

Chapter 5

Plant Structure-Function Relationships and Woody Tissue Respiration: Upscaling to Forests from Laser-Derived Measurements

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Summary

Land surface processes dominate the observed global signal of large inter-annual variability in the global carbon cycle, and this signal is itself dominated by responses of tropical forests to climatic variation and extremes. However, our understanding of the functioning of these forests is poorly constrained, not least in terms of the size and climate-sensitivity of gross ecosystem respiratory CO₂ emission. Woody tissue CO₂ effluxes contribute substantially to gross ecosystem CO₂ emissions, thereby influencing the net ecosystem exchange of carbon. Our ability to estimate this component of the forest respiration budget has been limited by our technical capacity to measure vegetation size and structure in sufficient detail and at sufficient scale. The outcome has been to leave large uncertainties in land-surface model performance and prediction. A key challenge in estimating woody tissue CO₂ efflux for the ecosystem has been the scaling of measurements made with chambers from the level of an organ to the stand. Appropriate scalars such as woody tissue mass, surface area and volume all require accurate structural information on both size and pattern. For individual trees, pattern is dominated by branching structure and this fundamentally determines how trees partition resources to address the trade-offs inherent in the simultaneous maintenance of structural integrity and metabolism. The detailed structural information needed to address this challenge has until recently been extremely scarce because of the difficulty of acquiring it, even for a single large tree. Recent developments in terrestrial light detection and ranging (LiDAR) technology have made possible a step change in our ability to quantify and describe tree form for continuous forest, for example describing hundreds of adjacent trees at the hectare scale. Connecting this new capability with tree physiology and fundamental theories of plant structure and metabolism offers to change the way we understand plant functional biology and its variation with environment, biogeography and phylogeny.

I. Introduction

Respiration in vegetation and soil is a fundamental component of ecosystem metabolism. When combined, total ecosystem respiration (R_{eco}) comprises marginally less than gross primary production (GPP), and the small difference between these two very large fluxes of approximately 60 Pg C year⁻¹ (60 Gt per year) equates to the net terrestrial carbon sink, estimated to be 3.0±0.8 Pg C

year⁻¹ (Le Quéré et al. 2014). This net carbon flux varies much more strongly on an inter-annual basis than its marine equivalent, dominating the dynamics of the global carbon cycle. For example during El Niño years, increased exposure to dry and warmer conditions, especially in the tropics, can lead to net emissions of carbon dioxide (CO₂) to the atmosphere at regional and sometimes globally-significant scales (Wang et al. 2013). Recent analysis suggests that the

inter-annual variation in the land carbon sink has grown by 50–100% in the last 50 years (Anderegg et al. 2015; Betts et al. 2016). The signal is dominated by tropical ecosystems, particularly tropical forests (Huntingford et al. 2009; Beer et al. 2010), and is influenced strongly by climatic extremes of warming, and in some regions, drought (Jung et al. 2017).

II. Tropical Forest Respiration

Understanding this variation in the tropical land-surface carbon cycle is a priority for Earth system science. Inter-annual variations in tropical-zone CO₂ emissions to the atmosphere have been attributed to temperature anomalies at large scale (Anderegg et al. 2015). Jung et al. (2017) examined the drivers of these emissions in a combined data- and model-based analysis. They found that differences in moisture availability explained much more inter-annual variance than temperature, effectively dominating process-responses at grid-scales up to 10° latitude, but that the spatial and temporal patchiness of the moisture effect led to a cancelling out at very large scale, leaving the residual temperature response as the spatially most consistent driver of tropical forest CO₂ emissions at the coarsest pan-tropical scale.

We thus need to disentangle both temperature and moisture effects more precisely (as well as other environmental constraints), but doing so requires a better understanding of the sub-processes contributing to whole-ecosystem fluxes, because these sub-processes respond semi-independently to climate and soil, and the discrete effects will not sum up linearly. Furthermore, while empirical observations may allow us to understand environmental responses within the range of observed conditions, process-based models are needed to predict how ecosystems will respond outside of those conditions, as is likely to be the case with future climate change (Evans 2012; Evans et al. 2012).

Therefore, the different components of the tropical carbon and water cycles on land, and especially those of forests, require careful quantification. It is here that a knowledge gap has become apparent. Ecosystem models are often parameterized with respect to representing the behavior of different components of an ecosystem with very limited reference to field data, sometimes due the difficulty of obtaining those data (Cleveland et al. 2015). Whilst multi-component datasets of, for example, the fluxes of carbon to/from woody tissue, soil, and leaves have begun to emerge for a few tropical forests (e.g. Metcalfe et al. 2010; Malhi et al. 2015; Anderson-Teixeira et al. 2016), they remain sparse and have not yet been used systematically to constrain model structure in any comprehensive way (Medlyn et al. 2015; Cleveland et al. 2015; Anderson-Teixeira et al. 2016). Further, although some components have been relatively intensively sampled such as leaf photosynthetic capacity (e.g. Domingues et al. 2010) and leaf dark respiration (e.g. Atkin et al. 2015; Rowland et al. 2016), extrapolating from one or few components to the behavior of the full carbon cycle system is inherently risky. The relationships and overall ratios among soil, woody and leafy tissue CO₂ effluxes may vary substantively across different forest ecosystems, or indeed across seasons, and model results can be very sensitive to these parameters. Current global vegetation models make fixed assumptions about these relationships, based on few or no data, meaning that any inherent inaccuracies (or accuracies) will be propagated strongly, with unknown consequences.

