

**Analysis of crown structure and evaluation of
growth strategies of canopy trees using UAV-LiDAR
in diverse natural forests of Japan**

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Abbreviations

AGB	Above-ground biomass
AGR	Absolute growth rate
AIC	Akaike's information criterion
AICc	Akaike's information criterion with correction for small sample sizes
A_L	Total leaf area
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
CA or A_c	Crown area
CF	Correction factor
CHM	Canopy height model
CNN	Convolutional neural network
CV	Coefficient of variation
DBH	Diameter at breast height
DSM	Digital surface model
DTM	Digital terrain model
GBH	Girth at breast height
H	Tree height
LAI	Leaf area index
LAR	Leaf area ratio
LiDAR	Light detection and ranging
LMR	Leaf mass ratio
LUE	Light use efficiency
M	Total plant mass
M_L	Leaf mass
MAT	Mean annual temperature
MAR	Mean annual rainfall
NAR	Net assimilation ratio
OLS	Ordinary least squared linear regression
PAR	Photosynthetically active radiation
R	Correlation coefficient

R ²	Coefficient of determination
RE	Relative error
RGB	Red, green, blue
RGR	Relative growth rate
RMSE	Root mean square error
RTK	Real-time kinematic position
SMRF	Simple morphological filter algorithm
SLA	Specific leaf area
SOE	Space occupation efficiency
SUE	Space use efficiency
TLS	Terrestrial laser scanning
UAV	Unmanned aerial vehicle
UAV-LiDAR	Unmanned aerial vehicle equipped with light detection and ranging
VIF	Variance inflation factor
WD	Wood density

Measurement units

Variable	Abbreviation	Unit
Above-ground biomass	AGB	kg
Absolute growth rate	AGR	kg year ⁻¹
Crown area	CA or A _c	m ²
Diameter at breast height	DBH	cm
Girth at breast height	GBH	cm
Light use efficiency	LUE	g MJ ⁻¹
Mean annual temperature	MAT	°C
Mean annual rainfall	MAR	mm
Photosynthetically active radiation	PAR	MJ m ⁻²
Relative growth rate	RGR	g g ⁻¹ year ⁻¹
Specific leaf area	SLA	cm ² g ⁻¹
Space occupation efficiency	SOE	m ² kg ⁻¹
Space use efficiency	SUE	kg m ⁻² year ⁻¹
Tree height	H	m
Wood density	WD	g cm ⁻³

Abstract

Accurate, efficient, and scalable measurements of forest canopy structures are crucial for effectively characterizing forest biomass and ecological functions. UAV-LiDAR technology enables detailed measurement of tree canopy structures including crown height (H) and crown area (CA). Yet, most of the previous research focused on commercial trees, with limited research on natural forest trees. This thesis investigates (1) crown sizes of canopy trees (H, CA) estimated with UAV-LiDAR, (2) canopy tree growth variations, and (3) species-specific growth strategies, in species-rich natural forests of Japan. Chapter 2 presents a novel crown-based growth analysis framework that utilizes UAV-LiDAR-derived CA as a proxy for light interception area in plant growth analysis in a natural forest stand in Wakayama. It decomposes the relative growth rate of canopy trees into underlying growth strategies, i.e., space occupation efficiency (SOE) and space use efficiency (SUE), which differed significantly between functional types (deciduous vs evergreen). Chapter 3 reports the allometric relationships between crown structural parameters (H, CA) and diameter at breast height (DBH) and above-ground biomass (AGB) of canopy trees for 149 species and functional types (deciduous broadleaf, evergreen broadleaf, conifers). Several alternative allometric models are evaluated to predict DBH and AGB from H and CA. Including both H and CA in the allometric models is better than H or CA alone, and consideration of functional type or species identity improved the predictive power. In Chapter 4 the approach reported in Chapter 2, i.e., the crown-based growth analysis to decompose relative growth rates to SOE and SUE, is applied to 23 natural forest sites spanning ca. 3000 km across Japan, to examine how growth strategies vary across environmental gradients. This broader scale analysis confirms that there are different crown strategies among canopy species in relation to their functional types and leaf traits. Overall, I conclude that tree crown sizes detected by UAV-LiDAR allow estimations of canopy structural variables relevant to tree growth and variations of growth strategies across environments. It should help advance forest ecosystem management, offering scalable solutions for assessing structural diversity and tracking AGB over larger scales.

Chapter 1: General introduction

1.1 Background

Conventional forest research that aims to characterize forest biomass stock or forest dynamics has relied on individual tree census data. As trees are often large and it is time-consuming to sample height and crown size, conventional surveys typically measure stem diameter at breast height (DBH), which is relatively easy to measure and amenable to repeated census (Anderson-teixeira et al., 2015; Davies et al., 2021). Such DBH data in combination with allometric models can be used to estimate biomass and its changes in individual trees. While DBH is a good predictor of biomass, there is a variation in biomass for a given DBH. Therefore, more elaborate allometric models incorporating tree height (H) and wood density to predict standing biomass have been established (Chave et al., 2005; Ishihara et al., 2011; Chave et al., 2014). However, measuring tree height in the field is time-consuming compared to DBH, so biomass estimation with tree height is relatively rare. Conventional forest surveys can provide accurate DBH measurements and species identity including sub-canopy trees. However, they are often limited in scope and scale due to their high cost and resource requirements, underscoring the need for more efficient approaches to scale-up measurements.

Recent advances in remote sensing technology, such as UAV (Unmanned Aerial Vehicle) and LiDAR (Light Detection and Ranging), offer a powerful alternative for forest monitoring. The UAV-LiDAR system (LiDAR mounted on a UAV) enables the collection of quantitative information that is (1) detailed, (2) of high-resolution, and (3) at large spatial scales (e.g., a few to hundred hectares). UAV-LiDAR systems use laser pulse returns to generate precise 3D (three-dimensional) point cloud data. LiDAR works by emitting laser pulses toward the target and measuring the time it takes for the pulses to return after bouncing back from solid objects. In the context of forest structural detections, a UAV-LiDAR system sends out thousands of laser pulses per second from above. When these pulses hit tree branches, leaves, or the ground, the system records the return time. From this information, the distance to the object is calculated, generating detailed 3D point cloud data (Fig. 1.1). By analyzing the 3D point cloud data, tree canopy structural metrics such as height, projected area, and shape of crowns can be accurately estimated (Guimarães et al., 2020). However, the direct estimation of stem DBH from point cloud data is not possible because of insufficient point cloud data available for reconstructing structures in the lower layers (e.g., the area within the rectangles indicated by red broken lines in Fig.1.1).

High-resolution RGB (Red, Green, Blue) images captured by UAV can be used to create an orthomosaic image – a geometrically corrected aerial image that has been adjusted to remove distortions caused by the camera angle, terrain relief, and lens distortions (Fig. 1.2a). These high-resolution orthomosaic images provide information on individual tree crown characteristics, including species identification, canopy density, and health status. Using point cloud data, several digital models can be derived; (1) digital surface model (DSM) (Fig. 1.2b), (2) digital terrain model (DTM) (Fig. 1.2c), and their differences - canopy height model (CHM) (Fig. 1.2d). DSM represents the surface of all features on the ground including vegetation,

buildings, and other objects. DTM represents the terrain elevation and topography, which can be used for various purposes such as terrain mapping, topographical analysis, and habitat associations. CHM represents the height of the top canopy surface. Moreover, the vertical distribution of point cloud data can be used to estimate leaf area index (Kamoske et al., 2019), and vertical distribution of foliage or branching architectures (McNeil et al., 2023) (Fig. 1.2e). In addition, it is possible to identify individuals of canopy trees (but not subordinate trees) from the CHM, therefore the crown area (CA) and canopy height (H) can be evaluated at individual tree levels at least for canopy individuals (Zhen et al., 2016; Apostol et al., 2020; Onishi & Ise, 2021; Ball et al., 2023).

Since tree CA and H are known to correlate with other tree dimensions, these parameters can be used for accurate estimation of tree DBH and above-ground biomass (AGB) (Wirth et al., 2004; António et al., 2007; Feldpausch et al., 2011; Goodman et al., 2014; Forrester et al., 2021). UAV-based allometric models for tree DBH or AGB predictions have primarily focused on monocultures or managed plantations where tree species and structure are homogenous (Moe et al., 2020; Hao et al., 2021; Iizuka et al., 2022). In contrast, the application of UAV-LiDAR data for predicting DBH and AGB in species-rich natural forests remains underexplored. Unlike plantations, natural forests exhibit structural complexity and high species diversity, which often pose challenges for developing allometric equations. Trees within natural forests vary in structure and growth patterns depending on species, forest types, and environmental conditions (Blanchard et al., 2016; Zhao et al., 2021). As a result, estimating DBH and AGB in these environments requires the use of tailored allometric models to account for species-specific and site-specific characteristics. In addition, a given forest stand may contain multiple functional types, including conifers and broadleaf species, as well as deciduous and evergreen trees. These functional types can differ not only in their canopy architectures such as crown shape, height, and leaf area, but also in their leaf phenology

(McNeil et al., 2023). Therefore, accounting for such structural and functional characteristics is crucial when developing UAV-based allometric models that can effectively convert UAV-LiDAR data into reliable estimates of DBH and AGB across natural forest stands.

In addition to tree DBH and AGB estimations, tree crowns play a crucial role in individual tree growth rates, because CA is closely linked to the amount of light interception that drives photosynthetic carbon assimilation and overall growth (Sterck et al., 2001). Hence, the projected CA can be used as a proxy of the total leaf area (Sterck et al., 2001; Binkley et al., 2013). In classical plant growth analysis, leaf area is a critical factor in understanding the variations in the relative growth rate (RGR), i.e., growth rates per unit biomass, ($\Delta M/M$, where M is plant mass and ΔM is the change in M over a unit time). In classical plant growth analysis, RGR is decomposed to net assimilation rates (NAR, $\Delta M/\text{leaf area}$) and leaf area ratio (LAR, $\text{leaf area}/M$), to provide insights into the growth strategies of individuals and species (Grime & Hunt, 1975). Yet, this approach cannot be readily applied to large trees due to technical difficulty in measuring total leaf areas for large trees. Instead, it is easier to measure the CA of canopy trees as a proxy of the total leaf area. Then, tree biomass growth rate per unit CA ($\text{kg m}^{-2} \text{ time}^{-1}$) can be analyzed as "space use efficiency" (SUE, $\Delta M/CA$) as a metric analogous to NAR (Webster & Lorimer, 2003; Pretzsch & Schütze 2005; Pretzsch et al., 2021) and CA per unit biomass ($\text{m}^2 \text{ kg}^{-1}$) can be analyzed as space occupation efficiency (SOE, CA/M) as a metric analogous to LAR. Thus, the RGR of a tree can be analyzed as the product of SUE and SOE ($\text{RGR} \approx \text{SUE} \times \text{SOE}$), allowing us to evaluate the relative importance of SUE and SOE in explaining the variations of RGR among individuals and different species.

A crown-based growth analysis approach can not only improve our understanding of individual tree growth strategies but also strengthen our ability to explore the broader ecological significance of variations. With UAV-LiDAR, the multiple CA of canopy trees can

now be measured in a shorter time across different forests. Thus, the crown-based approach allows us to investigate variations in SUE and SOE for multiple canopy species across various forests. Furthermore, CA values of multiple canopy trees collected from different forests can be analyzed in relation to their functional characteristics (conifer vs broadleaf; evergreen vs deciduous). This can provide deeper insights into underlying growth strategies since these groups significantly differ in canopy architecture, vertical leaf distribution, and leaf phenology (McNeil et al., 2023). Coniferous trees generally have narrow crowns for a given biomass, while broadleaf trees tend to have wider crowns, reflecting different biomass allocation strategies. They are also different in photosynthetic and light-capturing strategies. Evergreen species, which retain their leaves year-round, can continue photosynthesis for a greater proportion of the year, whereas deciduous species shed their leaves in winter. Evergreens typically have longer leaf lifespans, allowing them to capture light more efficiently in their deep crowns compared to deciduous species, which often have shallow crowns with low leaf density. Evergreen trees have more leaf areas per unit ground area (LAI) which may lead to self-shading. But they have relatively small leaves and adjust leaf angles as well as the overall canopy architecture (e.g., conical or layered), which may help mitigate the negative effects of self-shading and thereby optimize light capture in their deep crowns (Sprugel 1989). This may in turn result in higher gross production per unit projected CA in evergreen species than in deciduous species. Furthermore, by exploring how variations in SUE and SOE are related to functional types along environmental gradients, we can gain a better understanding of the ecological strategies employed by trees across regions. Therefore, the crown-based analysis approach offers a new foundation for a more detailed evaluation of forest dynamics through observation from above.

1.2 Rationale

Japan has unique geographical and ecological characteristics. Over a set of islands extending over 3000 km from the northern- to southernmost points, Japan's terrain is predominantly mountainous which makes up approximately 73% of the land (Mittermeier et al., 2004). The rugged and complex topography, with a wide range of mean annual temperatures under the influences of latitudes as well as cold and warm currents along the coasts, contribute to the heterogeneity of its forests. As a result, various forest types, including subboreal, cool temperate, warm temperate, and subtropical, are distributed (Fig 1.3a). According to the Japanese Forest Agency, forests cover 67% of the country's land area, 54% of which are natural forests (Forestry Agency, 2019). Japan has higher species diversity compared to temperate forests at similar latitudes in Europe and North America (Latham & Ricklefs, 1993) with approximately 1600 woody species thriving in the natural forests of Japan (Oohata, 1990). In Japan, woody species can be broadly categorized based on their taxonomic (conifer vs broadleaf) and phenological (deciduous vs evergreen) characteristics. Deciduous conifers are rare, and the only native one is Japanese Larch (*Larix kaempferi*). Other conifer species in Japan, including the wide-spread Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*), are evergreen and retain leaves throughout the year. Broadleaf trees include deciduous species such as maple (*Acer pictum*) and Japanese beech (*Fagus crenata*), which shed their leaves seasonally. Evergreen broadleaf species such as evergreen oaks (e.g., *Quercus glauca*, *Quercus acuta*) and *Camelia japonica* (the indicator species of warm-temperate evergreen broadleaf forests) maintain foliage year-round. These groups of functional characteristics are important for not only understanding forest composition but also for studying their ecological strategies across the diverse natural forests of Japan.

Japan also has a network of well-monitored vegetation plots, including a network of permanent forest monitoring sites established across Japan (Fig. 1.3b) as part of the Monitoring 1000 sites established in 2003 (Ishihara et al. 2011). All trees greater than 15 cm GBH (girth at breast height) typically in 1-ha (100 m $\times$ 100 m) plots have been mapped and identified to the species level. Tree GBH has been measured annually or at five-year intervals and tree dynamics such as growth, mortality, and recruitment have been monitored. These datasets are available to the public, and the sites can be accessed as research infrastructure with permission. Historically only a few sites have been able to gather LiDAR data due to the logistical constraints, the high costs, and the low availability of UAV-LiDAR systems. With the improved availability of UAV-LiDAR systems, there is a compelling need to expand LiDAR data acquisition to multiple monitoring sites in Japan. In this thesis, I targeted 23 forest census plots from diverse Japanese natural forests to test the generality and utility of UAV-LiDAR in estimating tree canopy information and other tree-size variables such as DBH and AGB. The existence of the forest monitoring site network serves as a foundation that enables UAV-LiDAR surveys to investigate variations of tree and forest biomass, as well as tree growth strategies across various environmental conditions.

1.3 Objectives

The main objectives and research questions addressed in each of the subsequent chapters of this thesis are as below.

- 1) In Chapter 2, I report a novel crown-based growth analysis framework using tree crown areas derived from the UAV-LiDAR data. This analytical framework is applied to a single forest site. The results demonstrate variations of individual tree growth strategies in terms of SUE (space use efficiency) and SOE (space occupation efficiency) among different species and functional types (i.e., evergreen vs deciduous).
- 2) Chapter 3 focuses on establishing reliable allometric models to estimate stem DBH

(diameter at breast height) and above-ground biomass (AGB) from two UAV-LiDAR-derived tree structural variables, i.e., crown area and height, across 149 species in 23 species-rich natural forests. Additionally, it evaluates the contribution of UAV-detected trees towards the total AGB in 1-ha permanent sample plots across 23 monitoring sites.

- 3) Chapter 4 reports variations in tree growth strategies (i.e., SUE and SOE) among species and functional types, encompassing 103 species across 23 natural forests. I also examined the relationships between the growth strategies and functional traits such as specific leaf area and wood density across 100 species. In addition, the chapter explores variations in their growth strategies in response to temperature, radiation, and snow cover. These analyses deepen our understanding of the ecological strategies of tree species thriving in diverse climate conditions.
- 4) Chapter 5 synthesizes the findings from all chapters, discussing the overall research findings, and their implications. Last, but not least, it provides future research directions that may prioritize and advance the UAV applications in ecological studies.

Figures

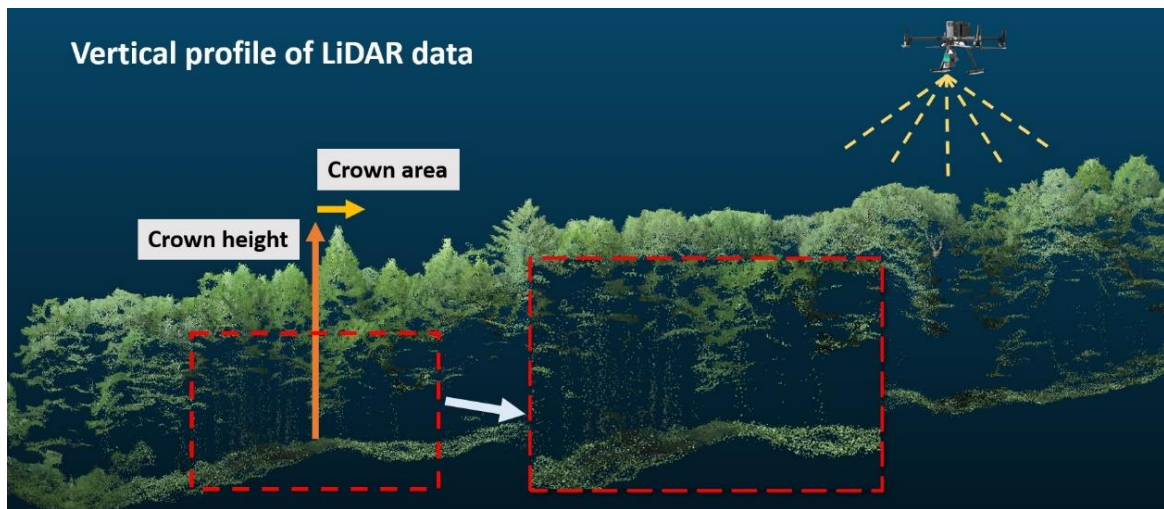


Fig. 1.1 Illustration of how UAV-LiDAR can estimate individual tree crown information and vertical distribution of tree bodies. The magnified red rectangle highlights the low acquisition of 3D point cloud data for estimating tree stems.

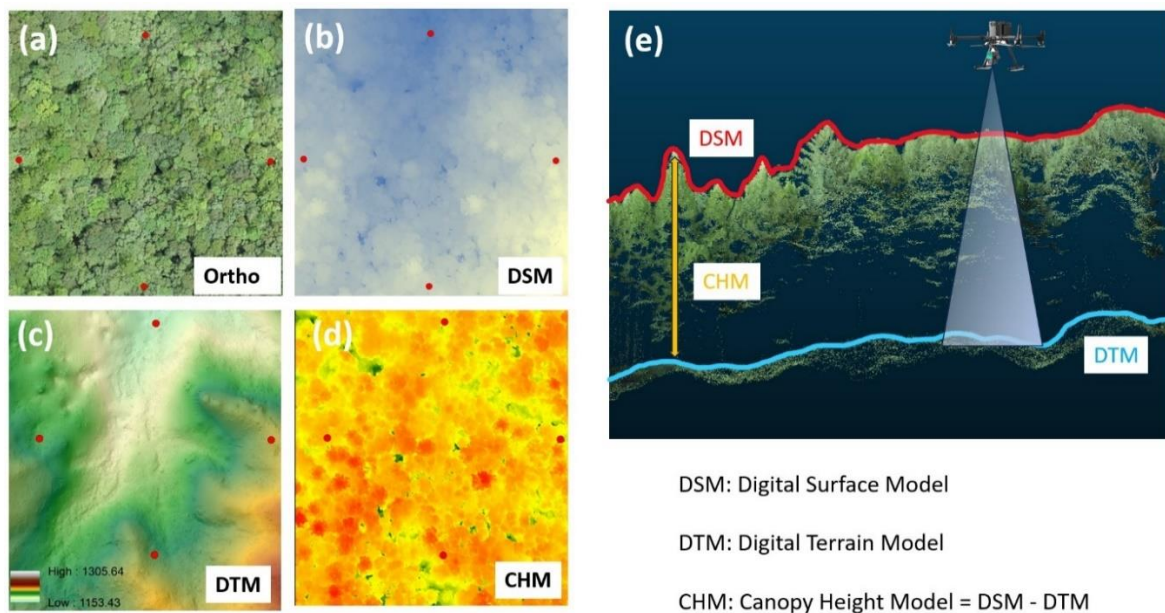


Fig. 1.2 (a) An example of an orthomosaic photo constructed from aerial images, (b) Digital Surface Model (DSM), (c) Digital Terrain Model (DTM), (d) Canopy Height Model using LiDAR point cloud data, and (e) vertical profile of point cloud data.

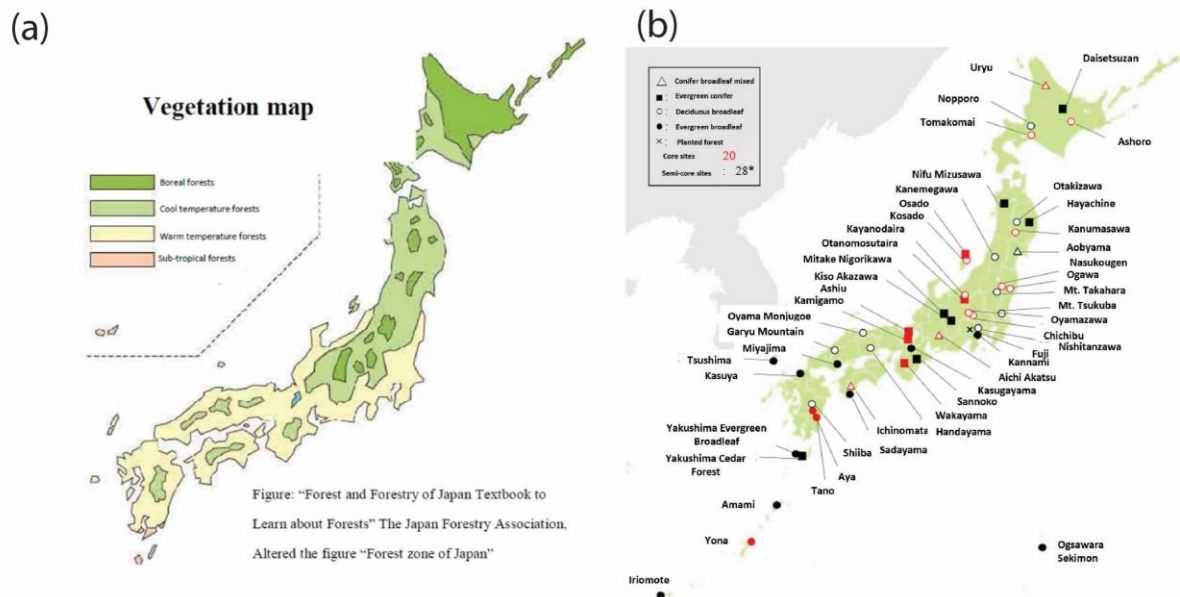


Fig. 1.3 Maps of **(a)** major forest types (Boreal, Cool temperate, Warm temperate, and Sub-tropical forests) and **(b)** permanent forest monitoring sites distributed across Japan. Maps are sourced and adapted from Forestry Agency, 2019 and Ministry of Environment, Biodiversity Center of Japan, 2022 reports.

Chapter 2: The space occupation and use by tree crowns explain variations of individual growth rates in an old-growth temperate forest in Japan

Abstract

Relative growth rates (RGR), i.e., growth rates per unit biomass ($\Delta M/M$, where M is plant mass and ΔM is the change in M over a period of time), reflect growth strategies of plant species. Partitioning of RGR to net assimilation rate ($\Delta M/\text{leaf area}$) and leaf area ratio (leaf area/ M) provides further insights into allocation strategies. To apply this analytical approach to large canopy tree species, we used crown area (A_c) as a proxy for leaf area to understand variations of RGR partitioned to space use efficiency (SUE, $\Delta M/A_c$) and space occupation efficiency (SOE, A_c/M). With UAV imagery, we measured A_c of 226 co-occurring individuals of 14 canopy tree species in a 1-ha stand in a temperate old-growth mixed-forest in Japan and analyzed how RGR was related to SUE and SOE. The results show that deciduous species exhibited higher SOE and lower SUE compared to evergreen species, even though their RGR values largely overlapped. Late successional species tended to have higher RGR through higher SUE than early-to-middle successional species. We also analyzed the relationship of absolute growth rates (AGR) with several functional traits including DBH (diameter at breast height), A_c , leaf- and stem traits. Both A_c and DBH were strong determinants of AGR across species. Low specific leaf area (SLA, leaf area per unit leaf mass) and high wood density positively contributed to AGR across species, offering long-term growth advantages for old-growth natural forest. The analytical framework introduced in this study may be useful to elucidate the variation of tree growth strategies of canopy trees in natural forest stands.

Keywords: crown area, functional traits, growth rates, tree growth analysis, UAV

2.1 Introduction

To understand tree growth strategies and forest production, a central focus has been placed on two key growth metrics: absolute growth rate (AGR or ΔM) and relative growth rate (RGR, $\Delta M/M$). Absolute growth rate, representing the actual increase in size over a period of time, offers insights into the growth of individual trees, their competitive performance, and the net primary productivity of the forest community. AGR of individual trees depends on the individual size (Stephenson et al., 2014; Sheil et al., 2017) such that larger trees generally exhibit higher AGR than smaller individuals because of their higher capacity to intercept essential resources such as light and nutrients (Binkley et al., 2013). In contrast, RGR, which is a growth rate normalized for size, is useful to compare potential growth rates among different species under an optimal condition or to analyze how allocation strategies, physiological differences, and environment affect growth trajectory.

RGR can be mathematically decomposed into the underlying allocation and physiological components. In classical plant growth analysis, RGR is often decomposed as follows (Grime & Hunt, 1975);

$$\text{RGR} \approx \Delta M/A_L \times A_L/M = \Delta M/A_L \times A_L/M_L \times M_L/M \quad \text{Eq.1}$$

where A_L is the total leaf area, M_L and M are leaf mass and total plant mass, respectively. $\Delta M/A_L$ is called the net assimilation rate (NAR) and A_L/M is the leaf area ratio (LAR). LAR is further decomposed as the product of A_L/M_L (specific leaf area, SLA) and M_L/M (leaf mass ratio, LMR) (Grime & Hunt, 1975; Poorter, 1989). This approach enables us to evaluate the relative importance of these underlying components in explaining the variation of RGR (e.g., Grime, 1975; Poorter, 1989; Kitajima, 1994), as an effective way to compare resource and biomass allocation strategies among herbaceous plants or seedlings of woody species.

In Eq.1, leaf area is considered as the core characteristic determining the growth rates because it reflects the amount of light interception. However, it is not easy to determine the

total leaf area of large trees. Instead, the projected crown area (A_c) represents the amount of light interception for canopy trees and thus can be used as the core characteristic determining the growth rates (Sterck et al., 2001; Webster & Lorimer, 2003). Empirical evidence also shows that the total leaf area of trees correlated with their projected crown area (Binkley et al., 2013), thus should correlate with the amount of light capture and whole-plant photosynthesis (Sterck et al., 2001; Binkley et al., 2010). Traditionally, A_c is calculated from crown radius measurements taken in four or eight directions around the tree with some geometric assumptions (Fleck et al., 2011). Such traditional estimation is time-consuming and labor-intensive but does not necessarily produce accurate estimates of the crown area because the actual crown shapes are often more complicated than the proximate geometric shapes such as ellipses or octagons (Owen & Lines, 2024). In addition, measuring crown dimensions on steep terrains, or in dense vegetation is often impractical.

With the increasing availability of Unmanned Aerial Vehicles (UAVs, a.k.a., drones), measuring A_c of canopy trees has become easier than before. UAVs equipped with global navigation satellite systems, digital cameras, and LiDAR sensors (UAV-LiDAR) can collect three-dimensional (3D) point cloud data and high-resolution RGB images over larger areas (e.g. a few to hundreds of hectares) in a short time. High-resolution UAV orthomosaic images provide individual tree crown characteristics such as color and shape from which we can estimate A_c of canopy individuals (Onishi & Ise, 2021; Ball et al., 2023). From point cloud data, several raster-based models such as the digital surface model (DSM), digital terrain model (DTM), and canopy height model (CHM) can be derived. Several methods have been developed and applied for individual tree detection and crown delineation from UAV-LiDAR data (Zhen et al., 2016; Apostol et al., 2020; Onishi & Ise, 2021; Ball et al., 2023). Therefore, the integration of UAV data with advanced image analysis has opened new possibilities for canopy-level analysis (Araujo et al., 2020; Cushman et al., 2022).

With the help of UAVs, the RGR of canopy trees can now be analyzed in relation to $\Delta M/A_c$ ($\text{kg m}^{-2} \text{ time}^{-1}$) which is analogous to NAR (Pretzsch & Schütze, 2005; Pretzsch et al., 2021), and A_c/M ($\text{m}^2 \text{ kg}^{-1}$) which is analogous to LAR.

$$\text{RGR} \approx \Delta M/M = \Delta M/A_c \times A_c/M \quad \text{Eq.2}$$

Hereafter, I refer to A_c/M as “space occupation efficiency (SOE)”, and $\Delta M/A_c$ as “space use efficiency (SUE)”. The latter is also known as “crown efficiency” (Sterba & Amateis, 1998) or “growing space efficiency” (Webster & Lorimer, 2003). This partitioning scheme allows us to evaluate the relative importance of SUE and SOE in explaining the variations of RGR among tree species. As illustrated in Fig.2.1, a given value of RGR may be achieved by various combinations of SUE and SOE values. Differences in SUE, SOE, and RGR are associated with successional positions and competitive strategies. For instance, late successional species may take a strategy to increase SUE (Smith & Long, 1992; Webster & Lorimer, 2003) because the canopy layer is typically fully packed in a late successional forest stand, and increasing competition with neighbors limits the increase of A_c . In such conditions, increasing SUE is likely to be a more effective way to maximize growth rates and competitive advantage.

Classical growth analyses with herbaceous and small plants have shown that SLA is a key underlying component in the variations of RGR. SLA is also a core trait in the Leaf Economics Spectrum (LES) which summarizes associations among gas-exchange rates, nutrient concentrations, and lifespan of leaves (Wright et al., 2004). High SLA species are often considered as fast growers under optimal conditions, while low SLA species tolerate stresses but grow slowly (Poorter, 1989; Kitajima 1994; Reich, 2014). As trees grow larger, the potential correlation between SLA and RGR becomes weak or sometimes even negative (Poorter et al., 2008; Wright et al., 2010; Paine et al., 2015; Gibert et al., 2016; Falster et al., 2018). High SLA is often associated with larger light-harvesting areas at juvenile stages, but this may not be the case in older and larger plants because the accumulation of multi-layered

foliage and leaf turnover need to be considered in larger plants. Large trees develop dense and multiple foliage layers, with upper leaves shaded on lower leaves. Leaves in shaded environments with reduced light availability may be less beneficial to high SLA. In addition, the rate of leaf turnover may decrease in larger and older plants as they have to prioritize long-term resource efficiency over rapid leaf replacement. Thus, the importance of SLA for RGR may differ between small and large trees. Wood density, which is negatively correlated with SLA across species, also exhibits size dependency in its correlation with RGR. Trees with high wood density often grow slower at juvenile stages (Kitajima, 1994; Kitajima & Poorter, 2010), but they are more tolerant to biotic and abiotic stresses, to live longer and achieve larger tree crowns (Anten & Schieving, 2010; Iida et al., 2012). Hence, wood density may contribute positively to RGR in larger woody species (King et al., 2006; Poorter et al., 2008; Rüger et al., 2012; Francis et al., 2017). These observations suggest that associations of leaf and stem traits with RGR may depend on individual size and forest structures (Yang et al., 2018; Iida & Swenson, 2020).

In this study, we analyzed the variation in both RGR and AGR of canopy trees in an old-growth warm-temperate forest. For RGR, we partition RGR into SOE and SUE, using A_c of individual canopy tree crowns measured with UAV imagery. For AGR, we examined how size (A_c and DBH) and plant functional traits (SLA, wood density) explain variations of AGR among individual trees and species. Specifically, we tested the following hypotheses:

- 1) Partitioning RGR into SOE and SUE clarifies the ecological strategies of species and functional types of canopy trees. Specifically, we expect that late successional species have higher SUE than early successional species and that evergreen species have higher SUE than deciduous species.
- 2) In an old-growth forest stand, the RGR of canopy trees should negatively correlate with species mean specific leaf area (SLA) and positively correlate with species mean wood

density (WD), because stress tolerance and resource competition are more important than potential RGR in explaining realized RGR measured over longer intervals.

- 3) Models of absolute growth rates of canopy trees can be improved with the inclusion of projected crown area, with further improvement by adding SLA and WD to the multiple regression model.

2.2 Materials and methods

2.2.1 Study site

This study was conducted in a long-term forest study plot in Wakayama Research Forest of Kyoto University, Japan (34 ° 04' N, 135 ° 32' E, 807 m above sea level). It is registered as one of the long-term monitoring plots in Japan and the inventory data since 2005 are available (Ishihara et al., 2011). All trees ≥ 5 cm DBH (diameter at breast height) in the 1-ha (100 m $\times$ 100 m) plot were annually measured using a measuring tape. Tree positions (x and y coordinates) were recorded, and stems were identified at the species level (Fig. S2.1). The dataset including individual tree ID, species, and DBH is publicly available from the official monitoring sites 1000 data archive. Details of the dataset were provided in supplementary material B. It is an old-growth stand dominated by evergreen conifer species such as *Abies firma* Siebold & Zucc. (fir) and *Tsuga sieboldii* Carrière (hemlock). Deciduous broadleaf trees such as *Quercus serrata* Murray, *Stewartia monadelphica* Siebold et Zucc., and *Fagus crenata* Blume, and some evergreen broadleaf trees such as *Quercus acuta* Thunb. are also present in the canopy layer. There are also several sub-canopy or understory species such as *Eurya japonica* Thunb. var. *japonica* and *Pieris japonica* (Thunb.) D.Don ex G.Don subsp. *japonica* within the 1-ha plot. The soil type is moderately moist brown forest soil (Ueda et al., 1994). The mean annual temperature and precipitation averaged over 1981-2010 are 10.5°C and 1926 mm year⁻¹ (Nomura et al., 2023).

2.2.2 Species traits data

We used the species mean values of leaf and wood traits from a previous study at the same site (Nomura et al., 2023). This study collected 12 leaf and wood traits for 59 tree species found in this region. In the present study, we initially considered six traits (SLA, WD, leaf nitrogen concentration (LNC), leaf area, leaf thickness, and force to punch), and later we decided to focus on SLA and WD because other traits showed little correlation with growth rates and their components (Fig. S2.2). We classified species to early/middle successional or late successional according to their relative abundance along different aged stands in the region, following Nomura et al. (2023). For instance, the late successional species such as *A. firma*, *Q. acuta*, and *T. sieboldii* were abundant in forest stands aged over 80 years whereas early/middle successional species such as *Q. serrata* and *Pinus densiflora* were abundant in stands that were 10-80 years old in the region. Therefore, *A. firma*, *Q. acuta*, and *T. sieboldii* were classified as late successional species while *Q. serrata* and *P. densiflora* were classified as early/middle successional species. Details of the classification are provided in Table S2.1.

