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Volume increment efficiency of *Picea mariana* in northern Ontario, Canada

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Abstract

Volume increment efficiency (VIE), a measure related to radiation use efficiency, is defined in this study as the annual total stemwood volume increment divided by the amount of global shortwave radiation intercepted by tree crowns during the photosynthetic season. We examined the influence of ecosite and of stand density on the VIE of *Picea mariana* in northern Ontario, Canada, using two data sets. The VIE of *P. mariana* differed significantly among ecosites, ranging from 0.071 $dm^3\ GJ^{-1}$ on poor-quality peatland sites to 0.345 $dm^3\ GJ^{-1}$ on fertile mineral soil sites. The VIE of *P. mariana* increased with increasing stand basal area and generally decreased with increasing radiation interception by individual trees, likely because allocation to branches is less in small trees and dense stands. VIE represents a straightforward way to relate volume growth to radiation interception in individual tree growth models.

Keywords: *Picea mariana*; Black spruce; Light capture; Radiation interception; Radiation-use efficiency; Volume increment efficiency; Productivity

1. Introduction

Monteith (1977) demonstrated that the dry matter production of agricultural crops is linearly related to the amount of radiation intercepted by the crop canopy. The slope of this relationship is commonly referred to as radiation use efficiency (ε), or light use efficiency (LUE). Tree growth is also closely related to the interception of radiation, both at the stand level (Cannell et al., 1987; Dalla-Tea and Jokela, 1991; Will et al., 2001; Allen et al., 2005), and at the individual tree level (Kaufmann and Ryan, 1986; Brunner and Nigh, 2000; MacFarlane et al., 2002).

The strong relationship between radiation interception and tree growth is the foundation for stand-level forest productivity models such as 3-PG, PROMOD and TRIPLEX (Landsberg and Waring, 1997; Battaglia and Sands, 1997; Peng et al., 2002), which estimate growth as the product of radiation intercepted by the forest canopy and the efficiency of the radiation to growth conversion. The development of models that estimate radiation interception by individual tree crowns (Brunner, 1998; Groot, 2004) makes it feasible to also construct individual-tree growth models based on radiation-use efficiency (Bartelink et al., 1997). Such models potentially could overcome the error aggregation and propagation that currently limit the effectiveness of both empirical and process-based individual-tree growth models (Mäkelä, 2003; Groot et al., 2004). The resource limitation imposed by the availability of solar radiation provides a stand-level limit on the aggregate modelled growth of individual trees, ensuring that modelled stand-level growth remains with constraints defined by resource availability.

In this study, we examine resource-use efficiency in terms of the total stem volume increment divided by the amount of global shortwave radiation intercepted by tree crowns during the photosynthetic season. We use stem volume increment as the measure of production because of its economic significance, and because it is typically the production measure of interest in forest management. Furthermore, a vast amount of information on individual tree and stand volume increment has been accumulated in the forestry literature. We use global shortwave radiation as the resource measure because measurement networks are more widely available for shortwave global

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radiation than for PAR. We recognize that LUE is normally reported in terms of PAR, but note that frequently the PAR component is estimated from global shortwave radiation using a conversion factor of 0.5 (e.g., Martin and Jokela, 2004; Allen et al., 2005).

In their review of the uncertainties and inconsistencies involved in estimates of LUE, Gower et al. (1999) argued that the term LUE should be reserved for the ratio of total net primary productivity to photosynthetically active radiation absorbed by green foliage during the growing season. Our measure of resource-use efficiency is distinct from, although related to, LUE. We therefore propose the term Volume Increment Efficiency (VIE) to represent the ratio of total stem volume increment divided by the amount of global shortwave radiation intercepted by tree crowns during the photosynthetic season Convenient units for volume increment efficiency are $dm^3\ GJ^{-1}$. We note that knowledge gained about light use efficiency in forest production ecology research can be made applicable in volume terms through the use of appropriate conversion factors (e.g., wood density, biomass allocation factor and PAR: global shortwave radiation ratio).

