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## 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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## 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 photosyn-

thesis 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.

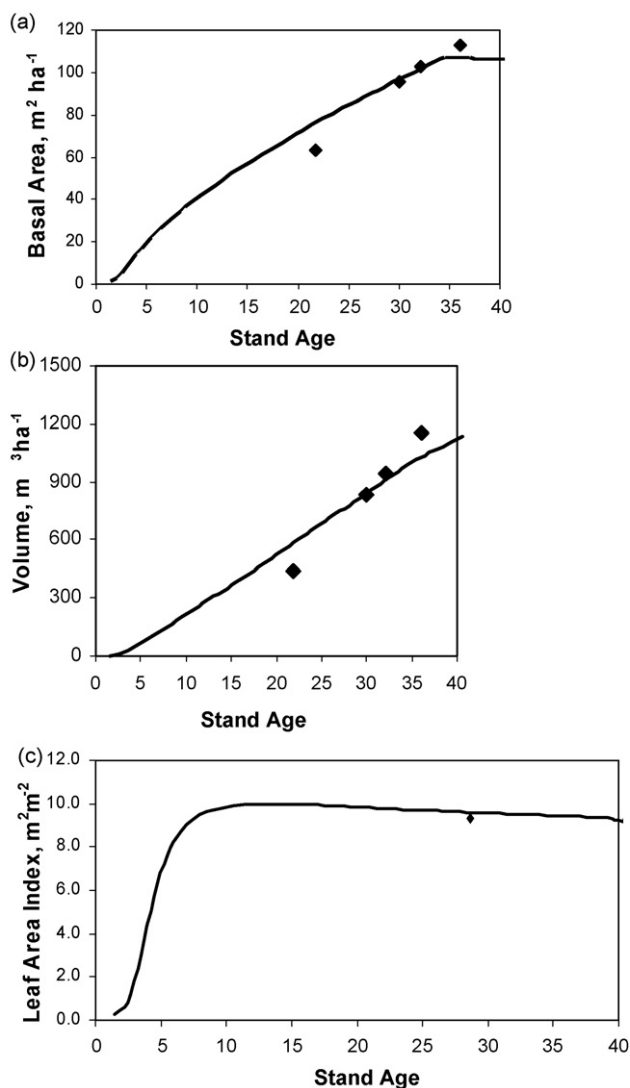
Gross primary production ( $P_G$ ) is calculated by multiplying  $\phi_{p.a.u.}$  by a canopy quantum efficiency coefficient ( $\alpha$ ), with a maximum value ( $\alpha_c$ ) set by the soil fertility ranking (ranging from 0 to 1.0 (see model parameters in Table 2)). In the analysis performed in this 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

