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RESEARCH ARTICLE

Vertical and horizontal light heterogeneity along gradients of secondary succession in cool- and warm-temperate forests

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Abstract

Aims: Light availability varies drastically in forests, both vertically and horizontally. Vertical light heterogeneity (i.e., patterns of light attenuation from the forest canopy to the floor) may be related to light competition among trees, while horizontal light heterogeneity (i.e., variations in light intensity at a given height within forests) may be associated with light-niche partitioning among tree species. However, light heterogeneity in vertical and horizontal directions and their associations with forest structure are rarely studied to date. Here we report the first comprehensive study to compare the vertical and horizontal light heterogeneity in differently aged forests in two forest types.

Location: Twelve forest stands of different ages in cool-temperate forests (consisting of deciduous broad-leaved trees) and five of different ages in warm-temperate forests (evergreen conifer and deciduous broad-leaved trees) in Japan.

Methods: We measured vertical light profiles at 1-m intervals from the understorey (1 m above the ground) to the top canopy (12–22 m depending on stands) at 16 locations for each stand (20 m × 20 m). We also measured structural parameters (diameter at breast height, height, and crown dimensions) for all major trees in these stands.

Results: Along the secondary successional gradients, the vertical and horizontal light heterogeneity changed in a systematic manner in both forests. The vertical light attenuation rate was steeper in early succession and more gradual in late succession, and the horizontal light heterogeneity was relatively small in early succession and more pronounced in late succession. The vertical light attenuation rate was different between the two forest types; the light intensity dropped more sharply from the canopy surface in the cool-temperate forests due to the crown being vertically shorter and denser (i.e., higher leaf density per unit volume).

Conclusion: In early succession, a steeper light attenuation rate is likely related to the strong light competition among co-occurring trees and thus a self-thinning process. In late succession, the high spatial light heterogeneity in forests (i.e., larger horizontal light heterogeneity and gradual light attenuation rate) may allow more species to partition light, and thus may enhance species coexistence and diversity.

KEYWORDS
forest structure, horizontal light heterogeneity, light attenuation rate, light competition, secondary succession, species coexistence, temperate forests, understorey light intensity, vertical light profile

1 | INTRODUCTION

Tall, uneven, and complex forest structures create light environments in forest stands that are much more heterogeneous than those in herbaceous stands (Kitajima et al., 2005). Such high spatial light heterogeneity in a forest is strongly associated with the forest dynamics; for instance, the vertical light heterogeneity in a forest — patterns of light attenuation from the forest canopy to the floor — may be related to light competition among tree individuals (Onoda et al., 2014; Parker, 2020) and to species coexistence through vertical light niche partitioning (e.g. forest architecture hypothesis; Kohyama, 1993). Similarly, horizontal light heterogeneity in a forest — the variation in light intensity at a given height — has been studied in relation to tree species coexistence as a consequence of horizontal light-niche partitioning (e.g. forest gap dynamics; Kitajima & Poorter, 2008). While the importance of vertical and horizontal light heterogeneity in tree performance and forest dynamics has been well recognized for many years, direct quantifications of such light heterogeneity have been rarely done (Yoda, 1974; Fauset et al., 2017).

The vertical light heterogeneity in a forest may be related to light competition among tree individuals, which is a driver for trees growing taller (Falster & Westoby, 2003) and also responsible for forest dynamics during succession through a self-thinning process (i.e. progressive decline in the density of a population of growing plants; Yoda et al., 1963; Schwinning & Weiner, 1998). Earlier research estimated vertical light profiles using Beer's law (Monsi & Saeki, 1953; Perot et al., 2017), which assumes that light intensity attenuates log-linearly with the cumulative leaf area from the forest canopy to the forest floor. While Beer's law may be useful for approximating the vertical light profile in horizontally homogeneous communities like crop stands (Monsi & Saeki, 1953), it may not be suitable for estimating the vertical light gradient in natural forests due to their more complex structure (Montgomery & Chazdon, 2001; Kitajima et al., 2005). Therefore, a direct quantification of vertical light profiles in forests is needed to capture the real variation in light intensity and to understand its importance in light competition and tree species coexistence and hence in forest dynamics.

In addition to vertical light heterogeneity, the horizontal light heterogeneity in a forest also has a major influence on forest dynamics. In the understorey, horizontal light heterogeneity, which is strongly associated with the presence of canopy gaps (Roncal, 2014), influences the patterns of recruitment, growth, and survival of tree seedlings and saplings, even at the scale of a few square meters (Jin et al., 2018). In the canopy layer, horizontal light heterogeneity may be associated with crown development patterns because canopy trees tend to expand their crowns toward a better light environment (Muth & Bazzaz, 2002). Although the horizontal light heterogeneity in forests has been well quantified in the understorey layer (e.g. Lebrija-Trejos et al., 2011; Sercu et al., 2017), there has been little quantification in the canopy layer (Matsuo et al., 2021). Therefore, quantifications of the horizontal light heterogeneity at multiple heights are important to determine which height has the highest heterogeneity and thus to understand how and where in a forest horizontal light heterogeneity plays a key role in the light-niche partitioning of tree species.

