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The need for a canopy perspective to understand the importance of phenotypic plasticity for promoting species coexistence and light-use complementarity in forest ecosystems

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Abstract Because of their overwhelming size over other organisms, trees define the structural and energetic properties of forest ecosystems. From grasslands to forests, leaf area index, which determines the amount of light energy intercepted for photosynthesis, increases with increasing canopy height across the various terrestrial ecosystems of the world. In vertically well-developed forests, niche differentiation along the vertical gradient of light availability may promote species coexistence. In addition, spatial and temporal differentiation of photosynthetic traits among the coexisting tree species (functional diversity) may promote complementary use of light energy, resulting in higher biomass and productivity in multi-species forests. Trees have evolved retaining high phenotypic plasticity because the spatial/temporal distribution of resources in forest ecosystems is highly heterogeneous and trees modify their own environment as they increase nearly 1,000 times in size through ontogeny. High phenotypic plasticity may enable coexistence of tree species through divergence in resource-rich environments, as well as through convergence in resource-limited environments. We propose that the breadth of individual-level phenotypic plasticity, expressed at the metamer level (leaves and shoots), is

an important factor that promotes species coexistence and resource-use complementarity in forest ecosystems. A cross-biome comparison of the link between plasticity of photosynthesis-related traits and stand productivity will provide a functional explanation for the relationship between species assemblages and productivity of forest ecosystems.

Keywords Complementarity theory · Diversity–productivity theory · Forest architecture theory · Niche differentiation · Species coexistence

Introduction

Trees are the largest organisms on Earth, and forests hold the greatest biomass among terrestrial ecosystems of the world. Trees are the primary producers that generate, through photosynthesis, the energy that flows through the food and detritus chains (Scheu 2005). Because of their overwhelming size over other organisms, trees are also the “engineers” (Jones et al. 1994) that build the structure of forest ecosystems and define its environmental and chemical properties, as well as the “habitat template” on which other organisms establish (Southwood and Kennedy 1983; Takeda and Abe 2001).

Trees are remarkable because they start out as tiny seedlings and grow to nearly 1,000 times in size during ontogeny. In a mature forest, individuals of various sizes coexist. Some species can acclimate to a wide range of resource availabilities and exist in multiple generations comprising understory seedlings to mature canopy trees. Within the same geographic region, natural forests that are well-developed vertically tend to hold greater diversity of tree species and maintain higher primary productivity than low statured forests (Franklin et al. 1989; Ishii et al. 2004). In this paper, we will review theories related to the structural development of forest ecosystems and how it may promote species coexistence. We will explore how spatial and temporal differentiation

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in resource use, especially light, among coexisting tree species may provide a functional explanation for why stand productivity increases with increasing species diversity. Finally, we discuss the importance of considering trait plasticity within individuals when assessing the functional diversity of forest ecosystems.

Vertical development, ecosystem productivity, and species diversity

From grasslands to forests, annual net primary production increases with increasing leaf area index (LAI) across the various terrestrial ecosystems of the world (LAI, leaf area per unit ground area, Asner et al. 2003). This is because the amount of light energy intercepted for photosynthesis by a plant canopy increases with increasing LAI, i.e., the greater the leaf area that is packed into a unit of ground area, the greater the ecosystem productivity. In forest ecosystems, LAI tends to increase with increasing canopy height, because biomass density (kg m^{-3}) is relatively constant across various forest types (Kira and Shidei 1967) and thus more leaf area can be stacked vertically in a tall forest. Forests with the largest LAI and greatest biomass in the world are found in the cool-temperate region of the Pacific Northwest coast of North America (Franklin et al. 2002; Fujimori et al. 1976; Sillett and Van Pelt 2007). In these forests, the canopy reaches 70–100 m in height and comprises the world's tallest trees. The dominant, evergreen conifer species include some of the tallest tree species in the world: *Sequoia sempervirens* (D. Don.) Endl., *Pseudotsuga menziesii* (Mirb.) Franco. var. *menziesii*, and *Picea sitchensis* (Bong.) Carr. These trees are not only tall, but extremely long-lived and stand age may reach 800–1,000 years in some areas (Franklin and Dyrness 1973). As a result, great amounts of carbon are stored both above and below ground (Harmon et al. 2004; Winner et al. 2004).

