Use of a physiological process model with forestry yield tables to set limits on annual carbon balances

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Summary   We present an approach that sets limits on annual carbon fluxes for different aged forests by using a simple process-based model (3-PG) and information derived from yield tables and local weather stations. Given a measure of height-growth potential, model predictions are constrained to match stand dynamics described in yield tables. Thus constrained, the model can provide reasonable annual estimates of gross photosynthesis under a specified climate, even with inexact knowledge of soil properties. If we assume that leaf litterfall and fine-root turnover approach equilibrium at canopy closure, maximum net annual ecosystem exchange can also be predicted from modeled estimates of these two detrital components and estimates of foliage, branch, stem and coarse-root production. The latter four components of production are predicted from allometric relationships with mean stem diameter. The approach is demonstrated for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands between Ages 20 and 150 years growing under conditions typical of those at Wind River, Washington, USA. Gross photosynthesis (P_g) by Douglas-fir at Ages 20, 70 and 150 years with leaf area indices (L) of 8.1, 6.9 and 4.0 was predicted at 1630, 1580 and 1160 g C m^{-2} year^{-1}, respectively. Maximum net ecosystem production (P_e) for the same range in age classes was predicted to average 275, 294 and 207 g C m^{-2} year^{-1}, respectively. The predicted reductions in L for older stands do not occur because other species fill the canopy gaps created by natural mortality of Douglas-fir. As a result of the development of an understory, total P_g is predicted to decrease only slightly with the aging of the overstory. Estimates of P_e exclude respiration from coarse woody debris, although additions of this component are provided annually by the model. The process-based modeling approach, constrained by yield table estimates of stand properties, sets reasonable limits on annual carbon exchange and suggests which environmental variables deserve careful monitoring to refine estimates of carbon fluxes.

Keywords: Douglas-fir, ecosystem production, 3-PG, primary production.

Introduction

As process models of canopy gas exchange have been field-tested in recent decades, evidence has emerged that simplifications in the description of canopy architecture can be made while still providing reasonable estimates of canopy photosynthesis (Lloyd et al. 1995, Williams et al. 1996, Law et al. 2000). By incorporating these simplifications, it has been possible to use photosynthetic models to simulate the growth of forest stands (Running and Gower 1991, Aber and Federer 1992, Cienciala et al. 1997). To ensure reasonable estimates of carbon allocation to aboveground production, Korol et al. (1996) and Landsberg and Waring (1997) modified process models to predict explicitly those stand characteristics presented in forestry yield tables: mean tree diameter, basal area, volume and tree mortality. Such constrained models have been shown to give good estimates of seasonal and annual carbon dioxide and water vapor exchange at intensively monitored sites (Cienciala et al. 1997, Law et al. 2000).

At the heart of all ecosystem process models are common elements that link the atmosphere, vegetation and soils. The models are driven by climatic variables that include precipitation, solar energy, means and extremes in temperature (including days below freezing), and the daytime atmospheric humidity deficit. Long-term changes in atmospheric CO_2 concentrations are also taken into account. Most models calculate complete water as well as carbon budgets: precipitation recharges the soil and enters streams, either as surface runoff or by percolation through the soil; the rest of the water is converted to vapor and evaporated or transpired back into the atmosphere. Major limitations on transpiration and photosynthesis are imposed by reductions in the rate that water vapor and CO_2 diffuse through stomata in response to stressful conditions.

The upper limits on photosynthesis are defined by the amount of light absorbed by the canopy and the canopy photosynthetic efficiency. The products of photosynthesis are partitioned into growth and autotrophic respiration. Growth is allocated to foliage, branches, stems and roots in proportions influenced by the extent to which nutrients and water are limiting. Eventually, plant components are shed and converted into detritus that is incorporated into soil organic matter, leached, or converted to CO_2 via heterotrophic respiration.

Our objective is to introduce an approach by which widely available growth data and long-term climatic records may be

used to constrain a physiological process model to set limits on ecosystem scale gross and net carbon uptake. We employ a simplified process model (3-PG) developed by Landsberg and Waring (1997) to estimate the carbon budget of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands of similar site quality and a climate representative of that at Wind River, Washington, USA. We applied the model to predict the annual carbon balance of 20- to 150-year-old Douglas-fir stands by using a narrow range of values for soil water holding capacity and soil fertility that generated aboveground growth properties closely matching those reported in a forest yield table (McArdle 1961).

Materials and methods

Study area

We used long-term climate data and site conditions characteristic of Wind River, Washington (45°49′ N, 121°38′ W) for our modeling. The forests are composed largely of Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red cedar (*Thuja plicata* Donn). The height-growth potential in both a 20- and 450-year-old Douglas-fir stand was assessed at 43 m at 100 years, which represents a Site III classification in yield tables (McArdle 1961). Soils of both stands are coarse textured and relatively nutrient-poor, having been developed on a 2- to 3-m-deep layer of volcanic ejecta (Franklin et al. 1972). A textural discontinuity is present at 70–80-cm depth that inhibits root growth. The storage capacity of available water varies considerably depending on whether roots penetrate this impervious zone.

