Exploring the Relationships Among Canopy Structure, Stand Productivity, and Biodiversity of Temperate Forest Ecosystems

Hiroaki T. Ishii, Shin-ichi Tanabe, and Tsutom Hiura

ABSTRACT. Impacts of human activity on forest ecosystems are most pronounced in the temperate region. Simplification of stand structure has resulted in diminished ecosystem function and biodiversity decline, raising much debate over future management policies. Ecosystem functions and biodiversity may be enhanced by managing forests for increased structural complexity. However, processes that determine relationships among structural complexity, ecosystem functions, and biodiversity of forest ecosystems remain unclear. In this review, we present examples of studies conducted at two canopy research facilities located in different types of temperate forest to illustrate that structural complexity of forest canopies enhances stand productivity and biodiversity: (1) development of structurally complex canopies comprising various tree species enhances stand productivity by promoting complementary resource utilization among species through spatial, physiological, and temporal differentiation; and (2) development of complex canopy structure enhances biodiversity of canopy-dwelling organisms by creating a resource-rich habitat. These ecological observations stress the importance of including three-dimensional structural attributes of forest canopies in management plans and silvicultural prescriptions that aim to maintain ecosystem functions and biodiversity. FOR. SCI. 50(3):342–355.

Key Words: Ecosystem function, ecosystem management, habitat template, canopy structure, structural complexity.

ONE OF THE PRONOUNCED EFFECTS of human activity on the global biosphere is the dramatic change in ecosystem productivity due to deforestation and the resulting loss of biological diversity (Wilson and Peter 1988, Perry and Maghembe 1989, Kimmins 1997). Various ecosystem functions and services may be negatively affected by the loss of biodiversity (Schulze and Mooney 1994). Several short-term experiments have shown that

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ecosystems with high species diversity are more productive and sequester more CO_2 than low-diversity ecosystems (e.g., Naeem et al. 1994, Tilman et al. 1997a, Hector et al. 1999). In the long-term, declining species diversity may lead to a decrease in the ecosystem's ability to buffer against perturbation (Schulze and Mooney 1994, Naeem and Shibin 1997), and this would be especially damaging for forest ecosystems that consist of long-lived tree species. Franklin et al. (1989) proposed that long-term productivity of natural forest ecosystems with high tree species diversity may be greater than that of forests with low diversity as a result of increased ecosystem resilience to disturbance.

Along with tree species diversity, we propose in this review that structural complexity (i.e., the variability of the three-dimensional spatial arrangement of trees and other structural elements within a forest) also enhances productivity of forest ecosystems. Structural complexity may increase ecosystem productivity by promoting complementary resource utilization among plant species (Naeem et al. 1994, Hooper and Vitousek 1997), especially for forest ecosystems where plants of various life forms coexist, creating complex three-dimensional structure. Structural complexity of forest ecosystems also enhances diversity of nontree species by creating resource-rich habitat. Several studies have indicated that complexity of habitat structure serves as a template for increasing species diversity (habitat template, c.f. Southwood 1977, Bell et al. 1991, Takeda and Abe 2001). In forest ecosystems, species diversity is generally greater in structurally complex, late-seral stands than in structurally simple, younger stands and plantations, and this difference has been attributed to the degree of development of habitat structure (e.g., Carey 1989, Schowalter 1995, Carey and Wilson 2001). Based on these findings, silvicultural prescriptions that aim to mimic structural characteristics of late-seral forests have been proposed in an effort to create habitat structure and to enhance biodiversity of managed forests (Kohm and Franklin 1997, Smith et al. 1997, Carey et al. 1999b, Hunter 1999).

Various measures of stand structural complexity have been proposed for guiding management (Solomon and Gove 1999, Staudhammer and LeMay 2001). However, we contend that current measures of stand structural complexity, most of which are based on conventional, ground-based measurements such as species composition and tree-size distribution, only indirectly reflect the three-dimensional structure of forest ecosystems and processes that define the relationship between ecosystem structure and function. Processes that determine productivity of forest ecosystems, such as photosynthesis and nutrient uptake, occur in the canopy and in the soil, not at breast height (Kira et al. 1969, Lowman and Nadkarni 1996). In addition, much of the biological diversity of forest ecosystems resides in the canopy and in the soil (Stork 1993). As such, we must find ways to integrate various ecosystem components, including canopy and belowground processes, into future ecosystem management strategies.

In this review, we focus on the structural complexity of forest canopies. Studying forest canopies is especially important because the three-dimensional structure of the canopy determines the distribution of light in a forest ecosystem and is a major determinant of stand productivity (Kira et al. 1969, Parker 1995). In addition, the three-dimensional distribution of habitat structure within the canopy contributes to enhancing biodiversity (Halaj et al. 2000). Thus, canopy research plays an important role in our understanding of the integrative relationships among structural complexity, stand productivity, and biodiversity of forest ecosystems. Here, we present examples from two canopy research facilities of the measurement and quantification of canopy structure and investigations of the processes that create structural complexity of forest canopies. We demonstrate that structural complexity of forest canopies enhances stand productivity and biodiversity. Based on these ecological observations, we stress the importance of considering three-dimensional structural development of forest canopies in ecosystem management plans and silvicultural prescriptions that aim to enhance productivity and biodiversity of temperate forest ecosystems.

Development of Canopy Structure

Measurement and quantification of canopy structure of natural forests is not an easy task. Casual observation suggests that late-seral natural forests, composed of various tree species and a wide range of tree sizes, are structurally "more complex" than plantations and younger natural forests comprising fewer species. But how do we measure structural complexity? What are the processes that create it? Quantification of the structural complexity of late-seral forests have been based on measurements made from the ground. For example, species composition, tree-size distribution, and abundance of snags and woody debris have been proposed as indices of late-seral forest structure for Pacific Northwest forests (Franklin et al. 1981, Spies and Franklin 1991, Wells et al. 1998). However, such conventional measures of stand structure include few elements of the forest canopy and only indirectly reflect aspects of structural complexity that affect productivity and biodiversity of the stand as a whole.