In order to parameterize VIE-based individual tree growth models, it is necessary to determine how VIE varies with site quality and stand structural characteristics. Variation in radiation use efficiency among forest types is not large when climatic constraints such as photosynthetic season length are taken into account (Runyon et al., 1994; Ahl et al., 2004). Much of the variation in net primary production is attributable to variation in the amount of radiation intercepted by the canopy during the growing season rather than variation in radiation use efficiency (Runyon et al., 1994; Bolstad et al., 2001). In contrast, forestry yield tables (e.g., Plonksi, 1974) show large variation in stand volume increment for fully occupied stands within regions with small climatic variation. It seems likely that much of this variation is a result of variation in VIE rather than variation in the amount of radiation intercepted.

It is also necessary to determine how characteristics such as stand density affect VIE. There is evidence that production efficiency increases with stand basal area or density (Burkes et al., 2003; McDowell et al., 2007), possibly because small and suppressed trees make more efficient use of resources such as radiation (Smith and Long, 1989; Reid et al., 2004).

The objective of this study was to quantify how radiation interception, volume increment and VIE vary with ecosite and stand density for *Picea mariana* (Mill.) B.S.P. (black spruce), a widely distributed and economically valuable species of boreal North America. This information will be used to parameterize a VIE-based individual tree growth model.

2. Materials and methods

2.1. Data description

We estimated VIE using measured volume increment and estimated shortwave radiation interception from two data sets collected in the Boreal Forest Region (Rowe, 1972) of northern Ontario:

PSP data set: We obtained data from 24 black spruce-dominated permanent sample plots ($400\ m^2$ plots in north-eastern Ontario, with locations bounded by 47°40′N, 49°37′N, 80°23′W, and 82°22′W) (Table 1). These plots were established and maintained through the growth and yield programs of the Ontario Ministry of Natural Resources and the Forest Ecosystem Science Co-operative Inc. (Forest Co-op) Growth and Yield Business Unit to provide information on the growth and yield of forest stands representing a range of ecoregions, site types, species compositions and site types (Lewis, 1995).

TL data set: We also obtained data from the Tyrol Lake black spruce thinning experiment (located in northwestern Ontario at 49°37′N, 88°15′W) which was established in black spruce plantations to compare stand growth and development following four levels of precommercial thinning (0, 20, 35, and 50% basal area removal) (Fleming et al., 2005). Stand basal area at age 24, just prior to thinning, averaged $27.9\ m^2\ ha^{-1}$. The soil in the experimental area was a cobbly, coarse loamy till overlying granitic bedrock. Each level of thinning was applied to three to five replicates (total of 18 plots). Treatment plot areas were 0.0625 ha, within which $225\ m^2$ measurement plots were located. The VIE estimates reported were derived from age 33 measurements made within the measurement plots.

Table 1
Mean characteristics of *Picea mariana* (PIm) radiation interception and stem volume increment (PSP data set)

Ecosite[a]	Number of plots	Dominant species[b]	Basal area[c] ($m^2\ ha^{-1}$)	Dominant height[c] (m)	Photosynthetic season length (days)	Age of site index trees (years)
ES2 + ES4	5	PIm (93)	28.5 (8.6)	18.3 (3.2)	170	49–140
ES5f	2	PIm (93)	16.3 (10.4)	14.7 (2.0)	168	40–101
ES6f	3	PIm (87)	42.6 (9.6)	20.3 (1.2)	168	75–99
ES8	2	PIm (84)	24.4 (17.5)	15.0 (0.8)	165	54–91
ES11	4	PIm (100)	21.4 (3.7)	13.8 (1.1)	169	61–154
ES12	3	PIm (96)	27.2 (4.5)	17.4 (1.5)	169	67–126
ES13	2	PIm (94)	18.3 (1.7)	15.3 (0.2)	163	144
ES14	3	PIm (99)	10.9 (3.7)	11.9 (0.8)	167	89–100

[a] Taylor et al. (2000): ES2: jack pine–coarse soil; ES4: black spruce–jack pine–coarse soil; ES5f: black spruce–fine soil; ES6f: black spruce–trembling aspen–fine soil; ES8: black spruce–feathermoss–sphagnum–moist soil; ES11: black spruce–labrador-tea–organic soil; ES12: black spruce–larch–labrador-tea–organic soil; ES13: black spruce–larch–speckled alder–organic soil–species poor; ES14: black spruce–leatherleaf–organic soil.

[b] Value in parenthesis is the percentage of the basal area represented by the dominant species.

[c] Values in parenthesis are standard deviations.