Climatic conditions

The climate at Wind River is characteristic of a temperate wet winter, dry summer region with annual precipitation averaging about 2500 mm, with less than 10% falling between June and September. Approximately 10% of the precipitation falls as snow. The 3-PG model requires values of short-wave incoming radiation (ϕ_s), mean daytime vapor pressure deficit (D), mean temperature and number of frost days. These values were calculated from long-term monthly averages of daily temperature extremes (1901–1977), obtained at http://www.wrcc.dri.edu, by means of standard equations (Running et al. 1987, Waring 2000) and are presented, along with monthly precipitation, in Table 1.

Conversion of temperature extremes into monthly estimates of solar radiation requires knowledge of latitude, elevation, slope and aspect. The extent that clouds, pollution and fog reduce solar radiation below the maximum is reflected in the difference between minimum and maximum temperatures (ΔT). We estimated monthly averaged radiation by taking into account daily changes in solar declination and day length and using Equations 1–3 (Bristow and Campbell 1984, Coops et al. 2000). First, clear sky transmissivity (Ω) was increased from 0.65 at sea level with elevation (Equation 1). Solar radiation (ϕ_s) was then estimated (Equation 2), after calculation of a β function (Equation 3).

$$\Omega = 0.65\,(\text{Elevation (m)})\,0.0008, \tag{1}$$

$$\phi_s = \Omega\left(1 - \exp^{-(\beta\Delta T)^{(\Delta T^{2.4})}}\right), \tag{2}$$

where

$$\beta = 0.035 \exp(-0.154\Delta T). \tag{3}$$

More sophisticated models are required to account for seasonal variation in the diffuse component of ϕ_s (MJ m^{-2} month^{-1}). However, because meteorological data were available from four sites in Oregon (http://www-eosdis.ornl.gov/DATACENTER_DOCS/otter.html, also see Goward et al. 1994, Runyon et al. 1994), we adjusted for this source of variation with a simple linear equation:

$$\phi_s = 0.74\phi_{sp} + 73, \ r^2 = 0.93, \tag{4}$$

where ϕ_{sp} is the initially predicted short-wave monthly radiation from the four meteorological stations. The standard error of estimate for the slope and intercept are ± 0.02 and ± 18 MJ m^{-2} month^{-1}, respectively.

Mean monthly atmospheric vapor pressure 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 (i.e., the minimum temperature is the dew point). 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 temperature (T_{min}) represents the mean maximum D for each month. Mean daytime D was assumed to be about 0.5 of the maximum, although 0.6 might be more appropriate (Waring 2000). The saturated vapor pressure (kPa) was estimated from a formula referenced by Running et al. (1987).

$$\text{Saturated vapor pressure} = 0.61078 \exp\left(\frac{17.269\,T_{min}}{237.3 + T_{min}}\right). \tag{5}$$

The number of days per month with subfreezing temperatures that could force stomatal closure was estimated from an empirical equation derived from data at three widely dispersed sites (N. Coops, CSIRO, Melbourne, Australia, unpublished data) where:

$$\text{Frost days per month} = T_{min}(-2.00) + 11.6, \tag{6}$$

if $T_{min}(-2.00) + 11.6$ is < 0, then 0 days frost, $r^2 = 0.83$.

Mean monthly temperatures (T_{av}) were derived by averaging mean monthly temperature extremes.

The 3-PG model structure

The 3-PG model (Physiological Principles Predicting Growth) developed by Landsberg and Waring (1997) incorporates five important simplifications, which have emerged from studies

Table 1. Meteorological data derived from mean monthly maximum and minimum temperatures and precipitation data averaged for years 1900–1977 at Wind River, Washington. Abbreviations: ϕ_s = solar radiation, Precip. = Precipitation, D = atmospheric vapor pressure deficit and T = temperature.

Variable	Jan	Feb	Mar	April	May	June	July	Aug	Sep	Oct	Nov	Dec	Sum or mean[*]
ϕ_s (MJ m^{-2})	114	174	315	457	567	590	580	504	368	243	138	98	4148
Precip. (mm)	429	320	292	154	91	60	17	33	76	213	381	466	2533
D (kPa)	0.16	0.22	0.33	0.53	0.75	0.89	1.23	1.19	0.96	0.55	0.25	0.15	0.60[*]
Mean T (°C)	0.0	2.1	4.6	7.9	11.9	14.9	17.8	17.4	14.6	9.7	4.3	1.8	8.9[*]
Frost days	19	16	13	10	4	0	0	0	0	6	12	14	94

conducted in a wide range of temperate forests, that can be summarized as follows. (1) At monthly time steps or longer, the ratio of net primary production to gross photosynthesis (P_n/P_g) approaches a constant (0.47 ± 0.04 SE) (Arneth et al. 1998, Waring et al. 1998, Law et al. 2001). This assumption greatly simplifies the calculation of respiratory losses. (2) Canopy conductance approaches a maximum above a leaf area index (L) of 3.0 (Kelliher et al. 1995). At $L > 3.0$, maximum canopy 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 L and simplify calculation of transpiration and photosynthesis. (3) The ratio of actual/potential photosynthesis decreases in response to the most restrictive (monthly) environmental limitation. This ratio simplifies calculations of the amount of carbon allocated monthly to roots (see Table 2, Runyon et al. 1994, Beets and Whitehead 1996, Waring and Running 1998). (4) The fraction of production not allocated to roots is partitioned among foliage, stem and branches based on species-specific allometric relationships with tree diameter. These allometric relationships are robust, and those between stem diameter and tree mass can easily be obtained from published tables of tree volume and wood densities. (5) Canopy quantum efficiency (α_c) is assumed to increase linearly with soil fertility (Waring et al. 1995, Linder and Murray 1998). This means that soil fertility can be quantified, so far as it affects photosynthesis, by measuring α_c.