2.2.3 LiDAR data collection and processing

LiDAR data were collected in May 2022 using a UAV-LiDAR system (DJI Matrice 300 RTK + Zenmuse L1, DJI, Shenzhen, China). D-RTK 2 high-precision GNSS mobile station was employed for accurate positioning. RGB raw images were taken with the 20-megapixel onboard camera. The flight plans were set up using the DJI Pilot App to achieve an 80% forward and side overlap rate, and a speed of 10 m s⁻¹. The LiDAR was set to 160 kHz, in non-repetitive mode, to capture three reflection positions with one laser irradiation (point density was on average 461 points m⁻²). The flight was conducted at a constant height of 100 meters above the ground (terrain follow mode) using a digital elevation model (DEM, 5 m resolution) that was downloaded from the Geospatial Information Authority of Japan. The terrain-follow

mode ensures a similar density and resolution of LiDAR data across the survey area, which is important to get accurate topography and forest structural information.

The overall analysis workflow is illustrated in Fig. S2.3. Initially, the raw data were processed to generate point cloud data with a standard protocol that involved data calibration and noise removal in DJI Terra software (Version 3.7.3) and saved in the “las” file format. From the point cloud data, three elevational models were constructed: a digital surface model (DSM), a digital terrain model (DTM), and a canopy height model ($CHM = DSM - DTM$). Firstly, the high-density point cloud data were thinned to reduce density using the “lasthin” function in ArcGIS 10.8. We reduced the data density by ensuring that 16 of the lowest points remained within each 1 square meter overlay grid cell. This process makes the data more manageable for analysis and processing. Subsequently, ground detection was performed with the Simple Morphological Filter (SMRF) algorithm (Pingel et al., 2013). Low ground points were missing especially under the dense canopy, we thus utilized a Poisson Surface Reconstruction to fill gaps (Kazhdan & Hoppe, 2013). Next, we merged the output from the initial Poisson filter with the detected ground points. Then, we applied a second round of Poisson filtering to generate dense points and merge the remaining gaps comprehensively. Measured ground point cloud data were interpolated to generate a high-resolution digital terrain model (DTM) with a 5 cm resolution. An orthomosaic image (2.3 cm resolution) was generated from the RGB images using DJI Terra software.

To separate individual crowns, we applied an auto image segmentation with a multiresolution segmentation algorithm in eCognition Developer v.9.0.0 (Trimble Inc., Sunnyvale, United States). According to previous studies, orthomosaic RGB layer, the canopy height model, and the surface slope model were combined for this segmentation (Onishi & Ise, 2021; Onishi et al., 2022). We set weights to the data layers (e.g., CHM layer = 2; surface slope layer = 3, see Table S2.2 for the detailed parameters) to determine their relative importance in

the image segmentation process. Higher weights were assigned to layers that provide more critical information for accurate segmentation. The weights were chosen by a number of trials using the information from the previous studies (Apostol et al., 2020; Moe et al., 2020; Onishi & Ise, 2021). The auto-segmented crown maps were manually edited and validated by the ground-truth work explained below.

2.2.4 Crown area extraction from the UAV survey

We carried out ground-truth work to check the size and shape of all the tree crowns detected by the UAV image, linking the crown polygons to the tree census ID tags. To do so, the RGB orthomosaic image, the segmented crown data, and stem location maps were uploaded to the iPad (Apple Inc.). In the field, the outlines of individual crowns were manually delineated on the orthomosaic image using Adobe Photoshop software, and their tag numbers were recorded (Adobe Systems Incorporated, USA). After the field survey, all individual crowns were digitized, and the crown area (A_c) was calculated in ArcGIS v.10.8.1 software (Environmental Systems Research Institute, Inc., Redlands, CA, USA). The mean canopy height (H) for each A_c was estimated using the zonal statistics tool in ArcGIS v.10.8.1.

2.2.5 Statistical analysis

All data analyses were conducted with the R statistical software (Version 4.1.1, R Core Team, 2022). Above-ground biomass (AGB) was estimated from the following allometric equation developed for Japanese forest trees (Ishihara et al., 2015):

$$\ln AGB = -1.196 + 1.622 \ln D + 0.338 (\ln D)^2 - 0.044 (\ln D)^3 + 0.708 \ln WD$$

where D is the diameter at breast height and WD is wood density. We used the species-specific wood density and field-measured DBH in the AGB calculation because intraspecific variations in wood density were typically small (Chave et al., 2006; Sungpalee et al., 2009; Osazuwa-Peters et al., 2014; Siefert et al., 2015). We did not consider below-ground biomass. The

absolute growth rate (AGR, kg year⁻¹) was calculated from changes in AGB over seven years (2010 to 2017) using linear regression. Relative growth rate (RGR) was calculated as follows:

$$\text{RGR} = (\ln(\text{AGB}_{2017}) - \ln(\text{AGB}_{2010})) / 7 \quad (\text{g g}^{-1} \text{ year}^{-1}) \quad \text{Eq.3}$$

Since the tree census data was available up to 2017, there was a five-year gap between the crown measurement and the available latest tree census data.

The understory or sub-canopy trees whose crowns could not be seen from the UAV (partially or completely overtopped by other crowns), or whose growth rates were zero or negative (11 out of 237 individuals) were excluded from the analysis. Therefore, the final data set consisted of 226 individuals. Species with low numbers of individuals ($n < 3$) were not included in the species-level analysis. The coefficient of variation (CV), which is defined as the standard deviation divided by the mean, was calculated for each variable.

The bivariate correlations between AGR, RGR, and several leaf- or wood traits were examined. All variables except for RGR were log₁₀-transformed to approximate normal distribution. The value of 1 was equally added to each individual AGR value to accommodate log transformation. Multiple linear regression models were used to model AGR as a function of a set of traits ($\text{AGR} \sim A_c + \text{DBH} + H + \text{WD} + \text{SLA}$). The variance inflation factor (VIF) was calculated with the ‘vif’ function in ‘car’ package (Fig. S2.4) to ensure that the values were sufficiently low in the range from 1.2 to 5.2 to avoid multicollinearity (Graham, 2003). The observed relationship between the growth rates and traits was sensitive to the presence/absence of conifers, thus separate analyses were performed for conifer species or broadleaf species. Species were categorized based on conifer or broadleaf trees, and evergreen or deciduous (2 × 2 categorizations). Since there were no deciduous conifer species in our study site, species were categorized into three functional types (deciduous broadleaf, evergreen broadleaf, and evergreen conifer species).

Akaike's Information Criterion with correction for small sample sizes (AICc) was used to assess the model performance with the 'AICcmodavg' package. The adjusted coefficient of determination (R^2) was compared to assess the relative explanatory power of variables. To examine the impact of broadleaf vs conifer on the relationship between variables, an analysis of covariance (ANCOVA) was conducted. To compare species for A_c at a given biomass or AGR at a given A_c , we calculated A_c and AGR at the reference values that were close to the overall mean values; 1000 kg for AGB (mean value is 1098.38 kg) and 33 m² for A_c (mean value is 33.42 m²).

2.3 Results

A total of 226 individual crowns belonging to 14 species (Table S2.3) were clearly observed in the UAV imagery, and successfully linked to the forest census data within the 1-ha study plot (out of 1337 individual stems with DBH $\geq$ 5 cm belonging to 37 species). The canopy trees detected by the UAV survey (226 individuals, 16.9%) accounted for 69% of the total above-ground biomass while the remaining 31% was accounted for by other remaining trees (1111 individuals, 83.1%) in 1-ha (Fig. S2.5). The most abundant two species were both evergreen conifers, *A. firma* (118 individuals) and *T. sieboldii* (30), and the third was a deciduous broadleaf species, *Stewartia monadelphica* (23). Among the five size and trait variables (H , A_c , DBH, SLA, WD), A_c showed the largest CV at 62 % (Table S2.4).

2.3.1 Partitioning of RGR into SUE and SOE in canopy trees

Species differed in space occupation efficiency (SOE) and space use efficiency (SUE). Deciduous species exhibited higher SOE compared to evergreen species (Fig. 2.2a, Fig. S2.6a). The mean SOE values varied from 0.02 to 0.06 m² kg⁻¹ among species with a mean SOE of 0.04 for all species. *P. densiflora* displayed the lowest SOE at 0.02, while higher values of SOE were found in *Q. serrata* (0.05) and *Carpinus laxiflora* (0.06). Evergreen species showed higher SUE than deciduous species (Fig. 2.2b, Fig. S2.6b). The mean values of SUE ranged

from 0.16 to 0.63 kg m⁻² year⁻¹ across species (mean SUE for all species = 0.40). The lowest mean SUE was observed for *C. laxiflora* (0.16) whereas the highest means were observed with *Q. acuta* (0.62) and *T. sieboldii* (0.63). Species mean RGR ranged from 0.8% to 1.9% per year. Early-to-middle successional species such as *P. densiflora* showed lower RGR (less than 1%) compared to late successional species such as *T. sieboldii* and *A. firma* (more than 1%) and *Q. acuta* (nearly 2%) (Fig. 2.2c). Fig. 2.2d shows species position within the SUE and SOE diagram with RGR isoclines. Deciduous species occupied the corners with high SOE and low SUE compared to evergreen species, even though RGR was not clearly different between the two groups.

Strong positive correlations ($R^2 = 0.65$) were observed between A_c and above-ground biomass, the two components of SOE, in Fig. S2.6c, in which the predicted value of A_c at biomass of 1000 kg for each species is shown (Table S2.5). In general, deciduous species achieved approximately 2.5 times greater A_c for the reference biomass value of 1000 kg compared to the evergreen conifer species (Fig. S2.6c, Table S2.5). Similarly, consistent positive correlations were found between AGR and A_c ($R^2 = 0.54$, Fig. S2.6d). Significant differences in the intercepts of the regression lines were found among species (Fig. S2.6cd).

2.3.2 Relationship of SUE and SOE with SLA and wood density

Species mean SOE was positively correlated with species mean SLA ($r = 0.87$, Fig. 2.3a). Species with lower SLA values, such as *A. firma*, *T. sieboldii* and *P. densiflora*, showed lower SOE while those with higher SLA values such as *Q. serrata* and *C. laxiflora* demonstrated higher SOE. In contrast, a negative correlation was observed between mean SUE and mean SLA ($r = -0.76$, Fig. 2.3b). Low SLA species displayed higher SUE, while species with higher SLA exhibited lower SUE. In contrast, wood density was not correlated with SOE or SUE (Fig. 2.3cd).

2.3.3 Modeling growth rates with leaf/stem traits and tree structural variables

In Fig. 2.4 we summarize the relationships of growth rates (AGR and RGR) with size- and morphology-related traits (A_c , DBH, SLA, and WD) for all species together, as well as for conifers and broadleaf trees separately. The difference in conifer vs broadleaf had significant effects on these relationships (Table S2.6). AGR was strongly correlated with A_c and DBH ($R^2 = 0.40$ and 0.46) (Fig. 2.4ab), but RGR was not correlated with A_c and slightly and negatively correlated with DBH ($R^2 = 0$ and 0.03 , Fig. 4ef). Neither SLA nor WD was correlated with RGR across all species. However, within broadleaf species, SLA showed a negative correlation with both AGR and RGR (Fig. 2.4cg). Conversely, positive correlations were found between WD and AGR, as well as WD and RGR among broadleaf species (Fig. 2.4dh).

Table 2.1 summarizes the multiple regression results, i.e., how AGR and RGR may be predicted by combinations of A_c , DBH, WD, and SLA. For all canopy trees, A_c alone accounted for 40% of the variation in AGR which was close to the explanatory power of DBH (46%). A_c and DBH together can explain the AGR variation by 50% ($R^2 = 0.50$). An additional 3% was explained by adding both SLA and WD into the model ($R^2 = 0.53$). For broadleaf species, the best model included A_c , DBH, WD, and SLA ($R^2 = 0.69$). A_c and DBH accounted for 51% and 58% and together explain 60% of the variation observed in the AGR. For conifers, A_c in combination with DBH was the best model ($R^2 = 0.34$). Both A_c and DBH showed the same contribution to AGR ($R^2 = 0.29$). The regression coefficients of the models are summarized in Tables S2.7 and S2.8.

When RGR was modeled with the same set of variables (A_c , DBH, WD, SLA), A_c hardly had any power to explain the variation in RGR, and DBH also showed very low prediction power in RGR (Table 2.1). Adding SLA and WD to that model explained an additional 13% of the variation in RGR ($R^2 = 0.18$). For broadleaf species, the best model included A_c , DBH, WD, and SLA ($R^2 = 0.22$). However, for conifer species, adding SLA and WD did not improve

the models partly due to the limited variation in SLA and WD among the conifer species (Table 2.1).

2.4 Discussion

This study demonstrates how a similar value of relative growth rate (RGR) may be achieved by variable combinations of space use efficiency (SUE = biomass growth rate/crown area) and space occupation efficiency (SOE =crown area/biomass) as components of RGR. Variations among species in SUE and SOE show predictable differences between functional types and between successional positions. For these canopy trees, crown area (A_c) was found to be a determinant of absolute growth rate (AGR) almost as strong as DBH. In addition, adding leaf and stem traits to A_c and DBH in multiple regression models slightly improved the prediction of AGR. Below we discuss further details associated with these key findings.

2.4.1 RGR, SOE, and SUE differences between functional types and ecological strategies

The old-growth forest stands in this study experienced no large disturbances for nearly 100 years (Furuno et al., 1986). The canopy layer was dominated by late successional species such as *Q. acuta*, *A. firma*, and *T. sieboldii*, which had higher or similar RGR compared to early or middle successional species, *P. densiflora* and *Q. serrata* over the 7-year period examined. These early/middle successional species may have lost vigor as the late successional species became dominant. This result differs from studies in early successional communities, in which early successional species grow faster than late successional species (Shukla & Ramakrishnan, 1986; Chen et al., 2017). We also found that late successional species had higher growth rates per unit A_c (high SUE), but not necessarily higher SOE than early successional species. This finding supports our first hypothesis. Similarly to our results, in an old-growth hemlock-hardwood forest in North America, late successional species (*Tsuga canadensis*) show higher SUE than the early successional species (Webster & Lorimer, 2003). We did not determine the leaf area index within individual crowns in the current study. But, in a mid-successional

tropical seasonal forest stand, late successional species take a strategy to accumulate foliage with longer leaf lifespans to capture light more completely compared to early successional species with shallow crowns with low leaf density (Kitajima et al., 2005). This means greater gross production per unit projected A_c in late successional species than early successional species.

We also found that deciduous species had higher SOE but lower SUE than co-occurring evergreen species, the net result of which was insignificant differences in RGR between the two groups. Similarly to our study, in a mixed stand of Norway spruce (evergreen) and European beech (deciduous), beech had higher SOE but lower SUE than spruce, even though they had similar RGR (Pretzsch & Schütze, 2005). In our study site, evergreen species included not only conifers but also one broadleaf species (*Q. acuta*), and the two types showed similar SOE and SUE.

Higher SOE in deciduous species than evergreen species were coupled with the higher SLA in the former (Fig. 2.3a). This correlation may not be expected *a priori* because SOE increases require allocation of woody mass to extend branches to widen the crown while SLA is solely determined by allocation within a single leaf. To our knowledge, this is the first report that shows the area-mass ratios are correlated between leaf- and crown-levels. The reason why deciduous species had larger A_c for a given biomass remains to be solved. One possibility is that deciduous species do not need to withstand heavy snow loads during winter unlike evergreen species, which may allow deciduous species to have larger A_c for a given standing biomass without the risks of breakages.

We propose two reasons why evergreen species may have higher SUE than deciduous species: (1) evergreen species continue photosynthesis for a greater proportion of each year than deciduous species, and (2) they have a higher efficiency of light capture (i.e., more light captured per unit projected crown area) than deciduous species. In our study site, deciduous

species expand their leaves in late April and maintain their leaves until November. Although evergreen species cannot photosynthesize during harsh winter days, they can photosynthesize during marginal periods when deciduous species are leafless but the ambient temperature is still above the lower threshold for photosynthesis (Miyazawa & Kikuzawa, 2005). Our study focused on the above-ground traits, and we did not study below-ground traits. But below-ground traits may also be important for the different performances between the functional types.

2.4.2 Influences of leaf and wood traits on RGR of canopy trees

Overall, correlations of RGR with leaf and wood traits were weak (Fig. 2.4gh, see also Laughlin et al., 2017; Wills et al., 2018). We found no clear trend between SLA and RGR among all canopy trees (Fig. 2.4g, $R^2 = 0.01$). However, we found a negative correlation between SLA and RGR in broadleaf trees ($R^2 = 0.14$). Positive correlations between SLA and RGR were found in seedling experiments (e.g., Poorter 1989; Walters et al., 1993, Kitajima, 1994). These seedling experiments were designed to assess potential RGR without competition with neighbors. Under such conditions, larger leaf areas for a given leaf mass (i.e., high SLA) enable them to capture more light and grow faster. In contrast, our objective was to reveal morphological and physiological factors that explain realized RGR in an old-growth forest with light competition, and other biotic and abiotic stresses. In later successional stages after canopy closure, late successional species with low SLA (i.e., high leaf mass per area) with longer leaf lifespan can accumulate larger leaf area per unit A_c , and as such, they are competitive for light by casting deep shade on their neighbors and may grow faster (Leuschner & Hagemeyer, 2020).

Similarly, we found no clear correlation between wood density and RGR across all canopy trees (Fig. 2.4h, $R^2 = 0.00$) but a positive correlation between WD and RGR in broadleaf trees ($R^2 = 0.17$). In broadleaf trees, late successional species tend to have higher wood density than early successional species, and they may be able to tolerate various stressors

(biotic/abiotic) and resist competitive displacement in old-growth forests. In contrast, conifers have typically lower wood density than broadleaf species, independent of successional stages. The two dominant late successional species in our study, *A. firma* and *T. sieboldii*, had lower wood density compared to other broadleaf species.

2.4.3 Absolute growth rates in relation to tree structural variables and other functional traits

We found that DBH is a good predictor of AGR partly because AGR is calculated from growth in DBH as well as other variables (height and wood density). However, we also observed that A_c , which was independently estimated, had comparable predictive power in the variation of AGR. Crown area A_c should be roughly proportional to the amount of light interception for canopy trees; therefore, A_c serves as a good predictor of AGR. Since SUE differed among species, the variation in AGR should be in part explained by species-specific traits. There were positive correlations between AGR and WD and negative correlations between AGR and SLA. In multiple regression models to explain AGR, the inclusion of SLA and WD to the model with A_c and DBH as the key predictor variables explained an additional 13% of the variation in AGR. In the best-selected model, WD had a positive coefficient and SLA had negative coefficients ($AGR = 0.63 + 0.38 A_c + 0.98 DBH + 1.48 WD - 0.71 SLA$, Table S2.7).

With UAV imagery, we can estimate A_c independently of DBH. Therefore, even without DBH data, it may be possible to predict AGR based on A_c for upper canopy trees and available species-specific leaf/wood traits. In our study, the model including A_c and leaf/wood traits explained 47% of the variation in AGR for all trees and 65% for broadleaf trees (Table S2.7). A study conducted in the subtropical forest of China also reported that a combination of leaf traits (i.e., specific leaf area, leaf physical strength) and crown size (i.e., crown length and projection area) can explain 42% of the variation in interspecific growth rates of saplings at early successional stage under open conditions (Li et al., 2017).

Since UAVs can cover much larger areas than ground surveys, the UAV approach should be powerful for estimating the AGR for canopy trees over extensive forested regions. While the present study was limited to 1-ha forest plot where the ground survey data are available, estimating AGR of canopy trees could be extended to neighboring areas where no forest census data are available. We note a couple of challenges in such scale-up: (1) accuracy of crown segmentations and (2) species identifications from UAV imagery. First, in the present study, the auto-segmented crown maps showed a reasonable match with the ground validation data, but there were some cases where a single tree was recognized as multiple trees or multiple trees were categorized as single trees (Fig. S2.7). We also note that auto-segmentation is often more difficult for broadleaf trees than conifer because canopy shape is more variable in broadleaf trees (Nuijten et al., 2019; Moe et al., 2020; Onishi et al., 2022). Individual tree crown segmentation is an active research area (e.g. Apostol et al., 2020; Silva et al., 2022; Ball et al., 2023; Vasquez et al., 2023), and we expect better algorithms will be developed and can be applied to different forest types. Second, while species identification based on UAV data was not employed in our study, UAV data (RGB images) can be used to identify species with a deep learning method (e.g. object-based convolutional neural network, CNN) (Onishi & Ise 2021). Onishi & Ise (2021) reported that the accuracy of species identification can be as high as 90% if the training data are obtained in the same region. Therefore, the combination of good algorithms of auto-segmented trees and species identification based on UAV data will enable us to obtain AGR of canopy trees for large areas. However, this method is applicable to canopy trees because UAV largely misses sub-canopy trees and understory trees. In our study, the UAV-captured canopy trees represented 17% of all the individuals ($DBH \geq 5$ cm) and 69% of the total AGB. Similar numbers are reported in previous studies; canopy trees constitute 40% of all trees ($DBH > 10$ cm) and 67% of total AGB (Araujo et al., 2020). A low detection rate of sub-canopy trees, below 30 cm DBH, was also reported in lowland tropical rainforests (Coomes

et al. 2017). However, the detection rate of under canopy trees can potentially be increased by integrating the analysis of canopy height models with the LiDAR point cloud data (e.g. Duncanson et al., 2014; Paris et al. 2016; Huo et al., 2022).

2.4.4 Conclusions and implications

We provide a framework to analyze tree growth rates in relation to A_c with the help of UAV imagery. Tree A_c is a critical trait that should be related to the amount of light interception and growth rates, enabling the decomposition of RGR ($\Delta M/M$) into space use efficiency (SUE, $\Delta M/A_c$) and space occupation efficiency (SOE, A_c/M). In temperate forests similar to our site, we also expect that deciduous broadleaf species excel in occupying space (higher SOE), whereas evergreen species excel in utilizing available space (higher SUE). More work is required to test whether the patterns recognized in this study are general in other forests. We believe that the analytical framework described in this study should be useful to understand tree growth strategies and improve our understanding of forest dynamics and ecosystem functions.

Table

Table 2.1 The adjusted coefficient of determination (R^2) for multiple linear regression models to estimate the absolute biomass growth rates (AGR) and relative growth rate (RGR) from the crown area (A_c), diameter at breast height (DBH), wood density (WD), and specific leaf area (SLA) for all individuals (n=226), conifers (n=162) and broadleaf trees (n=64).

Models	R^2					
	AGR			RGR		
	All	Conifer	Broadleaf	All	Conifer	Broadleaf
~ A_c	0.40	0.29	0.51	0.00	0.00	0.00
~ DBH	0.46	0.29	0.58	0.03	0.11	0.00
~ A_c + DBH	0.50	0.34	0.60	0.05	0.15	0.00
~ A_c + DBH + WD	0.50	0.33	0.68	0.06	0.16	0.20
~ A_c + DBH + SLA	0.50	0.33	0.69	0.13	0.16	0.22
~ A_c + DBH + WD + SLA	0.53	0.33	0.69	0.18	0.15	0.22

Note: we employ a $\log_{10}$ scale on AGR, A_c , DBH, SLA, and WD.

Figures

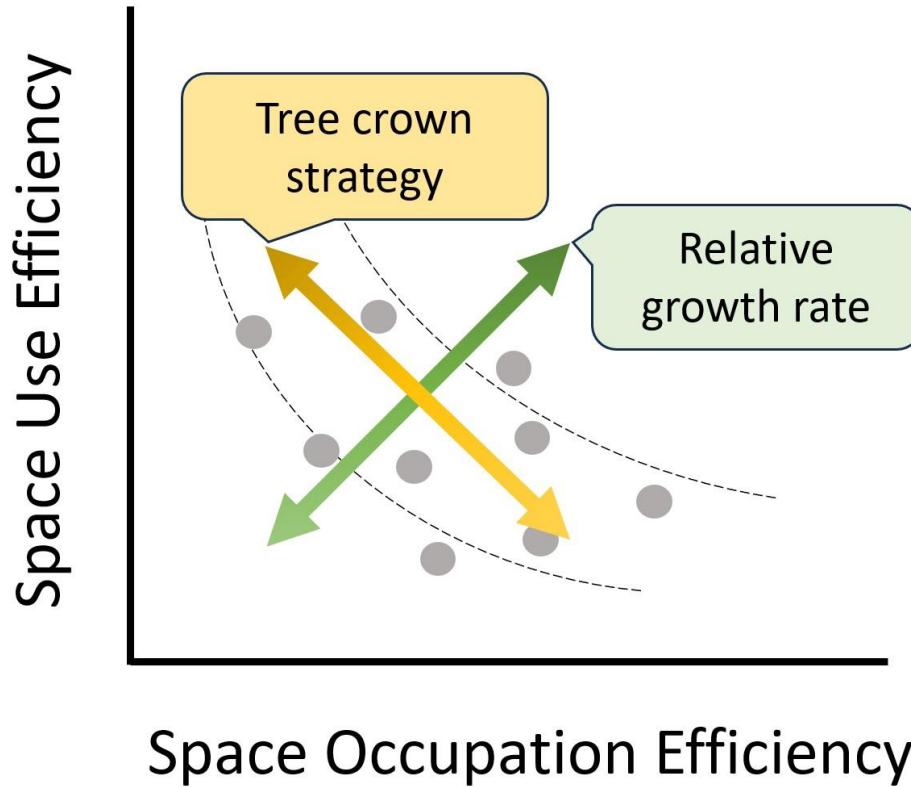


Fig. 2.1 A conceptual diagram illustrating how a given value of relative growth rate (RGR, $\Delta M/M$) may be achieved by variable combinations of space use efficiency (SUE, $\Delta M/A_c$) and space occupation efficiency (SOE, A_c/M), where M is tree biomass, ΔM is biomass growth rate and A_c is crown area. $RGR \approx SUE \times SOE$. Dashed black lines represent the isoclines of RGR. RGR increases from the bottom left (slow growers) to top-right (faster growers) along the green arrow, while the variation in tree crown strategy is roughly summarized from the top-left (efficient space users) to bottom right (fast colonizers) along the yellow arrow.

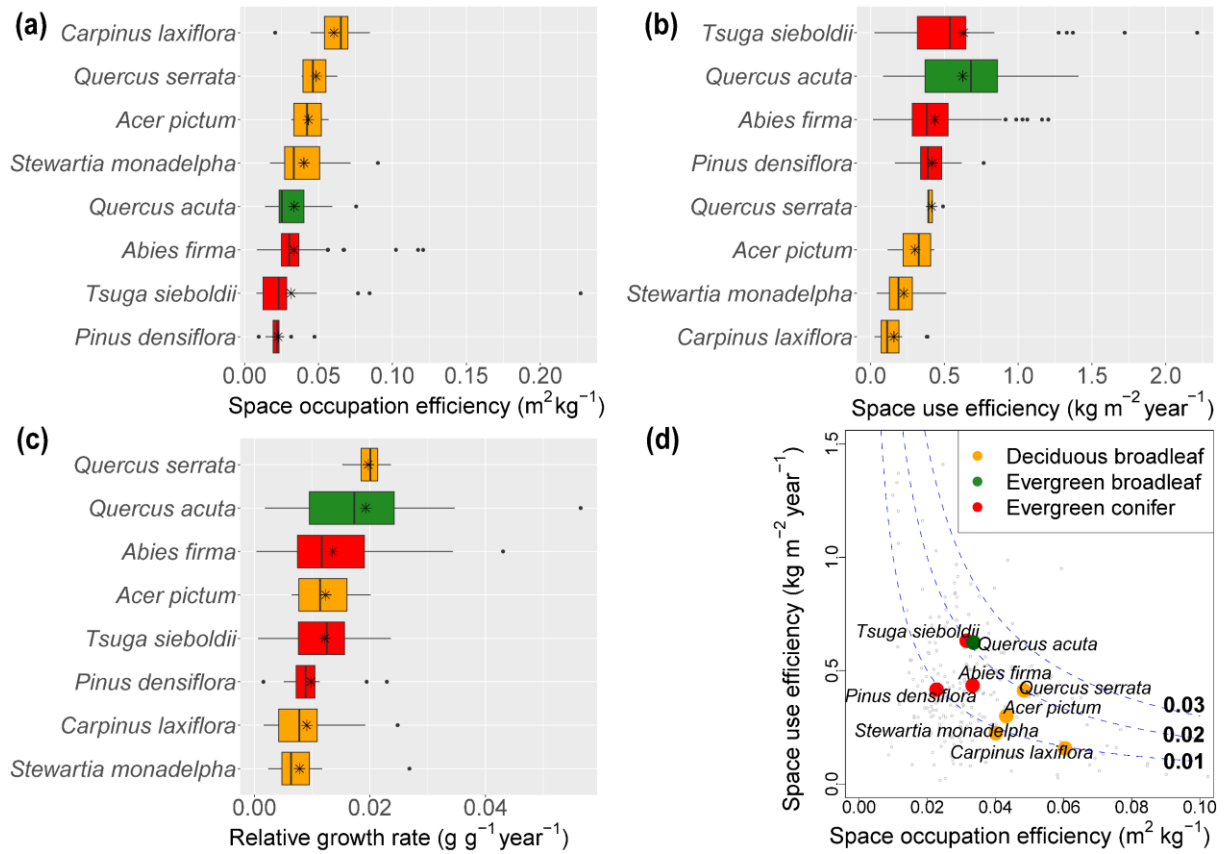


Fig. 2.2 Box plots of summarizing **(a)** space occupation efficiency (SOE), **(b)** space use efficiency (SUE), and **(c)** relative growth rate (RGR) for canopy individuals of eight species in an old-growth temperate forest in Japan. **(d)** Species mean values of SUE plotted against SOE along with the isoclines ($\text{RGR} = 0.01, 0.02, 0.03 \text{ g g}^{-1} \text{ year}^{-1}$). Deciduous broadleaf species, evergreen broadleaf species, and evergreen conifers are indicated by different colors.

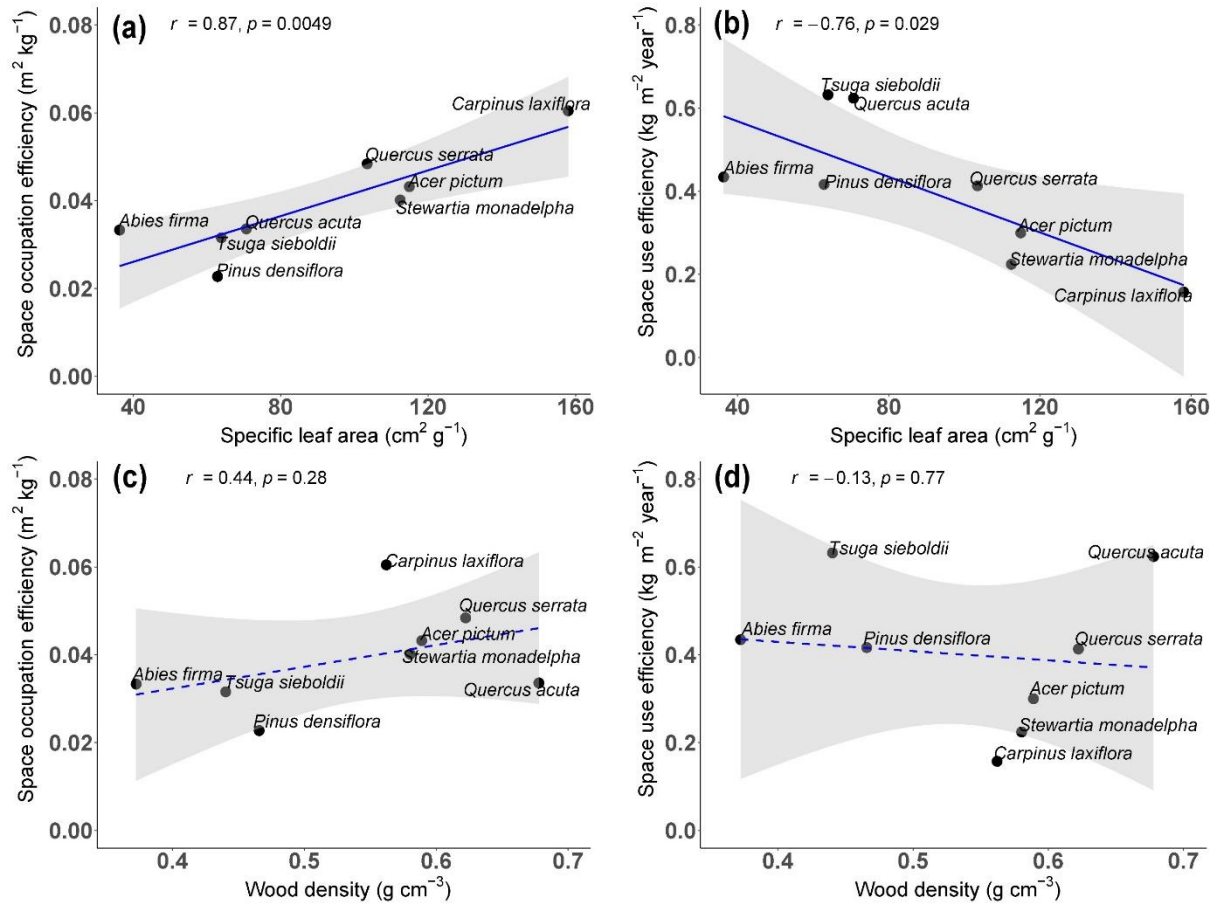


Fig. 2.3 Relationships between space occupation efficiency with **(a)** specific leaf area (SLA) and **(c)** wood density, and space use efficiency with **(b)** SLA and **(d)** wood density. Each dot represents the mean value for each species. Pearson correlation coefficient (r) is shown with a significant level. Statistically significant relationships are indicated by solid lines ($P < 0.05$).

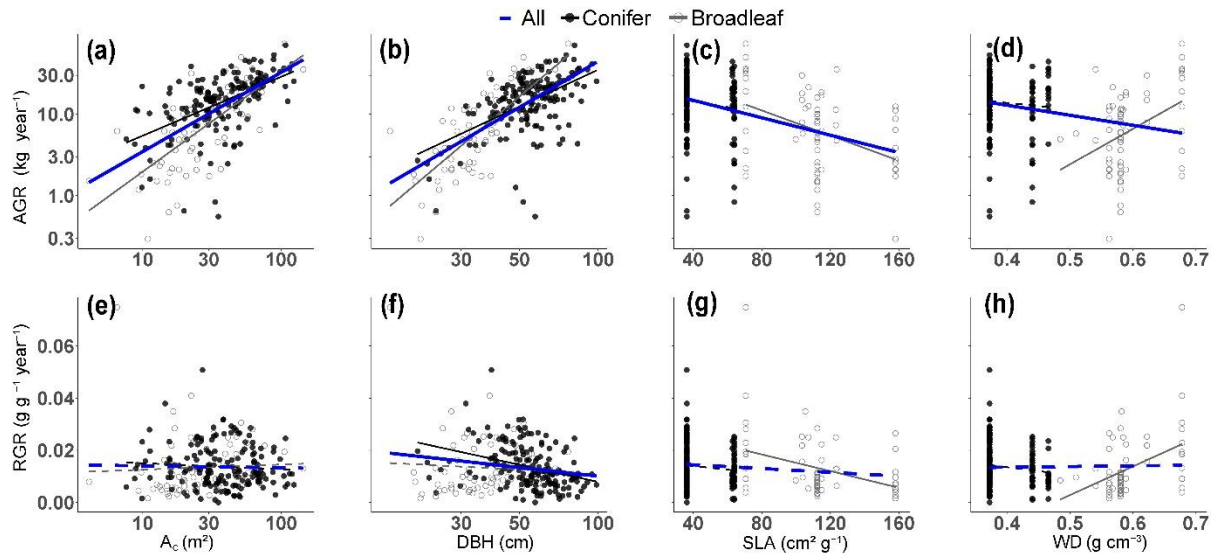


Fig. 2.4 Relationships of absolute growth rate (AGR, upper panels, **a,b,c,d**) and relative growth rate (RGR, lower panels, **e,f,g,h**) with tree structural variables and species-level functional traits across 226 canopy trees of 14 studied species. Horizontal axes are **(a, e)** Crown Area (A_c), **(b, f)** Diameter at Breast Height (DBH), **(c,g)** Specific Leaf Area (SLA), and **(d, h)** Wood Density (WD). Each data point represents an individual canopy tree, with filled symbols representing conifers ($n=162$), and open symbols representing broadleaf species ($n=64$). Thick blue lines represent all species while black and grey lines for conifer and broadleaf species, respectively. Statistically significant relationships are shown in solid lines ($P < 0.05$) while others are in dotted lines. Note: we employ $\log_{10}$ scale in AGR, A_c , DBH, SLA, and WD.