In grassland ecosystems, it has been shown experimentally that productivity increases with increasing species diversity (Hector et al. 1999; Tilman et al. 2001). Although stand productivity tends to be higher for more species-rich forest communities (e.g., Harmon et al. 1990; Ishii et al. 2004; Vila et al. 2003, but see Firn et al. 2007), it is difficult to obtain direct evidence supporting the diversity-productivity theory that pertains to forest ecosystems because, in natural forests, the various factors determining community assembly and ecosystem productivity are often confounded (Vila et al. 2005) and field experiments take several years to execute (Hector et al. 2011; Pretzsch 2005; Whittaker et al. 2001). The best test of the diversity-productivity relationship in forest ecosystems that we are aware of is that of Hiura (2001), who showed that species richness, LAI and total carbon are correlated positively with each other across 38 forest plots having different disturbance histories (Table 3 in Hiura 2001), all of which established on relatively flat topography after a volcanic eruption rendering uniform initial conditions.

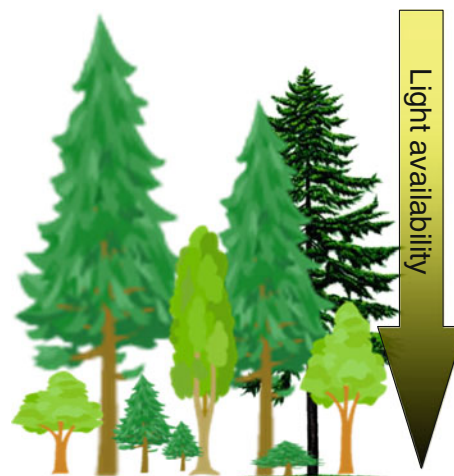


Fig. 1 Divergence of tree species along the vertical gradient of light availability in a vertically well-developed forest canopy represents niche differentiation along a gradient of resource availability, which may enhance both species diversity and stand productivity

A key factor linking diversity and productivity of forest ecosystems is the vertical development of the forest canopy (Ishii et al. 2004). Kohyama (1993) proposed the forest architecture theory of species coexistence, where differentiation of tree species into vertical strata promotes their coexistence through the trade-off between height growth and reproductive output (Kohyama and Takada 2009). Although in reality, species are not necessarily segregated into distinct strata (Parker and Brown 2000), divergence of tree species along the vertical gradient of light availability in a vertically well-developed forest canopy represents niche differentiation along a gradient of resource availability (Fig. 1). In vertically well-developed forests, niche differentiation may enhance both species diversity and stand productivity (Gravel et al. 2010). In the next section, we discuss the underlying mechanism that could explain how this may be possible.

Complementary resource use and functional diversity

A proposed mechanism for increased productivity with increasing species diversity is that it leads to complementary resource use (Hector 1998; Hooper 1998; Naeem et al. 1994). Complementarity is defined as the increase in resource-use efficiency of a mixed species community compared with that of a monoculture as a result of reduced niche overlap and competitive relaxation (Yachi and Loreau 2007). Because plants are the primary producers that define the structural and energetic properties of terrestrial ecosystems, the diversity of traits concerned with light capture and primary production are important determinants of ecosystem productivity. In grassland ecosystems, the presence of contrasting traits among species, such as foliar architecture and shade tolerance, promotes light-use complementarity and contributes to

increasing primary productivity (Vojtech et al. 2008; Zhang et al. 2012). Similarly, for woody species, trait divergence reduces niche overlap and relaxes competition, allowing even closely related species to coexist (Beltran et al. 2012). These observations suggest that not only the number of species per se, but their functional diversity (i.e., phenotypic variation) is an important factor underlying the diversity-productivity theory (Loreau 2010).

