INT. J. REMOTE SENSING, 2001, VOL. 22, NO. 18, 3797–3812

Estimation of potential forest productivity across the Oregon transect using satellite data and monthly weather records

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(*Received 8 March 1999; in final form 9 June 2000*)

Abstract. Detailed physiological and micrometeorological studies have provided new insights that greatly simplify the prediction of gross photosynthesis (P_G) and the fraction of production that goes into above-ground net primary production (NPP_A). These simplifications have been incorporated into a process-based forest growth model called 3-PGS (Physiological Principles Predicting Growth with Satellite Data). Running the model requires only monthly weather data, an estimate of soil texture and rooting depth, quantum efficiency (α), and a satellite-derived Normalized Difference Vegetation Index (NDVI) correlated with the fraction of visible light intercepted by foliage. The model was originally tested in Australia where seasonal variation in NDVI is extreme. In Oregon, NDVI varies much less seasonally and fully stocked coniferous stands maintain nearly constant canopy greenness throughout the year. We compared 3-PGS estimates of P_G and NPP_A across a steep environmental gradient in western Oregon where ground-based measurements at six sites were available from previous studies. We first tested the simplification in data acquisition of assigning the same quantum efficiency ($\alpha = 0.04\,\text{mol C/MJ APAR}$) and available soil water storage capacity ($\theta = 226\,\text{mm}$) to all sites. With these two variables fixed, the linear relation between predicted and measured P_G was $y = 1.45x + 2.4$ with an $r^2 = 0.85$. When values of θ were adjusted to match seasonal measurements of predawn water potentials more closely, and the quantum efficiency was increased to 0.05 mol C/MJ absorbed photosynthetically active radiation (APAR) on the most productive site, predicted and observed values of P_G and NPP_A were in near 1:1 agreement with $r^2 = 0.92$. Because maximum greenness (NDVI) reflects the seasonal availability of water, limits on soil water storage capacity can be inferred from calculated water balances derived following the onset of summer drought. The simplifications embedded in the 3-PGS model, along with the need to acquire only one mid-summer estimate of maximum greenness, make the approach well suited for assessing the productive capacity of forest lands throughout the Pacific Northwest, USA.

1. Introduction

The past 10–15 years have seen the development of a number of models designed to predict forest productivity on the basis of physiological processes. The models deal with processes at leaf (Nilson and Ross 1997), canopy (Martin and Aber 1996),

International Journal of Remote Sensing
ISSN 0143-1161 print/ISSN 1366-5901 online
http://www.tandf.co.uk/journals
DOI: 10.1080/01431160010014710

plot (Comins and McMurtrie 1993), region (Forest Biogeochemical Cycle—FOREST-BGC, Running and Coughlan 1988, Ollinger *et al.* 1997) and whole Earth (Prince and Goward 1995, Hunt *et al.* 1996) scales. To date, most of these models have been developed and used as research tools and have not been widely adapted or applied by forest managers. To make detailed process models more widely applicable to the general forestry community a number of important simplifications in model structure, data requirements, and output are required. In this paper we apply a model that was first developed in Australia to predict a number of variables relevant to forest managers, such as stem numbers, diameters, stand biomass and stem wood growth at annual time steps (Landsberg and Waring 1997). The stand level model was further simplified to enable the prediction of potential forest productivity across landscapes with satellite-derived data on vegetation greenness (Coops *et al.* 1998).

Our objective in this paper is to apply the landscape level model in western Oregon where evergreen coniferous forests dominate (Waring and Franklin 1979) and environmental conditions differ significantly from the vegetation, soils and climate in forested areas of most of Australia (Doley 1982). In making this comparison, we were fortunate in having available base meteorological, remote sensing, and physiological data collected as part of the US National Aeronautics and Space Administration (NASA) Oregon Transect Ecosystem Research (OTTER) project (Peterson and Waring 1994) as well as refined data from ongoing research at the OTTER sites since the completion of the project (Law *et al.* 1999).

