



## Why is the productivity of Douglas-fir higher in New Zealand than in its native range in the Pacific Northwest, USA?

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### ARTICLE INFO

#### Article history:

Received 18 October 2007

Received in revised form 22 March 2008

Accepted 26 March 2008

#### Keywords:

Climate analysis

Productivity

Process models

Douglas-fir

3-PG model

### ABSTRACT

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), a native to the Pacific Coast Range in North America, is recognized as a tree that is long-lived and can grow rapidly to standing volumes that approach the highest recorded for temperate conifers. Managed plantations in western Oregon register maximum periodic annual increments (PAI) at ages between 20 and 40 years of  $\sim 30 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ . The same seed source, when planted in New Zealand and elsewhere in the Southern Hemisphere, may attain a PAI of  $\sim 50 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ . Is this higher productivity mainly related to climate or to isolation from native pests? To evaluate the role of climate, we obtained meteorological data from plantation sites in New Zealand and Oregon, from which we established relationships between mean monthly temperature extremes and solar irradiance, air humidity deficits, and frost frequency. Using these empirical relationships, long-term weather records were converted to the meteorological variables required to drive a process-based forest growth model, 3-PG, for sites approaching the most productive in New Zealand and in Oregon. Annual precipitation is similar in both areas, but sites in Oregon receive only 10% during the growing season, resulting in humidity deficits 30% larger than those recorded in New Zealand. According to sensitivity analyses and direct measurements, the more productive Douglas-fir forests in Oregon avoid the limiting effects of summer drought by obtaining water from the subsoil and fractured bedrock. If such forests were under a reduced evaporative demand similar to that in New Zealand, we show that they would exhibit comparable productivity.

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### 1. Introduction

Douglas-fir, when planted in New Zealand, produces up to 40% more wood volume annually than that recorded on the best sites within its native range in the Pacific Northwest Region of the United States (Ledgard and Belton, 1985). Basal areas attained at 40 years on good sites in New Zealand on average exceed those recorded for old-growth forests in the Pacific Northwest (Ibid, Waring and Franklin, 1979). At Karioi State Forest on the North Island of New Zealand, unthinned plantations of Douglas-fir average standing volumes  $>1500 \text{ m}^3 \text{ ha}^{-1}$  at 50 years, representing a mean annual increment of  $30 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$  and a maximum periodic annual increment of  $\sim 50 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ . Similar yields are reported for plantations on the South Island north of Christchurch, Latitude  $46^\circ 30' \text{ S}$ , Longitude  $168^\circ 20' \text{ E}$  (A.

Nordmeyer, unpublished). Might these differences in growth rates be attributed to climate or could higher growth rates in New Zealand be associated with isolation of Douglas-fir from native pests? Douglas-fir is certainly not immune to infection or insect attack in New Zealand (Ledgard and Belton, 1985; Ledgard et al., 2005).

Many investigators have analyzed long-term weather data seeking correlations between forest productivity and annual precipitation and mean temperature (Lieth, 1975; Ledgard and Belton, 1985; Jiang et al., 1999). Locally, these correlations may be strong but interpretations can be misleading. Seasonal variation in precipitation and temperature may lead to periods that severely limit growth. In addition, cloud cover, often associated with periods of precipitation, reduces the evaporative demand as well as the irradiance available for photosynthesis.

To understand the extent that climate may limit growth requires an analysis incorporating seasonal constraints that might be imposed by drought, limiting irradiance, high air humidity deficits, and suboptimal temperatures, as well as other related

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factors (e.g., atmospheric CO<sub>2</sub>, NO<sub>x</sub>, ozone concentrations). Over the last two decades, a number of process-based forest growth models have been developed that consider most, if not all, of the above interactions (see reviews by Landsberg, 2003; Nightingale et al., 2004). These models require a suite of meteorological data rarely available from standard weather stations. Sites with high quality meteorological data, even if acquired for only a few years, provide the opportunity to establish relationships between maximum and minimum temperatures recorded at all weather stations with solar irradiance, air humidity deficits, and frost frequency (Running et al., 1987; Coops et al., 2000). Although based on sound principles, meteorological relationships include constants that tend to vary somewhat between maritime and continental climates. For this reason, it is desirable to calibrate such models before extrapolation to nearby areas where only long-term weather records are available.

In this paper, we first test meteorological relationships at two calibration sites, one in New Zealand and the other in the Coast Range of Oregon, USA. After calibration, we next derive meteorological variables from weather stations located near two other highly productive sites. Using a common set of allometric equations and other model parameters, we then match current levels of maximum mean periodic (decadal) increment recorded at the four sites. Finally, we perform sensitivity analyses with the forest growth model to determine the extent to which seasonal variation in climatic conditions might explain why growth rates of Douglas-fir in New Zealand are higher than those in Oregon. In the following sections we describe the sites, present the models, demonstrate their calibration, and report the results of sensitivity analyses.