Table 2 summarizes the inputs and outputs of the 3-PG model. The model can be run with either consecutive years of meteorological data or with long-term means. Running consecutive years of data is appropriate for short-term comparisons of net ecosystem exchange (Law et al. 2000). In this study, however, long-term means were used because height growth curves, which define the selection of an appropriate

Table 2. Inputs and outputs of the 3-PG model.

Inputs
Weather data: temperature, precipitation, humidity, solar radiation, subfreezing days
Initial biomass: foliage, stems, roots
Variables: soil water storage, initial stem numbers, stand age, age at maximum height
Parameters: canopy quantum efficiency, temperature optimum and limits for photosynthesis, ratio of autotrophic respiration to gross photosynthesis, maximum leaf and canopy conductances, specific leaf area, maximum annual litterfall, litter and root turnover rates, soil fertility ranking, parameters for allometric equations with stem diameter

Model calculates monthly
Canopy leaf area index from foliage mass and specific leaf area and monthly leaf litterfall
Degree that climatic variables limit stomatal or canopy conductance
Transpiration from Penman-Monteith equation, evaporation as a fraction of precipitation
Gross photosynthesis from utilizable PAR × quantum efficiency
Primary production as a fixed fraction of gross photosynthesis
Fraction of primary production allocated to coarse- and fine-roots
Fraction of primary production allocated to stems, branches and foliage
Autotrophic respiration as a fixed fraction of gross photosynthesis

Model calculates annually
Stem wood production, in units of mass, volume and basal area
Primary production, above and below ground
Natural mortality or mortality through thinning
Standing live biomass
Litter and root turnover, which represents heterotrophic respiration
Autotrophic respiration
Relative constraint imposed by each environmental factor on production

yield table, assume stable climatic patterns. Under these conditions, both carbon pools associated with leaf and root production and turnover, as well as fluxes of carbon in and out of the systems can be assumed to approach equilibrium, although in reality some woody debris may continue to accumulate until removed by fire or logging.

Photosynthetically active radiation (ϕ_{pa}) is considered to be 50% of short-wave incoming radiation (ϕ_s). The amount of ϕ_{pa} absorbed by the canopy is a function of canopy L and is calculated from Beer's law, which ignores foliage clumping (Table 3). The fraction of absorbed photosynthetically active radiation utilized (ϕ_{pau}) is obtained by reducing the value of ϕ_{pa} by amounts determined by modifiers (f_i)—dimensionless factors 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 vapor pressure deficits, soil drought and subfreezing temperatures. Gross photosynthesis is calculated as the product of ϕ_{pau} and α_c. The ratio ϕ_{pau}/ϕ_{pa} represents the constraints on photosynthesis associated with partial to complete stomatal closure.

As the vapor pressure deficit (kPa) increases, maximum stomatal conductance is assumed to decrease exponentially (using the default parameter published by Landsberg and Waring 1997).

$$g_c = g_{cmax} \exp(-0.5D), \tag{7}$$

where g_c is stomatal conductance and g_{cmax} is maximum stomatal conductance.

Similarly, because a water balance is calculated each month, after initialization at maximum soil water storage capacity θ_{max}, the available water supply will be reduced from the maximum if transpiration exceeds precipitation. As this happens, the relative available water content (r_θ) may be reduced from one to potentially zero. The soil water constraint (θ_f) on stomatal conductance is nonlinear and dependent on water-tension curves associated with different soils, because texture affects coefficients (c_θ), which range from 0.4 to 0.7, and power functions (n_θ), which range from 3 to 9, respectively, for clay and sandy soils (Landsberg and Waring 1997).

$$\theta_f = \frac{1}{1 + ((1 - r_\theta)/c_\theta)^{n_\theta}}. \tag{8}$$

A temperature function (T_f), which varies between zero and unity, was added to the model by Landsberg (1998) and Waring (2000) to take account of variations in mean monthly temperature (T_{mean}) that approach a threshold maximum or minimum departing from the temperature optimum (T_{opt}) for photosynthesis (Table 3). This monthly temperature function is multiplied by the maximum quantum efficiency set by soil fertility rankings.

If $T_{av} \leq T_{min}$ or $T_{av} \geq T_{max}$, then $T_f = 0$,

otherwise,

Table 3. Model functions and parameters used for Douglas-fir in this study. Abbreviation: APAR = absorbed photosynthetically active radiation.

