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SPECIAL FEATURE

**Plant responses to heterogeneous environments**

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# The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests

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**Abstract** Mixed forests comprising multiple tree species with contrasting crown architectures, leaf phenologies, and photosynthetic activity, tend to have high ecosystem productivity. We propose that in such forests, differentiation among coexisting species in their spatial and temporal strategies for light interception, results in complementary use of light. Spatial differentiation among coexisting tree species occurs as a result of adaptation of crown architecture and shoot/leaf morphology to the spatially variable light conditions of the canopy, sub-canopy, and understory. Temporal differentiation occurs as a result of variation in leaf phenology and photosynthetic activity. The arrangement of leaves in both space and time is an important aspect of plant strategies for light interception and determines photosynthetic carbon gain of the plant canopy. For example, at the shoot level, morphological and phenological differentiation between long and short shoots reflects their respective shoot functions, indicating that spatial and temporal strategies for light interception are linked. Complementary use of light is a consequence of the spatiotemporal differentiation in light interception among coexisting species. Because coexisting species may show differentiation in strategies for resource acquisition (functional diversification) or convergence with respect to some limiting resource (functional convergence), the relative importance of various crown functions and their contribution to growth and survival of individuals need to be evaluated quantitatively and compared among coexisting species.

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## Introduction

In temperate forest ecosystems, leaf area index (LAI) and stand productivity increase with increasing canopy height and proportion of evergreen tree species (Jarvis and Leverenz 1983; Perry 1994). Although both aspects are correlated with climatic conditions that allow for greater plant growth, canopy architecture and leaf phenology represent spatial and temporal strategies for light interception, respectively, and therefore influence ecosystem productivity. Ishii et al. (2004) proposed that spatial and temporal differentiation in crown architecture, leaf phenology, and photosynthetic activity among coexisting species would result in complementary use of light and increased productivity in temperate forest ecosystems. For example, ecosystem productivity is generally higher for mixed forests comprising both conifer and broadleaved trees than for forests consisting of only broadleaved trees (Aiba et al. 2007; Cannell et al. 1992; Midgley et al. 2002). Mixed forests may be more productive than single-species systems when the species mixture "uses the environment more fully" (enhanced resources use), there is facilitative resource use among species, or the mixture is "more stable" (Perry 1994). Complementary use of light by conifers and broadleaved trees, which is a consequence of their contrasting crown architecture and leaf phenology, may be regarded as enhanced resource use.

Mixed conifer-broadleaf forests occur across a wide range of climatic and elevational gradients throughout Japan. On Yakushima Island in southern Japan, where evergreen conifers (mainly *Cryptomeria japonica* D. Don and *Tsuga sieboldii* Carriere) occur together with evergreen broadleaved trees, the stand basal area of mixed forests is markedly higher than that of forests lacking conifers, suggesting that stand productivity may increase in mixed forests (Aiba et al. 2007). Mixed forests also occur in northern Japan (Hiura and Fujiwara 1999; Ishibashi 2000; Takahashi et al. 2003) and in the subalpine zones of central Japan (Franklin et al. 1979; Mori and Takeda 2004a, 2004b), where evergreen conifers (*Abies*, *Tsuga* and *Picea* species) occur together with deciduous broadleaved trees.

Although the term "mixed forest" usually refers to natural forests and plantations comprising both conifers and broadleaved trees, evergreen and deciduous broadleaved trees often occur together in the warm-temperate zone of Japan and this may also be considered one type of mixed forest consisting of broadleaved trees with different leaf habits. The late-successional forests in the warm-temperate zone of Japan are dominated by evergreen broadleaved trees of *Quercus*, *Castanopsis*, *Machilus*, etc. These forests are known as lucidophyllous forests (Hattori and Nakanishi 1985). Primary lucidophyllous forests are rare and most have been converted to secondary forests dominated by deciduous broadleaved trees. For many years, heavy human use of the forests for extraction of firewood and leaf litter had kept the forests at early successional stages, known as *satoyama* (Takeuchi et al. 2003). After fossil fuels and chemical fertilizers came into use, the secondary forests were abandoned. In recent years, they have become mixed forests comprising both early successional deciduous trees and late-successional evergreen trees. In abandoned secondary deciduous forests in central Japan, the abundance and basal area of late-successional evergreen trees have increased in recent years, resulting in increased stand biomass (Goto et al. 2003; Iwasaki and Ishii 2005).

