

Competitive asymmetry in a monospecific stand of the shade-tolerant tree *Fagus crenata* depends on gap formation

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Abstract

Competitive asymmetry is one of the most important determinants of size structure in plant communities. Many studies indicated that light competition is size-asymmetric in monospecific stands of herbaceous plants, as taller individuals preempt light. However, competition is size-symmetric in multispecific stands because shorter species adapted to shade. Then, a question arises on whether light competition is asymmetric or symmetric if a shade-tolerant species occupies the stand, such as climax forests. Moreover, it is also interesting how gap dynamics affect competitive asymmetry, given the fact that gap formation can improve light availability in lower layers of the canopy. In cool temperate and natural climax forest of northern Japan, dominated by a shade-tolerant tree, *Fagus crenata*, we investigated the plant size, growth rate, and three-dimensional distribution of foliage and light availability. We found that competitive asymmetry varied dynamically across the forest. In closed canopies, the relative growth rate (RGR) was higher in taller trees, indicating size-asymmetric growth. Shorter trees partly compensated for their light interception by having higher leaf area per aboveground mass (leaf area ratio; LAR) but did not achieve comparative RGR to taller trees. Conversely, in gaps, the RGR of shorter trees was equivalent to those of taller trees because of the improved light availability for smaller trees, indicating size-symmetric growth. These results suggest that changes in competitive asymmetry driven by gap dynamics can influence the spatiotemporal diversity of size structures in forests.

Introduction

Forests play an essential role in regulating the ecosystem functions on a global scale, and they are indispensable for the mitigation of climate change (IPBES 2019; Astigarraga et al. 2020). Natural forests consist of individual trees of different sizes and ages, and the size and age structures of a forest are major drivers of the ecosystem functions such as carbon sequestration (Forrester and Bauhus 2016; Ruiz-Benito et al. 2017; Kweon and Comeau 2019). For example, size inequality has been shown to increase the forest's primary productivity (Torresan et al. 2020). Due to the recruitment, growth, and death of trees, size structure changes temporally and locally even within the same forest. However, the ways through which the behaviors of the size structures of a forest are determined remain unclear.

The relationship between the growth rate and the size of individual plants is one of the important determinants of size structure in plant populations. If the growth rate is proportional to the size or the relative growth rate (RGR; growth rate per size) is the same among individuals, then size inequality does not change with time. If the growth rate is greater in larger individuals (to a more than proportional extent) or if the RGR is greater in larger individuals, then size inequality increases with time (Weiner 1990; Berntson and Wayne 2000), and the population will eventually consist of a smaller number of larger individuals along with a larger number of smaller individuals.

The growth-size relationship has been discussed in relation to the competitive asymmetry for resource acquisition (or the mode of competition) (Weiner and Thomas 1986; Hikosaka et al. 1999; Rüger et al. 2011; Guo et al. 2017). If the individuals compete for light, because the light comes directionally from

above, taller plants can preempt the light energy and suppress the light interception of shorter ones, but not *vice versa* (Weiner 1985; Weiner 1990; Nakashizuka and Kohyama 1995; Kikuzawa and Umeki 1996; Falster and Westoby 2003; Onoda et al. 2014; Guo et al. 2017). Taller plants absorb light more than proportionally to their size; i.e., size-asymmetric light interception. Conversely, the competition for below-ground resources such as water or nutrients may be reflecting a relatively size-symmetric acquisition, because these resources derive from all directions within the soil (Berntson and Wayne 2000; Hikosaka and Hirose 2001).

The growth-size relationship is influenced not only by resource acquisition but also by the plants' morphological and physiological characteristics allowing them to utilize the absorbed resources. Thus, the RGR can be decomposed as follows:

$$\text{RGR} = \text{LUE} \times \Phi_{\text{mass}} \text{ Eq. 1}$$

$$\Phi_{\text{mass}} = \Phi_{\text{area}} \times \text{LAR} \text{ Eq. 2}$$

where LUE is the light use efficiency defined as biomass production per unit light interception, Φ_{mass} is the light interception per unit of aboveground biomass, Φ_{area} is the light interception per unit of leaf area, and LAR is the leaf area ratio that is defined as the total leaf area per unit of aboveground biomass (Hirose and Werger 1995; Hikosaka et al. 1999). LUE may reflect physiological processes, including photosynthesis and respiration. Φ_{mass} represents the light acquisition efficiency, if the aboveground mass is regarded as the cost for acquiring light. Φ_{area} represents the light availability for the individual plant. LAR represents morphological characteristics, including biomass allocation.

To date, several studies determined these variables in herbaceous vegetations. In monospecific stands of annual herbs, the Φ_{mass} and the RGR have been shown to be higher for larger individuals, thereby suggesting that the light competition is size-asymmetric (Anten and Hirose 1998; Hikosaka et al. 1999, 2003; Matsumoto et al. 2008). Conversely, in herbaceous stands where multiple species coexist, the Φ_{mass} was not necessarily found to be higher in taller species than in shorter species, due to the fact that a greater LAR observed in shorter species can offset their lower Φ_{area} (Hirose and Werger 1995; Anten and Hirose 1999). In moorland stands, where deciduous and evergreen species coexist, the evergreen species have been shown to bear a lower Φ_{mass} than the deciduous species during summer, but when the Φ_{mass} was calculated at a leaf life span scale, it was found to be similar between the evergreen and the deciduous species; that was because the evergreen species could absorb more light during spring, where the leaves of the deciduous species are scarce (Kamiyama et al. 2010, 2014). These results suggest that the light competition in multispecific herbaceous stands is not necessarily size-asymmetric. In order for them to be able to coexist in a plant community, plants may need to demonstrate an equivalent Φ_{mass} (Hirose and Werger 1995; Kamiyama et al. 2014). In other words, the species inhabiting a shaded environment may require adaptive traits in order to achieve higher light interception efficiency; otherwise, they would be eliminated from the community as observed in shorter individuals in monospecific stands (Nagashima et al. 1995).

A few studies also focused on trees in multispecies forests. In the early secondary succession of tropical forests, the Φ_{mass} was found to be similar between taller and shorter species as well as between pioneer and later successional species (Selaya et al. 2008; van Kuijk et al. 2008), thereby suggesting that the light interception in multispecific forests is also size-symmetric. In a climax temperate forest, shorter species demonstrated a lower Φ_{mass} , thereby suggesting that the light interception was size-asymmetric (Onoda et al. 2014). However, shorter species were found to exhibit a higher LUE, which was able to offset their lower Φ_{mass} , and lead to a similar RGR between taller and shorter species (Onoda et al. 2014). These results also suggest that the RGR is similar between taller and shorter species in multispecific forests, and that the light interception among coexisting tree species is size-symmetric or asymmetric, but it can be compensated by higher light use efficiency in shorter species.