Variable	Functions and parameter values	Reference
Light conversion efficiency of photosynthesis	Maximum α_c set to vary from 0.043 to 0.05 mol C mol^{-1} photon (2.37–2.76 g C MJ^{-1} APAR)	This study
Temperature constraints on light conversion	T_{opt} was set at 20 °C, T_{min} at –2 °C and T_{max} at 40 °C	Lewis et al. 1999
Fraction of ϕ_s absorbed by canopy as function of L	$1 - (2.718 \exp(-0.5L))$	Landsberg and Waring 1997
Soil fertility rank (FR) (0 to 1)	0.42–0.50	This study
Available soil water storage (θ_{max})	100–300 mm	This study
Boundary layer conductance	0.2 m s^{-1}	Landsberg and Waring 1997
Maximum leaf stomatal conductance	0.006 m s^{-1}	Coops and Waring 2001a
Maximum canopy stomatal conductance (g_{cmax})	0.018 m s^{-1}	Coops and Waring 2001a
Stomatal response (g_c) to vapor pressure deficit (kPa)	$g_c = g_{cmax} \exp(-0.5D)$	Landsberg and Waring 1997
Specific leaf area	6.0 m^2 kg^{-1}	Matson et al. 1994
Allometric equation for stem mass (kg)	Stem mass = 0.0843(diameter (cm))$^{2.436}$	McArdle 1961, Site III
Allometric equation for foliage mass (kg)	Foliage mass = 0.1484 (diameter (cm))$^{2.167}$	This study
Allometric equation for coarse root mass (kg)	Coarse root mass = 0.0161(diameter (cm))$^{2.533}$	This study, derived from Gholz 1982
Foliage turnover	0.021 month^{-1}, 0.25 year^{-1}	Gholz 1982
Maximum stem biomass	220 Mg ha^{-1}	This study
Wood density	360–400 kg m^{-3}	This study and Brown et al. 1949
Age when trees approach maximum height (Age$_f$)	200 years	This study
Fraction of production allocated to roots (η_R)	$(\eta_x\eta_n)/\eta_n + (\eta_x - \eta_n)FR f_{i,min} Age_f$	Sands 2001
Maximum fraction allocated to roots (η_x)	0.8	
Minimum fraction allocated to roots (η_n)	0.25	

$$T_f = \frac{(T_{mean} - T_{min})}{(T_{opt} - T_{min})} \times \frac{(T_{max} - T_{mean})}{(T_{max} - T_{opt})}^{\left(\frac{T_{max} - T_{opt}}{T_{opt} - T_{min}}\right)}. \qquad (9)$$

As trees approach their maximum height, constraints are imposed that reduce the maximum stomatal conductance (Mencuccini and Grace 1996, Landsberg and Waring 1997, Ryan and Yoder 1997). We assumed that Douglas-fir trees, regardless of site, approach maximum height by 200 years; McArdle (1961) reported that tree heights at Age 200 are within 10% of those at Age 440. The relationship described in Equation 10 is nonlinear because lower branches continue to be replaced until trees approach maximum height, at which time branches remain functional longer, but exhibit increased hydraulic resistance (Waring and Silvester 1994, Ryan et al. 2000, Warren and Adams 2000).

Relative age (F_a) is the ratio of actual age (years) to the maximum age (taken to be 200 years in this case, when height growth almost ceases). The constant (0.95) causes the age effect (Age$_f$) to equal 0.5 when $F_a = 0.95$; the power in the denominator (n_{age}) controls the rate of change in the function, which we assumed equals 4. The values used for n_{age}, Age$_f$ and F_a are identical to those used by Landsberg and Waring (1997), based on measurements made on *Pinus sylvestris* L. plantations of different ages by Mencuccini and Grace (1996).

$$Age_f = \frac{1}{1 + (F_a / 0.95)^{n_{age}}}. \qquad (10)$$

Starting values of foliage, stem and root mass are required by the model, appropriate to the age of the stand at the beginning of a run, together with allometric equations describing the relationships between stem mass and diameter and foliage mass and stem diameter for the species. In this study, the allometric equation for stemwood growth as a function of mean stem diameter was derived from data presented in the yield table by first assuming a wood density of 400 kg m^{-3} (Brown et al. 1949) to convert from volume (m^3) to mass (kg) (Gholz 1982). A slightly better fit to the yield table data was attained by assuming a wood density of 360 kg m^{-3} in all model runs.

The foliage mass–stem diameter relationship for these stands was determined by using Beers law to estimate L from measurements of intercepted photosynthetically active radiation (fPAR) within two fully stocked stands of Douglas-fir with closed or nearly closed canopies obtained with a sunfleck ceptometer (Pierce and Running 1988). The two stands, growing in the H.J. Andrews Experimental Forest of the Willamette National Forest near Blue River, Oregon (R.H. Waring and J. Mayo, unpublished data) were aged 20 and 70 years; fPAR values averaged 0.98 and 0.96, equivalent to projected L of 8 and 6.5, respectively (Table 3). Coupled with values of specific leaf area (SLA; 6.0 m^2 kg^{-1}) published by Matson et al. (1994) and knowledge of mean tree diameters and stocking, the allometric equation presented in Table 3 was obtained. In the model, L is converted from foliage mass based on SLA. An estimate of annual leaf turnover (0.25 in Table 3) is also required to calculate leaf litterfall and monthly changes in L.