Photosynthesis is an important physiological function that determines the productivity and shade tolerance of a species (Anten 2005; Poorter and Bongers 2006; Valladares and Niinemets 2008; Werger et al. 2002). Thus we hypothesize that, if divergence of photosynthesis-related traits among species and their differentiation along the vertical gradient of light availability results in complementary resources use, it would lead to increased ecosystem productivity with increasing species diversity. There are several empirical examples that suggest our hypothesis may apply to forest ecosystems. When plantation forests of the same planting density are compared, productivity tends to be at least as high, or higher for mixed than monoculture stands (Garber and Maguire 2004; Kely et al. 1992; Piotta 2008). In some mixtures, the increase in productivity was attributed to light-use complementarity between species (Amoroso and Turnblom 2006; Forrester et al. 2005). In natural, mixed forests of Japan and New Zealand, where conifers and broadleaved trees coexist, the basal area of conifers is additive, meaning that stand biomass is higher in mixed forests than in forests comprising only broadleaved trees (Aiba et al. 2007; Midgley et al. 2002). In the mixed conifer-broadleaved forest on Yakushima Island in southern Japan, coexistence of conifers and broadleaved trees is realized through stratification along the vertical gradient of light availability (Inoue and Yoshida 2001; Ishii et al. 2010). Increased productivity and additive basal area of mixed forests may be the result of species differences in above-ground traits (height growth pattern, crown form, leaf morphology, shade tolerance, etc.) that determine photosynthetic gain, as well as below-ground traits (root growth, morphology, etc.) that determine uptake of water and nutrients. Functional differentiation among species may lead to competitive relaxation in mixed stands, whereas competition may be more intense in monocultures and less species-rich forests (Ewel and Mazzarino 2008; Jones et al. 2005; Kely 2006). A critical physiological function that underlies all of the above characteristics is photosynthetic production and allocation of photosynthate within individual trees (Poorter et al. 2006; Selaya et al. 2007).

In addition to spatial differentiation along the vertical gradient of light availability, temporal differentiation in light-use among coexisting species may also be an important factor that leads to complementary resource use in forest ecosystems (Ishii and Asano 2010). In vertically well-developed grasslands, seasonal variation in light interception promotes species coexistence (Anten and Hirose 1999). Similarly, in many forests, coexisting

tree species exhibit different leaf habits and phenologies, such as variation in the timing of new leaf production and leaf longevity, which reflects temporal differentiation across seasons. Temporal differentiation in light-use among species also occurs at longer time scales, such as during succession in a tropical secondary forest (Selaya et al. 2008). In many temperate forests of Japan, evergreen and deciduous trees coexist, and the difference in leaf habit and timing of leaf flushing may represent temporal differentiation among species (see, e.g., Maeno and Hiura 2000; Miyazawa and Kikuzawa 2005). At a shorter time-scale, the diurnal pattern of photosynthesis tends to vary among coexisting species. In a cool-temperate forest in Hokkaido, northern Japan, the diurnal patterns of change in leaf photosynthetic rates of *Acer mono* Maxim. and *Acer palmatum* Thunb. are opposite to those of *Betula maximowicziana* Regel and *Ostrya japonica* Sarg. (Fig. 2). This may be related to their stomatal response to diurnal changes in vapor pressure deficit, i.e., the two *Acer* species are isohydric (tight stomatal control of gas exchange), whereas *Betula* and *Ostrya* (Betulaceae) are more anisohydric (loose stomatal control), suggesting that variation in photosynthesis-related physiological traits among species results in different diurnal patterns of photosynthesis and leads to temporal differentiation in light-use among species. Given that no single species can maintain maximum photosynthetic rates throughout the day or year, stand-level productivity would increase if coexisting species diversified across time. We believe that our hypothesis: variation among species in photosynthesis-related traits leads to spatial/temporal differentiation and complementary resource use, would provide a functional