Stand-Level Canopy Structure

To date, efforts to quantify canopy structure of forests have been limited to measurements of tree height and gross crown dimensions (e.g., Ishizuka 1984, Dubrasich et al. 1997, Song et al. 1997, Chen and Bradshaw 1999, Zenner 2000) and measurements of vertical foliage distribution using indirect methods such as visual estimation, hemispherical photographs, and remote sensing (e.g., Koike 1985, Hedman and Binckley 1988, Easter and Spies 1994, Parker et al. 1989, Carey et al. 1999a, Yang et al. 1999). Detailed direct measurements of canopy structure (e.g., Sumida 1995, Fukushima et al. 1998, Kull et al. 1999) are time-consuming, require much effort, and cannot be done extensively. Detailed quantification of the canopy structure of late-seral forests has been especially hampered by the difficulty of access to the tall canopy. Recent developments in canopy access methods allow for safe and repeatable

measurements in the forest canopy (Lowman and Nadkarni 1996, Mitchell et al. 2002). These methods enable three-dimensional mapping of canopy structure (see Van Pelt and Nadkarni 2004 and Song et al. 2004) and in situ observations in the canopy to study the processes that enhance structural complexity.

At the Wind River Canopy Crane Research Facility (WRCCRF) in southwestern Washington State, several studies have quantified in detail the canopy structure of a 450-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*)–western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest (Van Pelt and North 1997, Parker 1997, Ishii et al. 2000, Thomas and Winner 2000, Song et al. 2004). These studies have elucidated important processes that drive structural development of the forest canopy. Late-seral Douglas-fir–western hemlock forests of the Pacific Northwest have complex canopy structure with a deep continuous canopy comprising various tree species (Franklin et al. 1981, Franklin et al. 2002). This is in contrast to the relatively simple canopy structure of early-successional stands and even-aged plantations of this region. In Douglas-fir–western hemlock forests, development of canopy structure begins with the dominance of Douglas-fir in the upper canopy of mixed-species, second-growth stands in early-successional stages (Wierman and Oliver 1979, Larson 1986). Douglas-fir continues to dominate in the upper canopy of late-seral forests for centuries into late-successional stages (Gholz et al. 1976, Stewart 1986b, Easter and Spies 1994). Ishii et al. (2000) predicted future canopy development at WRCCRF based on current height-growth and crown-expansion rates measured in the canopy. They concluded that at least 100 years will pass before western hemlock displaces Douglas-fir and attains dominant status in the upper canopy of this forest.

The canopy structure of the late-seral Douglas-fir–western hemlock forest at WRCCRF is characterized by the vertical distribution of species forming a continuous canopy (Figure 1). Tree abundance decreases markedly above 10 m, and horizontal spatial distribution of trees changes from aggregated distributions in the lower-canopy to increasingly regular distributions with increasing height (see also Song et al. 2004 for more detailed analysis). Moeur (1993) found that spatial distribution of trees became increasingly regular with increasing diameter in a western hemlock forest in northern Idaho and inferred that intense competition among spatially aggregated young trees results in mortality and increasingly regular spatial distribution as trees increase in size. While Mouer's model of canopy development is based on diameter measurements taken from the ground, the results from WRCCRF provide a three-dimensional perspective of canopy structural development and give support to the hypothesis that crown competition and tree mortality are important processes that drive development of canopy structure. Studies conducted at WRCCRF further suggest that, in early stages of stand development, deterministic processes such as species differences in timing of establishment, height-growth rate, maximum attainable height, crown form, crown competition, and recruitment
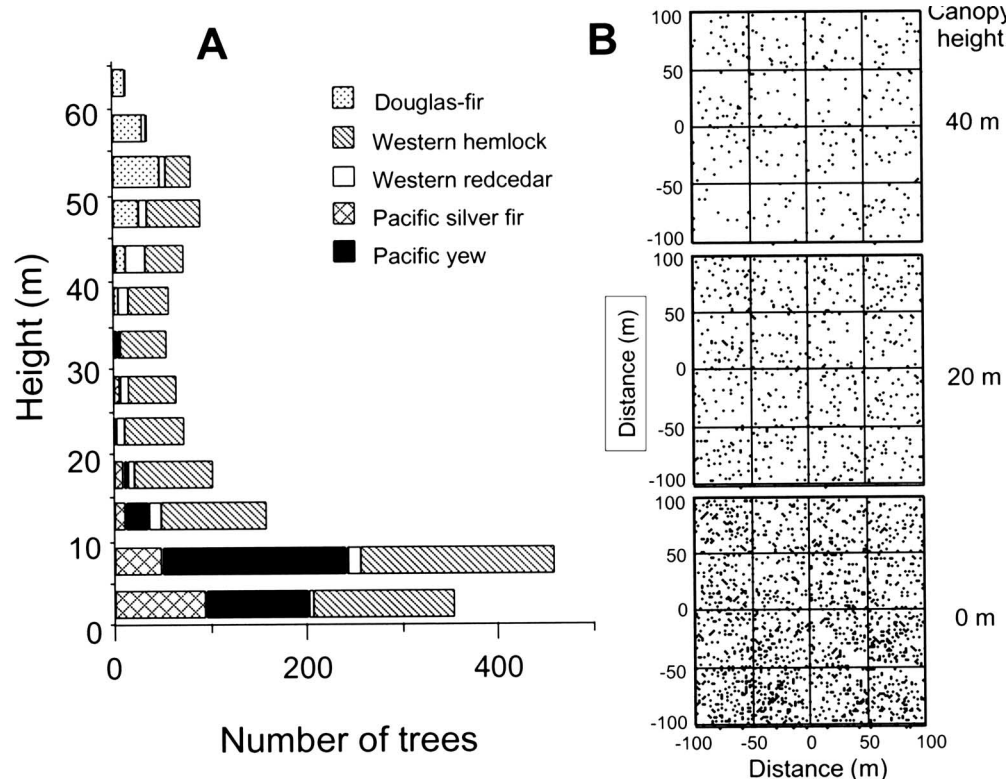

