

A process model analysis of environmental limitations on the growth of Sitka spruce plantations in Great Britain

R.H. WARING

Department of Forest Science, College of Forestry, Oregon State University, Corvallis, Oregon 97331, USA

Summary

The extent to which growth is limited by climatic factors or soil fertility is of significance to foresters concerned with the management of Sitka spruce plantations throughout Great Britain. A simplified physiologically based model, driven with monthly weather data, provided a means to assess growth limitations imposed by solar radiation, subfreezing and suboptimal temperatures, soil drought and atmospheric vapour pressure deficits, wind and soil fertility at sites differing in maximum wood volume production by fourfold. To drive the model, conventional weather station data were extrapolated to provide estimates of precipitation, solar radiation, vapour pressure deficits, suboptimal temperatures and frequency of subfreezing conditions. Variation in solar radiation associated with topography accounted for nearly half the differences observed in plantation growth. Unfavourable temperatures reduced annual photosynthesis and growth only by 10–15 per cent as they occur primarily in months with limited solar radiation. Drought and vapour pressure deficits do not appear to offer major constraints on growth. Soil fertility, however, significantly limited growth on a number of sites. The modelling approach provides a measure of nutrient availability by predicting the maximum accumulation of nitrogen in the canopy. The modelling analysis suggests that foresters could improve forecasts of Sitka spruce plantation growth throughout the UK with better estimates of solar radiation and canopy nitrogen content than with more conventional sets of measurements.

Introduction

Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is established throughout Great Britain as a major

commercial species. Although the species is adapted to a wide range of environments, growth rates vary by more than fourfold (Hamilton and Christie, 1971). The prediction of yield class

* E-mail: waring@fsl.orst.edu

($\text{m}^3 \text{ha}^{-1} \text{a}^{-1}$) in relation to elevation, soil type, climatic and topographic variables has been the subject of many papers (Macmillan, 1991; Worrell and Malcolm, 1990a, b; Proe *et al.*, 1996). Based on empirical models and field surveys, geographic variation in Sitka spruce yield classes has recently been mapped at a 1 km^2 resolution for Scotland and Wales (Allison *et al.*, 1994; Bateman and Lovett, 1998). Although empirical models are widely used, they are not designed to explain how changes in environmental conditions affect growth, or to make predictions beyond current conditions. With projected changes in atmospheric CO_2 , climatic conditions, and nutrient balances, there is increasing interest in more process-based forecasts of growth.

Over the last decade, much progress has been made in the development of more mechanistic forest growth models designed to couple water, carbon, and nutrient cycles (Running and Gower, 1991; McMurtrie and Landsberg, 1992; Friend *et al.*, 1993; Aber *et al.*, 1995; Mohren and Ilves-

niemi, 1995). At their heart, these process models have common elements that link the atmosphere, vegetation, and soils (Figure 1). A suite of climatic variables is required to drive the models that include precipitation, solar energy, temperature, and the atmospheric vapour pressure deficit (D). At longer intervals, changes in atmospheric CO_2 concentrations must also be taken into account.

The canopy and forest floor intercept radiation and precipitation. Some water recharges the soil and enters streams, the rest is converted to water vapour and is evaporated or transpired back into the atmosphere. The upper limit on photosynthesis is set by the amount of light (400–700 nm) absorbed by the canopy and the photosynthetic conversion (quantum) efficiency, the latter primarily a function of nutrition. Reductions in stomatal conductance limit the rates of water vapour loss via transpiration and CO_2 uptake via photosynthesis. Stomatal conductance is affected by all the climatic variables and by the availability of soil water. The products of photosynthesis are

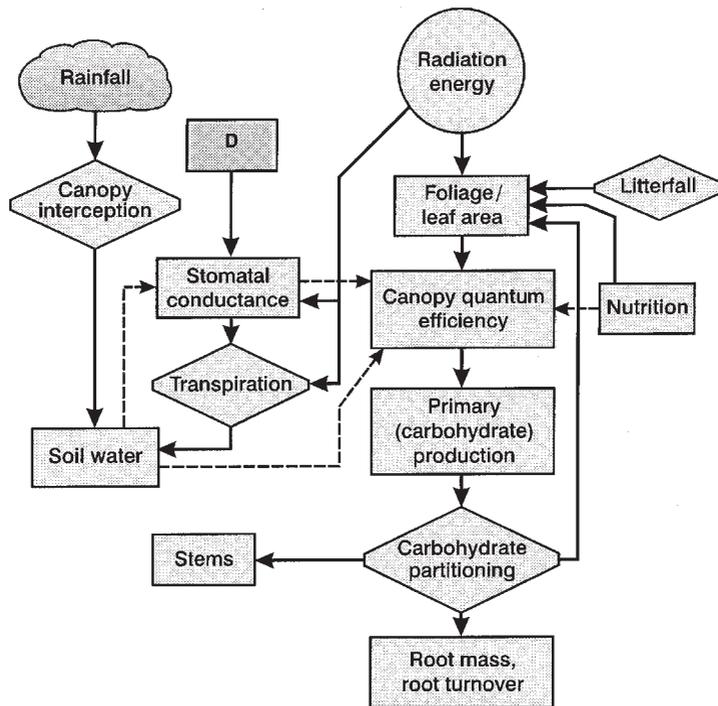


Figure 1. Schematic of a simplified process model to predict forest growth (Landsberg and Coops, 1999). D signifies atmospheric vapour pressure deficit.

partitioned into growth and plant respiratory losses of CO₂ back to the atmosphere. Carbon is partitioned into foliage, stems, and roots differentially, depending on the extent that resources limit photosynthesis and growth. Eventually, plant components are shed and converted into detritus which is incorporated into soil organic matter, leached, or converted into CO₂ via heterotrophic respiration (but not shown in Figure 1).

In the UK, annual solar radiation rarely exceeds 4000 MJ m⁻² a⁻¹. Of this, about half is visible light, so if 2000 MJ m⁻² a⁻¹ were completely absorbed by a dense canopy, and converted at maximum efficiency of 4 gC MJ⁻¹, 8000 gC m⁻² a⁻¹ could be fixed as photosynthate. Only about half of the fixed photosynthate can be utilized for growth (e.g. 4000 gC m⁻² a⁻¹); the rest is respired as CO₂. Assuming 50 per cent carbon content in dry matter, the maximum production of dry matter in the UK would then be ~8000 g m⁻² a⁻¹. Wood represents, at most, slightly more than 50 per cent of the total production, equivalent to ~4000 g m⁻² a⁻¹, which converts, assuming a density of 400 kg m⁻³, to a maximum current annual increment (CAI) of ~100 m³ ha⁻¹ a⁻¹. According to relationships indicated in the yield tables of Hamilton and Christie (1971), this is equivalent to a maximum mean annual increment (MAI) of 70 m³ ha⁻¹ a⁻¹ (0.68 of maximum CAI), a value nearly twice as high as any reported (Ford, 1982).