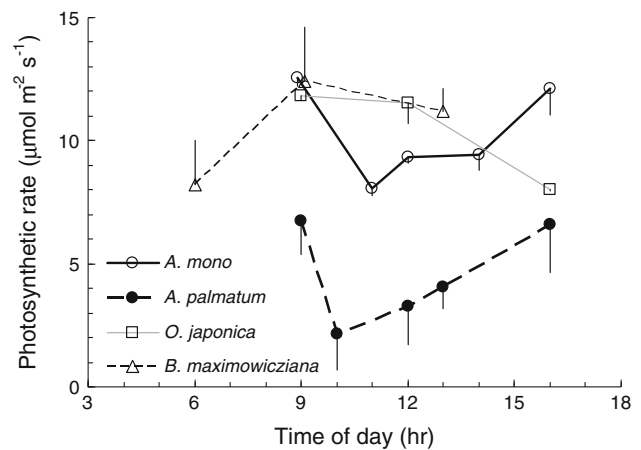


Fig. 2 Variation among four coexisting species (*Acer mono*, *Acer palmatum*, *Betula maximowicziana*, and *Ostrya japonica*) in the diurnal pattern of photosynthesis in a cool-temperate deciduous forest in Hokkaido, northern Japan. Measurements were made under in situ photosynthetic photon flux density (PPFD) and temperature and $370 \mu\text{mol mol}^{-1} \text{CO}_2$ concentration using the canopy crane at Tomakomai Experimental Forest, Hokkaido on clear days during summer (*B. maximowicziana*, Ishii et al. 2004; remaining species, E. N., unpublished data)

explanation for the diversity–productivity theory as it applies to forest ecosystems.

The importance of individual-level phenotypic plasticity in trees

Greater functional diversity among coexisting plant species may allow access to more of the total available resources, leading to increased productivity (Cadotte et al. 2009). For example, divergence of species across the spectrum of leaf functions, such as photosynthesis, longevity, herbivore defense, etc. (Onoda et al. 2011; Poorter and Bongers 2006; Wright et al. 2004), may promote species coexistence (Diaz and Cabido 2001; Kraft et al. 2008; Selaya and Anten 2010). Most studies comparing functional traits among coexisting species assign a mean trait to each species, when in reality there is a broad range of phenotypic plasticity both within and across individuals, especially for tall trees, and this range is highly variable among species. Because phenotypic plasticity is expressed at the metamer level in plants (DeKroon et al. 2005), such studies fail to address the importance of phenotypic plasticity and its contribution to species coexistence and ecosystem function.

Trees experience highly variable environmental conditions as they grow from seedlings to mature trees during their long life-span. Trees also modify their own environment as they increase nearly 1,000 times in size through ontogeny (Ford 1992; Thomas and Winner 2002). In trees, physiological acclimation occurs at the metamer level in response to the spatial/temporal variation in environmental conditions. Thus, it would be advantageous to retain high physiological plasticity over the course of their evolution (Schlichting 1986). This is readily visible if one observes the high variability of leaf morphology from the lower to upper crown of a single tree by accessing firsthand the canopy of tall forests. Although they are genetically identical, leaves near the tree top look very different from those at the bottom. In general, leaf orientation becomes more plagiotropic, the number of leaves attached to twigs decreases, and each leaf becomes flatter in cross-section, with fewer palisade cells toward the bottom of the canopy (Fig. 3a, Cavaleri et al. 2010; Ishii et al. 2007; Niinemets 2007; Oldham et al. 2010). A marked example is the vertical variation in leaf morphology of *S. sempervirens*, the world's tallest tree species. (Ishii et al. 2008; Koch et al. 2004; Mullin et al. 2009; Oldham et al. 2010). In *S. sempervirens*, leaf mass per area (LMA) can change as much as 2.5-fold within the crown of a single tree (Fig. 3b). The ability to produce highly shade-acclimated leaves with low LMA seems to be correlated with stand-level leaf area index. Among 12 conifer species in the western US, maximum LAI is higher for species that produce more shade-acclimated leaves (Leverenz and Hinckley 1990). This is because such species can develop deep crowns with leaves from the upper canopy down to deep shade. Among the 12 species, *S. sempervirens* exhibits the greatest