Natural cool temperate forests are often dominated by a single tree species. Then, a question arises: is light competition in a monospecific stand of a shade-tolerant tree species size-symmetric or asymmetric? A size-asymmetric competition would be expected from the point of view that light interception is generally size-asymmetric in monospecific stands of herbaceous species (Thomas and Weiner 1989; Anten and Hirose 1998; Hikosaka et al. 1999). Conversely, if the forest is dominated by a shade-tolerant species, a size-symmetric competition would be expected based on the fact that subordinate individuals of the shade-tolerant species would be able to survive under shade conditions for a long time, probably due to shade adaptation. However, as far as we know, no study so far focused on the competitive asymmetry in natural monospecific stands of tree species, and no study examined its relation to light acquisition and use.

Of course, other factors exist that may also influence the competitive asymmetry in natural forests. Gaps, for instance, are frequently formed by the fall of tall trees or large branches (Yamamoto 2000). Around these gaps, shorter trees in the low layer can intercept more light than those under a closed canopy (Dai 1996; Asner et al. 2004; Schliemann and Bockheim 2011). The expectation exists that the light interception-size relationship, and the competitive asymmetry are different between gaps and other forest areas. Another factor that one should consider is that natural forests consist of individuals with different ages. Plant age often influences various functions, even when the plant size remains the same. For example, older trees exhibit a higher leaf mass per area, higher water retentivity, lower photosynthetic capacity, stomatal conductance, and greater allocation of biomass in order to support tissues such as stems and branches (Ryan and Yoder 1997; Sillett et al. 2010; Azuma et al. 2019). Understandably, these factors may also influence the plant's competitive ability through alterations in its LUE and LAR.

We, herein, investigated the plant size, age, growth rate, light interception, and spatial leaf distribution in a natural forest dominated by a deciduous tree species, *Fagus crenata*. *F. crenata* is a representative late successional species of the cool temperate forests of Japan, and it exhibits a high dominance especially on the Japan sea side area (Hukusima et al. 1995). *F. crenata* is also known as a shade-tolerant species (Cao and Ohkubo 1999). It exerts a longer survivorship under a closed canopy and can regenerate in smaller gaps compared with other shade-intolerant tree species (Nakashizuka and Numata 1982;

Nakashizuka 1985; Yamamoto 2000). *F. crenata* can be expected to demonstrate high performances even under shaded conditions.

The current study aimed to address the following hypotheses: (i) the competition for light is size-symmetric in a *Fagus crenata* stand even in a closed canopy, because the shorter individuals of this species can adapt to shaded conditions (Hypothesis 1), (ii) the competition for light is size-asymmetric in a closed canopy, but less asymmetric in a gap (Hypothesis 2; where Hypotheses 1 and 2 are exclusive to each other), and (iii) the size dependence of RGR differs between young and older trees because of the age effects on physiological and/or morphological traits (Hypothesis 3).

Materials And Methods

We studied a monospecific stand of the shade-tolerant tree *Fagus crenata* in the Hakkoda mountains of the Aomori Prefecture, Japan (latitude: 40.634 N; longitude: 140.929 E, altitude: 776 m above sea level). The annual mean temperature and annual precipitation recorded at the Sukayu station, in the middle of the mountain range (altitude: 890 m above sea level), are 4°C–6°C and 1,300–2,300 mm, respectively (Shimazaki et al. 2011; Japan Meteorological Agency: <http://www.jma.go.jp/jma/indexe.html>). A permanent plot (50 × 50 m) was established in 2009 (the plot “800B” in Hikosaka et al. 2021). The diameter at breast height (DBH) of all trees (DBH > 4.7 cm) in this plot was measured annually. The number of individuals was 229 for *F. crenata* and 252 for all species in 2019. The tree height was measured with the use of a telescopic carbon pole (that can extend up to 15 m in length) in October 2019. The aboveground biomass was estimated by an allometric equation developed by Nakashizuka (1984), while the mean annual biomass production was calculated by data across the 2009–2019 annual surveys in order to finally calculate RGR.

In order to estimate the total leaf area of trees, a portable LIDAR system was used. This system is an electro-optical distance measuring instrument that can measure the vertical distance to any plant surfaces for 1,000 times per second (Onoda et al. 2014). The vertical profile of the total amount of foliage was measured by moving the LIDAR system horizontally at every 2.5 × 2.5 m grid in the plot (Onoda et al. 2014). The density of the foliage along the height was calculated by using the following equation (MacArthur and Horn 1969):

$$D(h) = - [d \{ \ln \phi(h) \} / dh] \text{ Eq. 3}$$

where $D(h)$ is the density of the foliage at height (h meters), and $\phi(h)$ is the probability of no laser interception from the LIDAR system up to h meters (the height of the LIDAR device was 1 m above the ground). By integration of the $D(h)$ for each height class, we were able to calculate the total amount of foliage and the leaf area index (LAI; leaf area per ground area) of each grid:

$$\int_{h_1}^{h_2} D(h) dh = \ln \left\{ \frac{\phi(h_1)}{\phi(h_2)} \right\} \text{ Eq. 4}$$

The total amount of foliage was calculated along with the height at 1-m intervals. The leaf area was calculated for each voxel (2.5 m width × 2.5 m width × 1 m height). For each individual tree, the voxels occupied by its crown were identified, and the whole-plant leaf area was calculated by summing up the leaf area over these voxels. When more than two individuals occupied the same voxel, the leaf area was distributed among the sharing individuals in a manner proportional to their DBH.

For the quantification of the whole-plant light interception, the 3D profiles of the photosynthetic photon flux density (PPFD, 400–700 nm) were created with the use of a PPFD sensor (LI-190SA, Li-Cor, USA) that was attached to the 15-m telescopic carbon pole, according to the approach described by Onoda et al. (2014). Vertical light profiles were measured from 1 to 15 m height, at 1-m intervals at the center of each grid. For each height, the average PPFD over 5 sec was logged in a data logger (LI-1400, Li-Cor). The PPFD was also determined outside the plot as the reference, and the relative PPFD was calculated for each measurement point. The measurement was subsequently executed under an overcast sky in order to avoid the confounding influence of direct sun light. When the 15-m height was not enough in order to reach above the canopy, the relative PPFD at that point was calculated based on the assumption that it increases linearly from the highest measuring point toward 100% at the top of the canopy.

Light absorption for each voxel ΔI_i was calculated by using the relative PPFD and the leaf area in the voxel (Monsi and Saeki 1953; Hikosaka et al. 1999) as follows:

$$\Delta I_i = I_{0i} \{1 - \exp(-KF_i)\} \text{ Eq. 5}$$

where I_{0i} is the relative PPFD on the upper surface of a given voxel i , F_i is the leaf area per ground area in a given voxel i as estimated by the LIDAR system, and K is the extinction coefficient of the study forest. The latter can be calculated by rearranging the following equation:

$$I_{ff} = \exp(-KF_{total}) \text{ Eq. 6}$$

where I_{ff} is the average relative PPFD at the forest floor, and F_{total} is the total LAI of the study forest, as estimated by the LIDAR system.