1.1 *Description of the stand growth model*

Landsberg and Waring (1997) developed a simple process-based forest growth model called 3-PG (Physiological Principles for Predicting Growth) that predicts a number of variables relevant to forest managers. The model uses a monthly time step and requires values for total short-wave incoming radiation, monthly mean vapour pressure deficits, total monthly rainfall, and an estimate of soil water storage capacity and soil fertility.

Absorbed photosynthetically active radiation (APAR) is estimated from global solar radiation, derived if necessary from an established empirical relationship based on average maximum and minimum temperatures. The utilized portion of APAR ($\mathrm{APAR_U}$) is obtained by reducing APAR by an amount determined by a series of modifiers derived from constraints that cause partial to complete stomatal closure: (a) subfreezing temperatures; (b) high daytime atmospheric vapour pressure deficit (VPD); (c) depletion of soil water reserves. A soil water balance is calculated as the difference between total monthly rainfall, plus available soil water stored from the previous month, and losses through interception and transpiration define the limits on soil water availability. The modifiers take values between zero and one (no constraint) (see Landsberg 1986, McMurtrie *et al.* 1994, Runyon *et al.* 1994). Each month the fraction of APAR actually utilised ($\mathrm{APAR_U}$) is determined by the most constraining environmental variable.

Gross photosynthesis (P_G) is calculated by multiplying $\mathrm{APAR_U}$ by a canopy quantum efficiency coefficient (α) assumed to vary with soil fertility. A major simplification in the 3-PG model is that it does not require calculation of respiration or root turnover, but rather assumes, based on more than a dozen studies, that total net primary production (NPP) in temperate forests approximates a fixed fraction (0.45 ± 0.05) of P_G (Landsberg and Waring 1997, Waring *et al.* 1998).

The leaf area index (L) determines radiation interception and photosynthesis, and the foliage biomass is calculated from measured or derived values of specific leaf area (Pierce *et al.* 1994); it is updated at the end of each month as a balance between new growth of foliage and fixed (or variable) rates of leaf litterfall. The model partitions NPP into root and above-ground foliage and stem mass. The fraction of total NPP allocated to root growth increases from 0.2 to 0.6 as the ratio APARu/APAR decreases from 1.0 to 0.2. Soil fertility becomes an important variable in months when other environmental factors are favourable. Proportionally more NPP is allocated to roots on progressively less fertile soils, up to an annual maximum of about 0.6 of NPP. The model can be summarized as a series of procedural steps as follows.

(1) Estimates of total incoming solar radiation are derived from temperature data, if not directly available. From modelled L, APAR is calculated using Beer's law assuming the PAR is 0.5 of the incoming radiation.
(2) If frost occurs, APAR is reduced in proportion ot the days per month below freezing or selected subfreezing temperature (-2°C in this paper, based on the work of Running *et al.* 1975).
(3) The available soil water balance is calculated as the difference between precipitation, storage capacity of the soil, and water transpired by or evaporated from the vegetation, carrying stored soil water forward from month to month. The soil water modifier is based on the ratio of currently available to total available water.
(4) The VPD modifier is calculated for each month from average values of VPD (see Landsberg and Waring 1997 for a detailed discussion). Either the soil water, frost, or the VPD modifier applies—whichever is the most severe in any month.
(5) The monthly P_G is calculated by multiplying APARu by the canopy quantum efficiency (user-specified) which, in unfertilized evergreen trees, is usually between 0.03–0.05 mol C/MJ APAR or 1.65–2.74 g C/MJ APAR (Landsberg and Waring 1997).
(6) NPP is calculated as $0.45 \times P_G$ (Landsberg and Waring 1997, Waring *et al.* 1998).
(7) The ratio APARu/APAR determines the fraction of NPP allocated to roots, with the remainder available for above-ground growth. Under otherwise favourable conditions, soil fertility determines the fraction of NPP allocated to roots.

1.2. *Structure of the satellite-driven model to predict potential forest productivity*

Coops *et al.* (1998) modified the 3-PG model to allow it to be driven with satellite observations to assess seasonal changes in the vegetative canopy (3-PGS). Both forms of the model are driven with monthly weather data from which estimates of incoming radiation and atmospheric vapour pressure deficits can be derived (Bristow and Campbell 1984, Kimball *et al.* 1997).

