Advances in understanding canopy development in forest trees

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1 Introduction

Canopy processes at once provide the fundamental building blocks for tree growth, health, and reproduction, and reflect the tree's ability to adapt to its immediate environment. Foresters' understanding of these processes informs their decisions about management activities that maintain and enhance forest vigor, health, and biodiversity while providing for desired ecosystem and economic benefits now and into the future. By manipulating density, foresters directly influence availability of light to the remaining trees and indirectly influence available water and nutrients. Forest canopies are highly variable within and among coniferous and broadleaf deciduous species, species genotypes, climates, and forest types; further, they vary with interspecies and intraspecies competition, forest disturbances, successional stage, and a myriad of other influences on forest development and reproduction (Barnes et al., 1998). Although most forest canopies are dominated by tree leaves, species within the *Chamaecyparis*, *Juniperus*, and *Thuja* genera have scales, which serve the same function as leaves. That is, they control evapotranspiration and respiration. Most importantly, they conduct photosynthesis. These tree species do not have preformed buds that require a period of dormancy and chilling before the tree can commence growth. For example, western red

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cedar (*Thuja plicata* Donn ex D. Don) readily responds to warming weather and initiates growth even in the winter. This premature activity subjects trees to damage when the weather turns cold again. Most angiosperm trees lose their leaves yearly; hence, they are deciduous and begin each growing season with new leaves. But some broadleaf species such as California live oak (*Quercus agrifolia* Née) are evergreen. As a corollary, most coniferous trees shed needles regularly with intervals as short as 2–5 years (e.g. western white pine [*Pinus monticola* Douglas ex D. Don] and ponderosa pine [*Pinus ponderosa* Lawson & C. Lawson]) and as long as 35 years or more (e.g. Great Basin bristlecone pine [*Pinus longaeva* D.K. Bailey], larch [*Larix* spp.], and baldcypress [*Taxodium distichum* (L.) Rich.]). Regardless of the type and temporal patterns of foliage, the complexities and sophistication of the evapotranspiration, respiration, and photosynthesis occurring in each leaf, needle, or scale (hereafter, collectively 'leaves') cannot be overstated. Foliage adapts to changing environments, weather, and disturbances (e.g. insects, diseases, fire, herbivory) so that these three essential processes will be sustained, providing the building blocks for tree growth, health, and reproduction. A common denominator throughout this complexity is how foliage interacts with light as light enters forest canopies and tree crowns, and subsequently comes in contact with a leaf.

In this chapter, we describe processes affecting physiological performance at the leaf level, including anatomical and morphological characteristics and how they shape, and are shaped by, environmental influences and physiological capabilities. These leaf functions can be scaled to the tree crown level to show how whole-tree photosynthesis and respiration influence growth, that is, the amount of carbon stored in stems, branches, and roots. Later in the chapter we explore how the spatial arrangement of leaves, branches, and stems – canopy structure – influences radiative transfer, water flux, and carbon flux between the atmosphere and the canopy. At this scale forest uses, treatments, and other stand-level disturbances (e.g. fire) along with forest succession and senescence are major drivers of how light influences forest development and such processes as carbon sequestration.

Canopy development in forest trees is the expression of the complex interactions of many structures, ranging from tree buds to massive tree crowns, to forested landscapes. Our understanding of this phenomenon is expanding with better data measurement achieved through more sophisticated technology, expansion of data collection around the world, and improved modeling of processes at a variety of scales. This chapter provides readers with highlights of advances in the research and tools that add to our knowledge of forest canopy development. Foresters can use this knowledge as a starting point to understand the processes in their forests and expand their knowledge with further study.

2 Physiological processes at the leaf level

2.1 Overview

As new leaves emerge and develop, light conditions within the forest canopy strongly influence leaf anatomy, morphology, biochemistry, and function (Hollinger, 1989; Niinemets et al., 1999; Coble and Cavaleri, 2014; Chin and Sillett, 2017). Within individual tree crowns and forest canopies, light conditions can vary drastically. Light transmittance from the top of the canopy to the forest floor can range from 100% of full sunlight conditions in low leaf area index (LAI) to <10% in high LAI (Pierce and Running, 1988; Parker et al., 2002). While light plays a dominant role in influencing leaf traits and function, additional factors such as gravitational effects (i.e. height) on leaf development and function may have the greatest influence in very tall trees (Koch et al., 2004; Woodruff et al., 2004).

Early greenhouse studies demonstrated that sun and shade leaves for perennials and shrubs display clear differences in anatomy, leaf traits, and function (Nobel et al., 1975; Chabot and Chabot, 1977; Chabot et al., 1979). Sun leaves were thicker, had a greater leaf mass per area (LMA, g m^{-2}), and had a greater photosynthetic capacity. Thicker sun leaves were thought to be the result of thicker palisade layers, a hypothesis supported by experiments that have observed similar increases over time in both leaf and palisade thickness during leaf development (Yano and Terashima, 2004). Due to their columnar shape, palisade cells play a fundamental role in facilitating light penetration at greater depths within the mesophyll (Vogelman and Martin, 2006), whereas the spongy mesophyll cells below palisade cells are capable of scattering light to increase light absorption.

While much of this research focused on shrubs and non-woody vegetation, research in forest canopies has observed differences between sun and shade leaves comparable to those reported for the greenhouse studies (Ellsworth and Reich, 1993; Coble and Cavaleri, 2017). Along vertical gradients, LMA, leaf nitrogen, and anatomical traits have been found to be strongly correlated with light conditions in temperate broadleaf deciduous and conifer trees (Hollinger, 1989; Ellsworth and Reich, 1993; Bond et al., 1999; Chin and Sillett, 2017). Accounting for differences in leaf morphology, chemistry, and function for both sun and shade leaves greatly improves modeling of photosynthesis at the crown and canopy level (de Pury and Farquhar, 1997). Within individual species, there is, however, an inherent limit on leaf morphology and functional traits at the extremes of light conditions (i.e. full sun and full shade). For example, shade-tolerant species that are capable of experiencing large changes in light conditions during their life cycle tend to have a greater leaf plasticity and ability to acclimate to changing light conditions (Goulet and Bellefluer, 1985; Coble et al., 2016). This observation has led to the hypothesis that leaf plasticity may play a role in forest succession (Goulet and Bellefluer, 1985).

In very tall conifer trees, the change in water potential due to gravity alone is enough to affect leaf turgor and leaf development (Koch et al., 2004; Woodruff et al., 2004; Meinzer et al., 2008). In the absence of transpiration, the gravitational potential gradient (-0.01 MPa m^{-1}) results in a lower leaf water potential at the top of the canopy (Scholander et al., 1965; Hellkvist et al., 1974). Turgor pressure in cells can be sustained through increases in osmotic concentration and subsequent decreases in osmotic potential. However, in tall Douglas-fir (*Pseudotsuga menziesii*) trees, turgor followed similar declines in leaf water potential due to a lack of osmotic adjustments with height (Woodruff et al., 2004; Meinzer et al., 2008). Leaf morphological and anatomical traits caused by the gravitational potential gradient of very tall conifer trees include greater LMA, smaller leaves, reduced intercellular air space, and greater carbon investments in transfusion tissue, which may explain limitations to photosynthesis at the top of very tall conifer trees (Koch et al., 2004; Woodruff et al., 2004; Ishii et al., 2008; Oldham et al., 2010). More recent investigations into cell water relations in tall trees have shown that tall conifer trees cope with the gravitational potential gradient through greater investment in transfusion tissue surrounding leaf veins (Oldham et al., 2010; Ishii et al., 2014; Azuma et al., 2016), greater leaf water storage and succulence (Ishii et al., 2014; Azuma et al., 2016), and decreasing turgor loss point with height via changes in tissue osmotica (Williams et al., 2017). These are all important mechanisms that helped to avoid turgor loss in the face of declining leaf water potential with height. These findings reinforce the strong role of the gravitational potential gradient in influencing leaf development and tissue water relations, as well as providing specific mechanisms that allow trees to grow to extreme heights.

