Institute for biological and chemical research on field cropt and herbage.

Durr, P. A. (2001). The biology, ecology and agroforestry potential of the raintree *Samanea saman* (Jacq.) Merr. *Agroforestry Systems, 51*, 223–237. https://doi.org/10.1023/A:1010765022497

Evans, J. (2009). Planted forests: uses, impacts and sustainability. CABI international and FAO, Rome, Italy..

Fetene, M. (2003). Intra- and inter-specific competition between seedlings of *Acacia etbaica* and a perennial grass (*Hyparrenia hirta*). *Journal of Arid Environments, 55*(3), 441–451. https://doi.org/10.1016/s0140-1963(03)00052-1

Firbank, L. G., & Watkinson, A. R. (1985). On the analysis of competition within two-species mixtures of plants. *Journal of Applied Ecology, 22*(2), 503–517. https://doi.org/10.2307/2403181

Friedman, J., & Waller, G. R. (1983). Seeds as allelopathic agents. *Journal of Chemical Ecology, 9*(8), 1107–1117. https://doi.org/10.1007/BF00982215

Gairola, K. C., Nautiyal, A. R., & Dwivedi, A. K. (2011). Effect of temperature and germination media on seed germination of *Jatropha curcas* Linn. *Advances in Bioresearch, 2*(2), 66–71.

Ghosh, S., Molla, K. A., & Ghosh, K. (2013). Allelopathic effect of *Albizia saman* F. Muell on three widely cultivated indian crop species. *IOSR Journal of Agriculture and Veterinary Science, 5*(2), 13–18.

Gibson, D. J., Connolly, J., Hartnett, D. C., & Weidenhamer, J. D. (1999). Designs for greenhouse studies of interactions between plants. *Journal of Ecology, 87*(1), 1–16.

Goldberg, D. E., & Barton, A. M. (1992). Patterns and consequences of interspecific competition in natural communities: A review of field experiments with plants. *The American Naturalist, 139*(4), 771–801.

Gotzenberger, L., de Bello, F., Brathen, K. A., Davison, J., Dubuis, A., Guisan, A., Leps, J., Lindborg, R., Moora, M., Partel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., & Zobel, M. (2012). Ecological assembly rules in plant communities-approaches, patterns and prospects. *Biological Reviews, 87*(1), 111–127. https://doi.org/10.1111/j.1469-185X.2011.00187.x

Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R. T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M. R., … Fargione, J. (2017). Natural climate solutions. *Proceedings of the National Academy of Sciences, 114*(44), 11645–11650.

Harper, J. L., Lovell, P. H., & Moore, K. G. (1970). The shapes and sizes of seeds. *Annual Review of Ecology and Systematics, 1*(1), 327–356. https://doi.org/10.1146/annurev.es.01.110170.001551

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal, 50*(3), 346–363. https://doi.org/10.1002/bimj.200810425

Iftekhar, M. S. (2006). Forestry in Bangladesh: An overview. *Journal of Forestry, 104*(3), 148–153. https://doi.org/10.1093/jof/104.3.148

Janzen, D. H. (1982). Cenízero tree (Leguminosae: *Pithecellobium saman*) delayed fruit development in Costa Rican deciduous forest. *American Journal of Botany, 69*, 1269–1276. https://doi.org/10.1002/j.1537-2197.1982.tb13372.x

Jolliffe, P. A., Minjas, A. N., & Runecles, V. C. (1984). A reinterpretation of yield relationships in replacement series experiments. *Journal of Applied Ecology, 21*(1), 227–243. https://doi.org/10.2307/2403049

Jones, E. I., Bronstein, J. L., & Ferriere, R. (2012). The fundamental role of competition in the ecology and evolution of mutualisms. *Annals of the New York Academy of Sciences, 1256*, 66–88. https://doi.org/10.1111/j.1749-6632.2012.06552.x

Kassambra, A. (2021). rstatix: Pipe-friendly framework for basic statistical tests. In (Version R package version 0.7.0.)

Khan, D., Uddin, A., & Zaki, M. J. (2017). Seed-size distribution pattern within pods of *Albizia lebbeck* (L.) Benth.-positional effect. *International Journal of Biology and Biotechnology, 14*(2), 293–301.