Wood growth is reduced below the potential not only because of limitations on the photosynthetic process, but because an increased proportion of growth is directed to root production as the environment becomes more stressful (Waring and Running, 1998). A shift in resource allocation to roots reduces not only stem growth, but also the amount of foliage that can be displayed to intercept light. Although the relationships controlling allocation of resources are not yet fully defined, there is little question that limiting nutrients, water, and frost all tend to increase the fraction of photosynthate allocated to roots. Wind may also stimulate trees to modify resource allocation below ground (Nicoll and Ray, 1996).

Most process models require an amount of information beyond that readily available to forest managers. In addition, few process models predict stand characteristics such as basal area, mean tree diameters and annual mortality. Landsberg and

Waring (1997) attempted to blend the interpretative power of a mechanistic process model with the mensurational features required by foresters in a simplified physiologically based process model for predicting growth (3-PG). The model is particularly well suited to evergreen, even-aged forests composed of a single species such as Sitka spruce. To provide the weather data required to drive 3-PG, spatial extrapolations of minimum/maximum temperatures and precipitation are necessary. In addition, algorithms must be applied to transform minimum/maximum temperature data into estimates of solar radiation, atmospheric vapour pressure deficits, and the frequency of subfreezing conditions each month (Running *et al.*, 1987).

The objective of this paper is to demonstrate the potential of 3-PG to forest managers by applying the model in a diagnostic mode. The approach involves deriving some parameter values, such as in the equations relating stem diameter growth with foliage and root growth, that give predictions of maximum CAI close to those observed on the most productive Sitka spruce sites with maximum CAI > 40 m³ ha⁻¹ a⁻¹. These sites represent, one may assume, places where solar radiation and sub-optimal temperatures offer the only limits of production. With parameter values established, the model will be used to diagnose the relative constraints exerted by other factors on less productive sites. In this analytic mode, the model predicts the maximum canopy leaf area index and the canopy nitrogen content, values that can be directly measured in the field. Because 3-PG also contains a water balance subroutine, sites can be identified where seepage or a high water-table can be assumed to play a role in ameliorating the effects of drought. In addition, the basic construction of 3-PG allows foresters to forecast plantation growth into the future under a variety of management practices and climatic conditions.

Location and site descriptions of plantations

The Forestry Commission provided information on 12 widely scattered sites where plantations of Sitka spruce have been established (Figure 2). In addition to physiographic information and growth rates, Forestry Commission staff provided some qualitative estimates of soil fertility and exposure

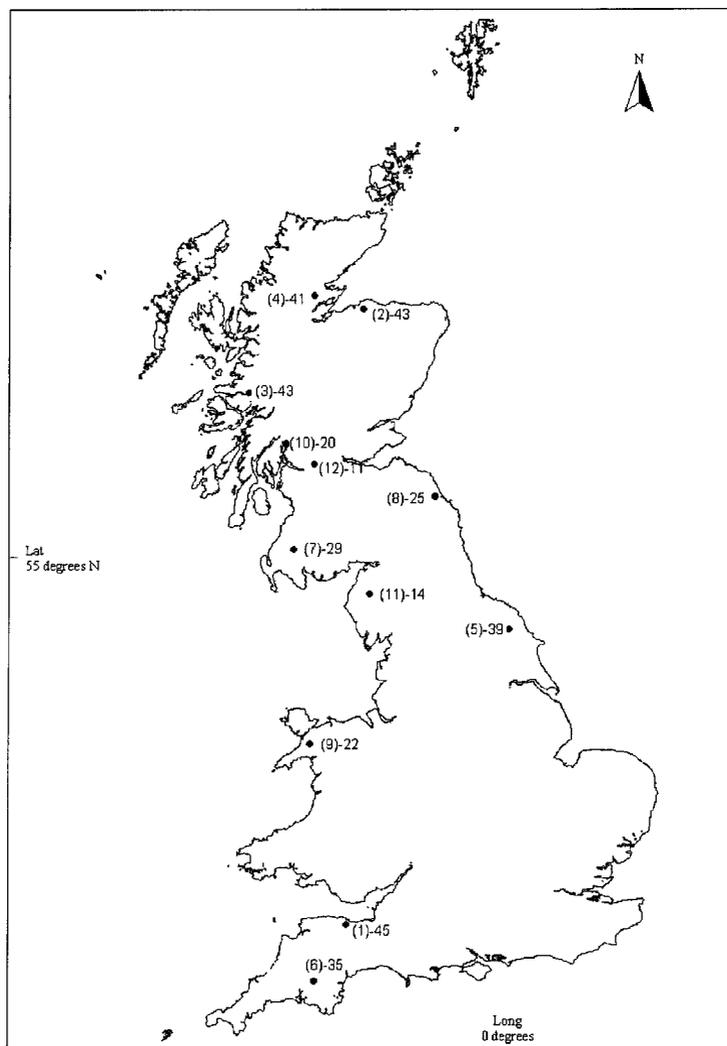


Figure 2. Geographic location of the 12 sites (numbers in parenthesis) followed by measured maximum CAI Map provided by Jane Fletcher, Forestry Commission, Northern Research Station, Bush Estate, Edinburgh.

to wind (Table 1). These latter two classifications were assumed to be tentative, and not employed directly in the diagnostic analysis.

3-PG model structure

3-PG incorporates a number of important simplifications that have emerged from studies conducted in a wide range of temperate forests, which can be summarized as follows:

- At monthly time steps or longer, the ratio of net production (P_N) to gross photosynthesis (P_G) approaches a constant (0.47 ± 0.04) (Arneth *et al.*, 1998; Waring *et al.*, 1998; Law *et al.*, 1999). This assumption simplifies the problem of calculating respiration losses.
- The maximum rates of water vapour and carbon dioxide exchange through leaf stomata approach a constant by the time a forest canopy reaches a leaf area index of 3.0 (Kelliher *et al.*,

Table 1: Information on the location of Sitka spruce plantations, physiographic setting, soil fertility, wind exposure and maximum current annual increments, provided by the UK Forestry Commission

Site number	Latitude (°N)	Longitude (°W)	Elevation (m)	Slope (degrees)	Aspect (degrees)	Soil fertility	Wind exposure 1 = no effect	Maximum CAI (m ³ ha ⁻¹ a ⁻¹)
1	50°05'	3°17'	350	5	225	poor	0.4†	46
2	57°22'	3°14'	100	20	135	poor	0.8	43
3	56°25'	5°20'	200	25	180	rich	0.6	43
4	57°26'	4°13'	190	3	225	poor	0.8	41
5	54°10'	0°24'	120	5	158	poor	0.9	39
6	50°20'	3°35'	430	4	180	poor	0.3†	35
7	55°03'	4°20'	120	5	112	poor	0.6	29
8	55°24'	1°32'	20	2	135	very poor	0.7	25
9	53°01'	4°06'	430	27	180	poor	0.5	22
10	56°07'	4°29'	270	21	45	poor	0.5	20
11	54°23'	3°06'	380	25	338	poor	0.6	14
12	55°09'	4°09'	180	6	180	poor	0.6	11

* Robert Matthews selected sites to represent a wide range in maximum CAI, averaged from inventories at 5-year intervals. Graham Pyatt provided estimates of soil fertility based on limited data. Bruce Nicholl added wind rankings founded on a topographic exposure classification (Quine and White, 1993).