## 2. Methods

### 2.1. Forest sites

The four sites selected for comparison support plantations of Douglas-fir 28–58 years old; their locations and climatic conditions are presented in Table 1. The plantations are situated on well-drained soils with high fertility (A. Nordmeyer, unpublished data; Mark Gourley, Starker Forests Inc., unpublished data). Mean annual average temperature and annual precipitation are similar at all sites, ranging from 8 to 11 °C and from ~1500 to 1800 mm, respectively (Table 1). Precipitation is distributed evenly across the seasons in New Zealand, averaging ~125 mm monthly. In contrast, the Oregon sites experience 4 months during the growing season that receive in total less than 10% of the annual precipitation.

With less precipitation and cloud cover, summer temperatures average 2–3 °C higher in Oregon than those at the New Zealand sites. Higher temperatures increase the evaporative demand (air humidity deficit,  $D$ ) to 30% above that recorded during the growing season in New Zealand. This increase in evaporative demand, combined with a reduction in precipitation, could severely limit photosynthesis and late season tree growth if soil water supply became limiting. On shallow soils, predawn tree water potentials have been recorded at –0.8 MPa in the Oregon Coast Range in summer (late June), falling to below –1.2 MPa by early autumn (September, R. Waring and M. Newton, unpublished). On deeper soils overlaying friable bedrock, Douglas-fir roots obtain sufficient water to maintain predawn water potentials at –0.5 MPa (James Irvine, unpublished data collected at Mary's River site in early September) (Runyon et al., 1994; Zwieniecki and Newton, 1996; Hubbert et al., 2001).

Frost is infrequent (~40 days annually) except at the high elevation site on the South Island of New Zealand where, on average, 120 frost days per year were recorded. The extent that drought, air humidity deficit, frost frequency affects photosynth-

esis and growth is dependent to a large extent on seasonal variation in the amount of light absorbed by the foliage. A process-based growth model, described below, gives us the ability to assess the monthly constraints on productivity.

### 2.2. 3-PG model

Landsberg and Waring (1997) developed a deterministic (i.e., non-statistical) forest growth model, 3-PG (Physiological Principles for Predicting Growth), based on a number of established biophysical relationships and constants. 3-PG, like other process-based models, contains subroutines to calculate rates of photosynthesis, transpiration, respiration, and growth allocation and litter production. It differs from most process models in that it predicts stand properties measured by foresters (tree spacing, basal area, mean diameters, standing volume, current and mean annual increment) as well as those of interest to ecologists such as leaf area index ( $L$ ), carbon and water balances. Relatively few variables are needed to run the model and these can be derived from literature or from field measurements (Table 2).

The monthly time-step model requires average daily short-wave incoming irradiance, mean air humidity deficit, mean monthly temperature, precipitation, and frost frequency (Table 1). At annual time steps, an estimate of the available soil water storage capacity ( $\theta$ ) and soil fertility ranking (FR) must be obtained if these vary, as they do when young trees have not established full root extension, or following application of commercial fertilizer.

Absorbed photosynthetically active irradiance (APAR,  $\phi_{p,a}$ ) is estimated from global solar irradiance (assumed at 50%) and leaf area index; the utilized portion ( $\phi_{p,a,u}$ ) is calculated by reducing  $\phi_{p,a}$  by an amount determined by a series of modifiers that take values between 0 (system 'shutdown') and 1 (no constraint) to limit photosynthesis (Landsberg and Waring, 1997). Fractional reductions in  $\phi_{p,a}$  are imposed depending on the degree to which stomatal conductance is limited by high (average) day-time  $D$ , subfreezing conditions, and inadequate precipitation as it affects the soil water balance. Drought limitations are imposed as a function of soil texture when the total monthly precipitation and soil water supply are significantly less than transpiration estimated using the Penman–Monteith equation.

Gross primary production ( $P_G$ ) is calculated by multiplying  $\phi_{p,a,u}$  by a canopy quantum efficiency coefficient ( $\alpha$ ), with a maximum value ( $\alpha_c$ ) set by the soil fertility ranking (ranging from 0 to 1.0 (see model parameters in Table 2)). In the analysis performed in this paper, we set  $\alpha_c$  at 3.0 g C MJ<sup>-1</sup> APAR, representing maximum reported values for Douglas-fir (Bond et al., 1999) at an optimum temperature of 15 °C (C. Thomas, unpublished eddy-flux data acquired at site 3, Table 1). Suboptimal temperatures reduce the canopy quantum efficiency, particularly when below 10 °C (Lewis et al., 2001). We chose to maintain a stable value for the temperature optimum, although we realize some adjustment is possible throughout much of the year (Lewis et al., 2001).

A major simplification in the 3-PG model is that it does not require detailed calculation of respiration. Autotrophic respiration and total net primary production ( $P_N$ ) in temperate forests are recognized to be relatively constant fractions (0.53 and 0.47, S.E.  $\pm$  0.04) of  $P_G$  (Waring et al., 1998; Gifford, 2003; but see Litton et al., 2007). The model partitions  $P_N$  into root and aboveground components of biomass (branches, stems, and foliage). The fraction of total  $P_N$  allocated below ground increases from 0.25 to 0.6 as the ratio of  $\phi_{p,a,u}/\phi_{p,a}$  decreases from 1.0 to 0.2. The remaining  $P_N$  is partitioned into above-ground components, based on species-specific allometric relations with mean stem diameter (Table 2). In this study, we first parameterized 3-PG for Douglas-fir to match yield table values for a highly productive plantation (site 4 in Table 1) in regard to

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