

Performance of seed-seedling continuum of two agroforestry tree species under inter-specific competition

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Abstract

The 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 altered physiological and developmental stages. However, most research investigated inter-specific competition at the mature stage. We examined seed germination and seedling growth of two con-familial species, i.e., *Albizia saman* and *Albizia lebbeck* and explored inter-specific competition at their early life stages grown in a different proportional mixture through a replacement series experiment. We found that the germination speed and percentage, the probability of seedling emergence and seedling height were significantly higher in *A. saman* than in *A. lebbeck*. Moreover, we observed that *A. saman* showed higher germination performance in mixtures compared to *A. lebbeck*, although the germination properties of the species did not significantly vary among treatments. Similarly, the seedling height growth did not vary significantly among treatments, when the seedlings of the studied species were mixed in different proportions. However, both species showed mutualistic relationships, which was significantly modulated by *A. saman*. Our study suggests that the knowledge of variation in early growth performance of these species and their inter-specific competition influence the recruitment success and will determine the population dynamics of a mixed-species plantation. Furthermore, studies examining the competitive relationship between different species would be invaluable for choosing suitable species and applying proper management approaches for the success of any mixed-species plantation at any afforestation and reforestation activities.

Introduction

Globally, planting trees is considered one of the most efficient strategies to combat climate change due to its ability to rapidly capture atmospheric carbon dioxide (CO₂) and for restoration potential in any degraded areas (Bastin et al., 2019; Griscom et al., 2017). However, the selection of suitable species is critical in any plantation and the suitability of plantation type 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 being recommended due to their multiple functional benefits compared to timber production from monoculture (Lamb et al., 2005; Li et al., 2022; Paquette & Messier, 2010). Especially, in a country with low per capita land mass and high climate vulnerability, like Bangladesh, mixed species plantations are encouraged through various form of plantations activities such as social forestry and agroforestry (Iftekhar, 2006).

Despite multiple benefits, the success of mixed-species plantations is challenging as the intra- and inter-specific competition among species has a strong influence on individual fitness and the ways these species co-exist into communities (Antonovics & Levin, 1980). At the very early stage of plant growth, the outcomes of competition are driven and defined by resource capturing and dominating available spaces quickly (Aschehoug et al., 2016; Trinder et al., 2013). Broadly, plant competitive ability has two components: i) the ability to suppress a neighbour, or competitive effect, and ii) the ability to tolerate a neighbour's competitive effect or competitive response (Goldberg & Barton, 1992). Trinder et al. (2013) stated resource competition as *sensu stricto* and considered competition for both direct and indirect resources including, light, water,

soil moisture and nutrients. When two plant species interact, the ability to response of both competitors determine the outcome of the competition, which is usually measured as the overall performance of each species (Tilman et al., 2014). Though, plant competition studies predominantly focus on individual and direct negative effects of competition [e.g., community assembly theory (Gotzenberger et al., 2012; Weiher & Keddy, 2001)], or co-occurring plant species where both affect and response to one another and these interactions influence structure, dynamics and evolution within plant communities (Mathias & Chesson, 2013; Silvertown, 2004; Tilman, 2004). Despite its importance, there is still debate and scope to address further inter-specific competitive phenomena (Connolly et al., 2001; Silvertown, 2004). More specifically, by focusing on mutualistic interactions of species from the same family or taxa (Jones et al., 2012).

Competition not only takes place within and between species, but also varies by growth stage; especially when plants go through different demographic phases such as seed germination, seedling growth dynamics, and even initial development of root-shoot (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 of the studies focused on the mature stages gain or dominance (Silvertown, 2004; Trinder et al., 2013). These posit to study covering such continuum is necessary to understand and execute different plantation strategies, especially under current global climate change scenarios.

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 (NAS, 1979). They are from Fabaceae family and have multiple potentials other than producing wood; namely, pasture trees, shade trees in agroforestry and medicinal uses (Nair et al., 1984). Besides, due to their nitrogen fixing capabilities they often are recommended for afforestation and reforestation activities (Durr, 2001; Mishra et al., 2010). They are commonly found in roadside, agroforestry and social forestry plantations with different admixture with other species in Bangladesh (Azad et al., 2006). *A. saman* has been identified with an allelopathic effect on other species when it appeared in combination with other species, as all plant parts (i.e., seed, stem and leaf) contain and leach considerable amount of allelochemicals, including tannins, flavonoids, steroids, glycosides and terpenoids (Ghosh et al., 2013; Noor & Khan, 1994).