In a recent cross-biome comparison, plant (i.e. autotrophic) respiration comprised 48–90% of ecosystem respiration, with woody tissue CO₂ effluxes representing 40–70% of this autotrophic total (Carnioli et al. 2016). The large size of the overall contribution of plants to the terrestrial ecosystem carbon budget means that estimating the total and component fluxes, and how

they might change as the atmosphere changes over the coming decades, is fundamental to our efforts to understand and predict the functioning of the Earth system. Autotrophic respiration fluxes reflect the intensity of metabolic activity as well as the mass of living cells. This activity may respond to physical drivers such as temperature and moisture stress, but will also be strongly moderated by physiological activity such as live tissue maintenance, growth and secondary compound synthesis (Amthor 1989). However, before the variations in the total respiration flux (R_{eco}) can be quantified, the underlying component fluxes need to be known. There is substantial uncertainty in these underlying component values, partly due to the difficulty of their measurement at the necessary scale. Most components of R_{eco} depend strongly on vegetation structure, but the visually striking three-dimensional structure of woody ecosystems has been very difficult to measure well, even for highly aggregated parameters such as biomass (Chave et al. 2014; Calders et al. 2015). Our limited ability to quantify structure (and in consequence component CO_2 effluxes) has led to the need to ascribe large error terms to values for respiration estimated at the stand scale, with uncertainty estimates ranging between 30 and 50% (e.g. Metcalfe et al. 2010; Campioli et al. 2016). Our analysis here focuses on tropical forests, but the outcomes and conclusions are widely applicable.

III. How, and How Much? Canopy Architecture and Metabolism

Vegetation structure is fundamentally important for determining resource capture by plants. Structure also shapes the associated demands imposed on woody vegetation through the need to transport and metabolize water and carbon between and within organs, and to retain structural integrity in the face of

differences in soil structure, wind stress, and gravity. This combination of demands has influenced the development of very general ecological theories that seek to explain and predict vegetation structure (e.g. Niklas 1994) and the trade-offs between structure and function (e.g. Enquist et al. 2007), which themselves may vary with the constraints imposed by different metabolites of interest (e.g. water, carbon) and characteristic plant form (von Allmen et al. 2012; Bentley et al. 2013).

Quantifying vegetative structure becomes increasingly difficult with plant size. Describing branching patterns in a herb is relatively straightforward, for example, but for a complex late-successional tree that may be 40–50 m tall, it is very challenging. In the humid tropics, where the variety of plant form is perhaps the largest, reflecting high species diversity, this challenge reaches its apogee. Recognizing this issue, and building on the pioneering ecological insights of Thompson (1917) and Corner (1964), the French biologist Francis Hallé developed a descriptive spectrum to account for the architectural variety found in tropical rainforests. He and colleagues, Oldeman and Tomlinson, described 23 distinct architectural forms, into which all tropical trees were supposed to fall (Hallé et al. 1978). The analysis of Hallé et al. represented a watershed in trying to reduce the complexity and diversity of tropical forests to something more tractable, and provided an early basis for the interpretation of form with respect to genetic differences and environment. However, efforts to associate ecological function with these forms have not been successful, partly because of their limitations in terms of quantitative description. Despite a few extended efforts to sample full-size trees destructively (e.g. Yoda et al. 1965; McWilliam et al. 1993; Mori et al. 2010; Bentley et al. 2013) and to address the underlying quantitative questions of structure and metabolism, it has hitherto been almost impossible to obtain

substantive structural-metabolic datasets for any woody ecosystem. Recent advances in laser (light) detection and ranging technology (LiDAR) promise to break this impasse.

The development of LiDAR-based terrestrial laser scanning (TLS) instruments has for the first time provided the potential to measure plant structure at the fine scales (mm-cm) needed to quantify whole plant form, from ground level to the canopy-tops of large trees. The use of TLS is still in its infancy for forest ecology, but already the outcomes are demonstrating the potential to revolutionize our ability to estimate plant structure, mass, and associated metabolic function. These datasets will emerge over the coming decade and will enable significant scientific advances, ranging from improved quantification of carbon storage on land (Calders et al. 2015; Gonzalez de Tanago et al. 2017; Disney et al. 2017) and improved estimates of carbon and water fluxes, through tests of fundamental theories of plant structure (Farnsworth and Niklas 1995) and metabolic scaling (Enquist et al. 2007), to the unexplored territory of understanding plant trait difference and convergence at the level of tree canopies, a step-advance from analogous studies at the leaf level (Wright et al. 2004).

IV. Respiration and Its Measurement in Woody Terrestrial Ecosystems

Respiration in plants and microbes drives the generation of the energy and biosynthesis required for metabolism, growth and reproduction. The underlying biochemistry and environmental response surfaces of plant respiration and its components are considered in detail elsewhere in this volume. Here we focus on CO₂ effluxes from woody tissue, noting that major constraints over absolute CO₂ effluxes and the drivers of change in these fluxes can be summarized under three connected headings: (i) metabolic and biochemi-

cal requirements for maintenance, growth, and defense; (ii) environmental influences (e.g. responses to temperature, drought, radiation load, seasonality); and (iii) apparent complications, such as microbial breakdown, mycorrhizal associations, and multiple carbon sources.

