



# Effects of light transmittance on growth and biomass of understory seedlings in mixed pine-beech forests

Ferhat Kara<sup>1</sup>

Received: 6 April 2022 / Revised: 11 July 2022 / Accepted: 27 September 2022 / Published online: 12 October 2022  
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## Abstract

Seedling growth as well as aboveground and belowground biomass allocation is mostly influenced by Light Transmittance (LT) (%) through the canopy. The knowledge of how understory light conditions affect seedling growth and biomass of different species in mixed forests is not well documented. Thus, it is essential to quantify the effects of light on the growth and biomass of understory seedlings. Given their advantages over pure forests, these quantitative understandings are especially crucial in mixed forests with species whose light demand and shade tolerance vary. This research examined the growth responses of natural-origin Scots pine (*Pinus sylvestris* L.), black pine (*Pinus nigra* Arnold.) and Oriental beech (*Fagus orientalis* L.) seedlings to LT (%) through the canopy in their mixed stands. Linear mixed-effect models were utilized to examine the influence of LT (%) on the seedlings. Moreover, allometric equations for estimating the aboveground biomass and belowground biomass of seedlings were developed for each species. Seedling height, and aboveground and belowground biomass after five years of germination were most significantly affected by LT (%) and tree species in the mixed pine-beech stand ( $p < 0.001$ ). Biomass models for each species included different variable combinations of seedling height, root-collar diameter, LT (%), and their interactions. This study demonstrates the importance of canopy structure and overstory disturbances for the maintenance of mixed pine-beech forests since canopy structure significantly contributes to the understory light environment.

**Keywords** Aboveground · Belowground · Canopy · *Fagus* · Pine

## Introduction

Forest managers are mostly interested in ensuring the successful growth and development of seedlings during stand establishment. Seedling growth and establishment are highly related to a complex interaction among environmental variables (Mason et al. 2004; Lhotka and Loewenstein 2008). Relationships among growth, biomass and environmental conditions such as the understory light regime are usually species-specific (Mediavilla and Escudero 2010). Therefore, species' shade tolerance as well as their response to light conditions should be well understood in all stages of their development. This is particularly essential when the

natural regeneration of mixed species forests through silvicultural practices is aimed. The environmental adaptability of species is related to their growth rate as well as above and belowground biomass allocation (Bonser and Aarsen 1994; Bachofen et al. 2019). Moreover, tolerance of seedlings to shade is also associated with their ability to adapt to varying environmental conditions (Humbert et al. 2007).

Light transmittance through the canopy can hinder or promote growth and biomass allocation of understory seedlings depending on their shade tolerance and light requirements (Petritan et al. 2009; Kara and Topaçoğlu 2018a). Quantitative approaches that relate understory light conditions to the growth of understory seedlings are of great importance, particularly in mixed-species forests. Quantifying the biomass of understory seedlings is also important since they are considered important components of nutrient cycling (Muukkonen et al. 2006). Unlike height and stem diameter of seedlings, measurements of their aboveground/belowground biomasses are generally costly, laborious, and time-consuming (Addo-Danso et al. 2016). The use of allometric

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Communicated by: Chirstian Ammer.

✉ Ferhat Kara  
fkara@kastamonu.edu.tr

<sup>1</sup> Faculty of Forestry, Kastamonu University,  
37100 Kastamonu, Turkey

equations is a more efficient method to estimate above and belowground biomasses in forests (Domenicano et al. 2011). Thus, developing allometric equations to estimate seedling biomass using easily measured parameters such as seedling height and root-collar diameter is also crucial for evaluating stand development through biomass accumulation (Shah-rokhzadeh et al. 2015).

Previous research commonly observed the influence of light on seedling growth and development mostly in pure forests of different species (Messier and Nikinmaa 2000; Hale 2003; Köseoğlu and Kara 2019), or in artificial light conditions and greenhouses (Daryaei et al. 2019). However, the effects of light on understory seedlings in mixed-species forests composed of species that present different levels of shade tolerance are not well documented and quantified (Sevillano et al. 2016). Previous studies examining growth-light relationships in mixed forests have cast doubt on this notion. Although some studies found similar seedling growth rates of intolerant and tolerant species under the canopy of mixed stands (Grubb et al. 1996), others reported greater growth rates of intolerant species compared to tolerant species (Modrzyński et al. 2015), or greater growth of tolerant species than that of intolerant species (Walters and Reich 2000). The inconsistency among previous studies highlights the remaining uncertainty in our knowledge of growth-light relationships in mixed forests. Moreover, although various collections of biomass equations of mature trees are available, these equations are limited for understory seedlings' biomasses, especially in mixed forests (Annighöfer et al. 2022). Such equations are particularly important for modelling seedling growth and carbon sequestration. Scots pine (*Pinus sylvestris* L.), black pine (*Pinus nigra* Arnold.) and Oriental beech (*Fagus orientalis* L.) are widespread and economically important tree species across Europe and Asia Minor (Atik 2013; Kara and Topacoglu 2018b). Mixed forests of these tree species cover vast areas within their natural ranges. Uncertainty remains about the response of seedlings of Scots pine, black pine and Oriental beech to light transmittance across the geographical range of their mixed forests. Moreover, despite the significant role of mixed pine-beech forests in the carbon cycle and carbon balance (Macaroğlu 2011), no aboveground/belowground biomass model for understory seedlings of these forests has been developed.