Forest structure changes along a gradient of secondary succession (e.g. increases in canopy height, above-ground biomass and crown size of canopy trees) and differs among different forest types (Olson et al., 2018; Cook-Patton et al., 2020). These differences in forest structure can have profound consequences for patterns of vertical and horizontal light heterogeneity in forests (Stark et al., 2012; Binkley et al., 2013). For instance, the light attenuation rate (i.e., the rate of light extinction per unit of vertical height) becomes steeper with increasing leaf area density, and the horizontal heterogeneity of the understorey light intensity decreases with the total crown area of a forest (Brown & Parker, 1994; Lebrija-Trejos et al., 2010).

This study aims to assess how the vertical and horizontal light heterogeneity in a forest differ along a gradient of secondary succession in two climatically different forest types: cool-temperate forests where deciduous broad-leaved trees dominate and warm-temperate forests where evergreen conifers and deciduous broad-leaved trees dominate. Due to the longer growth period in warm-temperate forests, forest height and stand size (above-ground biomass, total crown area, and mean crown depth) tend to be larger in warm-temperate forests than cool-temperate forests for a given forest age (see Figure 1). Specifically, we address the following two hypotheses:

(1) The vertical and horizontal light heterogeneity increases along the secondary successional gradient because of larger total crown area and longer mean crown depth in later successional stages in both forest types.

(2) The vertical and horizontal light heterogeneity in a forest is larger in warm-temperate forests than in cool-temperate forests for all successional stages because of larger total crown area and crown depth in the former.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted in two climatically different (cool and warm) temperate forests as described later (Appendix S1). Within each forest type, we studied forest stands of different ages (from

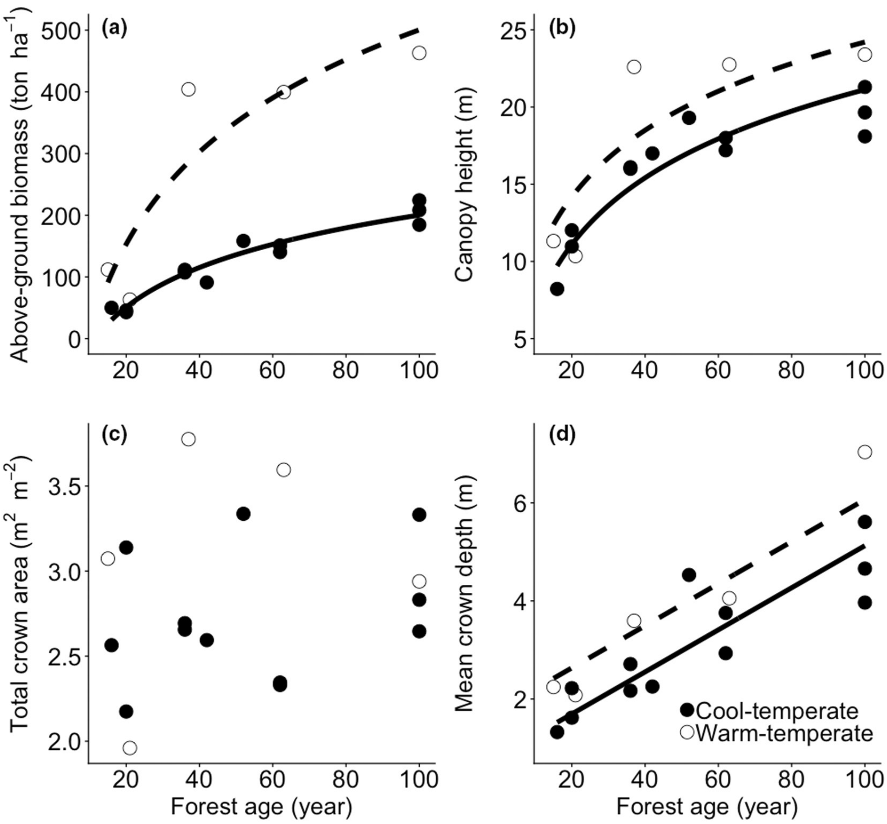

FIGURE 1 Successional trajectories of forest structural attributes in cool- and warm-temperate forests: (a) total above-ground biomass; (b) canopy height of the forest; (c) total crown area per unit of ground area; and (d) mean crown depth plotted against forest age. Continuous lines represent the regression lines for the cool-temperate forests, and hatched lines represent the regression lines for the warm-temperate forests. The detailed model results can be found in Appendix S3. Regression lines are (a) cool: $y = 213.44 \log_{10}(x) - 226.65$, warm: $y = 497.04 \log_{10}(x) - 493.59$; (b) cool: $y = 14.35 \log_{10}(x) - 7.57$, warm: $y = 14.35 \log_{10}(x) - 4.49$; (d) cool: $y = 0.043x + 0.84$, warm: $y = 0.043x + 1.78$

15 years to more than 100 years old) using a chronosequence approach to explore changes in forest structure and in vertical and horizontal light heterogeneity along the secondary successional gradients (Pickett, 1989). The cool-temperate stands are located in the Tomakomai Experimental Forest of Hokkaido University, Hokkaido, Japan (42°41′ N, 141°36′ E, 65 m elevation; see Hiura, 2001 for detailed site description). Secondary succession in this forest is in progress, either windthrown due to typhoons or after logging (Hiura, 2001). In cool-temperate forests, we studied 12 forest stands that differed in age from 16 years to more than 100 years according to the aerial images taken by the governments (Onoda, unpublished). The forest is mainly composed of deciduous broad-leaved trees; *Betula platyphylla* Sukaczev and *Cerasus maximowiczii* (Rupr.) Kom & Aliss. are the dominant species in the earlier successional stands, and *Quercus crispula* Blume and *Tilia japonica* (Miq.) Simonk. are the dominant species in the later successional stands, based on relative biomass (Appendix S2). Mean annual precipitation is 1351 mm, and the mean annual temperature was 8.1°C at Tomakomai meteorological station during 2009–2018.