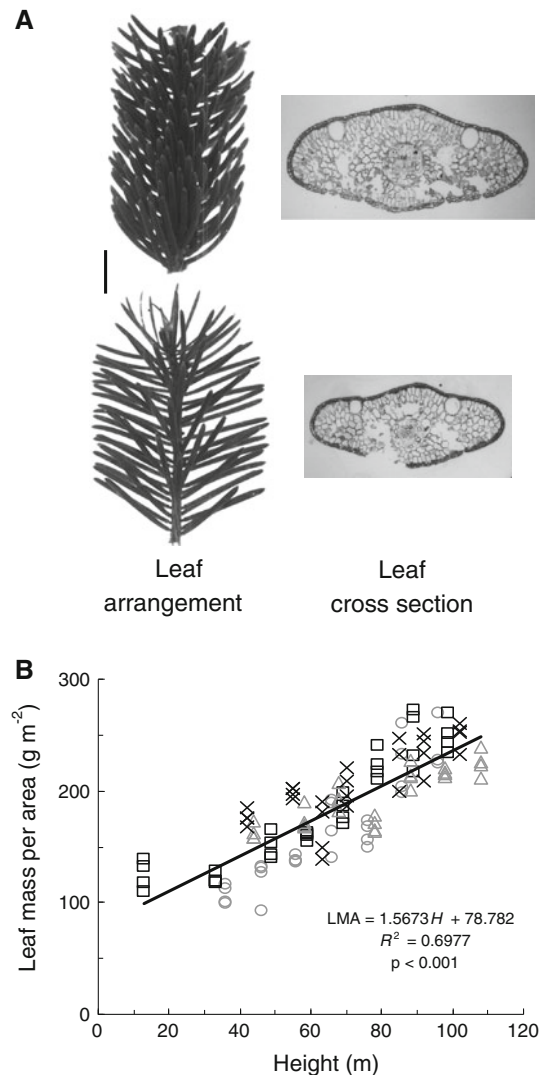


Fig. 3 Because phenotypic plasticity is expressed at the metamer level in plants, physiological acclimation to the vertical gradient occurs at the shoot and leaf levels within the crown of individual trees. In *Picea jezoensis*, the number of leaves attached to the shoot axis, leaf thickness and number of palisade cells decrease from the upper to lower crown (a). The line represents 1 cm and 1 mm in the left and right panels, respectively (after Ishii et al. 2007). In *Sequoia sempervirens*, the world's tallest tree species, leaf mass per area changes 2.5-fold from tree top to crown base (b). Symbols denote different trees that were climbed and sampled using ropes in Jedediah Smith Redwoods State Park, CA. Each data point represents a foliated shoot (1-year-old), of which three to five replicate samples were measured at each height (W. Azuma, unpublished data)

morphological plasticity and highest stand-level LAI. This suggests that species with greater plasticity in photosynthesis-related traits are able to exploit the vertical gradient in light availability, which may explain why *S. sempervirens* forests have such enormous biomass. When plasticity-induced exploitation of light occurs across species rather than within species, it would increase both diversity and productivity of forest communities.