**Table 1**  
Monthly and annual summaries of climate variables at Douglas-fir plantation sites

Variable Site 1	July	August	September	October	November	December	January	February	March	April	May	June	Monthly average	Annual sum
Solar irradiance (MJ m <sup>-2</sup> day <sup>-1</sup> )	4.9	7.6	11.6	15.4	18.6	20.4	20.6	17.6	13.6	9.5	6.1	4.4	12.5	4571
Air humidity deficit daytime (kPa)	0.27	0.31	0.43	0.54	0.60	0.79	0.76	0.84	0.66	0.44	0.35	0.22	0.52	
Precipitation (mm month <sup>-1</sup> )	128	152	132	174	139	131	108	73	92	114	126	113	124	1483
Frost days month <sup>-1</sup>	25	22	15	9	4	1	0	0	1	5	15	22	10.1	121
Average air temperature (°C)	2.3	3.5	5.7	8.1	9.7	12.0	13.5	13.9	11.9	8.9	5.6	2.9	8.2	
Variable Site 2	July	August	September	October	November	December	January	February	March	April	May	June	Monthly average	Annual sum
Solar irradiance (MJ m <sup>-2</sup> day <sup>-1</sup> )	6.1	8.6	12.6	16.7	19.4	20.3	20.0	18.1	14.5	10.1	7.0	5.7	13.3	4839
Air humidity deficit daytime (kPa)	0.26	0.30	0.36	0.46	0.56	0.61	0.71	0.72	0.65	0.52	0.33	0.28	0.48	
Precipitation (mm month <sup>-1</sup> )	168	162	148	131	125	163	108	75	96	107	145	136	130	1564
Frost days month <sup>-1</sup>	12	8	5	3	2	0	0	0	0	1	6	11	4.1	49
Average air temperature (°C)	4.9	5.9	7.5	9.6	11.2	13.3	15.2	15.1	14.0	10.8	7.4	5.4	10.0	
Variable Site 3	January	February	March	April	May	June	July	August	September	October	November	December	Monthly average	Annual sum
Solar irradiance (MJ m <sup>-2</sup> day <sup>-1</sup> )	4.2	4.8	7.3	13.3	16.7	16.8	21.2	19.0	15.4	10.1	2.9	3.4	11.3	4052
Air humidity deficit daytime (kPa)	0.24	0.18	0.23	0.49	0.79	1.04	0.95	0.76	1.14	0.63	0.26	0.21	0.58	
Precipitation (mm month <sup>-1</sup> )	165	260	174	120	51	27	4	0	23	45	459	229	126	1557
Frost days month <sup>-1</sup>	14	6	1	0	0	0	0	0	0	0	4	12	3.1	37
Average air temperature (°C)	3.0	5.4	6.8	8.3	11.9	14.6	16.4	14.7	15.7	10.3	6.6	4.0	9.8	
Variable Site 4	January	February	March	April	May	June	July	August	September	October	November	December	Monthly average	Annual sum
Solar irradiance (MJ m <sup>-2</sup> day <sup>-1</sup> )	3.3	5.9	9.9	14.9	18.1	19.3	18.8	16.3	11.9	7.1	3.9	2.8	11.0	4013
Air humidity deficit daytime (kPa)	0.27	0.36	0.45	0.58	0.70	0.79	1.03	1.06	1.03	0.71	0.37	0.27	6.3	
Precipitation (mm month <sup>-1</sup> )	273	236	206	142	89	63	24	26	61	121	280	313	153	1833
Frost days month <sup>-1</sup>	9	8	6	4	0	0	0	0	0	0	5	9	3.4	41
Average air temperature (°C)	4.7	6.2	7.6	9.6	12.1	14.5	16.8	17.0	15.7	12.0	7.5	5.1	10.7	

Site 1: Craigieburn calibration site: South Island, New Zealand. Latitude 43° 09'S, Longitude 171° 43'E, elevation 914 m asl. Derived from meteorological data: 1964–2001. Site 2: Karioi Forest, North Island, New Zealand. Latitude 39° 24'S, Longitude 175° 25'E, elevation 629 m asl. Derived from weather data: 1974–1980. Site 3: Mary's River, Oregon Calibration site. Latitude 44° 39' N, Longitude 123° 20' W, elevation 301 m asl. Derived from meteorological data: March 2006–2007. Site 4: Eddyville, Oregon, U.S.A., Latitude 44° 60'N, Longitude 123° 73'W, elevation 93 m asl. Derived from weather data: 1971–2000.



**Fig. 1.** 3-PG model predictions (solid line), calibrated with allometric equations from site-specific yield tables in Oregon (Waring et al., 2005; Table 2) compare reasonably well with measured values (diamond symbols) of: (a) basal area, (b) standing volume, and (c) leaf area index measured at the Craigieburn site, New Zealand (A. Nordmeyer, unpublished data).

tree spacing, mean diameter at breast height (*dbh*), basal area, and standing volume between 20 and 70 years (Waring et al., 2005).

With the same allometric equations we are able to predict the higher basal area values reported in New Zealand by increasing the average stem biomass at which self-thinning occurs from 110 to 440  $Mg ha^{-1}$  as site productivity increases (Fig. 1; Pittman and Turnblom, 2003). In New Zealand, site-specific volume tables for Douglas-fir are available for comparison at <http://www.forestry.ac.nz/software/index.shtml>. Although yield tables for fully stocked stands show correlations between maximum periodic annual increment, PAI, and maximum mean annual increment (MAI) the relationships break down when stands are thinned or otherwise disturbed. Thus we chose to report max PAI between stand ages of 10 and 40 years.

