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Quantifying aboveground components of *Picea sitchensis* for allometric comparisons among tall conifers in North American rainforests

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ABSTRACT

Tree biomass is one of the most important variables for studying and managing forest ecosystems. With emphasis shifting from young forests grown for timber production to forests with old-growth characteristics, the need to quantify various components of individual trees in natural settings is increasing. Destructive methods are inherently limited by what is feasible to cut down, dissect, and measure. In contrast, crown mapping is a minimally invasive technique for quantifying aboveground tree components such as wood, cambium, bark, and leaves. Despite being applied mostly to large trees, it is generalizable to any woody plant and can be adapted to answer diverse questions about biology, ecology, and ecosystem functions. We present a generalized approach for non-destructively quantifying the three-dimensional structure and aboveground components of whole trees along with a new programmatic tool for error-checking, visualizing, and interacting with tree-level data. Crown-mapping data from 60 lowland rainforest *Picea sitchensis* trees are presented to demonstrate the utility of this method for deriving allometric equations of tree components based on ground measurements. The 60 trees range from 14 to 495 cm trunk diameter at breast height, 10 to 94 m tall, and include simple to structurally complex individuals in dominant to suppressed positions within forests varying widely in density. Final allometric equations explain > 90% of the variability in volumes and masses of bark, wood, and leaves; are applicable to *P. sitchensis* throughout much of its geographic range; and are conservative relative to equations based on smaller dissected trees. Dendrochronology and allometric equations demonstrate that *Picea sitchensis* radically out-paces both *Pseudotsuga menziesii* and *Sequoia sempervirens* in accumulation of aboveground biomass and leaves, becoming heavier (155 ± 9 Mg) than any living *P. menziesii* and almost half as heavy as any living *S. sempervirens* in < 500 years.

1. Introduction

Accurate quantification of aboveground tree components such as leaves, bark, cambium, and wood is the basis for understanding the dynamics of forest biomass. Carbon accounting is a major goal of forest scientists and managers (Fahey et al., 2010), especially in replanted areas with rapid rates of carbon accumulation (Poorter et al., 2016) and in older forests where terrestrial carbon stores are high (Luyssaert et al., 2008). Equations predicting biomass and carbon are extrapolations with unknown accuracy unless derived from trees spanning the full range of sizes in a population, yet the maximum size of trees used to make such equations is often limited by how feasible they are to dissect. Quantifying carbon sequestration additionally requires integrating tree growth in the context of species-level differences in decay-resistance, vulnerability to fire, and consequent longevity (Franklin et al., 2002; Sillett et al., 2015a; 2015b; Sillett et al., 2018b).

Determining biomass and ages of large trees in old-growth forests is particularly challenging. While tree-level dissection is accurate and accounts for biomass separation into trunk, branches, and leaves (e.g. Bormann, 1990; Harrison et al., 2009), this method has disadvantages with increasing tree size. Branches are damaged in the falling process, destroying information about within-crown structure, and it is now socially unacceptable to kill the largest trees. Ground-based LiDAR scanning is able to produce impressive models of tree structure (Côté et al., 2011; Hackenberg et al., 2014) but is unable to distinguish leaves, bark, sapwood, heartwood, and deadwood necessary for accurate biomass accounting at the tree-level unless combined with destructive sampling. Remotely sensed methods for scaling biomass to large areas are subsuming many ground-based techniques because of their relative affordability at large scales and high resolution (Kane et al., 2010; Lisein et al., 2013; Tanago et al., 2017; Zolkos et al., 2013). Remote

methods rely on correlations between area-based metrics and ground plots (Kane et al., 2010; Lefsky et al., 1999), tree survey type data from tree segmentation (Lamb et al., 2017; Yao et al., 2011), or structural units centered on canopy dominant vegetation (Jeronimo et al., 2018). In all cases it is necessary to anchor the results of any scaling requiring accurate (as opposed to precise relative) estimates of biomass with ground-truthing to calibrate and validate such models (Goetz et al., 2009; Nelson et al., 2017).

An alternative approach to dissecting whole trees, and the one we promote in this study, is to climb and measure them directly. Crown mapping includes climbing and intensively measuring trees to create three-dimensional (3D) models of their structure. These maps along with extracted increment cores at multiple heights along the main trunk provides the empirical basis for computing tree component quantities and age. The term 'crown mapping' is preferred to 'tree mapping' even though we are mapping whole trees, because the latter is confused with mapping tree locations in ground-based plots. Although labor-intensive, crown mapping has been used to generate allometric equations for *Sequoiadendron giganteum*, *Sequoia sempervirens*, *Pseudotsuga menziesii*, and *Eucalyptus regnans* trees spanning the full size range (Sillett et al., 2015a; 2015b; Sillett et al., 2018b; Van Pelt and Sillett, 2008). Crown mapping further improves estimates of carbon by accommodating differences in wood density along trunks and between trunks and branches (Sillett et al., 2010; Wassenberg et al., 2015), and relatively portable equipment promotes sampling across a broad geographic range. Due to advances in equipment, climbing techniques, and standard methodologies, all portions of a tree crown can be safely accessed and quantified by trained technicians (Anderson et al., 2015; Jepson, 2000, Appendix A).