The model was run for 150 years with an initial stocking of 1500 seedlings ha^{-1} and initial biomass of foliage, roots and stems set at 1, 3 and 6 Mg ha^{-1}, respectively; i.e., the same values used by Landsberg and Waring (1997). The initial stocking density was chosen to delay self-thinning, using the −3/2 power law, beyond 20 years to simplify calculation of maximum net ecosystem production at canopy closure. The higher the initial stocking density is set, the smaller the diameter of trees will be when self-thinning begins. In this study, self-thinning was set to start when a standing biomass of 220 Mg ha^{-1} was attained (Table 3). The model produces values of stand gross photosynthesis (P_g), and then estimates stand net primary production (P_n; g C m^{-2} year^{-1}) by multiplying by 0.47, assuming the biomass contains 50% carbon. Stand basal area, the sum of all individual tree cross sections at 1.3 m height, is the most appropriate variable to evaluate when comparing model predictions to yield tables.

Maximum annual net ecosystem production (P_e) is obtained by subtracting autotrophic (R_a) and heterotrophic (R_h) respiration from 3-PG estimates of P_g. In 3-PG, R_a is assumed to be 0.53 of P_g (Waring et al. 1998). If we assume that decomposition consumes an amount of carbon equivalent to that contained in annual leaf litterfall (L_f) and fine-root production (R_f), and that these components approach equilibrium following canopy closure (Raich and Nadelhoffer 1989), then:

$$R_h = L_f + R_f. \qquad (11)$$

Although 3-PG estimates stem and coarse-root mortality since stand establishment, it does not estimate respiration from these sources. For such estimates, see Landsberg and Gower (1997) and Janisch and Harmon (2002).

Results

Implications of matching stand structural properties

The values of L produced by 3-PG were constrained to match those derived from measurements of light interception by the 20- and 70-year-old Douglas-fir stands at the H.J. Andrews Experimental Forest. Estimates of stand basal area were constrained to match yield table values for Site III stands aged from 20 to 150 years. Under the climatic regime summarized in Table 1, these constraints restricted maximum available soil water content (θ_{max}) to between 100 and 300 mm, soil fertility rating to between 0.42 and 0.50, and maximum α_c to between 0.043 and 0.050 mol C mol^{-1} photon. Only within these ranges of soil water content and fertility, could 3-PG reproduce yield table estimates of stem basal area, volume and stocking (Figure 1).

If θ_{max} was increased, soil fertility rating and α_c had to be decreased to provide comparable estimates of annual gross photosynthesis, and maintain close agreement with yield table values of growth and other mensurational properties (Figure 1). This tradeoff between soil fertility and soil water availability is illustrated for 20-year-old stands in Table 4 where
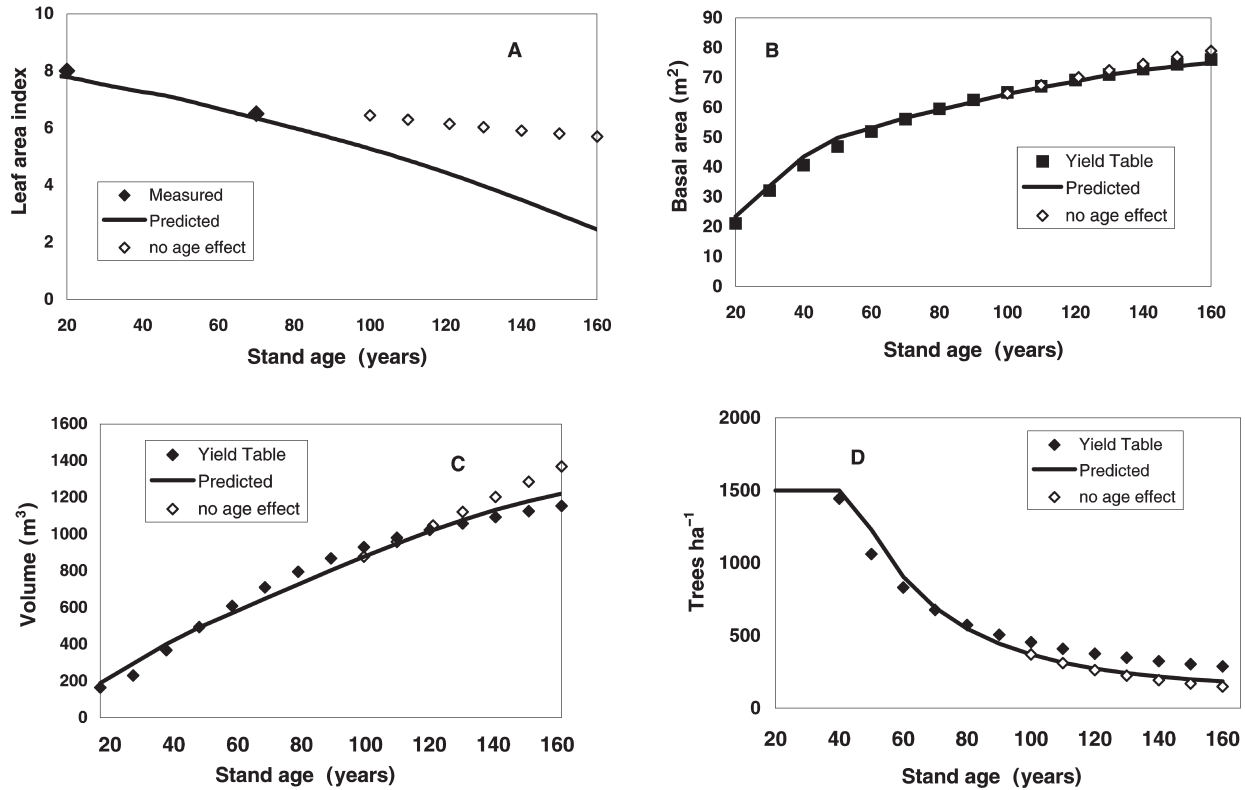
Figure 1. Modeled values of leaf area index (A), basal area (B), stem wood volume (C) and stocking density (D) between stand ages of 20 and 150 years have near 1:1 relationships (within 10%, with $r^2 > 0.98$) with yield table values for sites of equivalent productive capacity (43 m height at 100 years).

