Canopy ecophysiology: exploring the terrestrial ecosystem frontier

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Editorial: Recent advances in canopy ecophysiology research

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Introduction

Most physiological knowledge regarding trees is based on observations and experiments conducted on seedlings and small trees because they can be easily manipulated and measured (Pallardy 2008). Although forest canopy function cannot be inferred from studies of small trees in controlled environments, canopy trees present a research challenge due to their sheer size and difficulty of vertical access (Meinzer et al. 2010). Canopy ecophysiology has advanced greatly in recent years, due in part to the establishment of new canopy access facilities around the world (Mitchell et al. 2002), including cranes, lifts, platforms, ladders, and cable networks (Fig. 1). These facilities, along with the introduction of new equipment and techniques in arborist-style tree climbing, allow safer and easier repeated access to the canopy. Technological advances, such as small sensors, portable systems, and wireless data loggers, enable researchers to conduct detailed and continuous physiological measurements high in the canopy.

This special issue of *Tree Physiology* showcases canopy ecophysiology research from around the globe, covering wide geographical and spatial scales, conducted using various canopy access methods and measurement techniques, targeting tropical broadleaved forests to conifer plantations, and ranging from leaf to whole-tree ecophysiology. We also strive to continue the tradition of special issues published by the International Union of Forest Research Organizations (IUFRO), Canopy Processes Working Group (See Ryan 2002 for a brief history). Topics covered can be grouped into the following categories:

(1) Physiological responses of leaf respiration and photosynthesis to variable environmental conditions

(2) Water storage, water potential, and hydraulic conductivity at the leaf and whole-tree level

(3) Environmental drivers of vertical variation in leaf structure and function

(4) Growth and nutrient allocation in relation to reproduction

Here, we highlight individual papers on each topic and briefly discuss their unique methodologies, technical advances, and scientific findings. We hope this special issue of *Tree Physiology* will give readers a broad scope of recent advances in canopy ecophysiology and stimulate further research regarding forest canopy processes.

Responses of leaf respiration and photosynthesis to variable environmental conditions

Because trees are long-lived, sessile organisms, their persistence depends on the ability to acclimate to highly variable environmental conditions in order to maintain net positive carbon balance over the long term. Forest biomes alone represent approximately half of total global terrestrial carbon sequestration (Beer et al. 2010), and thus, are highly influential to global climate trajectories. The effects of a changing climate on tree canopy physiology, including responses to warmer temperatures and more variable rainfall, can be investigated using both observational and manipulative experiments. In this issue, Araki, et al. (2017) show that leaf respiration rates of 10-year-old hinoki cypress (*Chamaecyparis obtusa*) increased with height, leaf mass per area (LMA), and leaf nitrogen on a leaf area basis (N_{area}). While the temperature response of leaf respiration did not vary with canopy height, respiration rates did show seasonal down-regulation during the summer months, indicating thermal acclimation of canopy respiration (Araki et al. 2017). Investigations of variability in canopy respiration and acclimation potential across space and time can help to constrain parameterizations of Earth System Models, thus improving our ability to understand atmosphere-biosphere interactions and to forecast future global climate more accurately (Smith and Dukes 2012).

Adaptation or acclimation to variable rainfall is also important to consider when predicting how trees will function under future climate change. This special issue includes two studies showing how tree canopy photosynthesis was affected by too much or too little moisture. Aparecido et al. (2017) show that species from the wet tropics are morphologically and physiologically adapted to rainy conditions, with features such as trichomes that repel water, drip tips that drain water from leaf surfaces, or the ability to maintain high photosynthetic rates even when leaf surfaces were wet (Aparecido et al. 2017). A second study, also in the wet tropics, reports on responses of canopy physiology following a four-month rainfall exclusion experiment (Fig. 2). Inoue et al. (2017) found that photosynthesis in the drought-treated trees was maintained during morning hours, but did show midday depression compared to control trees. This study concluded that tropical species with anisohydric behavior (weak stomatal control) had leaves that were able to maintain turgor under water limitation and had high resilience to drought (Inoue et al. 2017). Such dynamic responses of tree photosynthesis to temperature and moisture variation have significant implications for stand-level estimates of carbon sequestration.