In 3-PGS, the fraction of photosynthetically active radiation absorbed by the firest canopies (fPAR) is estimated from a satellite-derived index, based on the normalized difference between reflectances measured in the near-infrared and red wavelengths, termed the NDVI. This spectral vegetation index has been shown, both empirically and theoretically, to be related to the *f*PAR absorbed by vegetation canopies (Kumar and Monteith 1982, Sellers 1985, 1987, Goward *et al.* 1994).

Coops *et al.* (1998) utilized 3-PGS to predict above-ground NPP ($\mathrm{NPP_A}$) at eight contrasting forested sites in Australia and New Zealand and compared them with estimated above-ground NPP derived from field data. In 3-PGS, biomass partitioning between foliage and stems, as well as leaf litterfall, root decomposition and self-thinning routines present in the 3-PG model are not implemented. For these reasons the analysis was restricted to comparisons of $\mathrm{NPP_A}$. Likewise, data from the coarse-scale US National Oceanic and Atmospheric Administrations's (NOAA) Advanced Very High Resolution Radiometer (AVHRR) instrument was used, thus making the scale of analysis broad (8 km by 8 km), reducing the requirement (or possibility) for recognizing species, size classes, individual plot treatments or annual rates of mortality. There was a linear relation between $\mathrm{NPP_A}$ predicted by the model and on the ground estimates of wood production (usually $>75\%$ of $\mathrm{NPP_A}$) for (potentially) fully stocked, rapidly growing stands ($r^2=0.82$). The analysis also provided an assessment of the relative importance of climatic variables upon production.

Coops (1999) demonstrated that the 3-PGS model could be utilized in management applications by linking coarse-scale NOAA AVHRR data with Landsat Multi Spectral Scanner (MSS) data to incorporate ‘snapshots’ of the forest using high spatial resolution data obtained at specific intervals of time. This high-resolution remotely sensed data provided a number of additional key spatial variables such as current forest age class, and greater detail on soil fertility and water holding capacity which could extend the application of the 3-PGS model. $\mathrm{NPP_A}$ was predicted and compared with measured field data in a *Pinus radiata* plantation in southern New South Wales, Australia. There was excellent agreement ($r^2=0.84$) between predicted and actual forest productivity at the site. As a result of incorporating both fine- and coarse-resolution data, non-climatic factors such as disturbance, which occur within individual stands, could be accounted for in the model.

In applying the 3-PGS model to evergreen forests in the Pacific Northwest we recognized that the maximum seasonally observed NDVI remained essentially stable for these ecosystems throughout the year (Spanner *et al.* 1994). Because perennial vegetation of all kinds tends to reach comparable maximum value of NDVI during mid-summer, unless disturbed by grazing, fire or logging, the maximum NDVI can be assumed to be linearly related to the potential *f*PAR for the site (Goward *et al.* 1985, 1994, Franklin *et al.* 1997).

In this paper we initially apply the 3-PGS model using minimal *a priori* assumptions as to the canopy efficiency (α) and soil water holding capacity (θ) of the OTTER sites. A constant α for the year was assumed (0.04 mol C/MJ APAR) based on the work of Landsberg and Waring (1997) and a fixed value for available soil water storage (θ) of 226 mm, as suggested by Running (1994), was also assumed.

These initial values were then adjusted based on more detailed field observations at each site with α increasing to 0.05 mol C/MJ APAR at a single site and using more realistic values of θ derived independently for each of six sites along the Oregon translated by Gholz (1982).

2. Methods

2.1. *Vegetation*

The OTTER project was established to assess the potential of developing ecosystem simulation models that might be *completely parameterized and driven* with information acquired from satellite-borne sensors (Peterson and Waring 1994). The transect represents a steep environmental gradient that supports a wide variety of coniferous forests with a range in NPP (dry mass) of 3 to >25 Mg ha^{-1} yr^{-1} (Gholz 1982, Runyon *et al.* 1994). Edited datasets from the OTTER project have been made widely available through the Internet and three CD-Roms (produced by NASA Ames Research Center, Moffett Field, California 94035, USA).

