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Foliage biomass and specific leaf area equations at the branch, annual shoot and whole-tree levels for lodgepole pine and white spruce in British Columbia

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ABSTRACT

The distribution and characteristics of foliage are important aspects of tree structure and have implications for the productivity of individual trees and whole stands. We modelled foliage biomass and specific leaf area (SLA) using a sample of 60 lodgepole pine (*Pinus contorta*) and 60 white spruce (*Picea glauca*) that were destructively sampled in British Columbia, Canada. We modelled foliage biomass and SLA at three scales of organization: individual primary branches, annual shoots (all branches on an annual increment of the main stem), and the whole tree. We used a variety of independent variables that range in scale from the branch to plot level. Models of foliage biomass and SLA differ substantially between the two species even though their basic architectural design is quite similar. Models differed notably among levels of organization. For branch-level biomass, relevant variables for both species included branch diameter, length, age, distance to the crown base, and a measure of crown contact; however, at the annual-shoot level, relevant explanatory variables were mostly different between the species. At the whole tree-level, only crown length was common to both species and all other explanatory variables differed. SLA was higher in spruce than pine for all age classes and canopy positions. Overall, the models allow prediction of important crown properties for two major conifers at a range of scales, and can thus contribute to better prediction of stand growth and other properties.

1. Introduction

Crown structure of trees controls the dynamics and growth of forest stands (Horn, 1971; Smith and Long, 1989; Han et al., 2014). The large differences that occur in crown shape among species often translate into substantial variation in light interception (Horn, 1971). Crown length and foliage display differ among species, often in relation to shade tolerance and stand density, which in turn influences competitive interactions (Antos et al., 2010; Lintunen et al., 2011). Branch distribution affects the overall shape of the crown (Linnell Nemec et al., 2012), which has a major influence on foliage display and thus canopy function.

The amount, distribution, and characteristics of foliage within crowns contribute to tree and stand growth (Kershaw and Maguire, 1996; Weiskittel et al., 2009; DeRose and Seymour, 2010). The vertical distribution of foliage biomass relates to shade tolerance, effects of neighbours, and tree development (Maguire and Bennett, 1996; Garber and Maguire, 2005). In general, foliage biomass is concentrated vertically in the central parts of the crown, increasing downward from the top of the tree to some maximum and then decreasing to the base of the crown (Kantola and Mäkelä, 2004; Schneider et al., 2011). In young trees, the foliage tends to be distributed relatively lower in the crown versus concentrated towards the upper part, especially if the tree is in a dominant position (Mori and Hagihara, 1991; Maguire and Bennett, 1996). Within a tree, the distribution of foliage and the associated branches can determine stem characteristics including taper and the size of knots, which affects the value of boles (Trincado and Burkhart, 2009; Linnell Nemec et al., 2012).

Leaf area is strongly linked to photosynthesis and productivity. In conifer species, light interception by needles is a complex function of thickness and orientation (Niinemets, 1999). Specific leaf area (SLA), the ratio of leaf area to leaf dry mass, is a useful measure that reflects potential photosynthetic rate (Reich et al., 1998). SLA is typically plastic within and among individuals of a

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species because it depends on the light level reaching the foliage (e.g., Richardson et al., 2000; Temesgen and Weiskittel, 2006). Many investigations (e.g., Borghetti et al., 1986; Marshall and Monserud, 2003; Weiskittel et al., 2008) have found that SLA increases from the top of the tree to the base of the crown as leaves or needles become thinner and thus the ratio of area to mass increases. Canopy position of trees within a stand will also relate to whole-tree SLA, with shaded individuals (suppressed or sub-canopy) having higher SLA than fully exposed dominant individuals of the same species (Marshall and Monserud, 2003; Weiskittel et al., 2008). Thus, trees in different social positions and of different absolute heights are apt to differ substantially in SLA.

The scale of observation is important when evaluating the distribution of foliage within forest stands. Within the crown, foliage distribution can be related to individual branches and systems of branches (e.g., Gillespie et al., 1994; Kershaw and Maguire, 1995; Schneider et al., 2011). Many conifers have rather rigid branching patterns with a central vertical stem supporting whorls of branches related to annual growth increments of the main stem (e.g., Schneider et al., 2011), which we will call annual shoots (Linnell Nemec et al., 2012).

Economically important species of *Pinus* and *Picea* dominate many temperate forests in the northern hemisphere. Consequently, these have been the focus of many studies modelling various aspects of crown structure (e.g., Gillespie et al., 1994; Baldwin et al., 1997; Kantola and Mäkelä, 2004). Both *Pinus* and *Picea* have a main stem with whorls of branches, but often differ in overall crown morphology. For example, studies of co-occurring *Pinus sylvestris* and *Picea abies* in Europe indicate substantial differences in foliage distribution and crown form (Mäkelä and Vanninen, 2001; Kantola and Mäkelä, 2004; Tahvanainen and Forss, 2008). Species differences within these genera can also be substantial – both for *Pinus* (Gillespie et al., 1994; Xu and Harrington, 1998; Schneider et al., 2011; Shaiek et al., 2011) and *Picea* (Power et al., 2012, 2014) – necessitating study of individual species in order to make precise predictions of foliage distribution and characteristics within and among trees.