Figure 1. Vertical changes in tree species abundance (A) and spatial distribution (B) in a 4-ha plot of Douglas-fir–western hemlock forest at the Wind River Canopy Crane Research Facility (WRCCRF) in southwestern Washington State.

drive development of canopy structure (see also Johnson et al. 1994, Dubrasich et al. 1997). Toward late-seral stages, stochastic processes such as small-scale disturbances that cause gap formation and crown damage/dieback work to enhance structural complexity of the forest canopy (Figure 2A, reviewed by Franklin et al. 2002).

Crown-Level Structural Complexity

Detailed measurement and quantification of stand-level canopy structure can elucidate important mechanisms that regulate stand structural complexity. However, we must also consider that many of the structural features that directly affect individual tree growth and habitat for canopy-dwelling organisms occur at individual tree-crown scales. Crown structure influences photosynthetic capacity and growth of trees (Ford 1986, Smith and Long 1989). Birds and small mammals use specific structural attributes of the crown, such as large-diameter branches, as nesting sites and dens (Ruggiero et al. 1991, Carey et al. 1997). Community structure of canopy epiphytes is largely determined by structural features of the tree crown (Pike et al. 1977, Clement and Shaw 1999). Despite this, few studies have made detailed measurements of crown structure in late-seral forests (e.g., Denison et al. 1972, Massman 1981).

Ishii and Wilson (2001) conducted a detailed study of the vertical structure and microenvironment of the crown of 450-year-old Douglas-fir trees at WRCCRF using rope-climbing techniques. They found that the crown of old Douglas-fir trees is more sparsely branched than younger trees and has several large vertical gaps over 2 m in depth. There are numerous dead branches, as well as young epicormic branches, indicating continuous turnover of branches within the crown. Epicormic branches account for 15–48% of the total number of live branches per tree, fill inner regions of the crown, and contribute to increasing crown depth of old Douglas-fir trees. Branch recruitment by production of epicormic branches increased branch-size variability with branch sizes ranging from large original branches more than 300 years old to small, relatively young epicormic branches. The structural characteristics of the crown created variable within-crown light environment. Instead of the steady decline in relative light intensity from upper to lower crown observed in younger stands, Ishii and Wilson (2001) found a local peak in light intensity near the middle crown of old Douglas-fir trees where light intensity increased due to increased lateral penetration of diffused light. This local peak in light intensity coincided with the height where large original branches ceased to exist, and live-branch biomass decreased markedly. Below this height, the crown consisted almost entirely of young epicormic branches.

The complex crown structure of old Douglas-fir trees develops as a result of branch growth, branch death, and production of epicormic branches (Figure 2B). Millet et al. (1998a) observed similar processes of dieback and regrowth within the crown of late-seral tree species in the temperate deciduous forests of southwestern Quebec. Sillett and Van Pelt (2000) also documented detailed crown structure and reiteration of several branches and vertical axes in an old redwood (*Sequoia sempervirens* (D. Don) Endl.) tree in northern California. Reiteration by epicormic shoot production also occurs within branches, increasing size variability of branch axes as well as complexity of the branching
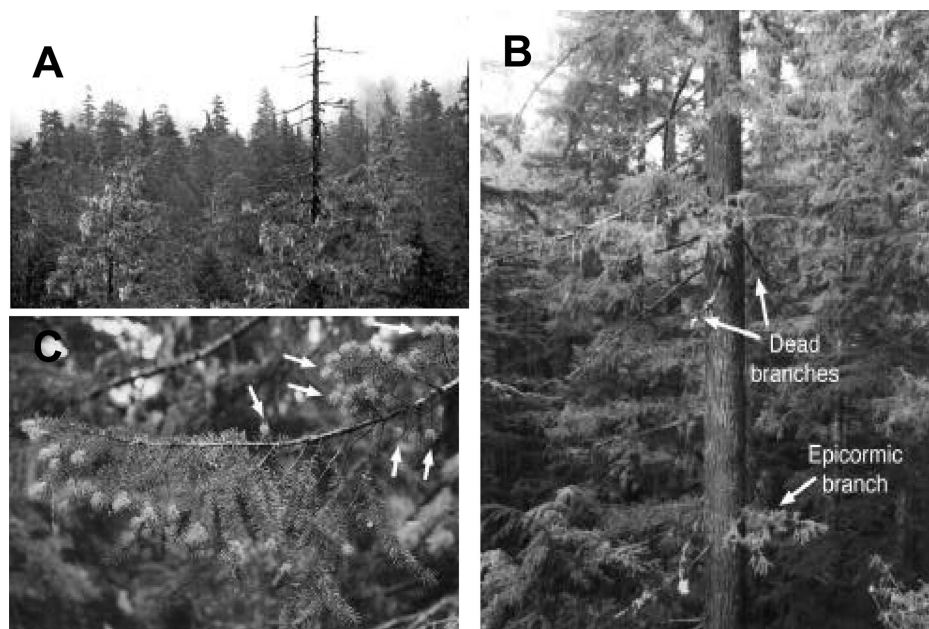

Figure 2. In late-seral Douglas-fir–western hemlock forest canopies, stochastic processes that result in gap formation and crown damage/dieback enhances structural complexity at the stand level (A). In old in Douglas-fir trees, branch death and recruitment by epicormic branching enhances structural complexity at the crown level (B). Within branches, epicormic shoot production (arrows) increases size variability of branch axes and enhances complexity of the branching structure (C; photo by M. Kennedy).

structure (Figure 2C, Ishii and Ford 2001, Ishii et al. 2002). Together with canopy-level dynamics, these within-crown processes enhance structural complexity of the late-seral forest canopy at smaller spatial scales.