Supplementary materials

Sampling protocols on measurements of leaf and wood traits

We used leaf- and wood-trait data from a previous study at the same site (Nomura et al. 2023). The leaf samples were collected from the top of tree crowns with a 15-m telescopic pruning pole (Taketani Trading Co., Osaka, Tokyo) near the study plot (within 10 km at a similar elevation). Wood core samples (diameter 5.05 mm, length ca. 50 mm) were collected from the same individuals (one per individual) with an increment borer (Haglöf, Sweden). More than six individuals were sampled for each species to encompass a range of canopy openness. Leaf area was calculated from scanned images using a flat-bed scanner (GT-S630, EPSON, Nagano, Japan) and image analysis software (Image J, NIH, USA). The dry weight (70 °C for more than two days) of the scanned leaves was measured by a digital balance, and LMA (m2) was calculated as leaf dry mass per unit leaf area. Specific leaf area (SLA) was calculated using the formula $SLA\ (cm^2) = (1/LMA) * 1000$. Wood density was calculated as dry weight divided by fresh volume, assuming that a stem core had a cylindrical shape. Trait values were normalized at 100% canopy openness for each species to avoid confounding effects of light and species on trait values.

Table S2.1 Species were categorized into early/middle succession or late succession according to the age-related occurrences and canopy openness from the study of Nomura et al. (2023) conducted in the Wakayama region. This table was referred from the supplementary table (Table S1) in Nomura et al. (2023).

Species	Forest age									Succession
	10	18	19	34	60	63	80	100a	100b	
<i>Abies firma</i> (19)							5-100	5-100	5-100	Late
<i>Acer pictum</i> (9)				10		20				Early/Mid
<i>Carpinus laxiflora</i> (11)			100	5-10	20	10-30	5-100	100	20-100	Early/Late
<i>Pinus densiflora</i> (19)			20-100	20-100	30-100	100				Early/Mid
<i>Quercus acuta</i> (13)			90-100				5	5-70	5	Late
<i>Quercus serrata</i> (25)	60-80		50-100	10-100	10-100	20-100	80-100			Early/Mid
<i>Stewartia monadelpha</i> (9)							10	80-100	5-60	Late
<i>Tsuga sieboldii</i> (16)							5-100	5-100	5-100	Late

Note: Canopy openness was visually categorized into 11 levels (100, 90, 80, 70, 60, 50, 40, 30, 20, 10, 5%). Numbers shown in the parenthesis () are numbers of individuals used for leaf and wood trait measurement in the study of Nomura et al. (2023).

Table S2.2 Parameters for the multiresolution segmentation function in eCognition software

Parameter	Value
Red, Green, Blue	1, 1, 1
Canopy Height Model	2
Surface Slope Model	3
Scale	200
Shape	0.2
Compactness	0.5

Table S2.3 List of recorded canopy species detected by drone in 1-ha permanent sample plot and mean species-specific leaf and wood traits

No.	Species	Family	N (226)	Wood density (g cm ⁻³)	Specific leaf area (cm ² g ⁻¹)
1	<i>Abies firma</i> Siebold & Zucc.	Pinaceae	118	0.37	36.3
2	<i>Acer amoenum</i> Carrière	Aceraceae	2	0.58	123.2
3	<i>Acer pictum</i> Thunb.	Sapindaceae	4	0.59	114.9
4	<i>Aria japonica</i> Decne.	Rosaceae	1	0.58	105.4
5	<i>Betula grossa</i> Siebold & Zucc.	Betulaceae	2	0.57	107.2
6	<i>Carpinus laxiflora</i> (Siebold & Zucc.) Blume	Betulaceae	11	0.56	158
7	<i>Castanea crenata</i> Siebold & Zucc.	Fagaceae	1	0.49	99.8
8	<i>Cerasus jamasakura</i> (Siebold ex Koidz.) H.Ohba	Rosaceae	1	0.51	103.9
9	<i>Fagus crenata</i> Blume	Fagaceae	2	0.54	123.7
10	<i>Pinus densiflora</i> Siebold & Zucc.	Pinaceae	14	0.47	62.9
11	<i>Quercus acuta</i> Thunb.	Fagaceae	13	0.68	70.7
12	<i>Quercus serrata</i> Murray	Fagaceae	4	0.62	103.5
13	<i>Stewartia monadelpha</i> Siebold & Zucc.	Theaceae	23	0.58	112.4
14	<i>Tsuga sieboldii</i> Carrière	Pinaceae	30	0.44	63.9

Note: Bold species with N > 3 were used for species-level analysis

Table S2.4 List of leaf and wood traits and tree structural variables, showing a range of species means among species and coefficient of variation (CV).

Variable	Sample size	Range (min–max)	Coefficient of Variation (%)
Wood density (g cm ⁻³)	14	0.37 – 0.68	22.02
Specific leaf area (cm ² g ⁻¹)	14	36.3 – 158	40.39
Diameter at breast height (cm)	226	16.08 – 98.45	32.89
Crown area (m ²)	226	4.07 – 144.60	62.39
Mean canopy height (m)	226	13.28 – 34.30	14.79

Table S2.5 Linear regression models including species as a random factor (i.e., interaction term). Specifically, we used a reference value of 1000 kg AGB (mean value is 1083.16 kg) and a reference value of 33 m² A_c (mean value is 33.15 m²) to estimate the corresponding A_c (m²) and absolute growth rates (AGR, kg year⁻¹) values for each species. The coefficient of determination (R²) value is presented for each model.

Model	R ²	Species	Predicted value
log ₁₀ (A _c) ~ log ₁₀ (AGB) * species	0.65	<i>Carpinus laxiflora</i>	52.94
		<i>Quercus serrata</i>	48.84
		<i>Acer pictum</i>	39.38
		<i>Abies firma</i>	33.58
		<i>Quercus acuta</i>	30.75
		<i>Stewartia monadelpha</i>	30.19
		<i>Pinus densiflora</i>	28.71
		<i>Tsuga sieboldii</i>	21.26
log ₁₀ (AGR) ~ log ₁₀ (A _c) * species	0.54	<i>Quercus acuta</i>	17.94
		<i>Quercus serrata</i>	15.01
		<i>Abies firma</i>	13.96
		<i>Pinus densiflora</i>	13.93
		<i>Tsuga sieboldii</i>	12.71
		<i>Acer pictum</i>	10.30
		<i>Stewartia monadelpha</i>	7.54
		<i>Carpinus laxiflora</i>	5.42

Table S2.6 ANCOVA summary table for determining the effects of conifer vs broadleaf on the absolute biomass growth rates (AGR) and relative growth rate (RGR) by wood density (WD), specific leaf area (SLA), diameter at breast height (DBH), and crown area (A_c). Note: we employ a $\log_{10}$ scale on AGR, A_c , DBH, SLA, and WD.

Response	Predictor	Interaction term	F value	p-value
AGR	A_c	Conifer vs Broadleaf	6.9184	0.009 **
AGR	DBH	Conifer vs Broadleaf	10.2209	0.002 **
AGR	SLA	Conifer vs Broadleaf	8.9828	0.003 **
AGR	WD	Conifer vs Broadleaf	16.8981	0.000 ***
RGR	A_c	Conifer vs Broadleaf	0.7448	0.389 ns
RGR	DBH	Conifer vs Broadleaf	2.8260	0.094 ns
RGR	SLA	Conifer vs Broadleaf	7.6971	0.006 **
RGR	WD	Conifer vs Broadleaf	20.840	0.000 ***

The significance levels: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns $P > 0.05$.

Table S2.7 Multiple linear regression models for estimating absolute growth rates (AGR) based on wood density (WD), specific leaf area (SLA), mean canopy height (H), diameter at breast height (DBH), and crown area (A_c). Significant variables ($P < 0.05$) are bolded. The adjusted coefficient of determination (R^2), Akaike's Information Criteria with a correction for small sample sizes (AICc), delta AICc, and their significant values are presented for each model. Note: we employ a $\log_{10}$ scale on AGR, A_c , DBH, H, SLA, and WD.

	R^2	AICc	$\Delta AICc$	P	Model
All (n = 226)					
A_c +DBH+WD+SLA	0.53	20.03	0.00	<0.001	$0.63 + 0.38 A_c + 0.98 DBH + 1.48 WD - 0.71 SLA$
A_c +DBH+WD+SLA+H	0.53	21.98	1.95	<0.001	$0.78 + 0.38 A_c + 1 DBH + 1.5 WD - 0.71 SLA - 0.12 H$
A_c +DBH+SLA	0.50	30.70	10.67	<0.001	$-0.79 + 0.41 A_c + 0.93 DBH - 0.16 SLA$
A_c +DBH	0.50	31.63	11.60	<0.001	$-1.30 + 0.39 A_c + 1.08 DBH$
A_c +DBH+WD	0.50	33.59	13.56	<0.001	$-1.31 + 0.39 A_c + 1.11 DBH + 0.08 WD$
DBH+WD+SLA	0.49	35.77	15.74	<0.001	$0.37 + 1.53 DBH + 1.65 WD - 0.72 SLA$
A_c +WD+SLA	0.47	46.13	26.10	<0.001	$1.98 + 0.73 A_c + 1.29 WD - 0.87 SLA$
DBH	0.46	47.48	27.44	<0.001	$-1.57 + 1.60 DBH$
A_c	0.40	69.42	49.39	<0.001	$-0.17 + 0.84 A_c$
WD+SLA	0.19	139.21	119.17	<0.001	$3.83 + 1.50 WD - 1.26 SLA$
SLA	0.17	144.86	124.83	<0.001	$2.33 - 0.70 SLA$
WD	0.08	167.06	147.02	<0.001	$0.68 - 1.20 WD$
H	0.08	167.63	147.59	<0.001	$-1.14 + 1.61 H$
Conifers (n = 162)					
A_c +DBH	0.34	16.96	0.00	<0.001	$-0.73 + 0.39 A_c + 0.76 DBH$
A_c +DBH+WD	0.33	19.00	2.04	<0.001	$-0.66 + 0.4 A_c + 0.75 DBH + 0.17 WD$
A_c +DBH+SLA	0.33	19.00	2.04	<0.001	$-0.82 + 0.4 A_c + 0.75 DBH + 0.06 SLA$
A_c +DBH+WD+SLA	0.33	21.16	4.20	<0.001	$-0.71 + 0.4 A_c + 0.75 DBH + 0.11 WD + 0.02 SLA$
A_c +DBH+WD+SLA+H	0.33	22.83	5.87	<0.001	$-1.47 + 0.4 A_c + 0.71 DBH - 0.4 WD + 0.2 SLA + 0.23 H$
A_c	0.29	26.34	9.37	<0.001	$0.17 + 0.65 A_c$
DBH	0.29	27.56	10.60	<0.001	$-1.1 + 1.32 DBH$
A_c +WD+SLA	0.29	30.01	13.04	<0.001	$1.27 + 0.65 A_c + 1.36 WD - 0.33 SLA$
DBH+WD+SLA	0.28	30.81	13.84	<0.001	$1.41 + 1.27 DBH + 2.32 WD - 0.91 SLA$
H	0.07	70.63	53.67	<0.001	$-0.56 + 1.24 H$
WD+SLA	0.05	75.26	58.30	0.006	$11.53 + 10.39 WD - 3.76 SLA$
SLA	0.01	81.19	64.23	0.128	$1.74 - 0.34 SLA$
WD	0.00	82.53	65.56	0.316	$0.91 - 0.67 WD$
Broadleaf (n = 64)					
A_c +DBH+SLA	0.69	-0.06	0.00	<0.001	$0.86 + 0.58 A_c + 1.02 DBH - 1.16 SLA$
A_c +DBH+WD+SLA	0.69	1.46	1.52	<0.001	$0.36 + 0.53 A_c + 1.11 DBH + 1.44 WD - 0.79 SLA$
A_c +DBH+WD	0.68	1.75	1.81	<0.001	$-1.01 + 0.43 A_c + 1.35 DBH + 3.49 WD$
A_c +DBH+WD+SLA+H	0.69	1.95	2.02	<0.001	$1.33 + 0.51 A_c + 1.25 DBH + 1.47 WD - 0.82 SLA - 0.79 H$
A_c +WD+SLA	0.65	7.37	7.43	<0.001	$2.34 + 0.97 A_c + 0.34 WD - 1.34 SLA$
DBH+WD+SLA	0.65	7.67	7.74	<0.001	$-1.08 + 2.04 DBH + 2.68 WD - 0.28 SLA$
A_c +DBH	0.60	13.66	13.72	<0.001	$-2.08 + 0.41 A_c + 1.55 DBH$
DBH	0.58	16.07	16.13	<0.001	$-2.56 + 2.24 DBH$
A_c	0.51	25.79	25.85	<0.001	$-0.54 + 1.02 A_c$
SLA	0.19	58.25	58.31	<0.001	$4.28 - 1.66 SLA$
WD+SLA	0.18	59.69	59.75	<0.001	$3.69 + 2.15 WD - 1.13 SLA$
WD	0.17	59.93	60.00	<0.001	$2.08 + 5.21 WD$
H	0.04	68.82	68.88	0.057	$-1.57 + 1.79 H$

Table S2.8 Multiple linear regression models for estimating relative growth rates (RGR) based on wood density (WD), specific leaf area (SLA), mean canopy height (H), diameter at breast height (DBH), and crown area (A_c). Significant variables ($P < 0.05$) are bolded. The adjusted coefficient of determination (R^2), Akaike's Information Criteria with a correction for small sample sizes (AICc), delta AICc, and their significant values are presented for each model. Note: we employ a $\log_{10}$ scale on A_c , DBH, H, SLA, and WD.

	R^2	AICc	$\Delta AICc$	P	Model
All (n = 226)					
A_c +DBH+WD+SLA+H	0.20	-1510.04	0.00	<0.001	0.16 + 0.01 A_c - 0.03 DBH + 0.06 WD - 0.04 SLA - 0.02 H
A_c +DBH+WD+SLA	0.18	-1506.43	3.62	<0.001	0.13 + 0.01 A_c - 0.03 DBH + 0.05 WD - 0.03 SLA
DBH+WD+SLA	0.15	-1499.71	10.33	<0.001	0.13 - 0.02 DBH + 0.06 WD - 0.03 SLA
A_c +DBH+SLA	0.13	-1493.98	16.06	<0.001	0.08 + 0.01 A_c - 0.04 DBH - 0.01 SLA
WD+SLA	0.07	-1480.51	29.54	<0.001	0.08 + 0.06 WD - 0.03 SLA
A_c +WD+SLA	0.07	-1479.87	30.17	<0.001	0.09 - 0.00 A_c + 0.06 WD - 0.03 SLA
A_c +DBH+WD	0.06	-1477.18	32.87	<0.001	0.04 + 0.01 A_c - 0.03 DBH - 0.01WD
A_c +DBH	0.05	-1475.74	34.31	<0.001	0.04 + 0.01 A_c - 0.02 DBH
DBH	0.03	-1471.22	38.83	0.006	0.03 - 0.01 DBH
H	0.03	-1470.95	39.09	0.007	0.05 - 0.03 H
SLA	0.01	-1466.84	43.20	0.071	0.00 - 0.01 SLA
A_c	0.00	-1463.67	46.38	0.741	0.01 - 0.00 A_c
WD	0.00	-1463.57	46.47	0.890	0.01 + 0.00 WD
Conifers (n = 162)					
A_c +DBH	0.15	-1116.17	0.00	<0.001	0.06 + 0.01 A_c - 0.04 DBH
A_c +DBH+WD	0.16	-1115.82	0.34	<0.001	0.05 + 0.01 A_c - 0.04 DBH - 0.02 WD
A_c +DBH+SLA	0.16	-1115.74	0.43	<0.001	0.07 + 0.01 A_c - 0.04 DBH - 0.01 SLA
A_c +DBH+WD+SLA	0.15	-1113.67	2.50	<0.001	0.05 + 0.01 A_c - 0.04 DBH - 0.03 WD + 0 SLA
A_c +DBH+WD+SLA+H	0.15	-1112.12	4.04	<0.001	0.07 + 0.01 A_c - 0.03 DBH - 0.01 WD - 0 SLA - 0 H
DBH+WD+SLA	0.12	-1108.56	7.61	<0.001	0.10 - 0.02 DBH + 0.02 WD - 0.02 SLA
DBH	0.11	-1108.34	7.82	<0.001	0.05 - 0.02 DBH
H	0.02	-1093.95	22.22	0.028	0.04 - 0.02 H
WD	0.01	-1091.52	24.65	0.119	0.00 - 0.03 WD
SLA	0.01	-1090.91	25.26	0.177	0.03 - 0.01 SLA
WD+SLA	0.01	-1090.46	25.71	0.179	- 0.09 - 0.13 WD + 0.03 SLA
A_c	0.00	-1089.95	26.22	0.348	0.02 - 0.00 A_c
A_c +WD+SLA	0.01	-1089.38	26.79	0.216	- 0.05 - 0.00 A_c - 0.09 WD + 0.02 SLA
Broadleaf (n = 64)					
A_c +DBH+WD+SLA+H	0.28	-397.73	0.00	<0.001	0.23 + 0.02 A_c - 0.03 DBH + 0.07 WD - 0.04 SLA - 0.06 H
A_c +DBH+SLA	0.22	-395.28	2.46	<0.001	0.17 + 0.02 A_c - 0.05 DBH - 0.05 SLA
A_c +DBH+WD+SLA	0.22	-393.82	3.91	<0.001	0.15 + 0.02 A_c - 0.04 DBH + 0.07 WD - 0.04 SLA
WD	0.17	-393.59	4.15	<0.001	0.05 + 0.15 WD
A_c +DBH+WD	0.20	-393.31	4.42	0.001	0.09 + 0.01 A_c - 0.03 DBH + 0.16 WD
WD+SLA	0.16	-391.82	5.92	0.002	0.07 + 0.11 WD - 0.01 SLA
DBH+WD+SLA	0.18	-391.77	5.96	0.002	0.1 - 0.01 DBH + 0.11WD - 0.02 SLA
SLA	0.14	-391.52	6.21	0.001	0.1 - 0.04 SLA
A_c +WD+SLA	0.15	-389.47	8.26	0.006	0.07 - 0 A_c + 0.11 WD - 0.01 SLA
H	0.04	-384.29	13.44	0.066	0.08 - 0.05 H
DBH	0.00	-381.00	16.74	0.636	0.02 - 0.00 DBH
A_c	0.00	-380.91	16.83	0.707	0.01 + 0.00 A_c
A_c +DBH	0.00	-380.48	17.25	0.386	0.03 + 0.01 A_c - 0.02 DBH

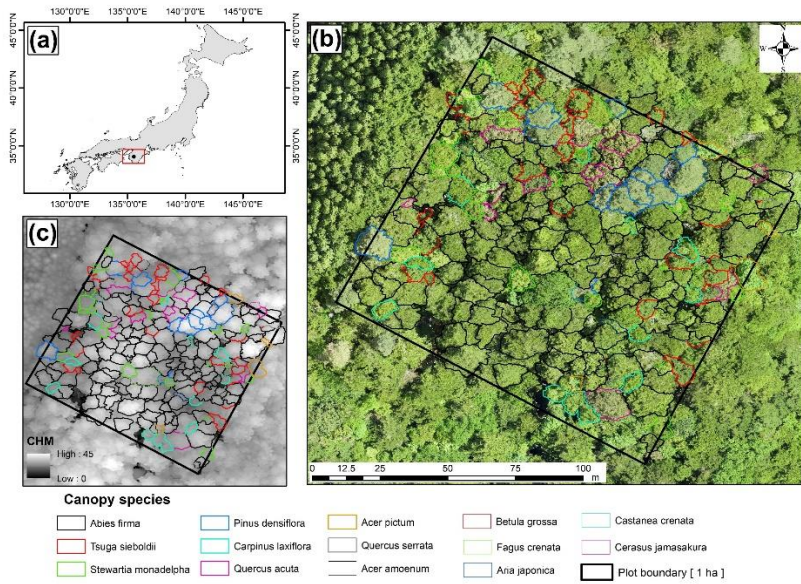


Fig. S2.1 (a) A map of Japan with the black dot indicating the study site, (b) Orthomosaic image of the study site based on drone imagery, and (c) Canopy Height Model (CHM) showing the height gradient in grey scale. The boundary of the forest monitoring plot is shown by a thick black line, whereas each tree crown is shown with thin lines with different colors depending on tree species.

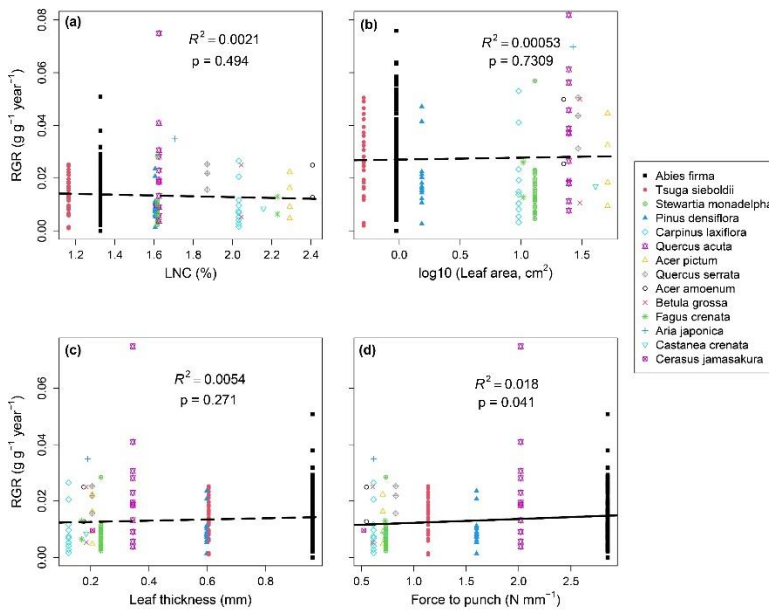


Fig. S2.2 The relationship between relative growth rate (RGR) and leaf traits, including (a) leaf nitrogen content (LNC), (b) $\log_{10}(\text{leaf area, cm}^2)$, (c) leaf thickness, and (d) force to punch. For each, the coefficient of determination (R^2) is shown with significance level (p). Statistically significant relationships are indicated by solid lines ($P < 0.05$) while dotted lines denote no significance.

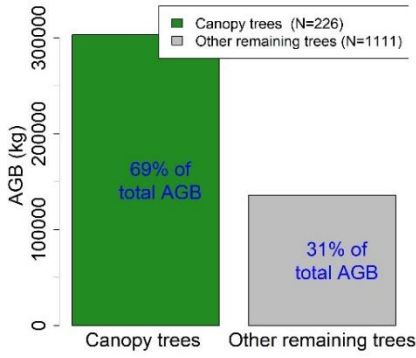


Fig. S2.5 Relative contribution of the canopy trees detected by drone survey and other remaining trees as components of the stand biomass of the 1-ha plot.

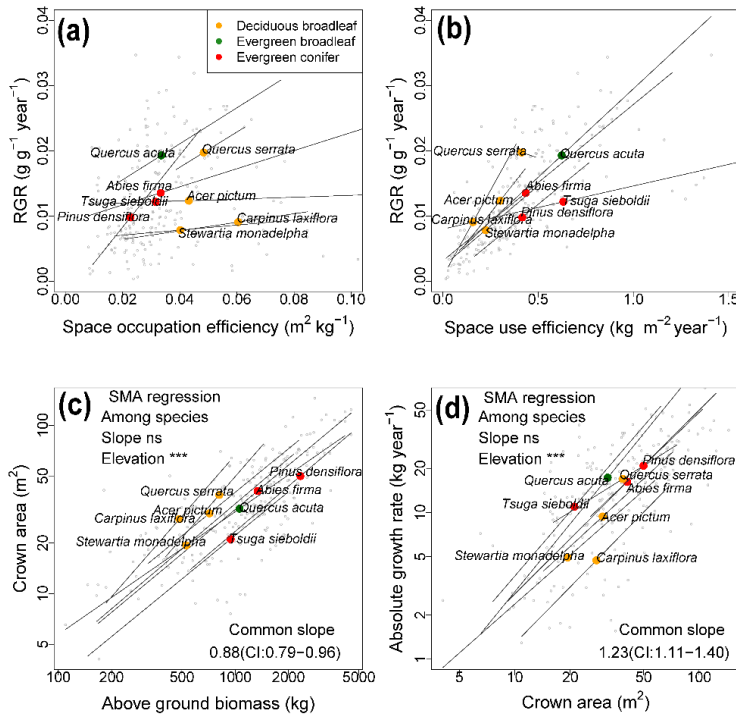
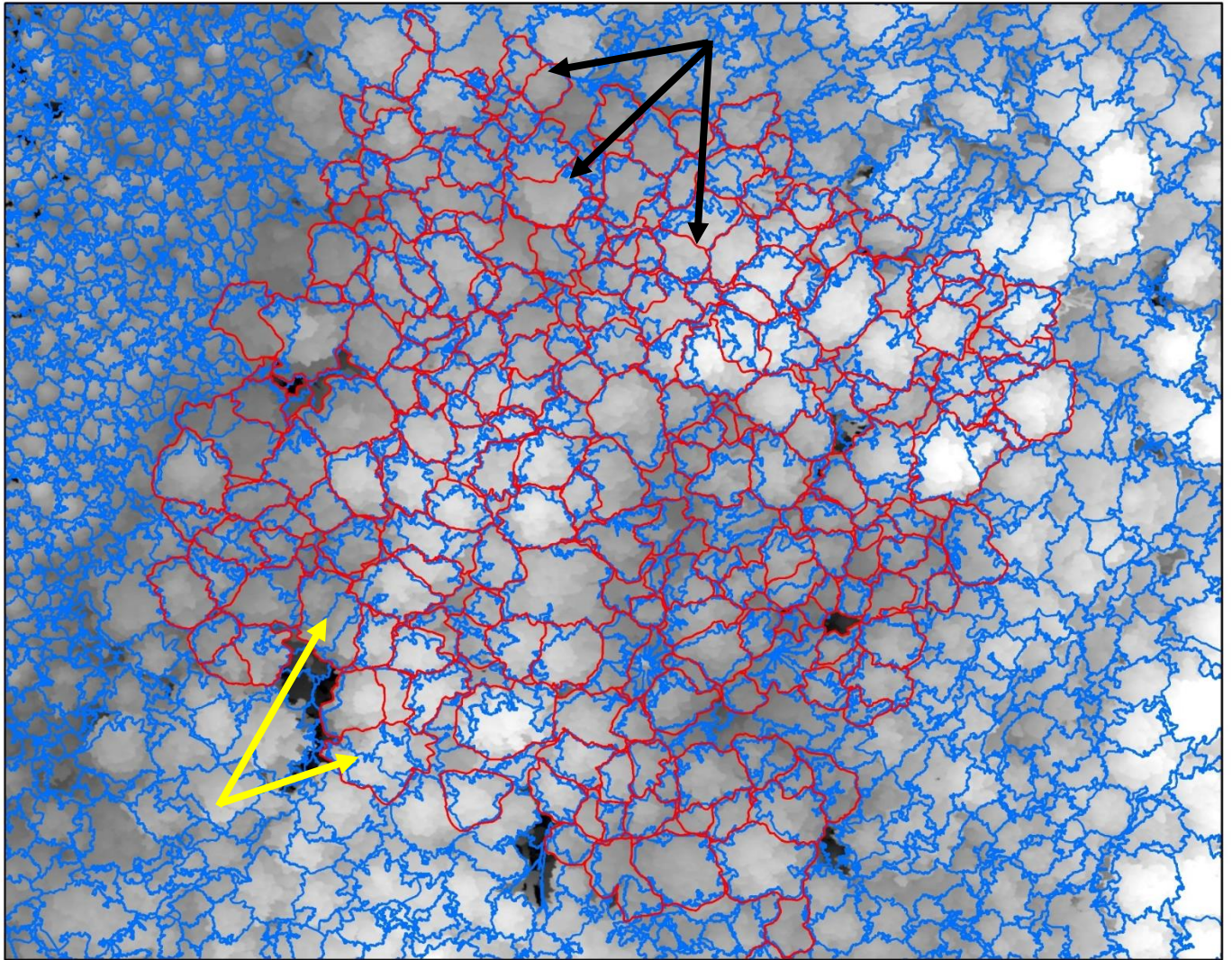


Fig. S2.6 Bivariate relationship between size- and growth-related variables among individual trees (grey points) for species with sufficient sample size (> 3 individuals) in the dataset. Relative growth rates (RGR, $\Delta M/M$) are plotted against (a) space occupation efficiency (SOE, A_c/M) and (b) space use efficiency (SUE, $\Delta M/A_c$), where M is tree above-ground biomass, ΔM is above-ground biomass growth rate and A_c is crown area. (c) Relationship between the two components of SOE; crown area and above-ground biomass, and (d) between the components of SUE; absolute growth rate, and crown area. Each colored point represents the mean values of each species on the species-specific regression line of standard major axis regression (SMA). Symbol colors indicate functional types (yellow for deciduous broadleaf species, green for evergreen broadleaf species, and red for evergreen conifers). Plots (c) and (d) employ the $\log_{10}$ scale on both axes. The significance levels of the SMA results for (c) and (d): *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns $P > 0.05$.



Auto-segmented tree crown area
 Field-validated tree crown area

Fig. S2.7 Comparison of the auto-segmented tree crowns and the manually edited tree crowns after field validation. The auto-segmentation was done using RGB layers, canopy height model (CHM) and surface slope model. Compared to visual delineations followed by the field valuation, the automatically produced results are typically either more fine-grained or coarse-grained, requiring additional aggregation (yellow arrows) or division (black arrows) steps to achieve accurate crown delineations.

Chapter 3: Development of crown-based allometric equations for estimating stem diameter and above-ground biomass using UAV-LiDAR in species-rich temperate forests

Abstract

Accurate measurement of individual tree structural variables, such as stem diameter, height, and crown dimension, is essential for assessing forest biomass and ecological functions. UAV-LiDAR technology enables detailed measurement of tree canopy structures including crown height (H) and crown area (CA) over extensive areas and has been used to estimate above-ground biomass (AGB). However, most previous studies have focused on commercial conifer trees, with limited research on natural forest trees. In this study, we measured H and CA for 149 canopy species encompassing 4355 individuals across 23 temperate natural forests in Japan, using UAV-LiDAR. We developed general, functional-type-, and species-specific allometric models to estimate stem diameter at breast height (DBH) and AGB based on H and CA. Our results demonstrate UAV-LiDAR as a reliable tool for accurately estimating H and CA across diverse forest types and regions. The models incorporating H and CA provide a substantial explanation of DBH (68%) and AGB (71%) variations across different forests and regions. The integration of functional types or species-specific information enhanced estimations by 9-13% in DBH and by 7-11% in AGB models, thereby the models can explain up to 81% in DBH and 82% in AGB variations. UAV-detected trees accounted for more than two-thirds of the total AGB in one-hectare plots across various forest types, underscoring the reliability of UAV surveys in capturing standing AGB. The crown-based allometric models developed in this study may be useful to accurately estimate DBH and AGB of canopy trees for larger areas in temperate natural forests.

Keywords: above-ground biomass, crown area, tree height, stem diameter, UAV-LiDAR

3.1 Introduction

Reliable estimations of forest above-ground biomass (AGB) are crucial for understanding the ecosystem functions and services (Pregitzer et al., 2004; Bonan, 2008; Pan et al., 2013). Accurate measurements of individual tree structural characteristics such as stem diameter, height, and crown dimensions (e.g. width and area) are important because tree species differ in their sizes and canopy structures. Allometric equations translate these measurable tree structural variables to AGB estimates, which could be compared across various forest types and regions (Chave et al., 2005). Therefore, precise data acquisition of individual tree structural characteristics and the development of robust allometric models are necessary for reliable AGB estimates.

Given that a whole tree is usually too large to measure directly, traditional forest surveys often took ground-based measurements of stem diameter at breast height (DBH) to estimate tree biomass and forest dynamics (Davies et al., 2021). DBH can be measured relatively quickly and consistently for many trees, providing a reliable metric for estimating tree biomass and growth rates. Various allometric models have been developed to estimate the standing AGB based on DBH values. More elaborate models incorporate additional variables such as tree height (H) and wood density, which lead to more accurate AGB estimates as they account for differences in tree architecture and wood traits (Chave et al., 2005; Ishihara et al., 2011; Chave et al., 2014). However, conventional forest census methods are time-consuming and labor-intensive, especially when applied to large census plots or areas with dense vegetation. These challenges often result in fewer trees being measured than ideal, or limited sampling of the target forested area, underscoring the need for more efficient approaches to scale-up measurements for broad assessments.

Recent advances in remote sensing technologies, such as Light Detection and Ranging (LiDAR) and Unmanned Aerial Vehicles (UAVs, a.k.a., drones), have emerged as promising

tools for estimating tree structural variables at the individual tree level across a larger scale (Dalponte & Coomes, 2016; Zhen et al., 2016; Weinstein et al., 2021; Rahman et al., 2022; Jackson et al., 2024). UAV equipped with LiDAR sensor (UAV-LiDAR) can gather precise three-dimensional (3D) point cloud data of forests. From such point cloud data, digital surface model (DSM), digital terrain model (DTM), and canopy height model (CHM) can be derived at high resolutions. The height of individual canopy trees can be derived from CHM, and their crown area (CA) can also be estimated from CHM and orthomosaic photo (Zhen et al., 2016; Apostol et al., 2020; Onishi & Ise, 2021; Ball et al., 2023). Therefore, UAV-LiDAR technology and the subsequent data analysis enable us to collect accurate and detailed tree canopy structural variables (H and CA) at broader scales and enhance our capacity in forest surveys.

Tree canopy structural variables (H and CA) are known to correlate with other tree dimensions. These relationships make them useful for estimating other important metrics such as DBH and AGB. Consequently, there is a growing interest in incorporating remote sensing-compatible variables (e.g., H and crown diameter), to improve DBH and AGB estimations (Jucker et al., 2017; Dalponte et al., 2018; Brede et al., 2022), especially for canopy trees which can be easily measured from UAV (Htoo et al., 2024). The accuracy and effectiveness of UAV-derived canopy structural variables have been extensively studied, primarily focusing on conifers and commercial species in homogeneous forests (Kuželka et al., 2020; Moe et al., 2020; Puliti et al., 2020; Hao et al., 2021; Iizuka et al., 2022). However, the potential of UAV-LiDAR data in predicting DBH and AGB in species-rich natural forests across diverse environments remains largely underexplored. Several factors contribute to the challenges of using UAV-LiDAR in natural forest ecosystems, including (1) diverse crown shapes, (2) uneven tree size distribution, (3) varying allometric relationships among species, and (4) species composition. Trees in natural forests exhibit a wide range of crown shapes,

many of which are not conical as in monospecific conifer stands. This complicates the detection and segmentation of individual crowns especially in broadleaf stands where canopy shape is more variable (Nuijten et al., 2019; Moe et al., 2020; Onishi et al., 2022). Tree size and growth patterns differ among tree species, forest types, and environmental conditions (Blanchard et al., 2016), which necessitates the development of different allometric equations. Furthermore, they comprise a mix of functional types, such as conifers and broadleaf species with distinct canopy architectures, vertical leaf distribution, and leaf phenology (McNeil et al., 2023). Moreover, it is also crucial to evaluate the extent to which canopy individuals detected by UAV surveys contribute to the total standing AGB across diverse forest types and regions. Such efforts will enhance the effective application of UAV-LiDAR in diverse natural forests, improving our understanding of AGB variations in natural forest stands.