Water relations at leaf and whole-tree level

As trees grow tall, both distance for water transport from roots to leaves and evaporative demand increase, potentially resulting in growth-limitation due to water stress (Koch et al. 2004, Ryan et al. 2006). Recent studies, however, suggest that tall trees have functions that hydraulically buffer the negative effects of vertical water transport (e.g., Ishii et al. 2014). In this issue, Williams et al. (2017) show that leaves of giant sequoia (*Sequoiadendron giganteum*; up to 95 m tall) have nearly double the hydraulic capacitance (water storage) compared to leaves of other species. Their measurements of diurnal changes in leaf water potential (Fig. 3) revealed giant sequoia leaves routinely, but safely, functioned near turgor loss point with the help of height-related adjustment of tissue osmotic and elastic properties, as well as the balance of water between the apoplasm and symplasm (Williams et al 2017). Similarly, Shiraki et al. (2017) show that treetop leaves of 100-year-old hinoki cypress acclimated to water-stressed conditions in the upper canopy by increasing transfusion tissue with height and decreasing leaf water potential at turgor loss point, thereby enabling greater hydraulic conductance and facilitating osmotic adjustment. Another interesting and related finding is the increase in vascular tissue with height in both ~23m sugar maple (*Acer saccarum*; Coble and Cavaleri 2017) and ~100m sitka spruce (*Picea stichensis*; Chin and Sillett 2017). Greater allocation to vascular tissue can help to improve transport of water and photosynthate under water-stressed conditions of the upper canopies of both broadleaved deciduous and coniferous trees.

Some unique applications of novel technologies have revealed insight into the biochemical changes with height that may mitigate treetop water stress of leaves. Azuma et al. (2017) employed infrared micro-spectroscopy to observe water and polysaccharide distributions within leaves sampled from four heights in a Japanese cedar (*Cryptomeria japonica*) canopy, and found evidence of higher concentrations of dissolved sugar and other polysaccharides in upper leaves, supporting the notion that osmotic control is a key acclimation to height-related water stress.

Acclimation to and buffering of height-related hydraulic constraints may be especially important under drought conditions. Yi et al. (2017) compared leaf-level gas exchange, tree-level sap flux, and stand-level eddy covariance among three canopy-dominant trees with different degrees of isohydricity over a three-year observation period to assess their response to severe drought. They found that nocturnal refilling of cavitated xylem was more important in anisohydric than isohydric species, suggesting reliance on stem hydraulic capacitance to mitigate the risk of hydraulic failure. Water stored in the leaves is also critical for maintaining daily transpiration rates in some species (Zweifel et al. 2001, Ishii et al. 2014). In this issue, Himeno et al. (2017) show leaves of Japanese cedar stored nearly twice as much water as sapwood tissue, contributed 5-8% of total daily transpiration, and in the morning, contributed 100% of whole-tree transpiration. De Guzman et al. (2017) compared the trade-off between safety and efficiency of water transport between tropical lianas and trees and found that lianas showed greater hydraulic conductance than trees, while trees were less vulnerable to cavitation and relied more on stored water to maintain leaf water status. These studies illustrate that various physiological adaptations allow tall trees to avoid, tolerate, or acclimate to hydraulic constraints and maintain physiological function.

Vertical variation in leaf structure and function

A tree's growing environment changes markedly through ontogeny from a tiny seedling to an adult nearly 1000 times in size, as well as along the vertical environmental gradient from upper to lower crown. Tree leaves acclimate to variable environmental conditions in time and space through phenotypic plasticity. In addition to the classic structural and functional changes observed along the sun/shade gradient, height also affects leaf structure and function reflecting vertical water transport limitations due to gravity (e.g., Cavaleri et al. 2010). In this issue, researchers found that in trees of markedly different sizes, growth forms, and leaf morphologies, light had stronger effects than height on morphological traits directly related to maximizing photosynthetic capacity. For example, greater light availability increased leaf width in sitka spruce (~100m, Chin and Sillett 2017), and palisade layer thickness in sugar maple (~23m, Coble and Cavaleri 2017). Height, on the other hand, appeared to be more influential to anatomical and morphological traits related to mitigating hydrostatic constraints. Coble and Cavaleri (2017) found LMA to be greater at higher heights due in part to increased vascular tissue. Similarly, Shiraki et al. (2017) found height to be the stronger driver of increased transfusion tissue. Such adaptations that overcome hydrostatic limitations are important for persistence in the canopy and for out-competing other species by growing tall.