The warm-temperate stands are located in the Wakayama Forest Research Station of Kyoto University and on nearby private land in the southern part of mainland Japan (34°04′ N, 135°32′ E); secondary succession in these stands is in progress after logging (Nomura, unpublished). In warm-temperate forests, we studied five forest stands in which four secondary forest plots were on private land and one old-growth forest plot was in the long-term monitoring area. The ages of the secondary stands range from 15 to 63 years, and the age of the old-growth plot is assumed to be approximately 100 years old according to aerial images taken by the governments (Nomura, unpublished). The canopy layer of these stands is dominated by evergreen conifers and deciduous broad-leaved trees; *Pinus densiflora* Siebold & Zucc. was the dominant conifer species in the 15-, 37-, and 63-year-old plots, *Lindera erythrocarpa* Makino is the dominant deciduous species in the 21-year-old plots, and *Abies firma* Siebold & Zucc. is the dominant conifer species in the roughly 100-year-old plots, based on the relative biomass (Appendix S1). In addition, evergreen broad-leaved species, such as *Eurya japonica* Thunb. and *Ilex pedunculosa* Miq. are abundant in the understorey in the 15-, 37-, 63-, and 100-year-old plots. Mean annual precipitation is 2332 mm, and the mean annual temperature was 14.0°C at Shimizu meteorological station, which is the nearest station to the studied sites, during 2009–2018.

2.2 | Field survey

Each study plot (in a size of 20 m × 20 m) was established in a typical location for each forest stand of a certain age. We avoided large gaps and tracks when establishing the study plots. Each plot was subdivided into 16 subplots (5 m × 5 m) and the vertical light profile was measured in the center of each subplot. As described later, the measurement of vertical light profile was labor-intensive work, and there was a trade-off between horizontal resolution and sampling effort for a given fieldwork effort. If the minimum horizontal resolution was too fine (for example, 1 m × 1 m) we could only measure horizontal heterogeneity of small areas covering only a few trees. On the contrary, if the minimum horizontal resolution was too coarse (for example, 10 m × 10 m) we would miss most of the local light heterogeneity between the measuring places. Therefore, we chose a 5 m × 5 m subplot as a minimum resolution and evaluated the horizontal light heterogeneity using the data of 16 subplots for each plot (in total 16 subplots × 17 plots = 272 vertical light profiles).

The vertical light profile in the forests was measured using a PPFD (photosynthetic photon flux density) sensor (DEFI2-L, JFE Advantech Co. Ltd, Hyogo, Japan) attached to a 20-m telescopic carbon rod (Taketani Trading Co. Osaka, Japan; Onoda et al., 2014). At the center of each of the 16 subplots, PPFD was measured at height intervals of 1 m, from 1 m to up to 22 m height (20 + 2 m height of the person holding the equipment). At each height, PPFD was recorded every second for 5 s, and the average value was used. Relative light intensity (%) at each height was calculated as the irradiance at a given height divided by the irradiance either above the canopy or measured simultaneously in an open area near the plot, multiplied by 100. Light intensity was measured under overcast sky conditions in July and August 2019 in the cool-temperate forests and in June 2018 in the warm-temperate forests in order to represent the average light environment during the growing season without the confounding influence of direct sunlight, such as sunflecks, consistent with Parker et al. (2002), who found that vertical light profiles measured under overcast skies were smoother than those under clear skies. The diffuse light under overcast sky conditions can also penetrate deeper into forest canopies than direct light and can thus influence more the light interception among tree individuals at different heights (Alton et al., 2007; Zhang et al., 2011).

2.3 | Forest structural attributes

We measured diameter at breast height (DBH), heights of the tops and bottoms of the crowns and crown radius for individuals in each plot. The heights of the tops and bottoms of the crowns were measured using a telescope rod or an ultrasound range finder (Vertex IV; Haglöf, Långsele, Sweden). When measured with an ultrasound range finder, the tree height measurement was done twice from different directions and the average value used in order to minimize measurement errors. Crown depth is defined as difference between the heights of the top and bottom of the crown. Because the plots in the cool- and warm-temperate forests were established for different purposes, the measurement criteria for smaller trees were slightly different. In the cool-temperate forests, all individual trees with a DBH of more than 1 cm were measured. In the warm-temperate forests, a hierarchical measurement design was used: all individual trees with a DBH of more than 5 cm were measured, but those with a DBH of 1–5 cm were measured only in the four corner subplots. The crown radius was measured in the four cardinal directions for all trees in the cool-temperate forests; in the warm-temperate forests, the crown radius was measured similarly for bigger trees, but only in two orthogonal cardinal directions (north–south and east–west) for smaller trees. To account for the different measurement criteria, we standardized data when calculating the forest structural attributes (see below for the detailed standardization method).