In temperate ecosystems, latitudinal gradients roughly correspond to the changes in temperature (De Frenne et al., 2013). As the climate transitions from warmer to colder temperate regions, the distribution and relative abundance of tree species change accordingly, with each adapting to their local environmental conditions (Suzuki et al., 2015). There are hundreds of canopy species within a given region and these species can be grouped into conifers (needle-leaved gymnosperms) vs. broadleaf (angiosperms) trees, each of which includes deciduous and evergreen species. Coniferous trees generally have narrow crowns for a given biomass, while broadleaf trees tend to have wider crowns, reflecting differences in canopy structure and biomass allocation. Additionally, evergreen and broadleaf species exhibit distinctions in their growth patterns: evergreens retain their leaves year-round, enabling them to photosynthesize over a greater proportion of the year, whereas deciduous species shed their leaves for some period during the year. Species-specific allometric relationships may be partly underpinned by these functional types in terms of biomass allocation and canopy structure, so functional type-based allometric equations could be a practical alternative, even when species

information is not available. Therefore, it is crucial to assess how much allometric relationships vary within species compared to between functional types to determine the feasibility of using such generalized models in temperate forests.

Japanese archipelago spans a wide latitudinal range of 45° N to 24° N, with large covers of forests mainly on mountains and hills. As a result, it hosts a wide range of forest types including subboreal, cold temperate, warm temperate, and subtropical forests (Kira, 1949; Numata et al., 1972; Miyawaki, 1990). Approximately 1600 tree species have been reported in Japan (Oohata, 1990). This high level of diversity is partly attributable to being part of East Asia, which benefited from abundant refugia during the last glacial period compared to Europe and America (Latham & Ricklefs, 1993). The relative dominance of functional types changes with latitudinal gradient (Suzuki et al., 2015). Due to the high species diversity, allometric equations per functional type may be practical for estimating stand-level biomass productions in Japanese natural forests, even though species-specific allometric equations may be more precise.

In the current study, we have the following objectives:

- 1) To establish a database of tree crown height and crown area using UAV-LiDAR for a diverse set of canopy tree species across 23 one-hectare permanent forest monitoring sites in Japan, spanning approximately 3000 km distance (Fig. 3.1).
- 2) To develop functional type- and species-specific allometric equations to estimate DBH and AGB based on crown height and crown area.
- 3) To examine the predictive performances of these multiple models, with or without incorporating functional types and species information, in estimating DBH and AGB.
- 4) To quantify the contribution of UAV-detected canopy trees to total AGB within the plots across diverse natural forests in Japan.

3.2. Materials and methods

3.2.1 Study area

The study was conducted in 23 permanent forest monitoring sites which covered a wide latitudinal range of 44.4° N to 26.7°N. These sites encompass diverse forest types ranging from subboreal forests in the north to subtropical forests in the south of Japan (Fig. 3.1 and Supplementary Information Table S3.1). They are part of a long-term monitoring project in Japan (the Monitoring Sites 1000 Project) with standardized plot size of 1-ha (100 m × 100 m) with tagging and identification of all trees ≥ 15 cm GBH (girth at breast height). Individual tree identification number (ID), species, and stem locations (x and y coordinates) are recorded, and their GBH and survival are measured at one- to five-year intervals. The time-series inventory data are publicly available for 2005 and onward (Ishihara et al., 2011). We downloaded the latest available dataset version as of a reference date of 2019/07/11 (<https://www.biodic.go.jp/moni1000/>). Site-level characteristics and forest census information were detailed in Table S3.1.

3.2.2 UAV-LiDAR data collection, processing, and process of crown mapping

In 2022–2023, we collected the LiDAR data in the 23 sites using a UAV-LiDAR system (DJI Matrice 300 RTK+ Zenmuse L1, DJI, Shenzhen, China). All data collection was done in the summertime when deciduous species were fully foliated and clearly visible from UAV images. Details of LiDAR data collection and processing are described in Htoo et al. (2024) with a schematic summary shown in Fig. S3.1. In brief, we collected raw LiDAR data with a standard flight configuration (100 m above the ground, speed 5–10 m/s) across the 23 sites (Table S3.2 for details of each flight). The raw LiDAR data were processed by the protocol (DF LAT, Deep Forest Technologies, Kyoto, Japan), which involved point cloud construction, thinning point cloud data, ground point detection, surface filtering, and merging with filtered data. From the

final point cloud data, three raster-based models were constructed: digital surface model (DSM), digital terrain model (DTM), and canopy height model ($CHM = DSM - DTM$).

From these data, individual tree crown segmentation was carried out in eCognition Developer v.9.0.0 (Trimble, Inc., Sunnyvale, United States). Previous research demonstrated that the combination of CHM, orthomosaic images, and the surface slope model enhanced the accuracy of crown segmentation (Onishi & Ise, 2021; Onishi et al., 2022). Therefore, along with the RGB layer, CHM, and surface slope models were jointly employed for image segmentation with a multiresolution segmentation algorithm (Fig. S3.2). We assigned weights to the data layers (e.g., RGB image layers=1, CHM layers=2) to determine their importance in the image segmentation process. The weights were determined by prior research findings (Apostol et al., 2020; Moe et al., 2020; Onishi & Ise, 2021; Htoo et al., 2024) and empirical testing to optimize the segmentation outcomes. We found variable combinations of segmentation parameters for each site. The detailed site-specific segmentation parameters for accurate crown area estimations are presented in Table S3.3.

The shape, size, and conditions (i.e., live, dead, or broken) of the segmented tree crowns and linking them with the tree census data were confirmed by the ground-based measurements in all 23 sites. We used the ArcGIS FieldMap application (ESRI, Inc., Redlands, CA, USA) which can accommodate and show multiple spatial layers such as RGB orthomosaic image, DTM, and CHM with current location information on these layers. In the field, we identified individuals of canopy trees, recorded their associated tag numbers, and manually delineated tree crowns using the FieldMap application on a tablet (Apple iPad iOS). After the fieldwork, all individual crowns were manually digitized in the lab, and the crown area (CA) was calculated using ArcGIS Desktop v.10.8.1 software (ESRI, Inc., Redlands, CA, USA). The maximum tree height (H) for each tree individual was estimated using the zonal statistics tool in ArcGIS Desktop. In the field, we also measured the tree heights of selected individuals (113

in total) across various forest types using an ultrasonic range finder (Vertex Hypsometer VI, Haglof Company Group, Sweden). While height estimates using ultrasonic range finders also contain potential errors because of the difficulty in detecting canopy tops from the ground, we usually found a good agreement between the two tree height estimates ($r=0.70$, Fig. S3.3).

3.2.3 Modeling

Our primary purpose was to build allometric models to predict DBH and AGB of trees using H and CA which are derived from UAV-LiDAR, and species information available from tree census data across 23 sites. Since we aimed to quantify the relative contribution of H , CA , site-to-site variability, functional types, and species to predict the stem DBH and AGB, we applied both ordinary least squared (OLS) linear regressions and mixed-effects models. Firstly, we applied OLS linear regressions, where both the predictor variables (H , CA) and response variables (DBH, AGB) were transformed to logarithmic scales to normalize distributions and reduce heteroscedasticity. We compared sets of models to assess the predictive power of each variable independently and in combination. Initially, we fitted the following general models using data from all sites:

$$\ln(Y) = a + b \ln(H) \quad (M1)$$

$$\ln(Y) = a + c \ln(CA) \quad (M2)$$

$$\ln(Y) = a + b \ln(H) + c \ln(CA) \quad (M3)$$

where $\ln$ is the natural log, Y is stem diameter (DBH, cm) or above-ground biomass (AGB, kg), H is maximum tree height (m), CA is crown area (m^2) and a , b , and c are the regression coefficients. The equations (M1- M3) are regarded as general allometric equations, assuming that the scaling relationships between variables DBH , AGB , H , and CA are constant irrespective of species, functional types, and sites.

Secondly, linear mixed-effects models (Leite et al., 2020; Moe et al., 2020; Adhikari et al., 2024) were built with sites, functional types, and species as random effects:

$$\ln(Y) = a_{site} + c_{site} \ln(CA) \quad (M4)$$

$$\ln(Y) = a_{fun} + c_{fun} \ln(CA) \quad (M5)$$

$$\ln(Y) = a_{spp} + c_{spp} \ln(CA) \quad (M6)$$

$$\ln(Y) = a_{site} + b_{site} \ln(H) + c_{site} \ln(CA) \quad (M7)$$

$$\ln(Y) = a_{fun} + b_{fun} \ln(H) + c_{fun} \ln(CA) \quad (M8)$$

$$\ln(Y) = a_{spp} + b_{spp} \ln(H) + c_{spp} \ln(CA) \quad (M9)$$

where *site* refers to the identity of the 23 forest monitoring sites, *fun* is the functional type (i.e., conifer, deciduous- and evergreen- broadleaf), and *spp* denotes the species identity of each tree crown.

In this study, the above-ground biomass (AGB) was calculated with a general biomass equation developed for Japanese natural trees (Ishihara et al., 2015). The equation incorporates not only diameter at breast height (*DBH*) but also maximum tree height (*H*) and species-specific wood density (*WD*) to increase the accuracy of biomass estimation:

$$\ln AGB = -1.876 + 2.174 \times \ln(DBH) + 0.283 \times \ln(H) + 0.611 \times \ln(WD)$$

We calculated *DBH* values from field-measured GBH, *H* values derived from the CHM, and species-specific *WD* from the wood density dataset (Aiba et al., 2016). We note that *H* is used for calculating AGB in the above equation, and also used as a predictor in the models M1, M3, M7, M8, and M9 when *Y* in these models are AGB. Even though autocorrelation may potentially increase R^2 values, our objective is to obtain practical model coefficients to predict AGB from UAV-based metrics, i.e. CA and H, rather than obtaining high R^2 .

We also quantify the relative contribution of the AGB of UAV-detected canopy individuals to the total stand AGB including subcanopy trees. In this calculation, since H data for non-canopy trees are not available, we calculated the AGB by using only DBH and WD values: $\ln AGB = -1.196 + 1.622 \ln(DBH) + 0.338 (\ln(DBH))^2 - 0.044 (\ln(DBH))^3 + 0.708 \ln(WD)$.

3.2.4 Statistical analysis

All the analyses were conducted in R programming software (R Core Team, 2023). The correlation coefficient (r) was calculated to determine the relationships between pairs of the study variables (DBH , H , CA , and AGB). Individuals whose crowns were dead or broken, partially-to-completely overtopped by others, or mismatched to the tree tags (56 out of 4411), were excluded from the allometry analysis. Therefore, we analyzed a total of 4355 individuals across 23 sites. Tree species were classified as conifer or broadleaf trees, as well as evergreen or deciduous. Because deciduous conifer species (e.g., *Larix kaempferi*) did not appear in our study sites, we compared three functional types: deciduous broadleaf, evergreen broadleaf, and evergreen conifer species. To examine the impact of functional types on the relationship between variables, an analysis of covariance (ANCOVA) was conducted with the “stats” package (version 4.2.2). We calculated the contribution of UAV-detected individuals to total AGB per hectare to compare across study sites. For two sites (Hanyama and Yona), we could not quantify for the entire 1-ha because 50 out of 302 trees were excluded due to technical reasons in Hanyama, and because approximately 23 % of the area could not be surveyed due to heavily damaged crowns by the past typhoons in Yona. Therefore, we estimated variables per ha for these sites to compare with other sites.

We fit linear models using the “stats” package, and mixed-effects models using “lme4” (version 1.1-33) (Bates et al., 2015) where random effects were specified based on site, functional type, and species to account for the hierarchical data structure. Model performance

metrics include the Akaike Information Criterion (AIC) extracted using the AIC function from the “stats” package. Root Mean Squared Error (RMSE) was calculated as the square root of the mean squared error between predicted and observed values. Conditional and marginal R-squared (R^2) values for mixed-effects models were computed using the “MuMIn” package (version 1.47.5) (Bartoń K, 2023). The conditional R^2 includes both fixed effects (H, CA) and the random effects (site-to-site variability or functional types or species), showing the total variance explained when accounting for these random factors (Nakagawa & Schielzeth, 2013). The marginal R^2 considers only fixed effects, highlighting the variance explained by predictors (H, CA). The relative error (RE%) was calculated as the average percentage difference between predicted and observed values using the formula: $RE = (|Y_{\text{predicted}} - Y_{\text{observed}}| / Y_{\text{observed}}) \times 100$ (Chave et al., 2005). The mean RE was obtained by averaging the relative errors across sites. The correction factor (CF) for each model was calculated to account for the bias introduced by the inverse log transformation, using the formula $CF = \exp(SEE^2/2)$, where SEE is the standard error of the estimate (Sprugel, 1983). The best linear unbiased prediction (BLUP) coefficients (a, b, c) from mixed-effects models were extracted using the “coef” function from the “lme4” package. We utilized the BLUP approach as it is suited for predicting species-specific functions for many species even when some of them had a relatively small number of samples (Robinson, 1991; Gelman, 2007).

3.3 Results

A total of 4355 living canopy tree individuals from 149 species were validated and recognized from the UAV imagery and linked to the tree census data from 23 one-hectare sites. These numbers accounted for 18.6% of total stems (23360 stems), 67.9% of total basal areas (1135 m^2), and 64.0% of all 233 species with DBH (diameter at breast height) ≥ 5 cm because UAV could capture only canopy trees and not sub-canopy tree crowns. A total of 1349, 1776, and 1230 records (tree crowns) belonged to the functional types of evergreen conifers, deciduous

broadleaf, and evergreen broadleaf, respectively. Among the tree structural variables measured, crown area (CA) exhibited the highest coefficient of variation (CV) within and among sites, with a mean of 81.8% for the 23 sites. Hence, there was considerable variability in crown size across different tree individuals, species, and sites. DBH also showed notable variation with a mean CV of 43.8%, while tree height (H) was the most consistent structural variable with a mean CV of 18.2% among sites, partly because only the canopy trees were detected by the UAV survey. Detailed descriptive statistics of these tree structural variables at individual sites were provided in Table S3.4.

The number of tree crowns detected per hectare by the UAV survey varied significantly across different sites and functional types. Conifer-dominated sites exhibited a higher detection rate, ranging from 10% to 47% of all stems more than 5 cm, and the highest detection rate was observed in conifer-dominated sites (Otanomosutaira). In contrast, sites dominated by evergreen broadleaf trees generally had lower detection rates of less than 20%. For example, at Aya site, only 10.37% of trees were detected by UAV survey, meaning a high abundance of sub-canopy and understory individuals in evergreen broadleaf forests. Likewise, at Yona, an evergreen broadleaf site, a low detection rate of 18% was recorded. Deciduous-broadleaf-dominated sites showed variable detection rates, ranging from 11% to 38%. These variations in detection rates across different sites underscore the influence of forest structure and composition on the effectiveness of UAV-based crown detection. In some cases, site-specific conditions further impacted the detection rate. Detailed site-specific variations in tree detection rates are provided in the supplementary Table S3.4.

3.3.1 Relationship between UAV-measured variables (CA and H) and DBH and above-ground biomass (AGB)

DBH was better correlated with CA ($r = 0.76$, Fig. 3.2a) than H ($r = 0.72$, Fig. 3.2c). Similarly, AGB was better correlated with CA ($r = 0.78$, Fig. 3.2b) than H ($r = 0.74$, Fig. 3.2d) across all

individuals and species. There were also significant variations in the relationships between DBH, H, CA, and AGB among three functional types (i.e., evergreen conifers, deciduous broadleaf, and evergreen broadleaf) according to the ANCOVA test (Fig. 3.2). In DBH-CA and AGB-CA relationships, conifers showed higher intercept values in the log-log relationship than broadleaf species.

3.3.2 DBH and AGB models

Table 3.1 summarizes multiple allometric models to predict DBH from UAV-measured H, and CA, in combination with sites, functional types, and species information as covariates. Whereas Models 1 to 3 are general linear models, models 4 to 9 are linear mixed-effects models that consider variations of intercepts (a) and slopes (b, c) among individual sites, functional types, and species. H alone accounted for 53% of the observed variation in DBH (M1, $R^2 = 0.53$), whereas CA alone accounted for 58% (M2, $R^2 = 0.58$). Combining H and CA enhanced model performance by 10% (M3, $R^2 = 0.68$). Models 4 to 6 focused on DBH estimation solely using CA, incorporating site, functional types, and species as random factors. Model 4 (CA + site) showed the same power as M3 with 68%. Consideration of functional type improved by 3% (M5, $R^2 = 0.71$), and species improved by 7% (M6, $R^2 = 0.75$). Furthermore, jointly considering H and CA with site identity led to a 12% improvement (M7), and a 9% improvement with functional types (M8). Notably, integrating CA and H with species as a random factor, achieved the highest R^2 of 0.81 (M9), along with the lowest AIC of 922.16 and an RMSE of 0.25.

Similarly, we conducted a comparison of models for estimating AGB using the same variables (H, CA, sites, functional types, and species). The performance of all models was comparable to those for DBH estimation. M1 (H only) explained 55% and M2 (CA only) explained 61% of AGB variations. M3 (CA to H) improved the prediction by 16% ($R^2 = 0.71$). The model incorporating sites, functional types, and species alongside H and CA showed the

R^2 values of 0.82, 0.78, and 0.82 respectively, demonstrating the importance of including these factors in AGB estimation (Table 3.2).

Table 3.3 summarizes the model coefficients along with their corresponding correction factors (CF) to predict DBH and AGB, for which we selected general models (M1, M2, M3) and functional types specific models (M5, M8). More details of fitted coefficients for each different site and species are summarized in Tables S3.5 and S3.6.

3.3.3 UAV-detected individuals and their contribution to total AGB

The contribution of UAV-detected individuals to the total AGB per hectare varied across different sites and functional types. Among the conifer-dominated sites, it ranged from 70% to 84%. Among the deciduous-broadleaf-dominated sites, it varied from 64% to 89% (Fig. 3.3a). In the evergreen-broadleaf sites, the contribution ranged from 64% to 71%. In general, UAV-detected trees represented approximately two-thirds of the total AGB of each 1-ha sample regardless of the sites. There was a significant positive relationship between the total AGB of UAV-detected individuals and ground-based AGB estimated for all trees $DBH \geq 5\text{cm}$ irrespective of sites and dominant functional types ($R^2 = 0.92$, Fig. 3.3b). This finding highlights the effectiveness of UAV in detecting the substantial portion of the canopy trees that contribute to the total AGB in diverse forest types.

3.4. Discussion

3.4.1 Performance of general and functional-type specific models

In this study, we found that crown area (CA) and crown height (H) estimated by the UAV-LiDAR method well predicted both DBH and AGB of individual canopy trees. In the global analysis, Jucker et al. (2017) demonstrated the effectiveness of incorporating crown diameter and H in predicting tree DBH with an R^2 value of 0.69. Various studies across different regions have shown the efficacy of utilizing crown information toward improving the accuracy of AGB

modeling (Wirth et al., 2004; António et al., 2007; Goodman et al., 2014; Forrester et al., 2021; Brede et al., 2022). In our study, only CA and H can explain a substantial portion of the variation without considering species or functional type identity, i.e., 68% in DBH models and 71% in AGB models. In developing these models, our primary goal was to provide simple and accurate models that could be applied across various forest types with minimal data requirements. The general models (M1-M3) are particularly useful when only CA and H information are available. By focusing only on H and CA, these models can predict both DBH and AGB with reasonably high accuracy, even in the absence of detailed functional types- or species-specific information. Therefore, models including H and CA could be used to predict the DBH and AGB of canopy trees for larger areas.

Consideration of functional types distinguishing conifers, deciduous broadleaf, and evergreen broadleaf species resulted in better prediction of DBH and AGB. In our study, the inclusion of functional types increased the DBH prediction by 9% (from 68 to 77%) and AGB by 7% (from 71 to 78%) (Table 3.1 and 3.2). A global study by Jucker et al. (2017) similarly found significant improvement in the model performance by incorporating biogeographical regions, forest types, and functional types (angiosperms vs gymnosperms). Conifers, deciduous broadleaf, and evergreen broadleaf species exhibit distinct architecture and biomass distributions. For instance, conifers tend to have greater DBH for a given CA, i.e., higher intercept values compared to broadleaf species (Fig. 3.2a; Table 3.3). Incorporating functional types allows consideration of these underlying structural differences.

Our study compared the UAV-based estimates of AGB with ground-based estimates to evaluate the utility of the UAV. In order to apply crown-based allometric equations for larger areas without ground-based measurements, it is essential to estimate tree CA and H from UAV. UAV-measured H agreed with field-measured H across diverse forest types, climates, and topographies ($r = 0.70$, Fig. S3.3), underscoring UAV-LiDAR's reliability and robustness in

measuring canopy H. However, auto-segmentation of individual tree crowns remains technically difficult with potential errors, particularly in mixed forests with broadleaf trees. We note that canopy shapes in these sites are more variable than in conifer-dominated forests, leading to greater variability in crown estimation (Table S3.3). Therefore, the crown validation process is still required. In this study, we searched for the best combination of site-specific crown segmentation parameters for our study sites. These parameters could be applied to similar types of natural forests in a given region. The field of individual tree crown segmentation continues to evolve rapidly (Silva et al., 2022; Ball et al., 2023; Vasquez et al., 2023; Dersch et al., 2024), and future advancements in algorithms are expected to improve segmentation accuracy across diverse forest types. In addition, UAV imagery can capture differences in crown shape, canopy texture, and color, which are often used to distinguish between coniferous and broadleaf species (Htun et al., 2023), or between deciduous and evergreen species (Onishi & Ise, 2021; Cloutier et al., 2024). Therefore, UAV imagery can provide valuable information for detecting functional types for large areas. By leveraging functional types that are distinguishable from UAV imagery, it can deliver more precise and reliable DBH and AGB estimates across broader areas and forest types.

3.4.2 Species-specific regression models

As expected, species-specific models outperformed general and functional-type specific models as evidenced in our study as in others (Moe et al., 2020; Iizuka et al., 2022). With additional species data, the models' explanatory power significantly increases, reaching up to 81% in DBH models and 82% in AGB models. Unlike previous studies that reported regression coefficients for only a limited number of species, our study included 149 tree species occurring in Japanese natural forests across a wide geographical range. These coefficients also shed light on species-specific strategies. For instance, conifer species tend to allocate more to the trunk biomass compared to broadleaf species, which generally prioritize lateral crown expansion

(Fig. 3.2b). Therefore, considering species-specific allometric relationships can reflect their specific strategies and improve the estimation accuracy. Yet there are many species with relatively low sample sizes ($n < 10$), therefore their allometric equations may have lower precision of estimates for rare species.

The species identification may be difficult from UAV images alone, especially in mixed forests, where diverse species coexist. In the current study, forest inventory data were utilized for species identification, but a broader application of this method outside of monitoring plots would require species identification from UAV images. In this regard, machine learning algorithms have the potential to automate the identification process, and UAV imagery in combination with deep learning techniques, such as object-based convolutional neural network (CNN), can predict accurately up to 90% in some sites (Onishi & Ise, 2021). Similarly, in heterogeneous temperate forests with a training dataset of target species can achieve up to 89% (Schiefer et al., 2020) and 92% accuracy (Beloïu et al., 2023). Species identification from UAV imagery is progressing, with future advancements in algorithms anticipated to enhance the accuracy across different forest types, thereby increasing the efficiency and scalability of forest assessments.

3.4.3 Efficacy of UAV surveys in AGB monitoring in diverse natural forests

In our study sites, among the tree structural variables, the CA of canopy trees turned out to be a critical factor that explained AGB variation (Fig. 3.2b; Table 3.2). In neotropical landscapes, Meyer et al. (2018) showed that CAs of large trees derived from the LiDAR data were significantly correlated with the stand-level AGB, explaining more than 75% of the forest biomass in large trees ($H > 27$ m, $CA > 100$ m²). In a study conducted in Brazil (Araújo et al., 2020), UAV-detected canopy trees, which make up only 40% of stem numbers with DBH > 10 cm, accounted for the majority of above-ground carbon (67%). In a similar study conducted in a 9-ha plot in the Yoko Forest in the Democratic Republic of the Congo, UAV could detect

only 23.4% of the trees with DBH >10 cm but they represent 75.1% of total AGB (Ndamiyehe et al., 2020). Although we found large variations in detection rates of canopy trees by UAV among sites, the results consistently revealed that UAV-detected individuals accounted for approximately two-thirds of the total biomass across a variety of forest structures and tree species composition. To our knowledge, the present study is the first to assess what proportion of trees and stand-level AGB can be detected by UAV in multiple forest types across various climatic zones.

Overall, we found that UAV-based AGB monitoring can be reliably applied in various ecological contexts, potentially offering a more scalable and less labor-intensive method compared to traditional ground surveys. At the same time, sub-canopy trees and understory trees missed by UAV still account for approximately one-third of total AGB (Fig. 3a, see also Coomes et al., 2017). The detection rate of under-canopy trees can potentially be increased by integrating the analysis of canopy height models with the LiDAR point cloud data (e.g. Duncanson et al., 2014; Paris et al., 2016; Huo et al., 2022), or by fusing LiDAR data with the terrestrial laser scanning (TLS), which can effectively scan the understory trees (Brede et al., 2022; Terryn et al., 2022; Terryn et al., 2024). However, these techniques are computationally demanding especially if we applied to larger areas and the algorithms still need to be well-tested for wider application across various forest types.

3.4.4 Conclusions and implications

In this study, we show that UAV-LiDAR technology is applicable to many different forest types, from subarctic to subtropical, to estimate DBH and AGB. We developed various crown-based allometric models – general, functional- and species-specific – that can estimate AGB with high accuracy depending on the availability of data. UAV provides an excellent method to estimate the height and crown area of canopy trees, to allow AGB estimation for much larger areas than traditional forest surveys can achieve. Moreover,

UAV surveys are particularly advantageous in remote or hard-to-access regions such as steep terrains, where conventional surveys are impractical. We hope that the models developed in our study will be useful for improving AGB estimates of canopy trees in natural forest stands. Future studies may evaluate the applicability of these models to larger forested areas and similar forest types in other biogeographical regions.

Tables

Table 3.1 Model comparison for estimating diameter at breast height (*DBH*) from crown area (*CA*) and maximum height (*H*). Models 1-3 were general linear models and from models 4-9, linear mixed-effects models were employed to allow intercept (*a*) and slopes (*b*, *c*) to vary for each site, functional types (*fun.*), and species. Akaike's Information Criteria (AIC), Root Mean Square Error (RMSE) and mean relative error in percentage (RE) are presented for each model. The adjusted coefficient of determination (R^2) is presented (Adj.) for linear models, while conditional (Cond.) and marginal (Marg.) R^2 values are shown for linear mixed-effects models.

No.	Model structure	Random factor	AIC	RMSE	RE (%)	R^2		
						Adj.	Cond.	Marg.
M1	$\ln(DBH) = a + b \ln(H)$	-	4393.83	0.40	9.35	0.53	-	-
M2	$\ln(DBH) = a + c \ln(CA)$	-	3829.22	0.38	8.97	0.58	-	-
M3	$\ln(DBH) = a + b \ln(H) + c \ln(CA)$	-	2728.27	0.33	7.78	0.68	-	-
M4	$\ln(DBH) = a + c \ln(CA)$	site	2492.79	0.31	7.29	-	0.68	0.53
M5	$\ln(DBH) = a + c \ln(CA)$	fun.	2548.68	0.32	7.50	-	0.71	0.57
M6	$\ln(DBH) = a + c \ln(CA)$	species	1803.04	0.28	6.33	-	0.75	0.52
M7	$\ln(DBH) = a + b \ln(H) + c \ln(CA)$	site	1364.14	0.27	6.20	-	0.80	0.68
M8	$\ln(DBH) = a + b \ln(H) + c \ln(CA)$	fun.	1569.55	0.29	6.54	-	0.77	0.66
M9	$\ln(DBH) = a + b \ln(H) + c \ln(CA)$	species	922.16	0.25	5.56	-	0.81	0.64

Table 3.2 Model comparison for estimating above-ground biomass (*AGB*) from crown area (*CA*) and maximum height (*H*). Models 1-3 were general linear models and from models 4-9, linear mixed-effects models were employed to allow intercept (*a*) and slopes (*b*, *c*) to vary for each site, functional types (*fun.*), and species. Akaike's Information Criteria (AIC), Root Mean Square Error (RMSE) and mean relative error in percentage (RE) are presented for each model. The adjusted coefficient of determination (R^2) is presented (Adj.) for linear models, while conditional (Cond.) and marginal (Marg.) R^2 values are shown for linear mixed-effects models.

No.	Model structure	Random factor	AIC	RMSE	RE (%)	R^2		
						Adj.	Cond.	Marg.
M1	$\ln(AGB) = a + b \ln(H)$	-	11181.43	0.87	11.95	0.55	-	-
M2	$\ln(AGB) = a + c \ln(CA)$	-	10516.88	0.81	11.60	0.61	-	-
M3	$\ln(AGB) = a + b \ln(H) + c \ln(CA)$	-	9268.05	0.70	9.71	0.71	-	-
M4	$\ln(AGB) = a + c \ln(CA)$	site	9362.97	0.69	9.65	-	0.68	0.55
M5	$\ln(AGB) = a + c \ln(CA)$	fun.	9647.33	0.73	10.20	-	0.70	0.60
M6	$\ln(AGB) = a + c \ln(CA)$	species	8883.59	0.62	8.60	-	0.75	0.53
M7	$\ln(AGB) = a + b \ln(H) + c \ln(CA)$	site	8024.14	0.59	7.89	-	0.82	0.71
M8	$\ln(AGB) = a + b \ln(H) + c \ln(CA)$	fun.	8382.35	0.63	8.48	-	0.78	0.70
M9	$\ln(AGB) = a + b \ln(H) + c \ln(CA)$	species	7679.97	0.54	7.17	-	0.82	0.68

Table 3.3 Comparison of allometric models for estimating both *DBH* and *AGB* from crown area (*CA*) and maximum height (*H*). Parameters *a*, *b*, and *c*. are the models' coefficients. M1 to M3 were regarded as global allometric equations, assuming that the scaling relationships remained constant across different species and functional types. In the functional type-specific models (M5 and M8), separate random intercepts (*a*) and slopes (*b*, *c*) were estimated for evergreen conifer, deciduous broadleaf, and evergreen broadleaf trees. CF refers to the correction factor for log transformation.

No.	Model structure	Fitted parameters						CF	
		<i>DBH</i>			<i>AGB</i>			<i>DBH</i>	<i>AGB</i>
		<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
M1	$\ln(Y) = a + b \ln(H)$	-0.358	1.301	-	-2.687	2.979	-	1.084	1.464
M2	$\ln(Y) = a + c \ln(CA)$	1.999	-	0.483	2.700	-	1.108	1.073	1.387
M3	$\ln(Y) = a + b \ln(H) + c \ln(CA)$	0.363	0.716	0.321	-1.026	1.629	0.739	1.056	1.278
M5	$\ln(Y) = a + c \ln(CA)$							1.053	1.304
	Evergreen conifer	2.370	-	0.452	3.487	-	1.009		
	Deciduous broadleaf	1.770	-	0.498	2.279	-	1.130		
	Evergreen broadleaf	1.813	-	0.531	2.267	-	1.250		
M8	$\ln(Y) = a + b \ln(H) + c \ln(CA)$							1.042	1.219
	Evergreen conifer	0.768	0.665	0.303	-0.197	1.534	0.662		
	Deciduous broadleaf	0.234	0.623	0.387	-1.648	1.593	0.849		
	Evergreen broadleaf	0.461	0.641	0.377	-1.403	1.738	0.832		

Figures

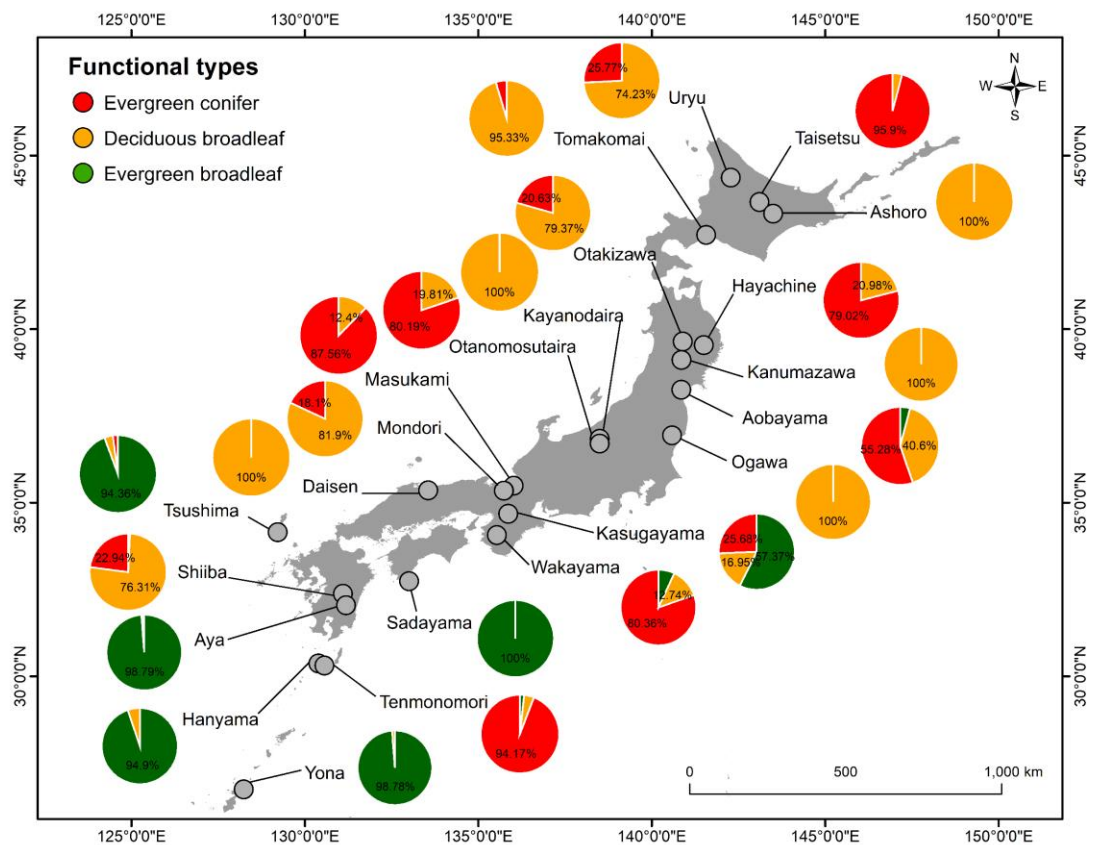


Fig. 3.1 Location map of 23 permanent forest monitoring sites (1-ha) across Japan. Different colors represent different dominant site-specific functional types (red for evergreen conifers, orange for deciduous broadleaf, green for evergreen broadleaf). Percent values indicate the relative contribution of each functional type to the total above-ground biomass of canopy trees detected by UAV at each site.