Canopy Complexity and Stand Productivity

In natural forests, structural complexity is often coupled with tree species diversity. Therefore, to examine the effects of structural complexity on stand productivity, we must first explore the factors that determine tree species diversity of a stand because trees form the structural framework of forest ecosystems. Mechanisms of the effect of diversity on ecosystem productivity may be grouped into two classes. First are local deterministic processes, such as niche differentiation, which increase the performance of communities, also termed "complementarity" effects (Tilman et al. 1997b). Second are local and regional stochastic processes, such as colonization and establishment probabilities, involved in community assembly. Wright (2001) proposed that, in tropical forests, deterministic processes such as niche differentiation may dominate in determining species assemblage rules and community dynamics. In forests affected by large-scale disturbances such as forest fire and typhoons, colonization ability, propagule persistence, and growth rate of individual species may be more important (Hiura 2001).

Several experiments on microcosms and grasslands have indicated that higher species diversity enhances ecosystem productivity as well as other ecosystem functions (e.g., Naeem et al. 1994, Tilman et al. 1997a, Hector et al. 1999, Mikola et al. 2002). These experimental studies mimicked stochastic processes of species assemblage by creating artificial communities randomly sampled from a species pool. On the other hand, comparative studies on natural ecosystems have been less conclusive because of the difficulty of controlling for variation in factors other than species diversity. Forest ecosystems present great biomass and high species diversity, but the mechanisms and relationships among biodiversity, structural complexity, and stand productivity remain unclear. Here, we present results from studies conducted at Tomakomai Experimental Forest (TOEF), the Japanese canopy crane site, to explore the relationship between structural complexity and stand productivity. The mixed-species deciduous forests at TOEF have been affected by large-scale disturbances including volcanic eruptions and typhoons. Therefore, stochastic processes play an important role in determining species composition and community dynamics (Hiura 2001). The topography is flat and site conditions are relatively homogeneous, making the forests at TOEF an excellent natural experiment for comparing tree species diversity and stand productivity among different types of stands. We show that, in this forest, coexistence of various tree species leads to the development of complex canopy structure and complementary resource utilization among species. These processes lead to the positive effect of species diversity on stand productivity.

Stand-Level Structure and Productivity

Mixed-species forests will generally have greater productivity than monocultures if facilitation among species and vertical stratification occurs (Cannell and Malcolm 1992, Kelty 1992, Hartley 2002). This implies that differentiation among species in resource utilization, growth, and form are important factors promoting productivity of mixed-species forests. In mixed-species natural stands, trees present various life forms, varying in size from saplings to mature trees, and from understory and subcanopy species to species that reach the upper canopy. This variation in tree sizes results in a multi-layered foliage structure and enhances structural complexity of the forest canopy. Vertical diversification among tree species and effective packing of biomass in the canopy allows for more efficient light capture and resource utilization by trees, leading to increased stand productivity (Kira et al. 1969, Smith and Long 1989, Hartley 2002). An ongoing long-term study at TOEF compares tree species richness, canopy structure, and stand productivity among 38 forest plots, all of which established after a catastrophic typhoon in 1954. The study plots range in size from 0.2 to 0.25 ha, and environmental conditions such as substrate and site index are similar among stands. Preliminary analyses based on observations for the first 8–9 years of the study indicated that tree species richness was positively correlated with leaf area index ($r = 0.498$, $P < 0.01$) and with basal area increment ($r = 0.460$, $P < 0.01$), suggesting that tree species diversity enhances structural complexity of the canopy and leads to increased productivity (T. Hiura, unpublished data).