We calculated the above-ground biomass (AGB) of each individual using the allometric equations developed for Japanese tree species (Ishihara et al., 2015) using DBH and species-specific wood density:

$$\ln(\mathrm{AGB}) = -1.196 + 1.622\ln(D) + 0.338\ln(D)^2 - 0.044\ln(D)^3 + 0.708\ln(\rho) \quad (1)$$

where AGB is the above-ground biomass (kg), D is DBH (cm), and ρ is the species-specific wood density ($\mathrm{g\,cm^{-3}}$). Wood density data for all tree species in the studied sites were obtained from Aiba et al. (2012) and Onoda (unpublished). The total AGB of a plot was calculated as the sum of the AGB of all individuals within that plot. The height of the highest individual per plot was used as the maximum canopy height of each plot. The total crown area per unit ground area was calculated as the sum of the individual crown areas divided by the plot size ($20\,\mathrm{m} \times 20\,\mathrm{m} = 400\,\mathrm{m}^2$), where each individual crown area (m^2) was calculated as $d_1 d_2 \pi/4$, where d_1 and d_2 are the crown diameters in orthogonal directions. The mean crown depth of the individual trees within each plot was the average of all crown depths. Because trees with a DBH between 1 and 5 cm were measured only for the four corner subplots in the warm-temperate forest (one quarter of the plot), we multiplied the total AGB, total crown area, and mean crown depth for trees with a DBH between 1 and 5 cm in the warm-temperate forests by 4 to account for the different sampling procedures.

2.4 | Vertical and horizontal light heterogeneity

To evaluate the light attenuation rate along the vertical axis, the following logistic sigmoid curve was applied to the relationship between the relative light intensity and the height above the ground (Matsuo et al., 2021):

$$\mathrm{RLI} = 100 / \left[1 + \exp\{-a \times (h - b)\}\right] \quad (2)$$

where RLI is the relative light intensity (%), a is the slope at the inflection point, h is the height above the ground (m), and b is the height of the inflection point of the logistic sigmoid curve (m). We used a as the indicator of the light attenuation rate (i.e., the rate of light extinction per unit of vertical height) in this study.

To quantify the horizontal light heterogeneity at each height in each plot, we calculated the coefficient of variation of the relative light intensity ($\mathrm{RLI_{cv}}$) among the 16 subplots at each height from 1 m to up to 22 m (Lebrija-Trejos et al., 2011; Matsuo et al., 2021):

$$\mathrm{RLI_{cv}} = \left(\mathrm{RLI_{sd}} / \mathrm{RLI_{average}}\right) \times 100 \quad (3)$$

where $\mathrm{RLI_{sd}}$ and $\mathrm{RLI_{average}}$ were the standard deviation and average, respectively, of the RLI among the 16 subplots per plot for each height class. $\mathrm{RLI_{cv}}$ was considered to be an indicator of the horizontal variation of light intensity at each height. Using this dataset, the patterns of the horizontal light heterogeneity along the vertical axis were analyzed to determine which height shows the greatest horizontal light heterogeneity within a plot.

To evaluate the mean horizontal light heterogeneity of the whole forest (integrating all horizontal light heterogeneity along the vertical axis, from the canopy top to the forest floor), we calculated the mean RLI_{cv} across all height classes and used it as the indicator of the horizontal light heterogeneity at the whole-forest level. We considered the RLI_{cv} at 1 m above the ground to be an indicator of the horizontal light heterogeneity in the understorey for tree seedlings and saplings.

2.5 | Data and statistical analysis

All data analysis was performed using R software (version 3.4.0, R Core Team, R Foundation for Statistical Computing, Vienna, Austria). We analyzed the vertical and horizontal light attributes as well as the forest structural attributes in relation to the forest ages and forest types. We used ANCOVA (Analysis of Covariance) with forest structural attributes or light attributes as response variables and with forest age, forest type (cool or warm-temperate), and their interaction as predictor variables (Equation 4); the best models were selected based on Akaike's Information Criterion (AIC) by considering equally plausible models under a delta AIC (Aho et al., 2014).

$$\text{Response variable} \sim \text{forest age} + \text{forest type} + \text{forest age: forest type} \tag{4}$$

We chose the best functions for the models from a linear function, a $\log_{10}$-transformed linear function, a rational function, and a quadratic function based on AIC. We also used ANCOVA to examine whether and how the canopy architectural traits were associated with the light attributes in cool- and warm-temperate forests.

3 | RESULTS

3.1 | Forest structure along the secondary successional gradient

The total AGB, canopy height of the forest, and mean crown depth were greater along the secondary successional gradients in both forests (Figure 1, Appendix S3). For each successional stage, these three attributes were greater in the warm-temperate forest than the cool-temperate forest (Figure 1, Appendix S3). However, the total crown area per unit of ground area did not vary among the differently aged stands that were between 15 and more than 100 years old, and did not differ between the cool- and warm-temperate forests (Figure 1c). The total AGB was in the range 42.9–463 ton ha^{-1}, the canopy height was in the range 8.2–23.4 m, the total crown area per unit of ground area was in the range 2.0–3.6 m^2 m^{-2}, and the mean crown depth was in the range 1.3–7.0 m (Figure 1).