More details on using yield tables to predict carbon balances with 3-PG are presented in Law et al. (2000) and Waring and McDowell (2002). These papers include a more complete listing of parameters than those presented in Table 2.

To maintain maximum *L* within reasonable bounds (between 8 and 12  $m^2 m^{-2}$ ) and to simplify the analyses, we set specific leaf

area at 4.0  $m^2 kg^{-1}$  for all sites as in Waring et al. (2005). The soil fertility ranking was compared at two values, the maximum,  $FR = 1$ , and 20% lower,  $FR = 0.8$ . On well-watered sites, the higher value results in about 5% less growth being allocated to roots and mycorrhizal activity with a concomitant increase in allocation above-ground. The available soil water capacity ( $\theta$ ) was compared at 200 mm and at 2000 mm, the latter designated as beyond any limitation, given that maximum summer transpiration rates at the Mary's River site are  $\sim 3 mm day^{-1}$  or 90  $mm month^{-1}$  (C. Thomas, unpublished eddy-flux data).

### 2.3. Meteorological relationships

The extent to which clouds and fog reduce solar irradiance below its maximum is reflected in the difference between minimum and maximum temperatures. We estimated monthly average irradiance by taking into account seasonal changes in solar declination and day length, using equations developed by Bristow and Campbell (1984) as modified by Coops et al. (2000). At calibration sites 1 (Craigieburn) and 3 (Mary's River) (Table 1), measured monthly irradiance averaged 23–25% less than that predicted. When modeled estimates were reduced accordingly, the values were in close agreement at site 1 where meteorological data were averaged for 37 years (slope: 1:1,  $r^2 = 0.98$ ). With only 1 year's data at site 3, the coefficient of determination was still respectable at 0.89. At sites 2 and 4 we made similar reductions in modeled estimates of monthly irradiance derived from mean monthly temperature extremes. More details on the formulas and errors in estimation of solar irradiance are provided in Waring and McDowell (2002).

Mean monthly air humidity deficit (*D*) for daylight periods was estimated by assuming that vapor pressure at the minimum temperature is equivalent to the saturated vapor pressure of the atmosphere. This is a valid assumption in most temperate forest regions (Kimball et al., 1997). The difference between the saturated vapor pressure at the maximum temperature and that at the minimum represents the mean maximum *D* for each month. Mean daytime *D* was assumed to be 60% of the monthly maximum but this fraction may vary (Almeida and Landsberg, 2003). At the calibration sites 1 and 3, measured and predicted monthly values of *D* were correlated with  $r^2 > 0.9$  and a slope near 1:1. We applied the above relationship to predict monthly average *D* at sites 2 and 4 where long-term averages of temperature extremes were available.

The number of days per month with sub-freezing temperatures that could result in stomatal closure was estimated from a linear correlation between minimum mean monthly temperatures at the two calibration sites, which showed agreement within 5% of measured values. We assumed the relationship with mean monthly minimum temperature and frost days applied at sites 2 and 4. In modeling the effect of frost on photosynthesis with 3-PG, we considered that photosynthesis would be reduced to zero on days when frost occurred each month, with gross photosynthesis reduced accordingly. This may overestimate the effect of frost, particularly in areas with cloudy conditions (Law et al., 2000).

### 2.4. Sensitivity analyses

We made a total of eight simulation runs at the four sites with the 3-PG model in the following order:

1. No water limitations,  $\theta = 2000 mm$ ,  $T_{opt} = 15 ^\circ C$ ,  $FR = 1.0$ , climate from Table 1.
2. Same as run 1, but with reduced water storage ( $\theta = 200 mm$ ).
3. Same as run 1, but with the monthly humidity deficit set at 0.5 kPa.