The OTTER study covered six areas chosen along a 250 km west to east transect at approximately 44 degrees northern latitude. Table 1 provides details on the geographic location and physiographic features of the OTTER sites. The six sites were selected to include vegetation zones ranging from lush coastal forests to dry juniper woodlands.

Site 1 at Cascade Hotel represents a costal rain forest composed of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Site 2 is situated in the interior Coast Range near Corvallis and is dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with a scattering of Oregon white oak (*Quercus garryana* Dougl.) and Pacific madrone (*Arbutus menziesii* Pursh). Site 3 represents a dense, young forest of western hemlock and Douglas-fir situated on the west slope of the Cascades near the town of Scio. Site 4 at Santiam Press represents a subalpine forest made up of mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), western white pine (*Pinus monticola* Dougl. ex D. Don) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.). Site 5 represents nearly a pure stand of ponderosa pine (*Pinus ponderosa* Doug. ex Loud.) near the Metolius River in the rain shadow on the eastern slopes of the Cascades (Gholz 1982, Law *et al.* 1999). Site 6 represents a Juniper woodland (*Juniperus occidentalis* Hook.) near Redmond, Oregon. More detailed information on the vegetation is available in works by Franklin and Dyrness (1973) and by Gholz (1982).

2.2. *Soils*

Estimates of water storage capacity of the soils at each of the six sites were available from previous work by Gholz (1982) who extracted a number of intact soil cores from soil profiles down to a maximum depth of 1 m. Running (1994) suggested (from simulation modelling with FOREST-BGC) that at site 3 water must be provided through down-slope seepage (confirmed by observation) and at sites 2 and 5 some water must be available below 1 m depth to account for measured predawn water potentials (Runyon *et al.* 1994). Successful simulations depend on

Table 1. Location and physiography of Oregon transect sites[a].

Site Site name	1 Cascade Head	2 Corvallis	3 Scio	4 Santiam Pass	5 Metolius	6 Juniper
Latitude	45°03′	44°36′	44°40′30″	44°25′30″	44°29′	44°17′30″
Longitude	125°57′30″	123°16′	122°36′40″	121°50′20″	121°37′	121°20′
Elevation (m)	240	170	800	1460	940	930
Aspect (°)	120	160	325	—	—	—
Slope (%)	12	13	12	0	0	0

[a] Data from Peterson and Waring (1994) and Law *et al.* (1999).

accurate estimates of soil water holding capacity because exhaustion of available water limits leaf conductance and the rates of photosynthesis and transpiration. Running (1994) suggested that it would be more realistic to use an available soil water storage capacity of 226 mm for all sites than to assume water was available only from the upper 1 m of soil. This value appears to be suitable for a variety of coniferous sites in the continental United States. As a result, initial simulations were undertaken with a fixed value for θ of 226 mm. These values were then refined at each site by utilizing independent data from Gholz (1982) who determined predawn water potential during extended periods of drought (see Waring and Running (1998) for detailed descriptions of methodologies).

2.3. *Meteorological data*

Runyon *et al.* (1994) installed automatic meteorological stations close to each site to collect air temperature, relative humidity, precipitation and incident solar radiation data. Measurements were made every minute, integrated hourly, and stored in data loggers. Monthly means were calculated from the daily data. Table 2 provides a summary of the monthly meteorological data compiled for each site for 1990, available on the OTTER CD-Roms. There was no meteorological station at the Juniper site so data from the station at site 5 was substituted to provide radiation, humidity and temperature values for site 6, supplemented with precipitation data from the nearest weather station at Redmond, Oregon.

3-PGS incorporates routines, first developed by Bristow and Campbell (1984), and later incorporated into a more general model by Hungerford *et al.* (1989), which relate diurnal air temperature amplitude to atmospheric transmittance and potential radiation (Garnier and Ohmura 1968, Buffo *et al.* 1972, Swift 1976, Hungerford *et al.* 1989). However, as monthly total incoming short-wave radiation data were collected at the OTTER sites these data were utilized rather than predicting radiation from the temperature observations.