In shorter trees, there is also an evidence for height effects on leaf development. In tropical broadleaf species, LMA was linearly and strongly correlated with height, yet LMA did not respond to light transmittance above 22% (Cavaleri et al., 2010). In temperate broadleaf deciduous forest species such as sugar maple (*Acer saccharum*), height effects were most apparent early in the growing season during leaf expansion, but light appeared to play a more dominant role after leaves acclimated to the local light conditions (Coble et al., 2016). In short temperate broadleaf deciduous trees, declining cell wall extensibility with height may be one possible mechanism associated with constraints on leaf development at the tops of trees (Zheng and Moskal, 2012). In both temperate broadleaf deciduous and conifer trees, investment in vascular tissue, including the xylem and parenchyma cells (total area and cell size) surrounding the leaf vein, increases with height (Shiraki et al., 2017; Coble and Cavaleri et al., 2017). Parenchyma cells surrounding the leaf vein in conifers are referred to as 'transfusion tissue', whereas in broadleaf species, parenchyma cells surrounding the leaf vein constitute the bundle sheath and bundle sheath extensions. Transfusion tissue and bundle sheaths provide a similar function in transporting water from the xylem to mesophyll cells and may play a role in water storage (Azuma et al., 2016; Ishii et al., 2014).

Regardless of the primary mechanisms influencing leaf development and morphology, the link between leaf function and morphology, as well as anatomy, is well documented. Leaf traits that are strongly associated with photosynthesis within forest canopies include LMA, leaf nitrogen, and leaf thickness (Field and Mooney, 1986; Ellsworth and Reich, 1993; Bond et al., 1999). An important implication of this work is that leaf anatomy and morphology can be used to understand and predict processes occurring at a larger scale, such as whole-tree and canopy photosynthesis. As is often the case, leaf morphological and anatomical traits are easier to measure than leaf photosynthesis, particularly in tall trees, due to logistical constraints. Factors that influence these traits such as light and leaf water potential are important to understand as they also affect carbon dioxide (CO_2) and water exchange at the crown and canopy level. Studies investigating specific mechanisms that allow trees to cope with the gravitational potential gradient provide insight into the limitations of tree height (Koch et al., 2004; Azuma et al., 2016; Williams et al., 2017), which have important implications for canopy structure of forests. Recent research in forest canopies has provided exciting insights into leaf responses to both light and height and has made additional progress in disentangling the two confounding factors in forest canopies. Future work that continues to investigate specific trade-offs of tolerating water stress, capturing light, and assimilating CO_2 in trees of all sizes will further advance our understanding of canopy ecophysiology.

2.2 Light gradient within the canopy

2.2.1 The effect of foliage clumping and leaf orientation

Light availability has a major role in regulating forest canopy development, and canopy structure determines how much light the forest can absorb (Atkins et al., 2018). The transmission of light through canopies results in vertical profiles of light intensity, which affect the photosynthetic activity and gas exchange of plants, their competition for light, and the canopy energy exchange. The attenuation of radiation passing through the canopy is directly affected by the density, size, and distribution (horizontal and vertical) of foliage and woody elements within the canopy, as well as spectral properties of leaves, woody elements, and the surface albedo beneath the canopy (Fig. 1).

Clumping (grouping) of foliage is a significant factor affecting the vertical light profile, particularly in forest canopies that are not completely closed (Nilson, 1992; Cescatti, 1997; Valladares and Guzman, 2006, Ni-Meister et al.,

Figure 1 Hemispherical photographs for canopy architecture and light transmission measurements (a) 28 April 2017, (b) 29 August 2017, (c) 10 May 2015. The image colors are enhanced for human vision. Photographs courtesy of Dr. Mait Lang.

2010). Clumping of canopy elements occurs in a hierarchical way in all forests: rosettes of leaves, shoots, crowns, trees, tree clusters, forest patches (Fournier et al., 1997). In conifers, successive levels of leaf clumping are present down to needle clumping in shoots, which may be an architectural strategy for the optimization of light absorption (Ford, 1992; Oker-Blom and Kellomäki, 1983; Stenberg et al., 1994). In terms of light interception, maintaining inefficient upper layers produces an even distribution of the irradiance on the total leaf area, and seems to be an architectural strategy of canopies to sustain higher amounts of foliage (up to LAI of 10 and more) (Larsen and Kershaw Jr., 1996; Russell et al., 1989; Stenberg, 1996).

Several optical field instruments and particularly hemispherical photography (Leblanc et al., 2005) can provide information about gap size distribution that is related to the foliage clumping index (for review of different methods see Gonsamo and Pellikka, 2009; Leblanc and Fournier, 2014; Raabe et al., 2017; Yan et al., 2019). The clumping index equals 1 when foliage is dispersed randomly throughout the canopy space and is in the range of 0–1 for clumped canopies (Chen and Black, 1992). Figure 2 illustrates vertical profiles of clumping obtained from digital hemispherical photography in two distinct canopies. The availability of range information from laser scanning systems also permits analysis of any vertical stratification in foliage clumping (van Leeuwen and Disney, 2018). Global and regional-scale clumping index maps have been generated using different approaches from a diverse set of Earth Observation multi-angle data sets across a wide range of scales (Pisek et al., 2015). It has been observed that satellite measurements are capable of capturing the structural elements at upper levels, whereas ground measurements may be biased by the lower vegetation layers (Pisek and Oliphant, 2013).

In addition to foliage clumping, leaf inclination angle distribution also affects the transmission of light along the canopy vertical gradient. Nilson (1968) solved theoretically the problem of optimizing the canopy structure for maximum production. He found that the optimal orientation of leaves is

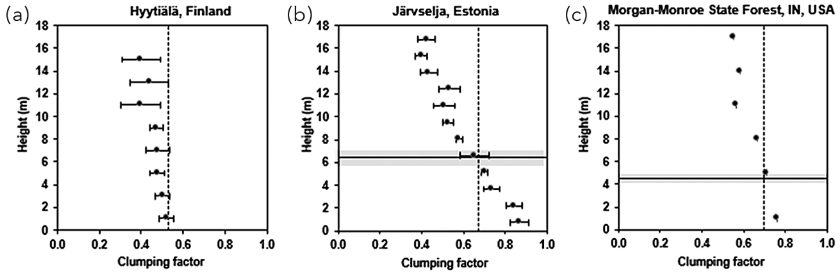

Figure 2 Vertical profiles of foliage clumping and gap fraction with ±1 standard deviation. Bars obtained with digital hemispherical photography. (a) boreal conifer (Scots pine) stand in Finland, (b) temperate deciduous broadleaf forest in Indiana, USA, (c) mixed hemiboreal forest in Estonia. Stand average clumping values from MODIS satellite data (He at al., 2012) are marked with vertical dashed black line. The mean height of undergrowth layer is marked by a grey horizontal line, shaded areas mark the ±1 standard deviation area.

erectophile (vertically oriented) in upper layers and planophile (horizontally oriented) in lower layers.

Leaf inclination angle distributions can change with canopy height, light exposure (McMillen and McClendon, 1979; Kull et al., 1999; Utsugi et al., 2006) and season (Hosoi and Omasa, 2009; Pisek et al., 2013). Seasonal changes are generally the most pronounced in early spring after the emergence of leaves and in late summer, before senescence (Raabe et al., 2015). Leaf inclination angle changes during spring can be caused by the unfolding of leaves, lengthening of the petiole, and increase in lamina mass (Niinemets, 1998). Later during the growing season, planophile leaf angles may become more erectophile due to simultaneous increases in lamina mass and area with an age-weakened petiole (Gordon and Promnitz, 1976; Hamerlynck and Knapp, 1996).