Whilst the efflux of CO₂ from woody tissue is sometimes quantified by chemical absorption or using mitochondria-sensitive stains, measurements are most frequently made by gas analysis. That is, a chamber is sealed to a woody limb connecting it with tubing to an infra-red gas analyzer to enable the change in CO₂ concentration in the chamber to be quantified, and the rate of CO₂ efflux from the bark calculated (e.g. Sprugel and Benecke 1991; Meir and Grace 2002). Several of the constraints and drivers of respiration listed above co-influence the gross emissions of CO₂ as measured from the surface of woody tissue. For example, although much CO₂ is generated by respiration of live cells in the cambium and parenchymal sapwood underlying any area of bark, there may be other sources of CO₂ that affect diffusion rates through to the bark surface, influencing the net measured efflux (Fig. 5.1). Static sources include microbes and macrofauna respiring CO₂ as they breakdown organic material in the trunks of large trees. Dynamic sources and potential sinks include the concentration of dissolved CO₂ in the fluids transported in the xylem and phloem (Zelawski et al. 1970). In particular, the transport of CO₂ dissolved in the xylem sap has been considered to potentially affect efflux rates. Soil water brought up *via* the roots may have a high concentration of dissolved CO₂ that can effuse outwards through the bark (Zelawski et al. 1970). Before emission to the atmosphere, this CO₂ may be partially consumed by photosynthesis in the bark of some woody limbs (Foote and Schaedle 1978), ultimately providing potential additional substrate for assimilation by the leaves. Pioneering measurements of these fluxes were made on *Betula pendula*

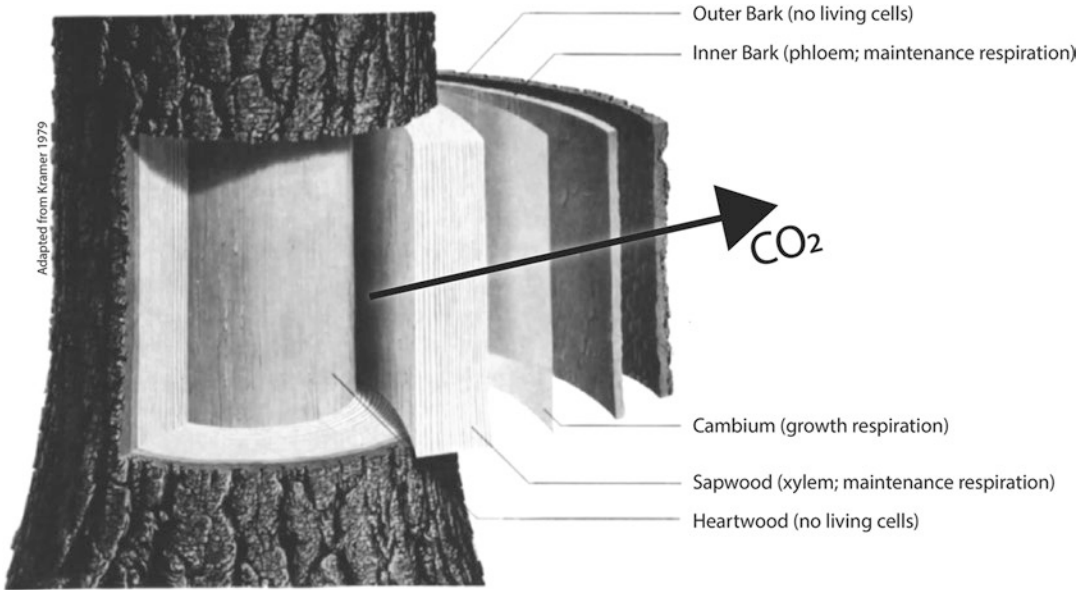


Fig. 5.1. The structure of woody tissue. Metabolically active cells are found from the sapwood parenchyma outwards. The sapwood parenchyma has a variable fraction of live cells, complicating estimates of respiration activity. The outer rings of cells are live and affect growth (cambium) or metabolite transport (phloem). As the tree gets larger the relationship between live sapwood volume and total circumference of cambium and phloem varies, affecting the overall efflux of CO₂ from the bark surface (Modified, from Kramer and Kozłowski 1979)

by Levy et al. (1999), who devised a chamber to quantify sap CO₂ concentration at atmospheric pressure and applied Henry's law and carbonate dissociative chemistry to the sap and co-incident CO₂ emissions. These different sources of CO₂ are thus additional to the respiratory flux from cambial and parenchymal tissue, and they may also vary in direction or size with the time-dynamic functional attributes of the tree. The consequence is that raw CO₂ efflux rates from bark may not always fully represent the respiration of the tissue immediately underlying the measurement chamber. A significant portion of the uncertainty can be accounted for by comparing efflux rates

when transpiration is occurring and when it has stopped, though hysteresis effects remain possible, depending on the relevant tissue CO₂ concentration (Kunert and Edinger 2015; Bužková et al. 2015). Full quantification is only possible by measuring in fine detail all the sources of CO₂ in a stem (Teskey and McGuire 2007), although isotopic tracing has also proved a useful additional technique (e.g. Angert et al. 2012). Debate continues as to the importance of static and dynamic sources of stem respiration measurement error. Static sources of CO₂ such as heartwood microbial decomposition are particularly understudied, and improved understanding of the response to climate by both

autotrophic and heterotrophic sources is needed for tropical forests.