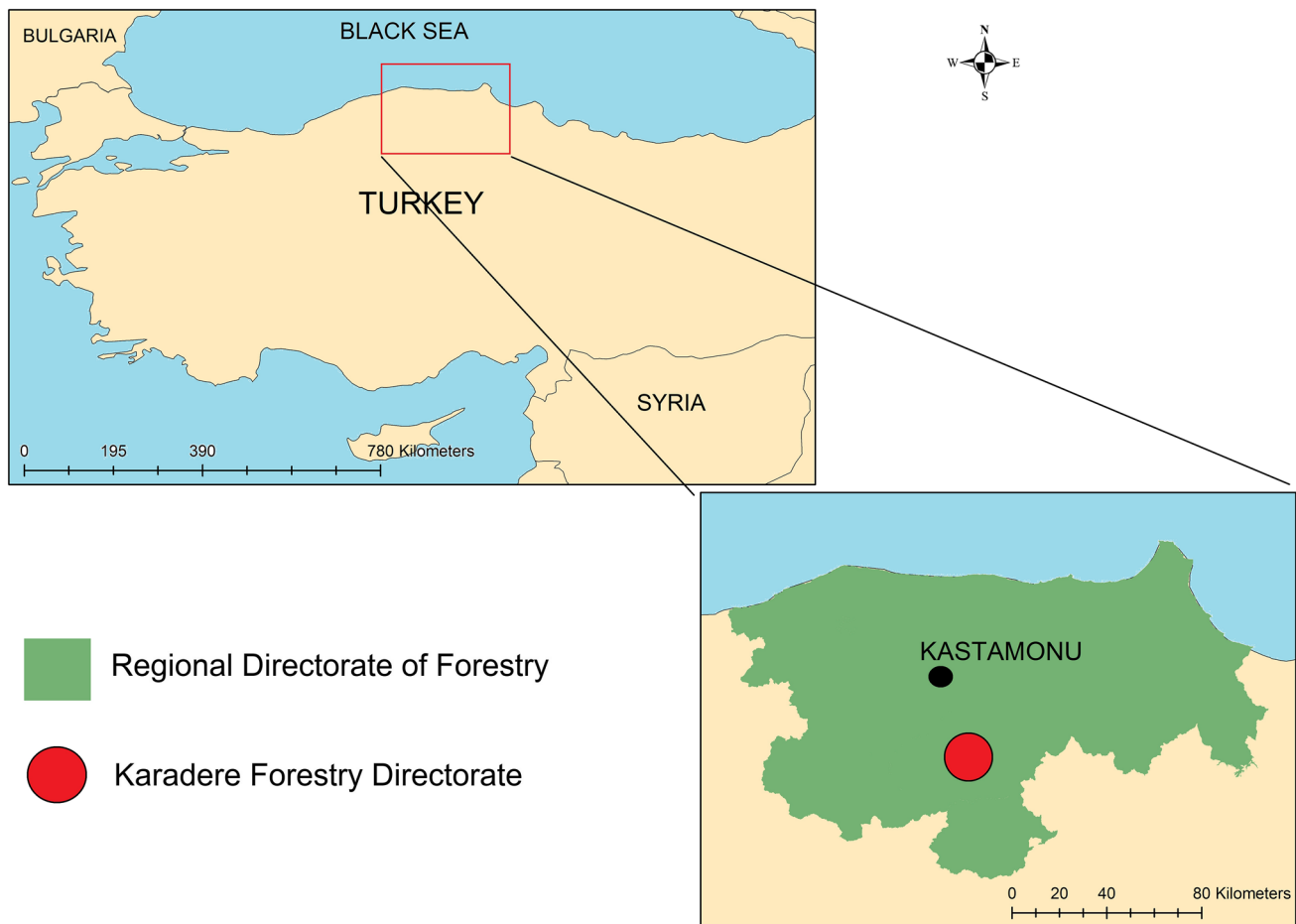
It should be noted that tree species richness can positively enhance forest productivity (Danescu et al. 2016), biological diversity (Pádua and Chiaravalotti 2012), and ecosystem functioning (Huang et al. 2018). However, natural regeneration in mixed forests composed of tree species, which exhibit different levels of shade tolerance (i.e., pine-beech mixture), is considered more difficult compared to natural regeneration in their pure stands (Odabaşı et al. 2004). Mixed Scots pine-black pine-Oriental beech forests