**Table 2**  
3-PG model parameters

Variable	Functions and parameter values	Reference
Maximum light use efficiency for photosynthesis	3.0 g C MJ <sup>-1</sup> APAR	Bond et al. (1999)
Minimum temperature ( $T_{\min}$ )	0 °C	Waring et al. (2005)
Temperature optimum ( $T_{\text{opt}}$ )	15 °C	Lewis et al. (2001)
Temperature maximum ( $T_{\max}$ )	40 °C	Waring et al. (2005)
Fraction of APAR absorbed by canopy as a function of $L$	$1 - (2.718 \exp(-0.5 L))$	Landsberg and Waring (1997)
Soil fertility rank (FR) (0–1)	0.8–1.0	This study
Maximum available soil water storage	200 and 2000 mm	This study
Fraction of total available soil water storage when constraints begin	0.6	Landsberg and Waring (1997)
Power coefficient in water constraint function	0.7	
Boundary layer conductance	0.2 m s <sup>-1</sup>	Landsberg and Waring (1997)
Maximum canopy stomatal conductance, $g_{\text{cmax}}$	15 mm s <sup>-1</sup>	This study
Stomatal conductance ( $g_c$ ) response to air humidity deficit, $D$ (kPa)	$g_c = g_{\text{cmax}} \exp(-0.05 D)$	Landsberg and Waring (1997)
Specific leaf area	4.0 m <sup>2</sup> kg <sup>-1</sup>	Waring et al. (2005)
Allometric equation for stem mass (kg), stem diameter ( $dbh$ , cm)	Stem mass = 0.0062( $dbh$ ) <sup>3.10</sup>	Waring et al. (2005)
Allometric equation for foliage mass (kg) Stem diameter ( $dbh$ , cm)	Foliage mass = 0.0167( $dbh$ ) <sup>2.13</sup>	Waring et al. (2005)
Foliage turnover	0.0275 month <sup>-1</sup> , 0.33 year <sup>-1</sup>	Waring and McDowell (2002)
Wood density	350 kg m <sup>-3</sup>	Ledgard and Belton (1985), Waring et al. (2005)
Maximum fraction allocated to roots	0.8	Landsberg and Waring (1997)
Minimum fraction allocated to root	0.25	Landsberg and Waring (1997)

- Same as run 1, but with the soil fertility ranking reduced from 1.0 to 0.8.
- Same as run 1, but with the temperature optimum increased from 15 to 20 °C.
- Same as run 1, but with precipitation equally distributed at 100 mm,  $\theta = 2000$  mm.
- Same as run 2, but with precipitation equally distributed at 100 mm,  $\theta = 200$  mm.
- Same as run 1, but absence of any frost.

This set of simulations, using the same allometric equations, allows us to evaluate the implications of seasonal variation in climatic conditions that would not emerge from comparisons of annual means. In addition, we are able to evaluate how soil properties: fertility and water holding capacity, interact with climate to affect growth of Douglas-fir. The extent that predicted maximum PAI match values recorded at the four sites is discussed in the next section.

### 3. Results

Douglas-fir at the Craigieburn site on the South Island of New Zealand, with 120 days of frost, and at Kariori Forest had a measured maximum PAI similar to those predicted in model run 1 (Table 3).

The PAI predicted in model run 1 for the Mary's River and Eddyville sites in Oregon are  $\sim 2$  m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup> larger than those

measured when water is not limiting. Model run 2 indicates that the Oregon sites would have yields reduced by >20% if soil water storage capacity were only 200 mm, whereas productivity would be unaffected for the New Zealand sites. Model run 3 suggests that reducing the humidity deficit to 0.5 kPa each month would increase productivity in Oregon by >20% but have only a modest (+4 to +8%) effect in New Zealand. Model run 4 demonstrates that a slight reduction in soil fertility (FR reduced from 1.0 to 0.8 in run 1) would be sufficient to match measured productivity at the Oregon sites.