estimates of P_g vary only between 1544 to 1628 g C m^{-2} year^{-1}.

Seasonal patterns of P_g differed considerably depending on the values set for θ_{max} (Figure 2). For example, if θ_{max} was set at 100 mm, drought restricted photosynthesis from June to September, whereas when θ_{max} was set at 200–300 mm, drought reduced P_g only in August and September. As a corollary, higher values of soil fertility and quantum efficiency were required at lower values of θ_{max} to allow the model to reproduce yield table values (Figure 2 and Table 4). The seasonal pattern in P_g associated with drought-prone soils ($\theta_{max} = 100$ mm), is similar to that reported for net ecosystem exchange at Wind River over a 2-year period that included summer

droughts (K.T. Paw U, University of California, Davis, CA, unpublished observations).

Limits on stand carbon balances

Table 5 summarizes the modeled carbon balances for the Douglas-fir stand aged 20, 70 and 150 years. Calculations were carried out with θ_{max} set at 200 mm with the corresponding values for soil fertility and α_c listed in Table 4; the results are similar for other combinations listed. Under the imposed range of climatic and soil conditions, 40–50% of P_n is predicted by the model to be allocated to fine-root growth. If soil fertility were increased to the maximum, allocation of P_n to fine-root growth would be reduced to < 25%, with a propor-

Table 4. 3-PG simulations starting at stand establishment with 1500 trees ha^{-1} and running to Age 20 show a range of possible values for soil water storage capacity (θ_{max}), soil fertility ranking and canopy quantum efficiency (α_c) that results in different estimates of annual transpiration (E), but similar values of gross photosynthesis (P_g): mean ± SE = 1600 ± 28 g C m^{-2} year^{-1}. This convergence in predicted P_g occurs because the model is constrained to match closely the values of leaf area index (8.0), basal area (21 m^2) and volume (165 m^3) associated with the site's productive capacity (43 m height of Douglas-fir at 100 years, McArdle 1961).

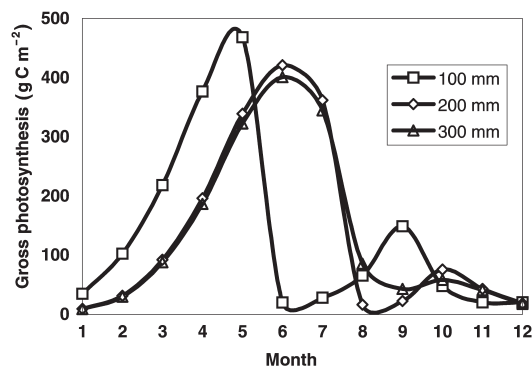| Simulation run	θ_{max} (mm)	Soil fertility rank	α_c (mol C mol^{-1} photon)	P_g (g C m^{-2} year^{-1})	E (mm year^{-1})
1	100	0.50	0.050	1544	540
2	200	0.45	0.045	1629	631
3	300	0.42	0.043	1628	666

Figure 2. Monthly gross photosynthesis (P_g) of a 20-year-old Douglas-fir stand in relation to maximum soil water holding capacity (θ_{max}). Annual gross photosynthesis is identified for all three scenarios and is set to maximize the fit between predicted and measured stand characteristic from yield tables (McArdle 1961), as shown in Figure 1. At lower values of θ_{max}, higher photosynthetic rates are required in the spring to offset drought stress in the summer. Recovery of photosynthetic activity, however, is more rapid during autumn as less precipitation is required to recharge soil moisture when $\theta_{max} = 100$ mm than at higher values.

tional increase in aboveground growth.