Shade-tolerant tree species tend to have more planophile leaves, whereas the leaves of shade-intolerant tree species are characterized by steeper leaf inclination angles (McMillen and McClendon, 1979; Pearcy et al., 2004). Different light exposure has a particularly strong effect on species with steeper leaf inclination angles, which, in conditions of limited exposure, display the optimal erectophile orientation at the top of the canopy and planophile leaves at the bottom of the canopy (Hollinger, 1989; Niinemets, 1998; Raabe et al., 2015). Steeply inclined leaves enable a greater amount of light penetration deeper into the canopy, whereas the planophile leaves at the bottom produce an increasing efficiency of light interception at lower intensities (Ford and Newbould, 1971; King, 1997). With high light availability, this stratification is not necessary. In contrast, species with planophile leaf inclination angle distribution remain relatively constant in different light conditions with a strategy of shading out other tree species instead of maximizing light interception (Hikosaka and Hirose, 1997).

Datasets of leaf inclination angles have been published (e.g. Chianucci et al., 2018), but this characteristic remains a highly variable one that depends on multiple factors. A preferred approach is to use distributions based on actual measurements obtained via digital photography (Ryu et al., 2010; Pisek et al., 2011; Raabe et al., 2015) or terrestrial LiDAR (Zheng and Moskal, 2012; Jin et al., 2015; Vicari et al., 2019) whenever feasible.

2.2.2 Acclimation of leaf traits along the canopy light gradient

Leaf capacity for light acclimation depends strongly on leaf age at the time of major modifications in light availability. Young developing leaves can respond much more plastically to changes in the light environment than can mature fully developed leaves (Yamashita et al., 2000; Oguchi et al., 2003, 2005). In tree canopies, the woody perennial branching framework remains for many years and regulates the positions of foliar elements within the canopy light gradient. In deciduous tree canopies with single flush leaf formation, the leaf light environment remains relatively constant during the entire leaf lifespan (Niinemets et al., 2004) allowing orchestrated light acclimation of anatomical, biochemical, and physiological leaf traits (Hallik et al., 2009a). Besides flush-type deciduous tree canopies, there exist fast-growing woody species with continuous shoot growth (Kull et al., 1998). Continuous canopy expansion of such fast-growing woody species results in shading of older leaves by newly developed leaves. This shading leads to foliage re-acclimation to altered light availability and can significantly modify relationships between leaf traits and light availability (Niinemets, 2016). Mature leaves have very limited capacity for anatomical changes in response to modifications in light availability. LMA is the most commonly measured foliar trait and reflects adjustments in leaf structure and anatomy. In flush-type deciduous canopies LMA increases strongly along the canopy light gradient since lower canopy layers have already become shaded during leaf formation and the early developmental stage, allowing full acclimation of structural leaf traits (Oguchi et al., 2003, 2005; Hallik et al., 2009a, 2012). There is also a light gradient inside the individual leaf. Sun leaves with high LMA and multiple palisade layers can distribute direct sunlight more evenly within the leaf. Lower LMA in shaded portions of the canopy helps to reduce self-shading inside the leaf. Leaf angle distributions of more vertical leaves in the upper canopy and more horizontally arranged leaves in the shaded lower parts of the canopy can further promote more uniform light interception along the full canopy light gradient. Here plastic acclimation responses combine with species-specific differences between shade-tolerant and intolerant species (Mänd et al., 2013).

Another commonly measured foliar trait is leaf nitrogen (N) content, which reflects the amount of the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and hence the leaf capacity for carbon fixation (Walker et al., 2014). Light acclimation of leaf nitrogen content follows patterns similar to LMA, suggesting that mature leaves have limited capacity for re-acclimation due to anatomical restrictions (Hallik et al., 2009b; Niinemets et al., 2015; Fajardo and Siefert, 2018). Since chlorophyll (Chl) is responsible for light capture and leaf N is primarily concentrated in Rubisco associated with carbon fixation, the Chl/N ratio can provide useful information about the stoichiometry of the photosynthetic apparatus. The light-harvesting part of the photosynthetic machinery produces adenosine triphosphate and nicotinamide adenine dinucleotide phosphate hydrogen (NADPH), which are used in the 'dark reactions' of the Calvin-Benson cycle to fix CO_2 into carbohydrates. In light-limited conditions, shaded leaves require a larger relative share of light-harvesting pigments within the photosynthetic apparatus in order to provide energy for carbon fixation. In conditions of excess light, total photosynthetic capacity could be even larger; however, a much smaller amount of the light-harvesting antenna complexes transferring light energy to the reaction center of a photosystem is needed to capture the same amount of energy, and the leaf needs to reduce the chlorophyll content to avoid damaging the photosynthetic apparatus. Hence, the light intensity has two opposing effects on foliar chlorophyll content. The positive effect is mediated via structural adjustments related to LMA and leaf thickness: A larger total amount of photosynthetic green biomass can be produced per unit of leaf area in high light conditions. Conversely, the direct effect of light intensity on leaf chlorophyll content is negative, resulting in a reduced Chl/N ratio (Hallik and Kull, 2008; Hallik et al., 2009b). Leaf light interception capacity also changes during the growing season due to the adjustments of amount and structural arrangement of pigments. Leaf optical properties (reflectance and transmittance) have been shown to change continuously until the end of the growing season (Mõttus et al., 2014).

The age and height of the individual tree can also affect the photosynthetic capacity of foliage. It has been shown that sink limitation can suppress photosynthesis in mature stands of Norway spruce (*Picea abies*), leading to a reduced photosynthetic capacity of older trees (Räim et al., 2012). Other stand characteristics manifested in species composition of neighboring trees have shown to influence foliar N content independent of light availability in silver birch (*Betula pendula*) but not in Scots pine (*Pinus sylvestris*) (Kaitaniemi et al., 2018). All these mechanisms in concert affect the relationship between light availability and photosynthetic capacity of foliage.

Plant functional trait-environment relationships are not unique, and different environmental drivers are responsible for trait combinations at local and global scales (Bruelheide et al., 2018). Light-driven plasticity in leaf traits should not be overlooked because most leaves exist in partial shade and only a small percentage of the total foliage is exposed to full sunlight. Ignoring this fact can lead to biased trait estimates at larger scales (Keenan and Niinemets, 2016). Photosynthetic light use efficiency (LUE) is enhanced under diffuse light in shaded conditions, which increases forest photosynthesis and can lead to biased carbon uptake predictions if unaccounted for in standard models (Lee et al., 2018). Dose-response curves have been used to quantitatively characterize the light responses of different traits among different species (Niinemets et al., 2015; Poorter et al., 2019).

In addition to plastic acclimation processes, species-specific differences can also significantly contribute to the observed relationship between leaf traits and light availability along a vertical canopy gradient. Leaf longevity is strongly related to LMA across different species. Evergreen species have a higher LMA than do shorter-lived species, a difference that forms the basis for the ‘leaf economics spectrum’ across plant functional types (Wright et al., 2004; Shiklomanov et al., 2018). Shade responses can alter this relationship. Increased leaf longevity generally improves species shade tolerance, but a higher LMA at a given leaf longevity can negatively affect species shade tolerance (Hallik et al., 2009b). This leads to two opposing effects of light availability on LMA. Therefore, it could be concluded that leaf trait values at certain canopy position can differ due to foliage reacclimation to modifications in light availability, leaf age, stand age, or species-specific differences (Hallik et al., 2012; Niinemets, 2016). In certain temperate and hemiboreal regions, the forest canopy can be formed by a mixture of evergreen conifers and winter-deciduous woody species that have either flush-type or continuous leaf formation. The presence of both types of species leads to simultaneous operation of the full range of trait responses to the dynamics of the light environment.