At the scale of understanding the ecosystem respiration budget, the uncertainties regarding CO₂ sources additional to those cells metabolizing immediately under any single measurement point may become less of a concern, as emissions not captured in one component should be captured in measurements of other components of the ecosystem. Eddy covariance can provide measurements of stand-scale total ecosystem respiration (R_{eco}) under the correct meteorological conditions, but the data do not distinguish the separate components of R_{eco} (e.g. leaf, wood, and soil respiration). This limitation obscures physiological insight and limits model evaluation and development that is based solely on eddy flux data. Carefully-designed chamber-based measurements may still offer the best widely-applicable measurement to quantify woody tissue CO₂ effluxes, especially in remote locations, but scaling the data to the canopy remains a key challenge, even in well-studied plantation species.

V. Scaling Woody Tissue CO₂ Effluxes from Organ to Ecosystem

At least five basic ecosystem respiration components must be quantified to understand R_{eco} : CO₂ emissions from soil, roots, coarse woody debris (CWD), leaves, and stems. The latter two comprise the biologically active component of the canopy. In contrast to woody tissue (stem) CO₂ effluxes, the scaling of leaf gas exchange to the stand-scale has proved a reasonably tractable challenge. It has been achieved through the combination of the bulk measurement of leaf area index (LAI) and the repeated observation that leaf gas exchange capacity acclimates to incident irradiance within a canopy, and to nutrient availability (e.g. Hollinger

1996; Meir et al. 2002). It turns out that real canopies allocate leaf gas exchange resources to optimize photosynthesis in a way that approximates theory surprisingly closely (Field and Mooney 1986; Sellers et al. 1992; Meir et al. 2002). With some modifications (e.g. De Pury and Farquhar 1997), and despite observed important departures from this optimal allocation model (Meir et al. 2002; Lloyd et al. 2010), some vegetation models assume optimal allocation of leaf nitrogen and leaf gas exchange capacity with respect to irradiance because the efficiency of calculation outweighs the error resulting from the approximation of real canopy properties to acclimation theory. However, the same assumptions cannot be made of woody tissue physiology. This probably reflects the contrast between the principal functions of leaves (light capture, gas exchange and nutrient assimilation) and the much more diverse functions woody tissue performs, from structural integrity, though the provision of an armature to support leaves, to gas exchange, and to metabolite transport and its transfer into cellular requirements. As a consequence, woody tissue CO₂ efflux measurements have been considered necessary to estimate canopy fluxes, although the best method for extrapolating these measurements to the stand-scale has remained unclear.

The first concerted effort to examine how structure determines whole-tree woody tissue respiration was made as part of the United Nations Man and Biosphere Program in the 1960s. Yoda et al. (1965) led the field using large-scale destructive harvest and static sodium hydroxide absorption and titration methods, all performed in tropical forest. They sought to identify the best scalar for extrapolating measurements of CO₂ efflux from excised sections of woody stems and branches, to determine respiration by the whole tree. They focused on woody tissue surface area and volume as likely scalars, and their

analysis, extended subsequently by Yoneda (1993), suggested that area was the best scalar for the trees they studied (Yoda 1983). However, as tree growth and metabolism takes place in cells that dominate both cross-sectional (e.g. sapwood parenchyma) and circumferential elements (e.g. cambium, xylem and phloem production), this left room for substantial uncertainty with regard to the influence on overall efflux rates of seasonal growth or other metabolic pulses, which could not be monitored using excised stem sections and static CO₂ absorption methods.

The arrival of commercially-available infra-red gas analyzers created a new potential to measure fluxes from live wood on a continuous basis over extended periods (Hutchinson and Livingston 1993). This helped understanding how sapwood volume rather than surface area determined overall flux rates (Sprugel 1990; Ryan et al. 1997). The approach was considered more mechanistic and worked well for intensively-studied species where sapwood volume was well quantified, despite uncertainty in the proportion of live cells in the estimated sapwood volume, a problem that remains unsolved (Carlquist 2001; Ziemińska et al. 2013). However, the sapwood volume approach was less useful for natural forests for which species-specific sapwood volume data were not available, as is usually the case for tropical forest trees. A pioneering study in tropical rainforest by Ryan et al. (1994) to connect sapwood volume with growth and maintenance respiration for two well-studied species in Costa Rica suggested that maintenance accounted for about 80% of total woody tissue CO₂ efflux. For less well-studied species, an elegant analytical approach was developed instead to determine whether volume or area dominated the efflux signal, using Sahelian shrubs (Levy and Jarvis 1998). For larger trees in tropical forest, an equation to simulate the changing influence with stem diam-

eter of both volume and stem surface area components predicted stem CO₂ efflux rate contributions accurately and in a way that correctly reflected the underlying live cellular structure (Meir and Grace 2002). This method also yielded maintenance costs for trees growing in closed-canopy forest as approximately 80% of total measured effluxes, consistent with those of Ryan et al. (1994) that had been obtained using sapwood volume estimates. Detailed in-canopy measurements in Costa Rica (Cavaleri et al. 2006) subsequently demonstrated that upper-canopy smaller branch sections had higher efflux rates than stem sections nearer the ground, suggesting higher metabolic rates, or a larger importance for fluid transport causing increased outward diffusion of CO₂ carried from elsewhere in the plant or soil. This pattern was not repeated in a detailed analysis in Bornean rainforest (Katayama et al. 2014), suggesting a need to examine the implications for additional studies.