For each individual of each studied tree species, the whole-plant light interception was calculated by summing up the light absorption over the voxels occupied by its leaves. When more than two individuals were included in the same voxel, the leaf area was assumed to be shared between the individuals in a manner proportional to their DBH. In order to calculate the absolute daily light interception, the light absorption for each voxel was multiplied by the grid area (6.25 m²) and the daily average PPFD (56.6 mol·m⁻²·day⁻¹), which was in turn calculated from the typical insolation in Aomori (15.7 MJ·m⁻²·day⁻¹; average of the growth season, from June to October across 2011–2020 in Aomori, as measured by the Japan Meteorological Agency) with the use of a conversion constant (4.57 mol·MJ⁻¹ under natural light; McCree 1972; Amthor 2010; Onoda et al. 2014).

In the study forest, where the maximum height was 30 m, each gap was defined as a grid where the relative PPFD at a 10-m height was more than 20%. Individuals whose leaves were included in the gap grid were regarded to be growing in a “gap,” while the rest individuals were regarded to be growing in a “closed canopy.” As the maximum height of the study forest was 30 m, a certain degree of time was thought to have passed from the point of the gap formation (e.g., as a result of a treefall), and a number of trees had already grown in the gaps, thereby suiting the aim of this study.

The tree age was determined from the increment cores sampled by increment borers in August of 2020. Increment borers were inserted as deeply as possible to the center of the trunk and pulled out its core. When the radius of tree stem at breast height was longer than the length of the increment borers, the tree age was estimated from the average width of the annual ring that was sampled from trees with a relatively thick trunk. In order to compare variables between the relatively young and the old trees, trees were grouped into height classes (5-m each) and were regarded as young or old individuals if they were younger or older than the average age identified for each height class.

In an attempt to test our hypotheses, multiple regression analysis was performed on the *F. crenata* individuals. The RGR, LUE, Φ_{mass} , Φ_{area} , and LAR were used as dependent variables, while the tree height, the presence of a gap (whether the individual was around the gap or not), and the tree age (relatively young or old in each height class) were used as independent variables. All variables were standardized in order to calculate the standard partial regression coefficient. Moreover, single regression analysis was performed in order to visualize the trends of the relationships between dependent and independent variables. Finally, the testing of multicollinearity between independent variables required the calculation of the variance inflation factor (VIF) as follows:

$$\text{VIF} = \frac{1}{1-r^2} \text{ Eq. 7}$$

where r is the correlation coefficient between independent variables. All analyses were performed with RStudio (version 1.1.453).

Results

The areas of the closed canopies and the gaps in the study plot were 2,125 m² and 375 m², respectively. In 2019, we identified 153 trees of *F. crenata* and 14 trees of other species growing in a closed canopy and 76 trees of *F. crenata* and 9 trees of other species growing in a gap. The LAI varied considerably among the plot grids (Fig. 1). LAI was found to be significantly higher in a closed canopy than in a gap (t -test; $P < 0.01$). The light attenuation in a closed canopy was stronger than that in a gap (Fig. 2). The average relative PPFD at the forest floor was 3%, while the total LAI of the study forest was estimated from the LIDAR system to be 6.43. The latter was very close to 6.49, which was estimated based on the litter trap collection (the product of the *F. crenata* LAI was 5.5 in 2011, and the ratio of the total basal area to the *F. crenata* basal area was 1.18 in 2011; Hikosaka et al. 2021), thereby suggesting that the herein

estimated LAI is valid. The extinction coefficient (K) of the study forest was calculated by using Eq. 6 and was found to be 0.55.

The RGR was significantly influenced by the height, the presence of a gap, and their interaction, whereas it was not related to the tree age (Table 1). The RGR increased along with an increasing height in the closed canopy, whereas it was independent of the height in the gap (Fig. 3a). In fact, the RGR of shorter trees was higher in the gap than in the closed canopy (Fig. 3a). The LUE was not significantly influenced by any of the independent variables alone (Table 1, Fig. 3b), but it was significantly influenced by the interaction of height and age (Table 1); the LUE of shorter individuals was higher in older than in younger trees, and the opposite was the case for the LUE of taller individuals (Fig. 4). The Φ_{mass} was significantly influenced by the presence of a gap alone, as well as by the interaction of the gap presence and the tree height, whereas it was not related to the tree height or the tree age alone (Table 1). With an increasing height, the Φ_{mass} increased in the closed canopy and decreased in the gap (Fig. 3c).

Table 1

Standard partial regression coefficient and significance in the multiple regression analysis of *Fagus crenata* individuals. Height (H) signifies the tree height; gap (G) signifies whether an individual tree was in a gap rather than in a closed canopy; age (A) signifies the tree age. The VIF of all combinations between independent variables was less than 3. Other abbreviations used: RGR, relative growth rate; LUE, light use efficiency; Φ_{mass} , light interception per unit of aboveground biomass; Φ_{area} , light interception per unit of leaf area; LAR, leaf area ratio; VIF, variance inflation factor. Significance: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; +, $P < 0.1$. Data of other species are not included.

	RGR	LUE	Φ_{mass}	Φ_{area}	LAR
Intercept	-0.09	0.10	-0.03	-0.04	-0.12
Height	0.54 ***	-0.20	0.02	0.82 ***	-0.42 ***
Gap	0.48 ***	-0.00	0.42 ***	0.34 ***	0.29 ***
Age	-0.38	0.25	-0.03	-0.08	-0.16
H × G	-0.32 **	-0.21	-0.31 **	-0.18 *	-0.34 **
G × A	0.16	0.30	-0.06	0.25 +	0.02
A × H	0.03	-0.27 *	0.07	0.10	0.19 +
H × G × A	-0.06	-0.02	0.00	-0.16 **	-0.02

The Φ_{area} was significantly influenced by the height, by the presence of a gap, by their interaction, as well as by the interaction of all three independent variables, whereas it was not related to the tree age (Table 1). The Φ_{area} increased with the increasing height in both the closed canopy and the gap, while the Φ_{area} of short trees was higher in the gap than in the closed canopy (Fig. 3d). The LAR was significantly influenced by the height, by the presence of a gap, and by their interaction, whereas it was

not related with the tree age (Table 1). The LAR decreased along with the increasing height in both the closed canopy and the gap, and it actually decreased more sharply in the gap than in the closed canopy (Fig. 3e).

Discussion

Our results demonstrate that the competitive asymmetry differs between a closed canopy and a gap, which is consistent with Hypothesis 2 rather than Hypothesis 1. In a closed canopy, both the Φ_{mass} and the RGR increased along with an increasing *F. crenata* tree height as larger individuals were able to acquire light and increase their own biomass in a more than proportional to their own size manner, thereby indicating that the competition for light was size-asymmetric. In contrast, the Φ_{mass} decreased with an increasing tree height in a gap, and the RGR of shorter trees was equivalent to that of taller trees, thereby indicating that – in this case – the competition for light was size-symmetric. This difference in competitive asymmetry was caused mainly by the difference in light attenuation, which was stronger in a closed canopy than in a gap (Fig. 2). The Φ_{area} , which represents the light interception per unit of leaf area, decreased sharply with depth in the closed canopy. Although the LAR of short trees was higher than that of tall trees, it did not compensate for the decrease in Φ_{area} , thereby leading to a lower Φ_{mass} in shorter trees. In contrast, light attenuation was not strong in gaps (Fig. 2). The decrease in the Φ_{area} of shorter trees was relatively small and sufficiently compensated for by the recorded increase in LAR, which led to an increase in the Φ_{mass} of shorter trees.