Khurana, E., & Singh, J. S. (2004). Germination and seedling growth of five tree species from tropical dry forest in relation to water stress: Impact of seed size. *Journal of Tropical Ecology, 20*(4), 385–396. https://doi.org/10.1017/S026646740400135X

Kumar, N., Handa, A. K., Dev, I., Ram, A., Uthappa, A. R., Shukla, A., & Chand, L. (2018). Effect of pre-sowing treatments and growing media on seed germination and seedling growth of *Albizia lebbeck* (L.) Benth. *Journal of Applied and Natural Science, 10*(3), 860–863.

Lamb, D., Erskine, P. D., & Parrotta, J. A. (2005). Restoration of degraded tropical forest landscapes. *Science, 310*(5754), 1628–1632.

Lawan, S. A., Saleh, A., Sani, B. G., & Fa'iza, A. M., & Sadiay, A. Z. (2017). Preliminary phytochemical constituents and phytotoxic effect of *Albizia lebbeck* (L.) benth on Sorghum bicolor. *Bayero Journal of Pure and Applied Sciences, 10*(1), 405–408. https://doi.org/10.4314/bajopas.v10i1.79S

Lenth, R. V. (2021). emmeans: Estimated marginal means, aka least-square means. In (Version R package version 1.6.2–1.) https://CRAN.R-project.org/package=emmeans

Lewis, S. L., Wheeler, C. E., Mitchard, E. T. A., & Koch, A. (2019). Restoring natural forests is the best way to remove atmosheric carbon. *Nature, 568*, 25–28. https://doi.org/10.1038/d41586-019-01026-8

Li, Y., Wang, J., Shen, C., Wang, J., Singh, Brajesh K., & Ge, Y. (2022). Plant diversity improves resistance of plant biomass and soil microbial communities to drought. *Journal of Ecology*, *n/a*(n/a). https://doi.org/10.1111/1365-2745.13900

Lowry, J. B., Prinsen, J. H., & Burrows, D. M. (1994). Albizia lebbeck-a promising forage tree for semiarid regions. *Forage Tree Legumes in Tropical Agriculture, 6*, 75–83.

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software, 6*(60), 3139.

Mariod, A. A., Saeed Mirghani, M. E., & Hussein, I. (2017). *Albizia lebbeck* (L. Benth.) Lebbeck tree seed. In A. A. Mariod, M. E. Saeed Mirghani, & I. Hussein (Eds.), *Unconventional Oilseeds and Oil Sources* (pp. 277–281). Academic Press. https://doi.org/10.1016/B978-0-12-809435-8.00041-X

Mathias, A., & Chesson, P. (2013). Coexistence and evolutionary dynamics mediated by seasonal environmental variation in annual plant communities. *Theoretical Population Biology, 84*, 56–71. https://doi.org/10.1016/j.tpb.2012.11.009

Mishra, S. S., Gothecha, V. K., & Sharma, A. (2010). *Albizia lebbeck*: A short review. *Journal of Herbal Medicine and Toxicology, 4*(2), 9–15.

Missanjo, E., Maya, C., Kapira, D., Banda, H., & Kamanga-Thole, G. (2013). Effect of seed size and pretreatment methods on germination of *Albizia lebbeck*. *ISRN Botany, 5*, 1–4. https://doi.org/10.1155/2013/969026

Mo, Q., Li, Z. A., Zhu, W., Zou, B., Li, Y., Yu, S., Ding, Y., Chen, Y., Li, X., & Wang, F. (2016). Reforestation in southern China: revisiting soil N mineralization and nitrification after 8 years restoration. *Scientific Reports, 6*(1), 19770. https://doi.org/10.1038/srep19770

Monaghan, P. (2008). Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B Biological Sciences, 363*(1497), 1635–1645. https://doi.org/10.1098/rstb.2007.0011

Mondal, K. K., Akhter, M. A., Mallik, M., & Hassan, S. Q. (2017). Study on rainfall and temperature trend of khulna division in Bangladesh. *Dew-Drop, 4*, 77–83.

Nair, P. K. R., Fernandes, E. C. M., & Wambugu, P. N. (1984). Multipurpose leguminous trees and shrubs for agroforestry. *Agroforestry Systems, 2*(3), 145–163. https://doi.org/10.1007/BF00147030

NRC. (1979). *Tropical legumes, resources for the future*. Books for business.