Recent attempts have also been made to understand the scaling of respiration based purely on mass. Whilst the use of dry mass as the sole scalar for whole-plant respiration may not appear intuitive for large high-biomass trees because of the likely increasing proportion of dead biomass in large stems (heartwood), a signal analysis by Reich et al. (2006), based mainly on measurements of small plants, suggested a well-defined exponential model. In a heroic extension of the pioneering work of Yoda, Mori et al. (2010) tested Reich's analysis by destructively harvesting and measuring respiration from 271 trees, across 9 orders of magnitude in mass, up to 10⁴ kg (10 tons), including many trees from tropical and subtropical locations. The outcome suggested consistent whole-plant scaling of respiration with total mass (Fig. 5.2), but required a double-exponential form to allow for large trees not considered by the Reich et al. (2006) study.

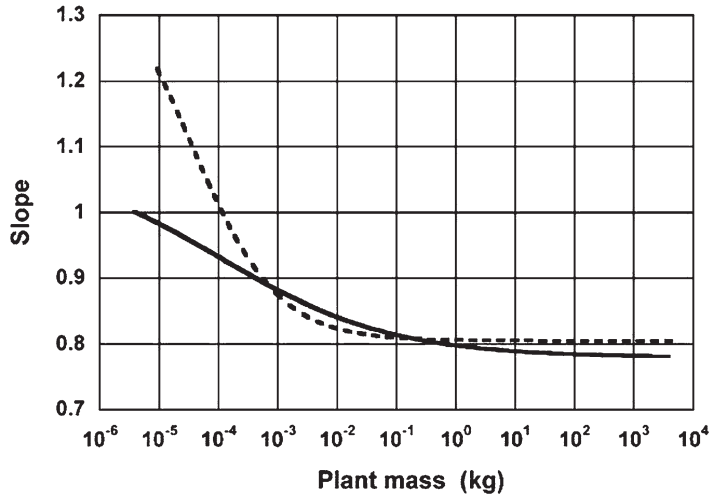


Fig. 5.2. The relationship between the slope (S) of the relationship between the respiration rate (Y) and plant mass (M), as a mixed power function derived to account for allometric scaling of respiration by trees over 9 orders of magnitude (Mori et al. 2010). The mixed power function is derived from a single exponential relationship $Y = FM^\alpha$, where F is a constant and α is an exponent varying between 0.75–1 (thus, $S = \alpha FM^{\alpha-1}$)

VI. Structural Data: A Transformational Opportunity

Despite the empirical (and theoretical) attraction of relatively recently-determined mass-based equations for estimating whole plant respiration in large trees, most recent empirical approaches for tropical forests have estimated stand-scale CO_2 efflux using surface area as the key scalar, making use of the relative ease of site-based chamber-derived flux measurements (e.g. Doughty et al. 2015). The measurements and calculations have broadly followed the specifics proposed by Chambers et al. (2004), themselves determined by Yoda’s work 30 years earlier, and the surface area calculations of Yoneda (1993). However, irrespective of what the best structural scalar is for any one tropical forest [that is, area (Yoda et al. 1965; Yoda 1983), volume (Levy and Jarvis 1998), both area and volume (Meir and Grace 2002), sapwood volume (Ryan et al. 1994) or mass (Mori et al. 2010)] it is necessary to quantify the selected scalar properly to obtain a satisfactory value for whole-tree and stand-scale

canopy CO_2 efflux. Getting accurate measurements of stem surface area or total plant mass has been notoriously difficult for forests, particularly tropical forests, and this has held back progress, until recently.

For biomass, the intensification of research into tropical forests, coupled with the stimulus to improve quantification to inform climate change-related land-use policy, has helped enabling incremental improvements to equations predicting biomass from stem diameter and tree height, using harvested trees where possible (Chave et al. 2014). In the tropics the need for so-called allometric scaling equations (ASEs) is made complex by biogeographic differences in diameter-height relationships (Feldpausch et al. 2010), complexity in tree trunk shape including buttressed stems, biogeographic variation in woody tissue density (Patiño et al. 2009), and diversity of crown shapes (Goodman et al. 2014), among other factors. ASEs are inevitably based on a limited number of destructively sampled trees, and hence contain much variance and uncertainty. This is especially true for large trees, which are

even more under-sampled because of the logistical difficulty of doing so (e.g. Chave et al. 2014; da Costa et al. 2010; Ometto et al. 2014). The same problem arises for estimating the surface area of individual trees. Furthermore, because fewer destructively sampled trees have also been analyzed for size-area relationships (especially for the crown in addition to the main stem of a tree), the uncertainties are substantially higher. Exemplifying this data-gap still further, information on the branching and limb-taper patterns in trees, which underlie detailed biomass, volume, or surface area analyses, is almost non-existent. Recent detailed examination of a few relatively small, hand-measured trees has been performed with promising results for understanding branching patterns and plant metabolism (Bentley et al. 2013), but extending this approach requires some form of automation.