2.4. *Forest survey data*

Runyon *et al.* (1994) made measurements of fPAR at each site between noon and 14:00 hr local time with a sunlit ceptometer, which measured radiation (400–700 nm) transmitted through the tree canopy. Between 60 and 200 point measurements were made in order to accommodate variation at each site. Canopy trans-

Table 2. Climatic variation at Oregon transect sites in 1990[a].

Location	Annual rainfall (mm)	Minimum temperature in coldest month (°C)	Maximum temperature in warmest month (°C)	Average daily solar radiation ($MJ\,m^{-2}\,day^{-1}$)	Total no. of frost days (yr)	Maximum daily VPD (kPa)
Cascade Head	2743	−1.1	22.1	10.3	10	1.32
Corvallis	1042	−2.5	28.6	12.3	25	2.48
Scio	1128	−2.3	25.8	12.2	18	1.78
Santiam Pass	1403	−12.3	23.7	13.3	159	1.95
Metolius	545	−10.4	27.1	15.3	161	2.57
Juniper	220	−10.4	27.1	15.3	161	2.57

[a] Data from OTTER CD-Rom, Volume 1, NASA Ames Research Center Moffett Field, CA, USA.

mittance was calculated by dividing average below-canopy PAR by average incident PAR. Estimates of the leaf area index (L) of overstorey trees at each site were made using Beer's law, assuming an extinction coefficient of 0.5 (Runyon *et al.* 1994).

Above-ground biomass of the overstorey trees was another important variable determined at each site during the OTTER project. To obtain accurate estimates of above-ground biomass, a minimum of 20 prism plots was randomly located within each site and the diameter at breast height (1.4 m) of each tree greater than 5 cm was measured. Tree counts and basal area measurements allowed the relative contribution of each tree species to the total basal area of the site to be calculated. Stem, bark and branch biomass were computed using regression equations developed for each species from destructive sampling of key regional species in the Pacific Northwest (Gholz *et al.* 1979). Above-ground biomass was estimated by multiplying the measure of averaged weighted basal area for each species by the biomass regression equations. Per cent cover and NPP were estimated for the understorey components of the sites and, at all but site 6, contributed less than 10% of the total accumulated biomass of the stand (Law and Waring 1994).

NPP (defined as new foliage production, branch stem and root growth) was calculated for each site during the measurement period. New foliage production and litterfall measurements served as correlates to estimate seasonal changes in canopy leaf area and foliar biomass (Marshall and Waring 1986). New foliage production was also estimated by sampling five branches collected for determining specific leaf area at each site. Growth in woody biomass of tree stems and branches (including bark) was determined by measuring changes in tree diameter estimated from growth-ring analysis using incremental cores taken from selected trees of each species. Measurements were made of the current year's growth and that of the previous 5 years. Below-ground production was estimated from a correlation between measured annual CO_2 efflux for the soil and litterfall derived for a range of forests in different climatic zones (Raich and Nadelhoffer 1989, Runyon *et al.* 1994, Law *et al.* 1999).

Runyon *et al.* (1994) showed the contribution of climatic components in restricting the efficiency with which radiant energy is utilized by forest canopies at the six OTTER sites. At the coastal site, no limitations from freezing temperatures or drought were experienced, resulting in only a minor constraint (8%) from summertime VPDs. At the other extreme, the Juniper site was limited by nearly 80% in response to subfreezing temperatures through most of the winter, and high VPDs and soil drought during the summer. In the OTTER analysis only sites 2, 5 and 6 experienced soil drought conditions sufficient to limit annual production. Frost occurred for more than 150 days each year at sites 4, 5 and 6 (table 2). Vapour pressure deficit has wide ranging effects at all sites.

Williams *et al.* (1997) took the NPP data from Runyon *et al.* (1994) and made two independent estimates of gross photosynthesis (P_G), one with a detailed process model and the other from an annual carbon balance analysis that estimated autotrophic respiration associated with the growth and maintenance of foliage, stems and roots throughout the year. We used the annual carbon balance analyses (assuming dry mass = 50% C) in deriving values for P_G and NPP_A for the six sites (table 3).