3 Physiological processes at the canopy (stand) level

3.1 Overview

Radiative transfer, carbon flux, and water flux occurring at the canopy level are strongly governed by processes, structure, and environmental responses occurring at the leaf and crown levels. The dominant physiological processes that control carbon flux and storage are leaf photosynthesis and respiration. Transpiration is the primary process that dictates whole-tree water use, and at the stand level, evapotranspiration, particularly during the growing season. Quantifying and modeling these processes involve some form of scaling of processes from a finer scale up the crown- and canopy-level. Other methods such as large, closed-air circulation chambers can be an effective method for measurement of whole-tree net photosynthesis and respiration for smaller trees

(Corelli-Grappadelli and Magnanini, 1993; Mori et al., 2010). Photosynthesis can also be estimated from canopy-level measurements, made using the eddy covariance method (Sec. 3.3), of the net ecosystem exchange of CO_2.

Photosynthesis is often measured and modeled at the leaf level and scaled up to the crown using the total leaf area of the crown or the vertical and horizontal distribution of leaf area across the length of the crown (Wang and Jarvis, 1990; Wang et al., 1990). Scaling photosynthesis and leaf respiration to the crown level requires an estimate of whole-tree leaf area or vertical distributions in leaf area, which can be estimated with a representative sample of leaves from branches throughout the crown. Different portions of crowns can photosynthesize more efficiently than other portions, with the central part often the most efficient, the top portion next most efficient and the bottom of the crown the least efficient at photosynthesis (Oliver and Larson, 1996). One approach to estimating whole-tree leaf area is by developing branch-scale allometric equations for a given species (Monserud and Marshall, 1999; McDowell et al., 2002). A similar approach can be used to estimate coefficients that describe the vertical and horizontal distribution of leaf area within crowns (Wang et al., 1990). In contrast to photosynthesis and respiration, whole-tree transpiration can be estimated with measurements of sap velocity at one or more depths in the sapwood and scaled to the tree-level (e.g. sapflow) using sapwood area of the stem or divisions of sapwood area at each measurement depth (Burgess et al., 2001; Alvarado-Barrientos et al., 2013).

Given that photosynthesis is difficult to measure continuously over a long period of time for many trees, photosynthesis is modeled using environmental response parameters derived from field measurements. For example, coefficients that describe light and temperature response curves are commonly used for photosynthesis (Leverenz and Jarvis, 1979; Ögren, 1993; Medlyn et al., 2002). Thus, microclimatic conditions at the location of individual leaves are a critical component to modeling photosynthesis at the leaf level and hence for scaling up to the crown and canopy levels. Due to the strong role of canopy structure in influencing light transmittance and absorbance in forest canopies, models of light interception usually incorporate some form of canopy structure.

A challenge to modeling whole-tree photosynthesis is the component of modeling light conditions for individual layers within the crown. Unlike canopy models that treat the canopy as one or more vertical, horizontally uniform layers, models that compartmentalize the canopy into discrete units (i.e. crowns) with horizontal and vertical dimensions must account for neighboring trees because of shading from those trees, in addition to within-crown shading. To account for this, Norman and Welles (1983) developed a three-dimensional array model for radiative transfer that can be applied to nearly any type of plant canopy, where the canopy is expressed as an array of ellipsoidal crowns. This model has been incorporated in canopy photosynthesis models (Wang and Jarvis, 1990;

Medlyn, 2004) and tested and validated using detailed measurements of light interception at individual layers within crowns (Bauerle et al., 2004).

A number of approaches to scaling photosynthesis and leaf respiration to the canopy have been used. Big-leaf and two-leaf models are a few examples that include less spatial detail than the spatially explicit models (Sellers et al., 1992; de Pury and Farquhar, 1997), but very useful in many regards such as modeling radiative transfer, evapotranspiration, and gross primary productivity at large spatial scales (Samson and Lemeur, 2001; Dai et al., 2004; Ryu et al., 2011). The big-leaf and two-leaf models integrate absorbed radiation and leaf nitrogen across the canopy using LAI (m^2 m^{-2}), extinction coefficients, open sky light conditions (for light), and upper canopy leaf nitrogen (de Pury and Farquhar, 1997). Canopy leaf nitrogen can be used to predict the canopy photosynthetic capacity, which is then used with absorbed radiation over time to predict instantaneous canopy photosynthesis. The two-leaf model separates sun and shade leaves, whereas the big-leaf does not make this distinction. A two-dimensional multi-layered model is another approach to modeling light conditions and photosynthesis at defined vertical layers and can also be used to scale to the canopy (Leuning et al., 1995). Information from light interception models can be used for evaluating light absorbed by canopies and can also be applied more broadly to modeling carbon- and water-flux in forest canopies. In many cases, estimates of carbon- and water-flux requires a light interception submodel, necessary for modeling photosynthesis and leaf energy balance.

The spatial arrangement of leaves, branches, and stems (i.e. canopy structure) is a key component of forests that influences microclimate, radiative transfer, water flux, and carbon flux between the atmosphere, tree crowns, and the canopy (Norman and Jarvis, 1975; Luo et al., 2001; Law et al., 2001; Whitehead et al., 2004). Quantifying crown and canopy structure facilitates modeling stand-level processes as well as scaling leaf-level measurements to the canopy. Canopy structure affects light transmittance, relative humidity, temperature, the amount of precipitation falling through the canopy, and the environment of other living organisms (Campbell and Norman, 1989).

Canopy structure and light transmittance are influenced by a number of factors that can be broadly grouped into three categories: (1) stand developmental changes over time associated with natural processes and disturbance, (2) silvicultural treatments, and (3) phenology and seasonal patterns of development and senescence (for further explanation of phenology, see Section 3.2). With respect to stand development, canopy structure changes as stands increase in age and through the process of forest succession and shifts in species composition (Hedman and Binkley, 1988; Parker, 1997; Frazer et al., 2000; Parker et al., 2002). In younger stands, light decreases rapidly with canopy depth over a very narrow vertical range, whereas old-growth stands display more gradual changes over a longer vertical range (Parker et al., 2002). Within old-growth forests, the transition zone of light conditions (~0.2–0.8 transmittance, fraction) occupies a much larger space of the canopy as compared with younger forests. Characteristics of this transition zone include a steep gradient and high variation in light conditions, and a mixture of beam and diffuse light; this zone coincides with the majority of leaf area in the canopy (Parker, 1997). Understory light conditions in old-growth forests also tend to be more heterogeneous than younger stands. Old-growth forests are likely to provide more opportunities for leaves and branches of different species to occupy a suitable range of light conditions throughout the canopy.

The change in species composition during succession, particularly the increasing presence of shade-tolerant species, results in transformations in canopy structure and light transmittance. In older mixed-species deciduous forests, there is often a vertical stratification of tree species and sizes, which all contribute to canopy structure (Hedman and Binkley, 1988; Parker et al., 1989). The vertical profile in light conditions is responsible for the vertical stratification of shade-tolerant and shade-intolerant species, and in turn, profiles in light transmittance are strongly influenced by that stratification (Canham et al., 1994). Shade-tolerant species with deeper crowns tend to cast more shade than shade-intolerant species (Canham et al., 1994).

Silvicultural treatments that selectively remove trees through thinning or patch cuts promote greater penetration of light through the canopy and expose more leaves of residual trees to high light conditions. A number of studies have found that stand density affects the leaf area distribution within crowns and canopies (Stephens, 1969; Gary, 1978; Vose et al., 1995; Medhurst and Beadle, 2001). Thus, the modified profile in light transmittance after thinning influences the canopy structure once leaves and branches have had sufficient time to acclimate to the change in light conditions, leading to adjustments in leaf area distribution throughout individual tree crowns. After forest thinning, leaf area distributions tend to display a normal distribution, where the maximum leaf area is near the center of tree crowns (Gary, 1978; Medhurst and Beadle, 2001). In unthinned stands, the leaf area tends to be more concentrated toward the top of the canopy. Consistent with these findings, Alcorn et al. (2013) found that leaf area was more distributed toward the top of the canopy when canopies were closed for longer. In contrast, other studies have observed upward shifts in leaf area distribution in response to thinning (Maguire and Bennett, 1996), or no change (Bidlake and Black, 1989). The studies described here occurred in even-aged stands or plantations. Further work that evaluates the effects of silvicultural prescriptions on canopy structure in more complex stands would further contribute to our understanding of forest management and ecology.