Terrestrial laser scanning (TLS) offers to resolve this limitation in quantifying structure and at high precision, thereby significantly advancing the scaling of fluxes from woody tissue segment to the stand. Recent work shows that TLS can be used to estimate woody tissue volume with very high precision,

down to centimeter-scale for large trees, and at higher resolution still for smaller trees or branches (e.g. Raumonen et al. 2013; Disney et al. 2017). Using TLS, full hemispherical canopy scans are taken on a regular grid within a forest plot (typically every 10 or 20 m), delivering millions of structural data points based on the laser return signal. By fitting cylinders to the LiDAR point clouds for each tree, so-called quantitative structural models (QSMs) can now be built describing tree architecture, including stem diameter and height, and woody tissue volume (Disney et al. 2017). The gain with respect to estimating tree volume is particularly important for large trees, notwithstanding some uncertainty in the size of possible internal trunk-cavities. Using standard ASEs, the uncertainty in estimating individual total biomass varies very strongly with diameter, with the error for larger trees rising 4–5 fold (Calders et al. 2015). However, with improved volume and shape estimates made possible with TLS-based measurements, this error-term is held nearly constant, irrespective of tree diameter (Calders et al. 2015; Fig. 5.3). The impact on stand-scale biomass estimates of reducing the error for large trees

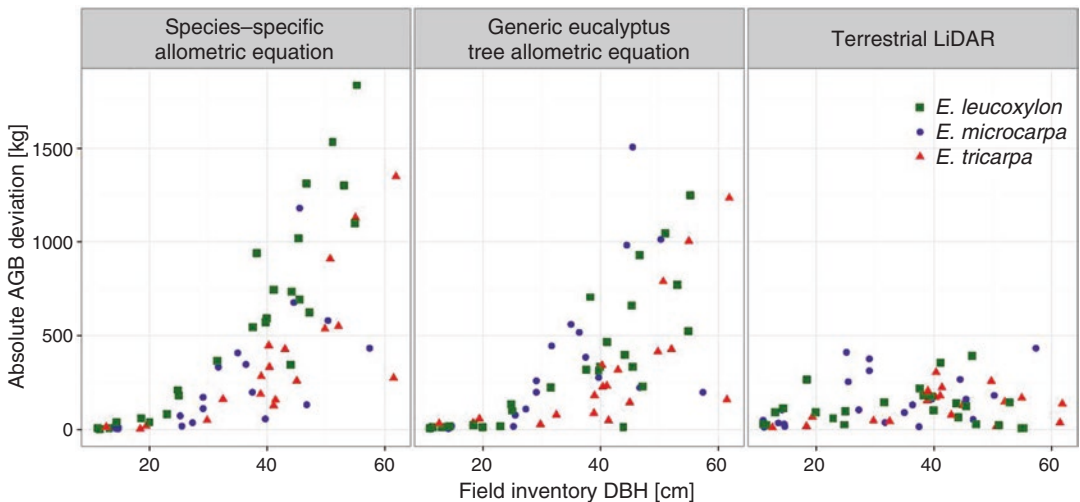


Fig. 5.3. Comparison of the absolute deviation (i.e. error, in kg) in estimated aboveground biomass using standard allometrically-derived estimates (in different species, left; generically for *Eucalyptus*, centre; and estimates derived using TLS, right). Note the lack of large deviation at large stem diameters using the TLS method. Surface area estimates should show similar patterns with tree size (Calders et al. 2015). AGB, aboveground biomass; DBH, diameter at breast height (in cm)

is significant because they often represent more than 50% of the total biomass in old-growth forests. Indeed, combined with woody tissue density data, TLS-based measurement of tree structure is already enabling newly-robust quantification of above-ground biomass, with the strong likelihood of altering estimates of terrestrial carbon storage regionally and globally (Disney et al. 2017).

The detailed nature of the new structural data also opens up whole new opportunities

for understanding differences in the fundamental connections among plant structure, branching patterns, plant physiology and the existence of ecological trait groupings based on whole-tree form. For example, recent TLS measurements made in the eastern Amazon have enabled a detailed tree-by-tree description of a mature tropical forest. The data also allow a range of branching metrics to be derived (Fig. 5.4). For example, whilst canopy volume and trunk length appear to