The quantity and distribution of foliar biomass and leaf area are important components of micro environment, tree growth and stand dynamics, which affects timber and non-timber forest values. Our goal is to evaluate and predict the distribution of foliar biomass and SLA in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) and white spruce (*Picea glauca* [Moench] Voss) (Hereinafter designated as pine and spruce, respectively). We consider foliage biomass and SLA at three scales: (1) primary branches on the main stem, (2) the set of branches emanating from each annual shoot on the main stem, including the main whorl at the distal end of the annual shoot and other secondary whorls or individual branches along the annual shoot, and (3) the entire tree. We ask what do characteristics at each level of organization contribute to the prediction of foliage biomass and SLA; what factors determine foliar biomass and SLA of branches; how does organization into annual shoots contribute; and, how are foliar biomass and SLA distributed vertically along the stem of the whole tree? Furthermore, we discuss how these two conifers differ in foliage characteristics.

2. Methods

2.1. Stand selection and field measurements

A total of 60 pine and 60 spruce were sampled in the dormant seasons of 2003/4 and 2004/5 and of 2007/8 and 2008/9, respectively (Table 1). Four or five relatively undamaged trees were typically selected from stands in each of three age classes (20–40, 41–70 and 71+). The stands were selected in two different geographic areas: near Kamloops and Quesnel for pine; and near Quesnel and Prince George for spruce.

Trees were selected to span the range of diameters in each stand. Other selection criteria included: having relatively symmetrical crowns, little damage, and a location so that they could be felled easily and safely. The crown perimeter of the sample tree was measured at 8–12 points. All trees with diameter at breast height (D_{BH}) $\geqslant$ 4 cm were mapped and species, diameter, and location recorded around the sample tree. Plots were circular and sizes ranged from 0.002 to 0.040 ha (radius 2.52–11.28 m) and included at least 10 neighbours. Trees were felled in a safe, open location to minimize branch breakage.

After felling, we recorded the height to each annual whorl in the live crown (including the leader) and measured in each of four quadrants around the stem, height to the base of live crown and to the free-growing portion of the crown, i.e., above contact zone of crowns of neighbouring trees. Evidence of branch abrasion was observed to determine the upper extent of crown contact. To check the accuracy of the whorl count, ring counts on disk samples were cross-referenced to ensure that nodal ages at each whorl matched both bole ages and branch ages. Complete disks were removed at three fixed heights (0.30, 0.70 and 1.3 m) and at 10 approximately equally spaced locations above breast height, dividing the bole into 13 sections. Sample locations were adjusted if necessary to avoid large branches or whorls. Occasionally the bottom sample above breast height was not removed on small trees if it was within one metre of the breast height disk. We recorded the diameter outside bark, double bark thickness, number of rings and the distance from the pith to the interface between heartwood and sapwood on two average radii for each disk.

A previously developed custom data logging program (Stem and Tree Analysis Recording System (STARS)) guided and recorded branch sampling. We define annual shoot as the portion of a bole from just above a branch whorl up to and including the next whorl up the bole, or the height growth (H_G) in each year. The STARS program randomly selects at least one annual shoot in each of the above bole sections containing live crown for detailed branch sampling, with at least six annual shoots chosen from each tree. For crowns occupying less than six bole sections, STARS randomly selects annual shoots in the middle third of the crown where most foliage exists. In each sample shoot, all branches in the live crown, both at the whorl and along the annual shoot, were located and measured for distance from the whorl, azimuth, vertical and horizontal diameters outside bark, and total length. The horizontal and vertical diameters were sampled close to the bole edge but outside notable branch swelling. Basal diameter of a branch (D_{BR}, Table 2) was calculated as the average of the vertical and horizontal diameters. Branches broken both prior to or after felling were assigned a damage code.

STARS randomly selects up to three branches per annual shoot for detailed subsampling with selection probability being proportional to branch cross-sectional area at the base. We measured angle to terminal bud, primary branch length, and distance to live foliage. We severed the branch and measured inside bark diameters (vertical and horizontal) and collected foliage for laboratory determination of biomass and leaf area. We defined first-order as branches that initiate from the main bole and second-order as those originating on the primary branch. For pine, we sampled along the entire branch when the number of second-order branches was less than seven. Otherwise, we drew a number between 1 and 3, and starting at the randomly-chosen second-order branch, sequentially sampled it and every third second-order branch. The number of second-order branches on spruce was considerably higher than pine, so that we sampled every 5th second-order branch after drawing a random start. Six excessively large spruce second-order branches were similarly sub-sampled by