Although upper-canopy trees contribute the greatest amount to biomass and production of mixed-species stands, the presence of shade-tolerant, understory tree species plays a significant role in enhancing stand productivity. Growth and survival of individual trees are determined not only by the rate of resource acquisition but also by the efficiency of resource utilization. Understory tree species show adaptation to low-light conditions: e.g., greater biomass allocation to leaves than to support tissue (King 1991, Bongers and Sterck 1998), to horizontal crown expansion than to height growth (Shukla and Ramarkrishnan 1986, Kohyama and Hotta 1990), and to leaf area than to leaf mass (Ellsworth and Reich 1992). These adaptations increase efficiency of light absorption per unit of aboveground biomass of understory species and sustains their contribution to stand productivity. In a mature deciduous broad-leaved forest at TOEF, three-dimensional distribution of foliage and light were investigated using a large scaffolding tower that included 139 trees of various species (Fukushima et al. 1998). In the upper canopy, eight dominant species contributed 80.3% of the total leaf area (Figure 3) and captured 90.5% of incident photosynthetically active photon flux density (PPFD; 400–700 nm), indicating that competition for light was markedly asymmetric. For the understory trees, leaf area ratio (LAR: leaf area/plant biomass) had a strong effect on the amount of light absorption per unit aboveground
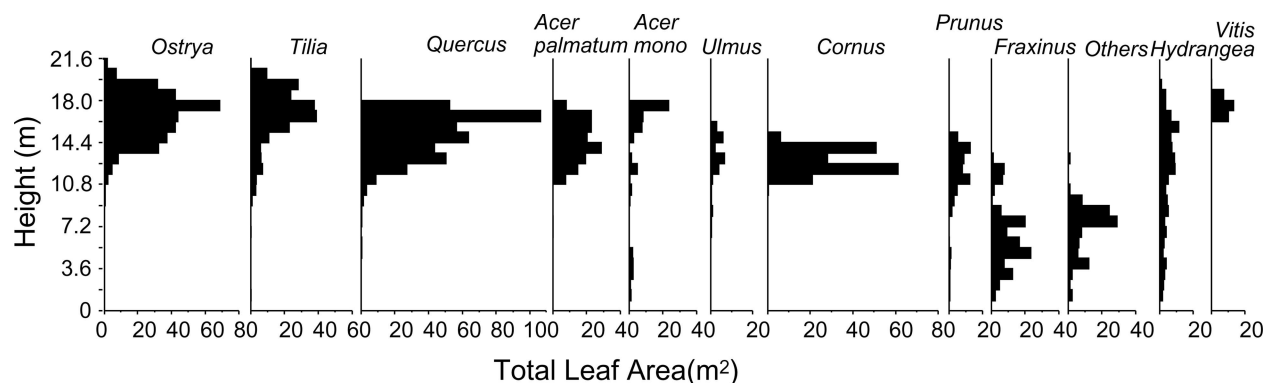
Figure 3. Vertical distribution of leaf area inside a scaffolding tower (15 × 15 × 22 m) at Tomakomai Experimental Forest (TOEF). Vertical axis shown in 1.8-m increments, dimensions of one cubic section of the scaffolding tower for which foliage areas were determined (see Fukushima and Hiura 1998). *Ostrya japonica, Tilia maximowiczii* Shirasawa, *Quercus mongolica, Acer palmatum* Thunb., *Acer mono*, and *Ulmus japonica* Sargent are canopy tree species, while *Cornus controversa* Hemsl., *Prunus ssiori* Fr. Schm., *Fraxinus lanuginosa* f. *serrata* Murata, and others are understory tree species. *Hydrangea petiolaris* Sieb. et Zucc. is a vine.

biomass. This suggested that biomass allocation is an important factor determining the efficiency of light capture and growth of understory trees contributing to their persistence in mixed-species forests. Canopy species have an advantage over understory species in receiving a large fraction of incident PPFD, while understory species show adaptations in biomass allocation to increase efficiency of light capture. The observed adaptations to different light conditions of the canopy and understory, and the resulting differences among species in the efficiency of light capture, are essential mechanisms for development of vertical canopy structure and stable coexistence of species in forest ecosystems (Kohyama 1993). Stable coexistence of multiple species enhances stand productivity through the development of complex, multi-layered canopy structure that promotes complementary resource utilization among species.

Species-Level Characteristics and Stand Productivity

Stand productivity may be enhanced not only by the development of complex canopy structure but also by differences among species in their photosynthetic characteristics. Because trees are sessile organisms, the amount of space occupied by their crown and root system directly influences the amount of resources gained. Each tree species has a characteristic crown form, which is partly genetically determined (Millet et al. 1998b). Photosynthetic characteristics should differ among species depending on their successional status, crown form, and within-canopy position. Because early-successional species have a relatively long residence time in the upper canopy than late-successional species, leaves of early-successional species are likely to show greater acclimation to high-light conditions of the upper canopy. In contrast, late-successional, shade-tolerant species generally have a relatively narrow range of morphological and physiological plasticity (Bazzaz 1979). Thus upper-canopy leaves of late-successional species may show a decline in photosynthetic rate induced by high leaf temperatures and degeneration of photosynthetic enzymes, as

well as stomatal closure due to high vapor pressure deficit, resulting from excessive amounts of light (Pathre et al. 1998, Ishida et al. 1999). Photosynthetic characteristics were compared among 17 species of varying successional status and canopy position using the TOEF canopy crane. Photosynthetic rates of leaves were measured at the canopy surface and in the layer 0.5–1.0 m below the canopy surface for tree species that have different crown shapes and successional status. For *Betula maximowicziana* Regel, an early-successional species, maximum photosynthetic rates (A_{max}) of leaves at the canopy surface were higher than that of leaves just below the surface ($P < 0.05$), corresponding to the vertical gradient in light intensity (Figure 4). In contrast, for *Acer mono* Maxim., a late-successional species, A_{max} of leaves at the canopy surface were significantly lower than those just below the surface ($P < 0.01$). In early morning, A_{max} of *A. mono* was higher than that of *B. maximowicziana*. However, A_{max} of *B. maximowicziana* increased and peaked in mid-morning, while A_{max} of *A. mono* declined. This indicated that while leaves of *B. maximowicziana* are adapted to high-light conditions of the
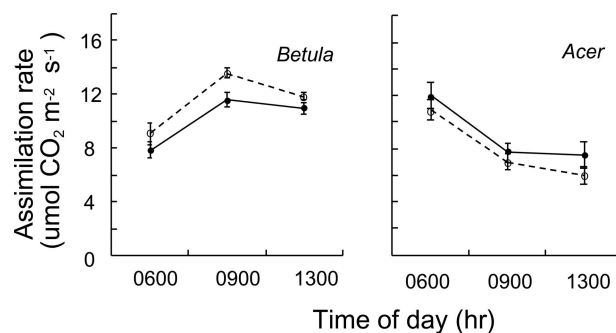

Figure 4. Diurnal changes in CO$_2$ assimilation rate (μmol m^{-2} s^{-1}) of leaves at the canopy surface (○) and the lower layer (●) for two species out of 17 studied at TOEF. *B. maximowicziana* and *A. mono* represent typical patterns observed for early- and late-successional tree species, respectively. The mean and standard error are shown for measurements taken on two trees of *B. maximowicziana* and three trees of *A. mono*, which were accessible from the canopy crane. Three leaves were sampled from each tree.

upper-canopy, leaves of *A. mono* were suffering from excess light during the day. These results suggested that differences among species in photosynthetic capacity of the crown and diurnal patterns of photosynthesis results in spatial and temporal differentiation of photosynthetic productivity.