There is a myriad amount of research on individual germination and growth with different seed treatment strategies for these species (Khurana & Singh, 2004; Kumar et al., 2018), answering how higher germination success can be achieved? Nevertheless, there is no research on their inter-specific interaction, especially from the community organisational perspective when they shared a same space and time. Understanding the competitive and mutualistic interactions between these two important species at different developmental stages will be critical for evaluating their seed germination capacity and seedling production. Such knowledge will ultimately ensure their success in production forestry as well as their establishment in restoration program.

Therefore, we investigated the germination and growth performance of *A. lebbeck* and *A. saman* at seed germination and seedling growth stage and their inter-specific competition with a replacement series (RS) experiment whereby variable mixtures of these species were grown alongside monospecific treatment.

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 two congeneric species grown in a mixture of variable proportions and 3) how to 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 characterised by hot summers (March–May), monsoonal rainy seasons (June–October) and mild winters (November–February) (Sultana et al., 2021). The 55 years of climate data between 1960 to 2015 had an average annual temperature in Khulna of 26.4°C and an average total annual rainfall of 1630mm (Mondal et al., 2017).

Seed collection and preparation

Both *A. saman* and *A. lebbeck* produce seeds in pods, which are matured in the subsequent dry season. The seed has typical hard impermeable testa. We first handpicked mature seed pods in February 2016 from mature and healthy mother trees with straight, well-formed bole, and spreading crowns situated in Khulna University campus. We carefully then extracted the seeds from the pods, rinsed them with flowing water, dried and subsequently stored them at room temperature until sowing.

Nursery bed preparation and seed sowing

We prepared 6m × 3.7m nursery bed and divided it into three blocks, which were later subdivided into five (1.2m × 0.6m) subplots and randomly allocated to each treatment for seed germination and seedling competition experiments, respectively. Stored seeds were soaked into water for 24 hours prior and randomly sowed in different frequencies to the allocated subplots. The whole bed was watered every afternoon by sprinkling to keep moist.

Theoretical framework and the experiment

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 magnitudes 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 mixtures. 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 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.

$$K_{ij} = Y_{1j}F_j / (Y_{ii} - Y_{ij})F_i$$

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 mixture with species J, the relative frequencies of the species being F_i and F_j . 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):

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

2

where Y_{ji} is the yield of species J in 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 demands on the same limiting 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.

$$R_{ji} = (Y_{ii} - Y_{ij}) / Y_{ii}$$

3

where R_{ji} is the relative effect of inter-specific competition from species J on the yield of species I. All the described indices were calculated based on seedling height in this study.

The experiment was conducted through a randomised complete block design (RCBD) **to measure the species mixture effect 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 used for each treatment.**

Table 1
Experimental description.

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

Measurements

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

$$Ger_{speed} = \frac{n_1}{d_1} + \frac{n_2}{d_2} + \frac{n_3}{d_3} + \dots$$

4

Where, Ger_{speed} is the germination speed per day, n indicates the number of germinated seeds, and d stands for the number of days.

Besides, seed germination, we measured an individual seedling's height with 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 subsequently back transformed to present graphically.

The cumulative seed germination percentage (%) was 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 Akaike information criterion (AIC) (Akaike, 1974); it began with a full model including

all possible explanatory variables and then 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 with 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 situation.

All statistical analyses were realised 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" function from "rstatix" package (Kassambra, 2021), "emmeans" function of "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 "glm" function from the base package by assuming a binomial distribution with "logit" link. Finally, all models were diagnosed by "performance" package (Lüdecke et al., 2021), and data wrangling and graphical operations were done through "tidyverse" (Wickham et al., 2019).