† Estimates made with less adequate data.

1995) and that at leaf area indices >3.0, maximum photosynthesis is a linear function of the amount of light intercepted and absorbed (Wang *et al.*, 1991).

These assumptions reduce the requirement for accuracy in assessment of canopy leaf area index (L) and simplify calculation of transpiration and photosynthesis.

- The ratio of actual:potential photosynthesis decreases in response to the most restrictive (monthly) climatic limitation, which affects the fraction of carbon allocated to roots (Runyon *et al.*, 1994; Waring and Running, 1998). This ratio expresses the combined effects of all climatic variables on photosynthesis and predicts the fraction of photosynthate allocated to roots (See Table 2).
- As soil fertility increases, proportionally less carbon is allocated to roots and proportionally more is available for above-ground growth (Beets and Whitehead, 1996; Waring and Running, 1998). The fraction of production not allocated to roots is proportioned between foliage and stem wood using species-specific allometric relations with tree diameter (Table 2). Soil fertility also affects the canopy quantum efficiency (Waring *et al.*, 1995; Linder and Murray, 1998).

A flow diagram outlining the calculations that comprise the model is presented in Table 3. The model uses a monthly time step and requires as input data:

- values of total short-wave (375–2500 nm) incoming radiation (ϕ_s);
- monthly mean day-time atmospheric vapour pressure deficit (D);
- total monthly precipitation;
- number of days per month below a threshold subfreezing temperature of -2°C .

The short-wave incoming radiation ϕ_s is assumed to be twice the visible, photosynthetically active radiation ϕ_{pa} . The amount of ϕ_{pa} absorbed by the canopy is a function of the canopy leaf area index (L) and is calculated from Beer's law (Table 2). The fraction of absorbed photosynthetically active radiation utilized ϕ_{pau} is obtained by reducing the value of ϕ_{pa} by amounts determined by modifiers (m) – dimensionless factors (f_i) with values varying between zero and unity. The modifiers reflect the constraints imposed on the utilization of absorbed radiation because of stomatal closure, associated with high atmospheric vapour pressure deficits (D), soil drought, defined by the ratio of the amount of water in the root zone to the maximum possible

Table 2: Model functions and parameters used for Sitka spruce in this study that may differ slightly from those in the original description of 3-PG (Landsberg and Waring, 1997)

Variable	Functions and parameter values	Reference
Light conversion efficiency of photosynthesis	Maximum canopy quantum efficiency α_c ranges from 1.9 to 3.8 gC MJ ⁻¹ ϕ_{pau} , increases linearly with soil fertility rank	Landsberg, 1998 Waring <i>et al.</i> , 1995 Linder and Murray, 1998
Constraints of light conversion efficiency associated with temperature	T_{opt} was set at 15°C, T_{min} -5°C, and T_{max} 35°C	Neilson and Jarvis, 1975 [see formula 1]
Fraction of radiation absorbed by canopy	$1 - (1.38 \exp(-0.6615 * L))$	Wang <i>et al.</i> , 1991
Stomatal response to humidity	$g_c = g_{\text{cmax}} \exp(-2.5 * D)$	Same function as in Landsberg and Waring, 1997
Specific leaf area	7.0 m ² kg ⁻¹	Matson <i>et al.</i> , 1994
Allometric equation for stem mass	Stem mass, kg = 0.0007 exp(2.1896 * dia., mm)	Hamilton and Christie, 1971 [Tariff Table 30]
Allometric equation for foliage mass	Foliage mass, kg = 0.002 exp(1.75 * dia., mm)	This study
Wood density in stands <20 years old	350 kg m ⁻³	Petty <i>et al.</i> , 1990
Maximum leaf litterfall	0.0143 month ⁻¹ of L , or 0.17 a ⁻¹	Miller <i>et al.</i> , 1992, 1996
Fraction of production allocated to roots, monthly	$0.5 / (1 + \phi_{\text{pau}} / \phi_{\text{pa}}) * 2.5 * \text{highest } f_i$ Selects the most restrictive environmental constraint (f_i), e.g., with value nearest zero; includes soil fertility and wind exposure	Changed numerator from 0.8 to 0.5 Landsberg and Waring, 1997

L , leaf area index, m² m⁻²; ϕ_{pa} , photosynthetically active solar radiation, MJ m⁻² month⁻¹; ϕ_{pau} , photosynthetically active solar radiation utilized, MJ m⁻² month⁻¹; g_{cmax} , maximum stomatal conductance, m s⁻¹; D , monthly mean daily vapour pressure deficit, kPa; dia., average stem diameter, mm; T_{opt} , optimum temperature for photosynthesis; g_c , stomatal conductance, m s⁻¹.

amount available (θ) and the effects of subfreezing temperatures (T). Gross photosynthesis is calculated as the product of ϕ_{pau} and the canopy quantum efficiency (α_c). The ratio of $\phi_{\text{pau}}:\phi_{\text{pa}}$ represents the relative constraints on photosynthesis associated with partial to complete stomatal closure.

A temperature function (T_f), which varies between zero and unity, was added to the model by Landsberg (1998) to take account of variations in monthly mean temperature (T_{mean}) that approach a threshold maximum (Th_{max}) or minimum (Th_{min}) departing from the temperature optimum (T_{opt}) for photosynthesis. This monthly temperature function is multiplied by the

maximum canopy quantum efficiency (max. α_c) set by soil fertility rankings (0–1) between 1.9 and 3.8 gC MJ⁻¹ ϕ_{pau} .

$$T_f = \frac{(T_{\text{mean}} - Th_{\text{min}})}{(T_{\text{opt}} - Th_{\text{min}})} \times \frac{(Th_{\text{max}} - T_{\text{mean}})}{(Th_{\text{max}} - T_{\text{opt}})} \left[\frac{(Th_{\text{max}} - T_{\text{opt}})}{(T_{\text{opt}} - Th_{\text{min}})} \right] \quad (1)$$

Starting values of foliage, stem and root mass are also required, appropriate to the age of the stand at the beginning of a run, together with allometric equations for the species and some soil parameters. Parameter values and allometric equations for Sitka spruce are presented in Table 3. Leaf area index is determined from foliage

mass and input values of specific leaf area ($\text{m}^2 \text{kg}^{-1}$). In this study, the model was run for 20 years at a stocking of 2500 seedlings ha^{-1} , with the initial biomass of foliage, roots, and stems set at the same values used by Landsberg and Waring (1997): 1, 3, and 6 Mg ha^{-1} , respectively. To simplify the analysis, the thinning routines, which include self-thinning using the $-3/2$ power law, were switched off because the initial stocking level chosen was near that predicted at 20–25 years from normal yield tables (Hamilton and Christie, 1971).