The stable coexistence of multiple tree species is an important factor contributing to increased productivity of mixed forests (Cannell et al. 1992; Perry 1994). Tree species coexistence in mixed forests has been explained through differences among species' regeneration patterns, i.e., patterns of seed dispersal and seedling establishment in response to various factors such as disturbance, topography, and micro sites (Ishikawa and Ito 1989; Lusk and Smith 1998; Mori and Takeda 2004a, 2004b; Tang and Ohsawa 2002; Youngblood 1995). Such effects can persist for many years influencing the differential non-equilibrium demography among tree species in late-successional forests, which appear to be fairly stable. For example, in a late-successional mixed subalpine forest in Gifu Prefecture, central Japan, the spatial distribution of canopy trees of deciduous *Betula ermanii* Cham., which established soon after stand-initiating disturbance several decades ago, determined the distribution of seasonal gaps and influenced the survival of shade tolerant conifer saplings in the understory (Mori et al. 2007).

In mixed forests, tree species with different crown architectures and leaf phenologies coexist, forming a forest canopy that is diverse, both spatially and temporally. In this paper, we propose that spatiotemporal differentiation among coexisting species in their respective strategies for light interception results in complementary use of light. Variation among species in crown architecture and shoot/leaf morphology represents spatial differentiation, while variation in leaf phenology and photosynthetic activity represents temporal differentiation. We discuss how such variation can lead to complementary use of light among coexisting species and contribute to increasing stand productivity.

## Spatial differentiation: crown architecture and shoot/leaf morphology

In vertically well-developed forests, spatial differentiation among coexisting tree species occurs as a result of adaptations of crown architecture, shoot/leaf morphology, and photosynthetic characteristics, to the spatially variable light conditions of the canopy, sub-canopy, and understory. The vertical light gradient in a plant canopy has been modeled as an exponential loss function (Monsi and Saeki 2005):

$$I = I_0 \mathrm{e}^{-KF} \qquad (1)$$

where $I$ is the light intensity at a given canopy layer, $I_0$ is the light intensity above the canopy, $K$ is the extinction coefficient, and $F$ is the LAI above a given canopy layer. Because light intensity decreases exponentially, there is a steep gradient of light availability from upper to lower canopy. In a mature deciduous broadleaved forest in northern Japan, eight dominant, upper-canopy species contributed 80.3% of the total leaf area and intercepted 90.5% of incident photosynthetically active photon flux density (PPFD; 400–700 nm), indicating that canopy species have an advantage over understory species in receiving a large fraction of incident PPFD (Ishii et al. 2004). The understory species, on the other hand, show adaptations in crown architecture and shoot/leaf morphology such as high leaf area ratio (LAR: leaf area/plant biomass) and low leaf mass per area, which increase light interception per unit biomass invested in leaf area, an important characteristic for plant survival in the light-limited understory (Seino 2009; Valladares and Niinemets 2008).

In mixed forests, the light environment of the understory is highly spatially variable: between evergreen and deciduous canopy trees, as well as between canopy gaps and the understory. Understory species respond to increased light availability in canopy gaps through morphological and physiological adjustments in growth rate, branching pattern, leaf number, photosynthesis, etc. (e.g., Canham 1988; Niinemets 1998; Oguchi et al. 2005; Seino 2009; Sipe and Bazzaz 1994; Sterck 1999; VanPelt and Franklin 1999; Veres and Pickett 1982). Because of their conical crown architecture, natural conifer forest canopies have several vertical gaps (Ishii et al. 2004; Parker 1997) and this allows more light to penetrate into the lower canopy (Parker et al. 2004). In mixed forests in New Guinea, tall *Araucaria hunsteinii* K. Schum. trees have emergent crowns that cast little shade allowing other broadleaved tree species to coexist below the diffuse canopy (Midgley et al. 2002). In forests comprising emergent conifers, vertical development of the canopy may allow complementary use of light by coexisting species that differentiate among the various canopy layers (Enright et al. 1999; Ishii and Ford 2002).