The horizontal arrangement of foliage related to grouping or clumping also influences light transmittance through canopies, which is relevant for density management in forests (see Section 2.2.1). Accounting for clumping in light interception models is particularly important in low-density and sparse stands where foliage is clumped within discrete units around tree stems (Oker-Blom and Kellomäki, 1983; Whitehead et al., 1990; Law et al., 2001). Models that incorporate clumping indices typically result in greater light transmittance values deeper into the canopy and at the forest floor, as would be expected in a low-density stand (Oker-Blom and Kellomäki, 1983; Whitehead et al., 1990; Law et al., 2001). Models that do not account for clumping assume a random horizontal distribution of leaf area, which is more appropriate for stands with a high stand density or basal area with a closed canopy. Another approach to accounting for clumping is through the use of three-dimensional models that account for the crown architecture of individual trees and their locations (Norman and Welles, 1983; Wang and Jarvis, 1990; Medlyn, 2004).

3.2 Canopy phenology and the PhenoCam method

Seasonal variation in both the amount of foliage and its physiological activity plays a key role in governing many canopy processes including light attenuation, photosynthesis, and transpiration (Parker and Tibbs, 2004; Richardson et al., 2013a). Conventional observations of canopy phenology have focused on characterizing the timing of specific phenological events such as budburst and leaf-off dates. However, the overall seasonal trajectory is more relevant in the context of canopy processes. From year to year this trajectory varies in response to weather. For example, in temperate deciduous forests leaves may emerge a week (or more) earlier than normal in years with a warm spring, driving increases in springtime ecosystem productivity (Richardson et al., 2009).

High-frequency field measurements of canopy LAI are labor-intensive and hence are rarely conducted often enough to precisely detect interannual variation in the seasonal trajectory. Radiometric methods, such as measurement of fAPAR (the fraction of photosynthetically active radiation that is absorbed by the canopy) or broadband NDVI (a version of the normalized difference vegetation index derived from measurements of incident and reflected photosynthetically active radiation and shortwave radiation), have been suggested as alternative proxies (Jenkins et al., 2007; Richardson et al., 2013b). Satellite remote sensing also can be used to track canopy phenology (Zhang et al., 2003) although spatial and temporal resolutions are commonly identified as limiting factors.

Digital cameras or ‘phenocams’ have increasingly been used to monitor vegetation phenology in many forests, as well as in other ecosystem types (Richardson et al., 2007b; Richardson, 2018). Unlike most satellite remote sensing, this method has the advantage of providing information on the state of the canopy at daily temporal resolution. And unlike tower-based radiometric measurements which integrate across the canopy, it is possible to distinguish among individual organisms with phenocam imagery.

3.2.1 The PhenoCam approach

Typically, PhenoCam imagery is recorded at least once daily, and images are stored as minimally compressed JPEG files. The images provide a permanent record of the state of an ecosystem at a point in time and can be inspected visually to determine phenological transition dates, or phenophases. But the camera can also be viewed as a multi-channel imaging sensor, and thus quantitative data can be extracted directly from the imagery. Image processing consists of using very simple routines to extract information about vegetation color, in the form of red, green, and blue (RGB) channel intensities or pixel values, calculated across a user-defined region of interest. From the RGB data, seasonal changes in vegetation color can be characterized using a variety of ratio indices. One such index is the green chromatic coordinate (G_{cc}), calculated as the mean green channel intensity, normalized against the sum of the RGB channel intensities (Wingate et al., 2015; Richardson et al., 2018a). Other indices have been proposed and shown to be superior in some applications (Mizunuma et al., 2013; Nasahara and Nagai, 2015), and alternative methods leveraging the near-infrared sensitivity of the imaging sensors commonly used in today's digital cameras have also been developed (Petach et al., 2014; Filippa et al., 2018). These indices are analogous to the indices routinely calculated from airborne and satellite remote sensing images, such as enhanced vegetation index (EVI), NDVI, and chlorophyll carotenoid index (CCI).

The timing and amplitude of seasonal changes in canopy color vary among forests. Temperate deciduous broadleaf forests (Fig. 3a) tend to have the largest seasonal amplitude of canopy greenness. The color of the canopy at any given time is driven by the amount of leaf area, and the color of individual leaves (Keenan et al., 2014). Greenness increases rapidly in spring with the flush and expansion of new leaves, which drop off more gradually in the fall as they change color and are shed. In evergreen needleleaf forests (Fig. 3b), seasonal changes in canopy greenness are generally driven by biochemical changes within existing foliage. Specifically changes occur in foliage concentrations of chlorophyll, carotenoid, and xanthophyll cycle pigments, which are associated with seasonal upregulation and downregulation of photosynthetic capacity (Bowling et al., 2018). By comparison, in tropical evergreen broadleaf forests (Fig. 3c), the seasonal changes in canopy greenness may be negligible.

3.2.2 Extracting phenological transition dates

Just as methods have been developed to extract phenophase transition dates, corresponding to the start and end of the growing season, from satellite remote

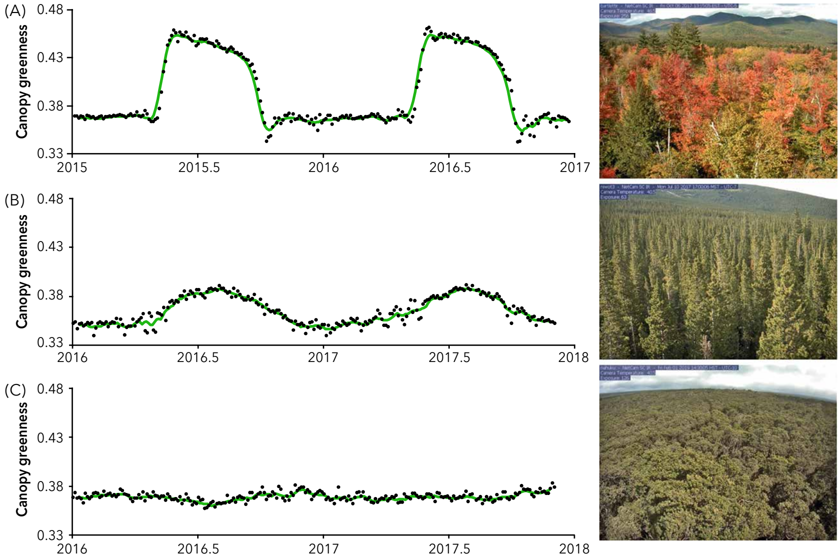

Figure 3 Representative examples of seasonal changes in canopy greenness for different forest ecosystems, quantified from PhenoCam imagery using the green chromatic coordinate. (a) temperate deciduous broadleaf forest: Bartlett Experimental Forest, New Hampshire, USA, (b) montane evergreen conifer forest: Niwot Ridge, Colorado, USA, (c) tropical evergreen broadleaf forest: Nahuku, Hawaii, USA. The y-axis range is the same in all figures.

sensing indices such as NDVI (Zhang et al., 2003), it is also possible to extract similar transition dates from camera-based indices such as G_{CC}. Spline, sigmoid, and piecewise regression approaches have all been used with good success (Klosterman et al., 2014; Wingate et al., 2015; Filippa et al., 2016; Richardson et al., 2018a). Particularly for deciduous broadleaf forests, the derived transition dates have been shown to correlate well with biologically relevant phenological transition dates observed by people on the ground (Richardson et al., 2018a) or inferred from visual inspection of the camera imagery (Klosterman et al., 2014; Kosmala et al., 2016), and transition dates derived from satellite remote sensing platforms including MODIS, VIIRS and Landsat (Klosterman et al., 2014; Melaas et al., 2016b, Zhang et al., 2018; Richardson et al., 2018b). These transition dates have been widely used to develop and parameterize improved phenological models using data from across a wide spatial domain (Melaas et al., 2016a; Hufkens et al., 2018).