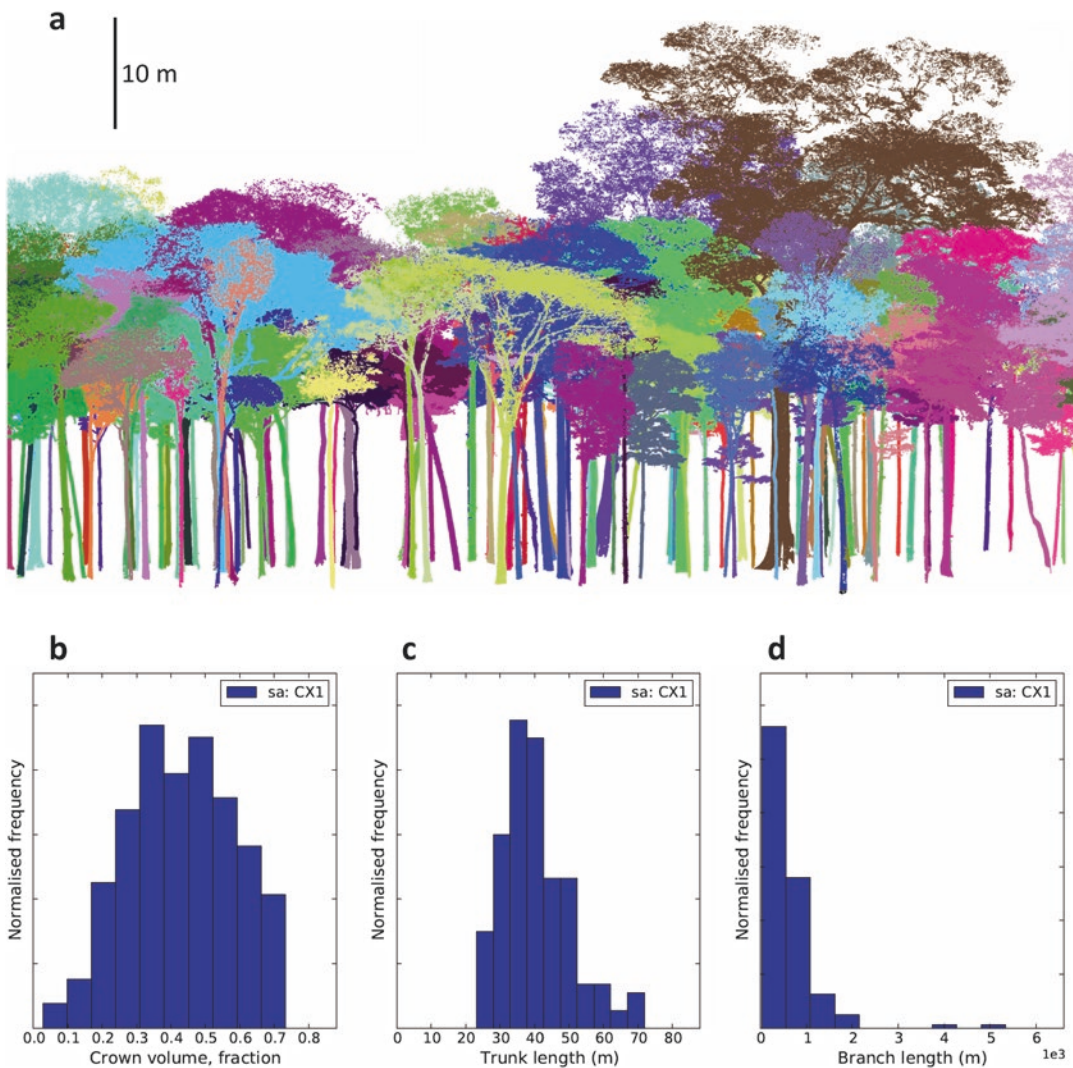


Fig. 5.4. Tree reconstruction (a) and architectural metrics (b) for an eastern Amazon rainforest in Caxiuanã National Forest Pará, Brazil, using TLS. In panels b–d, architectural metrics are given for frequency distributions of crown volume, trunk length (m) and branch length (m, $\times 10^3$). Note that some trees at this site have 5 km of branches or more. The tallest trees in this scan-based image are up to 50 m in height

approximate a normal distribution with stem diameter, variation in branch length is clearly inverse-J shaped, with the larger trees supporting over five kilometers of branch length in one Amazonian forest (Fig. 5.4). Extending the branching and surface area analysis further, separation of leaf area from woody-tissue structures is rapidly becoming possible, and offers an entirely new and comparatively rapid method of determining the variation of leaf area density with position in the canopy, and of leaf area index (LAI) at stand-scale compared with existing

methods (e.g. Kull et al. 1999; Meir et al. 2001). These new data streams will transform the quantitative determination of basic surface area or volume metrics, but they will also open up the opportunity to explore entirely new relationships describing plant form (e.g. Lin and Herold 2016) and function. For example in Fig. 5.5, a new TLS-derived analysis of tropical tree structure shows that previously-accepted estimates of woody surface area become increasingly inaccurate at larger stem diameter, reaching errors of over 100% (Fig. 5.5a). It is now