The value of the extinction coefficient (*K*) in Eq. (1) varies widely among species. Conifers tend to have higher LAI and deeper canopies than broadleaved trees, suggesting that light penetrates deeper into conifer canopies (Jarvis and Leverenz 1983; Norman and Jarvis 1975). This may be because conifer leaves are small and tend to filter light through to the lower canopy (Leverenz and Hinckley 1990; Smolander and Stenberg 2001; Therezien et al. 2007), in contrast to the flat leaves of broadleaved trees, which cast more shade. In addition, clumping of small leaves on shoots creates a "penumbra effect" that allows light to penetrate deep into conifer canopies (Chen et al. 1997; Norman and Jarvis 1975; Palmroth et al. 1999; Stenberg 1998). Within the same geographical region, the canopy of closed, evergreen conifer forests intercept a higher proportion of the incident light than broadleaved canopies (Aubin et al. 2000; Messier et al. 1998). Furthermore, conifers and broadleaved trees utilize different regions of the spectral space (Smolander and Stenberg 2003) and this may contribute to complementary use of light between conifers and broadleaved trees in mixed forests.

These observations suggest that in mixed forests, differences in crown architecture and shoot/leaf morphology between conifers and broadleaved trees may result in complementary use of light and increased stand productivity. For example, in the mixed forests of Yakushima Island, *C. japonica* dominates the upper canopy and seem to set the upper limit of height growth for the broadleaved trees (Takashima et al. 2003). However, growth of the broadleaved trees does not seem to be suppressed by *C. japonica* and their stable coexistence (Aiba et al. 2007; Suzuki and Tsukahara 1987) suggests that the broadleaved trees are able to utilize light that has filtered through the *C. japonica* canopy. Theoretical exploration has shown that trees having conical crowns (conifers) can coexist with trees having spherical crowns (broadleaved trees) under variable conditions (Fig. 1, Yokozawa et al. 1996). This prediction matches the observed dynamics of conifers and broadleaved trees in many mixed forests (Kubota and Hara 1995; Takashima et al. 2003). Thus, complementary use of light, which is a consequence of stable coexistence of conifers and broadleaved trees, may explain why stand productivity is higher for mixed forests than for forests comprising broadleaved trees only.

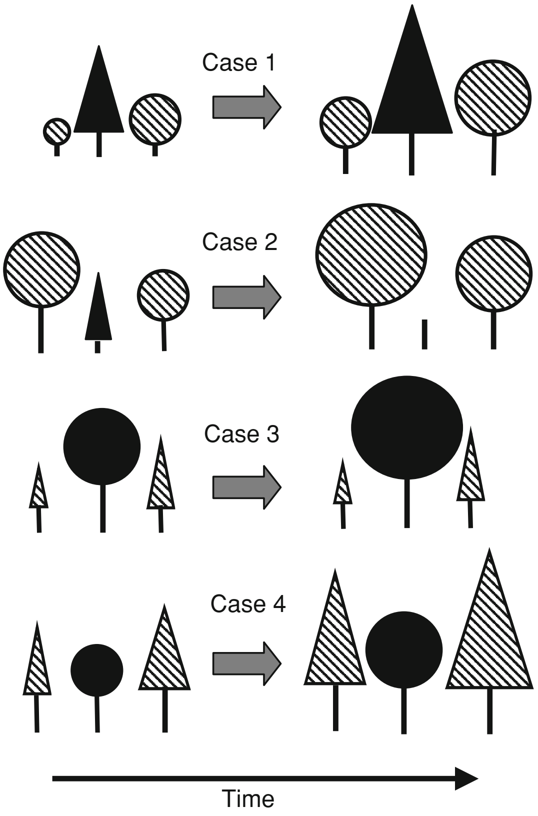

**Fig. 1** Theoretical models of coexistence between conifers (*triangular crowns*) and broadleaved trees (*spherical crowns*). *Solid* or *hatched crowns* indicate fixed or variable physiological parameters, respectively, representing low or high physiological plasticity. In case 1, broadleaved trees with high physiological plasticity that established after the conifer tree with low physiological plasticity can reach the canopy. In case 2, a conifer tree with low physiological plasticity that established after the broadleaved trees with high physiological plasticity cannot survive. In case 3, conifer trees with high physiological plasticity that established after a broadleaved tree with low physiological plasticity can persist. In case 4, a broadleaved tree with low physiological plasticity that established after the conifer trees with high physiological plasticity can reach the canopy (after Yokozawa et al. 1996)