3.2.3 Long-term observations and camera-based phenological networks

In the years since the PhenoCam method was first developed (Richardson et al., 2007b), the method has been widely adopted for forest monitoring around the world. Time series from some individual cameras are more than a decade in length. For example, at Harvard Forest, Massachusetts, USA, the same StarDot NetCam SC camera has been recording images continuously, every half hour from 4 a.m. to 10 p.m., from 2008 through 2019 – over 125 000 images to date. These data reveal the seasonal rhythms of green-up and senescence in relation to interannual variation in weather. Spring green-up dates have varied by more than 2½ weeks over that period, from day 121 (May 1) to day 139 (May 19) of a year, and green-down dates in the fall have varied by more than 3 weeks, from day 277 (October 4) to 298 (October 25). The green canopy duration – measured as the number of days between green-up and green-down – thus varies from year to year by 17 days, or 10%, which has important implications for CO_2 uptake and primary production (Richardson et al., 2010a).

Regional-to-continental scale camera-based phenological observatory networks have also been established. The PhenoCam network, which targets ecosystems across North America, currently includes imagery from over 500 cameras. Data are available in near real time through the project web page (http://phenocam.sr.unh.edu), and fully processed and curated data sets derived from PhenoCam imagery have been made publicly available (Richardson et al., 2018a). Other networks have been established in Asia (Nasahara and Nagai, 2015), Europe (Wingate et al., 2015), Australia (Moore et al., 2016), and Brazil (Alberton et al., 2014). These networks can contribute to monitoring and tracking forest responses to global change.

3.3 Ecosystem physiology and the eddy covariance method

Although modeling canopy-level fluxes of carbon and water require difficult scaling from leaves to canopy, methods to measure canopy-level fluxes have been developed and are now widely used. The eddy covariance method uses high-frequency (5–20 Hz) measurements of trace gas concentrations, air temperature, and the horizontal and vertical wind components to quantify the exchange, or flux, of matter (e.g. uptake and release of CO_2 and other trace gases) and energy (sensible and latent heat fluxes) between the land surface and the atmosphere (Aubinet et al., 2012; Burba, 2013). The ideas behind the method originated with Sir Osborne Reynolds in the late 1800s (Baldocchi, 2013), and by the mid-twentieth century the method was fully conceptualized (Aubinet et al., 2012). However, instrument technology lagged behind theory and several decades would pass before the necessary instruments – fast-response infrared gas analyzers and sonic anemometers – were developed. 'Modern' eddy covariance measurements over crops were conducted by Shashi Verma and students in the 1980s (Anderson et al., 1986), and beginning in 1991 Steve Wofsy and collaborators initiated continuous, long-term measurements above a temperate deciduous forest (Wofsy et al., 1993). Wofsy's measurements at Harvard Forest, Massachusetts, USA, which continue to this day, represent the longest continuous record of forest-atmosphere CO_2 flux in the world, and they provide an important benchmark for tracking forest responses to global change.

The eddy covariance method has relevance to ecological and global change studies because it can be applied both to characterize the canopy-level integrated ecosystem response to external and internal forcing and to evaluate these responses over different time scales, from hourly to decadal. These measurements place a top-down constraint on estimates of ecosystem-atmosphere flux scaled up from small-scale or cuvette-based measurements of matter and energy exchange, such as chamber measurements of leaf-level photosynthesis or transpiration, or soil CO_2 flux (Carbone et al., 2019). Eddy covariance measurements thus provide insights into forest ecophysiology at the ecosystem scale (Richardson et al., 2007a), annual carbon budgets (Baldocchi, 2008; Baldocchi et al., 2018), and surface-atmosphere interactions and coupling (Bonan, 2008; Richardson et al., 2013a)

3.3.1 Half-hourly to interannual time scales

Eddy covariance measurements are commonly calculated at the half-hourly time step (17 520 measurements per year). Figure 4 shows the half-hourly net ecosystem exchange (NEE) of CO_2 over the first 14 years (2004–2017) of measurements at a deciduous forest in Bartlett, New Hampshire, USA (Lee et al., 2018). NEE represents the balance between photosynthetic uptake by plants and cellular respiration by all living organisms, including soil

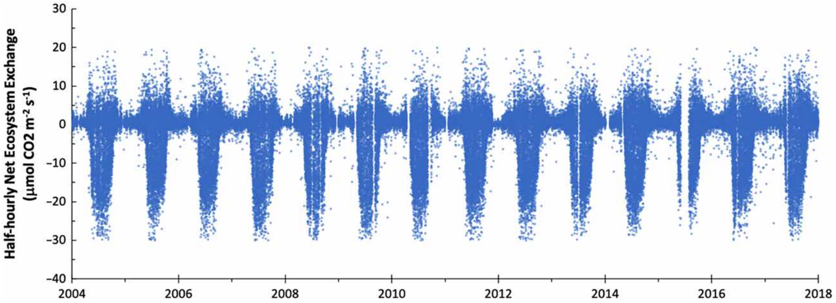

Figure 4 Half-hourly forest-atmosphere CO_2 fluxes (net ecosystem exchange, or NEE) at Bartlett Experimental Forest, New Hampshire, USA, measured over 14 years using the eddy covariance method. Negative fluxes indicate net uptake of CO_2 by the forest, while positive fluxes indicate net release of CO_2 by the forest. The obvious seasonal rhythms relate to both biotic and abiotic factors that lead to low CO_2 exchange during the winter (dormant season) and both high respiratory (efflux) and high photosynthetic (uptake) fluxes during the summer (growing season).

microbes. Following the micrometeorological convention, negative values of NEE correspond to a flow of carbon from the atmosphere to the ecosystem (C-uptake, photosynthesis > respiration) whereas positive values of NEE correspond to a flow of carbon from the ecosystem to the atmosphere (C-efflux, respiration > photosynthesis).

At Bartlett, the obvious seasonality of NEE is driven by a variety of factors, both biotic and abiotic. Bartlett's dominant deciduous species (sugar maple [*Acer saccharum*], American beech [*Fagus grandifolia*], yellow birch [*Betula alleghaniensis*]) have an LAI close to zero during the dormant season, but about 4 m^2 m^{-2} during the growing season. The seasonality of leaf area places a top-down constraint on photosynthetic productivity. Likewise, respiratory fluxes are small in magnitude during the winter when metabolism of all organisms is limited by temperature, but these fluxes are much higher in summer as metabolic activity increases approximately exponentially with increasing temperature. Although the seasonal patterns in Fig. 3 are superficially similar across years, the corresponding differences in annual NEE, canopy photosynthesis, and ecosystem respiration (Table 1) are substantial, with annual NEE varying by a factor of five between 2005 (-48 ± 36 g C m^{-2}) and 2007 (-244 ± 44 g C m^{-2}).