Sitka spruce plantations are normally established where soil moisture in the rooting zone is rarely exhausted. In this analysis, monthly transpiration was assumed to match any losses that might have otherwise occurred through evaporation of free water from the canopy. This assumption inflates the amount of water extracted via roots and required therefore that θ_{max} be set at or above 200 mm. If the model predicted that the soil water supply would be exhausted during any month of the year, θ_{max} was further increased in

increments of 100 mm until the soil water balance remained above zero.

Conversion of weather data

Conventional weather data from the UK Meteorological Office were compiled by Thomas Connolly and Graham Pyatt at the Northern Research Station of the Forestry Commission to provide long-term averages of monthly precipitation and minimum/maximum temperature for stations near each of the selected plantation sites. Both temperature and precipitation data were adjusted to take into account rain shadows and temperature differences associated with topography and elevation in manners similar to those outlined by Running *et al.* (1987).

The topographically adjusted minimum/maximum temperature data served as a basis for calculating all additional meteorological variables (apart from wind exposure). Mean monthly temperatures were calculated from the average of

Table 3: Flow diagram: 3-PG

Inputs

Weather data: temperature, precipitation, humidity, radiation, subfreezing days

Initial biomass: foliage, stems, roots

Variables: max. available soil water, initial stem number, stand age, max. stand age

Parameters: canopy quantum efficiency, temperature optimum and limits for photosynthesis, ratio of $P_N:P_G$, max. leaf and canopy conductance, specific leaf area, maximum litterfall rate, root turnover rate (if soil carbon balance is of interest), soil fertility ranking, wind exposure ranking, and parameters for the allometric equations

Model calculates monthly

Leaf area index from foliage mass and specific leaf area and monthly litterfall

Max. degree that a climatic variable limits stomatal or canopy conductance

Transpiration from Penman–Monteith equation

Gross photosynthesis from utilizable PAR * quantum efficiency

Net primary production (P_N) as a fixed fraction of gross photosynthesis

Fraction of P_N allocated to roots

Fraction of P_N allocated to stems and foliage

Model calculates annually

Stem wood production (mass and volume)

Net production, above and below ground

Natural mortality and mortality through thinning

Updates tree biomass (alive and dead)

Litter and root turnover

Autotrophic respiration

Relative constraint imposed by each environmental factor on production

maximum and minimum temperatures. The number of days per month with subfreezing temperatures $< -2^{\circ}\text{C}$ was estimated from mean monthly minimum temperatures based on an empirical relation established in Oregon ($44^{\circ} 30' \text{N}$, $121^{\circ} 37' \text{W}$) from data furnished by Peter Anthoni, Oregon State University:

$$\text{Number of days per month } < -2^{\circ}\text{C} = T_{\min} * -1.57 + 11.62; \text{ if } < 0, \text{ then } 0 \text{ days } < -2^{\circ}\text{C} \quad (2)$$

The mean monthly daytime atmospheric vapour pressure deficit (D) is estimated by assuming that the minimum temperature is equivalent to the saturated vapour pressure of the atmosphere. The difference between the saturated vapour pressure at the maximum temperature and that at the minimum represents the maximum average D for

the month, the mean daytime D is approximately two-thirds of the maximum D , based on data from the same site in Oregon used to derive the relation between T_{\min} and number of subfreezing days per month (see Figure 3a). The saturated vapour pressure was estimated from a formula referenced by Running *et al.* (1987).

$$\text{Saturated vapour pressure, kPa} = 0.61078 \exp[17.269 T_{\min}/(237.3 + T_{\min})] \quad (3)$$

Estimates of monthly mean solar radiation were derived from minimum/maximum temperature data following procedures described by Bristow and Campbell (1984). With knowledge of the location, elevation, slope and aspect, the maximum potential radiation can be estimated, taking into account the seasonal variation in the

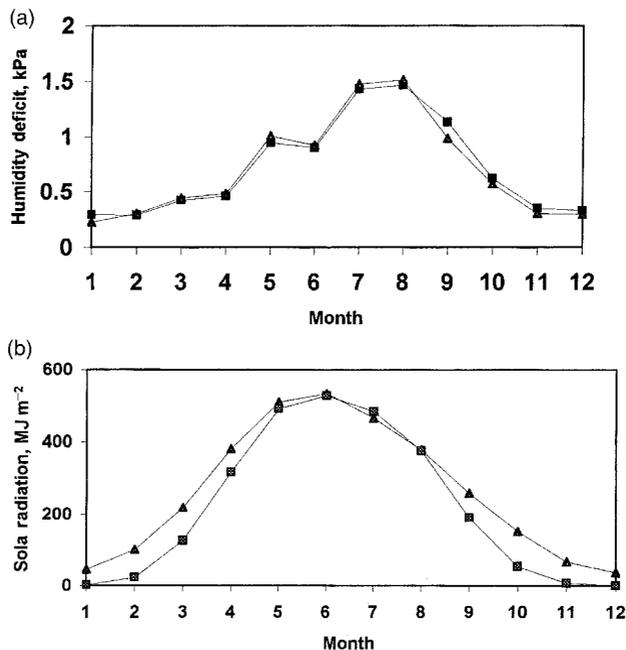


Figure 3a. Mean monthly daytime vapour pressure deficit (D) can be accurately estimated from minimum/maximum temperature data (see formula 3). Triangles represent measured values; squares represent predicted values. Data acquired by Peter Anthoni, Oregon State University at $44^{\circ} 30' \text{N}$, $121^{\circ} 37' \text{W}$, elevation 940 m (Law *et al.*, 1999). D_{measured} , kPa = $1.0 * D_{\text{predicted}}$, $r^2 = 0.98$.