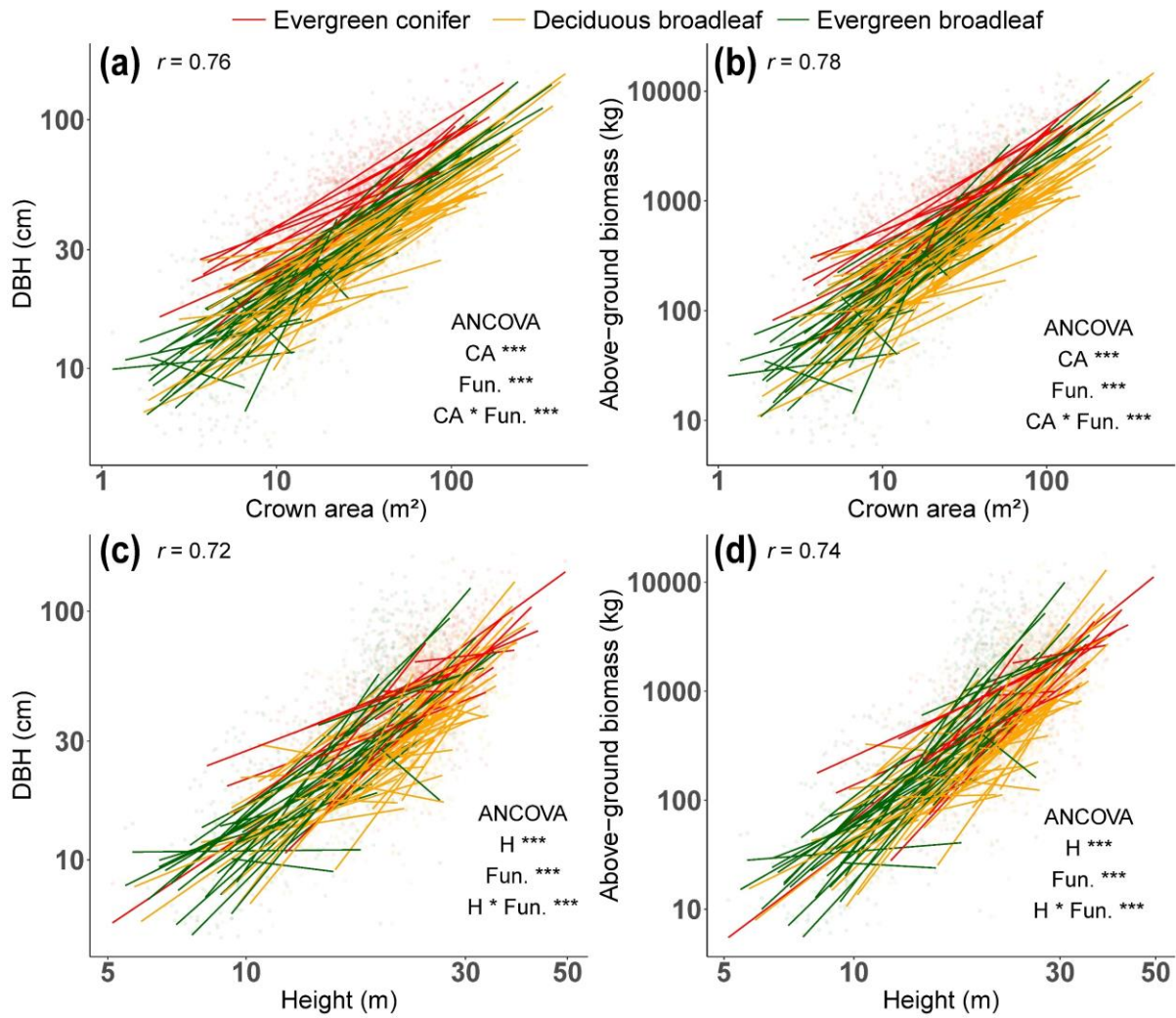


Fig. 3.2 Relationships between **(a)** DBH (diameter at breast height) vs crown area (CA), **(b)** Above-ground biomass vs CA, and **(c)** DBH vs Height (H) and **(d)** Above-ground biomass vs H. Each data point represents each tree while symbol colors indicate functional types (red for evergreen conifers, yellow for deciduous broadleaf species, and green for evergreen broadleaf species). Each line represents a species-specific regression line of linear regression. Note: regression lines were shown for species with the number of individuals ≥ 4 . The correlation coefficient (r) is shown for all the individuals (4355). Significance levels for ANCOVA results are marked as: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns $P > 0.05$.

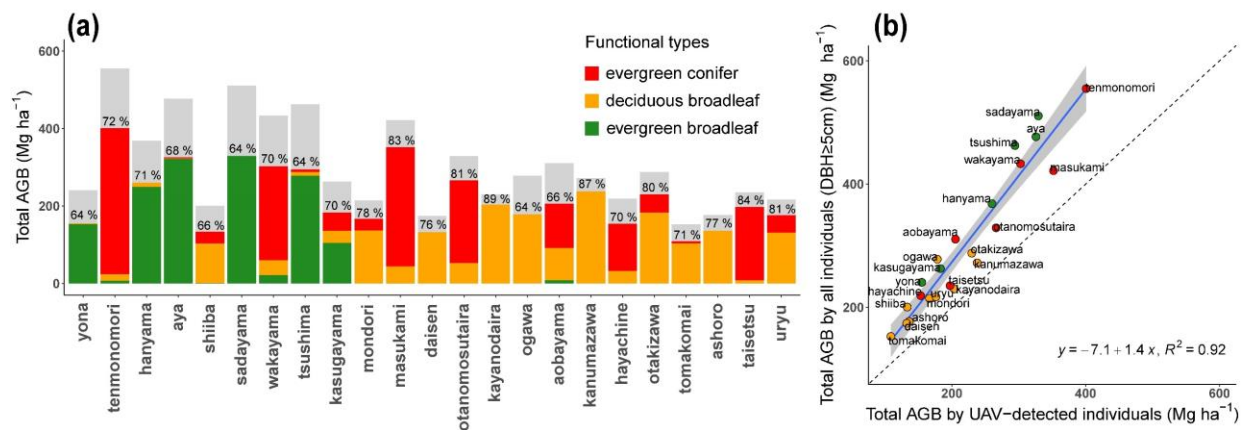


Fig. 3.3 (a) Contribution of UAV-detected individuals toward the total above-ground biomass (AGB) in 1-ha in 23 forest monitoring sites. The sites are arranged from the lowest latitudes to the highest (from left to right). The grey color represents the total amount of AGB represented by all individuals whose $DBH \geq 5$ cm in 1-ha while the contributions of UAV-detected individuals towards total AGB by each functional type (evergreen conifers, deciduous broadleaf, and evergreen broadleaf) are indicated by different colors. **(b)** Correlation between total AGB by all individuals whose $DBH \geq 5$ cm and UAV-detected individuals.

Supplementary materials

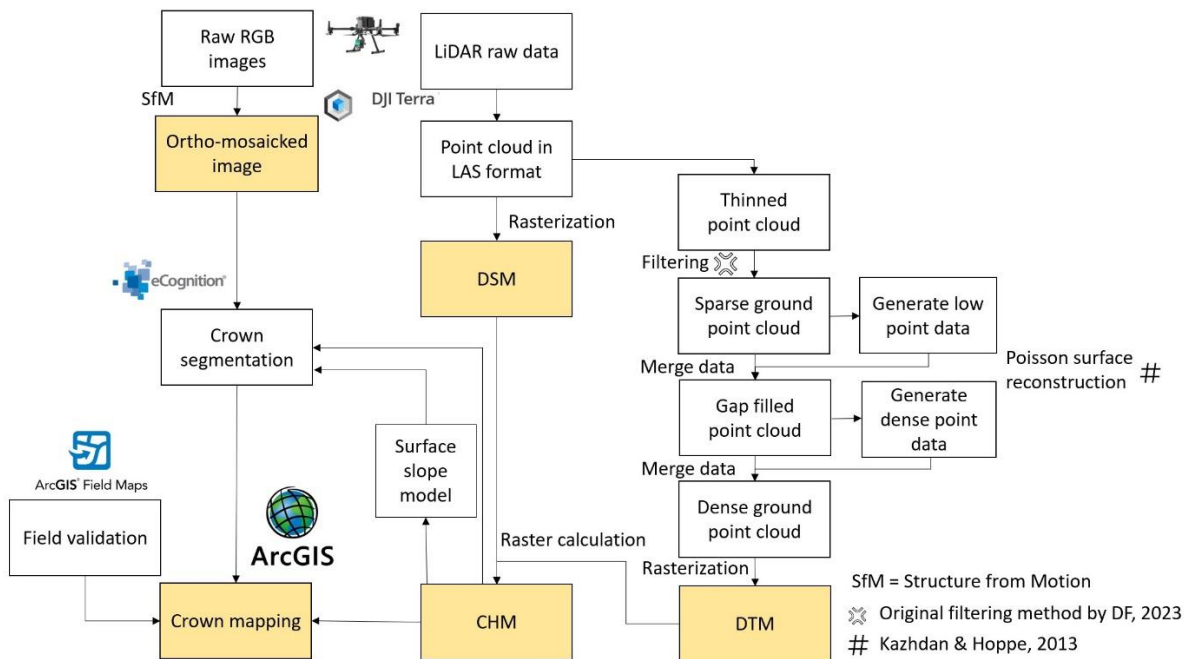


Fig. S3.1 Schematic diagram showing the workflow of processing the UAV–LiDAR data and individual tree crown data

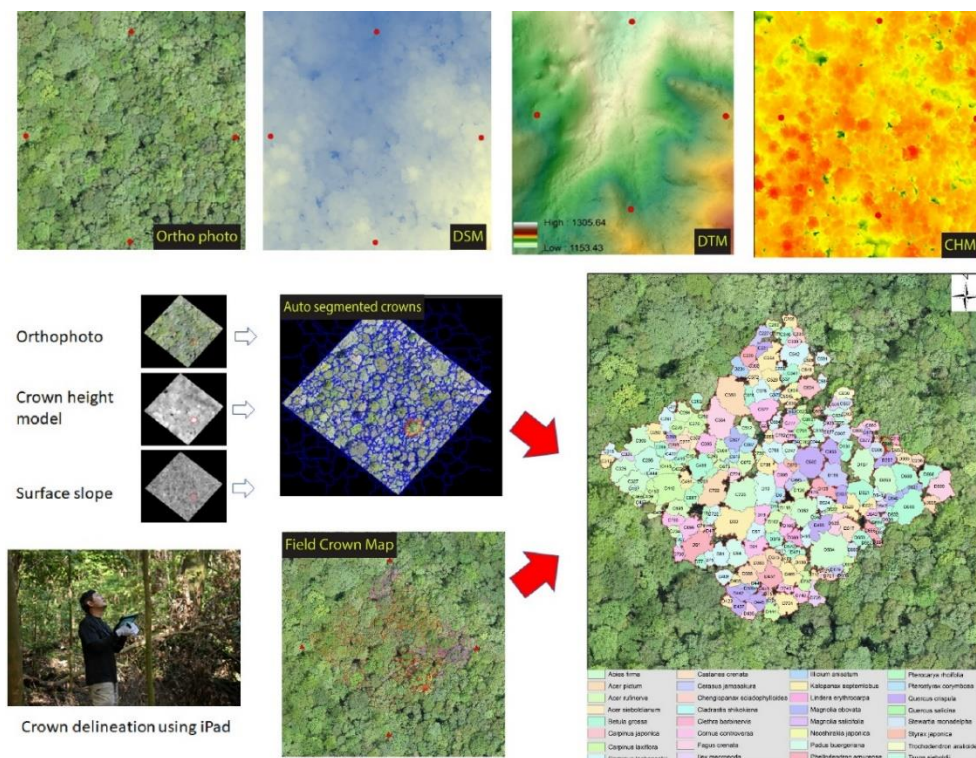


Fig. S3.2 Schematic diagram showing the workflow of processing the UAV-LiDAR data and individual tree crown data

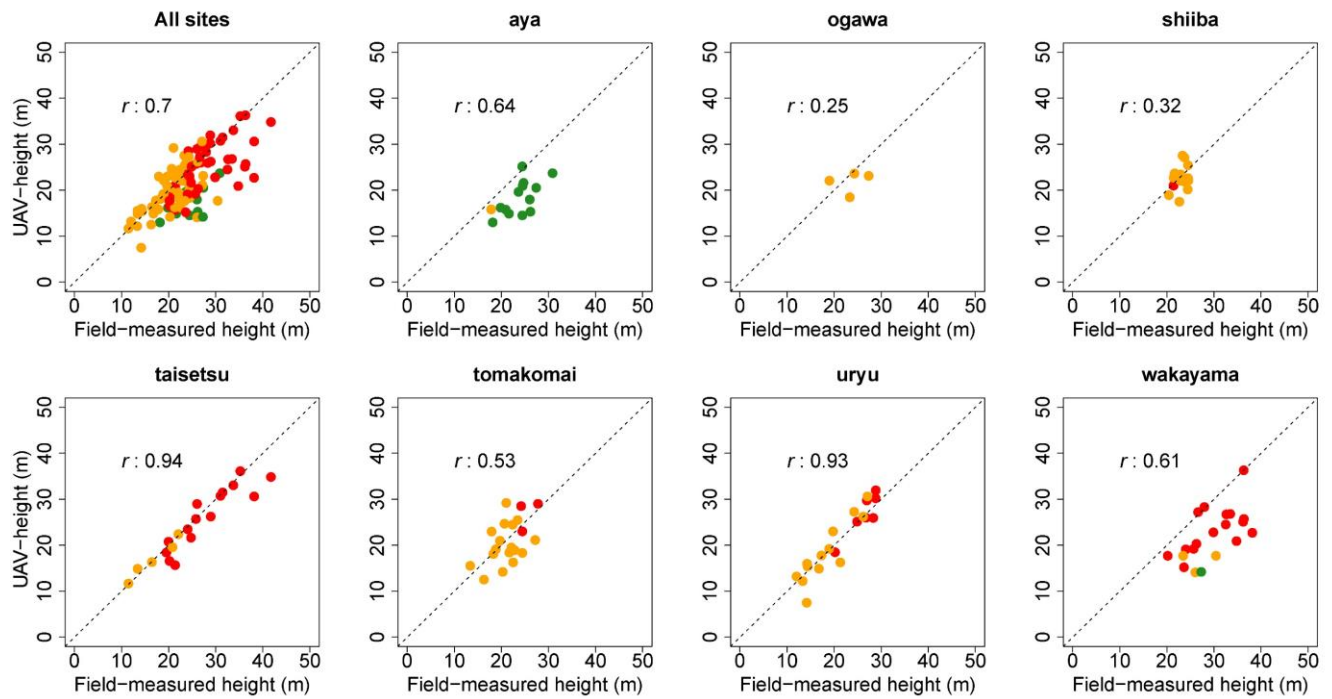


Fig. S3.3 Relationship between UAV-measured height and Field-measured height at different forest types across Japan. Each data point represents each individual tree and the colors represent different functional types (red for evergreen conifer, yellow for deciduous broadleaf, and green for evergreen broadleaf). Pearson correlation coefficient (r) is presented for all sites (113 in total) (top left panel).

Table S3.1 Field inventory and LiDAR data acquisition in the 23 sites across Japan and their site characteristics

Site	Plot ID	Location			Climate		Forest census data			LiDAR data
		Latitude(°N)	Longitude (°E)	Elevation (m)	MAT (°C)	MAR (mm)	Period	Forest types	Plot size (ha)	Data collection period
Uryu	UR-BC1	44.3643	142.2785	362	3.7	1424	2014-2018	Broadleaf /Conifer	1.05	July, 2022
Taisetsu	TA-EC1	43.6629	143.1053	1023	1.5	1221	2008-2018	Conifer	1	July, 2022
Ashoro	AS-DB1	43.3235	143.5017	355	4.3	935	2014-2018	Deciduous Broadleaf	1	July, 2022
Tomakomai	TM-DB1	42.7109	141.5682	101	7.1	1255	2014-2018	Deciduous Broadleaf	1	July, 2022
Otakizawa	OZ-DB1	39.6435	140.8941	476	7.7	2030	2008-2018	Deciduous Broadleaf	1	August, 2023
Hayachine	HY-EC1	39.5398	141.4995	1212	4.2	1659	2005-2015	Conifer	1	August, 2023
Kanumazawa	KM-DB1	39.1114	140.8551	466	7.4	2144	2018-2022	Deciduous Broadleaf	1	August, 2023
Aobayama	AO-BC1	38.2544	140.8539	131	11.8	1228	2006-2015	Broadleaf /Conifer	1	July, 2023
Ogawa	OG-DB1	36.9389	140.5862	660	8.6	1680	2014-2018	Deciduous Broadleaf	1	September, 2022
Kayanodaira	KY-DB1	36.8390	138.4996	1516	4.5	1854	2014-2018	Deciduous Broadleaf	1	September, 2023
Otanomosutaira	OT-EC1	36.7028	138.4995	1747	3.8	1734	2014-2018	Conifer	1	September, 2023
Daisen	DI-DB1	35.3577	133.5535	1142	6.1	2634	2006-2016	Deciduous Broadleaf	1	August, 2022
Masukami	AU-EC1	35.3463	135.7413	791	9.6	2222	2014-2018	Conifer	1	June, 2022
Mondori	AU-DB1	35.3458	135.7354	742	9.8	2200	2008-2013	Deciduous Broadleaf	1	June, 2022
Kasugayama	KA-EB1	34.6796	135.8631	384	13.5	1403	2007-2016	Evergreen Broadleaf	1	October, 2023
Tsushima	TT-EB1	34.1497	129.2165	163	14.5	2128	2007-2017	Evergreen Broadleaf	1	June, 2023
Wakayama	WK-EC1	34.0672	135.5355	847	9.6	2262	2014-2018	Conifer	1	May, 2022
Sadayama	SD-EB1	32.7396	133.0021	329	16.1	2443	2007-2017	Evergreen Broadleaf	1	August, 2023
Shiiba	SI-DB1	32.3776	131.0967	1182	9.4	3086	2009-2015	Deciduous Broadleaf	1	August, 2022
Aya	AY-EB1	32.0485	131.1861	496	14.7	2836	2014-2018	Evergreen Broadleaf	1	August, 2022
Hanyama	YK-EB1	30.3690	130.3895	192	16.8	3677	2007-2018	Evergreen Broadleaf	1	September, 2023
Tenmonomori	YS-EC1	30.3109	130.5650	1218	12.6	4171	2007-2012	Conifer	1	September, 2023
Yona	YN-EB1	26.7421	128.2354	269	20.5	3129	2012-2016	Evergreen Broadleaf	1	October, 2023

Note: Forest census data (Tree ID, species, GBH (girth breast height)) were downloaded from the official website of monitoring 1000 sites data archive. The data set version for this analysis is as of 2019/07/11. https://www.biodic.go.jp/moni1000/findings/data/index_file.html

Table S3.2 UAV-LiDAR flight configurations at 23 forest monitoring sites

Site	Density (point/m2)	Orth GSD (cm/pixel)	Terrain-follow height (m)	Speed (m/s)	Overlap (Front/Side)	Return mode	Sampling rate	Scanning mode	RTK Latitude	RTK Longitude	Ellipsoida l height
Uryu	461	2.73	100	10	80	Triple	160 KHz	Non-repetitive	44.364342365	142.278520379	372.216
Taisetsu	461	2.73	100	10	80	Triple	160 KHz	Non-repetitive	43.662935068	143.105294691	994.722
Ashoro	461	2.73	100	10	80	Triple	160 KHz	Non-repetitive	43.323497765	143.501696998	443.425
Tomakomai	461	2.73	100	10	80	Triple	160 KHz	Non-repetitive	42.710891566	141.568215789	124.212
Otakizawa	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	Network	Network	Network
Hayachine	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	39.541334915	141.500859787	1241.053
Kanumazawa	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	39.108823797	140.858325182	503.544
Aobayama	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	Network	Network	Network
Ogawa	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	36.938893802	140.586158567	688.633
Kayanodaira	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	36.834072345	138.500176805	1496.503
Otanomosutaira	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	Network	Network	Network
Daisen	461	2.73	100	10	80	Triple	160 KHz	Non-repetitive	35.357714260	133.553517096	1189.99
Masukami	322	2.73	100	10	70	Triple	160 KHz	Non-repetitive	35.343456826	135.733666349	834.707
Mondori	322	2.73	100	10	70	Triple	160 KHz	Non-repetitive	35.343456826	135.733666349	834.707
Kasugayama	583	2.73	100	7.9	80	Triple	160 KHz	Non-repetitive	Network	Network	Network
Tsushima	658	2.73	100	7	80	Triple	160 KHz	Non-repetitive	Network	Network	Network
Wakayama	461	2.73	100	10	80	Triple	160 KHz	Non-repetitive	34.067192800	135.535469774	736.012
Sadayama	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	Network	Network	Network
Shiiba	461	2.73	100	10	80	Triple	160 KHz	Non-repetitive	32.377551263	131.096737073	1162.302
Aya	461	2.73	100	10	80	Triple	160 KHz	Non-repetitive	32.048476007	131.186118745	578.656
Hanyama	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	30.369143941	130.387633943	175.572
Tenmonomori	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	Network	Network	Network
Yona	921	2.73	100	5	80	Triple	160 KHz	Non-repetitive	26.740298258	128.237689383	336.497

Table S3.3 Site-specific segmentation parameters for multiresolution segmentation in eCognition Developer software v.9.0.0

Site	Red	Green	Blue	CHM	CHM (Slope)	CHM (SD)	Scale	Shape	Compactness
Uryu	1	1	1	1	1	2	258	0.2	0.7
Taisetsu	1	1	1	1	2	1	230	0.5	0.6
Ashoro	1	1	1	2	1	1	275	0.2	0.7
Tomakomai	1	1	1	1	2	1	260	0.2	0.7
Otakizawa	1	1	1	3	1	1	220	0.4	0.8
Hayachine	1	1	1	3	1	1	190	0.4	0.8
Kanumazawa	1	1	1	3	1	1	280	0.2	0.7
Aobayama	1	1	1	2	1	1	220	0.3	0.7
Ogawa	1	1	1	1	1	1	230	0.2	0.7
Kayanodaira	1	1	1	3	1	1	250	0.3	0.6
Otanomosutaira	1	1	1	2	1	1	190	0.4	0.8
Daisen	1	1	1	2	1	3	190	0.2	0.6
Masukami	1	1	1	2	1	1	170	0.2	0.8
Mondori	1	1	1	2	1	1	180	0.2	0.5
Kasugayama	1	1	1	3	1	1	270	0.4	0.6
Tsushima	1	1	1	2	1	1	250	0.3	0.6
Wakayama	1	1	1	2	3	1	200	0.2	0.5
Sadayama	1	1	1	3	1	1	250	0.5	0.6
Shiiba	1	1	1	1	1	1	195	0.2	0.7
Aya	1	1	1	1	2	1	250	0.3	0.6
Hanyama	1	1	1	3	1	1	250	0.3	0.7
Tenmonomori	1	1	1	3	1	1	260	0.5	0.7
Yona	1	1	1	2	1	1	220	0.3	0.6

Note: CHM = Canopy Height Model, SD = standard deviation

Table S3.4 Summary of tree crown surveys in 23 monitoring sites and their tree structural characteristics.

Site	Census in 1 ha		Crowns linked to census			DBH (cm)			H (m)			CA (m ²)		
	(DBH $\geq$ 5cm)		in 1 ha											
	No.	Species	No.	Species	% census	Mean	Range ($\pm$ SD)	CV%	Mean	Range ($\pm$ SD)	CV%	Mean	Range ($\pm$ SD)	CV%
Uryu	789	16	242	13	30.67	32.02	7.45- 123.63 ($\pm$ 20.66)	64.53	19.54	9.00-32.77($\pm$ 4.67)	23.89	32.89	3.29-198.95($\pm$ 30.64)	93.16
Taisetsu	578	7	174	5	30.10	46.26	7.35- 114.75 ($\pm$ 22.32)	48.24	26.60	5.12-41.73($\pm$ 6.43)	24.17	36.94	4.07-140.83($\pm$ 23.39)	63.32
Ashoro	574	32	163	18	28.40	37.66	5.51-79.90 ($\pm$ 15.01)	39.85	25.06	13.16-33.69($\pm$ 3.25)	12.96	44.91	4.01-213.41($\pm$ 36.41)	81.08
Tomakomai	925	32	161	18	17.41	33.48	6.24-79.10 ($\pm$ 13.71)	40.94	20.69	5.91-27.78($\pm$ 3.98)	19.25	38.99	3.16-184.16($\pm$ 32.18)	82.54
Otakizawa	373	24	141	12	37.80	52.13	11.27-140.82 ($\pm$ 19.94)	38.25	30.61	13.75-41.20($\pm$ 5.82)	19.02	56.90	3.27-254.73($\pm$ 47.02)	82.64
Hayachine	755	15	300	10	39.74	30.70	6.59-68.72 ($\pm$ 11.96)	38.96	14.52	5.71-19.82($\pm$ 2.74)	18.85	25.50	1.85-247.78($\pm$ 27.53)	107.97
Kanumazawa	520	24	103	12	19.81	59.50	11.40-170.10 ($\pm$ 28.90)	48.57	26.31	10.23-37.96($\pm$ 5.01)	19.05	81.54	6.25-448.46($\pm$ 69.78)	85.58
Aobayama	1097	47	204	19	18.60	44.19	19.74-98.29 ($\pm$ 15.59)	35.28	26.00	14.36-37.86($\pm$ 3.39)	13.05	41.05	4.48-159.34($\pm$ 25.80)	62.84
Ogawa	937	44	116	23	12.38	45.60	10.35-128.95 ($\pm$ 22.49)	49.32	25.05	13.95-35.29($\pm$ 4.16)	16.62	67.30	7.33-422.36($\pm$ 60.72)	90.21
Kayanodaira	931	20	99	7	10.63	55.12	14.39-101.25 ($\pm$ 20.45)	37.09	20.73	9.09-27.59($\pm$ 3.61)	17.43	77.41	7.45-226.68($\pm$ 45.37)	58.61
Otanomosutaira	555	8	259	6	46.67	43.13	11.30-78.62 ($\pm$ 11.75)	27.24	22.28	8.22-28.67($\pm$ 2.78)	12.48	33.54	3.20-152.58($\pm$ 27.18)	81.04
Daisen	776	23	104	12	13.40	43.50	10.73-82.95 ($\pm$ 18.83)	43.28	21.51	9.73-31.42($\pm$ 4.43)	20.60	53.15	5.37-239.83($\pm$ 38.58)	72.58
Masukami	1069	29	299	11	27.97	51.28	13.11-111.22 ($\pm$ 15.73)	30.66	23.04	11.42-33.24($\pm$ 3.57)	15.51	29.64	3.10-170.21($\pm$ 21.89)	73.85
Mondori	574	43	109	16	18.99	47.84	8.05-155.84 ($\pm$ 26.00)	54.35	25.24	9.29-36.66($\pm$ 5.32)	21.07	65.09	5.02-380.29($\pm$ 63.64)	97.77
Kasugayama	1198	44	182	25	15.19	37.31	5.09-158.74 ($\pm$ 20.76)	55.65	22.01	7.62-49.46($\pm$ 6.15)	27.93	40.58	3.75-225.42($\pm$ 33.80)	83.31
Tsushima	947	28	131	18	13.83	52.31	11.65-141.27 ($\pm$ 29.19)	55.79	19.22	12.12-24.57($\pm$ 2.93)	15.26	54.02	4.03-240.52($\pm$ 50.01)	92.59
Wakayama	1281	38	225	14	17.56	51.08	15.41-98.55 ($\pm$ 16.84)	32.98	28.41	17.60-40.55($\pm$ 4.12)	14.49	40.12	4.07-144.60($\pm$ 25.16)	62.71
Sadayama	1088	39	138	12	12.68	57.68	22.47-129.71 ($\pm$ 21.69)	37.61	21.28	15.90-34.53($\pm$ 3.55)	16.70	62.21	9.07-375.42($\pm$ 53.78)	86.44
Shiiba	1342	48	218	28	16.24	32.61	14.51-99.92 ($\pm$ 14.00)	42.93	23.01	14.51-32.91($\pm$ 2.40)	10.41	32.57	3.51-164.69($\pm$ 27.07)	83.10
Aya	1591	30	165	18	10.37	48.96	9.29-135.82 ($\pm$ 23.78)	48.58	22.92	15.24-31.60($\pm$ 3.47)	15.15	51.92	4.66-275.66($\pm$ 43.81)	84.39
Hanyama	1688	42	252	27	14.93	34.03	7.32-109.50 ($\pm$ 17.20)	50.53	16.86	5.46-25.06($\pm$ 3.38)	20.04	25.03	2.91-183.47($\pm$ 24.38)	97.40
Tenmonomori	1203	27	116	8	9.64	85.57	8.50-165.90 ($\pm$ 27.83)	32.53	28.21	9.06-37.37($\pm$ 4.07)	14.43	53.13	7.76-198.53($\pm$ 36.02)	67.79
Yona	2569	67	454	43	17.67	20.54	4.87-61.15 ($\pm$ 11.13)	54.19	13.45	5.66-24.49($\pm$ 4.23)	31.49	11.61	1.15-71.78($\pm$ 10.50)	90.37

Note: In the Yona site, a crown mapping field survey was able to be carried out in approximately 77 % of the 1-ha plot area due to many heavily damaged tree crowns in 23 % of the area during observation.

Table S3.5 Parameter predictions of the linear regression and linear mixed-effects models to estimate tree diameter at breast height (DBH) and above-ground biomass (AGB) using height (H), and crown area (CA). Functional types (i.e., Evergreen conifer, Deciduous broadleaf, and Evergreen broadleaf) and sites are treated as random factors in linear mixed effects models. Note: a = intercept, b = slope of H, c = slope of CA, and CF = correction factor for log transformation.

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				a	b	c	a	b	c		
M1	$\ln(y) = a + b \ln(H)$	-	4355	-0.358	1.301	-	-2.687	2.979	-	1.084	1.464
M2	$\ln(y) = a + c \ln(CA)$	-	4355	1.999	-	0.483	2.700	-	1.108	1.073	1.387
M3	$\ln(y) = a + b \ln(H) + c \ln(CA)$	-	4355	0.363	0.716	0.321	-1.026	1.629	0.739	1.056	1.278
M4	$\ln(y) = a + c \ln(CA)$	Sites								1.051	1.274
		Uryu	242	1.299	-	0.629	1.204	-	1.421		
		Taisetsu	174	1.579	-	0.621	1.652	-	1.416		
		Ashoro	163	1.964	-	0.450	2.711	-	1.016		
		Tomakomai	161	1.916	-	0.449	2.519	-	1.041		
		Otakizawa	141	2.652	-	0.330	4.105	-	0.790		
		Hayachine	300	2.179	-	0.400	2.992	-	0.927		
		Kanumazawa	103	1.959	-	0.493	2.537	-	1.137		
		Aobayama	204	2.734	-	0.284	4.402	-	0.647		
		Ogawa	116	1.994	-	0.441	2.903	-	0.989		
		Kayanodaira	99	1.808	-	0.510	2.246	-	1.179		
		Otanomosutaira	259	2.955	-	0.238	4.850	-	0.558		
		Daisen	104	1.834	-	0.491	2.367	-	1.124		
		Masukami	299	2.973	-	0.286	4.595	-	0.694		
		Mondori	109	1.975	-	0.463	2.544	-	1.090		
		Kasugayama	182	1.821	-	0.488	2.391	-	1.123		
		Tsushima	131	1.971	-	0.510	2.922	-	1.118		
		Wakayama	225	2.423	-	0.414	3.919	-	0.868		
		Sadayama	138	2.464	-	0.394	4.058	-	0.852		
		Shiiba	218	2.195	-	0.381	3.400	-	0.825		
		Aya	165	2.071	-	0.467	3.034	-	1.071		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
M5	$\ln(y) = a + c \ln(CA)$	Hanyama	252	2.128	-	0.445	3.003	-	1.037	1.053	1.304
		Tenmonomori	116	2.890	-	0.394	4.564	-	0.889		
		Yona	454	1.765	-	0.513	2.157	-	1.192		
		Functional types									
		Evergreen conifer	1349	2.370	-	0.452	3.487	-	1.009		
		Deciduous broadleaf	1776	1.770	-	0.498	2.279	-	1.130		
		Evergreen broadleaf	1230	1.813	-	0.531	2.267	-	1.250		
M7	$\ln(y) = a + b \ln(H) + c \ln(CA)$	Sites								1.039	1.192
		Uryu	242	-1.105	1.057	0.405	-4.159	2.360	0.918		
		Taisetsu	174	-1.385	1.274	0.279	-5.072	2.893	0.637		
		Ashoro	163	-0.444	0.855	0.353	-2.451	1.840	0.801		
		Tomakomai	161	0.024	0.781	0.313	-2.153	1.932	0.703		
		Otakizawa	141	0.448	0.788	0.203	-1.039	1.840	0.494		
		Hayachine	300	-0.174	1.052	0.247	-2.536	2.471	0.567		
		Kanumazawa	103	0.430	0.617	0.376	-0.879	1.394	0.865		
		Aobayama	204	-0.653	1.142	0.192	-2.111	2.195	0.470		
		Ogawa	116	-0.932	1.074	0.308	-4.340	2.652	0.664		
		Kayanodaira	99	-0.320	0.924	0.351	-3.229	2.371	0.774		
		Otanomosutaira	259	0.707	0.796	0.171	-0.552	1.909	0.400		
		Daisen	104	-0.215	0.832	0.360	-2.595	2.020	0.806		
		Masukami	299	0.192	1.015	0.164	-1.439	2.201	0.429		
		Mondori	109	-0.376	0.911	0.313	-2.853	2.096	0.741		
		Kasugayama	182	-0.327	0.942	0.274	-2.806	2.277	0.608		
		Tsushima	131	-0.654	1.030	0.396	-3.862	2.652	0.832		
		Wakayama	225	0.728	0.570	0.355	-0.142	1.365	0.728		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
M8	$\ln(y) = a + b \ln(H) + c \ln(CA)$	Sadayama	138	2.626	-0.051	0.393	4.361	-0.086	0.842		
		Shiiba	218	1.403	0.280	0.355	1.566	0.654	0.758		
		Aya	165	-1.057	1.177	0.316	-5.245	3.105	0.681		
		Hanyama	252	0.308	0.779	0.319	-1.670	1.997	0.715		
		Tenmonomori	116	-0.106	0.983	0.323	-1.860	2.108	0.739		
		Yona	454	0.381	0.707	0.318	-1.365	1.800	0.696		
		Functional types								1.042	1.219
		Evergreen conifer	1349	0.768	0.665	0.303	-0.197	1.534	0.662		
		Deciduous broadleaf	1776	0.234	0.623	0.387	-1.648	1.593	0.849		
		Evergreen broadleaf	1230	0.461	0.641	0.377	-1.403	1.738	0.832		

Table S3.6 Parameter predictions of the linear mixed-effects model to estimate tree DBH and above-ground biomass (AGB) using height (H), and crown area (CA). Species information is treated as a random factor.