3.2 | Vertical and horizontal light heterogeneity along the secondary successional gradient

Light intensity declined from the top canopy toward the forest floor in all studied plots, but the pattern varied between the subplots within a forest stand (Figure 2a, Appendix S4) and between differently aged stands (Figure 2b). Similarly, the horizontal light heterogeneity, expressed as the coefficient of variation of the relative light intensity (RLI_{cv}) for a given height, varied widely along the vertical axis within a stand as well as between differently aged stands (Figure 2c, Appendix S5). The peak horizontal variation was found in the middle layer in all the studied stands: at ca. 40% of canopy height for earlier successional stages and at ca. 80% for later successional stages (Figure 2c).

The light attenuation rate (i.e., the rate of light extinction with height) was steeper in the earlier than in the later successional stage, irrespective of forest types (Figure 3a, Appendix S6). $RLI_{average}$ at 1 m above the ground was, on average, 4.0% ± 1.9% in the cool-temperate forests and 3.8% ± 2.6% in the warm-temperate forests (see Appendix S7 for the detail information) but did not systematically vary among differently aged stands within either forest (Figure 3b). The horizontal light heterogeneity in the understorey — that is, RLI_{cv} at 1 m above the ground — showed a U-shaped pattern along the secondary successional gradient, with the lowest value at the middle successional stages (Figure 3c, Appendix S6). The horizontal light heterogeneity in the whole forest, measured as the mean RLI_{cv} across all heights, was in the range 24.2%–73.3% and was larger in the later successional stage in both forest types (Figure 3d, Appendix S6).

3.3 | Different patterns of light distribution in cool- and warm-temperate forests

Unlike the forest structural attributes, the light attributes did not differ between the cool- and warm-temperate forests, except for the light attenuation rate (Figure 3, Appendix S6). The light attenuation rate was higher in the cool than in the warm-temperate forests for a given forest age, meaning that the light intensity declined faster within canopy layers in cool temperature forests.

3.4 | Vertical and horizontal light heterogeneity in relation to canopy architecture

The vertical and horizontal light heterogeneity was driven by the canopy architecture irrespective of the forest types, except for horizontal light heterogeneity at 1 m above the ground (Figure 4, Appendix S8). Stands with more total crown area per unit of ground area had lower $RLI_{average}$ at 1 m above the ground (Figure 4a), while stands with longer crown depth had more gradual vertical light attenuation and greater horizontal light heterogeneity of a whole forest (Figure 4c,d).

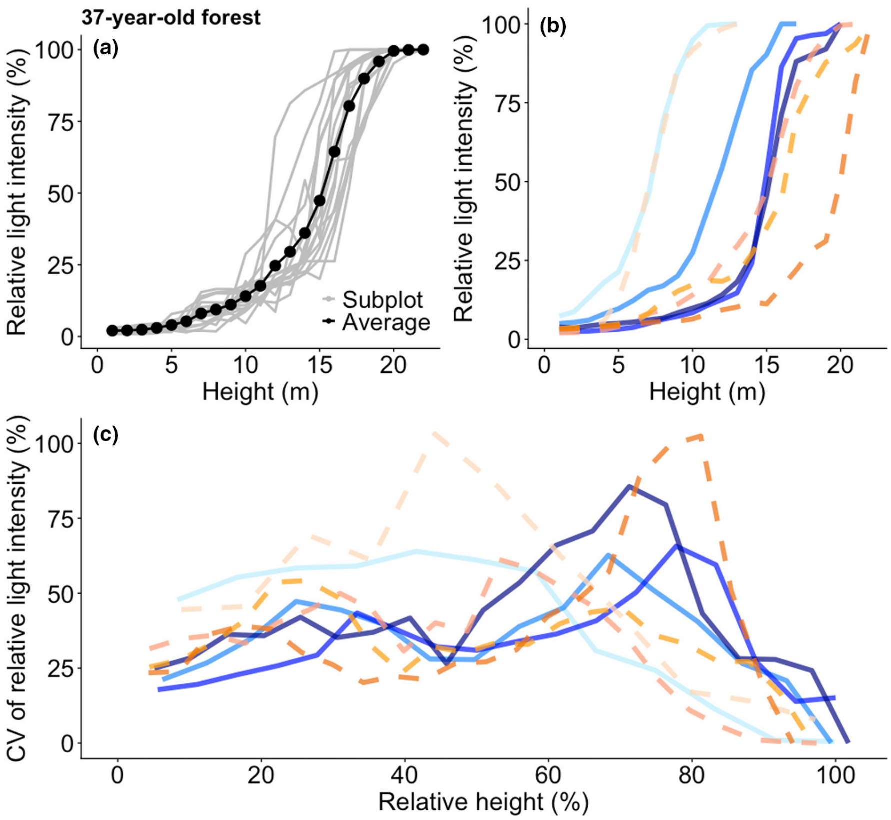

FIGURE 2 Forest light profiles at four secondary successional stages (early, mid-early, middle, and late) in cool- and warm-temperate forests. (a) An example of vertical light profiles in a plot (37-year-old forest stand in the warm-temperate forest); (b) average vertical light profiles per plot (n = 16 per plot) in stands of different age; and (c) the coefficient of variation (cv) of the relative light intensity among 16 subplots for a given height in relation to relative height (%) — that is, with the highest tree per plot normalized to 100%. In (b) and (c), only one representative plot per successional stage in each forest type is shown; blue solid lines represent the cool-temperate forest and orange dashed lines the warm-temperate forest. The lighter color indicates the plots in early successional stages whereas the darker color indicates the plots in late successional stages