Results

Germination performance

The cumulative germination percentages were significantly varied between species ($F_{1,18} = 85.20$, $p < 0.05$), and *A. saman* had a higher seed germination percentage than *A. lebbeck* (Fig. 1). Significant variation was also found within and between different proportional mixtures for two different species ($F_{4,18} = 4.51$, $p < 0.05$). However, none of the different species' mixtures were significantly different in their post-hoc comparison to their pure (100% conspecific) treatment. Interestingly, the highest percentages of *A. lebbeck* seed germination occurred when shown in a pure stand, while *A. saman* had the highest germination percentages in moderate to dominant mixtures (i.e., AS75 and AS50).

Status of seed emergence

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

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

Species	Treatment	Ger_{speed}
<i>A. saman</i>	AS100	7.201
	AS75:AL25	5.650
	AS50:AL50	3.095
	AS25:AL75	1.803
<i>A. lebbeck</i>	AL100	3.854
	AS75:AL25	0.974
	AS50:AL50	1.927
	AS25:AL75	1.846

Height growth

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

Inter-specific competition

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

Table 3

Inter-specific competition indices in replacement series for height yield of *A. lebbeck* and *A. saman*. AS = *A. saman*; AL = *A. lebbeck*; K = crowding coefficient; RYT = relative yield total; R = inter-specific competition index and 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).

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	26.078	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

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. 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 amongst the species.

At the germination state, this study demonstrated that *A. saman* outperformed *A. lebbeck* for 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 to initiate the onset of metabolism and complete the seed germination (Ali & Elozeiri, 2017; Bewley, 2001). *A. saman* has a normal oval shaped thick seed compared to the concave centred seed of *A. lebbeck* indicating its higher relative food abundance for embryos which may have accelerated its seed germination (Harper et al., 1970; Mariod et al., 2017; NAS, 1979). Moreover, the thickness of the seed coat may have an influence on the 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 *A. saman*'s seed was confirmed by the requirements of harsh 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 emerge with time. Unfortunately, investigating this phenomenon was out of the capacity of this experiment to investigate the condition of ungerminated seeds or the overall germination success (Solberg et al., 2020).

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 soil through the passive release of CO₂ 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, and take advantages of the competitive environment (Towers et al., 2022). Our findings of a higher probability of seedling emergence of *A. saman* than *A. lebbbeck* 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. lebbbeck*. The inhibitory allelopathic impacts of *A. saman* on the associated species are well documented (Ghosh et al., 2013; Noor & Khan, 1994). However, the mechanisms of seeds as an allelopathic agent for different species are not well studied (Friedman & Waller, 1983). The allelopathic influence of *A. saman* seeds on *A. lebbbeck* 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; NAS, 1979) and prohibit seed germination of *A. lebbbeck* in mixtures (Lawan et al., 2017). Furthermore, the physical movement of soil caused by each germinant 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 soil physical condition to become more unfavourable for the germination of *A. lebbbeck* seeds.

Seedling height growth followed a similar trend as seed germination and *A. saman* was 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. lebbbeck* may also be influenced by slower germination speed.

Among three different competition indices, the non-significant difference of crowding coefficient (K) indicates a mutualistic or weak relationship as both species were from the same family, though a negative influence was observed in the seed germination stage. On the other hand, the significant difference in relative yield total (RYT) and inter-specific competition (R) indicates that the species were actively seeking and consuming resources other than their local competitive pools which is common in the mixture of nitrogen-fixing species, as they produce a certain level of complementarity as the competition between studied species were significant (Fetene, 2003). The R-value in our study indicated a weak negative interactive effect from *A. saman* which may have driven *A. saman*'s 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 plant tree species.

Overall, our findings from this study suggest that seed germination and seedling growth of these economically important agroforestry species perform better when they are grown individually, and mixing them in nursery seedbed or in the field might negatively influence each other through inter-specific competition, allelopathy or other mechanisms. 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 agroforestry or restoration plantation. However, further information about their inter-specific competition and coexistence after the seedling stage is needed. Furthermore, including more species in such experimentation would be valuable and more representative 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, e.g., biomass partitioning, leaf area. Moreover, following a more structured seed deployment strategy and adding of later stage, e.g., sapling to this competition continuum would shade further understanding of this complex relationship.