are commonly managed using the traditional shelterwood method in northern Turkey, and specific light demands of the species are usually ignored. Understanding the response of understory seedlings to canopy openings is important when conducting shelterwood cuttings that allow the regeneration and seedlings' growth in these forests. But, due to the lack of knowledge on the relationships between understory light conditions and seedling growth and biomass, some regeneration activities have resulted in a decline in species richness in these mixed forests (Genç 2020). Pine seedlings may not recruit under low light conditions following small-scale overstory disturbances, and consequently, mixed pine-beech stands may turn into pure beech stands in long term (Pretzsch et al. 2015; Topaçoğlu and Genç 2019). The quantitative knowledge about light-growth relationships would help forest managers to understand how understory seedlings may respond to light conditions following canopy disturbances when aiming to regenerate, promote and maintain tree mixture (Daryaei et al. 2019). It would give forest managers the ability to implement silvicultural treatments that modify the understory light availability and response of seedlings through overstory disturbances (Assenac 2000; Lhotka and Loewenstein 2008). Therefore, in this study, the main objectives were; (1) to examine the growth and biomass of understory seedlings under varying levels of light transmittance in mixed forests of Scots pine-black pine-Oriental beech, (2) to quantify the relationships between light transmittance through canopy and seedling growth and biomass, and (3) to develop allometric equations to estimate belowground and aboveground seedling biomass for these mixed forests. Moreover, specific objectives were to observe the influences of light transmittance on seedling quality and seedling shoot–root ratio. Novelty includes the first model quantifying seedling growth–light relationships for mixed pine-beech forests and the first allometric equations to estimate seedling biomasses for mixed pine-beech forests.

## Materials and methods

### The study area

This study was carried out in Karadere Forestry Directorate under Kastamonu Regional Directorate of Forestry, Kastamonu city, northern Turkey (Fig. 1). This region is included within the Euro-Siberian phytogeographic region, which is in the natural range of the species (i.e., Scots pine, black pine and Oriental beech). The study area represents the typical characteristics of a continental climate with cold winters and rainy summers. The mean monthly temperature and the mean total annual precipitation are 9.8 °C and 490 mm, respectively. The lowest and highest temperatures are measured in January (− 1 °C) and July (20.3 °C) on



**Fig. 1** Location of the study area

average, while the maximum and minimum monthly precipitation occur in May (68.8 mm) and February (28.5 mm), respectively. Soil is mostly moderately deep ranging from 50 to 90 cm and is primarily brown forest soil. The study area is mountainous with a topography ranging from gently sloping to steep slopes, while altitude varies from 800 to 1700 m above sea level.

According to the reports of the General Directorate of Forestry, the total forested acreage of the region is approximately 900.000 ha. Main tree species, which constitute approximately 60% of the total forested area in the region, are black pine (%27), oak (*Quercus* spp.) (%12), Scots pine (%9), Oriental beech (%6), and Trojan fir (*Abies nordmanniana* subsp. *equi-trojani*) (%5). Approximately 46% of the forested area consists of the mixed forests of the main species, while the pine-beech mixture is not more than 5%. Hornbeam (*Carpinus* spp.), Calabrian pine (*Pinus brutia* Ten.) and Anatolian chestnut (*Castanea sativa* Mill.) are other tree species that establish pure and mixed forests. Common hazel (*Coryllus avellana* L.), raspberry (*Rubus* spp.) and common juniper (*Juniperus communis* var. *saxatilis* Pall.) form the

commonly observed understory cover within these forests. Forests are state-owned in the country, and managed by the General Directorate of Forestry. Natural regeneration of the forests is persistently recommended by the Turkish Forestry doctrine.

### Sampling and measurements

A mixed pine-beech stand dominated by Scots pine, black pine and Oriental beech was selected for the study. A stand composed of these tree species was selected due to differences in their shade tolerance, and their economic and ecologic significance (Çalışkan 1992). The stand had an area of approximately seven ha, and has been naturally regenerated using the traditional shelter-wood system for decades, and represents even-aged stand structure. In this approach, a seeding cutting, which aims to establish new regeneration and to assure the seedlings' eventual light demand in advance, was carried out reducing canopy closure to 50–60%. The seeding cutting is usually conducted in a good seed crop year of pines aiming to establish new pine

seedlings. It is believed that reducing canopy closure with the seeding cutting would recruit advanced beech reproduction that survived under the canopy, and establish new beech seedlings as well. Dominant trees' ages range from 80 to 100 based on the management plan of the stand. There has not been any treatment for more than twenty years within the selected stand, and natural stand dynamics prevailed in this period.

Forty-five circular plots with an area of 100 m<sup>2</sup> were installed within the study stand in 2021. When installing a plot, first, a spot where three seedlings (i.e., one from each species) were present was found within the stand. Then, the plot center was located near the selected seedlings aiming to minimize the distance of the seedlings to the center. The plot installation process was repeated until a well-distribution of the plots across the stand was achieved. In each plot, the number of seedlings was counted for each species, and converted to calculate seedling density ha<sup>-1</sup> in 2021. Average seedling density was approximately 3250, 1930 and 1300 seedling ha<sup>-1</sup> for Scots pine, black pine and Oriental beech, respectively. Next, in each plot, one five-year-old seedling of each species (i.e., forty-five seedlings of each species, and a total of 135 seedlings) was randomly selected. Seedlings' ages were confirmed by counting the whorls, while small single branches between major whorls were not included when counting age as suggested (DeYoung 2016). Since only a restricted number of seedlings were allowed to be harvested by the officials, the number of seedlings sampled had to be limited to forty-five for each species. Moreover, seedling quality was determined with Dickson's Quality Index (QI) (Bayala et al. 2009) using the formula below.

$$QI = \frac{\text{Seedling dry weight(g)}}{\left( \frac{\text{Height}}{\text{RCD}} + \frac{\text{SDW}}{\text{RDW}} \right)}$$

where RCD is the root-collar diameter (mm), while SDW and RDW are shoot dry weight (g) and root dry weight (g), respectively. Measurement of seedling quality using morphological attributes is considered reliable and has been commonly used in previous studies (Puttonen 1997). The aspect, slope and altitude of each plot were also recorded.