Figure 3b. Monthly solar radiation was predicted from mean monthly minimum/maximum temperature data from Glasgow, Scotland (Lebens, 1986) using equations 4–6 (Bristow and Campbell, 1984). Triangles represent measured values; squares represent predicted values. With low sun angle and much cloud cover, diffuse radiation contributes more than predicted with the simple model. A linear equation with a slope of 0.87 and an intercept of $73 \text{ MJ m}^{-2} \text{ month}^{-1}$ provides a closer fit to measured radiation ($r^2 = 0.98$).

sun's solar angle of declination to the Earth's surface. The extent that clouds, pollution, or fog reduce solar radiation below the potential is reflected in the difference between minimum and maximum temperatures (ΔT). Although a good relationship can often be obtained using only mid-month estimates of solar declination (Coops *et al.*, 1998), the estimates are improved when changes in solar declination are taken into account at more frequent intervals (Running *et al.*, 1987). In this study, monthly averaged radiation was estimated by taking into account daily changes in solar declination and day length (see Figure 3b). Clear sky transmissivity (Ω) was increased from 0.65 at sea level with elevation.

$$\Omega = 0.65 * \text{Elevation, (m)} * 0.0008 \quad (4)$$

$$\phi_s = \Omega * \left(1 - \exp\left(-\left(\beta * \Delta T^{(2.4)}\right)\right)\right) \quad (5)$$

$$\text{Where } \beta = 0.035 \exp(-0.154 * \Delta T) \quad (6)$$

The long-term average radiation recorded at Glasgow (56° 45' N, 4° 18' W) agreed closely with a year's worth of data acquired northwest of Perth (56° 54' N, 3° 72' W) by John Moncrieff from the University of Edinburgh. In the simplified model, the ratio of diffuse:direct solar radiation was assumed constant at 0.15. Because of extensive cloud cover in the UK, the actual ratio of diffuse: direct solar radiation is usually above 0.6 (Lebens, 1986). All predictions of solar radiation derived from extrapolated minimum maximum temperature data were therefore

adjusted, using a linear relationship with a positive intercept.

$$\text{Actual Solar Radiation } (\phi_s), \text{ MJ m}^{-2} \text{ month}^{-1} = 73 + 0.87 (\text{Predicted } \phi_s) \quad (7)$$

Results

The first step in the analysis involved the sensitivity of model predictions of maximum leaf area index and maximum CAI to changes in slope and aspect. In Table 4 a comparison of four plots with maximum CAI > 40 m³ ha⁻¹ a⁻¹ illustrates that as the slope increases from 3° to 25° (refer to Table 1), there is increasing variation in the predicted values of maximum leaf area index and maximum CAI. In general, the effect of slope appears to be reduced approximately by half, probably in response to the large amount of diffuse radiation associated with overcast skies in the UK (Jones, 1992). As a result of this analysis, solar radiation estimated for sites on sloping ground was calculated at half the true slope angle. The maximum L values, it should be noted, are similar to the average reported by Miller *et al.* (1992) for six fertilized pole-sized Sitka spruce plantations ($L = 12.3$, assuming a specific leaf area = 7.0 m² kg⁻¹) and for highly productive forests in the Pacific Northwest United States (Waring *et al.*, 1982).

The second step in the analysis was to establish to what extent solar radiation contributed to Sitka spruce productivity. As seen in Table 5, differences in estimated solar radiation varied by almost two-fold from 2200 to 4100 MJ m⁻² a⁻¹. These differences are sufficient to account for

Table 4: Comparison of model predictions of maximum leaf area index and maximum current annual increments for four highly productive sites indicates that the effect of slope in the UK is reduced by about half that predicted for the true slope and aspect, as a result of increased diffuse radiation associated with overcast skies. See Table 1 for information on slope and aspect of the sites

Site	Maximum leaf area index			Maximum current annual increment			
	Flat	True slope and aspect	Half slope	Flat	True slope and aspect	Half slope	Observed max. CAI
1	13	14	14	42	46	43	45
2	10	15	13	32	52	43	43
3	10	18	13	28	63	41	43
4	13	13	13	43	45	42	41

Table 5: Summary table with predicted solar radiation and precipitation at a dozen Sitka spruce plantation sites. Adjustments were made in soil water storage and soil fertility ranking to allow 3-PG to predict maximum CAI close to that observed (last column). In addition to max CAI, the model predicts the ratio of transpiration to precipitation, the maximum quantum efficiency, maximum leaf area index, and maximum nitrogen content in foliage

Site no.	Solar radiation ϕ_s (MJ m ⁻² a ⁻¹)	Annual precipitation (mm a ⁻¹)	Transpiration: precipitation ratio	Soil water storage capacity* (mm)	Soil fertility rank [†] (High = 1.0)	Maximum quantum efficiency [‡] (gC MJ ⁻¹) ϕ_{pau}	Maximum leaf area index (m ² m ⁻²)	Max. canopy nitrogen content (kg ha ⁻¹)	Predicted maximum CAI [§] (m ³ ha ⁻¹ a ⁻¹)	Observed maximum CAI [#] (m ³ ha ⁻¹ a ⁻¹)
1	3400	1548	0.60	200	1.00	3.8	14	390	43	45
2	3700	1051	0.86	300	1.00	3.8	13	380	43	43
3	3300	1513	0.64	200	1.00	3.8	13	370	41	43
4	3700	1548	0.59	200	1.00	3.8	13	380	42	41
5	3200	790	1.09	400	1.00	3.8	12	340	37	39
6	3600	1834	0.54	200	0.60	2.8	11	260	35	35
7	2800	1177	0.74	200	0.85	3.4	9	240	27	29
8	2800	858	0.93	200	1.00	3.8	8	220	22	25
9	4100	1964	0.50	200	0.25	1.8	7	130	21	22
10	2200	1588	0.57	200	0.7	3.0	7	170	20	20
11	2200	1622	0.55	200	0.5	2.5	5	110	13	14
12	2200	1224	0.72	200	0.3	1.9	4	70	10	11

* Soil water capacity is somewhat inflated because losses associated with interception of precipitation by the canopy were ignored; all evaporation was assumed to be attributed to water uptake from the soil and loss through transpiration.

† On half of the sites, soil fertility was assumed non-limiting (rank = 1.0); on the remaining sites, the soil fertility rank was adjusted to match more closely observed growth.

‡ Maximum quantum efficiency is a linear function of the soil fertility ranking.

§ Maximum CAI is approximately a third higher than the maximum mean annual increment used to define Yield Class.

production ranging from $25 \text{ m}^3 \text{ ha}^{-1} \text{ a}^{-1}$ at Site 8 to $45 \text{ m}^3 \text{ ha}^{-1} \text{ a}^{-1}$ at Site 1 with soil fertility (and wind exposure rankings) set at 1.0, and the quantum efficiency at the theoretical maximum ($3.8 \text{ gC MJ}^{-1} \phi_{\text{pau}}$). For all sites, however, solar radiation alone only accounted for 47 per cent of the variation in measured maximum CAI.