The lower RGR and Φ_{mass} values of shorter *F. crenata* individuals observed in a closed canopy are inconsistent with the expectation from earlier studies for multiple species stands, in which the shade-tolerant species successfully compensate for the lower light availability (Φ_{area}) through a higher LAR (Hirose and Werger 1995) or a higher LUE (Onoda et al. 2014). This could be partly explained by the differences in the maximal height; although *F. crenata* is known as a shade-tolerant species (Nakashizuka and Numata 1982; Nakashizuka 1985; Yamamoto 2000), small *F. crenata* individuals require a biomass investment in stems in order to achieve a high stature in future, thereby leading to a decrease in the LAR and the LUE due to a higher stem respiration, compared to short understory species.

LAR is known to be higher in shorter shaded plants (Nakashizuka 1988; Hirose and Werger 1995; Anten and Hirose 1998; van Kuijk et al. 2008; Pooter et al. 2008; Onoda et al. 2014). LAR can be decomposed as a product of the specific leaf area (SLA; leaf area per leaf mass) and the leaf mass fraction (LMF; leaf mass per aboveground). By analyzing individuals with different heights in monospecific stands with a different stand height of an annual herb, Anten and Hirose (1998) showed that the SLA is negatively correlated with light availability rather than with the plant height, whereas the LMF is negatively correlated with the plant height rather than with light availability. Thus, we could expect that the LAR of shorter individuals is higher in a closed canopy than in a gap. However, our results revealed that the LAR of shorter *F. crenata* individuals was lower in a closed canopy than in a gap. Although we did not analyze the SLA and the LMF of *F. crenata* individuals in our site, previous studies showed that the SLA is greater in shady than in sunny environments for the *Fagus* species (Kimura et al. 1998; Oguchi et al. 2005;

Yasumura et al 2005; Bachofen et al. 2020), thereby implying that the SLA might be higher in a closed canopy in our site, not being able to explain why the LAR is higher in a gap. Conversely, a lower LMF in shaded individuals has often been observed in some tropical tree species (Sterk 1997; Poorter 2001; ter Steege et al. 1994). This trend may be explained by some level of self-shading within the individual. As tree species tend to exhibit a large number of leaves around its main stem, mutual shading among these leaves does occur to an extent. Further increment of the leaf number may not contribute to an increase in the whole-plant photosynthesis, because such leaves may receive a light intensity that is lower than the light compensation point, especially under closed canopy conditions. This may not be the case for understory species, as they can avoid self-shading by their horizontal (rather than vertical) development of their branch architecture.

In our study, the LUE was not significantly influenced by variables except for the interactions of age and height (Table 1). Hikosaka et al. (1999, 2003) calculated the LUE as the daily whole-plant photosynthesis per daily absorbed PPFD of individuals in monospecific stands of an annual herbaceous species. They showed that the LUE was similar among large and middle individuals but very low in shorter individuals. The lower LUE of the shorter individuals was ascribed to a low light availability, in which their carbon assimilation was close to zero or negative. Such individuals would be eliminated in the course of a canopy development. In the studied forest, probably because individuals with a low LUE might have already been eliminated, we observed similar LUE values among the studied individuals.

The tree age is suggested to have a small direct effect on the competition for light. It alone did not significantly influence any of the studied dependent variables (Table 1). However, the interaction of age and size was significant; when larger individuals were compared, older trees demonstrated a lower LUE than younger trees (Table 1, Fig. 4). This result suggests that the negative effect on LUE is stronger in large and old individuals, which is partly consistent with our Hypothesis 3. This is the first report demonstrating that the plant age influences light competition when plants of the same size are compared.

Our results suggest that the competitive asymmetry changes in a dynamic manner in *F. crenata* forests. In a closed canopy, the competition for light is size-asymmetric. Size inequality is enlarged with time, and small individuals are eliminated. However, when a large individual falls due to age or disturbances, the occurring gap formation improves the light availability for individuals under or near the gap, and the light competition becomes size-symmetric until the gap closure (Fig. 5). Such dynamics of competitive asymmetry may also occur in multispecific forests.

During the early succession of secondary tropical forests, the Φ_{mass} was found to be similar among individuals (symmetric light interception) (Selaya et al. 2008; van Kuijk et al. 2008), whereas in a climax temperate forest, the Φ_{mass} was found to be lower in shorter species (asymmetric light interception) (Onoda et al. 2014). The symmetric light interception that occurred in the former was probably due to the fact that the early secondary succession is similar to the gap closure process. However, competitive asymmetry differs among forests depending on the developmental stages of the latter, and it can even

differ spatiotemporally within the same forest depending on the gap formation, thereby causing a diversity of size structure.

Conclusions

Our study demonstrated that the competitive asymmetry changes dynamically in a forest dominated by *F. crenata*. In a closed canopy, the competition is size-asymmetric even though the stand is dominated by a shade-tolerant tree. The RGR is higher in larger individuals as smaller individuals cannot sufficiently compensate for the lower light availability through their morphological (LAR) and physiological (LUE) characteristics. Conversely, the light availability of smaller individuals in a gap is improved, and the competition for light is size-symmetric. Such dynamic changes in competitive asymmetry can strongly influence the size structure of individuals and can cause a spatiotemporal diversity of size structures in forests.

Declarations

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References

1. **Amthor JS. 2010.** From sunlight to phytomass: on the potential efficiency of converting solar radiation to phyto-energy. *New Phytologist* 188:939–959.