All live trees larger than 5 cm in diameter at breast height (DBH) were measured using a diameter tape in each plot, and their tree species were recorded. Stand basal area (BA) (m<sup>2</sup> ha<sup>-1</sup>) for each stand was also calculated using the DBH measurements. The average BA was approximately 28.7 m<sup>2</sup> ha<sup>-1</sup>, while the number of trees per ha was about 634 in the stand. The approximate proportion of species within the stand was 50, 35 and 15% of total BA for Scots pine, black pine and Oriental beech, respectively.

To determine LT (%) at the location of each selected seedling, first, photosynthetically active radiation (PAR) was measured above each seedling using a CI-110 Plant Canopy

Imager (CID Bio-Science Inc., Washington, USA). PAR measurements were taken on a nearly cloudless day, preferably between 11:00 am and 1:00 pm as suggested (Kara et al. 2018). The device was leveled during PAR measurements, and special care was taken to restrain the operator's shadow from falling across the sensors. Another PAR measurement was taken simultaneously in an open area. Then, LT (%) through the canopy was calculated using the following formula for each selected seedling.

$$LT(\%) = \frac{\text{PAR above seedling}}{\text{PAR in open}} \times 100$$

Previous studies have suggested that there is a considerable relationship between understory vegetation cover (UVC) (%) and seedling biomass of most species (Chiarucci et al. 1999; Röttgermann et al. 2000). Therefore, at the location of each selected seedling, UVC (%) was visually estimated in a 1 m<sup>2</sup> subplot centered at the points where light measurements took place, as outlined by Messier et al. (1998). UVC (%) was defined as the vertical crown projection of the understory vegetation within the subplots (Muukkonen et al. 2006). The stem height (cm) of each selected seedling was measured with a ruler to obtain the total height of the seedlings after five years, in September 2021. RCD (mm) of the seedlings was also measured using a digital caliper. Then, measured seedlings were uprooted and brought to the laboratory. The seedlings were thoroughly cleaned from soil and other debris, and their needles and leaves were removed. Next, they were divided into the main stem, branches and root. All parts (i.e., roots, branches, leaves/needles and stems) were oven-dried for 72 h at 70 °C as outlined by Yamashita et al. (2016). Then, dried samples were weighed with a precision balance, and belowground (i.e., root) and aboveground (i.e., stem, branches and leaves/needles) biomass of seedlings were attained.

## Analyses

The effects of light transmittance (%) (hereafter, LT) on the height, belowground and aboveground biomass were examined using a mixed-effect multiple regression model. Apart from LT (%), seedling species, BA, UVC (%), slope, aspect, and elevation were all treated as fixed effects, while seedlings were used as random effects in the models. It should be noted that an individual seedling was considered as the experimental unit (i.e., replicate). Height, belowground and aboveground biomass were used as the response variables (i.e., dependent variables). To develop allometric equations for estimating aboveground and belowground biomasses for each species, the mixed-effect multiple regression model was utilized as well. The models were defined by the following equation.

**Table 1** Descriptive statistics for the variables of studied seedlings by species

Variables	Scots pine		Black pine		Oriental beech	
	Mean	SD	Mean	SD	Mean	SD
Height (cm)	36.88 (19.7–55.4)	8.5	43.43 (16.5–71)	12.1	55.56 (22.43–94.2)	14.87
RCD (mm)	6.71 (3.96–11.5)	1.74	8.43 (2.54–14.7)	3.13	8.21 (3.34–13.8)	2.36
AGB (g)	7.11 (1.53–22.9)	4.18	12.43 (1.14–26.7)	6.46	15.54 (2.93–41.8)	8.64
BGB (g)	2.01 (0.51–5.16)	1.22	5.13 (0.89–12.05)	2.63	11.09 (1.24–26.5)	6.67
LT (%)	56.5 (23.9–86.2)	17.99	52.44 (9.13–96.1)	21.46	43.3 (6.14–93.1)	27.89

RCD, AGB, BGB and LT refer to root-collar diameter, above-ground biomass, below-ground biomass and light transmittance, respectively. Numbers in parenthesis give the range. SD donate to standard deviation

$$Rv = \beta_o + Re + X^T + \varepsilon$$

where  $Rv$  is the response variable (i.e., aboveground and belowground biomass),  $\beta_o$  is the intercept,  $Re$  is the random effect,  $X^T$  is the transposed matrix of the fixed effects and  $\varepsilon$  is the error term. Model fitting started with a full model. Then, candidate models were also fit, and all models were compared using Akaike's information criterion (AIC), which aims to compare different models on a given outcome based on an AIC score (AICs) (Snipes and Taylor 2014). The best models were defined with the lowest AICs as suggested (Arnold 2010). To test the differences in height, belowground and aboveground biomasses, and needles/leaves biomasses among the species, analyses of variance (ANOVA) statistical model ( $\alpha$ -level=0.05) was used. Multiple comparisons of means of the species were performed using Tukey's test. A linear regression model was also utilized to define the relationships between UVC (%) and the above-mentioned response variables, as well as the relationships between LT (%) and seedling quality (i.e., QI), and between LT (%) and BA. Normality and homogeneity of variance of data were tested with residual analysis, and no departures from these model assumptions were found. Multicollinearity among the selected parameters was examined with the variance inflation factor (VIF); VIF greater than 10 indicates high collinearity among variables (Dormann et al. 2013). It should be noted that no VIF value greater than 2 was detected in the models. Pearson correlation matrix was calculated for the measured variables. During statistical analyses, "lme", "anova", "TukeyHSD" and "cor.test" functions of R-Statistical software (R Development Core Team 2021) were utilized.