Navarro-Cerrillo, R. M., Manzanedo, R. D., Rodriguez-Vallejo, C., Gazol, A., Palacios-Rodríguez, G., & Camarero, J. J. (2020). Competition modulates the response of growth to climate in pure and mixed *Abies pinsapo* subsp. Maroccana forests in northern Morocco. *Forest Ecology and Management, 459*, 117847. https://doi.org/10.1016/j.foreco.2019.117847

Noor, M., & Khan, M. A. (1994). Alleopathic potential of *Albizia samans* MERR. *Pakistan Journal of Botany, 26*(1), 139–147.

Paine, T. C. E., Harms, K. E., Schnitzer, S. A., & Carson, W. P. (2008). Weak competition among tropical tree seedlings: Implications for species coexistence. *Biotropica, 40*(4), 432–440.

Paquette, A., & Messier, C. (2010). The role of plantations in managing the world's forests in the Anthropocene. *Frontiers in Ecology and the Environment, 8*(1), 27–34.

R core team. (2022). R: A language and environment for statistical computing. In R Foundation for Statistical Computing. https://www.R-project.org/

RStudio team. (2021). RStudio: Integrated Development Environment for R. In RStudio, PBC. http://www.rstudio.com/

Shahid, S. (2010). Recent trends in the climate of Bangladesh. *Climate Research, 42*(3), 185–193.

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology & Evolution, 19*(11), 605–611. https://doi.org/10.1016/j.tree.2004.09.003

Snaydon, R. W. (1991). Replacement or additive designs for competition studies? *Journal of Applied Ecology, 28*(3), 930–946. https://doi.org/10.2307/2404218

Solberg, S. Ø., Yndgaard, F., Andreasen, C., von Bothmer, R., Loskutov, I. G., & Asdal, Å. (2020). Long-term storage and longevity of orthodox seeds: A systematic review. *Frontiers in Plant Science*. https://doi.org/10.3389/fpls.2020.01007

Soliveres, S., DeSoto, L., Maestre, F. T., & Olano, J. M. (2010). Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. *Perspectives in Plant Ecology, Evolution and Systematics, 12*(3), 227–234. https://doi.org/10.1016/j.ppees.2010.02.003

Sultana, N., Limon, S. H., Rahman, M. S., Akther, A., Salekin, S., Meason, D. F., & Bloomberg, M. (2021). Germination and growth responses to water stress of three agroforestry tree species from Bangladesh. *Environmental Challenges*. https://doi.org/10.1016/j.envc.2021.100256

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competiion, invasion, and community assembly. *Proceedings of the National Academy of Sciences, 101*(30), 10854–10861.

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics, 45*(1), 471–493.

Towers, I. R., Merritt, D. J., Erickson, T. E., Mayfield, M. M., & Dwyer, J. M. (2022). Variable seed bed microsite conditions and light influence germination in Australian winter annuals. *Oecologia*. https://doi.org/10.1007/s00442-021-05091-7

Trenbath, B. R. (1976). Plant interactions in mixed crop communities. In *Multiple Cropping* (pp. 129–169). https://doi.org/10.2134/asaspecpub27.c8

Trinder, C. J., Brooker, R. W., Robinson, D., & Thompson, K. (2013). Plant ecology's guilty little secret: Understanding the dynamics of plant competition. *Functional Ecology, 27*(4), 918–929. https://doi.org/10.1111/1365-2435.12078

Troup, R. S., & Joshi, H. B. (1983). *Forage tree legumes in tropical agriculture*. CAB International.

Wang, F., Li, Z., Xia, H., Zou, B., Li, N., Liu, J., & Zhu, W. (2010). Effects of nitrogen-fixing and non-nitrogen-fixing tree species on soil properties and nitrogen transformation during forest restoration in southern China. *Soil Science and Plant Nutrition, 56*(2), 297–306. https://doi.org/10.1111/j.1747-0765.2010.00454.x

Weiher, E., & Keddy, P. (2001). *Ecological assembly rules: Perspectives, advances, retereats*. Cambridge University Press.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pederse, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P. S. V., Takahashi, K., … Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software, 4*(43), 1686.

Xia, Z.-C., Kong, C.-H., Chen, L.-C., Wang, P., & Wang, S.-L. (2016). A broadleaf species enhances an autotoxic conifers growth through belowground chemical interactions. *Ecology, 97*(9), 2283–2292.