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
M6	$\ln(y) = a + c \ln(CA)$	Species								1.041	1.225
		<i>Abies firma</i>	188	2.462	-	0.426	3.660	-	0.954		
		<i>Abies mariesii</i>	231	2.517	-	0.320	3.801	-	0.735		
		<i>Abies sachalinensis</i>	112	2.129	-	0.453	2.841	-	1.042		
		<i>Acer amoenum</i>	9	2.111	-	0.379	3.181	-	0.853		
		<i>Acer cissifolium</i>	2	1.925	-	0.434	2.564	-	0.994		
		<i>Acer japonicum</i>	12	1.548	-	0.454	1.738	-	1.049		
		<i>Acer maximowiczianum</i>	6	1.733	-	0.466	2.215	-	1.080		
		<i>Acer micranthum</i>	1	1.730	-	0.448	2.047	-	1.051		
		<i>Acer nipponicum</i>	10	1.496	-	0.527	1.550	-	1.220		
		<i>Acer pictum</i>	166	1.672	-	0.509	2.117	-	1.160		
		<i>Acer rufinerve</i>	14	2.010	-	0.441	2.841	-	0.994		
		<i>Acer shirasawanum</i>	1	1.802	-	0.431	2.284	-	1.004		
		<i>Acer sieboldianum</i>	15	2.253	-	0.337	3.451	-	0.766		
		<i>Acer tschonoskii</i>	3	1.415	-	0.486	1.193	-	1.167		
		<i>Acer ukurunduense</i>	23	1.648	-	0.417	1.721	-	0.989		
		<i>Actinodaphne acuminata</i>	52	2.308	-	0.385	3.385	-	0.879		
		<i>Adinandra ryukyuensis</i>	1	1.559	-	0.483	1.734	-	1.126		
		<i>Aesculus turbinata</i>	66	2.023	-	0.491	2.887	-	1.095		
		<i>Aidia canthioides</i>	1	1.194	-	0.539	1.084	-	1.236		
		<i>Alnus hirsuta</i>	1	1.838	-	0.419	2.341	-	0.972		
		<i>Ardisia sieboldii</i>	22	2.141	-	0.397	3.031	-	0.924		
		<i>Aria alnifolia</i>	4	2.113	-	0.393	3.088	-	0.883		
		<i>Aria japonica</i>	3	2.103	-	0.422	3.106	-	0.950		
		<i>Betula corylifolia</i>	9	2.014	-	0.408	2.710	-	0.942		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Betula ermanii</i>	112	1.794	-	0.460	2.359	-	1.032		
		<i>Betula grossa</i>	42	1.847	-	0.483	2.589	-	1.072		
		<i>Betula maximowicziana</i>	5	1.954	-	0.416	2.683	-	0.963		
		<i>Camellia japonica</i>	20	2.224	-	0.339	3.372	-	0.772		
		<i>Camellia sasanqua</i>	4	1.859	-	0.435	2.503	-	0.998		
		<i>Carpinus cordata</i>	4	1.819	-	0.450	2.423	-	1.032		
		<i>Carpinus japonica</i>	3	2.067	-	0.389	3.042	-	0.884		
		<i>Carpinus laxiflora</i>	78	2.388	-	0.302	3.801	-	0.679		
		<i>Carpinus tschonoskii</i>	30	2.192	-	0.371	3.381	-	0.825		
		<i>Castanea crenata</i>	10	2.311	-	0.372	3.408	-	0.852		
		<i>Castanopsis cuspidata</i>	31	1.954	-	0.464	2.677	-	1.060		
		<i>Castanopsis sieboldii</i>	198	1.846	-	0.565	2.369	-	1.285		
		<i>Celtis sinensis</i>	1	1.869	-	0.431	2.441	-	0.997		
		<i>Cerasus jamasakura</i>	12	2.168	-	0.419	3.278	-	0.939		
		<i>Cerasus leveilleana</i>	23	2.596	-	0.282	4.245	-	0.633		
		<i>Cerasus maximowiczii</i>	2	1.363	-	0.507	1.226	-	1.197		
		<i>Cerasus sargentii</i>	3	1.885	-	0.448	2.473	-	1.032		
		<i>Cerasus spachiana</i>	1	2.048	-	0.434	2.912	-	0.985		
		<i>Cercidiphyllum japonicum</i>	23	1.877	-	0.543	2.445	-	1.227		
		<i>Chamaecyparis obtusa</i>	9	2.529	-	0.399	3.919	-	0.884		
		<i>Chengiopanax sciadophylloides</i>	14	1.782	-	0.454	2.094	-	1.039		
		<i>Cinnamomum camphora</i>	21	2.296	-	0.412	3.521	-	0.921		
		<i>Cinnamomum doederleinii</i>	1	1.408	-	0.515	1.266	-	1.219		
		<i>Cinnamomum sieboldii</i>	1	2.062	-	0.438	2.891	-	0.996		
		<i>Cinnamomum tenuifolium</i>	13	2.212	-	0.370	3.212	-	0.845		
		<i>Cladrastis shikokiana</i>	3	2.078	-	0.415	3.125	-	0.921		
		<i>Clerodendrum trichotomum</i>	1	1.146	-	0.546	0.658	-	1.300		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Cleyera japonica</i>	26	2.028	-	0.367	2.757	-	0.877		
		<i>Cornus controversa</i>	38	2.171	-	0.368	3.259	-	0.820		
		<i>Cornus macrophylla</i>	3	2.330	-	0.383	3.623	-	0.862		
		<i>Cryptomeria japonica</i>	396	2.575	-	0.448	3.772	-	1.021		
		<i>Daphniphyllum teijsmannii</i>	8	1.993	-	0.438	2.555	-	1.036		
		<i>Dendropanax trifidus</i>	4	1.623	-	0.530	1.779	-	1.228		
		<i>Diospyros morrisiana</i>	10	1.699	-	0.475	2.048	-	1.103		
		<i>Diplospora dubia</i>	3	1.730	-	0.476	2.095	-	1.104		
		<i>Distylium racemosum</i>	172	2.106	-	0.466	3.183	-	1.064		
		<i>Elaeocarpus japonicus</i>	12	1.934	-	0.330	2.401	-	0.818		
		<i>Elaeocarpus zollingeri</i>	3	1.968	-	0.478	2.628	-	1.098		
		<i>Euonymus planipes</i>	1	1.516	-	0.490	1.689	-	1.137		
		<i>Eurya japonica</i>	2	1.469	-	0.503	1.542	-	1.168		
		<i>Fagus crenata</i>	247	2.153	-	0.425	3.179	-	0.963		
		<i>Fagus japonica</i>	32	2.673	-	0.268	4.435	-	0.602		
		<i>Ficus ampelas</i>	1	1.488	-	0.516	1.621	-	1.185		
		<i>Ficus benguetensis</i>	1	1.711	-	0.476	2.092	-	1.097		
		<i>Ficus erecta</i>	2	1.791	-	0.467	2.378	-	1.061		
		<i>Fraxinus lanuginosa</i>	7	1.909	-	0.421	2.609	-	0.972		
		<i>Fraxinus mandshurica</i>	7	1.831	-	0.436	2.441	-	1.007		
		<i>Hovenia trichocarpa</i>	1	1.946	-	0.435	2.632	-	1.002		
		<i>Idesia polycarpa</i>	24	2.719	-	0.268	4.373	-	0.587		
		<i>Ilex goshiensis</i>	9	1.769	-	0.492	2.135	-	1.140		
		<i>Ilex integra</i>	3	1.851	-	0.442	2.505	-	1.013		
		<i>Ilex liukiuensis</i>	12	2.054	-	0.350	2.857	-	0.839		
		<i>Ilex macropoda</i>	11	2.241	-	0.371	3.399	-	0.838		
		<i>Ilex rotunda</i>	3	2.265	-	0.371	3.428	-	0.837		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Ilex warburgii</i>	1	1.332	-	0.520	1.123	-	1.229		
		<i>Illicium anisatum</i>	3	1.468	-	0.472	1.431	-	1.122		
		<i>Kalopanax septemlobus</i>	57	1.716	-	0.530	2.086	-	1.207		
		<i>Lagerstroemia subcostata</i>	7	1.979	-	0.492	2.794	-	1.106		
		<i>Laurocerasus spinulosa</i>	2	1.801	-	0.427	2.332	-	0.996		
		<i>Lindera erythrocarpa</i>	8	2.687	-	0.261	4.380	-	0.587		
		<i>Lithocarpus edulis</i>	14	1.935	-	0.411	2.799	-	0.935		
		<i>Litsea coreana</i>	3	2.249	-	0.422	3.398	-	0.944		
		<i>Lyonia ovalifolia</i>	1	2.254	-	0.389	3.421	-	0.873		
		<i>Machilus japonica</i>	23	1.850	-	0.473	2.453	-	1.077		
		<i>Machilus thunbergii</i>	53	2.005	-	0.491	2.786	-	1.115		
		<i>Magnolia kobus</i>	7	1.453	-	0.546	1.402	-	1.262		
		<i>Magnolia obovata</i>	64	1.976	-	0.444	2.588	-	1.024		
		<i>Magnolia salicifolia</i>	3	1.850	-	0.435	2.341	-	1.009		
		<i>Mallotus japonicus</i>	6	1.478	-	0.457	1.347	-	1.095		
		<i>Meliosma myriantha</i>	1	1.451	-	0.468	1.395	-	1.114		
		<i>Meliosma rigida</i>	6	1.830	-	0.419	2.247	-	0.989		
		<i>Meliosma squamulata</i>	4	1.788	-	0.436	2.114	-	1.038		
		<i>Morella rubra</i>	9	1.824	-	0.559	2.420	-	1.257		
		<i>Myrsine sequinii</i>	3	1.605	-	0.448	1.969	-	1.038		
		<i>Neolitsea aciculata</i>	35	1.606	-	0.521	1.757	-	1.211		
		<i>Neolitsea sericea</i>	8	1.805	-	0.476	2.173	-	1.113		
		<i>Neoshirakia japonica</i>	1	1.965	-	0.437	2.558	-	1.023		
		<i>Ostrya japonica</i>	77	2.410	-	0.343	3.893	-	0.760		
		<i>Padus buergeriana</i>	5	2.296	-	0.361	3.530	-	0.805		
		<i>Padus grayana</i>	14	2.006	-	0.342	2.529	-	0.838		
		<i>Padus ssiori</i>	17	1.830	-	0.410	2.333	-	0.955		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Phellodendron amurense</i>	17	1.716	-	0.448	1.972	-	1.035		
		<i>Picea glehnii</i>	17	2.208	-	0.475	3.089	-	1.074		
		<i>Picea jezoensis</i>	89	1.885	-	0.571	2.290	-	1.307		
		<i>Pinus densiflora</i>	14	2.382	-	0.454	3.706	-	1.004		
		<i>Pinus parviflora</i>	1	2.025	-	0.460	2.763	-	1.034		
		<i>Podocarpus macrophyllus</i>	4	1.953	-	0.509	2.572	-	1.152		
		<i>Pterocarya rhoifolia</i>	60	1.858	-	0.477	2.221	-	1.088		
		<i>Pterostyrax corymbosa</i>	4	2.094	-	0.402	2.968	-	0.922		
		<i>Quercus acuta</i>	104	2.328	-	0.412	3.837	-	0.911		
		<i>Quercus crispula</i>	98	1.310	-	0.621	1.367	-	1.398		
		<i>Quercus gilva</i>	8	1.957	-	0.487	2.753	-	1.124		
		<i>Quercus glauca</i>	5	1.812	-	0.427	2.575	-	0.978		
		<i>Quercus miyagii</i>	16	1.413	-	0.569	1.598	-	1.292		
		<i>Quercus salicina</i>	60	2.257	-	0.408	3.588	-	0.916		
		<i>Quercus serrata</i>	51	2.237	-	0.396	3.542	-	0.882		
		<i>Quercus sessilifolia</i>	29	1.919	-	0.465	2.697	-	1.077		
		<i>Rhaphiolepis indica</i>	5	1.738	-	0.474	2.286	-	1.073		
		<i>Rhododendron tashiroi</i>	2	1.779	-	0.462	2.197	-	1.073		
		<i>Sapindus mukorossi</i>	4	1.809	-	0.424	2.317	-	0.985		
		<i>Schefflera heptaphylla</i>	44	1.844	-	0.538	2.174	-	1.241		
		<i>Schima wallichii</i>	133	1.997	-	0.452	2.685	-	1.054		
		<i>Sorbus commixta</i>	34	1.710	-	0.435	2.109	-	1.006		
		<i>Stewartia monadelphica</i>	29	2.260	-	0.412	3.591	-	0.902		
		<i>Stewartia pseudocamellia</i>	3	2.107	-	0.429	3.073	-	0.968		
		<i>Styrax japonica</i>	9	2.027	-	0.358	2.763	-	0.841		
		<i>Styrax obassia</i>	7	1.737	-	0.401	2.132	-	0.945		
		<i>Symplocos kuroki</i>	3	2.007	-	0.423	2.811	-	0.963		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Symplocos prunifolia</i>	4	1.227	-	0.591	0.805	-	1.390		
		<i>Syzygium buxifolium</i>	1	2.014	-	0.430	2.928	-	0.962		
		<i>Ternstroemia gymnanthera</i>	20	1.637	-	0.516	1.901	-	1.199		
		<i>Tetradium glabrifolium</i>	3	1.206	-	0.632	0.739	-	1.466		
		<i>Thujopsis dolabrata</i>	39	2.625	-	0.347	4.176	-	0.782		
		<i>Tilia japonica</i>	24	1.891	-	0.453	2.406	-	1.028		
		<i>Tilia maximowicziana</i>	49	2.173	-	0.408	2.929	-	0.936		
		<i>Trochodendron aralioides</i>	3	2.467	-	0.405	3.870	-	0.896		
		<i>Tsuga diversifolia</i>	189	2.926	-	0.272	4.858	-	0.604		
		<i>Tsuga sieboldii</i>	60	2.716	-	0.382	4.385	-	0.849		
		<i>Turpinia ternata</i>	3	1.832	-	0.450	2.315	-	1.047		
		<i>Ulmus davidiana</i>	9	2.008	-	0.407	2.829	-	0.928		
		<i>Ulmus laciniata</i>	1	2.291	-	0.428	3.468	-	0.953		
		<i>Vernicia cordata</i>	3	1.851	-	0.452	2.130	-	1.075		
		<i>Wendlandia formosana</i>	1	1.616	-	0.493	1.830	-	1.146		
		<i>Zanthoxylum ailanthoides</i>	7	1.830	-	0.431	2.262	-	0.981		
		<i>Zelkova serrata</i>	2	1.930	-	0.461	2.615	-	1.057		
M9	$\ln(y) = a + b \ln(H) + c \ln(CA)$	Species								1.033	1.164
		<i>Abies firma</i>	188	1.173	0.442	0.373	0.179	1.196	0.810		
		<i>Abies mariesii</i>	231	1.478	0.429	0.262	0.863	1.214	0.569		
		<i>Abies sachalinensis</i>	112	-0.144	0.910	0.269	-2.775	2.255	0.584		
		<i>Acer amoenum</i>	9	0.464	0.611	0.295	-1.319	1.653	0.638		
		<i>Acer cissifolium</i>	2	0.354	0.654	0.312	-1.563	1.719	0.671		
		<i>Acer japonicum</i>	12	0.575	0.484	0.350	-0.977	1.348	0.759		
		<i>Acer maximowiczianum</i>	6	0.052	0.720	0.304	-2.254	1.901	0.659		
		<i>Acer micranthum</i>	1	0.237	0.710	0.311	-1.725	1.818	0.674		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Acer nipponicum</i>	10	−0.456	0.831	0.332	−3.478	2.146	0.712		
		<i>Acer pictum</i>	166	0.111	0.654	0.382	−1.960	1.707	0.831		
		<i>Acer rufinerve</i>	14	0.395	0.625	0.344	−1.435	1.646	0.746		
		<i>Acer shirasawanum</i>	1	0.202	0.705	0.299	−1.877	1.838	0.649		
		<i>Acer sieboldianum</i>	15	0.662	0.614	0.260	−0.745	1.618	0.562		
		<i>Acer tschonoskii</i>	3	−0.067	0.811	0.306	−2.405	2.040	0.663		
		<i>Acer ukurunduense</i>	23	0.539	0.566	0.313	−1.363	1.592	0.678		
		<i>Actinodaphne acuminata</i>	52	0.285	0.852	0.265	−1.581	2.097	0.578		
		<i>Adinandra ryukyuensis</i>	1	−0.050	0.720	0.328	−2.548	1.912	0.709		
		<i>Aesculus turbinata</i>	66	0.904	0.403	0.434	−0.318	1.145	0.939		
		<i>Aidia canthioides</i>	1	−0.202	0.655	0.372	−2.957	1.837	0.791		
		<i>Alnus hirsuta</i>	1	0.472	0.599	0.289	−1.358	1.624	0.612		
		<i>Ardisia sieboldii</i>	22	1.114	0.471	0.291	0.188	1.302	0.631		
		<i>Aria alnifolia</i>	4	0.761	0.559	0.319	−0.480	1.470	0.690		
		<i>Aria japonica</i>	3	0.402	0.670	0.319	−1.316	1.726	0.694		
		<i>Betula corylifolia</i>	9	0.640	0.634	0.306	−0.770	1.625	0.665		
		<i>Betula ermanii</i>	112	0.232	0.613	0.389	−1.774	1.619	0.845		
		<i>Betula grossa</i>	42	0.460	0.501	0.429	−1.308	1.394	0.931		
		<i>Betula maximowicziana</i>	5	0.384	0.652	0.286	−1.525	1.739	0.619		
		<i>Camellia japonica</i>	20	0.419	0.740	0.249	−1.116	1.846	0.538		
		<i>Camellia sasanqua</i>	4	−0.173	0.907	0.267	−2.378	2.190	0.570		
		<i>Carpinus cordata</i>	4	0.397	0.598	0.320	−1.476	1.626	0.690		
		<i>Carpinus japonica</i>	3	0.343	0.673	0.287	−1.540	1.776	0.620		
		<i>Carpinus laxiflora</i>	78	1.126	0.440	0.261	0.190	1.257	0.565		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Carpinus tschonoskii</i>	30	0.668	0.542	0.322	−0.813	1.482	0.699		
		<i>Castanea crenata</i>	10	0.973	0.534	0.282	−0.134	1.421	0.607		
		<i>Castanopsis cuspidata</i>	31	−0.233	0.898	0.308	−2.725	2.217	0.674		
		<i>Castanopsis sieboldii</i>	198	0.300	0.719	0.419	−1.581	1.835	0.912		
		<i>Celtis sinensis</i>	1	0.309	0.674	0.302	−1.656	1.773	0.652		
		<i>Cerasus jamasakura</i>	12	0.950	0.474	0.339	−0.140	1.306	0.737		
		<i>Cerasus leveilleana</i>	23	0.814	0.613	0.231	−0.450	1.612	0.500		
		<i>Cerasus maximowiczii</i>	2	−0.324	0.765	0.337	−3.286	2.050	0.728		
		<i>Cerasus sargentii</i>	3	0.268	0.688	0.315	−1.728	1.791	0.681		
		<i>Cerasus spachiana</i>	1	0.360	0.687	0.314	−1.436	1.762	0.681		
		<i>Cercidiphyllum japonicum</i>	23	0.210	0.668	0.409	−1.801	1.700	0.889		
		<i>Chamaecyparis obtusa</i>	9	0.743	0.642	0.317	−0.451	1.568	0.690		
		<i>Chengiopanax sciadophylloides</i>	14	0.726	0.450	0.371	−0.976	1.304	0.803		
		<i>Cinnamomum camphora</i>	21	0.131	0.773	0.309	−1.946	1.941	0.671		
		<i>Cinnamomum doederleinii</i>	1	−0.251	0.836	0.320	−2.875	2.116	0.693		
		<i>Cinnamomum sieboldii</i>	1	0.407	0.684	0.319	−1.314	1.740	0.692		
		<i>Cinnamomum tenuifolium</i>	13	0.360	0.709	0.282	−1.530	1.821	0.613		
		<i>Cladrastis shikokiana</i>	3	0.403	0.611	0.325	−1.471	1.655	0.699		
		<i>Clerodendrum trichotomum</i>	1	−0.824	0.945	0.335	−4.339	2.422	0.725		
		<i>Cleyera japonica</i>	26	0.690	0.659	0.204	−0.691	1.711	0.440		
		<i>Cornus controversa</i>	38	0.628	0.549	0.318	−0.958	1.494	0.689		
		<i>Cornus macrophylla</i>	3	1.200	0.454	0.296	0.480	1.246	0.641		
		<i>Cryptomeria japonica</i>	396	0.727	0.695	0.331	−0.951	1.777	0.720		
		<i>Daphniphyllum teijsmannii</i>	8	0.834	0.598	0.280	−0.472	1.579	0.608		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Dendropanax trifidus</i>	4	0.100	0.759	0.348	-2.026	1.912	0.759		
		<i>Diospyros morrisiana</i>	10	-0.206	0.877	0.286	-2.642	2.173	0.618		
		<i>Diplospora dubia</i>	3	0.488	0.643	0.310	-1.062	1.645	0.667		
		<i>Distylium racemosum</i>	172	1.077	0.444	0.381	0.311	1.236	0.830		
		<i>Elaeocarpus japonicus</i>	12	1.284	0.343	0.240	0.305	1.111	0.516		
		<i>Elaeocarpus zollingeri</i>	3	0.455	0.695	0.318	-1.174	1.752	0.695		
		<i>Euonymus planipes</i>	1	0.274	0.558	0.351	-1.944	1.595	0.759		
		<i>Eurya japonica</i>	2	-0.448	0.893	0.317	-3.179	2.214	0.680		
		<i>Fagus crenata</i>	247	0.970	0.461	0.359	-0.119	1.283	0.781		
		<i>Fagus japonica</i>	32	0.563	0.725	0.210	-0.979	1.855	0.458		
		<i>Ficus ampelas</i>	1	-0.227	0.807	0.336	-2.667	2.021	0.722		
		<i>Ficus benguetensis</i>	1	0.270	0.698	0.316	-1.515	1.758	0.681		
		<i>Ficus erecta</i>	2	0.022	0.764	0.319	-2.089	1.927	0.683		
		<i>Fraxinus lanuginosa</i>	7	0.501	0.609	0.290	-1.168	1.629	0.625		
		<i>Fraxinus mandshurica</i>	7	0.237	0.650	0.299	-1.927	1.764	0.645		
		<i>Hovenia trichocarpa</i>	1	0.369	0.670	0.308	-1.480	1.746	0.670		
		<i>Idesia polycarpa</i>	24	0.505	0.717	0.242	-1.102	1.777	0.520		
		<i>Ilex goshiensis</i>	9	0.754	0.564	0.332	-0.511	1.475	0.722		
		<i>Ilex integra</i>	3	0.347	0.666	0.304	-1.380	1.718	0.656		
		<i>Ilex liukiuensis</i>	12	1.175	0.459	0.218	0.422	1.278	0.463		
		<i>Ilex macropoda</i>	11	0.569	0.633	0.285	-0.995	1.658	0.617		
		<i>Ilex rotunda</i>	3	0.298	0.752	0.280	-1.528	1.890	0.608		
		<i>Ilex warburgii</i>	1	-0.371	0.874	0.316	-3.032	2.171	0.684		
		<i>Illicium anisatum</i>	3	-0.224	0.863	0.292	-2.638	2.126	0.632		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Kalopanax septemlobus</i>	57	0.012	0.697	0.393	-2.321	1.802	0.853		
		<i>Lagerstroemia subcostata</i>	7	0.794	0.556	0.376	-0.195	1.391	0.826		
		<i>Laurocerasus spinulosa</i>	2	0.399	0.638	0.297	-1.342	1.674	0.649		
		<i>Lindera erythrocarpa</i>	8	1.079	0.587	0.219	0.257	1.507	0.474		
		<i>Lithocarpus edulis</i>	14	0.137	0.730	0.287	-1.857	1.884	0.621		
		<i>Litsea coreana</i>	3	0.636	0.654	0.321	-0.636	1.627	0.701		
		<i>Lyonia ovalifolia</i>	1	0.655	0.642	0.288	-0.646	1.627	0.618		
		<i>Machilus japonica</i>	23	0.230	0.719	0.338	-1.665	1.827	0.734		
		<i>Machilus thunbergii</i>	53	-0.313	0.980	0.329	-2.834	2.374	0.723		
		<i>Magnolia kobus</i>	7	0.099	0.598	0.395	-2.357	1.648	0.855		
		<i>Magnolia obovata</i>	64	0.645	0.557	0.325	-0.982	1.497	0.703		
		<i>Magnolia salicifolia</i>	3	-0.041	0.816	0.306	-2.375	2.052	0.665		
		<i>Mallotus japonicus</i>	6	-0.523	0.947	0.282	-3.651	2.402	0.610		
		<i>Meliosma myriantha</i>	1	-0.373	0.849	0.297	-3.260	2.189	0.641		
		<i>Meliosma rigida</i>	6	0.079	0.791	0.282	-2.128	2.007	0.612		
		<i>Meliosma squamulata</i>	4	0.379	0.645	0.305	-1.675	1.743	0.669		
		<i>Morella rubra</i>	9	-0.055	0.851	0.390	-2.038	2.015	0.861		
		<i>Myrsine seguinii</i>	3	0.280	0.646	0.292	-1.442	1.669	0.622		
		<i>Neolitsea aciculata</i>	35	-0.781	1.164	0.222	-3.961	2.801	0.484		
		<i>Neolitsea sericea</i>	8	-0.467	1.003	0.288	-3.313	2.448	0.627		
		<i>Neoshirakia japonica</i>	1	1.093	0.474	0.299	0.213	1.290	0.648		
		<i>Ostrya japonica</i>	77	-0.207	0.889	0.290	-2.677	2.222	0.633		
		<i>Padus buergeriana</i>	5	0.312	0.703	0.295	-1.598	1.809	0.639		
		<i>Padus grayana</i>	14	0.940	0.581	0.201	-0.274	1.568	0.429		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Padus ssiori</i>	17	0.008	0.763	0.287	-2.321	1.965	0.620		
		<i>Phellodendron amurense</i>	17	0.019	0.726	0.313	-2.406	1.887	0.673		
		<i>Picea glehnii</i>	17	-0.462	1.007	0.300	-3.279	2.408	0.651		
		<i>Picea jezoensis</i>	89	-0.811	1.091	0.304	-4.184	2.625	0.663		
		<i>Pinus densiflora</i>	14	0.616	0.634	0.350	-0.746	1.581	0.758		
		<i>Pinus parviflora</i>	1	0.488	0.655	0.347	-1.137	1.671	0.744		
		<i>Podocarpus macrophyllus</i>	4	0.316	0.707	0.370	-1.487	1.764	0.803		
		<i>Pterocarya rhoifolia</i>	60	0.036	0.721	0.337	-2.402	1.840	0.724		
		<i>Pterostyrax corymbosa</i>	4	0.420	0.662	0.293	-1.400	1.730	0.634		
		<i>Quercus acuta</i>	104	1.368	0.337	0.388	0.931	1.008	0.847		
		<i>Quercus crispula</i>	98	-0.983	0.939	0.458	-4.324	2.328	0.997		
		<i>Quercus gilva</i>	8	0.177	0.720	0.349	-1.928	1.874	0.777		
		<i>Quercus glauca</i>	5	0.904	0.414	0.309	-0.418	1.285	0.666		
		<i>Quercus miyagii</i>	16	-0.994	1.080	0.360	-4.125	2.568	0.793		
		<i>Quercus salicina</i>	60	2.108	0.069	0.392	2.537	0.419	0.856		
		<i>Quercus serrata</i>	51	0.241	0.687	0.334	-1.733	1.802	0.730		
		<i>Quercus sessilifolia</i>	29	0.087	0.824	0.272	-1.886	2.057	0.598		
		<i>Rhaphiolepis indica</i>	5	0.662	0.581	0.325	-0.314	1.413	0.702		
		<i>Rhododendron tashiroi</i>	2	0.352	0.720	0.298	-1.318	1.796	0.643		
		<i>Sapindus mukorossi</i>	4	0.404	0.615	0.297	-1.526	1.674	0.639		
		<i>Schefflera heptaphylla</i>	44	-0.008	0.890	0.330	-2.391	2.201	0.721		
		<i>Schima wallichii</i>	133	0.628	0.659	0.284	-0.869	1.710	0.618		
		<i>Sorbus commixta</i>	34	0.847	0.405	0.344	-0.439	1.189	0.744		
		<i>Stewartia monadelphica</i>	29	0.602	0.560	0.365	-0.914	1.505	0.794		

No.	Model structure	Random factor	Sample size	Fitted parameters						CF	
				DBH			AGB			DBH	AGB
				<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>		
		<i>Stewartia pseudocamellia</i>	3	0.419	0.684	0.315	-1.232	1.737	0.685		
		<i>Styrax japonica</i>	9	0.709	0.548	0.270	-0.881	1.525	0.583		
		<i>Styrax obassia</i>	7	1.278	0.254	0.306	0.298	0.915	0.657		
		<i>Symplocos kuroki</i>	3	0.388	0.682	0.313	-1.307	1.736	0.680		
		<i>Symplocos prunifolia</i>	4	-0.965	1.084	0.335	-4.447	2.639	0.730		
		<i>Syzygium buxifolium</i>	1	0.484	0.655	0.307	-0.943	1.648	0.657		
		<i>Ternstroemia gymnanthera</i>	20	-0.058	0.919	0.257	-2.182	2.227	0.559		
		<i>Tetradium glabrifolium</i>	3	-1.188	1.103	0.375	-5.048	2.700	0.812		
		<i>Thujopsis dolabrata</i>	39	1.007	0.573	0.275	-0.051	1.493	0.599		
		<i>Tilia japonica</i>	24	0.441	0.571	0.360	-1.485	1.534	0.775		
		<i>Tilia maximowicziana</i>	49	0.379	0.688	0.287	-1.623	1.756	0.620		
		<i>Trochodendron aralioides</i>	3	0.662	0.678	0.314	-0.568	1.658	0.683		
		<i>Tsuga diversifolia</i>	189	1.136	0.627	0.243	0.193	1.636	0.528		
		<i>Tsuga sieboldii</i>	60	1.386	0.456	0.340	0.820	1.219	0.740		
		<i>Turpinia ternata</i>	3	0.379	0.679	0.304	-1.411	1.751	0.658		
		<i>Ulmus davidiana</i>	9	0.298	0.671	0.299	-1.694	1.770	0.646		
		<i>Ulmus laciniata</i>	1	0.403	0.734	0.320	-1.184	1.801	0.697		
		<i>Vernicia cordata</i>	3	0.396	0.660	0.315	-1.748	1.789	0.685		
		<i>Wendlandia formosana</i>	1	-0.034	0.760	0.329	-2.387	1.951	0.713		
		<i>Zanthoxylum ailanthoides</i>	7	-0.247	0.853	0.308	-2.986	2.171	0.657		
		<i>Zelkova serrata</i>	2	0.304	0.686	0.326	-1.598	1.773	0.712		

Chapter 4: Functional types explain variations of canopy tree growth strategies across environmental gradients in diverse temperate natural forests

Abstract

Understanding tree growth variations and underlying growth strategies across diverse environments is important for comprehending forest dynamics. Plant growth analysis, in which relative growth rate (RGR, growth rate/biomass) is decomposed into net assimilation rates (NAR, growth rate/leaf area) and leaf area ratio (LAR, leaf area/biomass) can provide insights into variations in plant growth strategies. Similarly, UAV-derived crown area as a proxy for leaf area can be used to decompose the RGR of canopy trees to space use efficiency (SUE, growth rate/crown area) and space occupation efficiency (SOE, crown area/biomass). This approach was applied in 23 (1-ha) sites of temperate natural forests across Japan, to reveal variations of tree growth strategies of 103 species from 3,747 canopy individuals along a wide range of environmental gradients (mean annual temperature (MAT), photosynthetically active radiation (PAR) and snow cover). Tree growth strategies differed among functional types and leaf characteristics. Deciduous trees with low specific leaf area (SLA) had higher values of SOE, whereas evergreen species with high SLA had higher values of SUE. RGR values were similar between the functional types. Across sites, SOE increased with decreasing MAT and PAR, while SUE increased with increasing MAT and PAR. In other words, deciduous species in cold and low-light areas spread crown to maximize light capture, while species in warmer sites focused on growth per unit crown area. Snow further modulated these patterns, with deciduous species maintaining higher SOE across snow gradients compared to evergreens. These findings suggest that species with contrasting leaf and crown traits respond differently to variations in temperature, light availability, and snow cover.

Keywords: crown area, environments, growth rates, tree crown strategies, UAV-LiDAR

4.1 Introduction

Tree species exhibit significant variations in growth rates across environmental gradients (Foster et al., 2016; Bauman et al., 2022). As such, understanding these growth variations and the underlying strategies is crucial for comprehending forest dynamics, sustainable management of those ecosystems, and predicting their responses to environmental changes (Clark et al., 2011). In temperate ecosystems, latitudinal gradients correspond to changes in mean annual temperature and its seasonality, light availability in the growing season, and rainfall seasonality. At lower latitudes, trees experience relatively stable and warm conditions year-round. Trees in these environments can exhibit faster growth rates with greater total solar radiation and higher temperatures year-round, especially where abundant rainfall is available. In these regions, evergreen broadleaf species with low specific leaf area (SLA) tend to dominate (Wang et al., 2016). In higher latitudes including warm and cold temperate zones, seasonal variations in temperature and sunlight become more pronounced (Saikkonen et al., 2012), and trees in these areas experience shorter growing seasons. Deciduous species, characterized by high SLA, can dominate in these regions, producing short-term thinner leaves that allow for rapid photosynthesis to maximize growth during the limited growing season. Evergreen coniferous species can also dominate in forests within this climate zone. They have relatively low SLA leaves which are durable, long-lasting, and resistant to freezing stress (Poorter et al., 2009; Onoda et al., 2011). Evergreen species in seasonal environments can continue photosynthesis during the marginal periods when deciduous species shed their leaves. These variations in tree growths and leaf traits underscore the adaptability of different functional types or species to their specific environmental conditions and reflect the ecological strategies they employ.

In classical plant growth analysis, the leaf area of a plant is a critical factor in understanding variations in the relative growth rate (RGR; growth rates per unit biomass). The

equation for RGR can be rearranged as the product of net assimilation rate (NAR; growth rates/leaf area) and leaf area ratio (LAR; leaf area/biomass) (Grime & Hunt, 1975; Poorter, 1989). This partitioning approach has been applied to herbaceous plants and seedlings of woody species and provided valuable insights into different growth strategies among individuals and species. However, applying this method to large trees is challenging due to the technical difficulties in measuring the total leaf area of a large tree. Instead, the projected crown area (CA) can be used as a proxy of the total leaf area (Binkley et al., 2013; Htoo et al., 2024), as CA should correlate with the amount of light capture that drives photosynthesis (Sterck et al., 2001). CA per unit above-ground biomass called space occupation efficiency (SOE) is analogous to LAR, whereas growth rates per unit CA which can be called space use efficiency (SUE), is analogous to NAR. SOE and SUE vary among species and functional types (broadleaf vs conifer or evergreen vs deciduous) since they differ significantly in canopy architecture, vertical leaf distribution, and leaf phenology (McNeil et al., 2023). For instance, coniferous trees generally have narrow crowns for a given biomass (i.e., low SOE), whereas broadleaf trees tend to have wider crowns (i.e., high SOE), reflecting different biomass allocation strategies between groups. Evergreen species can photosynthesize the greater portion of the year and utilize light captured per unit CA (i.e., high SUE), while deciduous species shed their leaves in winter (i.e., low SUE). Therefore, by utilizing CA in a manner similar to the leaf area in classical plant growth analysis, differences in underlying growth strategies among species and individuals can be revealed for canopy trees.

Traditionally, the CA of a tree is estimated from ground-based measurements of crown radius in four to eight compass directions in the field (Fleck et al., 2011). However, this process is time-consuming and challenging, especially for big trees on steep terrains or in dense vegetation. Recent advances in Unmanned Aerial Vehicle (UAV, a.k.a., drone) and LiDAR (Light Detection and Ranging) technology have made it possible to measure CA more

accurately and efficiently. UAV-LiDAR enables the collection of detailed, high-resolution, and repeated measurements of tree canopy structures from a few to hundreds of hectares. UAV-LiDAR emits laser pulses over the forests to capture precise three-dimensional (3D) point cloud data. From LiDAR point cloud data, digital surface model (DSM), digital terrain model (DTM), and canopy height model ($\text{CHM} = \text{DSM} - \text{DTM}$) can be derived at high resolutions. Most importantly, it is possible to identify individual canopy trees (but not subordinate trees) from the CHM (Coomes et al., 2017), and consequently CA can be measured at individual tree levels (Apostol et al., 2020; Onishi & Ise, 2021; Ball et al., 2023). Therefore, classical plant growth analysis can now be applied more easily to canopy trees with technological advances (Htoo et al., 2024).

Whereas some studied SOE and SUE for plantation trees (Webster & Lorimer, 2003; Pretzsch & Schütze, 2005), investigations on species-rich natural forests have been rare. In a previous study, the variations in RGR of hundreds of canopy individuals were analyzed in relation to SUE and SOE in an old-growth mixed forest in Japan (Htoo et al., 2024). It was found that deciduous species tended to have higher SOE while evergreen species showed higher SUE and $\text{RGR} (\approx \text{SOE} \times \text{SUE})$ showed similar values between them. Such UAV-based growth analysis can be applied to various forests along the environmental gradients quantified by mean annual temperature, mean annual precipitation, and degrees of snow cover. I hypothesize that higher SUE can be found in warmer areas where the growing season is longer and that heavy snow load may limit SOE, especially for evergreen species. In addition, the increased data availability of crown traits can allow us to examine potential associations between crown traits and leaf or wood traits which have been widely measured across many species (Aiba et al., 2016; Kattge et al., 2020). The previous study in an old-growth warm temperate forest found a positive relationship between SOE and SLA, and a negative relationship between SLA and SUE (Htoo et al., 2024). We can examine these relationships

as well as other potential associations across many canopy species from different forests to understand general patterns in tree growth strategies among species.