While, the breadth of physiological plasticity allows species to diverge along the vertical gradient of light



Fig. 4 Tree species may coexist through functional convergence in resource-limited environments, such as the shaded understory of mature forests. Branches of *Abies amabilis* (left) and *Tsuga heterophylla* (right) growing adjacent to each other in the understory of a mature temperate forest in southern Washington State, exhibit similar shoot/leaf morphologies and light-interception efficiencies (photo: H. Ishii)

availability within the canopy, convergence of physiological traits may allow their coexistence in the light-limited understory. For example, saplings of *Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes and *Tsuga heterophylla* (Raf.) Sarg. often occur adjacent to each other in the understory of cool-temperate conifer forests of the Pacific Northwest coast of North America (Fig. 4). Although leaf mass per area is greater and leaf longevity longer for *A. amabilis* than for *T. heterophylla*, the two species exhibit convergence in morphological and physiological traits associated with efficient light interception in the light-limited understory (Ishii et al. 2009). In the understory of a lowland tropical rainforest in Panama, 24 species of contrasting crown architectures exhibited convergence of traits associated with light-interception efficiency (Valldares et al. 2002). Functional convergence also occurs in response to hydraulic limitation in the upper canopy. Height-related changes in morphological and physiological traits, converge among 13 coexisting deciduous broad-leaved tree species (Miyata et al. 2011), as well as among three *Acer* species (Nabeshima and Hiura 2008) in Hokkaido, northern Japan. In forest ecosystems, resource availability is highly spatially and temporally heterogeneous. Thus, plasticity of photosynthesis-related traits may enable coexistence of tree species through divergence in resource-rich environments, as well as through convergence in resource-limited environments (Kraft et al. 2008; Lebrija-Trejos et al. 2010).

Conclusions

Because humans are confined mostly to the ground, we have been able to observe only what is happening at the



Fig. 5 Using newly developed, safe, and reliable canopy access techniques, we can make the same measurements in the canopy as we do on the ground. **a** Measuring the trunk diameter of a *Cryptomeria japonica* tree at 15 m above ground in Yakushima Island, Japan (Photo: H. I.). **b** Micrometeorological sensors installed atop a 111-m *Sequoia sempervirens* tree in California (Photo: S.C. Sillett)

foot of tall forests. We contend that a three-dimensional, canopy perspective is needed in order to fully understand forest ecosystem functioning. The canopy perspective adds depth (literally) to our understanding of forest ecosystems. In the early days of forest canopy ecology, it was exciting just to describe this new ecosystem, which had been largely unexplored. How diverse

are the canopy flora and fauna? What are their ecological roles? Dr. Tamiji Inoue, a pioneer of forest canopy ecology in Japan once said that we should appreciate the pure value of the diversity of organisms in the forest canopy and the intricate symbiotic relationships among them. With the development of safe and reliable canopy access techniques, canopy ecology has matured to a more process-based science (Lowman and Rinker 2004). Now, we can make the same measurements and address the same questions as we do on the ground. For example, we can measure the trunk diameter and sample increment cores from breast height to tree top, tag and measure every epiphytic plant, measure photosynthesis and transpiration rates of leaves in situ, and install micrometeorological stations in tall trees (Fig. 5). Using these enhanced techniques, we can provide functional explanations to the larger scale questions that could not be answered from measurements on the ground.

Experiments conducted in grasslands have provided much insight regarding diversity–function relationships in plant communities. We must use caution, however, when applying theories derived from low-statured ecosystems to forest ecosystems (Scherer-Lorenzen et al., 2005). As we have illustrated, elucidation of the underlying physiological mechanisms may provide a functional explanation for the diversity–productivity theory as it applies to forest ecosystems. Among these, we believe that individual-level phenotypic plasticity of photosynthesis-related traits is especially important because the breadth of physiological plasticity is what allows tree species to coexist along the vertical gradient of light availability within the forest canopy, as well as in the light-limited understory. In contrast to the view from the ground, a canopy perspective reveals the breadth of phenotypic plasticity of each species contributing to their coexistence and various ecosystem functions. It may also reveal new relationships between functional diversity and ecosystem functioning previously undiscovered in grassland experiments, where the vertical variation in the light environment and leaf functions is much less than in forest ecosystems. A cross-biome exploration of the link between plasticity of photosynthesis-related traits and stand productivity may provide a functional explanation for the relationship between species assemblages and productivity of forest ecosystems.

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