At 150 years, L is predicted to be 4.0 (Figure 1a), which represents a reduction in intercepted light of 10–12% from that predicted for younger Douglas-fir stands. A major reduction in photosynthesis is attributed to hydraulic constraints, which are assumed to become progressively more severe after 100 years. Together, these two canopy properties reduced P_g and P_n by 30% in 150-year-old Douglas-fir stands compared with younger stands. Net primary production equaled 765 and 741 g C m^{-2} $year^{-1}$ in 20- and 70-year-old stands, respectively, and declined sharply to 545 g C m^{-2} $year^{-1}$ in a 150-year-old stand (Table 5). Maximum net ecosystem production was similar for the younger stands, 275 to 294 g C m^{-2} $year^{-1}$, but decreased to 207 g C m^{-2} $year^{-1}$ in the 150-year-old Douglas-fir stand (Table 5). Annual tree mortality was estimated to represent a transfer of 68 g C m^{-2} $year^{-1}$ to the detrital pool at Age 70 and 47 g C m^{-2} $year^{-1}$ at Age 150. No mortality occurred in the 20-year-old stand because stand biomass was < 220 Mg ha^{-1}

with initial stocking set at 1500 trees ha^{-1}.

Setting limits on the contributions of understory trees and shrubs

The fraction of L contributed by Douglas-fir at Wind River declines with stand age from 95% at 20 years to about 30% at 450 years (Tomas and Winner 2000, N. McDowell, unpublished data). To set upper limits on P_g and P_e attributed to understory species, we assumed that all shade-tolerant trees and shrubs would establish in light gaps and would compete with Douglas-fir on an equal basis for water and nutrients. Under these circumstances, an estimate of maximum P_g for multistoried stands is obtained by assuming that the understory P_g represents the difference between the maximum attained at 20 years and that attributed to Douglas-fir at later stages in stand development. Following this logic and using values presented in Table 5, the maximum P_g by an understory beneath a Douglas-fir canopy, would be 52 and 469 g C m^{-2} $year^{-1}$ at Ages 70 and 150, respectively.

If we further assume that the P_e/P_g ratio of 0.17 observed in 20-year-old stands applied in older stands, then the maximum P_e contributed by understory vegetation in 70- and 150-year-old stands would be 9 and 80 g C m^{-2} $year^{-1}$, respectively. None of the estimates of P_e made with 3-PG include respiration from coarse woody debris; however, this source has been modeled for different age classes of Douglas-fir forests by Janisch and Harmon (2002).

Discussion

A critical first step in this analysis was to obtain a good fit to a broad array of yield table data for a specified site index. With appropriate allometric equations, 3-PG reproduced stand dynamics accurately, and gave reasonable estimates of L at Ages 20 and 70 (Figure 1). Beyond a stand age of 100 years, an age-imposed reduction in photosynthesis was required to match yield table values, but even before Age 100, the model predicts a decrease in L from that observed at Age 20. This early decrease in L is largely a function of differences in the way foliage and stem wood are allocated as trees grow, and

Table 5. 3-PG simulations set limits on the annual carbon balance and related variables (Columns 2–4) for different aged stands of Douglas-fir at Wind River, Washington with soil water storage capacity (θ_{max}) set at 200 mm. Tree mortality, net primary production (P_n), gross photosynthesis (P_g), autotrophic respiration (R_a), leaf litterfall (L_f), fine root production (R_f) and ecosystem production (P_e) and other values that appear in Columns 5–15 have units of g C m^{-2} $year^{-1}$. Fine-root production (Column 14) was determined by subtracting coarse-root production (R_c, Column 10), derived from an allometric equation (Table 3), from total root production (Σroots, Column 9) predicted by the model. Respiration from woody debris, including current tree mortality, is excluded from these calculations. The model estimates that tree mortality (representing suppressed trees averaging two thirds the diameter of surviving trees) contributed 40 Mg C ha^{-1} between 40 and 70 years to woody detritus and an additional 38 Mg C ha^{-1} between 70 and 150 years.

Age (years) (1)	L (m^2 m^{-2}) (2)	Stocking (trees ha^{-1}) (3)	Diam. (cm) (4)	Tree Mortality (5)	ΣP_n (6)	P_n Foliage (7)	P_n Stem (8)	P_n Σroots (9)	P_n R_c (10)	P_g (11)	R_a (12)	L_f (13)	R_f (14)	P_e (15)
20	8.1	1500	14	0	765	169	219	377	55	1629	863	169	322	275
70	6.9	694	32	68	741	143	231	367	62	1577	836	143	305	294
150	4.0	195	70	47	545	80	160	305	46	1160	615	80	259	207

limits imposed on the amount of biomass that can accumulate before self-thinning begins. Based on the power functions (2.436/2.167) presented in Table 3, wood accumulates 12% more rapidly than foliage as stem diameter increases. At the same time, the total biomass of Douglas-fir stem wood cannot exceed 220 Mg ha^{-1}, a value close to the 229 Mg ha^{-1} for stem biomass reported for all tree species in an old-growth forest at Wind River (M.E. Harmon et al. 1998, Oregon State University http://www.fsl.orst.edu/lter/pubs/permplot.htm). Combined with age-imposed reductions in photosynthesis, it is reasonable to expect Douglas-fir at Age 150 to support an L near that predicted (4.0). Thomas and Winner (2000) show that by Age 450, Douglas-fir further reduces its L to 2.5.