## Temporal differentiation: leaf phenology and photosynthetic activity

In forests comprising multiple species, temporal differentiation occurs as a result of variation among species in leaf phenology and seasonal/diurnal pattern of photosynthetic activity (Ishii et al. 2004). Leaf phenology is defined as the arrangement of leaves in time and consists of three components: leaf habit, leaf emergence, and leaf longevity (Kikuzawa 1995; Valladares 2003). Variation in the leaf habit of the canopy trees may influence the growth and survival of understory trees in mixed forests. Mori and Takeda (2004a, 2004b) found that saplings of shade-tolerant conifers were distributed on the north side of canopy trees of *B. ermanii*, where irradiance levels were higher compared to areas beneath the crown of evergreen conifers. For evergreen trees in mixed forests, photosynthesis during winter when the deciduous canopy trees shed their leaves may contribute a significant amount of their annual carbon gain (Miyazawa and Kikuzawa 2005). Many understory shrubs depend on light made available by "seasonal gaps" that occur as a result of temporal variation in leaf emergence of the canopy trees. Understory species are known to adjust their phenology in response to the seasonal variation in the light environment (e.g., Kikuzawa 1984; Maeno and Hiura 2000; Nitta and Ohsawa 1997; Uemura 1994). Phenology may also change with ontogeny such that small, juvenile trees expand their leaves early to intercept light in early spring before the leaves of canopy trees emerge (Augspurger 2008; Augspurger and Bartlett 2003; Seiwa 1999). Differentiation in phenology among coexisting canopy and understory species may be interpreted as complementary use of light across time.

Seasonal variation in photosynthetic activity is also observed among canopy trees of different successional status. In a mature broadleaf forest in northern Japan, maximum photosynthetic rates of *Betula maximowicziana* Regel, an early successional species, and *Magnolia hypoleuca* Sieb. et Zucc., a gap-phase species were high in spring and declined in summer (Ishii et al. 2004). On the other hand, the maximum photosynthetic rate of *Acer mono Maxim*. and *Carpinus cordata* Blume, both late-successional species, were not as high as that of the early successional species in spring, but remained constant during most of the growing season. Photosynthetic activity also varies with leaf age (e.g., Reich et al. 2009; Warren 2006), such that leaves of evergreen understory trees may mature later in the season so that their photosynthetic capacity is high when leaves of the deciduous canopy trees begin to shed in autumn.

In addition to seasonal variation, diurnal variation in photosynthetic activity may result in complementary use of light among coexisting tree species during the course of the day. In a mature broad-leaved forest in northern Japan, the diurnal pattern of photosynthesis varies among canopy tree species, such that maximum photosynthetic rates were observed in early morning for *A. mono*, a late-successional species, while that of *B. maximowicziana* were observed in mid-morning, resulting in a 3-h difference in the time of maximum photosynthetic activity between the two species (Ishii et al. 2004). Although diurnal patterns of photosynthesis may be the result of limitation, such as water stress leading to mid-day decline in photosynthetic rate, variation among species in their tolerance to stress may be interpreted as differential investment in stress tolerance versus avoidance, resulting in variation in photosynthetic activity over time. In other words, stress tolerance and stress avoidance may be interpreted as strategies for sustaining or abandoning photosynthesis under stressful conditions. Investment in stress-tolerant characteristics may allow some species to be productive while the stress avoiders are not. For example, in tropical dry forests, photosynthetic activity and growth of lianas is greater than that of coexisting tree species during the dry season (Cai et al. 2009). The difference in leaf phenology contributes to the coexistence of evergreen and deciduous *Quercus* species in dry Mediterranean forest (Montserrat-Marti et al. 2009). Seasonal variation in photosynthetic activity among species resulting from stress tolerance or avoidance may be interpreted as complementary use of light, because if the stress-tolerant species were absent, stand productivity would decrease during the dry season. Even if the stress avoiders were to fill this niche, stand productivity would decrease because their photosynthetic activity would be lower than that of the stress tolerators. Similar interpretation may be possible for differences among species in their diurnal pattern of photosynthetic activity. Because environmental conditions are heterogeneous in time and space, and there is no optimal morphology that dominates all plant functions (Kennedy 2009), a single species cannot achieve full performance across the entire time/space spectrum of available resources. Thus, complementary use of light among diverse species, where one species can perform better than the other and vise versa under different conditions, leads to increased productivity.