2. **Anten NPR, Hirose T. 1998.** Biomass allocation and light partitioning among dominant and subordinate individuals in *Xanthium canadense* stands. *Annals of Botany* 82:665–67.
3. **Anten NPR, Hirose T. 1999.** Interspecific differences in above-ground growth patterns result in spatial and temporal partitioning of light among species in a tall-grass meadow. *Journal of Ecology* 87:583–597.
4. **Anten NPR, Miyazawa K, Hikosaka K, Nagashima N, Hirose T. 1998.** Leaf nitrogen distribution in relation to leaf age and photon flux density in dominant and subordinate plants in dense stands of a dicotyledonous herb. *Oecologia* 113:314–324.
5. **Asner GP, Keller M, Silva JNM. 2004.** Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon. *Global Change Biology* 10:765–783.
6. **Astigarraga J, Andivia E, Zavala MA, et al. 2020.** Evidence of non-stationary relationships between climate and forest responses: increased sensitivity to climate change in Iberian forests. *Global Change Biology* 26(9):5063–5076.
7. **Azuma W, Ishii HR, Masaki T. 2019.** Height-related variations of leaf traits reflect strategies for maintaining photosynthetic and hydraulic homeostasis in mature and old *Pinus densiflora* trees. *Oecologia* 189:317–328.
8. **Bachofen C, D’Odorico P, Buchmenn N. 2020.** Light and VPD gradients drive foliar nitrogen partitioning and photosynthesis in the canopy of European beech and silver fir. *Oecologia* 192:323–339.
9. **Berntson GM, Wayne PM. 2000.** Characterizing the size dependence of resource acquisition within crowded plant populations. *Ecology* 81:1072–85.
10. **Cao KF, Ohkubo T. 1999.** Suppression and release during canopy recruitment in *Fagus crenata* and *Acer mono* in two old-growth beech forests in Japan. *Plant Ecology* 145:281–290
11. **Dai XB. 1996.** Influence of light conditions in canopy gaps on forest regeneration: A new gap light index and its application in a boreal forest in east-central Sweden. *Forest Ecology and Management* 84:187–197.
12. **Falster DS, Westoby M. 2003.** Plant height and evolutionary games. *Trends in Ecology and Evolution* 18:337–343.
13. **Forrester DI, Bauhus J. 2016.** A review of processes behind diversity–productivity relationships in forests. *Current Forestry Reports* 2:45–61.
14. **Guo, Q., Chi, X., Xie, Z., Tang, Z. 2017.** Asymmetric competition for light varies across functional groups. *Journal of Plant Ecology* 10:74–80.
15. **Hikosaka K, Hirose T. 2001.** Nitrogen uptake and use by competing individuals in a *Xanthium canadense* stand. *Oecologia* 126:174–181.
16. **Hikosaka K, Kurokawa H, Arai T, et al. 2021.** Intraspecific variations in leaf traits, productivity and resource use efficiencies in the dominant species of subalpine evergreen coniferous and deciduous broad-leaved forests along the altitudinal gradient. *Journal of Ecology* 109:1804–1818.

17. **Hikosaka K, Sudoh S, Hirose T. 1999.** Light acquisition and use by individuals competing in a dense stand of an annual herb, *Xanthium canadense*. *Oecologia* 118:388–396.
18. **Hikosaka K, Yamano T, Nagashima H, Hirose T. 2003.** Light-acquisition and use of individuals as influenced by elevated CO₂ in even-aged monospecific stands of *Chenopodium album*. *Functional Ecology* 17:786–795.
19. **Hirose T, Werger MJA. 1995.** Canopy structure and photon flux partitioning among species in a herbaceous plant community. *Ecology* 76:466–474.
20. **Hukusima T, Takasuna H, Matsui T, Nishio T, Kyan Y, Tsunetomi Y. 1995.** New phytosociological classification of beech forests in Japan. *Japanese journal of ecology* 45:79-98 (In Japanese with English summary).
21. **IPBES. 2019.** *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. In Díaz S, Settele J, Brondízio ES, Ngo HT, Guèze M, Agard J, Zayas CN, Eds. Bonn, Germany: IPBES Secretariat.
22. **Kamiyama C, Oikawa S, Kubo T, Hikosaka K. 2010.** Light interception in species with different functional groups coexisting in moorland plant communities. *Oecologia* 164:591–599.
23. **Kamiyama C, Oikawa S, Hikosaka K. 2014.** Seasonal change in light partitioning among coexisting species of different functional groups along elevation gradient in subalpine moorlands. *New Phytologist* 204:913–923.
24. **Kikuzawa K, Umeki K. 1996.** Effect of canopy structure on degree of asymmetry of competition in two forest stands in northern Japan. *Annals of Botany* 77:565-571.
25. **Kimura K, Ishida A, Uemura A, Matsumoto Y, Terashima I. 1998.** Effects of current-year and previous-year PPFDs on shoot gross morphology and leaf properties in *Fagus japonica*. *Tree Physiology* 18:459–466.
26. **van Kuijk M, Anten NPR, Oomen RJ, van Bentum DW, Werger MJA. 2008.** The limited importance of size-asymmetric light competition and growth of pioneer species in early secondary forest succession in Vietnam. *Oecologia* 157:1–12.
27. **Kweon D, Comeau PG. 2019.** Relationships between tree survival, stand structure and age in trembling aspen dominated stands. *Forest Ecology and Management* 438:114–122.
28. **MacArthur RH, Horn HS. 1969.** Foliage profile by vertical measurements. *Ecology* 50:802–804.
29. **Matsumoto Y, Oikawa S, Yasumura Y, Hirose T, Hikosaka K. 2008.** Reproductive yield of individuals competing for light in a dense stand of an annual, *Xanthium canadense*. *Oecologia* 157:185–195.
30. **McCree KJ. 1972.** Test of current definitions of photosynthetically active radiation against leaf photosynthesis data. *Agricultural Meteorology* 10:443–453.
31. **Monsi M, Saeki T. 1953.** Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Japanese journal of botany* 14:22–52.

32. **Nagashima H, Terashima I, Katoh S. 1995.** Effects of plant density on frequency distributions of plant height in *Chenopodium album* stands: analysis based on continuous monitoring of the height-growth of individual plants. *Annals of Botany* 75:173–180.
33. **Nakashizuka T. 1984.** Regeneration process of climax beech (*Fagus crenata* Blume) forests V. population dynamics of beech in a regeneration process. *Japanese journal of ecology* 34:411–419.
34. **Nakashizuka T. 1985.** Diffused light conditions in canopy gaps in a beech (*Fagus crenata* Blume) forest. *Oecologia* 66:472–474.
35. **Nakashizuka T. 1988.** Regeneration of beech (*Fagus crenata*) after the simultaneous death of undergrowing dwarf bamboo (*Sasa kurilensis*). *Ecological Research* 3:21–35.
36. **Nakashizuka T, Kohyama T. 1995.** The significance of the asymmetric effect of crowding for coexistence in a mixed temperate forest. *Journal of Vegetation Science* 6:509–51.
37. **Nakashizuka T, Numata M. 1982.** Regeneration process of climax beech forests I. Structure of a beech forest with the undergrowth of Sasa. *Japanese journal of ecology* 32:57–67.
38. **Oguchi R, Hikosaka K, Hirose T. 2005.** Leaf anatomy as a constraint for photosynthetic acclimation: differential responses in leaf anatomy to increasing growth irradiance among three deciduous trees. *Plant Cell and Environment* 28:916–927.
39. **Onoda Y, Saluñga JB, Akutsu K, Aiba SI, Yahara T, Anten NP. 2014.** Trade-off between light interception efficiency and light use efficiency: implications for species coexistence in one-sided light competition. *Journal of ecology* 102:167–75.
40. **Poorter L. 2001.** Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. *Functional Ecology* 15:113–123.
41. **Poorter L, Rozendaal DMA. 2008.** Leaf size and leaf display of thirty-eight tropical tree species. *Oecologia* 158:35–46.
42. **Rüger N, Berger U, Hubbell SP, Vieilledent G, Condit R. 2011.** Growth strategies of tropical tree species: disentangling light and size effects. *PLOS ONE* 6:e25330.
43. **Ruiz-Benito P, Ratcliffe S, Zavala MA, et al. 2017.** Climate- and successional-related changes in functional composition of European forests are strongly driven by tree mortality. *Global Change Biology* 23:4162–4176.
44. **Ryan MG, Yoder BJ. 1997.** Hydraulic limits to tree height and tree growth. *BioScience* 47:235–242.
45. **Schliemann SA, Bockheim JG. 2011.** Methods for studying treefall gaps: A review. *Forest Ecology and Management* 261:1143–1151.
46. **Selaya NG, Oomen RJ, Netten JJC, Werger MJA, Anten NPR. 2008.** Biomass allocation and leaf life span in relation to light interception by tropical forest plants during the first years of secondary succession. *Journal of Ecology* 96:1211–1221.
47. **Shimazaki M, Sasaki T, Hikosaka K, Nakashizuka T. 2011.** Environmental dependence of population dynamics and height growth of a subalpine conifer across its vertical distribution: an approach using high-resolution aerial photographs. *Global Change Biology* 17:3431–3438.