Table 1 Interannual variation in annual net ecosystem exchange (NEE) of CO_2, gross primary production (GPP, a proxy for canopy photosynthesis), and ecosystem respiration (Re) at the Bartlett Experimental Forest AmeriFlux site, a temperate deciduous forest in New Hampshire, USA

Year	NEE	GPP	Re
2004	−203 ± 32	1215 ± 42	1012 ± 62
2005	−48 ± 36	1121 ± 50	1073 ± 75
2006	−120 ± 29	1215 ± 53	1095 ± 71
2007	−244 ± 44	1393 ± 59	1149 ± 83
2008	−206 ± 34	1323 ± 50	1116 ± 72
2009	−158 ± 46	1429 ± 100	1271 ± 124
2010	−120 ± 44	1302 ± 63	1182 ± 83
2011	−174 ± 32	1233 ± 43	1059 ± 63
2012	−114 ± 49	1291 ± 71	1177 ± 113
2013	−120 ± 39	1309 ± 100	1189 ± 123
2014	−114 ± 30	1314 ± 46	1200 ± 61
2015	−102 ± 41	1268 ± 88	1166 ± 94
2016	−110 ± 40	1378 ± 129	1269 ± 156
2017	−69 ± 38	1383 ± 54	1315 ± 76

Half-hourly NEE measurements were gap-filled and partitioned to GPP and Re using the methods of Barr et al. (2013). Reported uncertainties indicate 95% confidence intervals, determined by Monte Carlo simulation. Units are g C m^{-2} y^{-1}.

Year-to-year variation in NEE is related to both biotic (phenology) and abiotic (weather) factors.

3.3.2 Seasonality of CO_2, water, and energy fluxes

The seasonality of surface-atmosphere fluxes also varies both among forest types and in response to environmental factors. In Figs. 5 and 6, we compare this seasonality for a sub-tropical evergreen forest (Tumbarumba, New South Wales, Australia) (Leuning et al., 2005), a sub-boreal evergreen forest (Howland, Maine, USA) (Hollinger et al., 2004), and a temperate deciduous forest (Bartlett). The seasonality of fluxes is offset between the southern (Tumbarumba) and northern (Howland and Bartlett) hemisphere sites. This is most clearly captured by the daily integral of incident shortwave radiation (Rg) (Fig. 5a), which represents the input of solar energy to the ecosystem. This energy input drives the seasonality of available energy (net radiation minus ground heat flux) and hence the sum of sensible (H) and latent heat (LE, equal to ecosystem evapotranspiration, expressed in energy rather than H_2O units) fluxes. The partitioning between H and LE (i.e. the Bowen ratio, $B = H/LE$) is further influenced by moisture availability and vegetation activity (Figs. 5b and c). For example, at the temperate deciduous Bartlett site in early spring, most of the available energy is directed toward H. Once foliage begins to emerge, LE increases rapidly as forest transpiration moves water from the soil column into the atmosphere. As the canopy develops, LE consumes an ever-increasing amount of the available energy. And, with more of the available energy being used to evaporate water, this leads to a corresponding drop in H despite the continued increase of Rg through midsummer. For further discussion of how phenology influences partitioning of the surface energy budget, see Richardson et al. (2013a).

The seasonality of Rg also plays a critical role in driving the seasonality of ecosystem-atmosphere CO_2 fluxes. In the evergreen ecosystems, Tumbarumba and Howland, canopy photosynthesis generally scales in a saturating manner with increasing Rg, unless temperature, soil water, or vapor pressure deficit is otherwise limiting. In the deciduous ecosystem, Bartlett, seasonal variation in the amount of photosynthetically active leaf area is also a primary constraint. As described earlier, the seasonality of ecosystem respiration is mostly driven by temperature. The seasonality of daily NEE thus varies among sites and reflects both ecological and climatological differences among ecosystems (Fig. 6a). Differences in daily CO_2 exchange then show up clearly as differences in the phasing and magnitude of cumulative net ecosystem CO_2 uptake over the calendar year (Fig. 6b). The seasonality of canopy-level photosynthetic activity (GPP) (Fig. 6c) is also markedly different among these three ecosystems. For example, at Tumbarumba, seasonal variation in GPP parallels that of Rg, but even

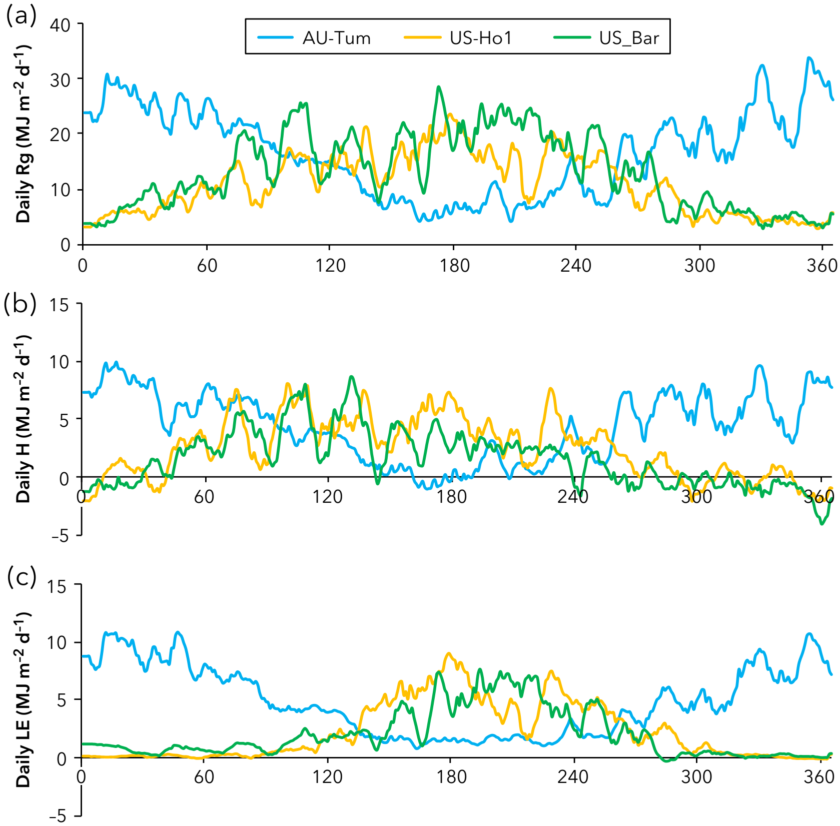

Figure 5 The seasonal cycle of forest-atmosphere energy fluxes measured at a subtropical evergreen forest (Tumbarumba, New South Wales, Australia, AU-Tum), a subboreal evergreen forest (Howland, Maine, USA, US-Ho1), and a temperate deciduous forest (Bartlett, New Hampshire, USA, US-Bar). Rg is incident shortwave radiation, H is sensible heat flux, and LE is latent heat flux (evapotranspiration, expressed in energy units). The seasonality of fluxes is offset between the southern (Tumbarumba) and northern (Howland and Bartlett) hemisphere sites. Day-to-day variability in Rg, superimposed on the seasonal cycle, is driven by weather and the amount of cloud cover. For H and LE, the sign convention is that a positive flux indicates the flow of energy from the ecosystem to the atmosphere. Data are from the FLUXNET La Thuile data set.

during the depths of the austral winter (days 180 to 240) the evergreen canopy is photosynthetically active. By comparison, at both Bartlett and Howland there is negligible canopy activity from day 300 to day 60. In late spring the evergreen canopy at Howland begins photosynthetic uptake around day 90 compared to day 120 for the deciduous canopy at Bartlett. The evergreen canopy at Howland also maintains photosynthetic uptake in the fall later than the deciduous canopy at Bartlett. Eddy covariance measurements thus illuminate temporal and across-ecosystem patterns of variation in ecosystem function.

Figure 6 The seasonal cycle of forest-atmosphere CO_2 fluxes measured at a sub-tropical evergreen forest (Tumbarumba, New South Wales, Australia, AU-Tum), a sub-boreal evergreen forest (Howland, Maine, USA, US-Ho1), and a temperate deciduous forest (Bartlett, New Hampshire, USA, US-Bar). NEE is the net ecosystem exchange of CO_2, which has been partitioned to ecosystem respiration and gross primary production (GPP, a proxy for canopy photosynthesis) using the method of Reichstein et al. (2005). Data are from the FLUXNET La Thuile data set.