Model run 5 indicates that a temperature optimum for photosynthesis of 15 °C (model run 1), which is close to summer monthly temperature means (Table 1), is more favorable for growth than 20 °C in both New Zealand and the Oregon Coast Range. Model runs 6 and 7 show that an even distribution of 100 mm of precipitation each month would sustain growth rates, even with a soil water storage capacity of 200 mm. Model run 8 indicates that if no frost occurred, yields might be increased up to 17% at Craigieburn with 120 days of frost annually but only 3–8% at the other three sites (Table 1).

### 4. Discussion

The sensitivity analyses reported in Table 3 demonstrate the importance of seasonal variation in temperature and precipitation on productivity. Although the mean annual values of temperature

**Table 3**  
Sensitivity analyses of the effects of environmental variables on maximum mean periodic increment (PAI), m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup>, of Douglas-fir plantations

Simulation run	Variables	Craigieburn, South Island, NZ site 1	Kariori North Island, NZ site 2	Mary's River Oregon, USA site 3	Eddyville, Oregon, USA site 4
1	$T_{\text{opt}} = 15$ °C, $\theta = 2000$ mm FR = 1.0, standard climate	36 reference	47 reference	29 reference	34 reference
2	$T_{\text{opt}} = 15$ °C, $\theta = 200$ mm FR = 1.0, standard climate, reduced water storage	36 (0%)	47 (0%)	20 (-23%)	27 (-21%)
3	$T_{\text{opt}} = 15$ °C, $\theta = 2000$ mm FR = 1.0, $D = 0.5$ kPa each month reduced humidity deficit	39 (+8%)	49 (+4%)	35 (+21%)	42 (+24%)
4	$T_{\text{opt}} = 15$ °C, $\theta = 2000$ mm FR = 0.8 reduced soil fertility	33 (-8%)	44 (-6%)	27 (-7%)	32 (-6%)
5	$T_{\text{opt}} = 20$ °C, $\theta = 2000$ mm FR = 1.0 increased optimum temperature	30 (-17%)	40 (-15%)	25 (-12%)	31 (-9%)
6	$T_{\text{opt}} = 15$ °C, $\theta = 2000$ mm FR = 1.0 precip = 100 mm month <sup>-1</sup> fixed monthly precip	36 (0%)	47 (0%)	29 (0%)	34 (0%)
7	$T_{\text{opt}} = 15$ °C, $\theta = 200$ mm FR = 1.0 precipitation = 100 mm month <sup>-1</sup> fixed monthly precip, reduced water storage	36 (0%)	47 (0%)	29 (0%)	34 (0%)
8	$T_{\text{opt}} = 15$ °C, $\theta = 2000$ mm FR = 1.0, Frost = 0 no effect of frost	42 (+17%)	51 (+8%)	30 (+3%)	35 (+3%)

Values in parentheses refer to change (%) from current climate with standard parameters.

**Table 4**

3-PG modeled transpiration ( $T$ ), gross primary production ( $P_G$ ), and water use efficiencies (WUE) show that New Zealand sites (November–March) have higher WUE values than sites in Oregon (May–September) during the respective growing seasons