48. **Sillett SC, Van Pelt R, Koch GW, *et al.* 2010.** Increasing wood production through old age in tall trees. *Forest Ecology and Management* 259:976–994.
49. **ter Steege H, Bokdam C, Boland M, Dobbelsteen J, Verburg I. 1994.** The effect of man made gaps on germ- ination, early survival and morphology of *Chlorocardium rodiei* seedlings in Guyana. *Journal of Tropical Ecology* 10:245–260.
50. **Sterck FJ. 1997.** Trees and light. Tree development and morphology in relation to light availability in a tropical rain forest in French Guiana. PhD Thesis, Wageningen Agricultural University, The Netherlands.
51. **Thomas SC, Weiner J. 1989.** Growth, death and size distribution change in an *Impatiens pallida* population. *Journal of Ecology* 77:524–536.
52. **Torresan C, del Río M, Hilmers T, *et al.* 2020.** Importance of tree species size dominance and heterogeneity on the productivity of spruce–fir–beech mountain forest stands in Europe. *Forest Ecology and Management* 457:117716.
53. **Weiner J. 1985.** Size hierarchies in experimental populationns of annual plants. *Ecology* 66:743–752.
54. **Weiner J. 1990.** Asymmetric competition in plant populations. *Trends in Ecology and Evolution* 5:360–364.
55. **Weiner J, Thomas SC. 1986.** Size variability and competition in plant monocultures. *Oikos* 47:211–222.
56. **Yamamoto S. 2000.** The Gap Theory in Forest Dynamics. The botanical magazine, Tokyo, 105:375–383.
57. **Yasumura Y, Onoda Y, Hikosaka K, Hirose T. 2005.** Nitrogen resorption from leaves under diferent growth irradiance in three deciduous woody species. *Plant Ecology* 178:29–37.

Figures

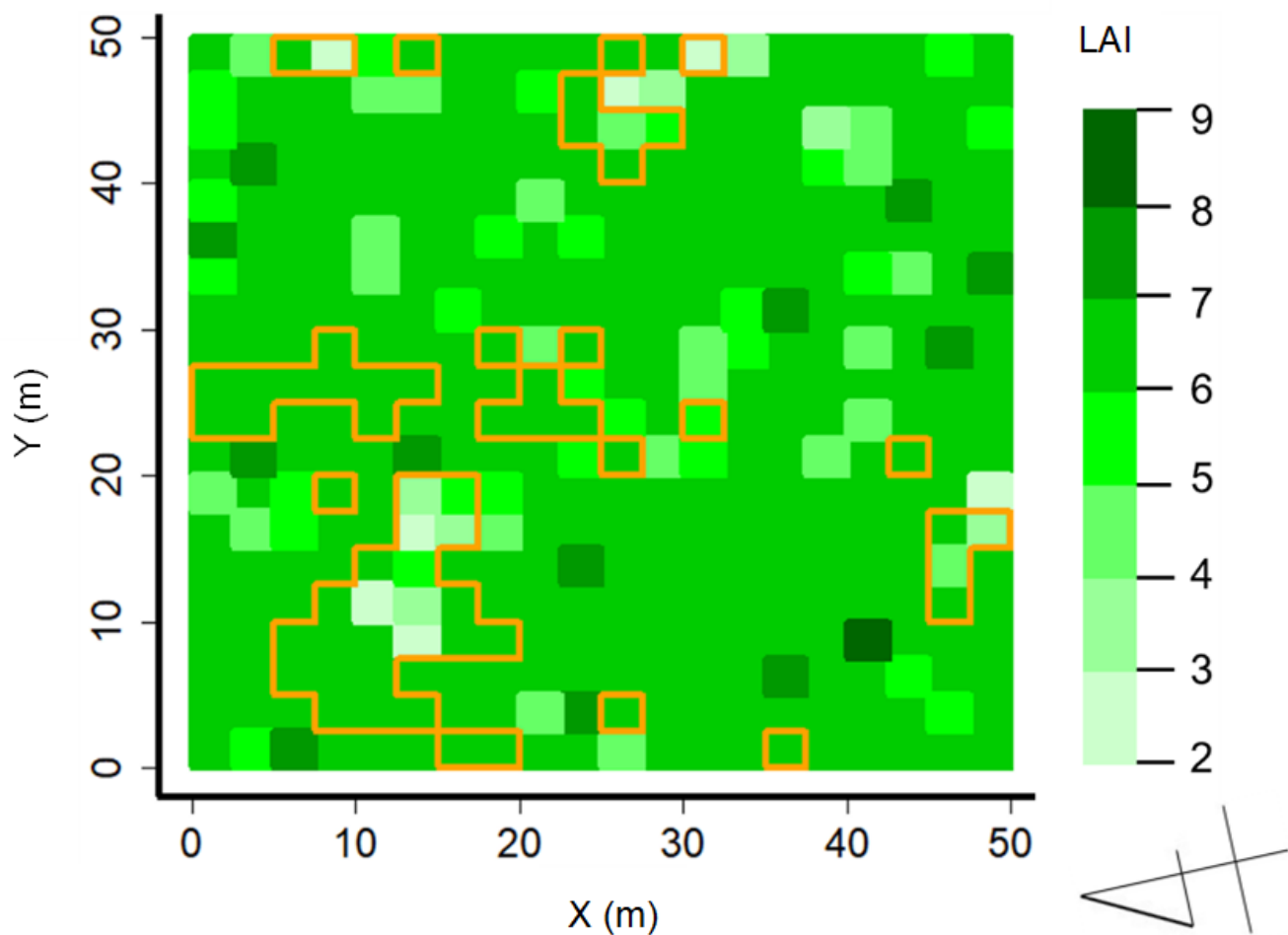


Figure 1

Horizontal distribution of leaf area per ground area (LAI) and of the gap in the study site (50 × 50 m) that was highly dominated by a shade-tolerant tree, *Fagus crenata*. Green intensity represents the LAI of each grid, while the areas surrounded by orange frames represent a gap.