4 | DISCUSSION

To our knowledge, this is the first comprehensive study examining how the vertical and horizontal light heterogeneity within forest stands varies with forest age and forest types. As expected, along the secondary successional gradient, the horizontal light heterogeneity of the whole forest became larger and the vertical light attenuation rate became more gradual (i.e., a slower rate of light extinction with height) with the increases in forest height and stand size (AGB and mean crown depth) in both forest types. Contrary to our hypotheses, the different patterns in the light attributes between cool- and warm-temperate forests were found only for the light attenuation rate despite that the warm-temperate forest showed more AGB and bigger height than the cool-temperate forest for a given age. The light intensity dropped more sharply from the canopy surface in the cool-temperate forests than in the warm-temperate forests for all successional stages. These results imply how successional patterns in forest light attributes influence the light competition among trees and the coexistence of tree species in temperate forests along the secondary successional gradients.

4.1 | Vertical and horizontal light heterogeneity along the secondary successional gradient

In the early successional stage, canopy trees form a shallower (vertically shorter crown) and denser foliage layer (similar amount of total crown area within shorter vertical height, Figure 1c,d; Kitajima et al., 2005), which can result in a steeper light attenuation rate from the forest canopy to the forest floor. As succession advances, the mean crown depth increases without an increase in the total crown area per unit of ground area partly due to the increase in the abundance of evergreen conifer trees in both forest types (Appendix S9). This suggests that older forests have lower leaf density per unit of volume (Stark et al., 2012) and a more gradual light attenuation rate than young forests (Figure 3a). In the late successional stage, the number of canopy trees per unit of ground area is lower likely due to long-term competition (i.e., self-thinning, Appendix S7; Oliver, 1981; Chanthorn et al., 2017), creating more spatially heterogeneous foliage distributions along the vertical axis (Mizunaga & Fujii, 2013). These heterogeneous foliage distributions can be responsible for larger horizontal light heterogeneity at the whole-forest level in the late successional stage (Figure 3d).

The horizontal light heterogeneity in the understorey was higher in the early and late successional stages than in the middle successional stage (Figure 3c, Appendix S7). In the early successional stage, small gaps exist due to the spatially heterogeneous patterns of tree recruitment (i.e., different tree densities in space by chance; Kepfer-Rojas et al., 2014). In the middle successional stages, canopy trees form a relatively uniform canopy layer in which no obvious gaps are observed. In the late successional stage, gaps can be created because some old trees are prone to natural disturbances, including storms and diseases (Hiura, 2001). Such gaps therefore tend to be more abundant in the early and late successional stages than in the middle successional stage, which can result in the U-shaped pattern of horizontal light variation along the successional gradient in the understorey (Figure 3c; Yao et al., 2015).

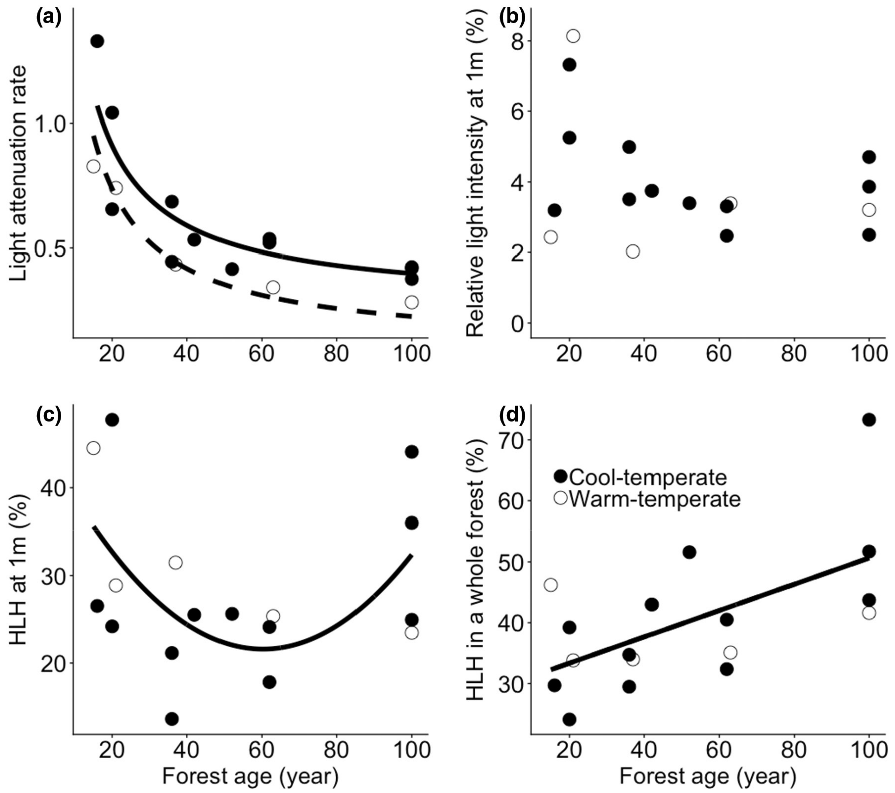

FIGURE 3 Successional trajectories of the forest light attributes in cool- and warm-temperate forests: (a) light attenuation rate (i.e., the rate of light extinction by height); (b) relative light intensity at 1 m above the ground; (c) horizontal light heterogeneity (HLH) at 1 m above the ground (the coefficient of variation of the relative light intensity at 1 m above the ground across 16 subplots); and (d) the HLH of a whole forest (the mean value of the coefficient of variation of relative light intensity across all height classes among 16 subplots in each plot) plotted against the different stand ages. In (a), continuous lines represent the regression lines of the cool-temperate forest, and hatched lines represent the regression lines of the warm-temperate forest. In (c, d), a single regression line was drawn for pooled data because there was no difference between the cool- and warm-temperate forests. The detailed model results can be found in Appendix S6. Regression lines are (a) cool: $y = 12.78/x + 0.27$, warm: $y = 12.67/x + 0.098$; (c) $y = 0.0068x^2 - 0.83x + 46.47$; (d) $y = 0.22x + 29.03$

