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Species differences in total and vertical distribution of branch- and tree-level leaf area for the five primary conifer species in Maine, USA

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ABSTRACT

Vertical distribution of leaf area largely governs both tree structure and function. Models of this important tree attribute have been constructed for several commercially important conifers. However, a limited number of studies have compared alternative modeling techniques and inherent species differences. This study used several existing datasets for the five primary conifer species in Maine, namely balsam fir [*Abies balsamea* (L.) Mill.], northern white-cedar [*Thuja occidentalis* (L.)], eastern hemlock [*Tsuga canadensis* (L.) Carr.], eastern white pine [*Pinus strobus* (L.)], and red spruce [*Picea rubens* (Sarg.)] to examine species variation in total and vertical distribution of projected leaf area at the individual branch- and tree-levels. In addition, multiple methods for modeling the vertical distribution of leaf area were examined across the species. For a given branch diameter and location within the crown, eastern hemlock branches held the greatest amount of leaf area, followed by balsam fir, northern white-cedar, white pine, and red spruce. At the tree-level, eastern white pine held the greatest amount of leaf area followed by eastern hemlock, balsam fir, red spruce, and northern white-cedar for a given tree size. Across species, the two-parameter, right-truncated Weibull distribution performed the best for predicting vertical distribution of leaf area when compared to the four-parameter beta and Johnson's S_B distributions (reduction of root mean square error of 1.7–21.1%). Northern white-cedar had a relative distribution of leaf area distinctly different than other species in this study with a mode shifted towards the upper crown. In contrast to red spruce and white pine, the mode of the relative distribution of leaf area for balsam fir and eastern hemlock occurred lower in the crown. Results of this study suggest that differences in total and vertical distribution of leaf area exist between species, but significant amounts of their variation are largely accounted for by bole and crown size.

1. Introduction

Vertical distribution of leaf area is an important determinant of both tree structure and function since it influences stem cross-sectional area increment (Kershaw and Maguire, 2000), light transmittance (Vose et al., 1995), radial pattern of sap flux density (Fiora and Cescatti, 2008), and natural sway frequency (Moore and Maguire, 2005). At the individual tree-level, vertical distribution of leaf area has been shown to be influenced by tree age (Kantola and Mäkelä, 2004), relative social position in the stand (Maguire and Bennett, 1996), and crown size (Weiskittel et al., 2006). Stand age (Kantola and Mäkelä, 2004), stand density (Xu and Harrington, 1998), species composition (Garber and Maguire, 2005), and defoliation caused by a foliar disease (Weiskittel et al., 2006) have been found to be important factors at the stand-level.

Vertical distribution of leaf area has been effectively modeled for several conifer species, including coastal Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco] (Maguire and Bennett, 1996); loblolly pine [*Pinus taeda* (L.)] (Xu and Harrington, 1998); Norway spruce [*Picea abies* (L.) Karst.] (Kantola and Mäkelä, 2004); grand fir [*Abies grandis* (Dougl. ex D. Don) Lindl.] (Garber and Maguire, 2005); Scots pine [*Pinus sylvestris* (L.)] (Mäkelä and Vanninen, 2001); and hinoki [*Chamaecyparis obtusa* (Endl.)] (Mori and Hagihara, 1991). Although a variety of studies have been conducted on vertical distribution of leaf area, most of these previous studies have concentrated on a single species rather than comparisons of multiple species. Garber and Maguire (2005) recently found that vertical distribution of leaf area for three conifers in eastern Oregon in an even-aged, mixed-species stand was dependent on the interaction of species composition and initial density. In addition, Garber and Maguire (2005) found that

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species with differing levels of shade tolerance were quite plastic in their vertical distribution of foliage in response to stand structure. Thus, a further understanding of species inherent differences in vertical distribution of leaf area is needed.

Previous studies have generally modeled vertical distribution of leaf area with probability density distributions, which have included the normal (Stephens, 1969), chi-square (Massman, 1982), lognormal (Schreuder and Swank, 1974), gamma (Schreuder and Swank, 1974; Massman, 1982), Weibull (Gillespie et al., 1994; Baldwin et al., 1997; Xu and Harrington, 1998), Johnson's S_B (Jerez et al., 2005), and beta (Maguire and Bennett, 1996; Garber and Maguire, 2005). The beta, Johnson's S_B, and truncated Weibull are all logical distributions to use because they are both highly flexible and have fixed endpoints that correspond with top and bottom of the live crown. To our knowledge, the relative accuracy and precision of these distributions for modeling vertical distribution of leaf area has yet to be simultaneously examined across multiple species. Furthermore, most previous studies on vertical distribution of leaf area have divided the crown into a predetermined number of segments for modeling purposes. For example, ten relative segments have been used in several recent studies (Maguire and Bennett, 1996; Garber and Maguire, 2005; Weiskittel et al., 2006). The accuracy of grouping branches and different levels of grouping for modeling vertical distribution of leaf area has also yet to be examined.