## Results

LT (%) measured above the seedlings ranged from 6.1 to 96.1% across the species, suggesting that the selected seedlings were distributed under a wide range of light transmittance. On average, Oriental beech seedlings appeared to be under relatively lower light conditions followed by black

pine and Scots pine within the study stand (Table 1). In addition, Oriental beech seedlings had higher total height, and above and belowground biomasses compared to the pine seedlings after five years of germination. Moreover, a relatively greater mean RCD of black pine seedlings was observed, followed by Oriental beech and Scots pine (Table 1). Seedling height, aboveground biomass and belowground biomass among the three species were significantly different ( $p < 0.001$ ,  $p < 0.001$ , and  $p < 0.001$ , respectively). Moreover, differences in needles/leaves biomasses among the species were significant ( $p = 0.012$ ), as greater biomass of beech leaves than pine needles was obtained. A significant relationship between LT (%) and stand BA was also attained ( $p < 0.001$ ), as LT (%) decreased with increasing BA across the study plots.

The linear mixed effect models indicated that total seedling height, after five years of germination was significantly affected by LT (%) ( $p < 0.001$ ), BA, and tree species in their mixed stand ( $p < 0.05$ ) (Table 2). It should be noted that seedling height was not significantly different between Scots pine and black pine. The interaction between LT (%) and species was only significant for seedling height between black pine and Oriental beech ( $p < 0.001$ ) (Table 2). As for aboveground biomass and belowground biomass, they were influenced by LT (%) and tree species in their mixed stand ( $p < 0.05$ ) (Table 2). Above and belowground biomasses were not significantly different between Scots pine and black pine ( $p > 0.05$ ), while it was significant between black pine and Oriental beech (Table 2). BA was not included in the best-fit biomass models. Effects of the slope, aspect, elevation and UVC (%) on height, above-ground and below-ground biomass were insignificant ( $p > 0.05$ ). The interaction effects of LT (%) and BA, and LT (%) and UVC (%) on the response variables were also insignificant ( $p > 0.05$ ).

The best-fitted models of seedling height, and above-ground and belowground biomass did not include UVC (%), however, significant effects of UVC (%) on height ( $p < 0.0001$ ), aboveground biomass ( $p < 0.0001$ ) and belowground biomass ( $p = 0.0014$ ) of beech seedlings were attained. Figure 2 represents the influence of LT (%) on above and belowground biomasses of seedlings

**Table 2** Influences of light transmittance (LT) (%), basal area (BA) and species on height, above-ground biomass (AGB) and below-ground biomass (BGB)

Variables	Height (cm)	AGB	BGB
Intercept	30.399 (6.43)***	3.427 (1.73)*	1.519 (1.27)*
LT	29.949 (5.74)***	15.592 (2.71)***	6.255 (1.99)***
Species: SP (vs BP)	- 3.827 (5.32) ns	- 5.152 (2.74) ns	- 1.718 (2.02) ns
Species: OB (vs BP)	23.463 (4.10)***	4.684 (2.11)*	5.399 (1.56)***
BA	- 0.184 (0.14)*	-	-
LT × Species: SP (vs BP)	- 4.814 (8.15) ns	- 1.334 (4.19) ns	- 2.704 (3.09) ns
LT × Species: OB (vs BP)	- 15.785 (6.45)*	- 0.495 (3.33) ns	2.215 (2.45) ns

SP, BP, OB and SE refer to Scots pine, black pine, Oriental beech and standard error, respectively. AIC values were 986.44, 812.42 and 733.63 for height, AGB and BGB models, respectively. Numbers in brackets within the results refer the standard error (SE)

ns, \*, \*\*, \*\*\* are not significant,  $p > 0.05$ ,  $p < 0.05$ ,  $p < 0.01$ , and  $p < 0.001$ , respectively