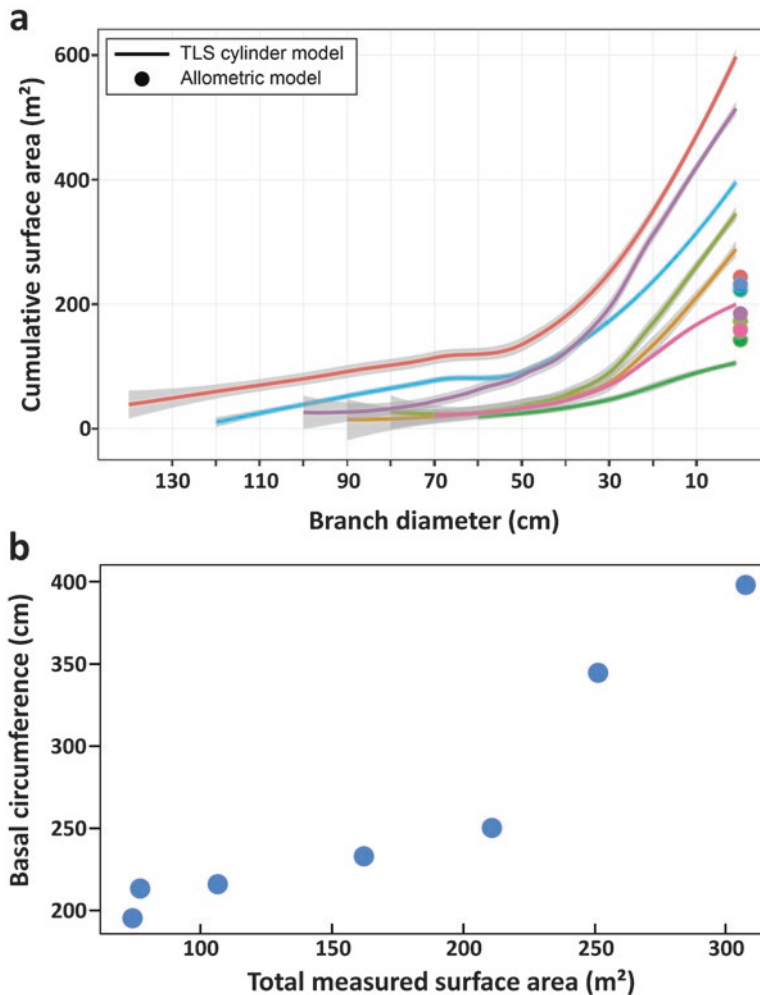


Fig. 5.5. Metrics of tree structure. (a) Comparison of TLS-derived surface area (when plotted against branch diameter) with standard derivations from Chambers et al. (2004) and hand measurement (dots) for different tree species (colours). (b) Total calculated surface area (m²) plotted against tree basal circumference (cm), derived from TLS data

possible to relate total tree surface area or woody tissue volume to metrics such as basal circumference (Fig. 5.5b). Future work will investigate this, including detailed analysis of leaf area and branching structure, from branch tip to central stem. In this way we will, for the first time, begin to relate structural differences and canopy-level trait variations, and their ecological significance, in an interpretive integrated framework analogous to the more familiar study of leaf trait ‘economics’ (Wright et al. 2004).

VII. Implications of Terrestrial Laser Scanning (TLS) and Perspectives

The step-change in our capability to describe plant structure using TLS has immediate application in quantifying woody tissue CO₂ efflux rates and their variation with environment, insofar as respiration depends on structure. Using metrics of surface area, height, and diameter-frequency distributions by position in the canopy, spatially-detailed and environmentally-driven models of woody tissue CO₂ efflux will soon be achievable. It will therefore be possible to compare the extrapolation of field-based measurements of CO₂ efflux using different scalars, from the more complex but biologically appropriate models considering both woody volume and surface areas (Meir and Grace 2002), to the simpler approaches of scaling by surface area (Chambers et al. 2004) or mass alone (Mori et al. 2010). Current methods of estimating total woody tissue respiration based on surface area alone look likely to be significant underestimates for large trees, given the discrepancies in Fig. 5.5 between standard calculations of surface area, and those based on TLS. How these biases scale to stand-level estimates will likely emerge in the near future. Fully independent empirical tests of each scaled product will remain challenging, and may need to fall back on comparison with carefully-selected eddy covariance data, for example,

examining data for periods of high turbulence during the day or night. But a clear step forward will have been gained in representing this key contribution to understanding ecosystem respiration, ultimately informing how we specify the efflux of CO₂ from woody tissue in vegetation models, and how it varies in concert with other components of the carbon cycle during either unconstrained growth conditions, or in response to stress, such as caused by El Niño climate perturbations.

The capability to calculate respiration coupled with detailed branching information also promises to inform general ecological theory that has been used to predict size, growth, and energy use based on natural selection over evolutionary timescales. The detailed empirical work of Mori et al. (2010) suggested that metabolism, represented by whole plant respiration, scales with mass such that the exponent on plant mass varies from 1 to 0.75, dependent on an increasing presence of dead non-metabolically active cells (Fig. 5.2). Application of TLS-derived structural metrics to chamber-based CO₂ efflux measurements and related anatomical data would provide an independent test of this double-power law rule that could be applied to very large numbers of trees in different locations.

More generally, the metabolic scaling theory of West et al. (1997); ‘WBE’ also makes assumptions that are testable using new TLS-derived structural metrics. The WBE model uses the principle that energy is minimized for the flow of water and nutrients from trunk to petioles along a specific space-filling and area-preserving branching pattern. The model has far-reaching predictive power in relation to form and function, though large variation occurs around the mean tendencies. It has attracted significant attention, both supportive and critical, but remains almost untested in terms of the assumed branching structure that underpins it. The primary model requires that branching in all plants is symmetrical such that at

each node, every daughter branch has identical length and radius, making the network self-similar (or fractal) though it has been extended recently to address implications of asymmetry (Brummer et al. 2017). Initial manual measurements of branching structure in nine ecologically contrasting temperate-zone tree species suggested some consistency with the predictions of the WBE model in terms of space-filling by the observed branching, but inconsistency with the WBE model in terms of the conservation of inter-node lengths, which were found to be more variable than predicted, and of branch diameters, which were found to be highly conserved (Bentley et al. 2013). This outcome suggested partial failure of the original WBE model, though it was consistent with the physical expectation that branch diameter alters hydraulic resistance much more strongly than length (the Hagen-Poiseuille law), and therefore may be highly conserved. TLS-derived branching data will enable a much more complete examination of the generality of these early tests of theory, addressing for example the trade-offs at whole-tree scale of the transport and use of carbon, as well as water. How mass, branching structure and leaf area reflect the different needs of structure, metabolism and metabolite transport fundamentally underpins our understanding of functional plant biology. In combination with plant ecophysiology, TLS offers to help open up this field for large woody plants.

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