In addition to differences among species in spatial and diurnal patterns of photosynthesis, variation among species in seasonal patterns were also observed (T. Hiura and K. Shimizu, unpublished data). For *B. maximowicziana*, an early-successional species, and for *Magnolia hypoleuca* Sieb. et Zucc., a gap-phase species, A_{max} declined in summer (July and Aug.). In contrast, late-successional species, such as *A. mono* and *Carpinus cordata* Blume, maintained a moderate but stable A_{max} during most of the growing season, and leaf number and nitrogen concentrations were relatively constant during this time. Other species, such as *Ostrya japonica* Sarg., a midsuccessional species, and *Quercus mongolica* Fischer ssp. *crispula* Blume, a late-successional species, reached their maxima in July and gradually declined thereafter. These results indicated that although early-successional species can use intense irradiance in the upper canopy, hot and dry mid-summer conditions induce a decline in photosynthetic rate. In contrast, late-successional species are able to maintain a moderate level of photosynthesis throughout the growing season.

The studies at TOEF showed that spatial and temporal differentiation among species in photosynthetic productivity contributes to spatial and temporal partitioning of light resources in the canopy of mixed-species forests. These processes explain, at least in part, how increasing tree species diversity enhances structural complexity of forest canopies and leads to increased stand productivity by promoting complementary resource utilization among species through spatial, physiological, and temporal differentiation in photosynthetic capacity.

Canopy Complexity and Biodiversity

Structurally complex habitats enhance biodiversity by increasing environmental heterogeneity such as the variation of microhabitats and the range of microclimates (Klopfer and MacArthur 1960, Pianka 1978, Carey et al. 1999a). Southwood (1977) proposed the term "habitat template" to represent the physical features of habitats relevant to organization of ecological communities. In forest ecosystems, trees produce and maintain the overall physical structure of habitats (Jones et al. 1997) and thus define fundamentally the templates for structural complexity and environmental heterogeneity. Ectogenous processes such as disturbance can carve the templates and also contribute to enhancing structural complexity at various spatial scales (Franklin et al. 2002). Although other mechanisms such as the development of complex food webs and sufficient time for colonization also enhance species diversity, the bottom-up effect of the development of habitat structure may be especially important in organizing ecological communities in forest ecosystems where plants predominantly produce the structural framework (Power 1992, Hunter and Price 1992).

Structural complexity of forest habitats affects biodiversity of a variety of organisms, including understory plants (North et al. 1996, Van Pelt and Franklin 2000, McKenzie et al. 2000, Brosofske et al. 2001), epiphytes (Rhoades 1987, McCune 1993, Lyons et al. 2000), birds (MacArthur and MacArthur 1961, Hansen et al. 1995, Beese and Bryant 1999), small mammals (Emmons 1987, Carey 1996), and arthropods (Schowalter 1995, Ozanne et al. 1997, Hijii et al. 2001). Franklin (1993) stresses the importance of considering various scales of structural organization in evaluating the importance of structural complexity for conservation of biodiversity in forest ecosystems. Stand, tree, branch, and leaf represent decreasing scales of structural organization that are ecologically meaningful (Strong et al. 1984, Juniper and Southwood 1986, Lowman 1997). Here, we examine the role that structural complexity plays in enhancing biodiversity of forest inhabitants, particularly of animal inhabitants, in temperate forests across various spatial scales. We are especially interested in canopy-dwelling arthropod communities, because arthropods still remain largely untapped in actual management of forest ecosystems despite rapidly increasing awareness of the usefulness and importance of terrestrial arthropod diversity as a biological indicator for forest conservation planning (Kim 1993, Kremen et al. 1993, Samways 1993).

Stand-Level Relationships

Numerous studies indicate, either explicitly or implicitly, the importance of forest habitat structure in organizing animal communities. These studies compare different forests varying greatly in one or some stand-level structural properties, such as vertical foliage complexity (MacArthur and MacArthur 1961, Southwood et al. 1979, August 1983, Gardner et al. 1995, Robertson and Hackwell 1995), horizontal forest structure (Roth 1976), and plant architecture and species composition (Southwood et al. 1979). The presence or absence of certain structural components (snags, logs, flowers, and fruits), their size, density, and decay state are also relevant to the organization of forest animal communities (Southwood et al. 1979, Franklin et al. 2002).