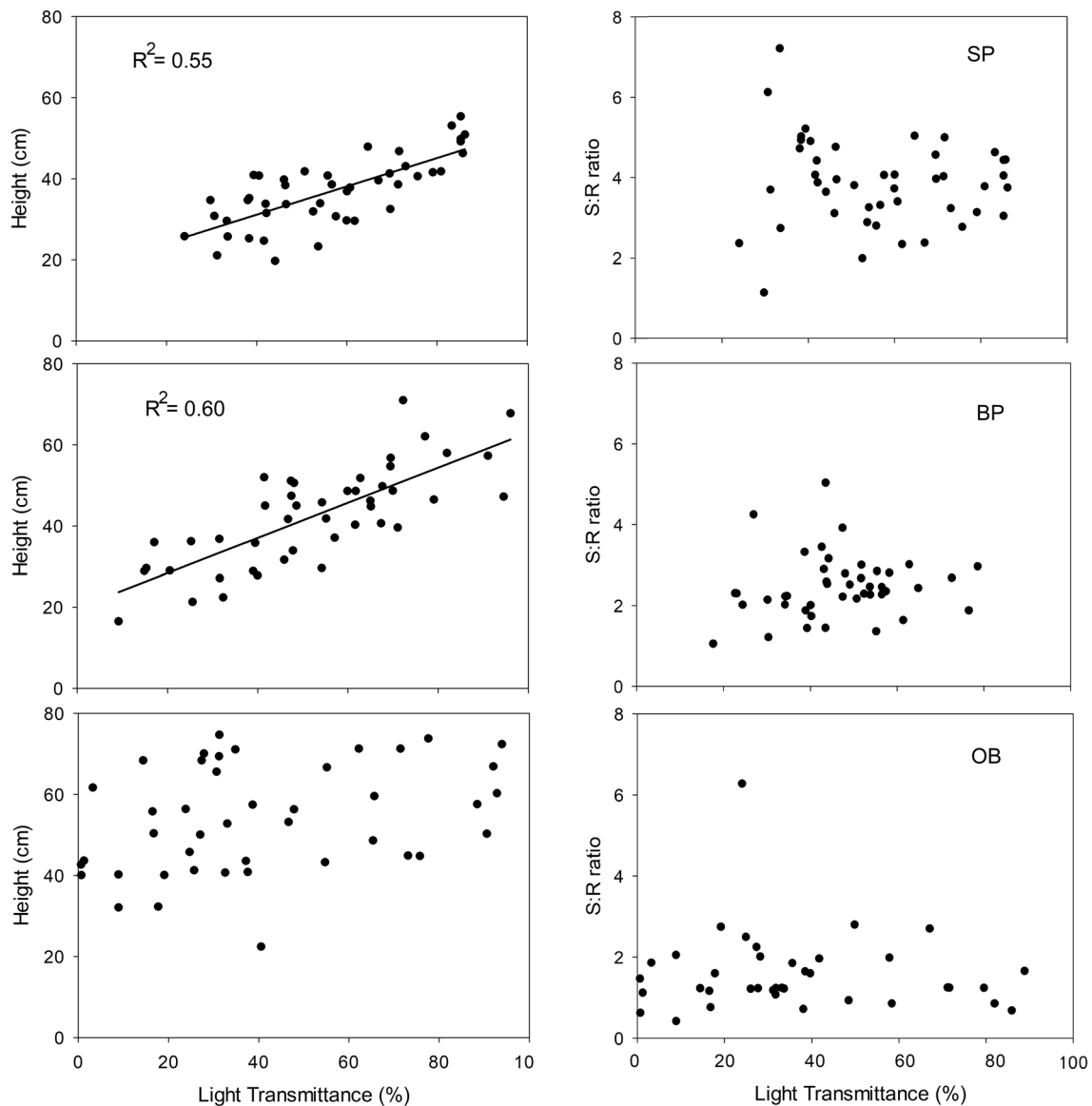


**Fig. 2** Relationship between the available light and aboveground and belowground biomass for Scots pine (SP), black pine (BP), and Oriental beech (OB)

by species, while the relationships between LT (%) and total seedling height are shown in Fig. 3. Moreover, the effects of LT (%) on the shoot: root ratio, which refers to the ratio of shoot dry mass to root dry mass, is also presented in Fig. 3. Above and belowground biomasses of seedlings increased with increasing LT (%) for Scots pine and black pine in the study stand (Fig. 2). As for Oriental beech seedlings, there was a linear positive association between LT (%) and aboveground biomass, while no significant relation of LT (%) with belowground biomass was detected. A positive correlation between LT (%) and seedling height was present for Scots pine and black pine, while this relationship was insignificant for Oriental beech seedlings (Fig. 3). Moreover, no significant relation of LT

(%) with shoot: root ratio was examined across seedlings of all species. But, the influence of LT (%) on overall seedling quality was statistically significant ( $p < 0.001$ ). The overall seedling quality index ranged from 0.23 to 8.11 across all species.

All of the measured variables of the seedlings were highly correlated with Pearson's  $r$  ranging between 0.51 and 0.88 (Table 3). Aboveground seedling biomass had a strong degree of correlation with belowground biomass for all species. The strongest correlation between RCD and height of seedlings was observed in black pine seedlings followed by Scots pine and Oriental beech. RCD and height were more correlated to aboveground biomass compared to belowground biomass (Table 3).