Temperature played a secondary role in limiting production. Although subfreezing conditions were predicted to occur from 40 to 70 days throughout the year on the four most productive sites, less than a 2 per cent increase in growth was predicted when the effect of subfreezing conditions were ignored. At the same sites, the monthly mean temperature function (T_f) was within 5 per cent of the assumed optimum for photosynthesis (15°C) from June through September. In October and May, T_f still averaged 0.89 of optimum; in November and April T_f fell to between 0.74 and 0.78, and by December and January, to a low of 0.60. At latitudes $51\text{--}57^\circ\text{N}$, more than half the annual radiation is distributed during the months June through September when T_f is near optimum. In winter, limitations in solar radiation predominate over constraints imposed by suboptimal and subfreezing temperatures. For these reasons, annual growth of Sitka spruce plantations in the UK is reduced only 10–15 per cent, compared with production rates when T_f is set at optimum for every month.

Monthly mean vapour pressure deficits ranged from less than 0.1 to 1.4 kPa throughout the year at the 12 sites with average maximum of 1.2 kPa in July and an annual mean of 0.7 kPa. These are modest vapour pressure deficits and offer essentially no restrictions on photosynthesis or growth using the function presented in Table 2.

Soil water storage capacity was not expected, nor assumed to be a major constraint on photosynthesis or growth of Sitka spruce. On 10 of the 12 sites, setting the water storage capacity in the rooting zone at 200 mm was sufficient to maintain at least 25 per cent of the available water storage every month throughout the year. The ratio of estimated annual transpiration:precipitation in these cases averaged 0.64 (Table 5). At three sites, the ratio of annual transpiration:precipitation exceeded 0.85 (Sites 2, 5, and 8). In all these cases, original survey notes indicated the presence of ground water or seepage (personal communication from Robert Matthews and colleagues at the

Forestry Commission Branch, Alice Holt). Process models that run at hourly to daily time steps can separate evaporation from transpiration. In this analysis, however, all losses of water to the atmosphere were assumed to be through transpiration, and on rainy days evaporation was assumed to be at rates equivalent to those calculated for transpiration under average conditions with a dry canopy. These assumptions are justified on the basis that the maximum rates of evaporation and transpiration from dense coniferous canopies are similar (0.5 mm h^{-1} or 5 mm day^{-1} (Jarvis and Stewart, 1978).

The third and last step in the analysis involved increasing the constraints on production attributed to infertile soils. When soil fertility was set at 1.0, e.g. non-limiting, predicted growth was higher than observed at half of the 12 sites. To match observed growth more closely with that predicted, soil fertility rankings were adjusted downward for sites 6, 7, 9, 10, 11 and 12 (Table 5). These adjustments in rankings resulted in changes in leaf area index, quantum efficiency, and nitrogen content in the foliage. Nitrogen concentration in foliage was assumed to increase from 1 to 2 per cent across the range in soil fertility rankings (Miller *et al.*, 1992). The predicted N content ranged from a minimum of 70 kg ha^{-1} to a maximum of 390 kg ha^{-1} (Table 5). There was only a fair relationship between maximum L and maximum canopy N content ($r^2 = 0.64$) because a whole suite of environmental variables besides nutrition affect carbon allocation to foliage. The average N content in the four fastest growing plantations averaged 380 kgN ha^{-1} , comparable to measured values (averaging 350 kgN ha^{-1}) reported for six pole-sized stands that were heavily fertilized (Miller *et al.*, 1992).

Discussion

Model functions and parameter values

Although 3-PG is a general model, its performance is improved when detailed knowledge is available for a particular species and for the environment in which it is growing. Sitka spruce is a species on which a vast amount of research has been conducted over the last 30 years. Nevertheless, from the perspective of process modelling, some gaps

stand out, while other areas are more than adequately covered for developing functions and assigning parameters (Table 2).

Much effort has gone into modelling light penetration through Sitka spruce canopies and in modelling the process of photosynthesis. Sitka spruce reflects only about 4 per cent of visible light, compared with 10–15 per cent by other species. This difference in reflectivity is incorporated in the formula developed by Wang *et al.* (1991), but this refinement hardly matters because leaf area indices above 6.0 generally intercept >95 per cent of incoming radiation. Although Sitka spruce is known to be sensitive to moderate vapour pressure deficits (Watts *et al.*, 1976), in applying monthly averaged data, the general response previously employed proved reasonable; in fact, a more sensitive stomatal response to vapour pressure deficits would not have provided rates of photosynthesis adequate at maximum conversion efficiency to match observed growth.

The temperature functions can be important when comparing temperate forest species that evolved from boreal in contrast to subtropical stock (Hawkins and Sweet, 1989). As was shown in this analysis, however, ignoring seasonal departures from optimum temperature and subfreezing conditions results in an increase in predicted growth of only 10–15 per cent. Allometric equations were determined from volume tables and from empirical fitting of constants to give a smooth increase in leaf area index and stability when self-thinning begins. The general conclusions from the simulations would not be significantly altered using even more general allometric equations, although the accuracy would no doubt be less. Simplifications in the model in the ways that transpiration and photosynthesis are calculated also ease the burden of deriving allometric equations to predict foliage biomass from stem diameter. Similarly, with generally high leaf area indices, estimates of annual litterfall can vary from 0.15 to 0.20 of total leaf area with little effect on photosynthesis or wood production.

Wood density and specific leaf area are variables that are known to vary with stocking. Petty *et al.* (1990) give values that range from about 320 to 360 kg m⁻³ for Sitka spruce stands in Scotland. Specific leaf area values were obtained from

an average of seasonal estimates made on dense coastal Sitka spruce and western hemlock forests growing in Oregon. Lower values might be expected in more open stands, but variation in this parameter does not significantly change the fraction of light intercepted once leaf area index >6.0.

Environmental limitations to Sitka spruce growth

From the analysis, the relation between soil fertility and maximum quantum efficiency is one that deserves special attention. The range in maximum α_c is well established but the relationships with nitrogen and chlorophyll concentrations are derived from a variety of species. These relationships need to be established specifically for Sitka spruce. The least known of all relationships deals with allocation to roots. Inferences have been made from annual budgets on fertilized and unfertilized pine plantations and from a range of native forests (see Waring *et al.*, 1998). In the allocation formula (Table 2), the numerator in the equation was set at 0.5 for Sitka spruce rather than 0.8, a change that resulted in not more than 35 per cent of net primary production going to roots on an annual basis. In contrast, more deeply rooted species may allocate as much as 60 per cent to roots (Runyon *et al.*, 1994). These changes in the allocation formula seem reasonable, and in the case of Sitka spruce, necessary to match measured stem wood growth >40 m³ ha⁻¹ a⁻¹.