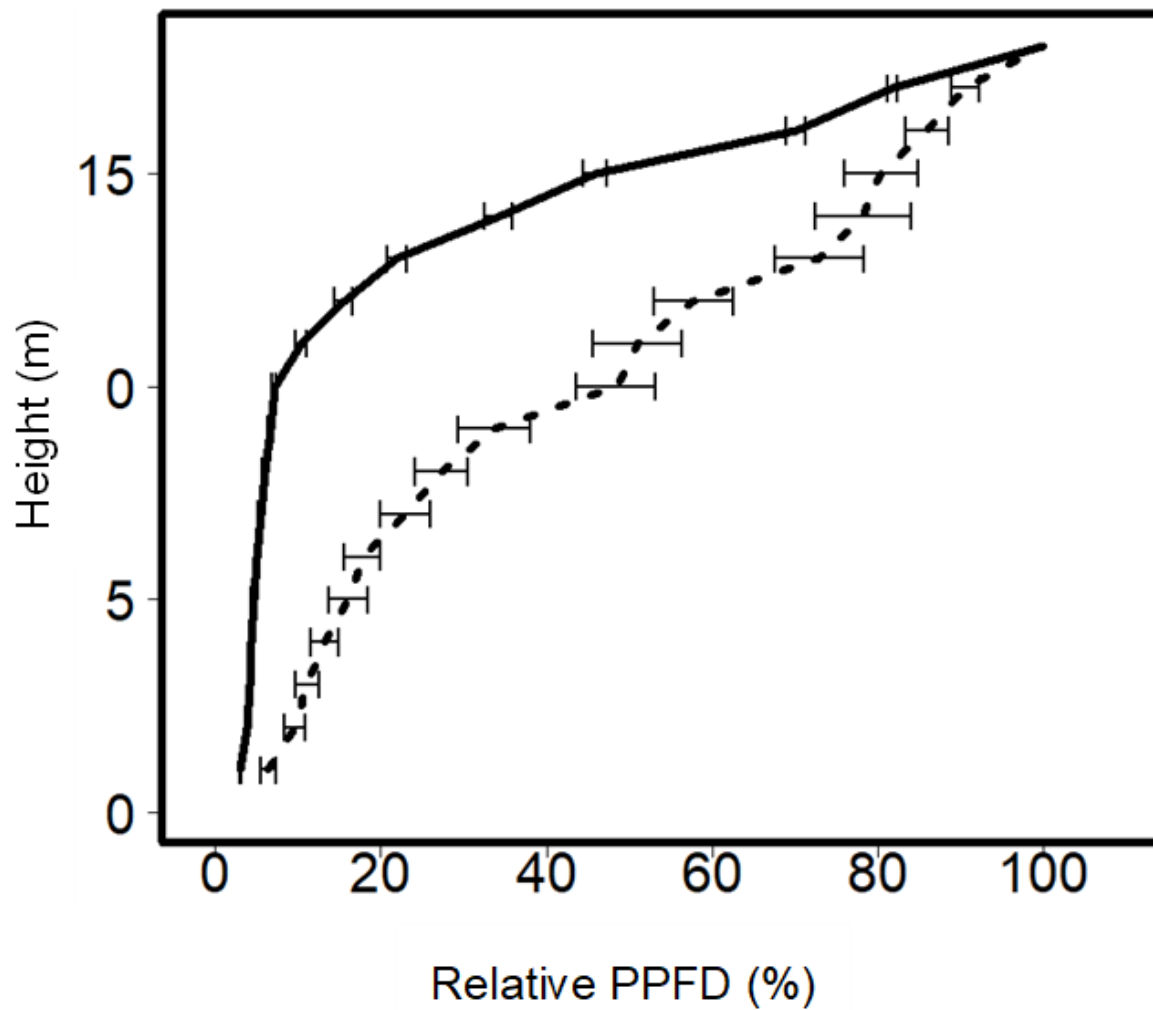


Figure 2

Relationships between height and relative photosynthetic photon flux density (PPFD) in the study site. Solid and dotted lines represent the light attenuation pattern in a closed canopy and in a gap, respectively. Bars denote SE ($n = 340$ for closed canopy; $n = 60$ for gap).