Species' responses may also vary depending on ecological niche. For example, Coble et al. (2017) suggest that acclimation responses and plasticity may differ among species with different leaf habit corresponding to the timing of leaf emergence and maturation. Light was a stronger driver of LMA gradients than height for species with determinate and indeterminate growth strategies, while determinate growth species showed greater plasticity in response to light. High light-acclimation plasticity could offer a competitive advantage by enabling canopy foliage to occupy a broader range of light conditions along the vertical canopy gradient (Coble et al. 2017).

Canopies of different structural complexity may also result in variation in foliar morphological and physiological gradients. Using light detection and ranging (LiDAR) data, Fotis and Curtis (2017) compared the foliar traits and canopy surface roughness (rugosity) across four temperate tree species, and found that even when canopies had the same amount of total light interception, higher rugosity lead to greater LMA. This effect may be related to the effect of height on LMA, as rugosity also increased with canopy height (Fotis and Curtis 2017). Such variations among species in response to stand level light environments and canopy complexity have ecological implications for tree species coexistence and community structure in natural forests (Ishii and Asano 2010).

Growth and nutrient allocation in relation to reproduction

In addition to persistence of individual trees through acclimation to changing environments, reproductive capacity is an important factor determining the persistence of species and their geographical distribution. Using pulse ^{15}N labelling, Han et al. (2017) , found that fruiting trees of Japanese beech (*Fagus crenata*) increased nitrogen uptake from soil compared to non-fruiting trees, but that fruiting did not affect final N concentration in leaves or branches. Han et al. (2017) also found leaf biomass of fruiting trees decreased by ~34%. Similarly, Kabeya et al. (2017) found reproduction to negatively affect vegetative growth of Japanese beech. In fruiting trees, radial growth rate of the trunk was reduced, while growth duration was not, suggesting resource allocation for fruiting and branch development resulted in trunk growth reduction in mast years (Kabeya et al. 2017).

Future research

Researchers represented here accessed the crowns of mature trees and presented exciting findings about their physiological function not previously known from experiments using small trees. Scaling up from detailed, *in-situ* measurements of the physiological functions of canopy trees is an important approach for accurately predicting how trees and forests will be affected by future climate change. Moreover, scaling down from field experiments that include canopy measurements can elucidate ecosystem level fluxes of carbon, water, and nutrients.

Several studies in this issue addressed the responses of trees to variable environmental conditions. Being long-lived, sessile organisms, trees have retained high phenotypic plasticity through their evolutionary history (Ishii et al. 2013). In the face of global climate change and uncertainties about future environmental conditions, phenotypic plasticity is likely to play a key role in determining persistence of long-lived organisms like trees (Valladares et al. 2014), which could be relevant for tree breeding. Rather than employing conventional breeding to narrow down traits and select for useful phenotypes, we should select for individuals that are more likely to acclimate to unpredictable environmental change, i.e., those with high phenotypic plasticity. Tree longevity, however, makes it difficult to study phenotypic plasticity through ontogeny. Measurements of within-tree trait variation (e.g., along the vertical gradient) can be used to indicate phenotypic plasticity and acclimation potential.

Finally, several studies in this issue combined physiological measurements with anatomy to infer function (e.g., Chin and Sillett 2017; Coble and Cavaleri 2017; Shiraki et al. 2017). Functional anatomy is a newly emerging discipline that promises to be fruitful in elucidating physiological function of canopy trees. We hope that the wide variety of exciting studies presented in this special issue will stimulate further research in forest canopies, the terrestrial ecosystem frontier!

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Figure captions

Fig. 1. (a) A researcher samples branches of Japanese beech using a pole-pruner while standing on a pole-ladder attached to the trunk (Photo by Daisuke Kabeya). (b) Accessing canopy leaves using a boom-lift to measure leaf gas exchange at Morgan-Monroe State Forest, IN, USA (Photo by Koong Yi). (c) Steel cable network connecting the crowns of three 25+ m sugar maple trees at the Michigan Technological University Ford Forestry Center near Alberta, Michigan. Researchers access foliage vertically with arborist-style single rope climbing techniques and traverse in the horizontal direction with zip-line style pulleys (photo by Molly Cavaleri).