Picea sitchensis is an ideal species with which to demonstrate this methodology because it is a dominant structural element in many coastal forests (Franklin and Dyrness, 1988; Van Pelt et al., 2006) and no published allometrics yet span its full size range up to > 90 m tall and > 400 cm diameter (Chin and Sillett, 2017; Van Pelt, 2001). Native to the northwest coast of North America from Alaska to California, *P. sitchensis* grows in forest receiving over 500 to under 65 cm of annual rainfall (Burns and Honkala, 1990). A suite of traits indicate that *P. sitchensis* has evolved a "grow-fast-die-young" strategy. First, it is relatively shade tolerant, capable of reproducing in gaps under its own canopy (Taylor, 1990), and its foliar morphology is geared toward maximizing photosynthesis with increasing light. Unlike other tall conifers, individual *P. sitchensis* leaves are twice as wide and have more stomata in well-illuminated upper crowns compared to the deeply shaded lower crowns of tall trees, and mesophyll cells are uniquely organized to promote rapid gas exchange (Chin and Sillett, 2017). Second, wood defense investment is low in *P. sitchensis*, whose heartwood is pale and vulnerable to many decay fungi, including *Phaeolus schweinitzii*, *Porodaedalea pini*, and *Armillaria mellea* (Hennon, 1995; Kimmey, 1956, *personal observation*). Third, *P. sitchensis* does not produce thick bark, averaging just 3 cm thick below 10 m height on trees > 60 m tall (this study) and is consequently not resistant to fire. Growing in rainforests with long fire return intervals, its primary disturbance agents are wind (Greene et al., 1992), fungi (Hennon, 1995), and avulsion by stream channels (Van Pelt et al., 2006). The combination of efficient photosynthesis and low investments in decay and fire resistance may be why *P. sitchensis* trees can gain $1 \, \mathrm{m^3 \, yr^{-1}}$ for more than a century, and area-based annual production is among the highest of any conifer (Ford, 1982; Van Pelt et al., 2006).

Producing estimates of tree-level components for allometric equations is just one application of crown mapping. Extending the applications to a broader range of species and scientific inquiry requires a critical mass of scientists with diverse perspectives. Thus far, consistent use of this method is limited to a closely linked group of researchers (Appendix A), partially due to lack of a detailed and comprehensive set of methods. The primary goal of this study is to present crown mapping in an easy-to-use form and demonstrate its use by creating allometric

equations for *P. sitchensis*. Although crown mapping is mostly used in larger trees, it is generalizable and adaptable to any tree species (Appendix B). We have three specific objectives: 1) to provide a user-friendly guide to our current crown mapping methodology, including a new programmatic tool for error checking and visualizing 3D data, 2) to develop allometric equations for predicting aboveground components of *P. sitchensis* based on 60 intensively measured trees spanning the full size range of the species, and 3) to validate this approach for tall forests via comparison to previously published allometrics for this species.

2. Methods

2.1. Overview

Crown mapping consists of modelling all aboveground external and internal components of the tree by combining low-impact external measurements with minimal extractive sampling of branches and increment cores. The basic principal behind crown mapping is to locate positions and associated diameters of tree components in 3D Cartesian coordinate space, calculate or predict the volumes and surface areas of these components, and then to sum them for each tree. Like trees themselves, these methods are modular and can be used selectively depending on research objectives once the overarching concepts are clear (Fig. 1). For the remainder of this study, we refer to the tree components of heartwood, sapwood, bark, cambium, and leaves collectively as **tissues** and to their separation into component portions as **tissue components** recognizing that plant anatomists may define them differently (Esau, 1965). This terminology allows us to compartmentalize the tree hierarchically into **components** such as trunks and appendages and their breakdown into tissues. We first present generalized methods and then specific methods for *P. sitchensis*.

Crown mapping relies on the repeating nature of genetically programmed tree architecture (Tomlinson, 1983). It quantifies trees in terms of main trunks and segmented appendages treated one way, while branches with a simple architecture are treated another way (Fig. 2, Table 1). Trunks and segments are modeled as conic frusta whose volumes and surface areas are calculated directly. In contrast, branches are tabulated with their location, diameter, and orientation, which are then used to predict separation into tissue components using allometric equations developed by dissecting a sample of branches. Obtaining tree-level tissue masses and leaf quantities requires additional subsampling of trunks and appendages with increment cores and branch dissection to measure their density ($\mathrm{kg \, m^{-3}}$) and specific leaf area and number ($\mathrm{m^2 \, kg^{-1}}$, # $\mathrm{kg^{-1}}$). From these data, we can create tissue-level scalars and height-dependent equations (e.g. wood density, leaf area) to apply to each tree component.

To determine the location of tree structures it is easier to collect cylindrical or polar coordinates and convert to Cartesian with the help of the program *SITCHENSIS* (see below, Fig. 3). Partitioning the tree into components, mapping their locations, and summing them at the tree-level is conceptually simple, but its implementation is not. There are many specific terms and measurements (Table 2) attributed to tree components, making it potentially confusing. Data templates are available in the GitHub distribution of *SITCHENSIS* (see **Error checking and 3d geometry**) to aid data collection and input. The following sections describe the most efficient approach to mapping each tree component.

2.2. Main trunk measurements

The basis for all crown mapping is the center, or pith, of the tree at ground level and is henceforth called the **origin**. The origin has the Cartesian coordinates of (0, 0, 0), and the main trunk is mapped as a collection of vertically stacked conic frusta above it. Conic frusta of the main trunk are called trunk **sections**. The position of all subsequent segments and branches are referenced to the trunk or to other positions