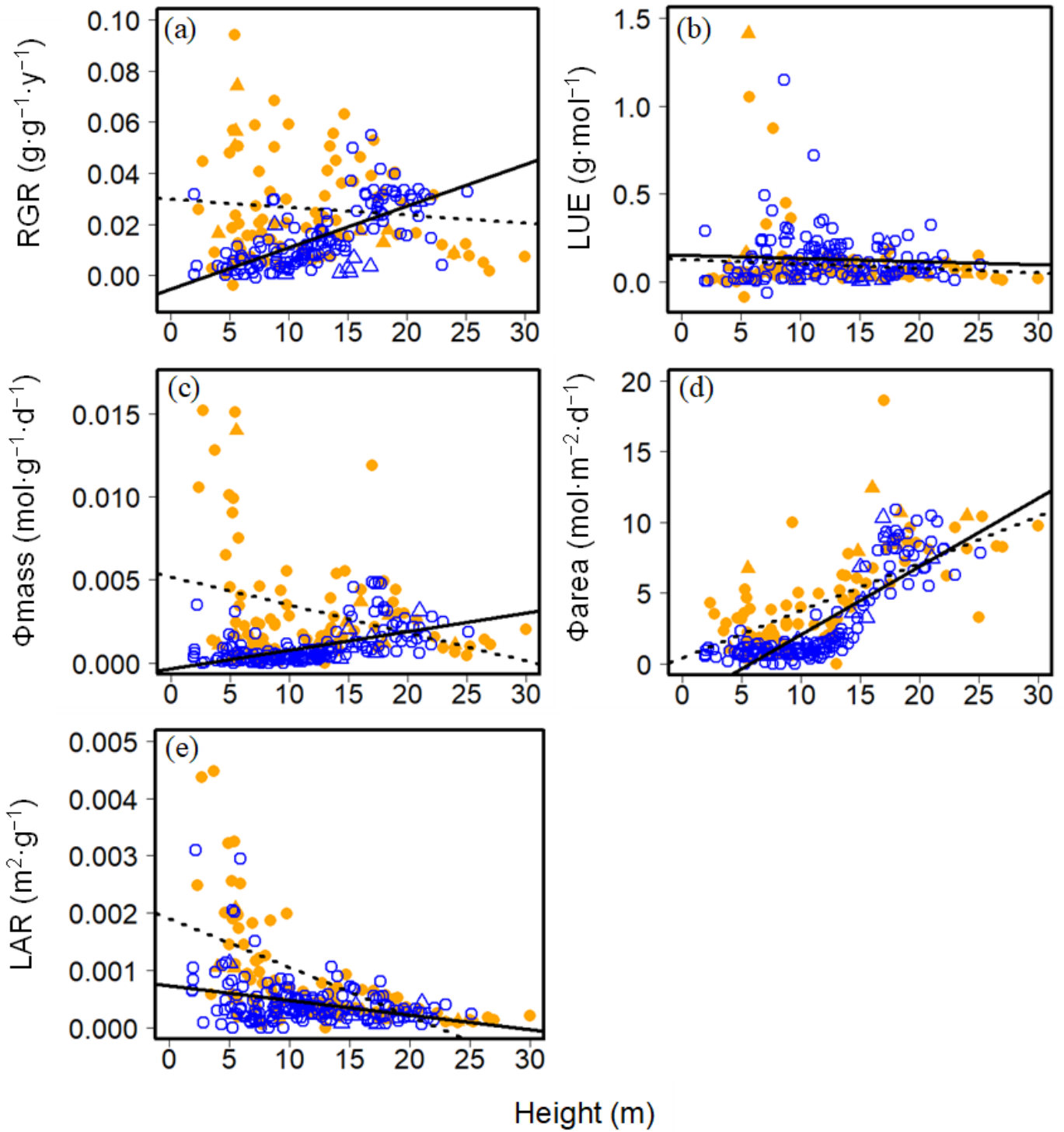


Figure 3

(a) Relative growth rate (RGR), (b) light use efficiency (LUE), (c) light interception per unit of aboveground biomass (Φ_{mass}), (d) light interception per unit of leaf area (Φ_{area}), and (e) leaf area ratio (LAR) of individuals in a closed canopy and in a gap, as a function of the tree height in the study site. Circles and triangles represent individuals of the *Fagus crenata* and of other species, respectively. Blue and orange symbols represent individuals in a closed canopy and in a gap, respectively. Solid and dotted lines

represent the linear regression of *F. crenata* individuals in a closed canopy and in a gap, respectively. Data of other species were not included in the regression analysis.

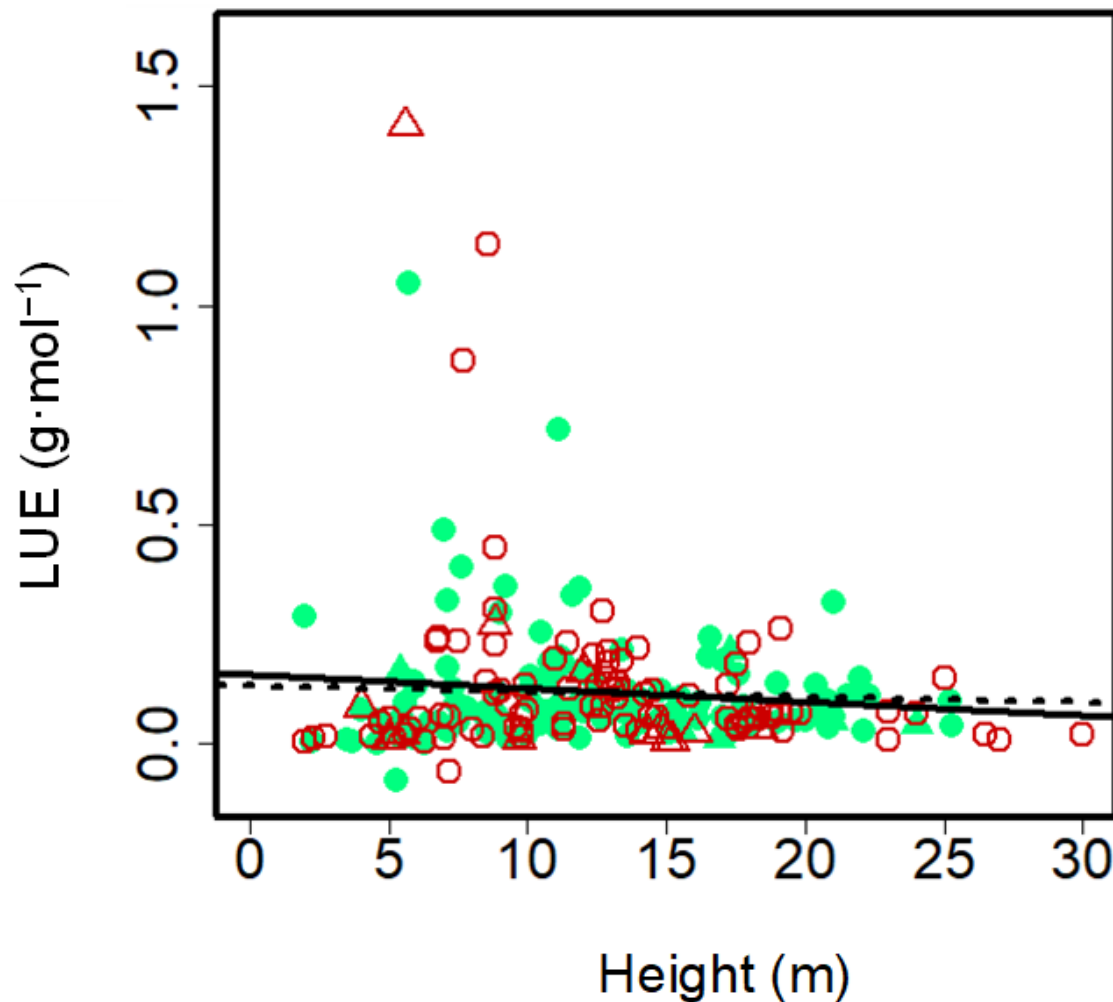


Figure 4

Light use efficiency (LUE) in relatively old and young individuals in the study site *versus* tree height. Circle and triangle symbols denote *Fagus crenata* and other species, respectively. Red and green symbols denote individual value of relatively old and young individuals in each size class, respectively. Solid and dotted lines represent the linear regression of relatively old and young *F. crenata* individuals, respectively. Data of other species were not included in the regression analysis.

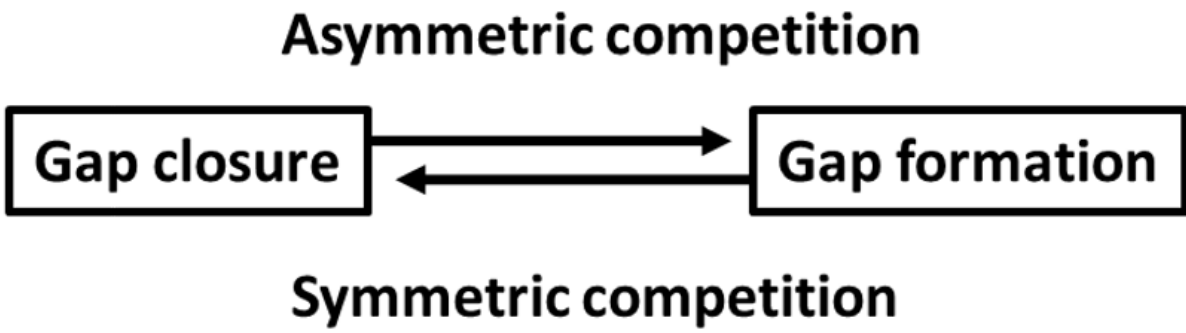


Figure 5

Dynamics of the size inequality of forests due to changes in light availability.