4.2 | Different patterns of light distribution in cool- and warm-temperate forests

The sharper decline in light intensity from the canopy surface in the cool-temperate forest than in the warm temperature forest was likely associated with the different leafing patterns of the two forest types. Deciduous broad-leaved trees are dominant in the cool-temperate forests (Appendix S9), and they deploy almost all leaves at the beginning of the growth season (spring), resulting in a shallower (i.e., vertically shorter crown) and denser canopy (i.e., higher leaf density per unit volume). In contrast, evergreen conifers and broad-leaved trees are more abundant in the warm-temperate forests (Appendix S9), and they accumulate leaves over the course of years, resulting in a longer (i.e., vertically longer crown) and sparser canopy (i.e., lower leaf density per unit volume; Lusk, 2002).

Although previous studies have found significant differences in the understorey light environment between various rainforests (Canham et al., 1989; Brenes-Arguedas et al., 2011), in this study, the relative light intensity in the understorey was not different between the two forest types. The similar understorey light environments might be related to the relatively high total crown area per unit of ground area in both forest types (2.0 – 3.6 m^2 m^{-2}). A large total crown area per unit of ground area, which may be associated with a higher leaf area index and lower frequency of gaps (Montgomery & Chazdon, 2001), should contribute to monotonically dark forest floors in our studied forests throughout succession.

4.3 | Implications for light competition

A steeper light attenuation rate may reflect stronger light competition because trees with similar statures engage in intense competition for light by deploying leaves in the top canopy layers (Kitajima et al., 2005). The light attenuation rate was the highest in the early successional stage, meaning that a difference in height of only 1 m can result in a large difference in light availability. Competing trees can thus increase the amount of light intercepted much more by height growth in the early successional stage than by the same growth in later stages. Such intense competition for light may put a premium on the fast growth in height of pioneer species, which is strongly associated with relatively fast development of forest height at the beginning of secondary succession (Figure 1b; Poorter et al., 2006; Sterck et al., 2006). Intensified

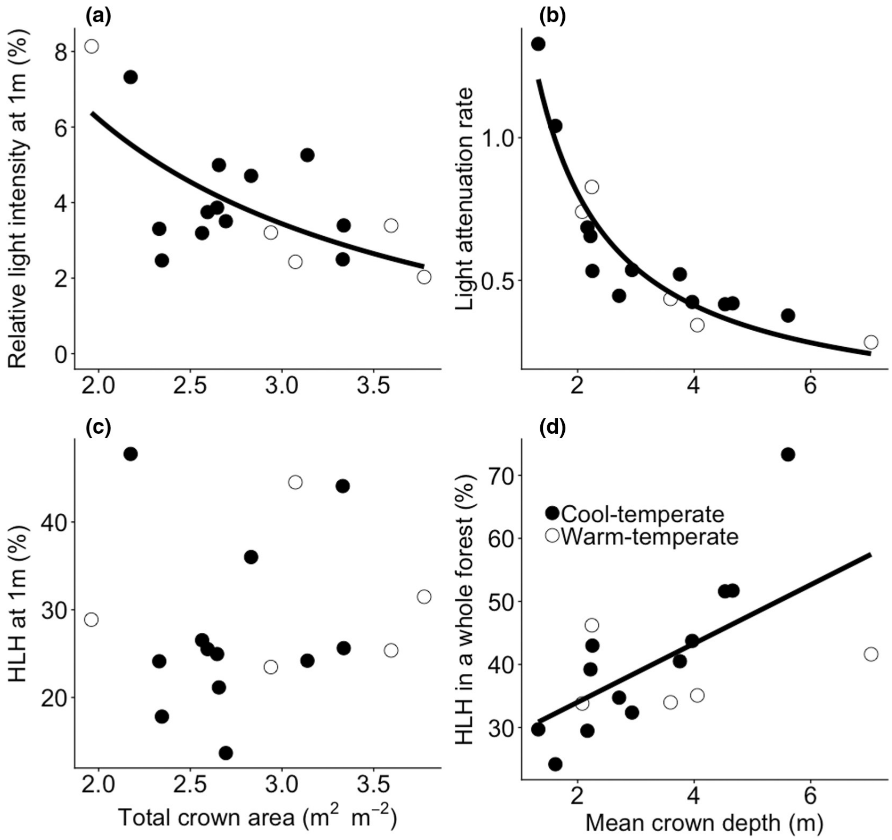

FIGURE 4 Forest light attributes in relation to forest structural attributes across forest stands of different ages in cool- and warm-temperate climates. (a) The relative light intensity (RLI) at 1 m above the ground plotted against the total crown area per unit of ground area; (b) the light attenuation rate (i.e., the rate of light extinction with height) plotted against the mean crown depth; (c) horizontal light heterogeneity (HLH) at 1 m above the ground (coefficient of variation of RLI at 1 m above the ground across 16 subplots) plotted against the total crown area per unit of ground area; and (d) the HLH of a whole forest (the mean value of the coefficient of variation of RLI across all height classes among 16 subplots in each plot) plotted against the mean crown depth. In (a,b,d), a single regression line was drawn for pooled data because there was no difference between the cool- and warm-temperate forests. The detailed model results can be found in Appendix S8. Regression lines are (a) $y = 16.62/x - 2.10$; (b) $y = 1.57/x + 0.020$; (d) $y = 4.66x + 24.69$