The present study examined the variations in growth rates and their underlying components in 3747 canopy individuals of 103 tree species for 23 one-hectare forest plots across a wide range of mean annual temperature (MAT) from 1.5 to 20.5 °C in Japan. The 103 species can be classified into three functional types (evergreen conifer, evergreen broadleaf, and deciduous broadleaf trees, as deciduous conifer trees were absent in the study sites). Specifically, the following hypotheses were tested:

- 1) Deciduous broadleaf species should have higher space occupation efficiency (SOE) than evergreen broadleaf species and evergreen conifers, whereas space use efficiency (SUE) is higher in the latter than the former, and relative growth rates ($RGR \approx SOE \times SUE$) were similar among the three functional types.
- 2) Crown display strategies (SOE and SUE) should be correlated with leaf traits. Specifically, SOE is expected to be positively correlated with SLA, while SUE is expected to be negatively correlated with SLA.
- 3) SOE and SUE should vary along the environmental gradients of temperature, photosynthetically active radiation (PAR), and snow depth.

More specifically about the last hypothesis, I expect that SUE is positively correlated with temperatures and PAR since longer growing seasons mean more light per unit crown area and greater SUE. On the other hand, SOE may increase with decreasing temperature and/or lower annual PAR as trees in colder environments face shorter growing seasons and may allocate biomass more efficiently to capture light through greater crown area (high SOE). However, snow load could modulate this relationship because snow accumulation on the crown is potentially disastrous as it can break branches. Evergreen species are particularly

sensitive to snow load while deciduous species are free of this risk as they are leafless and do not accumulate snow on their crown in winter.

4.2 Materials and methods

4.2.1 Study sites

The study was conducted in 23 permanent forest monitoring sites in Japan (Fig. 4.1). These sites are part of the long-term forest monitoring network, called as Monitoring 1000 project, encompassing various functional types of dominant trees and a wide range of climates. In almost all of them, 1-hectare (100 m $\times$ 100 m) survey plots were established, and all stems with a girth at breast height (GBH) $\geq$ 15 cm have been censused annually in those designated to be core sites (11) and five-year intervals in the rest with measuring tapes (Ishihara et al., 2011). Tree census data, including individual tree identification number (ID), GBH, stem locations (x and y coordinates), and species-level information are publicly available at the official data archive. The datasets for this study were downloaded from their website (<https://www.biodic.go.jp/moni1000/>). The census information available for each site is detailed in Table S1. Given the diverse forest types and species compositions of these sites, the relative biomass contributions of dominant functional types (conifer, deciduous broadleaf, and evergreen broadleaf) in each site are summarized in Fig. 4.1. For details of site-specific characteristics such as forest types, locations, and environmental variables such as mean annual temperature, total photosynthetically active radiation during the growing season, and snow cover data are listed in Table 4.1.

4.2.2 UAV-LiDAR acquisition, LiDAR data analysis, and crown mapping surveys

LiDAR data collections were conducted during 2022-2023 (Table S4.1) by using the UAV-LiDAR system (DJI Matrice 300 RTK+ Zenmuse L1, DJI, Shenzhen, China). The detailed step-by-step procedures of UAV-LiDAR data acquisition, analysis of LiDAR data, individual tree crown area (CA) estimations, and validation process in the field were thoroughly outlined

in Htoo et al. (2024), which was conducted in the Wakayama site, which is included in the current study, too. In brief, we collected three-dimensional (3D) LiDAR point cloud data following a consistent data collection protocol across all 23 sites (flight height 100 m, speed 5–10 ms⁻¹). From the collected LiDAR data, three digital models – Digital Surface Model (DSM), Digital Terrain Model (DTM), and Canopy Height Model (CHM = DSM – DTM) were constructed following Htoo et al. (2024) to generate comparable datasets across sites. Individual tree crown mapping surveys were conducted concurrently with the UAV-LiDAR surveys for all sites to verify the size, shape, and conditions (i.e., live, dead, or broken) of the individual tree crown, and link with the individual tree ID numbers from the tree census data. After all, the final dataset was compiled from all sites including individual trees with their corresponding tree ID, GBHs, projected crown areas, and corresponding species names.

4.2.3 Data analysis

All analyses were conducted in R Statistical Software (R Core Team, 2023). Above-ground biomass (AGB) was calculated using the following allometric equation developed for Japanese natural forest trees (Ishihara et al., 2015):

$$\ln AGB = -1.196 + 1.622 \ln DBH + 0.338 (\ln DBH)^2 - 0.044 (\ln DBH)^3 + 0.708 \ln WD$$

where *DBH* is the diameter at breast height and *WD* is wood density. *DBH* values were calculated from field-measured GBH values. We used species-specific mean *WD* (Aiba et al., 2016) in AGB calculation because intraspecific variations in wood density are typically smaller than the interspecific variations (Chave et al., 2006; Sungpalee et al., 2009; Osazuwa-Peters et al., 2014; Siefert et al., 2015). The biomass growth rate (GR, kg year⁻¹) was calculated using linear regression based on the average slope for a recent five-year period at each site. For core sites, where GBHs are measured annually, we used the latest yearly data available for five consecutive years. In semi-core sites where GBH measurements are taken every five years, we

thus used the most recent publicly available data covering the latest five-year interval at each site. We employed linear regression to calculate GR and estimated relative growth rates (RGR) as GR divided by the final AGB of each measurement period. This calculation of RGR is an approximation ($RGR \approx GR/AGB$) because AGB was measured over longer intervals and final biomass was utilized instead of mean AGB during the interval.

A total of 4355 individual trees, from 149 species, were analyzed. Tree species were classified based on whether conifer or broadleaf trees, and evergreen or deciduous. However, as no deciduous conifer species were present in our study sites, species were grouped into three main functional types (evergreen conifer, deciduous broadleaf, and evergreen broadleaf), and there were 1349, 1776, and 1230 individuals in these functional types, respectively. Individuals with negative growth rates (192 out of 4355 individuals) were excluded from the analysis, resulting in a dataset of 4163 individuals from 147 species. For species-level analysis, we focused on trees with a mean canopy height equal to or greater than 10 meters and a sample size of at least 3 individuals to ensure our analysis on canopy trees. This resulted in 3747 individuals for 103 species across sites. The choice of 10 m was made based on the distribution of tree heights in the dataset, where the 10th percentile value was approximately 10.36 meters, indicating that 90% of the trees were taller than this height. Trees below this height were mostly suppressed individuals or gap colonizers and their light availability might be influenced by the surrounding trees, therefore we did not consider them as canopy trees and excluded them from the analysis. We set a minimum sample size of three individuals per species. Details of sample sizes along with their species names were provided in Fig. 4.2.

We employed linear mixed-effects models to account for the variation in species-level characteristics (Bates et al., 2015). CA, AGB, and GR were $\log_{10}$ transformed, and two linear mixed-effects models were fitted: CA relative to AGB ($CA/AGB = SOE$), and GR relative to CA ($GR/CA = SUE$), both with random slopes and intercepts for each species. In my analysis,

I used the AGB and CA estimated at the most recent time (i.e., at the endpoint of the interval for which GR was estimated). The best linear unbiased prediction (BLUP) coefficients from these models were extracted and assigned to each species. For species-level comparisons, we examined CA and GR at reference AGB and CA values, which were close to the overall mean values across species: 1300 kg for AGB (the mean of 3747 individuals was 1248.23 kg) and 43 m² for CA (mean was 42.75 m²). This approach allowed us to standardize size heterogeneity among species for comparisons of SOE and SUE values. To assess the significant differences in tree growth strategies (RGR, SOE, and SUE) among functional types, an analysis of variance (ANOVA) was conducted.

Specific leaf area (SLA, cm² g⁻¹) values were sourced from a previous study (Aiba et al., 2016), which collected five traits including leaf mass per area (LMA, an inverse of SLA) and wood density for 200 species from natural forests across Japan. For details of sampling procedures, please refer to Aiba et al. (2016). For each species, the mean SLA and WD values across different sites were calculated and correlated with the species-specific SOE and SUE values to explore their relationships. In total, we were able to correlate with SLA and WD data for 100 species out of 103 species.

Environmental variables such as monthly mean temperature (°C), monthly maximum snow depth (cm), and daily mean radiation (MJ m⁻²) data were available for the 23 monitoring sites from which the mean annual temperature (MAT) and maximum snow cover were calculated. To focus on the growing season when photosynthesis is active, we calculated the periods when the mean temperatures exceeded 5 °C. Temperature and radiation values were first extracted for each month. Radiation values were filtered, retaining only values from months with mean temperatures above 5 °C. For each site, we summed the filtered radiation values and scaled them to annual totals. A conversion factor of 0.5 was applied to account for the fraction of solar radiation that is photosynthetically active (PAR) (Landsberg & Waring,

1997). Finally, MAT, PAR, and snow cover data were assigned to each corresponding species at each site and mean values were calculated for each species.

4.3 Results

4.3.1 SOE, SUE, and RGR across species and functional types from different forests

Functional types exhibited distinct patterns in terms of space occupation efficiency (SOE) and space use efficiency (SUE) across 103 canopy species from various forests. Deciduous broadleaf species had significantly higher SOE and lower SUE than evergreen species either conifer or broadleaf trees, while no significant differences were found between evergreen conifer and evergreen broadleaf species (Fig. 4.2). The average SOE values for evergreen conifer, evergreen broadleaf and deciduous broadleaf were 0.027, 0.029 and 0.041 m² kg⁻¹ respectively (Fig. 4.3a). The mean SUE values were 0.330 for evergreen conifer, 0.308 for evergreen broadleaf, and 0.238 kg m⁻² year⁻¹ for deciduous broadleaf species (Fig. 4.3b). However, the mean relative growth rates (RGR) were similar among the three functional types: 0.009 for evergreen conifer, 0.009 for evergreen broadleaf, and 0.010 g g⁻¹ year⁻¹ for deciduous species (Fig. 4.3c). The species-specific differences in the relationship between SOE and SUE were plotted along with their RGRs which were indicated by the isoclines (RGR= 0.01, 0.02, 0.03) in Fig. 4.3d. RGR values differed among species, with the majority achieving RGR between 0.005 and 0.02 per year. Although evergreen and deciduous species displayed contrasting patterns in SOE and SUE, their RGR values were not significantly different among the functional types, suggesting that there were contrasting crown strategies among canopy species to achieve similar growth performances within each functional type as well as across functional types. In general, deciduous species showed higher crown areas than both evergreen conifers and evergreen broadleaf species (Fig. S4.1).

4.3.2 Relationship between SOE, SUE, and species functional traits

The species mean SOE was positively correlated with the species mean specific leaf area (SLA) among species ($r = 0.48$, Fig. 4.4a). Species with low SLA leaves (i.e., smaller area for a given leaf mass), such as evergreen conifers and evergreen broadleaf species, tended to have lower SOE, i.e., less effective in occupying canopy space for a given above-ground biomass. In other words, species with high SLA leaves such as deciduous broadleaf excelled in space occupation at both canopy- and leaf-levels. Conversely, there was a significant negative correlation between SUE and SLA across species ($r = -0.45$, Fig. 4.4b). Species with lower SLA values, mostly evergreen species, grew more per unit projected crown area. The mean SLA values significantly differed among functional types, lowest in evergreen conifer followed by evergreen broadleaf and deciduous broadleaf species (Fig. S4.2a). Wood density was neither correlated with SOE nor SUE across species, while mean wood density was significantly different between functional types, lowest in evergreen conifer followed by deciduous broadleaf and evergreen broadleaf species (Fig. 4.4cd.). The mean wood density in evergreen broadleaf species (0.58 g cm^{-3}) was 1.44 times higher than evergreen conifer species (0.40 g cm^{-3}), while deciduous broadleaf species showed in between (0.52 g cm^{-3}) (Fig. S4.2b).

4.3.3 SOE, SUE across environmental gradients

The mean SOEs of species were significantly and negatively correlated with both mean annual temperature (MAT) ($r = -0.44$; Fig. 4.5a) and total photosynthetically active radiation (PAR) during the growing season ($r = -0.46$; Fig. 4.5c). This indicates that species in colder places receiving less total annual radiation had greater canopy space occupation per unit biomass. Conversely, SUE was positively correlated with both MAT ($r = 0.21$; Fig. 4.5b) and PAR across species ($r = 0.22$; Fig. 4.5d), meaning that species in warmer and high-light regions achieved higher growth for a given crown area. The ratio of SUE and PAR can be considered as a light use efficiency (biomass growth per unit PAR, g MJ^{-1}), and most of the species fell

between 0.1 to 0.2 g MJ⁻¹ with slightly higher values in evergreen conifer species (Fig. 4.5d). Within functional types, SUE of deciduous broadleaf and evergreen conifer species showed a positive correlation with both MAT and PAR, but evergreen broadleaf species showed a negative trend, possibly due to the past typhoon damage in our warmest site (Yona site with MAT of 20.5°C). Reduced crown area per unit biomass may be advantageous to avoid wind damage from typhoons, but this may result in lower growth rates compared to other evergreen broadleaf-dominated sites.

Maximum snow cover showed a positive relationship with SOE in the pooled data ($r = 0.31$; Fig. 5e), but no significant correlation was found within functional types. Evergreen broadleaf species were confined in almost fewer snow regions (<10 cm), while evergreen conifer species were distributed across a wide range of snowfall by showing low SOE. In contrast, SUE was negatively correlated with maximum snow cover in pooled data ($r = -0.24$; Fig. 4.5f) and also within functional types.

4.4 Discussion

In this study, we applied the growth-analytical framework to hundreds of canopy species using UAV-LiDAR across diverse natural forests in Japan. We found distinct growth strategies among functional types. Evergreen species, both conifers and broadleaf trees, exhibited higher space utilization (SUE; growth rates/crown area) but lower space occupation efficiency (SOE; crown area/biomass) compared to deciduous broadleaf trees. These strategies are associated with species-specific leaf traits, particularly with specific leaf area (SLA). Species with high SLA are more efficient in occupying space, whereas low SLA species are better at space utilization. These results offer new insights into the ecological strategies of canopy trees in diverse environmental conditions as discussed in detail below.

4.4.1 Different tree growth strategies among functional types

In this study, we found that variations in crown display and use strategies (SOE and SUE) differed among the three functional types. Deciduous species showed wider crowns for a given biomass, while evergreen species generally had narrower crowns for a given biomass. While both evergreen conifer and evergreen broadleaf species showed similarly lower SOE, the underlying mechanism may be different. Conifer species have generally narrower crown areas than broadleaf species (Fig. S4.1) irrespective of leaf habits, which may be a major reason for the lower SOE in conifer species. Instead, evergreen broadleaf species can have wider crowns compared to conifers but they have denser and mechanically stronger wood (Fig. S4.2b). High-density wood provides structural support and resilience against environmental stressors such as strong winds, heavy rainfall, and storms. On the other hand, the higher SOE in deciduous broadleaf species than both evergreen conifer and evergreen broadleaf species may be explained by two factors (1) wider crown than conifer species and (2) relatively lower wood density than evergreen broadleaf species that restrict the extension of branches to horizontal directions.

Despite these contrasting underpinnings, i.e., crown architecture and wood density, a simple positive correlation was found between SOE and SLA across species from three functional types (Fig. 4.4a). This means species with a larger area-mass ratio at the leaf level (high SLA) also have a larger area-mass ratio at the canopy level (high SOE). This correlation may not be expected *a priori* because SOE increases require allocation of woody mass to extend branches to widen the crown while SLA is solely determined by allocation within a single leaf. Although SLA and SOE both describe area-to-mass relationships, they operate at different levels of structural organization. SLA is determined by leaf-level traits and involves a relatively small fraction of total biomass, while SOE depends on crown expansion, which requires significant biomass investment in woody structures such as branches. However, the

biological correlation between SOE and SLA implies that deciduous species prioritize light interception at both leaf and branch levels compared to evergreen broadleaf species and evergreen conifer species. A previous study also reported similar findings in eight canopy species in a warm-temperate forest (Htoo et al., 2024). But in this study, we confirmed the generality of these findings. To our knowledge, this is the first study to clarify that leaf- and crown-level area-mass-ratios were coordinated over a hundred canopy species in diverse temperate natural forests.

The higher SUE in evergreen species than deciduous species may be attributed to the length of the growing season and the leaf traits they possessed. Evergreen species, which retain their leaves year-round, can perform photosynthesis for a greater proportion of the year (Miyazawa & Kikuzawa, 2005). Evergreens typically have longer leaf lifespans, allowing them to capture light more efficiently in their deep crowns compared to deciduous species, which often have shallow crowns with low leaf density (McNeil et al., 2023). This may in turn result in higher gross production per unit projected crown area in evergreen species than in deciduous species. We found a negative relationship between SUE and SLA. Species with lower SLAs such as evergreen conifers and evergreen broadleaf species, may optimize the available space via more durable and long-lived leaves which maintain photosynthesis over a prolonged period without needing to regenerate leaves frequently (Fig. 4.4b).

The convergence of relative growth rate was found across species, despite the wide range of crown strategies within each value of RGR. Previous studies (Pretzsch & Schütze, 2005; Htoo et al., 2024) also observed similar RGR values among species, attributable to high SOE and lower SUE in deciduous broadleaf trees, compared to evergreen species. The current study demonstrates the generality of these contrasting growth strategies across 103 canopy species from diverse environments. The convergence of RGR suggests that regardless of the strategy employed, species can achieve similar growth outcomes, highlighting that there are

multiple successful strategies for growth in canopy species. We also found notable variations in RGRs among canopy species within each site. These variations are attributable not only to species-specific traits and functional types but also to differences in successional positions. For instance, Htoo et al. (2024) found that at the Wakayama site, late-successional species achieve higher RGR through high SUE than early-middle successional species. Because in the late successional forest stands, the canopy layer is fully packed and limited space for crown expansion. Therefore, increasing SUE is an effective strategy to increase growth in late-successional stands. Conversely, early-successional species, which often specialize in colonization and rapid growth in treefall gaps, prioritize rapid crown expansion and resource acquisition, resulting in higher RGR.

4.4.2 Canopy tree growth strategies across the environmental gradients

SUE was higher in warmer sites in the pooled data as well as within deciduous species and conifer species. This may be primarily due to the longer growing season in warmer areas. Trees can get more light for their crown area in longer growing seasons, which can increase growth rates per unit crown area. This interpretation is supported by a similar correlation between SUE and PAR (Fig. 4.5d). Light use efficiency seems to be similar ($0.1 \sim 0.2 \text{ g MJ}^{-1}$) between deciduous broadleaf species and evergreen broadleaf species across a wide range of temperatures (Fig. 4.5d), while conifer species may achieve slightly higher light use efficiency.

SOE increased with decreasing mean annual temperature (MAT) and annual photosynthetically active radiation during the growing season (PAR), especially among broadleaf species, indicating that species in colder climates and lower amounts of PAR environments were more efficient at occupying canopy space. This could be an adaptation to maximize light capture in energy-limited environments, particularly where the growing season is short. In these environments, the ability to spread out and capture light becomes crucial for growth. In these sites, deciduous species are dominant and consistently showed higher SOE.

Enhancing growth through high SOE is advantageous, especially in regions where seasonal changes are pronounced, which is likely to compensate for their lower SUE in the shorter growing season. Conversely, high SOE species are largely absent from warmer environments. Evergreen broadleaf species with high wood density are dominated and show lower SOE. This kind of investment in durable wood with lower SOE may reflect an adaptation to environments with prolonged growing seasons and exposure to high pressure of storms e.g., typhoons and herbivory damages in warmer areas.

While snow accumulation is usually not considered in leaf trait variation, it can be important for crown structure as snow load can lead to increased mechanical stress on branches and a higher chance of branch failure. This mechanical limitation has important implications for the crown architecture of canopy trees in snowy regions. In our study, sites with heavy snowfalls and accumulation are primarily dominated by deciduous broadleaf and evergreen conifer trees. Evergreen broadleaf species are notably absent in these areas (Fig. 4.1), likely that the combination of needle leaves with ever-greenness or broadleaves with deciduousness offers advantages that other leaf habit combinations do not (Sprugel, 1989). Trees with wide evergreen crowns do not exist in snowy areas probably because these combinations cannot survive under heavy snow loads. In Japan, tree species distributions are influenced by both snow cover duration and snow depth (Shidei, 1979; Gansert, 2004). In particular, in subalpine and cool temperate zones, tall deciduous broadleaf species are better adapted to bearing snow loads than evergreen conifers (Shidei, 1979). Deciduous trees can have wider crowns as they shed their leaves during winter, reducing the surface area for snow to accumulate. This helps deciduous species minimize snow-loading stress in winter, allowing for larger crowns under snowy conditions. Evergreen conifers, on the other hand, cannot have wider crowns due to heavy snow loads but they can achieve higher SUE than deciduous species. The coexistence of these contrasting strategies is more prevalent, especially in mixed forests. This interpretation

is consistent with the evidence that mixed forests of deciduous broadleaf and evergreen conifers are widespread across many regions of Japan (Suzuki et al., 2015).

4.4.3 Conclusions

In this study, we used UAV-derived crown area to apply the plant growth analysis to canopy trees by decomposing their relative growth rates (growth rates/biomass) into underlying components; space occupation efficiency (crown area/biomass) and space use efficiency (growth rates/crown area). We found that deciduous species excelled at space occupation, while evergreen species were more efficient at space utilization, which were found across environmental gradients. We also found that crown traits are partly coupled with leaf traits perhaps through adaptation to different lengths of growing seasons. We believe the crown-based growth analysis as was done in this study offers a novel approach for assessing canopy tree growth strategies and understanding forest dynamics in natural forest stands.

Table

Table 4.1 Site-specific characteristics and environmental variables in 23 forest monitoring sites across Japan. MAT refers to the mean annual temperature in degrees Celsius, MAR represents mean annual rainfall in millimeters and PAR stands for photosynthetically active radiation in megajoules per square meter per year. The sites are arranged in ascending order along the latitudinal gradient, starting from the lowest latitude at the bottom to the highest latitude at the top.

Site	Forest types	Location			Environmental variables			
		Latitude (°N)	Longitude (°E)	Elevation (m ASL)	MAT (°C)	MAR (mm)	Total PAR in growing season (MJ m ⁻² yr ⁻¹)	Snow cover max. (cm)
Uryu	Broadleaf /Conifer	44.3643	142.2785	362	3.7	1424	1396.13	184
Taisetsu	Conifer	43.6629	143.1053	1023	1.5	1221	1321.60	74
Ashoro	Deciduous Broadleaf	43.3235	143.5017	355	4.3	935	1379.40	49
Tomakomai	Deciduous Broadleaf	42.7109	141.5682	101	7.1	1255	1303.35	76
Otakizawa	Deciduous Broadleaf	39.6435	140.8941	476	7.7	2030	1606.00	90
Hayachine	Conifer	39.5398	141.4995	1212	4.2	1659	1438.71	138
Kanumasawa	Deciduous Broadleaf	39.1114	140.8551	466	7.4	2144	1567.98	162
Aobayama	Broadleaf /Conifer	38.2544	140.8539	131	11.8	1228	1627.29	16
Ogawa	Deciduous Broadleaf	36.9389	140.5862	660	8.6	1680	1779.38	16
Kayanodaira	Deciduous Broadleaf	36.8390	138.4996	1516	4.5	1854	1499.54	209
Otanomosutaira	Conifer	36.7028	138.4995	1747	3.8	1734	1470.65	147
Daisen	Deciduous Broadleaf	35.3577	133.5535	1142	6.1	2634	1580.15	179
Masukami	Conifer	35.3463	135.7413	791	9.6	2222	1771.77	52
Mondori	Deciduous Broadleaf	35.3458	135.7354	742	9.8	2200	1771.77	51
Kasugayama	Evergreen Broadleaf	34.6796	135.8631	384	13.5	1403	2047.04	4
Tsushima	Evergreen Broadleaf	34.1497	129.2165	163	14.5	2128	2250.83	0
Wakayama	Conifer	34.0672	135.5355	847	9.6	2262	1780.90	9
Sadayama	Evergreen Broadleaf	32.7396	133.0021	329	16.1	2443	2728.38	0
Shiiba	Deciduous Broadleaf	32.3776	131.0967	1182	9.4	3086	1846.29	6
Aya	Evergreen Broadleaf	32.0485	131.1861	496	14.7	2836	2293.42	4
Hanyama	Evergreen Broadleaf	30.3690	130.3895	192	16.8	3677	2466.79	0
Tenmonomori	Conifer	30.3109	130.5650	1218	12.6	4171	2167.19	0
Yona	Evergreen Broadleaf	26.7421	128.2354	269	20.5	3129	2451.58	0

Figures

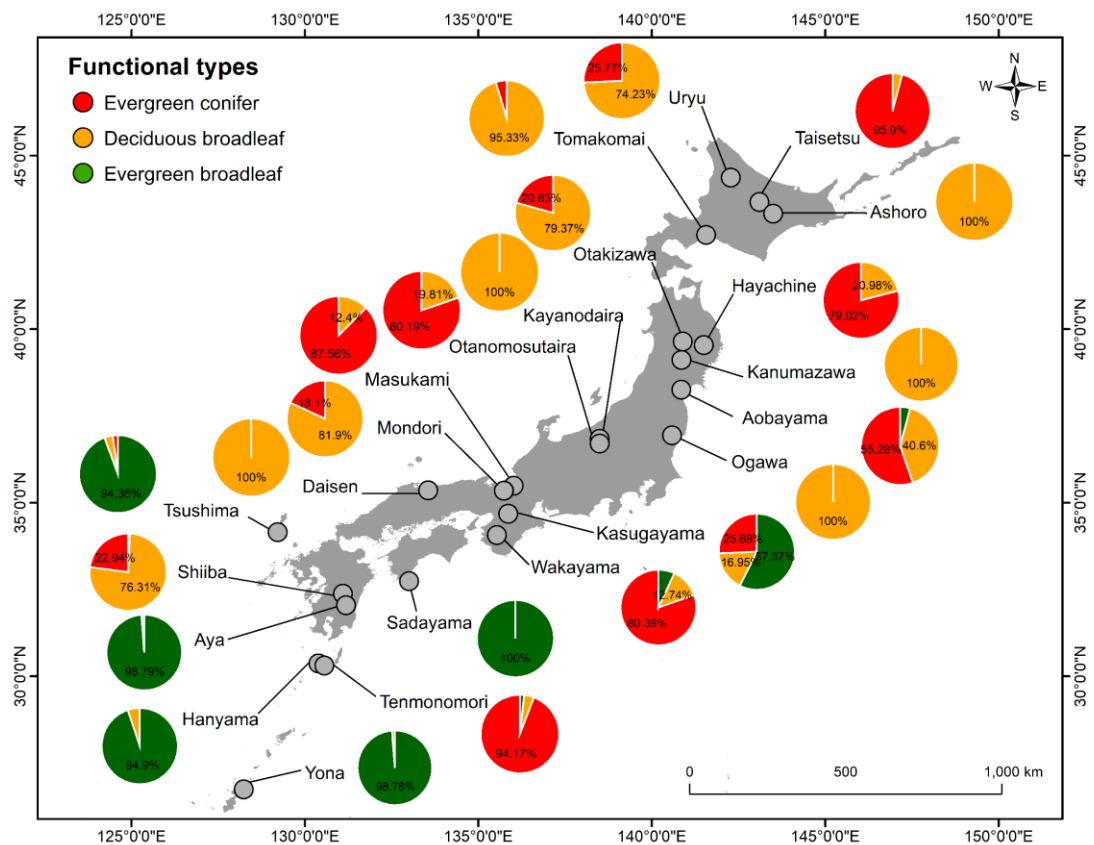


Fig. 4.1 Location of 23 studied forest sites across Japan. Different colors represent different above-ground contributions of site-specific functional types. Percent values indicate the relative contribution of each functional type to the total above-ground biomass of trees detected by UAV at each site.

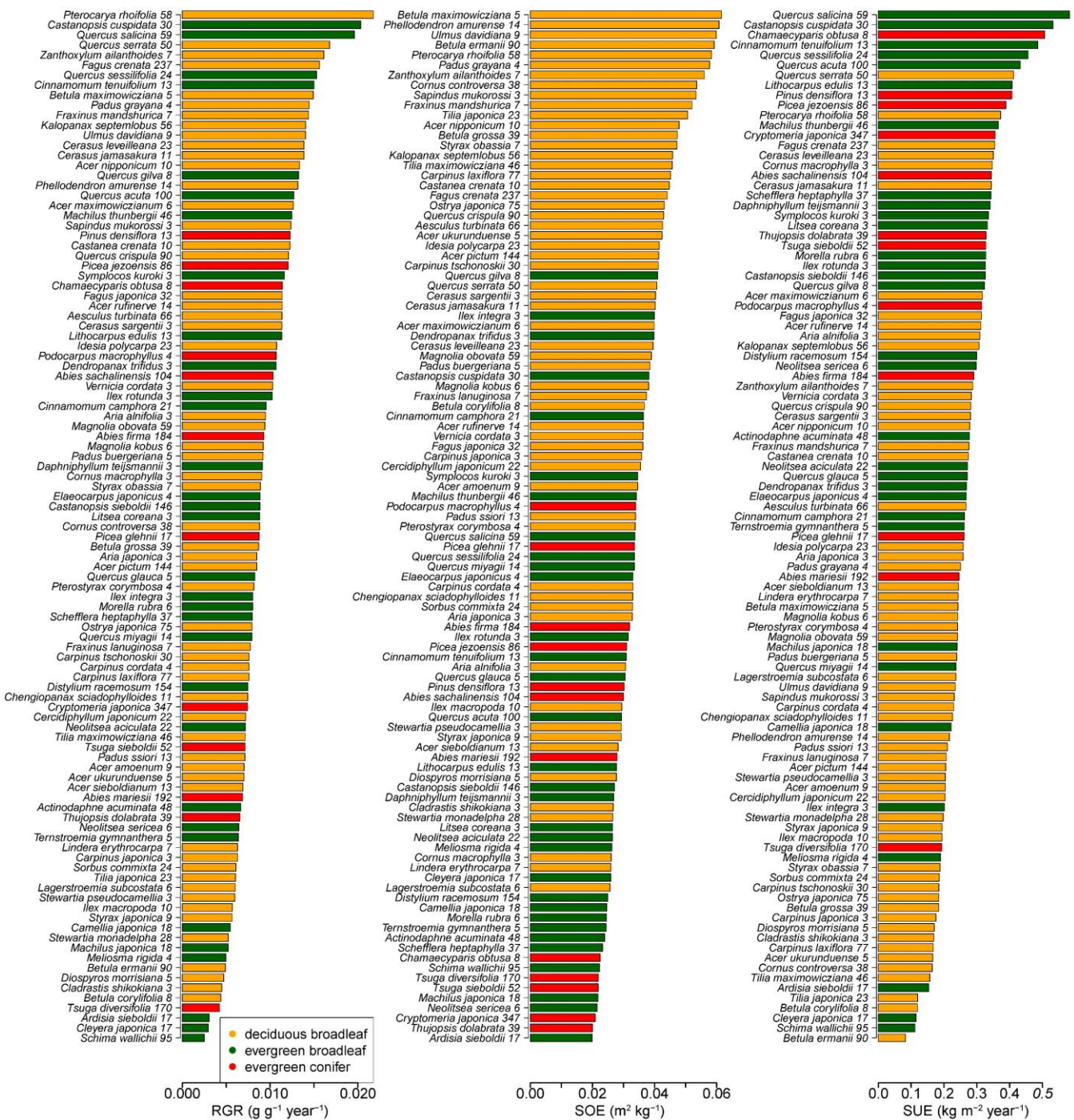


Fig. 4.2 Species-specific RGR, SOE and SUE with their sample size for 103 species across 23 forest sites. The values are normalized per size (see main text for details). The numbers next to species names indicate the number of individuals used for the analysis.

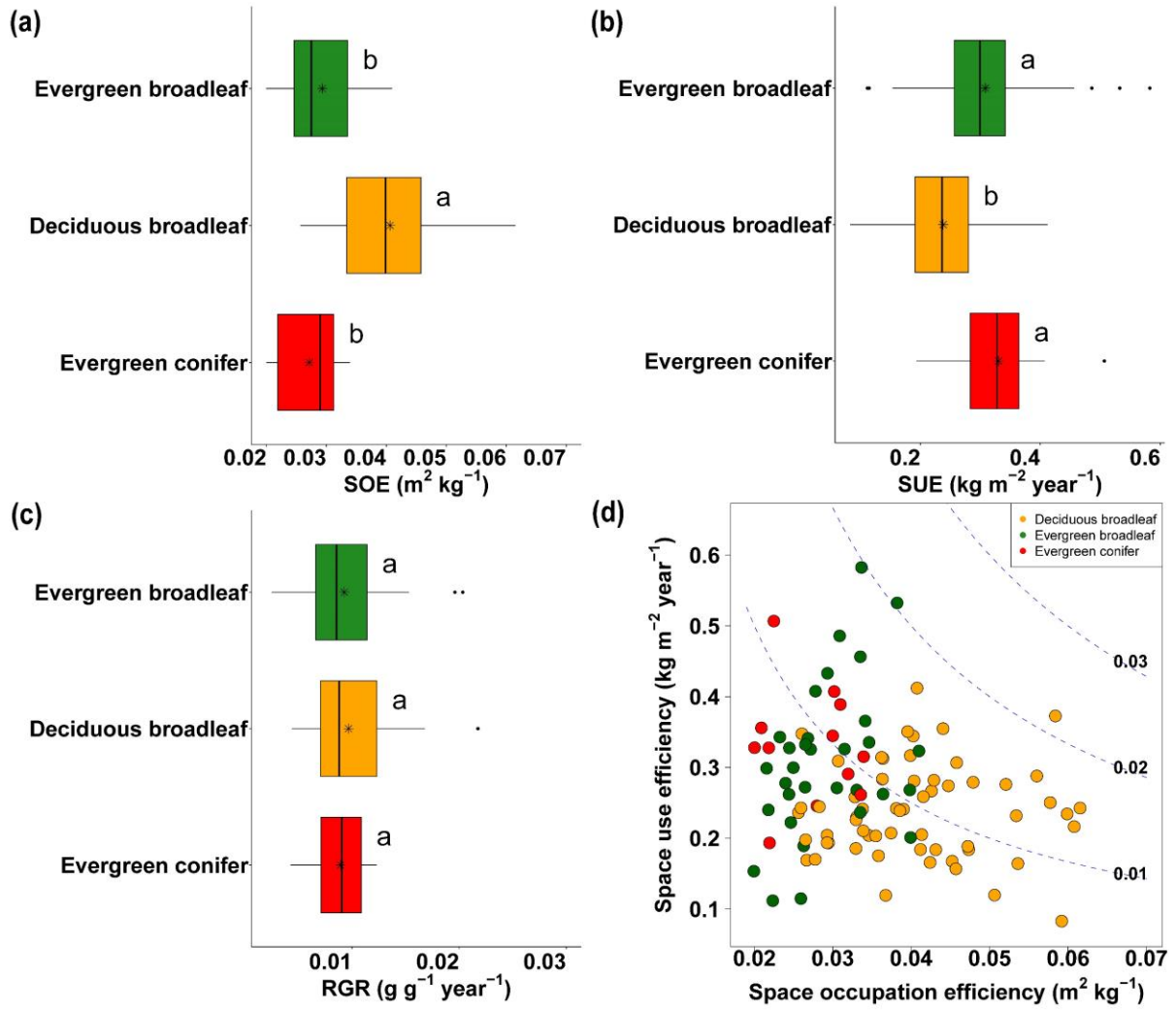


Fig. 4.3 Box plots of **(a)** space occupation efficiency (SOE), **(b)** space use efficiency (SUE), and **(c)** relative growth rate (RGR) for 103 canopy species across 23 study sites. **(d)** Species-specific mean values calculated from each regression line between SUE and SOE are presented along with dashed blue curves (isoclines) that indicated values of RGR (0.01, 0.02, 0.03 $\text{g g}^{-1} \text{year}^{-1}$). Symbol colors indicate functional types (yellow for deciduous broadleaf species, green for evergreen broadleaf species, and red for evergreen conifers). Functional types in subplots (a), (b), and (c), not sharing lowercase letters are significantly different from each other ($P < 0.05$).