The goal of this study was to model and compare vertical distribution of leaf area in the five primary conifer species in Maine. The species included balsam fir [*Abies balsamea* (L.) Mill.], northern white-cedar [*Thuja occidentalis* (L.)], eastern hemlock [*Tsuga canadensis* (L.) Carr.], eastern white pine [*Pinus strobus* (L.)], and red spruce [*Picea rubens* (Sarg.)]. The specific objectives of the study were: (1) develop predictive equations for branch- and tree-projected leaf area across the examined species; (2) quantify the relative performance of beta, Johnson's S_B, and truncated Weibull for modeling vertical distribution of tree leaf area across multiple species; and (3) model differences in vertical distribution of leaf area between species with varying shade tolerances.

2. Methods

2.1. Study area

Data for this study came from a range of locations in central and northern Maine. The state is comprised of nine separate climatic zones, which strongly influence composition and structure of the forest (Briggs and Lemin, 1992). Across the climatic zones, average annual precipitation is 110 cm with a range of 95–125 cm, while mean growing degree days (sum of daily mean temperatures above 5 °C) is 2133 (range of 1508–2976) (Briggs and Lemin, 1992). Glacial till is the principal soil parent material with soil types ranging from well-drained loams and sandy loams on glacial till ridges to poorly and very poorly drained loams on flat areas between these low-profile ridges. In general, the northern conifer sites from which many of the trees were sampled in this study are underlain by somewhat poorly to very poorly drained loams and silt loams.

The forest canopy is dominated by a mixture of species, primarily red spruce, balsam fir, and eastern hemlock with lesser amounts of white spruce [*Picea glauca* (Moench.)], black spruce [*Picea mariana* (Mill.) BSP], northern white-cedar, white pine, red maple [*Acer rubrum* (L.)], paper birch [*Betula papyrifera* (Marsh.)], and gray birch [*Betula populifolia* (Marsh.)]. Red spruce, white spruce, and balsam fir dominate the relatively low-lying sites of poorer drainage, but the proportion of eastern hemlock and white pine increases as drainage improves.

2.2. Data

To achieve the objectives of this study, multiple existing datasets were combined (Table 1). Each dataset is briefly described by species below.

2.2.1. Balsam fir

Data on balsam fir vertical distribution of leaf area were obtained from Gilmore et al. (1996) and Meyer (2005). The Gilmore et al. (1996) dataset consisted of 39 sample trees from two locations in north central Maine. Thirty-nine sample trees came from study sites located on University of Maine's Dwight B. Demeritt Forest and the Penobscot Experimental Forest. Basal area of the sampled stand ranged from 2 to 38 $m^2\ ha^{-1}$ and average quadratic mean diameter varied from 5.7 to 19.0 cm. The sites were intermediate in productivity as the site index ranged from 15 to 20 m at a base age of 50 years at breast height. The trees were systematically sampled across four crown classes, namely open grown ($n = 9$), codominant ($n = 17$), intermediate ($n = 10$), and suppressed ($n = 3$). These trees were sampled in July and August of 1992 and 1993, two or more weeks after bud set. In August 1993, an additional 12 codominant trees were sampled from a 23-year-old balsam fir–red spruce stand in Bald Mountain Township, which is approximately 100 km northwest of Orono. The stand was naturally regenerated after a winter clearcut and released by a variety of herbicides as described in Newton et al. (1992).

Table 1
Attributes of the sample trees by species. Variables include diameter at breast height (DBH; cm), total tree height (HT; m), height to crown base (HCB; m), height to lowest live branch (HLLB; m), tree leaf area (TLA; m^2), and relative height in the stand (RHT).

Attribute	Mean	Standard deviation	Minimum	Maximum
Balsam fir (n = 84)				
DBH (cm)	14.4	6.9	2.5	31.8
HT (m)	11.7	3.9	3.9	19.7
HCB (m)	5.3	3.1	0.2	12.9
HLLB (m)	4.4	2.8	0.0	11.5
TLA (m^2)	38.3	40.9	0.3	190.2
RHT	0.69	0.22	0.27	1.00
Northern white-cedar (n = 25)				
DBH (cm)	29.9	9.1	14.1	46.3
HT (m)	15.6	2.8	10.5	19.9
HCB (m)	10.6	3.1	5.5	16.3
HLLB (m)	8.1	2.9	3.8	15.2
TLA (m^2)	62.1	30.7	23.2	118.9
RHT	0.86	0.09	0.70	1.00
Eastern hemlock (n = 20)				
DBH (cm)	28.2	12.6	6.8	48.4
HT (m)	14.7	4.9	5.6	20.9
HCB (m)	5.3	2.5	1.6	10.8
HLLB (m)	3.4	1.9	0.9	7.5
TLA (m^2)	179.2	124.1	9.5	417.3
RHT	0.62	0.21	0.24	0.88
Red spruce (n = 62)				
DBH (cm)	20.1	10.6	4.9	50.0
HT (m)	14.8	4.4	5.7	23.4
HCB (m)	8.9	3.5	2.1	14.6
HLLB (m)	7.8	2.9	0.0	14.6
TLA (m^2)	45.4	53.1	0.6	250.9
RHT	0.66	0.17	0.25	1.00
White pine (n = 48)				
DBH (cm)	17.8	12.9	1.6	61.3
HT (m)	14.8	7.2	2.8	29.6
HCB (m)	11.8	3.6	1.5	18.6
HLLB (m)	8.7	5.2	0.9	18.3
TLA (m^2)	43.6	69.55	0.3	587.9
RHT	0.88	0.14	0.41	1.00