**Fig. 3** Relationship between the available light and height and shoot: root (S:R) ratio for Scots pine (SP), black pine (BP), and Oriental beech (OB)

**Table 3** Pearson correlation matrix for measured variables by species

Species	Variables	Height	AGB	BGB
Scots pine	RCD	0.65***	0.82***	0.75***
	Height	–	0.64***	0.51**
	AGB	–	–	0.86***
Black pine	RCD	0.85***	0.72***	0.73***
	Height	–	0.66***	0.67***
	AGB	–	–	0.88***
Oriental beech	RCD	0.62***	0.76***	0.64***
	Height	–	0.72***	0.57***
	AGB	–	–	0.80***

RCD, AGB and BGB refer to root-collar diameter, above-ground biomass and below-ground biomass, respectively

ns, \*, \*\*, \*\*\* are not significant,  $p > 0.05$ ,  $p < 0.05$ ,  $p < 0.01$ , and  $p < 0.001$ , respectively

**Table 4** Allometric equations for estimating above-ground biomass (AGB) and below-ground biomass (BGB) by species

Species	Equation	$R^2$	SEE	$p$ -value
Scots pine	AGB = 3.539 - 0.195 H + 0.042 H × RCD	0.73	2.23	< 0.001
	BGB = - 1.532 + 0.527 RCD	0.56	0.071	< 0.001
Black pine	AGB = - 1.668 + 1.008 RCD + 0.106 LT	0.59	4.259	< 0.001
	BGB = - 0.574 + 0.428 RCD + 0.04 LT	0.57	1.752	< 0.001
Oriental beech	AGB = 0.524 + 0.023 H × RCD + 0.086 LT	0.75	4.421	< 0.001
	BGB = 2.240 + 0.018 H × RCD	0.45	5.01	< 0.001

$R^2$  refers to coefficient of determination while SEE, RCD, LT (%) and H are standard error of estimate, root-collar diameter, light transmittance and height, respectively

To determine the effects of LT (%) on the precision of height, aboveground and belowground biomass allometric equations, a mixed-effect multiple regression model was utilized (Table 4) because of the strong correlations among the variables presented above (Table 3). The coefficient of the determination ( $R^2$ ) of the equations ranged from 0.45 to 0.75 across the species (Table 4). Biomass models for each species included different variable combinations. For example, the model for aboveground biomass of Scots pine contained seedling height and its interaction with RCD, while RCD and LT (%), and height, RCD and LT (%) were included in the aboveground biomass models of black pine and Oriental beech, respectively.

## Discussion

Light is considered one of the most influential factors that hinder or prompt the growth and biomass of understory seedlings (Daryaei et al. 2019), and is vital for the survival and development of seedlings. Light transmitted through the forest canopy is usually associated with stand BA, as observed in the present study. In mixed forests composed of

species with different levels of shade tolerance, seedlings can develop different strategies to overcome the insufficiency of light. Scots pine and black pine are more light-demanding species than Oriental beech which is known to be a very tolerant species to shade (Odabaşı et al. 2004). In general, shade-intolerant species have greater height growth rates in their early stages, and their early height growth is more dependent on the understory light environment, compared to shade-tolerant species (Walters and Reich 2000). The present study supported this assertion revealing a significant influence of LT (%) on the height growth of the pine species. Previous studies found LT (%) as one of the most significant predictors of growth for Scots pine and black pine seedlings understory (Pardos et al. 2007; Kara and Topaçoğlu 2018b), as monitored in the present study.

Scots pine and black pine usually appear where canopy closure is relatively lower in stands mixed with shade-tol-

erant species such as Oriental beech. Despite their intolerance to shade, approximately 5000 pine seedlings  $\text{ha}^{-1}$  were present in the understory under the varying levels of LT (%), while about 1300 beech seedlings  $\text{ha}^{-1}$  were observed. This is because seedlings of Scots pine and black pine require partial canopy, and can survive under the shade of parent trees in their early stages (Gaudio et al. 2011; Odabaşı et al. 2004). Due to the wide range of LT (%) across study plots, the light requirements of pine seedlings were likely met. The relatively lower number of beech seedlings  $\text{ha}^{-1}$  can be associated with the proportion of beech trees in BA across the stand. Despite the existence of pine seedlings under shade, the lack of light in the understory negatively influences their further growth rather than their survival (Castro et al. 2004; Tiscar and Linares 2014). The average RCD and height of understory seedlings attained after five-year post-germination were consistent with previous studies that were conducted on Scots pine (Kara and Topaçoğlu 2018b; Gerelbaatar et al. 2015), black pine (Mercurio et al. 2009; Köseoğlu and Kara 2019) and Oriental beech seedlings (Akbenar and Keshavarz 2005; Parhizkar et al. 2011).

Even though beech seedlings can survive under a closed canopy for a long time due to their tolerance to shade, their growth is highly associated with understory light conditions (Madsen 1994). This study found that LT (%) affected the aboveground biomass of Oriental beech seedlings, but not seedling height. Similarly, Parhizkar et al. (2011) monitored the height growth of Oriental beech seedlings under different light conditions, and they did not find any relationship between light intensity and seedling height. In another study, Collet et al. (2001) observed that light through the canopy initially has more influence on seedling biomass than on their height growth, which supports our findings. The hypothesis by Messier et al. (1999) stating that shade-tolerant species delay their height growth and develop their root system under low light conditions to increase their chance of survival also substantiates our findings.