Fig. 2: Rainfall exclusion equipment laid out like an umbrella around a mature canopy tree in a Malaysian tropical rain forest (Photo by Yuta Inoue).

Fig. 3. Canopy researcher measures water potential while secured to a limb 62 m above the ground in a giant sequoia tree (Photo by Rikke. Reese Næsborg).

Cover photo: Canopy researcher ascends a 250-year-old Japanese cedar tree at Nibuna Mizusawa Forest Reserve, Akita Prefecture in early morning fog. Leaves sampled from four heights in the canopy of a 51-m tree were analyzed using infra-red micro-spectroscopy mapping to investigate the distribution of water and polysaccharides within leaf tissue (Azuma et al., 2017).

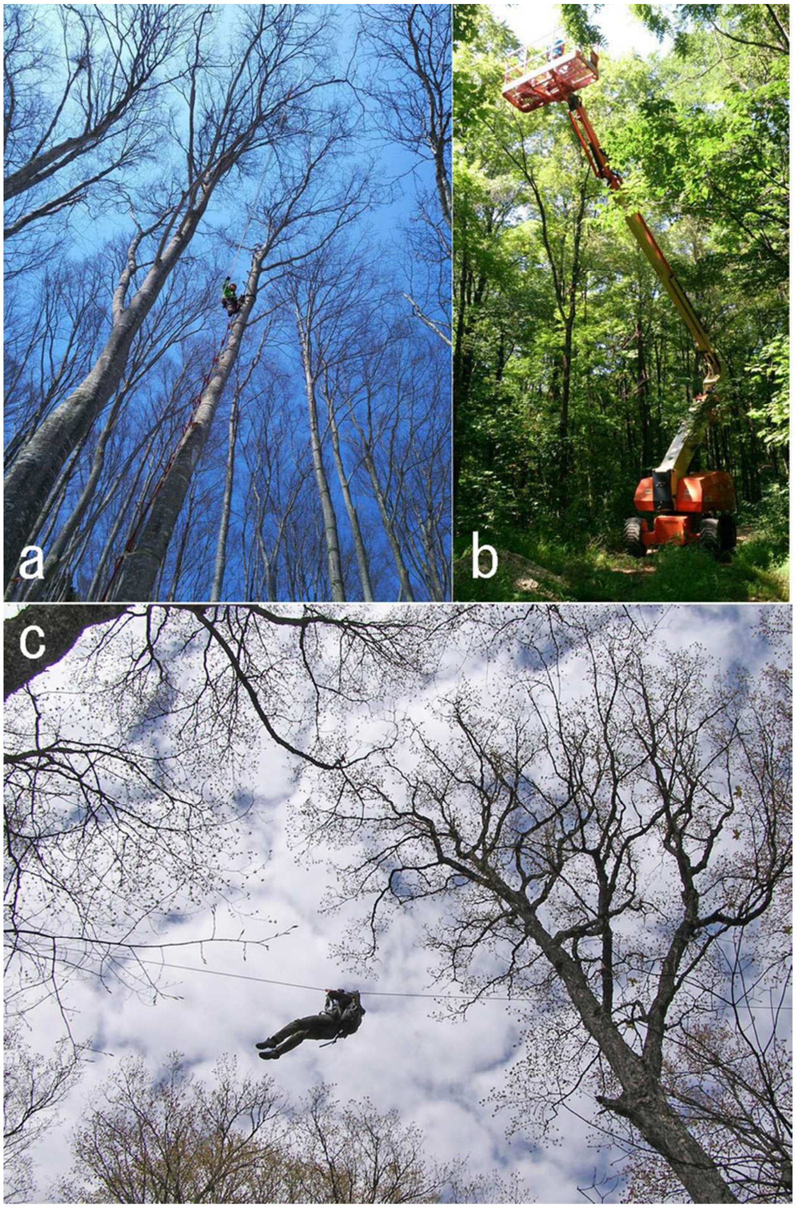

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Fig. 2: Rainfall exclusion equipment laid out like an umbrella around a mature canopy tree in a Malaysian tropical rain forest (Photo by Yuta Inoue).

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Fig. 3. Canopy researcher measures water potential while secured to a limb 62 m above the ground in a giant sequoia tree (Photo by Rikke. Reese Næsborg).

33x45mm (300 x 300 DPI)