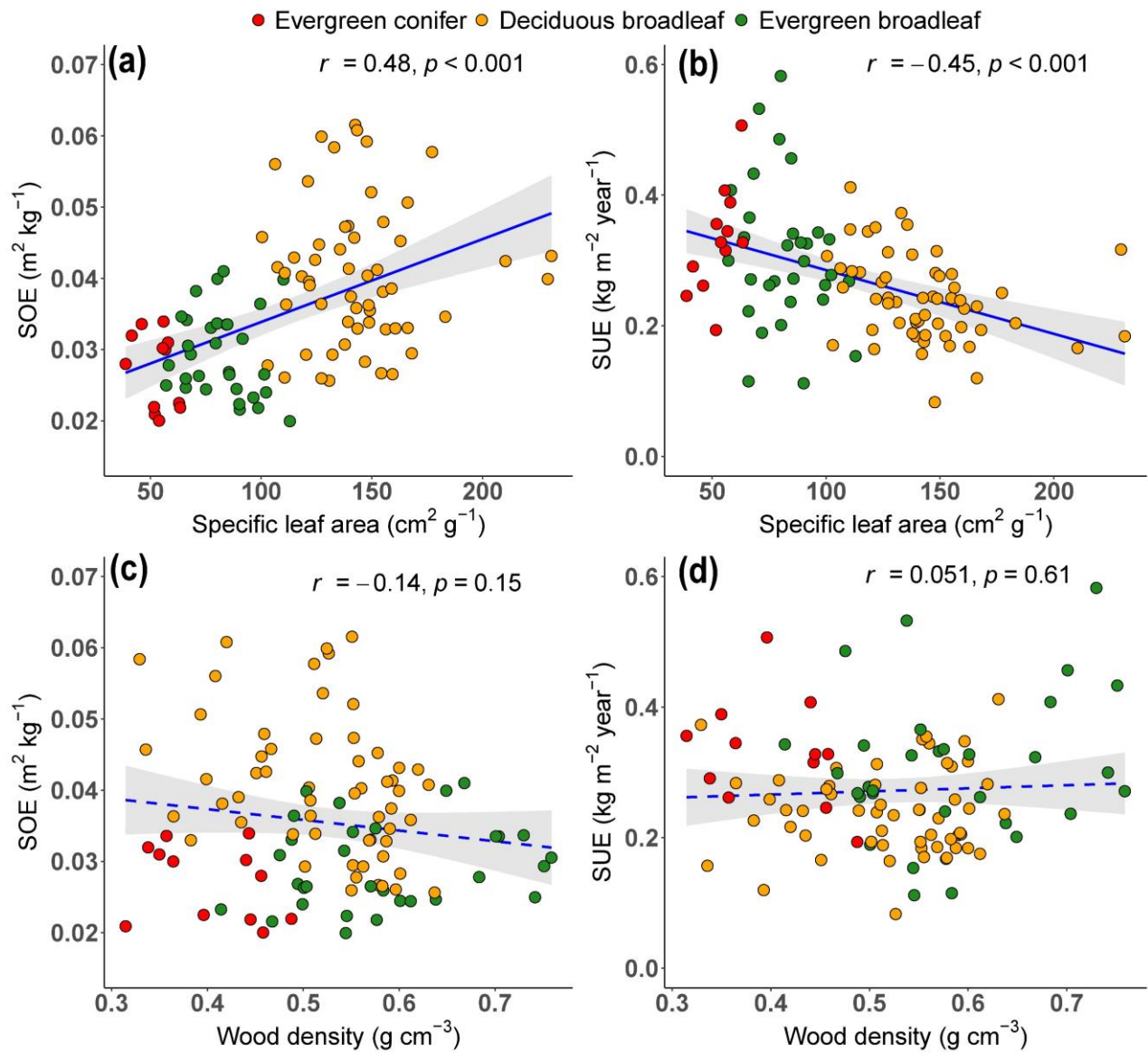


Fig. 4.4 Space occupation efficiency (SOE) and space use efficiency (SUE) are plotted against (a,b) specific leaf area and (c,d) wood density. Each dot represents the mean value for each species. Pearson correlation coefficient (r) is shown with a significant level. Statistically significant relationships are indicated by solid lines ($P < 0.05$). Symbol colors indicate functional types; yellow for deciduous broadleaf species, green for evergreen broadleaf species, and red for evergreen conifers.

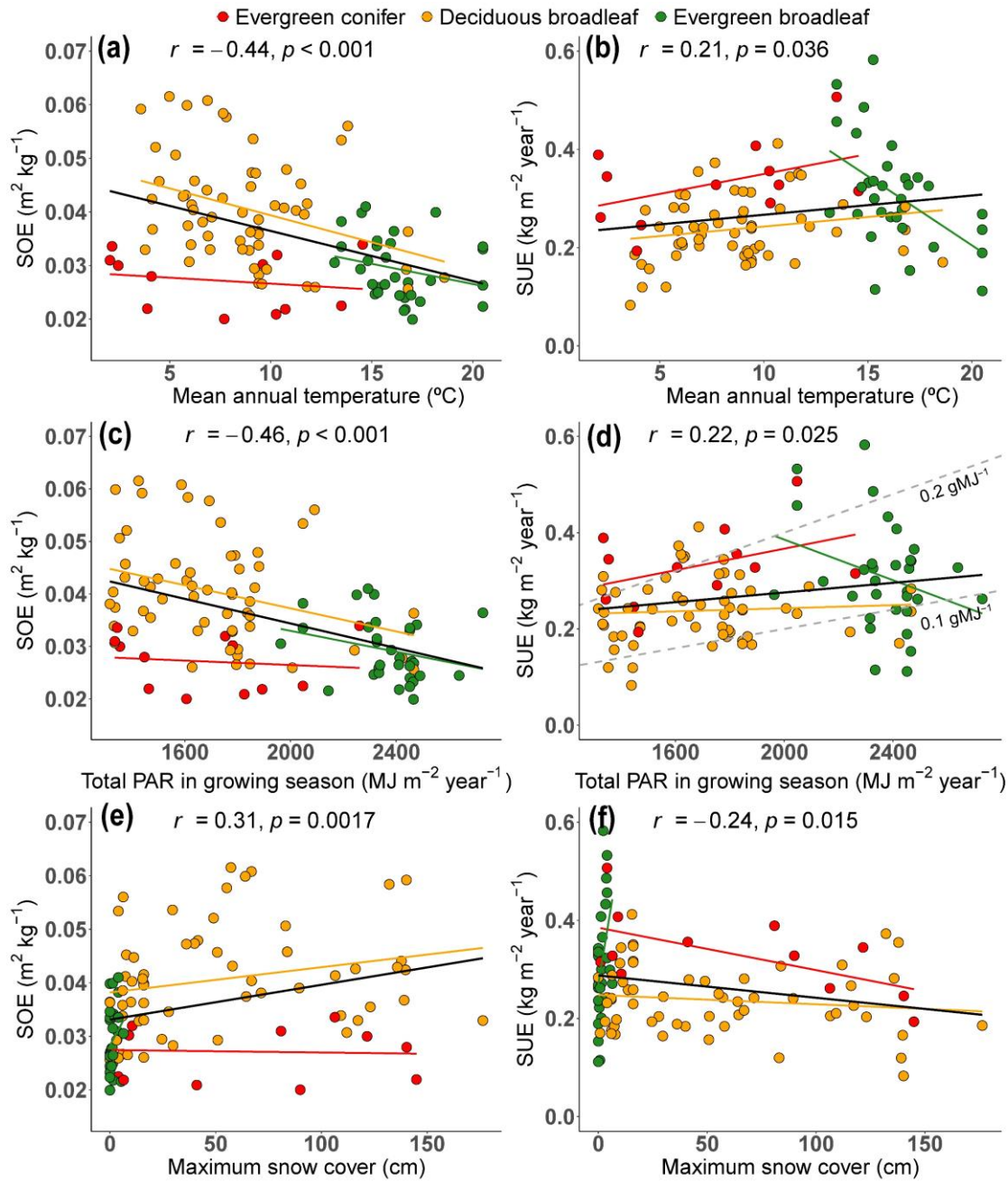


Fig. 4.5 Space occupation efficiency (SOE) and space use efficiency (SUE) are plotted against (a,b) mean annual temperature, (c,d) total photosynthetically active radiation (PAR) during the growing season, and (e,f) maximum snow cover. In (d), the dashed gray lines denote isoclines of light use efficiency (the ratio of SUE to PAR) at 0.1 and 0.2 g MJ⁻¹. Each dot represents the mean value for each species. Pearson correlation coefficient (r) is shown for all individuals and a statistically significant relationship is indicated by black solid line ($P < 0.05$). Symbol colors indicate functional types; yellow for deciduous broadleaf species, green for evergreen broadleaf species, and red for evergreen conifers.

Supplementary materials

Table S4.1 Site-specific characteristics, available latest tree census data, and UAV-LiDAR surveys in 23 forest monitoring sites across Japan. Sites are arranged in ascending order along the latitudinal gradient, starting from the lowest latitude at the bottom to the highest latitude at the top.

Site	Tree census data			LiDAR data
	Period	Forest types	Size (ha)	Collection Period
Uryu *	2014-2018	Broadleaf /Conifer	1.05	July, 2022
Taisetsu	2013-2018	Conifer	1	July, 2022
Ashoro *	2014-2018	Deciduous Broadleaf	1	July, 2022
Tomakomai *	2014-2018	Deciduous Broadleaf	1	July, 2022
Otakizawa	2013-2018	Deciduous Broadleaf	1	August, 2023
Hayachine	2010-2015	Conifer	1	August, 2023
Kanumasawa *	2018-2022	Deciduous Broadleaf	1	August, 2023
Aobayama	2010-2015	Broadleaf /Conifer	1	July, 2023
Ogawa *	2014-2018	Deciduous Broadleaf	1	September, 2022
Kayanodaira *	2014-2018	Deciduous Broadleaf	1	September, 2023
Otanomosutaira *	2014-2018	Conifer	1	September, 2023
Daisen	2011-2016	Deciduous Broadleaf	1	August, 2022
Masukami *	2014-2018	Conifer	1	June, 2022
Mondori	2008-2013	Deciduous Broadleaf	1	June, 2022
Kasugayama	2011-2016	Evergreen Broadleaf	1	October, 2023
Tsushima	2012-2017	Evergreen Broadleaf	1	June, 2023
Wakayama *	2014-2018	Conifer	1	May, 2022
Sadayama	2012-2017	Evergreen Broadleaf	1	August, 2023
Shiiba	2009-2015	Deciduous Broadleaf	1	August, 2022
Aya *	2014-2018	Evergreen Broadleaf	1	August, 2022
Hanyama	2013-2018	Evergreen Broadleaf	1	September, 2023
Tenmonomori	2007-2012	Conifer	1	September, 2023
Yona *	2012-2016	Evergreen Broadleaf	1	October, 2023

Note: Sites shown with an asterisk (*) are core sites with yearly GBH (girth at breast height) measurements while others are semi-core sites where GBH measurements are made every five years. Tree census data (ID, GBH, species) were downloaded from the official website of monitoring 1000 sites data archive. The data set version is as of 2019/07/11.

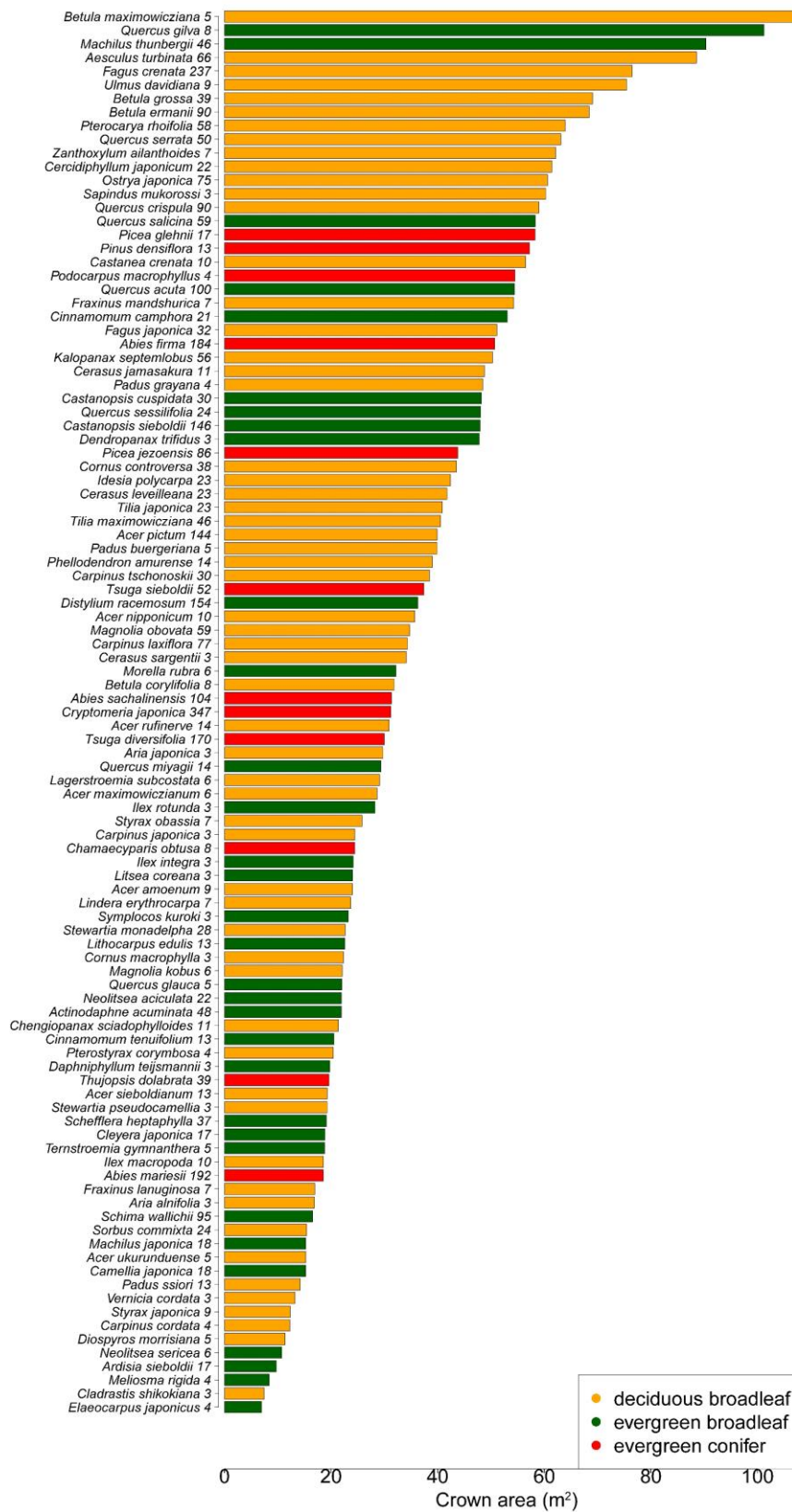


Fig. S4.1 Species-specific mean crown areas with their sample sizes for 103 species across 23 forest sites.

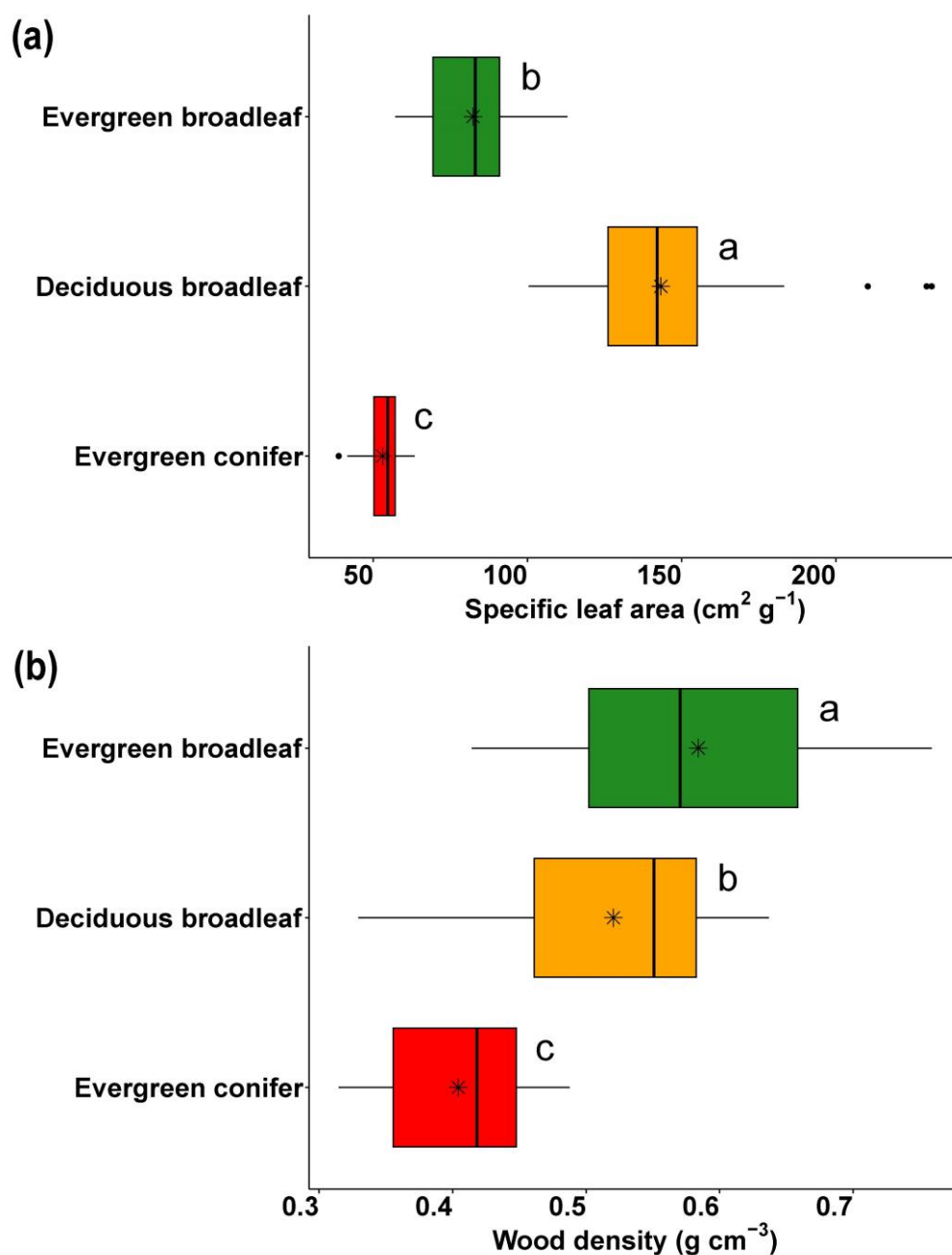


Fig. S4.2 Box plots summarizing **(a)** specific leaf area and **(b)** wood density based on the functional types for 100 canopy species across 23 study sites. Functional types in subplots (a) and (b), not sharing lowercase letters are significantly different from each other ($P < 0.05$).

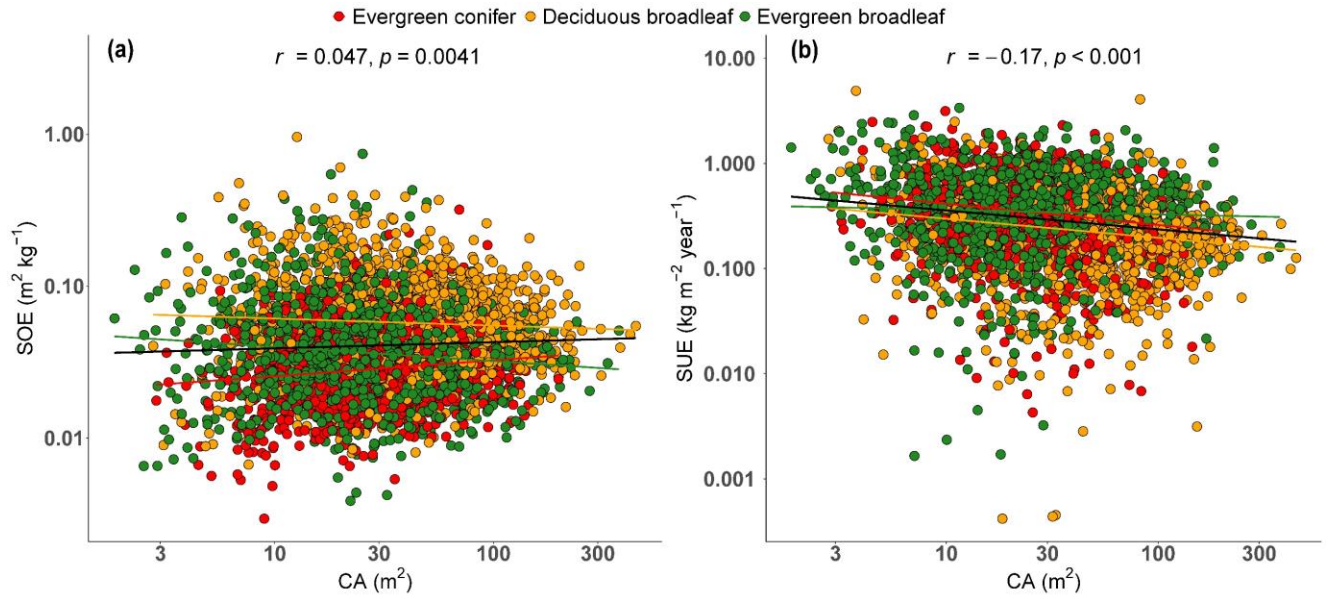


Fig. S4.3 Relationship between **(a)** space occupation efficiency (SOE), **(b)** space use efficiency (SUE), and crown area (CA) across 3747 individuals from 103 canopy species from 23 forest sites. Each point represents individual canopy trees with different colors representing different functional types. Note: we employ the log₁₀ scale in SOE, SUE, and CA. Pearson correlation coefficient (r) is shown for all individuals and a statistically significant relationship is indicated by black solid line ($P < 0.05$).

Chapter 5: General discussion

5.1 Synthesis of all chapters

The overall objective of this thesis was to evaluate how tree crowns quantified by UAV-LiDAR can achieve (1) estimating major forest parameters and (2) understanding canopy tree growth variations and underlying strategies in various natural forests across a wide range of environments in Japan. To achieve this, the thesis was structured into three major chapters (Chapters 2,3,4), each contributing to key research questions in ecology and management of natural forests. These chapters collectively aimed to deepen our understanding of natural forests by integrating novel UAV-LiDAR technology. This synthesis section integrates the findings from those chapters, highlighting their broader implications for forest management and monitoring.

Chapter 2 focused on how UAV-LiDAR-derived tree crown area could be a proxy of total leaf area to analyze canopy tree crown architecture strategies to extend plant growth analysis. I proposed a new framework of growth analysis such that the variation in relative growth rate (approximated as biomass increase per unit final biomass) is partitioned to space occupation efficiency ($SOE = \text{crown area}/\text{biomass}$) and space use efficiency ($SUE = \text{growth rates}/\text{crown area}$). Analysis with this partitioning scheme is

improved with the use of UAV-LiDAR and demonstrated that this approach provides new insights into tree growth dynamics in a warm temperate old-growth forest. Chapter 4 extended and tested this analytical framework to 23 forest monitoring sites across Japan to examine the generality and validity of tree growth strategies among different forest types and climate conditions. The variations in the growth strategies across 103 canopy species differed in relation to their functional types. I found that deciduous species were better at canopy space occupation relative to their biomass (high SOE), while evergreen species excelled at growth efficiency per unit crown area (high SUE). In addition, I found correlations between tree growth strategies and leaf characteristics, demonstrating that species with high SLA (specific leaf area) have high SOE whereas low SLA species have high SUE. This result indicates a general pattern that the allocation of woody mass (i.e., expansion of crown area per unit mass) is associated with leaf mass allocation strategy (i.e. expansion of leaf area per unit mass). I also found a diversity of species' ecological strategies along the environmental gradients of mean annual temperature, total photosynthetically active radiation during the growing season, and snow cover across 23 study sites. Species at lower temperatures and lower amounts of radiation during the season tend to have higher SOE but lower SUE than those at warmer and more radiation-rich environments. In addition, in snowy areas, deciduous species show larger SOE while evergreen species have smaller SOE possibly due to heavy snow load during winter. These analyses shed light on the tree species' adaptation to their environments and provide quantitative evidence on why and how canopy species growth strategies were differentiated in various climatic conditions. These findings are novel as previous studies cannot accurately quantify crown traits for a large number of canopy species across the environmental gradients. This research provides the first quantitative and reliable evaluation of previously unknown canopy tree growth strategies across species and functional types. Overall,

Chapters 2 and 4 made significant contributions to understanding the diversity of tree growth strategies across large environmental gradients.

Chapter 3 determined crown height (H) and crown area (CA) using UAV-LiDAR data and linked these traits with stem diameter at breast height (DBH) and biomass for 4355 individuals in 149 species from 23 temperate natural forests. I demonstrated that the models incorporating CA and H well predict the variations of DBH and biomass across different forests and climatic regions. The integration of functional types or species-specific information into the models further enhanced the accuracy of DBH and biomass. This improvement was particularly evident in the highly diverse Japanese natural forests. Chapter 3 also showed that the UAV-detected canopy trees account for 64–89% of the total standing biomass in 1-ha across 23 monitoring sites, suggesting the effectiveness of the UAV survey in capturing reliable estimations of biomass across various natural forest types. This study is the first quantitative study to assess what proportion of canopy trees and stand-level biomass can be detected by UAV-LiDAR in multiple forest types across various climatic zones. These findings underscore UAV-LiDAR as a scalable and cost-effective tool for estimating forest canopy structure and biomass assessments for a broader range of temperate natural forests in Japan.

While this thesis made significant contributions to improving biomass estimation and understanding tree growth strategies of canopy trees across diverse natural forests, several research areas can be improved or potentially integrated for future investigations. These research areas can offer significant opportunities for enhancing and expanding the findings of this thesis. In particular, these future perspectives contribute to advancing applications of UAV in the field of forest ecology and ecosystem ecology.

5.1.1 Leaf area index (LAI) within the crown area and shape

In Chapters 2 and 4, I calculated space occupation and use efficiency by focusing only on the two-dimensional (2D) projected crown areas of the canopy trees. I did not determine the leaf area index (LAI) within individual crowns and crown shape which can be estimated from UAV-LiDAR point cloud data (Kamoske et al., 2019). Since species significantly differ in canopy architecture, vertical leaf distribution, and crown volume and shape (Kitajima et al. 2005, McNeil et al., 2023), it will be exciting how these traits influence the growth rates and their ecological strategies. Therefore, analyzing 3D point cloud data within the individual crown could further improve understanding of how crown architectures and leaf area distribution impact tree growth strategies, enhancing the ecological applications of UAV-LiDAR.

5.1.2 Comparison of growth rates per unit crown area across forest types

In studies of forest ecosystem productivity, net primary production (NPP) is often reported as the total amount of biomass or carbon fixed by primary producers (e.g., plants) per unit area over a period (Lieth & Whittaker, 1975). NPP is a key indicator of forest productivity and is measured as biomass per unit land surface area ($\text{kg m}^{-2} \text{ year}^{-1}$) (Giardina et al., 2003; Van Tuyl et al., 2005; Huston & Wolverton, 2009). Understanding factors underlying variations of NPP at the level of individual canopy trees can offer more detailed insights into species-specific growth strategies and ecological functioning. By calculating the crown areas of individual canopy trees, their growth can be evaluated (i.e., SUE in this study). Such calculation allows for comparisons of growth rates ($\text{kg m}^{-2} \text{ year}^{-1}$) in a more standardized manner not only among individuals within a single forest system but also across different types of ecosystems, including agricultural systems. This type of growth comparison is important because traditional forest growth metrics, such as DBH growth rates (cm year^{-1}), are often difficult to compare across studies and ecosystems. In contrast, SUE provides a metric of growth efficiency that can

be readily applied across a wide range of ecosystems. Furthermore, SUE can be used to derive other important metrics, such as light use efficiency (LUE; g MJ^{-1}), which is calculated as biomass growth per unit of photosynthetically active radiation (PAR) received (Landsberg & Waring, 1997). In general, tree plantations tend to exhibit higher LUE than the natural forests with over 1 g MJ^{-1} . In the present study, most of the tree species occurring across Japanese natural forests exhibited LUE values between 0.1 and 0.2 g MJ^{-1} , with evergreen conifers showing slightly higher LUE values compared to other species. This suggests that conifers may have a slight advantage in converting light into biomass, likely due to their ability to photosynthesize for a greater portion of the year in temperate environments and also due to their efficient partitioning of light within their longer crowns. Future research could further expand on these findings by investigating how LUE varies across different forest types and geographical locations. Such comparisons could reveal broader patterns in species' light-use strategies, contributing to the understanding of how species respond to differing light regimes. In addition, these analyses could inform forest management practices where maximizing light capture and use efficiency is crucial for enhancing the productivity of the forest stands. When comparing SUE and LUE across studies, the target variables may be different. For example, some studies may target total biomass production, while others focus only on above-ground biomass or stem growth per se. Differing in the measurement variables may yield varying insights into tree growth and ecosystem productivity. In sum, the integration of SUE and LUE into future research will help further elucidate the underlying factors that drive the productivity and functions of forest ecosystems.

5.1.3 Scaling up biomass estimations to larger areas and similar forest types

Chapter 3 developed both general models and species-specific models for 149 canopy species to estimate stem DBH and biomass for Japanese natural forest trees. These modeling approaches account for a diverse set of canopy species and significantly enhance the

precision of DBH and biomass estimates for Japanese natural trees. However, the current analysis was limited to a 1-ha survey plot where the ground census data was available. While my data provides a robust foundation for model development, the broader potential of UAV-LiDAR is to apply the developed models to larger survey areas with minimal data requirements and field activities. As the UAV-LiDAR survey provides a broader spatial coverage of canopy tree H and CA measurements compared to traditional forest surveys, the analysis can be extended to surrounding and larger areas where ground census data may not be available (Fig. 5.1). This approach could enable a broader analysis of forest structure and biomass estimations of canopy trees in natural forest stands. Future research may evaluate the general applicability of these models in larger areas and similar forests in different geographic regions.

5.1.4 Improved detection of understory trees by UAV-LiDAR

In this study, the analysis was currently limited to canopy trees as the UAV-LiDAR survey missed the under-story individuals (11 ~ 36% of the total biomass with the detection rates varying among forests). These undetected trees can be particularly important when assessing forest dynamics, as smaller individuals play crucial roles in forest regeneration, mortality, and long-term biomass accumulation. For instance, Piponiot et al. (2022) highlight the importance of including smaller trees in assessments of above-ground wood productivity and mortality. It is suggested to include these smaller individuals for a complete understanding of forest dynamics. To overcome these limitations, future research could explore the integration of UAV-LiDAR data with the terrestrial laser scanning (TLS) approach (Fig. 5.2). TLS is shown to be effective in scanning the internal structure of forests including the smaller individuals under the canopy trees (Brede et. al., 2022; Terryn et al., 2022). Thus, the combined use of those approaches could provide a more comprehensive quantification of forest structure and

dynamics. Testing these methods for broader applications in diverse natural forests would significantly enhance the full potential of UAV-LiDAR in estimating forest structure and dynamics.

5.2 Conclusions

This thesis presents a comprehensive and detailed evaluation of UAV-LiDAR technology in analyzing natural forest ecosystems, with a particular focus on canopy-level analyses. The findings across chapters underscore UAV-LiDAR as a powerful and effective tool for estimating essential forest parameters, understanding canopy tree growth variations, and revealing species-specific growth strategies across diverse environmental gradients. I developed a novel crown-based growth analysis framework, as well as general models to estimate forest biomass, which can incorporate functional- and species-specific factors for future ecological studies. The use of UAV-LiDAR opens up new opportunities for advancing forest ecosystem management, offering scalable approaches for assessing canopy structural diversity, tracking biomass, and monitoring forests across larger scales.

Figures

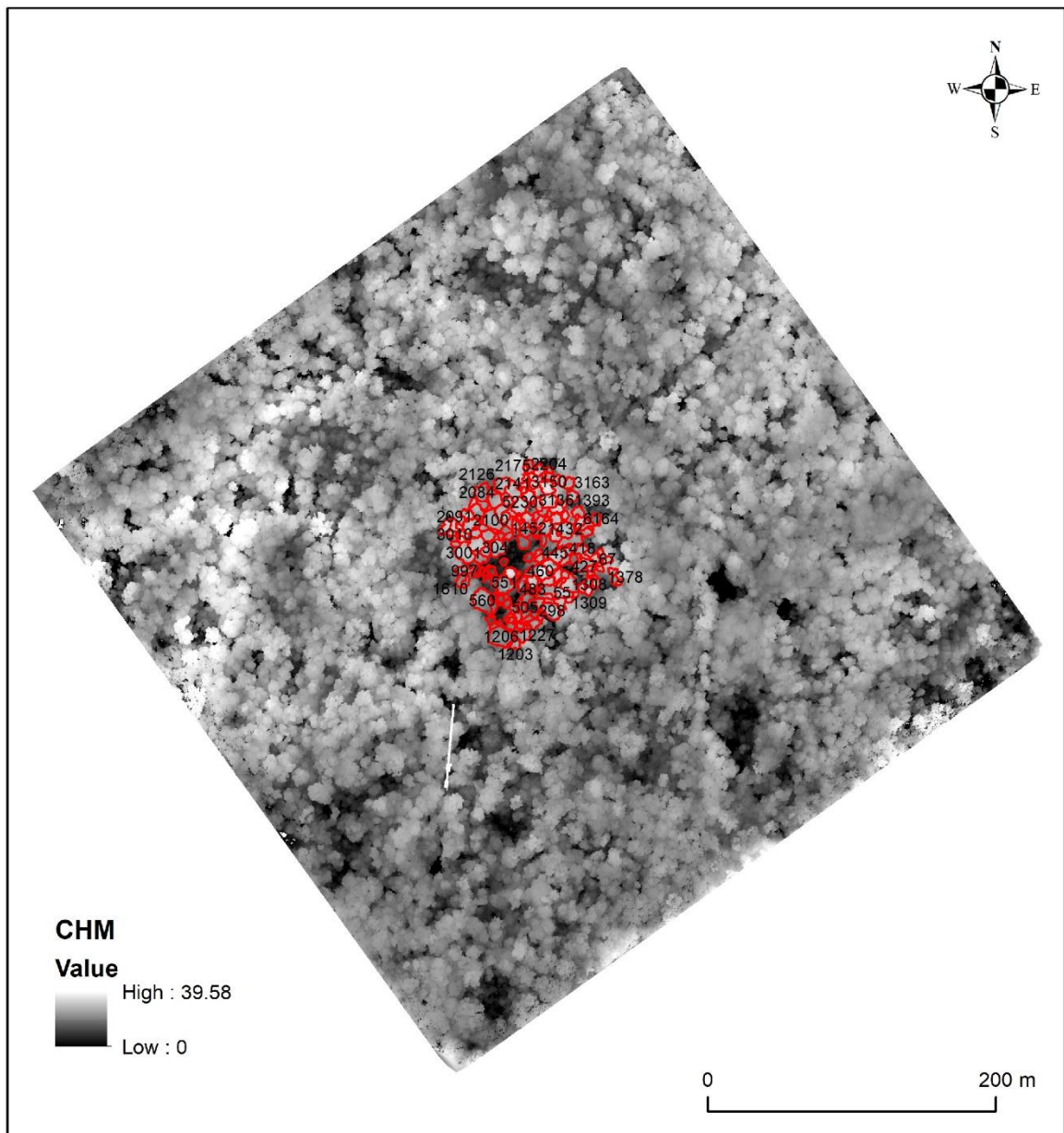


Fig. 5.1 Crowding mapping in 1-hectare sample plot where tree census data is available. Each tree crown is shown with thin red lines tracing over the canopy height model (CHM) which shows the height gradient in a gray scale.



Fig. 5.2 A vertical profile of BLK2GO mobile Terrestrial Laser Scanner (TLS) data which can effectively scan under-canopy trees. An example from the Tsushima evergreen broadleaf forest in southern Japan.

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