Given the effects of UVC (%) and LT (%) on Oriental beech seedlings, it is likely that competition of beech seedlings with understory vegetation for resources seems to be a more limiting factor than LT (%). Similarly, Kuusipalo (1983) examined the relationships between understory vegetation cover and biomass of shade-tolerant *Vaccinium myrtillus* L., and found that percentage cover alone accounted for a greater amount of the variation in aboveground biomass than light. UVC may hinder the natural regeneration of Scots pine and black pine (Hallikainen et al. 2007; Tardós et al. 2019); however, some studies reported that some understory vegetation may even have positive effects or no influence on seedling growth of Scots pine and black pine (Hyppönen et al. 2013). The relationships between UVC and seedling growth can be associated with climatic conditions. In this respect, UVC usually negatively affect seedling growth in harsh climate conditions in pine stands (Juntunen and Neuvonen 2006). Moreover, the early growth rate of the pine seedlings, which is greater than beech seedlings (Odabaşı et al. 2004), may also explain why UVC had a positive influence on beech seedlings while no influence on pines was detected.

Under low-level light conditions, seedlings of intolerant species invest more in aboveground biomass than belowground biomass to recruit upper stories (Babaei et al. 2017), as examined in pine species in the present study. In other words, when light is not a limiting factor, seedlings may spend more of their energy developing their root systems (i.e., belowground biomass). Aboveground biomass of Oriental beech seedlings was significantly influenced by LT (%). Shade tolerant species such as beech, mostly generate larger and more leaves to intercept a greater amount of light under shade conditions (Petrovska et al. 2021). Under low light availability, they usually allocate more aboveground biomass than belowground biomass compared with shade-intolerant species (Sevillano et al. 2016), which appears consistent with our findings. In a previous study conducted

by Petritan et al. (2009) on beech, maple, and ash, it was found that beech had a greater leaf area, leaf area index and leaf plasticity compared to other species. In another study, Welander and Ottosson (1998) examined the effects of light on dry matter of beech seedlings and found that light had more effects on stem biomass than on root biomass. The present study also found that LT (%) can influence the quality of understory seedlings. Although this relationship was available across all species in the present study, previous studies have indicated that LT (%) is more critical for the quality of understory beech seedlings than shade-intolerant species (Niinemets 1996; Čater et al. 2013). High-quality beech seedlings usually develop under moderate canopy shelter, and the growth form of beech seedlings tends to be more decurrent in low light conditions (Wagner et al. 2010).

Regeneration of mixed forests is considered more difficult than that of pure forests, when trees of the mixture present different levels of light demand. Canopy structure significantly contributes to the understory light environment (Hale 2003; Lhotka and Loewenstein 2008). The present study points out that canopy structure and canopy openness is important for the recruitment of understory seedlings in mixed pine-beech forests. If intervention in the forest canopy is impeded in mixed forests, their conversion to pure stands is inevitable in favor of shade-tolerant species. Therefore, shade tolerance and light demand of understory seedlings should be well understood in their seedling and sapling stages, when silvicultural practices, which aim to increase light transmittance through the canopy, are conducted. Moreover, the timing and intensity of overstory disturbances are also crucial for maintaining the mixture in pine-beech forests. Beech can respond to canopy opening at varying ages ranging from 1 to 12 (Collet et al. 2001); however, delayed treatments can result in poor responses of the pine seedlings to increasing light, and result in a high mortality rate (Odabaşı et al. 2004).

Biomass equations for understory seedlings are mainly limited (Annighöfer et al. 2016). Even though mixed pine-beech forests play a significant role in the carbon cycle and carbon balance (Macaroğlu 2011), there are no biomass models available for the understory seedlings of these forests. Such models are particularly essential for modeling seedling growth and sequestration. Prediction of belowground biomass using aboveground attributes is especially of great interest in recent studies (Annighöfer et al. 2022). Biomass models for each species included different variable combinations such as seedling height, RCD, LT (%), and their interactions. Similar variables have been utilized to develop biomass models in previous studies (Daryaei et al. 2019). Whilst the models provide insight into the relationships between LT (%), seedling size (i.e., height and RCD), and biomass, the predictive power of some models may be considered relatively low to recommend for prediction

purposes. The applicability of the models may be limited because some variables of the models are not typically measured parameters in large-scale inventories. The variances not explained by the models can be associated with microclimatic factors and site heterogeneity in the study (Puttonen 1997; Assenac 2000).

## Conclusions

Mixed forests have several advantages over pure forests. Thus, the sustainability and maintenance of these forests have gained much interest among forest managers. One of the most important steps is to well document the shade tolerance and light demand of understory seedlings of the species in mixed forests. This study points out the importance of light transmittance for the seedlings of different species in pine-beech forests. The present study also points out the importance of timing and intensity of overstory disturbances for the successful natural regeneration of mixed forests. Thus, forest managers should take into account the silvics of the species and silvicultural prescriptions that influence the understory light environment in mixed forests. Future monitoring is recommended for the development of the species in these mixed forests over time. Initial data in this research would create a basis for our knowledge on how different species respond to varying levels of light in mixed forests.

**Acknowledgements** The authors would like to thank Kastamonu Regional Directorate of Forestry for providing access to the study area for this research. Moreover, the authors would acknowledge Emre Genç, Erol Kaya and Abdurrahman Göksu for their help during the fieldworks.

**Author contributions** FK conceived the idea, developed the framework, collected data and compiled the literature, and worked with the writing and editing. FK conceptualized the study, collected the data, performed the statistical analyses, created figures and wrote the whole manuscript.

**Funding** This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

**Code availability** Not Applicable.

## Declarations

**Conflict of interest** The author has no conflict of interest.

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