Conclusion

We have presented results from two confamilial species addressing the seed-seedling continuum's competition/interactions strategy through replacement series experiments. Competitive interaction started from the seed germination stage, and diminished at the seedling growth stage. Germination patterns were markedly different for the two species, despite being confamilial. Initially, they followed basic competition theories; firstly, capturing base resources and then, altering microhabitats for seed germination. In later growth phase in terms of seedling height, the relationship turned into competitive irrelevance and promoted a moderate complementary effect, which indicates their possible coexistence.

Finally, this study highlights the necessity 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 making such forest plantations more resilient, sustainable, and increasing management efficiency. Such seed-seedling continuum study for multipurpose tree species would enable decision makers to choose proper species mixture and apply appropriate management scenarios.

Declarations

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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 investigation, formal analyses and

drafted the manuscript. All authors contributed meaningfully to the final draft and gave final approval for publication.

Competing interests

Authors declare no competing interests.

Data availability statement

The full data will be made available through an open public repository following acceptance of the manuscript.

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Figures

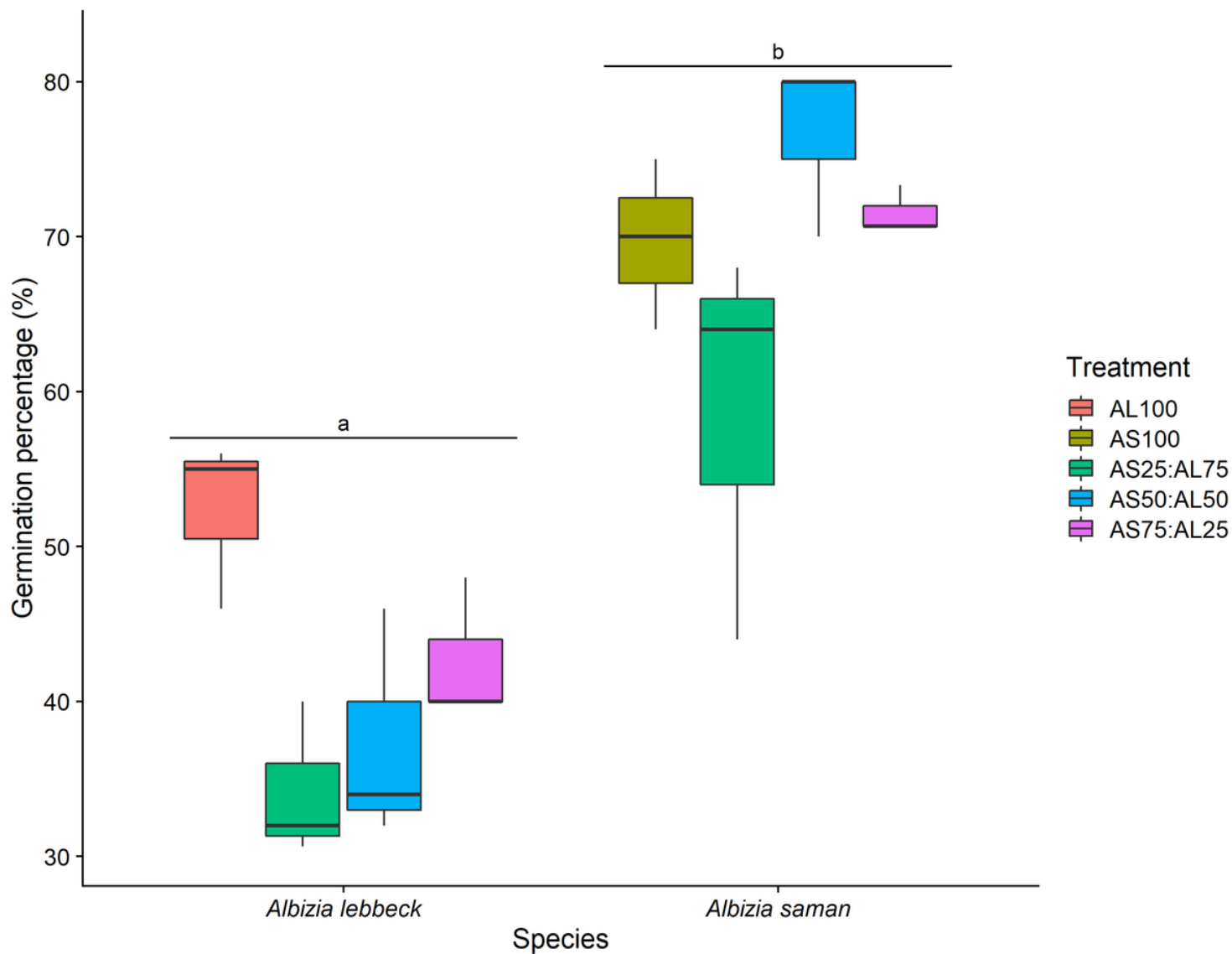


Figure 1

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

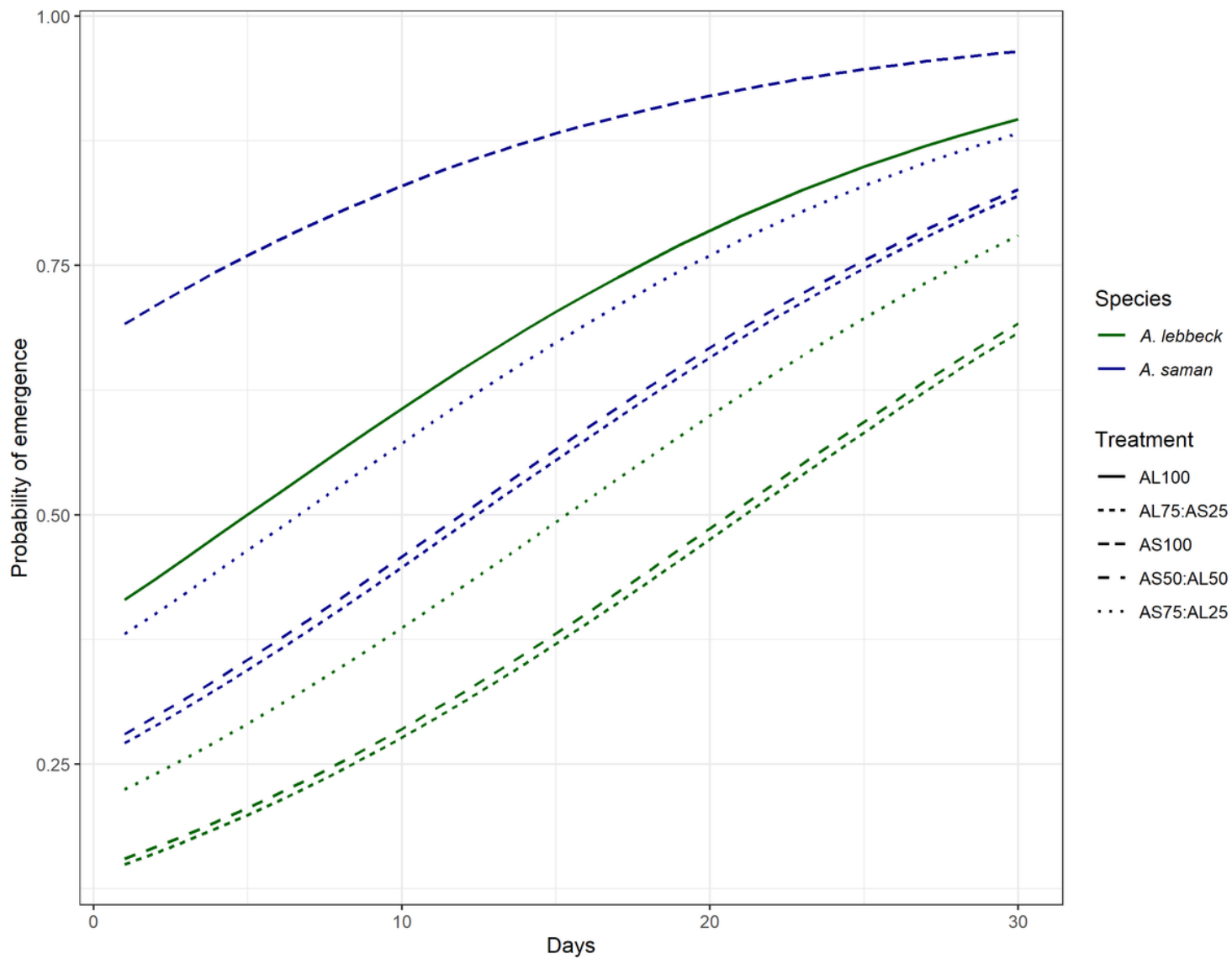


Figure 2

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

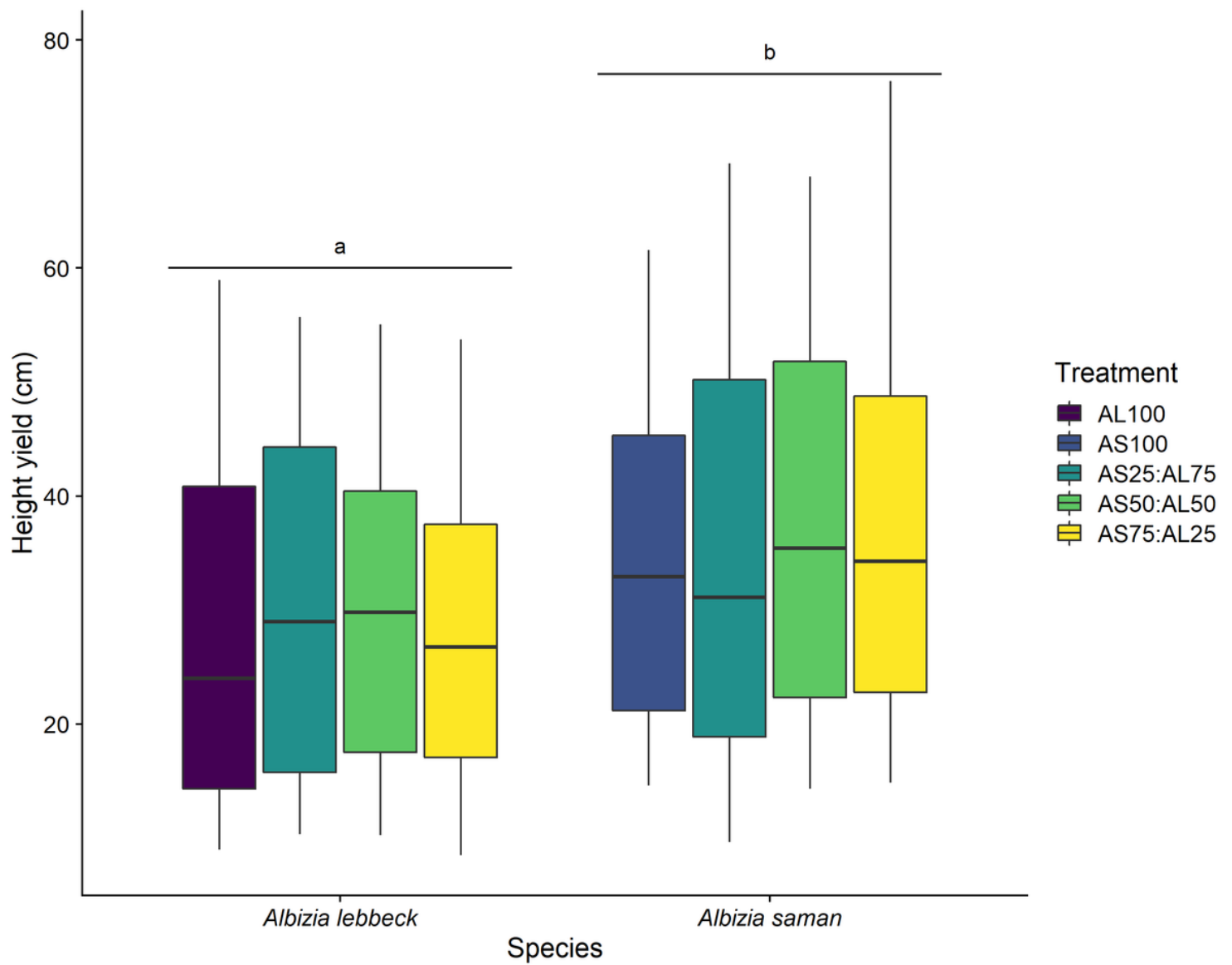


Figure 3

Height yield (cm) of two different species with different treatment. Different letter indicates significant differences at $p < 0.05$.