Reduction of Douglas-fir L at ages beyond 50 years allows for the development of other trees and shrubs in the understory. However, the total L for all vegetation in the stand remains nearly constant across a range in age classes from 20 to 450 years; as indicated by data collected by R.H. Waring and J. Mayo at 70 years (unpublished data), R. McKane (U.S. Environmental Protection Agency) at 150 years (personal communication), and at 450 years (Thomas and Winner 2000). This stability in total L across many stages in forest development serves as a reference in regional analyses using satellites to assess site productivity (Coops and Waring 2001a).

Sensitivity analyses revealed that as long as the model is constrained to reproduce stand dynamics, annual estimates of P_g were conservative as were values assigned to θ_{max}, soil fertility and α_c. In general, parameter values set for running the model at Wind River seem reasonable. Quantum efficiencies around 0.03 mol C mol^{-1} photon are typical of mixed hardwood stands growing on glacial till at Harvard Forest in Massachusetts (Waring et al. 1995). Values between 0.04 and 0.055 mol C mol^{-1} photon, however, are more typical of coniferous forests in the Pacific Northwest (Coops et al. 2001). The moderate soil fertility ratings and α_c used in modeling growth at Wind River suggest that nitrogen concentrations in foliage are likely to be about 1% or slightly higher (Waring 2000), a prediction close to foliage nitrogen concentration reported in 20-year-old Douglas-fir at Wind River (N. McDowell, unpublished data).

Experience indicates that some variables are consistently more critical than others in modeling stand growth. Repeated analyses have shown that the initial conditions set at Age 1 can vary widely without substantially changing the estimates of P_g or L after 20 years. Similarly, the maximum temperature for photosynthesis is relatively unimportant because humidity deficits and extended drought overwhelm the influence of high temperatures (Landsberg 1998). Also, because the preponderance of subfreezing conditions occur when solar radiation limits photosynthesis, analysis shows that gross photosynthesis would increase by only 16% if subfreezing conditions did not occur at Wind River. Whether the T_{min} is set at 0 or −2 °C makes a somewhat larger difference, particularly when θ_{max} = 100 mm because higher rates of photosynthesis are required in the late winter and early spring to maintain annual P_g (Figure 2).

The 3-PG model assumes constant ratios of P_n/P_g and R_a/P_g near 0.5, which is somewhat controversial (Medlyn and Dewar 1999), and values are likely to be lower under extreme climates (Ryan et al. 1997). In temperate coniferous forests, however, detailed gas-exchange analyses from young and old ponderosa pine forests (*Pinus ponderosa* Dougl. ex Loud.) support the ratios assumed in our analysis (Law et al. 2001). As a result, we find estimates by M.E. Harmon (unpublished observations) of a P_n/P_g ratio of 0.31 for the old-growth forest at Wind River to be surprisingly low. Eddy-flux analyses for the same old-growth forest indicate that variation for a 2-year period ranges between 1550 and 1590 g C m^{-2} year^{-1} and total respiration is estimated to be 1400 g C m^{-2} year^{-1} (K.T. Paw U, unpublished observations). These values compare closely with those estimated by 3-PG for Douglas-fir at Age 20 (P_g = 1544–1629 g C m^{-2} year^{-1} from Table 4; $R_a + R_h$ = 1354 g C m^{-2} year^{-1} from Table 5).

The allometric equations that we used to predict stem and coarse-root growth are nearly identical to those measured for Douglas-fir in the Pacific Northwest (Gholz 1982). The allometric equation derived to predict growth of foliage, however, differs substantially from that given by Gholz because his equations reflect net increment in foliage with increases in diameter, whereas the equation in 3-PG takes into account that a quarter of the total canopy leaf area turns over annually. Small increases in SLA could increase L; however, in stands as dense as those at Wind River, increases in $L > 5$ have little effect on photosynthesis or growth.

Where drought conditions occur, θ_{max} must be assessed. The most direct means of evaluating drought is through periodic measurement of predawn water potential (Law et al. 2000, Coops and Waring 2001a). As trees grow, their root systems extend to deeper soil horizons, tapping resources not available to younger plants. Also, where seepage or hydraulic redistribution of water occurs, predawn measurements of water potential define water availability better than most alternative methods. Measurements of predawn water potentials are recommended throughout multiple seasons to help further constrain model estimates.

Ideally, all process models should be tested at sites where there is continuous monitoring of both water vapor and carbon dioxide exchange. Detailed information, such as that being gathered at the Wind River Crane site, should clarify the appropriate θ_{max} through comparison of modeled values with seasonal measurements of transpiration and gross photosynthesis (see Law et al. 2000). On the other hand, once physiological process models have been calibrated with yield table data, they provide a basis for extrapolating across landscapes and allow consideration of a wide range of environmental changes on forest growth (Coops and Waring 2001b). Scaling these estimates to the landscape requires additional information on disturbance, changes in forest age and composition.

In summary, this paper demonstrates how the process model, 3-PG, when constrained by yield table information and long-term mean monthly climatic data, sets reasonable limits on ecosystem net carbon exchange. At the same time, 3-PG

has provided insights into which environmental variables deserve careful monitoring at Wind River, notably soil water holding capacity, soil fertility and maximum quantum-use efficiency.

Acknowledgments

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