The relative importance of various stand structural attributes in organizing forest animal communities varies with locality or forest type (Roth 1976), the kinds of organisms under investigation, and varies with time (Southwood et al. 1979). Animal species diversity in many herbivorous communities, most of which are insects, is positively correlated with diversity of plant species, the primary food resource (Southwood et al. 1979). On the other hand, such correlations are not observed in nonherbivorous communities (Gardner et al. 1995). For some insects, physical attributes of the forest canopy, such as vertical and horizontal distribution of foliage, may be more important. At TOEF, Tanabe (2002) showed that foliage height diversity (FHD, MacArthur and MacArthur 1961) was correlated with species richness in forest-dwelling fruit fly communities (Diptera: Drosophilidae), while horizontal variation in vertical foliage distribution and tree species diversity did not affect fruit fly diversity (Figure 5A). They proposed that
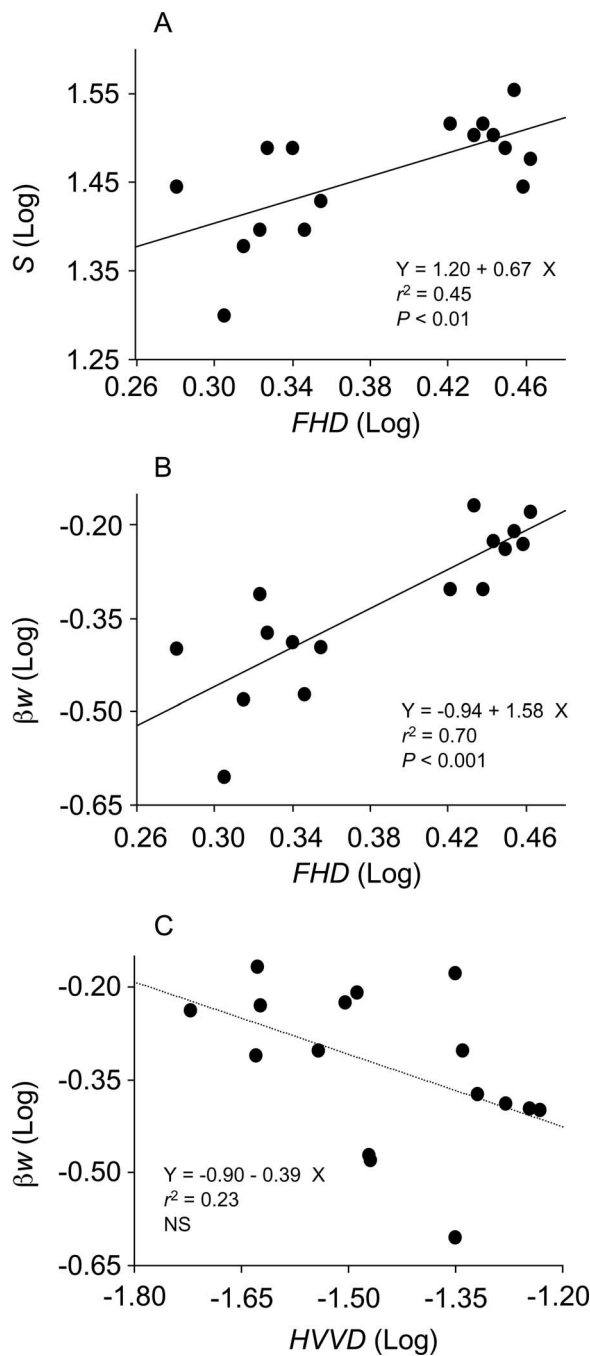
Figure 5. Relationships between canopy-dwelling fruit fly community organization and forest structural properties in mixed-species deciduous forests at TOEF. A, Foliage height diversity (FHD; MacArthur and MacArthur 1961) in relation to total number of species (S). B, FHD in relation to vertical variation in species composition (βw; an index of β diversity, Whittaker 1960). C, Horizontal variation in vertical distribution of foliage (HVVD; a measure of horizontal variation in FHD among subplots, Tanabe 2002) in relation to βw. Lines and equations show results of ordinary least-squares regression analyses. Occasional migrant or rare species (singletons) were excluded from the dataset.

increasing FHD affected species diversity of the fruit fly community by promoting microhabitat segregation among species (Figure 5B). The relatively low horizontal variation in the vertical distribution pattern of foliage may contribute

to maintaining stable vertical stratification among species by enhancing the predictability of the vertical gradient in microenvironment (Figure 5C). For other organisms, horizontal forest structure can be an important habitat parameter responsible for between-forest variation in species diversity. Roth (1976) found that horizontal patchiness was significantly correlated with bird species diversity for several shrub and forest areas. He suggested that the presence of additional patches facilitates horizontal segregation among bird species and increases species diversity in the habitat. These studies suggest that spatial segregation is an important process defining the relationship between structural complexity and species diversity at the stand level.

Within-Forest Relationships

Structural complexity at the crown or canopy stratum level may explain the spatial variation of biodiversity within a forest stand. Many forest-living organisms show species-specific, vertically stratified patterns of distribution within the three-dimensional habitat space of the stand (Sutton et al. 1983, Whitmore 1998, Tanabe et al. 2001). Animal communities are also vertically heterogeneous in terms of species composition (Longino and Nadkarni 1990, Rodgers and Kitching 1998, Brokaw and Lent 1999). Furthermore, many studies conducted in forests have found vertical gradients of biodiversity, with a species-rich fauna in the canopy (Erwin 1983, Wilson and Peter 1988, Stork 1993). This within-forest pattern of variation in biodiversity is often independent of differences in stand-level structural properties. For example, at TOEF, Tanabe (2002) showed that the total number of fruit fly species collected at a stratum (trap height) increased from the ground to the canopy, and that this pattern was consistent among forests differing markedly in vertical foliage structure (Figure 6). The consistent vertical pattern of fruit fly community structure across different forest types suggests that the unvarying nature of within-stand environmental gradients in forests with continuous, closed canopies plays an important role in organizing fruit fly communities. Because structural features in the canopy
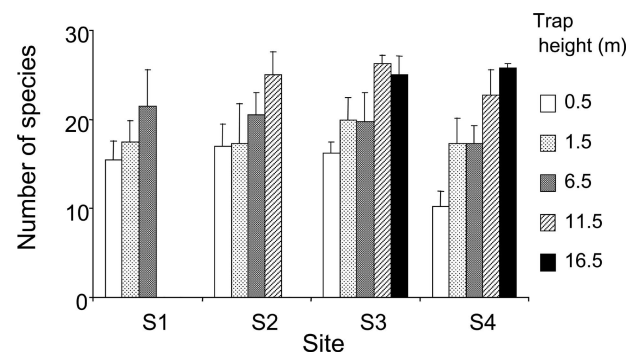