From the 3-PG diagnostic analysis, the most important limitation on wood production by Sitka spruce in the UK appears to be incident solar radiation, which varies by nearly twofold, and secondarily, soil fertility, which varies by more than fourfold (Table 5). Most of the variation in solar radiation is associated with slope and aspect. The four plots with maximum CAI >40 m³ ha⁻¹ a⁻¹ averaged ϕ_s 3500 MJ m⁻² a⁻¹ whereas the three least productive sites analysed received ϕ_s 2200 MJ m⁻² a⁻¹, almost 40 per cent less. Solar radiation alone, however, is an insufficient basis on which to predict yields. Site 9 received more than 4000 MJ m⁻² a⁻¹, yet grew less than half the maximum CAI reported.

Soil fertility is not an easy variable to correlate with soil morphology as noted by the lack of

correspondence between estimates provided by the Forestry Commission in Table 1 with those generated by the model in Table 5. A poor correlation is to be expected in environments where precipitation, including fog drip, carry high concentrations of nitrogen and other elements. In the UK, as in the coastal fogbelt of the Pacific Northwest region of North America, aerosol impaction of sea salts is an important process. Thus, although soils may have low inherent fertility, trees may obtain calcium, magnesium, potassium and sulphur largely from atmospheric sources (Bockheim and Langley-Turnbaugh, 1997). In the UK, aerosols are also enriched in nitrogen. Emmett and Reynolds (1996) state that 97 per cent of the area of coniferous forests in Wales, which is predominantly Sitka spruce, is currently receiving nitrogen deposition in excess of $11 \text{ kgN ha}^{-1} \text{ a}^{-1}$, and 72 per cent are receiving between 10 and $20 \text{ kgN ha}^{-1} \text{ a}^{-1}$.

In addition to aerosol deposition, commercial fertilizers are generally added during early stages in plantation development (Miller *et al.*, 1992). At ages beyond 25 years, little response to fertilization has been reported, supporting the supposition that much of the nutritional needs are met through reallocation from older foliage. Miller *et al.* (1992, 1996) present data that indicate canopy N content can reach or exceed 350 kg ha^{-1} and that less than 10 per cent of that value is normally recycled in litterfall. New foliage production, which may often exceed $>3000 \text{ kg ha}^{-1} \text{ a}^{-1}$, would require at optimum nutrition that at least half the nitrogen be obtained via translocation from older foliage. Nitrogen content of the canopy has been shown in plantations of *Pinus radiata* in New Zealand to be linearly correlated with volume production (Hunter *et al.*, 1987). The diagnostic analysis suggests that from a standpoint of forecasting plantation growth, canopy nitrogen content and solar radiation are two variables worthy of more attention. The role that diffuse radiation plays on sloping ground deserves clarification as few plantations are established on flat terrain.

3-PG was developed with the expressed goal that many of the driving variables, key parameters, and predicted outputs could be assessed by employing remote sensing technology. The first application of 3-PG used monthly weather satellite data to estimate the productive capacity of

forest lands in Australia and New Zealand (Coops *et al.*, 1998). Goward *et al.* (1994) and Prince and Goward (1995) demonstrated with other satellite-borne sensors the possibility of estimating solar radiation and ambient air temperatures with surprising accuracy. They also used satellites to quantify seasonal drought and seasonal variation in the canopy light absorption. Although instruments are available that measure canopy nitrogen content remotely (Matson *et al.* 1994; Gitelson and Metzlyak, 1997; Martin and Aber, 1997), no satellite at present carries such sensors.

Conclusion

This paper demonstrates how conventional inventory techniques can be used with a simplified process model, such as 3-PG, to diagnose present climatic limitations. Locations where soil fertility might be improved through fertilization or drainage can also be identified following procedures outlined. The approach has the potential to be expanded across the UK using geographic information systems and remote sensing technology (Waring and Running, 1999). One limitation, however, is that the typical disciplinary structure of government and academic research is not designed to foster truly integrative work. The forestry enterprise in the UK has the talent available to do much more, given the opportunity to address problems with a broader perspective built on fundamental principles.

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References

- Aber, J.D., Ollinger, S.V., Federer, C.A., Reich, P.B., Goulden, M.L., Kicklighter, D.W. *et al.* 1995 Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Clim. Res.* 5, 207–222.
- Allison, S.M.U., Proe, M.F. and Matthews, K.B. 1994 The prediction and distribution of general yield classes of Sitka spruce in Scotland by empirical analysis of site factors using a geographic information system. *Can. J. For. Res.* 24, 2166–2171.
- Arneth, A., Kelliher, F.M., McSeveny, T.M. and Byers, J. 1998 Net ecosystem productivity, net primary productivity and ecosystem carbon sequestration in *Pinus radiata* plantation subject to soil water deficit. *Tree Physiol.* 18, 785–793.
- Bateman, I.J. and Lovett, A.A. 1998 Using geographic information system (GIS) and large area data bases to predict yield class: a study of Sitka spruce in Wales. *Forestry* 71, 147–160.
- Beets, P.N. and Whitehead, D. (1996) Carbon partitioning in *Pinus radiata* in relation to foliage nitrogen status. *Tree Physiol.* 16, 131–138.
- Bockheim, J.G. and Langley-Turnbaugh, S. 1997 Biogeochemical cycling in coniferous ecosystems on different aged marine terraces in coastal Oregon. *J. Environ. Qual.* 26, 292–301.
- Bristow, K.L. and Campbell, G.S. 1984. On the relationship between incoming solar radiation and daily maximum and minimum temperature. *Agric. For. Meteorol.* 31, 159–166.
- Coops, N.C., Waring, R.H. and Landsberg, J.J. 1998 Assessing forest productivity in Australia and New Zealand using a physiologically-based model driven with averaged monthly weather data and satellite derived estimates of canopy photosynthetic capacity. *For. Ecol. Manage.* 104, 113–127.
- Emmett, B.A. and Reynolds, B. 1996 Nitrogen critical loads for spruce plantations in Wales: Is there too much nitrogen? *Forestry* 69, 200–214.
- Ford, E.D. 1982 High productivity by a pole-stage Sitka spruce stand and its relation to canopy structure. *Forestry* 55, 1–17.
- Friend, A.D., Shugart, H.H. and Running, S.W. 1993 A physiology-based gap model of forest dynamics. *Ecology* 74, 792–797.
- Gitelsen, A.A. and Merzlyak, M.N. 1997 Remote sensing of chlorophyll concentration in higher plant leaves. *Int. J. Remote Sens.* 18, 2691–2697.
- Goward, S.N., Waring, R.H., Dye, D.G. and Yang, J. 1994 Ecological remote sensing at Otter: Satellite macroscale observations. *Ecol. Appl.* 4, 322–343.
- Hamilton, G.J. and Christie, J.M. 1971 Forest Management Tables (Metric). *Forestry Commission Booklet* No 34. HMSO, London.
- Hawkins, B.J. and Sweet, G.B. 1989 Photosynthesis and growth of present New Zealand forest trees relate to ancient climates. *Ann. Sci. For.* 46, 512–514.
- Hunter, I.R., Hunter, J.A.C. and Graham, J.D. 1987 *Pinus radiata* stem volume increment and its relationship to needle mass, foliar and soil nutrients, and fertiliser inputs. *N. Z. J. For. Sci.* 17, 67–75.
- Jarvis, P.G. and Stewart, J. 1978 Evaporation of water from plantation forest. In *The Ecology of Even-aged Forest Plantations*. E.C. Ford, D.C. Malcolm, and J. Atterson (eds). Proceedings of the Meeting of Division 1. IUFRO, Edinburgh, Scotland, 327–345.
- Jones, H.G. 1992 *Plants and Microclimate*. Cambridge University Press, 428pp.
- Kelliher, F.M., Leuning, R., Raupach, M.R. and Schulze, E.-D. 1995 Maximum conductances for evaporation from global vegetation types. *Agric. For. Meteorol.* 73, 1–16.
- Landsberg, J. 1998 *Calibration, Performance and Further Development of the Forest Productivity Model 3-PG*. CSIRO Division of Lands and Water, Internal Report.
- Landsberg, J. and Coops, N.C. 1999 Modelling forest productivity across large areas and long periods. *Nat. Res. Modelling* (in press).
- Landsberg, J.J. and Waring, R.H. 1997 A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95, 209–228.
- Law, B.E., Waring, R.H., Aber, J.D. and Anthoni, P.M. 1999 Measurements of gross and net ecosystem productivity and water vapor exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biology* (in press).
- Linder, S. and Murray, M. 1998 Do elevated CO₂ concentrations and nutrients interact? In *European Forests and Global Change*. P.G. Jarvis (ed.). Cambridge University Press, 215–235.
- Lebens, R. 1986 *Climate in the United Kingdom*. Department of Energy. HMSO, London, 391pp.
- Macmillan, D.C. 1991 Predicting the general yield class of Sitka spruce on better quality land in Scotland. *Forestry* 64, 359–372.
- McMurtrie, R.E. and Landsberg, J.J. 1992 Using a simulation model to evaluate the effects of water and nutrients on the growth and carbon partitioning of *Pinus radiata*. *For. Ecol. Manage.* 52, 243–260.
- Martin, M.E. and Aber, J.D. 1997 High spectral resolution remote sensing of forest canopy lignin, nitrogen, and ecosystem processes. *Ecol. Appl.* 7, 431–443.