3.3.3 Derived quantities and applications to modeling

Beyond the investigation of seasonal patterns or annual budgets, flux measurements can be applied to several other end-uses. For example, simple light-response functions can be used to estimate canopy-level light-saturated photosynthetic rates (Ollinger et al., 2008). Alternatively, by using methods based on the Farquhar photosynthesis model, more sophisticated approaches can be used to estimate the maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}) at canopy level (Knauer et al., 2018). These can then be directly compared with estimates derived from leaf-level field measurements, or used for model parameterization. Another approach is to use the derived quantities to characterize sources of seasonal or interannual variation, or long-term trends, in ecosystem function (Groenendijk et al., 2011; Keenan et al., 2012). Alternatively, the flux measurements can be used to constrain ecosystem and land surface model parameters and states using a model-data fusion approach (Williams et al., 2009). This method is most successful when data on ecosystem carbon pools are also incorporated (Richardson et al., 2010b).

The eddy covariance methods have also been used to quantify the changes in ecosystem C fluxes associated with disturbance and succession; these data show that following disturbance, most forest ecosystems recover rapidly and within 10–20 years are strong carbon sinks (Amiro et al., 2010), and that contrary to conventional ecosystem development theory, even mature forests can be strong C sinks (Curtis and Gough, 2018).

3.3.4 A global perspective

Initially, short-term to long-term (months to years) studies of ecosystem-atmosphere exchanges at individual sites were important because they provided needed information about how specific ecosystem responded to environmental forcing. However, it was soon recognized that national and international collaborations, facilitating cross-site syntheses, would more directly lead to generalizable knowledge. FLUXNET, a global network of sites using the eddy covariance method (Baldocchi et al., 2001), was established in 1998, and hundreds of sites globally contribute data to the FLUXNET database (Pastorello et al., 2017). Important synthesis papers from FLUXNET have demonstrated that the network is far greater than the sum of its parts, as a large number of sites across a diverse array of ecosystem types have enabled increasingly improved upscaling of ecosystem function to global scales (Beer et al., 2010; Jung et al., 2010, 2011). However, underrepresented ecosystems, particularly in South America, Africa, and Southeast Asia, remain a persistent challenge.

3.3.5 Limitations and uncertainties

The eddy covariance method is not perfect. Random errors associated with the stochastic nature of turbulence result in substantial uncertainties in the high-frequency (30 minute) flux measurements (Richardson et al., 2006). Systematic errors, or biases, can occur if critical assumptions are not met, or if the necessary corrections are not applied (Richardson et al., 2012). Unlike random errors, which 'average out', systematic errors accumulate over time; hence, small biases can become more pernicious when data are integrated to longer time scales. Energy balance closure has long been recognized as an important issue (Wilson et al., 2002; Foken, 2008). Eddy covariance flux measurements are also detrimentally influenced by advection, uneven topography, and spatial heterogeneity (Massman and Lee, 2002). In spite of these limitations, this method has, as described here, provided remarkable insights into how forest canopies function.

4 Conclusion and future trends

In this chapter, we examined the progression of physiological processes from leaf to crown to canopy and presented select scientific analyses at different scales within a forest. An overarching theme was the mutual reinforcement of structure and function. Shade-tolerant and shade-intolerant species assume different leaf orientations as befitting their physiological needs, but these behaviors may adjust as environmental conditions change, both physically in a canopy and temporally during the growing season. For most tree species, light and water availability are the primary drivers of physiological responses. There are differences between species in their capacity for photosynthesis and transpiration, and the relative performance of the two. For example, both sweet birch (*Betula lenta*) and northern red oak (*Quercus rubra*) may be considered 'drought endurers'. But in a study of the physiological performance of juvenile and mature cohorts of co-occurring species, sweet birch proved itself unable to cope with late-summer water stress. The leaves lost turgor and stomata eventually closed. Meanwhile, the oaks' superior water and transport system allowed photosynthesis to continue (Moser, unpublished data). These basic physiological behaviors translate into whole-canopy performance. Height is often limited by the ability of the tree to supply water and nutrients to the leaves at the very top, although there are interspecific and intraspecific differences in this limit (e.g. *Sequoia sempervirens* vs. *Pseudotsuga menziesii*, or *Pseudotsuga menziesii* var. *menziesii* (Coast Douglas-fir) vs. *Pseudotsuga menziesii* var. *glauca* (Rocky Mountain Douglas-fir)).

Foliage clumping affects light transmission in canopies. Clumping can be hierarchical, progressing from leaf level to trees and then to forest-level clusters. Various studies have found differential amounts of foliage clumping at different heights within the crowns of conifer, broadleaf, and mixed forests in the Northern Hemisphere. We also reported studies of the variation of leaf angle by species, age of tree, position in the crown, and the date within the growing season. A balance must be achieved between the anatomical makeup of the leaf and available light. If light levels are too high with respect to leaf capacity to use the energy, the leaf structure and chemistry could be damaged. If light levels are too low, carbon uptake will be inadequate, limiting the supply of carbohydrates to fuel respiration and growth. The leaf traits observed along light gradients reflected the interconnectedness of structure and function referred to earlier.

Scaling up from leaf-level processes to crown and canopy levels requires estimates of total leaf area or foliar biomass, taking into account the distribution of leaves within crowns and canopies. Photosynthesis is difficult to measure continuously for long periods of time, so researchers rely on estimates interpolated from periodic measurements of canopy-scale biosphere-atmosphere fluxes. Evapotranspiration is easier to estimate over the long term with the use of sapflow measurements. To account for the scaling up of leaf-level data to crowns and canopies, most models at these larger scales incorporate some measure of canopy structure.

Canopy structure and the associated light transmittance are influenced by natural disturbances, such as wind; anthropogenic disturbances, such as silvicultural treatments; or phenological and seasonal patterns. Any of these influences can mitigate or accelerate ongoing trends in canopy development. Canopies tend not to be uniform, and more recent models of canopy development incorporate clumping as one of the factors influencing light transmittance – and hence, photosynthesis and productivity.

Given the seasonal variation in foliage, methods that estimate canopy phenology across the growing season are particularly valuable. The PhenoCam approach not only measures intraseasonal transition of leaf area, but through the use of red-blue-green channels can record leaf color and compare site-specific data to those of airborne and satellite platforms. Timing and amplitude of these color measurements are unique to individual forest types. These measurements can be used to evaluate the health and productivity of a particular forest via repeated measures or combined into a global network to examine planet-level changes in forest performance. Measures of phenophases matched with climatic data can serve as a benchmark of tree performance, particularly in situations where climatic factors may be changing but severe disturbance has not occurred.

As mentioned earlier, taking individual photosynthesis measurements and interpolating to model at the crown or canopy level can be challenging. Eddy covariance methods of recording canopy fluxes can overcome these difficulties. This method allows for flexibility in choosing timescales. Furthermore, the method puts an upper limit on biosphere-atmosphere flux estimates, dampening estimates that may arise from individual-tree measurements, particularly in deciduous forests.

Canopy processes drive forest productivity and foresters manipulate canopies to achieve their management goals. Variability in crown structure, coupled with leaf-level productivity and interspecific differences, provides the opportunity for forest managers to maximize productivity on a site. For example, these very principles of canopy density, light transmission, and interspecific differences in shade tolerance and photosynthesis allow mixed-species stands of northern red oak and eastern hemlock (*Tsuga canadensis*) to be more productive than stands with northern red oak alone (Kelty, 1986, 1989). Knowledge of these characteristics and an understanding of how they are evaluated are valuable tools for foresters managing current and future forests under the conditions of uncertain future climate scenarios.

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