## Linking spatial and temporal strategies at the shoot level

Crown architecture is the cumulative result of shoot production and elongation, and reflects the spatial strategy of the plant for light interception and maximizing carbon gain (Kawamura 2009; Valladares and Niinemets 2007). Many woody species show differentiation between long and short shoots (Caesar and MacDonald 1984; Jones and Harper 1987; Miyazawa and Kikuzawa 2004; Wilson 1991; Yagi 2004). Long shoots function to expand the crown and explore new space through high investment in elongation growth. In contrast, short shoots function to exploit acquired space with minimum investment in support tissue. Even for those species that do not show clear differentiation between long and short shoots, variability in current-year shoot lengths reflect a gradient in shoot function between crown expansion versus crown maintenance (Takenaka 1997; Yagi 2000; Yagi and Kikuzawa 1999).

Shoot phenology, on the other hand, reflects the temporal strategy for light interception (Harada and Takada 1988; Kikuzawa 1995). Woody species vary in the seasonal pattern of bud break, shoot elongation, leaf emergence, and shedding. In some species, shoot elongation occurs within a short period after bud break and leaves emerge and shed simultaneously. In other species, shoot elongation occurs over an extended period during the growing season and leaves emerge and shed successively. In a temperate deciduous forest in northern Japan, understory shrubs adapted to limited, but stable light environment of the understory exhibit simultaneous leaf emergence with long leaf longevity, whereas species adapted to more open, unpredictable habitats present successive leaf emergence with high leaf turnover

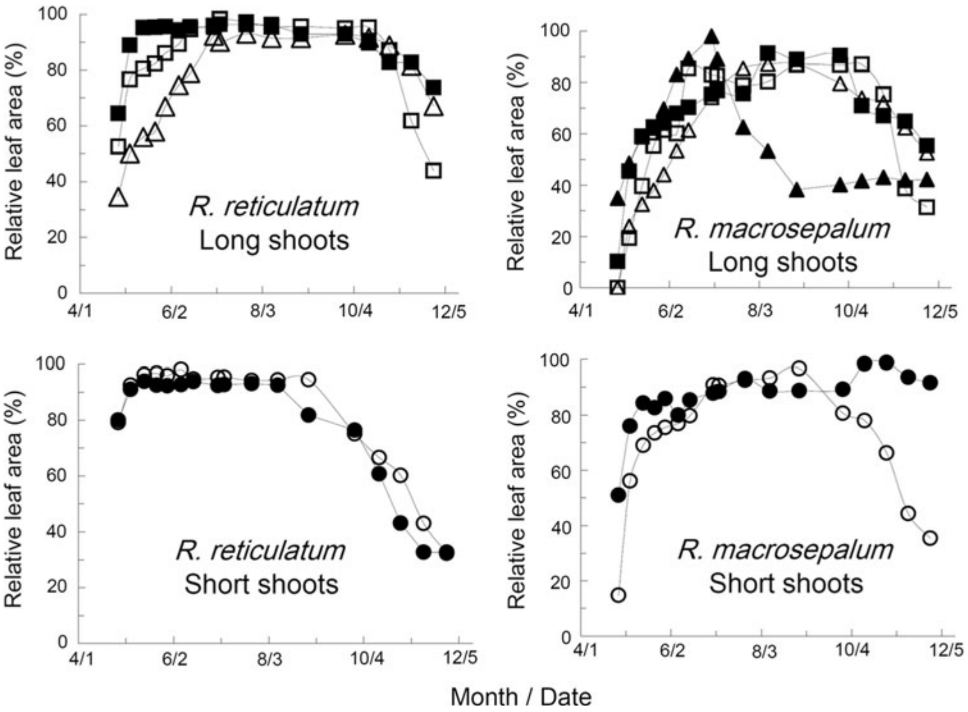

**Fig. 2** Seasonal changes in relative leaf area (leaf area of emerged leaves relative to the total leaf area produced during the growing season) of current-year shoots of *R. reticulatum* and *R. macrosepalum* growing in the gap and understory of a secondary forest in Kyoto Prefecture, central Japan. Mean patterns are shown for each shoot type ($n$ = 5–7 shoots). *Symbol shapes* indicate shoot type: monopodial long shoot (*circles*); sympodial long shoot (*triangles*), and short shoots (*squares*). *Open* and *filled symbols* indicate gap and understory, respectively (after Asano 2007)

rates (Kikuzawa 1984). Species adapted to gaps show intermediate patterns: simultaneous followed by successive leaf emergence.