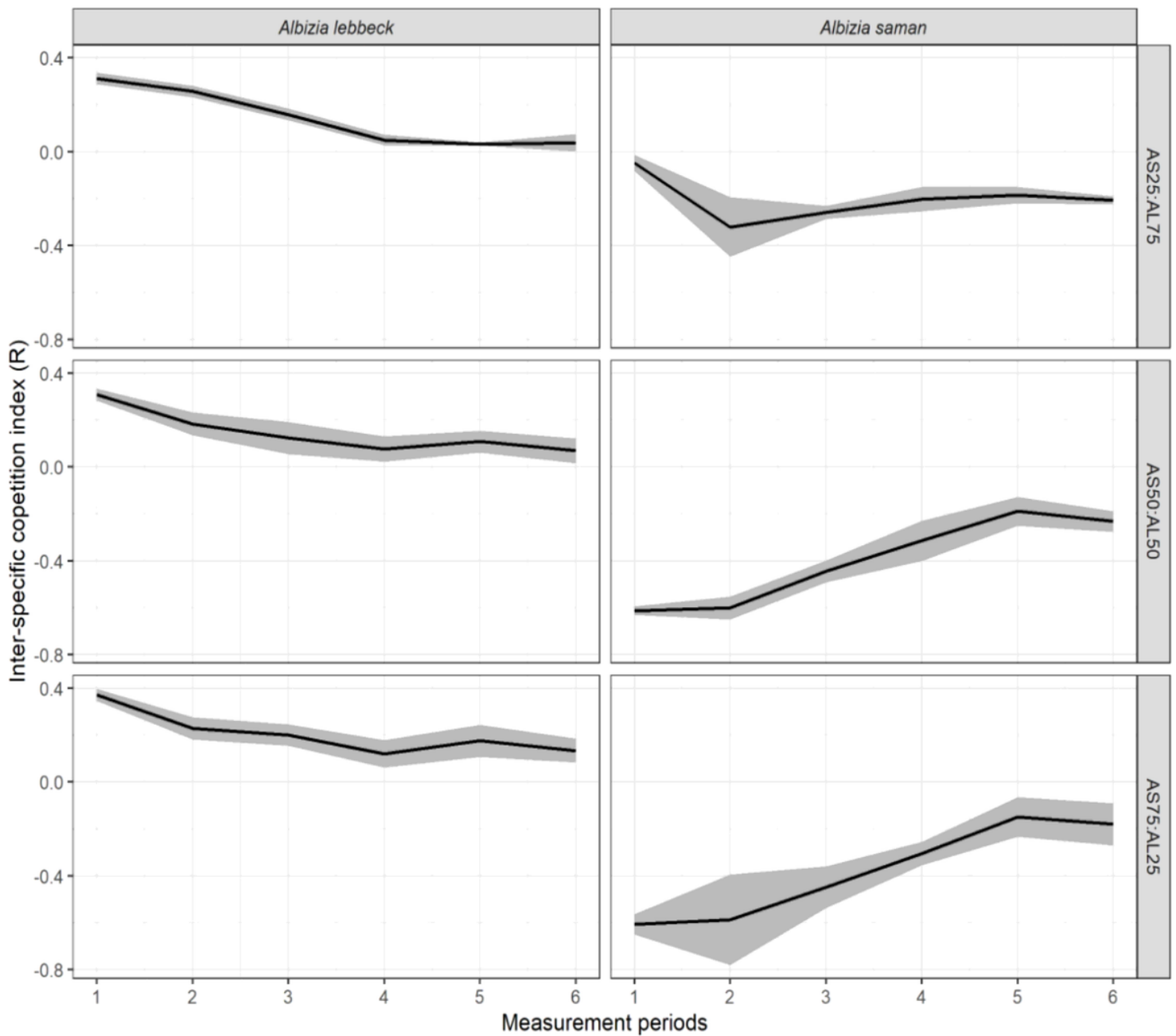


Figure 4

Relative inter-specific competition by height for two experimental special at different treatments level. Grey shaded area indicated confidence intervals at alpha level of 0.05.

Supplementary Files

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