light competition among tree individuals can also increase the mortality rate of suppressed tree individuals (i.e., self-thinning) and thus create a size hierarchy among co-occurring tree individuals along the successional gradient (Yoda et al., 1963).

In the late successional stage, light intensity attenuated more gradually along the vertical axis. This means that there may be very limited return for growing taller for light interception, which may slow down the vertical growth of newly entered seedlings and thus contribute to the long-term stability of the forest structure (i.e., stable size hierarchy among co-occurring individuals) unless large natural disturbances occur (e.g. storms, severe drought, pathogens, or insects; Mitchell, 2013; Senf & Seidl, 2021).

4.4 | Implications for species coexistence

Since tree species differ in their light requirements and therefore partition their niches along both horizontal and vertical gradients of light availability (Kitajima & Poorter, 2008; Kohyama & Takada, 2012), the higher horizontal light heterogeneity of the whole forest in the later successional stages (see also Appendix S6) may allow many tree species to coexist through horizontal light-niche partitioning (e.g. gap dynamics). The more gradual light attenuation rate at later successional stages may imply that the intensity of light competition was relaxed, and therefore may allow individuals of different statures to persist and coexist through vertical light-niche partitioning (e.g. forest architecture hypothesis).

Horizontal light heterogeneity was the greatest in the middle layer (at heights of between 20% and 80% of the forest height) in all the studied stands (Figure 2c, Appendix S5), meaning that horizontal light niche partitioning may be most important in the middle layer. Based on this result, we think that the chance of coexistence between light-demanding and shade-tolerant species may be highest in the middle layer — the light-demanding species can survive and utilize the relatively well-lit space, while the darker spaces can be exploited mostly by shade-tolerant species. Such light -niche partitioning among tree species along the spatial gradient of light availability may be associated with higher tree species coexistence in late-successional forests (Poorter et al., 2006). In the understorey layer, the relative light intensity was less than 5% throughout succession across forest stands more than 15 years old, hence limiting opportunities for small seedlings or saplings to recruit. However, slightly higher horizontal light heterogeneity in the understorey in the late successional stage may enhance the chances of seedling recruitment and potentially increase species richness (Nicotra et al., 1999; Denslow & Guzman, 2000).

Our results also suggest that the vegetation cover (i.e. total crown area per unit ground) can recover quickly and the light absorption by vegetation can saturate (>90%) within roughly a decade after large disturbances in our study regions. These findings may be consistent with the recent meta-analysis of multidimensional forest recovery that showed that forest structural attributes can recover faster compared to species diversity and composition along secondary successional gradients (Poorter et al., 2021). In early succession, there is a steeper light attenuation rate, which can drive strong light competition among trees and thus result in faster tree growth and stand development. In contrast, horizontal light heterogeneity in a forest, which may be more related to species coexistence and diversity through light-niche partitioning, may emerge more slowly and become more important in later successional stages.

5 | CONCLUSION

Sunlight is attenuated sharply within forests, and only a small percentage of light may reach the floor. Vertical and horizontal light heterogeneity change systematically along a secondary successional gradient in both cool- and warm-temperate forests; steeper vertical light attenuation in earlier successional stages becomes more gradual later, while horizontal light heterogeneity at the whole-forest level is lower in earlier stages, becoming more pronounced later. The approach we develop in the present study will be useful to test how spatial light heterogeneity is associated with light competition among trees and the coexistence of species through light-niche partitioning across time and space.

AUTHOR CONTRIBUTIONS

Tomonari Matsuo and Yusuke Onoda designed the research with support from Tsutom Hiura; Tomonari Matsuo and Yusuke Onoda performed fieldwork; Tomonari Matsuo performed data analysis. Tomonari Matsuo and Yusuke Onoda drafted the manuscript, and all the authors contributed meaningfully to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

The data on average light measures and structural attributes per stand is stored in DANS: https://doi.org/10.17026/dans-zvy-k5xe.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Three-dimensional images of forest structure in cool- and warm-temperate forests

Appendix S2. A list of dominant species per plot

Appendix S3. Results of ANCOVA between forest structural attributes and forest age between two climatically different forests

Appendix S4. Vertical profiles of relative light intensity in all plots in cool- and warm-temperate forests

Appendix S5. Vertical profiles of horizontal light heterogeneity along the secondary successional gradients in cool- and warm-temperate forests

Appendix S6. Results of ANCOVA models between forest light attributes and forest age between two climatically different forests
Appendix S7. Detailed information of the studied plots
Appendix S8. Results of simple regression models between forest structural attributes and forest light attributes
Appendix S9. Relative biomass of each functional group along the secondary successional gradients in cool- and warm-temperate forests

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