Mary's River, OR (site 3)													
Month	January	February	March	April	May	June	July	August	September	October	November	December	Annual sum or average
$T$ (mm month <sup>-1</sup> )	26	19	29	57	82	90	94	83	92	24	10	22	629
$P_G$ (g C m <sup>-2</sup> month <sup>-1</sup> )	36	91	212	384	504	449	609	605	392	314	71	42	3709
WUE (g C m <sup>-2</sup> /mm water)	1.4	4.8	7.2	6.7	6.1	5.0	6.5	7.3	4.3	4.8	2.8	1.9	5.9
Eddyville, OR (site 4)													
Month	January	February	March	April	May	June	July	August	September	October	November	December	Annual sum or average
$T$ (mm month <sup>-1</sup> )	21	29	48	66	86	94	107	98	81	57	28	19	734
$P_G$ (g C m <sup>-2</sup> month <sup>-1</sup> )	49	96	216	360	537	546	481	412	298	210	88	43	3337
WUE (g C m <sup>-2</sup> /mm water)	2.4	3.3	4.5	5.4	6.2	5.8	4.5	4.2	3.7	3.7	3.2	2.3	4.5
Craigieburn, NZ (site 1)													
Month	July	August	September	October	November	December	January	February	March	April	May	June	Annual sum or average
$T$ (mm month <sup>-1</sup> )	30	37	51	65	71	86	85	77	71	49	39	23	684
$P_G$ (g C m <sup>-2</sup> month <sup>-1</sup> )	10	36	136	311	481	597	653	484	424	245	76	18	3470
WUE (g C m <sup>-2</sup> /mm water)	0.3	1.0	2.7	4.8	6.8	6.9	7.7	6.3	5.9	5.0	1.9	0.8	5.1
Karioi Forest, NZ (site 2)													
Month	July	August	September	October	November	December	January	February	March	April	May	June	Annual sum or average
$T$ (mm month <sup>-1</sup> )	31	38	47	61	69	76	81	72	72	56	38	31	671
$P_G$ (g C m <sup>-2</sup> month <sup>-1</sup> )	64	127	241	407	500	623	620	500	447	271	134	66	3999
WUE (g C m <sup>-2</sup> /mm water)	2.1	3.4	5.2	6.6	7.2	8.2	7.6	7.0	6.2	4.9	3.5	2.1	6.0

and precipitation were similar at all sites, as was solar irradiance, the much higher yields recorded in New Zealand can be attributed to differences in temperature extremes recorded in Oregon during the summer growing season. These higher temperatures lead to higher daytime air humidity deficits which result in a reduction in stomatal conductance and hence photosynthesis. The water use efficiency (carbon gain per unit of water transpired) is much higher during summer months in New Zealand, averaging 7.0 g C m<sup>-2</sup>/mm water between November and March compared with 5.4 g C m<sup>-2</sup>/mm water in Oregon between May and September (Table 4). Without the higher summer humidity deficits, Oregon plantations would, according to the sensitivity analyses with  $D$  set at 0.5 kPa, grow nearly as well as the trees in New Zealand. Even with a reduced humidity deficit during the summer, plantations in Oregon could not continue to grow without deep roots to obtain sufficient water.

With 100 mm of precipitation per month throughout the year, the simulations indicate that drought would be highly unlikely, even on shallow soils in Oregon. At Karioi Forest, the same yields are predicted if annual precipitation were reduced from 1400 to 800 mm, as long as 100 mm of precipitation were received in each of the 4 months of the growing season (results not shown). Precipitation during winter months in both New Zealand and Oregon is far in excess of that required to maintain optimal tree water relations because transpiration rates decrease to <1 mm day<sup>-1</sup> during the winter (C. Thomas, unpublished eddy-flux data).

In the analysis, we assumed that photosynthesis in all canopies was highly efficient at optimum temperatures and that soil nutrients were well supplied. These assumptions are reasonable, considering that  $L$  exceeded 8 m<sup>2</sup> m<sup>-2</sup> and foliar nitrogen concentrations were >1.2% at all four sites. At the New Zealand sites, phosphorus and calcium are more readily available (A. Nordmeyer, unpublished) than in Oregon (M. Gourley, Starker Forests Inc., personal communication). *Alnus rubra*, a nitrogen-fixing species in Oregon, can add up to 200 kg N ha<sup>-1</sup> year<sup>-1</sup> (Binkley et al., 1994). When Douglas-fir is grown on such sites,

however, the large amount of nitrogen added by *Alnus* may create nutritional imbalances that make Douglas-fir more susceptible to pathogens (Perakis et al., 2006; Sinkhorn, 2007).

In summary, with a process-based model we were able to assess the relative importance of various abiotic constraints on productivity in different environments. The approach may be extended to evaluate the performance of different species (or genotypes) in both past and future environments (Coops et al., 2005).

Although it may be possible to use process-based models to identify forests under stress, through recognition of simulated reductions in  $L$  and yields, the actual damage caused by pests can only be estimated. We do not rule out, therefore, that Douglas-fir in its home range may be more limited by pests than it is in New Zealand.

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