Figure 6. The total number of fruit fly species collected at different canopy heights in four forest sites at TOEF. The four sites differed markedly in vertical foliage structure (Tanabe 2002). S1 and S2 are secondary forests. Canopy heights are 5–6 m and 11–12 m, respectively. S3 and S4 are primary forests. Canopy heights are 17–18 m and 20–21 m, respectively. Bars show the mean of four plots within each forest type. Error bars indicate one standard deviation.

are primarily responsible for spatial variability in environmental conditions such as light, temperature, humidity, and wind, crown- and canopy-level structural complexity should be considered as a potentially important factor affecting three-dimensional variation of biodiversity within forests.

Structural complexity at smaller scales defines the microhabitat of many organisms and thus has significant implications on biodiversity. Many studies have found that structural properties of trees (Lawton 1983, Strong et al. 1984), branches (Halaj et al. 2000), and leaves (Neuvonen and Niemelä 1981, Kennedy and Southwood 1984) affect variation in diversity of animal communities. Processes or mechanisms underlying the relationships between structural complexity and biodiversity remain unclear even at these lower levels because of the general lack of experimental manipulation. However, some recent studies manipulated structural complexity at the branch level and observed significant effects on species diversity and community organization (Gunnarsson 1990, Halaj et al. 1998, Halaj et al. 2000). For example, Halaj et al. (2000) manipulated needle density and branching complexity of Douglas-fir branches by removing needles, thinning branch axes, and tying branches. They found that spider species richness increased in structurally more complex habitats. The results of experimental manipulation of habitat structure suggested that structural complexity affects diversity and organization of spider communities by changing habitat quality and prey availability (Halaj et al. 2000), as well as predation rate by birds (Gunnarsson 1996). Halaj et al. (2000) also showed that abundance of highly mobile, airborne arthropods such as Diptera and Hymenoptera were not affected by manipulation of branch structural complexity, while relatively immobile, foliage-dwelling arthropods such as Collembola and Psocoptera showed marked responses. Furthermore, responses to variation in habitat structure differed even among members of the same arthropod order: e.g., spiders with different web-forming habits (Halaj et al. 2000). These studies indicate that structural complexity at various spatial scales need to be considered in accordance with body size, mobility, and ecological habits of the species in question to explain variation in diversity and patterns of community organization of canopy arthropods.

Discussion and Conclusions

As illustrated by the above studies at the two canopy research facilities located in different types of temperate forest and other studies conducted on forest canopies, detailed measurement and quantification of canopy structure at various spatial scales have refined our definition of stand structural complexity. Scaling up ecophysiological measurements made in situ in the canopy has provided better understanding of the relationship between canopy structure and stand productivity. Relating the spatial distribution of flora and fauna to canopy structure at various spatial scales has elucidated mechanisms of habitat structure that enhance biodiversity. We contend that three-dimensional structural attributes of forest stands is as important as tree species composition, size distribution, and other ground-based mea-

sures of stand structural complexity. The goal for studies of canopy structure should not be to develop a single index of stand structural complexity (e.g., Lähde et al. 1999, Zenner and Hibbs 2000, Staudhammer and LeMay 2001). Often, simplified indices of structural complexity show only weak correlations with species diversity (Neumann and Starlinger 2001). Rather, we should aim to elucidate important processes at various spatial scales that create structural complexity, increase stand productivity, and enhance biodiversity, thus providing ecological guidelines for managing forest ecosystems to carry out important ecological functions.

The impacts of human activity are most pronounced in the temperate regions (Martin 1996, Norton 1996), and this has raised much debate over future policies for managed and natural ecosystems (Kimmins 1997). Several studies have elucidated the effects of various management practices on structural complexity (Zenner 2000, Lindenmayer and McCarthy 2002), biodiversity (North et al. 1996, Beese and Bryant 1999), and ecosystem functions (Perry and Amaranthus 1997), with the general conclusion that simplification of stand structural complexity leads to decline of biodiversity and ecosystem functions (Bunnell and Huggard 1999). Forest management plans have been developed that consider multiple values (Gillis 1990, McComb et al. 1993), including conservation of biodiversity (Hunter 1999, Hartley 2002), long-term productivity (Franklin et al. 1989), and ecosystem health and integrity (Kimmins 1997). Önal (1997) proposed that management of forests to enhance biodiversity may be achieved by managing to increase stand structural complexity. For managed forests, this must be balanced with other potentially conflicting interests such as economic gain (Buongiorno et al. 1994, Carey et al. 1999b).

Forest ecologists are beginning to understand the role of canopy structure in enhancing various ecological functions, such as stand productivity and community organization. Management plans and silvicultural prescriptions should include not only conventional ground-based measures of stand structure, but also the three-dimensional structural attributes of forest canopies to realize multi-purpose management of forest ecosystems. Retention harvests and mixed-species plantations may not produce increased yield without sufficient development of multi-layered canopies that promotes complementary resource utilization among species. Likewise, a managed stand having species composition and tree-size distribution closely resembling those of natural forests may not support as many arboreal species if the structural habitat of the canopy is not sufficiently developed. The "canopy perspective" should not be overlooked in managing forests for structural complexity. Additionally, monitoring and manipulation of canopy structure should be considered in silvicultural prescriptions to enhance ecosystem integrity of managed forests (Berg et al. 1996).

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