- Matson, P., Johnson, L., Billow, C., Miller, J. and Pu, R. 1994 Seasonal patterns and remote spectral estimation of canopy chemistry across the Oregon transect. *Ecol. Appl.* 4, 280–298.
- Miller, J.D., Cooper, J.M. and Miller, H.G. 1992 Response of pole-stage Sitka spruce to applications of fertilizer nitrogen, phosphorus and potassium in upland Britain. *Forestry* 65, 15–33.
- Miller, J.D., Cooper, J.M. and Miller, H.G. 1996 Amounts and nutrient weights in litterfall, and their annual cycles, from a series of fertilizer experiments on pole-stage Sitka spruce. *J. For.* 69, 289–302.
- Mohren, G.M.J. and Ilvesniemi, H. 1995 Modelling effects of soil acidification on tree growth and nutrient status. *Ecol. Model.* 83, 263–272.
- Neilson, R.E. and Jarvis, P.G. 1975 Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). *J. Appl. Ecol.* 12, 879–892.
- Nicoll, B.C. and Ray, D. 1996 Adaptive growth of tree root systems in response to wind action and site conditions. *Tree Physiol.* 16, 891–898.
- Petty, J.A., Macmillan, D.C. and Steward, C.M. 1990 Variation of density and growth ring width in stems of Sitka and Norway spruce. *Forestry* 63, 39–49.
- Prince, S.D. and Goward, S.N. 1995 Global primary production: a remote sensing approach. *J. Biogeogr.* 22, 815–835.
- Proe, M.F., Allison, S.M. and Matthews, K.B. 1996 Assessment of the impact of climate change on the growth of Sitka spruce in Scotland. *Can. J. For. Res.* 26, 1914–1921.
- Quine, C.P. and White, I.M.S. 1993 Revised wind-throw hazard classification. *Forestry Commission Information Note No 230*. Forestry Commission, Farnham, Surrey.
- Running, S.W. and Gower, S.T. 1991 FOREST-BGC, A general model of forest ecosystem processes for regional applications II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiol.* 9, 147–160.
- Running, S.W., Nemani, R.R. and Hungerford, R.D. 1987 Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. *Can. J. For. Res.* 17, 472–483.
- Runyon, J., Waring, R.H., Goward, S.N. and Welles, J.M. 1994 Environmental limits on net primary production and light-use efficiency across the Oregon transect. *Ecol. Appl.* 4, 226–237.
- Wang, Y.P., Jarvis, P.G. and Taylor, C.M.A. 1991 PAR absorption and its relation to above-ground dry matter production of Sitka spruce. *J. Appl. Ecol.* 28, 547–560.
- Waring, R.H. and Running, S.W. 1998 *Forest Ecosystems: Analysis at Multiple Scales*. Academic Press, San Diego, CA. 370pp.
- Waring, R.H. and Running, S.W. 1999 Remote sensing requirements to drive ecosystem models at the landscape and regional scale. In *Integrating Hydrology, Ecosystem Dynamics, and Biogeochemistry in Complex Landscapes*. J.D. Tenhunen and P. Kabat (eds). John Wiley, Chichester, UK, 23–38.
- Waring, R.H., Schroeder, P.E. and Oren, R. 1982 Application of the pipe model theory to predict canopy leaf area. *Can. J. For. Res.* 12, 556–560.
- Waring, R.H., Law, B.E., Goulden, M.L., Bassow, S.L., McCreight, R.W., Wofsy, S.C. and Bazzaz, F.A. 1995. Scaling gross ecosystem at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. *Plant Cell Environ.* 18, 1201–1213.
- Waring, R.H., Landsberg, J.J. and Williams, M. 1998 Net primary production of forests: a constant fraction of gross primary production? *Tree Physiol.* 18, 129–134.
- Watts, W.R., Neilson, R.E. and Jarvis, P.G. 1976 Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). *J. Appl. Ecol.* 13, 623–638.
- Worrell, R. and Malcolm, D.C. 1990a Productivity of Sitka spruce in northern Britain. 1. The effects of elevation and climate. *Forestry* 63, 105–118.
- Worrell, R. and Malcolm, D.C. 1990b Productivity of Sitka spruce in northern Britain. 2. Prediction from site factors. *Forestry* 63, 119–128.

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