The arrangement of leaves in both space (crown architecture) and time (phenology) is an important aspect of plant strategies for light interception (Kawamura 2009; Kikuzawa 1995) and determines photosynthetic carbon gain of the plant canopy (Kikuzawa et al. 2009). Shoot morphology and phenology, therefore, are inevitably linked. Kikuzawa (1995) proposed that shoots with successive leaf emergence should be vertically oriented, while those with simultaneous leaf emergence should be horizontally oriented to avoid mutual shading among leaves. Although this theory has been criticized as being an oversimplification (Valladares 2003), it represents a working hypothesis for exploring the link between spatial and temporal strategies for light interception.

In many woody species, morphology and phenology are correlated such that phenology varies among different types of current-year shoots within individuals. For example, short shoots of *Betula grossa* Sieb. et Zucc. produce early leaves simultaneously after bud break and maintain them for 65–80 days, whereas long shoots produce early leaves followed by successive late leaves, which have shorter leaf longevity (Miyazawa and Kikuzawa 2004). In the understory of a secondary forest in Kyoto Prefecture, central Japan, the morphological and phenological response to the light environment differed between long and short shoots of two coexisting *Rhododendron* species (Asano 2007). *Rhododendron reticulatum* D. Don exhibited less plasticity in shoot morphology compared with *Rhododendron macrosepalum* Maxim. However, *R. reticulatum* exhibited greater plasticity in shoot phenology such that leaf emergence of short shoots was simultaneous and that of long shoots was successive (Fig. 2). No such distinction was observed for *R. macrosepalum*. The two *Rhododendron* species coexist in the understory of secondary deciduous forests in central Japan. *R. reticulatum* is deciduous, while *R. macrosepalum* is semi-deciduous (retains leaves in winter and sheds them in spring). In addition to differences in leaf habit, variation in current-year shoot morphology and phenology may result in differentiation between the two species in their respective spatiotemporal strategies for light interception. Thus, stable coexistence and complementary use of light between the two dominant understory *Rhododendron* species may contribute to increased understory productivity.

## Conclusions

Studies of crown architecture taking into account the link between spatial and temporal strategies for light interception and carbon gain of individual crowns have provided insights on how different strategies contribute to species coexistence (Niinemets 2009). However, descriptive research comparing differences in crown architecture and leaf phenology is not sufficient because apparently different crown architectures can realize similar levels of physiological function (Valldares et al. 2002). For example, in the old-growth coniferous forests of the Pacific Northwest coast of USA, small trees of *Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes and *Tsuga heterophylla* (Raf.) Sarg. often occur adjacent to each other in the understory. The two species have a contrasting branching pattern, but showed convergence in measures of photosynthetic light interception efficiency, including leaf display and shoot-silhouette-area-based photosynthetic rate (Ishii et al. 2009). Although mass-based photosynthetic rates were lower for *A. amabilis*, leaf longevity was nearly twice that of *T. heterophylla*. In addition, similar relative growth rates at the branch and tree levels suggested that there is no difference between *A. amabilis* and *T. heterophylla* in time-integrated net carbon gain. This suggests that despite having different branching patterns and crown architectures, the convergence of leaf display and photosynthetic characteristics for maximizing light-interception efficiency may contribute to the persistence of both species in the understory of old growth forests.

Because coexisting species may show differentiation in strategies for resource acquisition (functional diversification) or convergence with respect to some limiting resource (functional convergence, Meinzer 2003; Valladares 2003), the relative importance of various crown functions and their contribution to growth and survival of individual trees need to be evaluated quantitatively and compared among coexisting species. Accumulation of studies evaluating the functional significance of crown architecture should lead to a unified theory of how the spatial and temporal variation in light interception among coexisting species contributes to ecosystem productivity. Although light is the primary resource for photosynthesis and growth, crown architecture reflects other important functions related to plant survival, growth, and reproduction, including hydraulic architecture, mechanical stability, efficient flower display and, in arid environments, minimizing surface evaporation (Farnsworth and Niklas 1995; Kennedy 2009). In addition, species may differ in their unit of response to environmental change (Kawamura 2009). For example, light-interception efficiency may be modified at various spatial and temporal scales from chlorophyll content of leaves to biomass allocation to leaves within whole plants (Niinemets 2009). Therefore, we must develop methods to evaluate and compare quantitatively the multi-functional aspect of crown architecture and its plasticity, and how they contribute to tree growth and survival, and ultimately to stand productivity.

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