At the Metolius pine site (site 5) a number of harvesting treatments were imposed as part of the OTTER project. As a result a significant proportion of the standing biomass was removed from the stand. In order to obtain data on the productive capacity of the site, OTTER vegetation data for that site were supplemented with

Table 3. Measured LAI, *f*PAR, NPP_A and calculated P_G at sites on the Oregon transect[a].

Site	1	2	3	4	5	6
Site name	Cascade Head	Corvallis	Scio	Santiam Pass	Metolius[b]	Juniper
LAI, projected	6.6	5.7	10.6	1.9	1.5	0.5
*f*PAR	0.96	0.94	0.99	0.61	0.53	
NPP_A ($Mg\,ha^{-1}\,yr^{-1}$) (dry mass)	10.5	11.6	17.5	5.1	2.7	1.2
Above-ground biomass ($Mg\,ha^{-1}$) (dry mass)	711	471	408	370	196	11
P_G ($Mg\,ha^{-1}\,yr^{-1}$) (dry mass)	28.0	33.3	48.1	17.6	13.0[c]	6.0
Water holding capacity (cm)	13.1	6.1	4.4	6.2	16.6	10.1

[a] From Runyon *et al.* (1994), Williams *et al.* (1997), Waring *et al.* (1998) and Gholz (1982).

[b] From Law *et al.* (1999).

[c] Calculated from ratios of NPP_A/NPP (0.89) and NPP/GPP (0.44) estimated for OTTER site 5 by Waring *et al.* (1997). Using similar assumptions regarding below-ground allocation (Raich and Nadelhoffer 1989), Law *et al.* (1999) estimated P_G to be $14.4\,Mg\,ha^{-1}\,yr^{-1}$ for 1996, an exceptionally wet year.

data from an adjacent site established by Law *et al.* (1999) which was undisturbed. Subsequently, table 3 combines OTTER data for sites 1–4 and 6 and Law *et al.* (1999) data for site 5.

Ongoing research at site 5 has measured α to be 0.04 mol C/MJ APAR (Law *et al.* 1999) using eddy-flux studies of CO_2 exchange and detailed curvette measurements (Arneth *et al.* 1998, Law *et al.* 1999), indicating that the default value of α was appropriate at that site. At site 3, the most productive on the transect, α was independently measured using similar methods to be 0.05 mol C/MJ APAR (Dr Barbara Bond, Oregon State University, 1999, Personal communication). In the application of 3-PGS we first apply the model with default values of α (0.04 mol C/MJ APAR) at all sites and then increase α to 0.05 mol C/MJ APAR at site 3. Similarly, we initially assume a default value for available soil water storage (θ) of 226 mm as suggested by Running (1994), and later compare predictions of P_G and NPP_A with more realistic values of θ for each of the six sites along the Oregon transect as calculated by Gholz (1982).

2.5. *Satellite data*

The current AVHRR sensor on board the NOAA species of weather satellites provides data in five spectral channels from the visible, near-infrared and thermal regions of the spectrum (Kidwell 1988). The archive accumulated from these sensors over 15 years has become a major resource in global change research following efforts by NOAA and NASA to produce an edited ‘Pathfinder’ dataset (Agbu and James 1994).

The interpretation of satellite imagery to produce vegetation attributes can be a complex problem, with multiple factors affecting the signal recorded by the satellite sensor. Despite these difficulties, there are some clear relationships between photosynthetic behaviour of forest vegetation, regardless of species or age, and the spectral response of the vegetation in a number of key spectral wavelengths, in particular, the visible and near-infrared. The NDVI (derived from the differences between reflectances measured in the near-infrared and red wavelengths, divided by the sum of these two reflectances) is a commonly applied index and, although a full explanation of the observed correlation between NDVI and canopy properties is still to be fully achieved, studies have shown that there is a linear, or near linear, relationship between the fraction of PAR absorbed by vegetation canopies and the NDVI (Kumar and Monteith 1982, Sellers 1985, 1987, Goward *et al.* 1994). There are several possible limitations to such an inference but it appears that an approximation to the *f* PAR, integrated over the diurnal cycle, can be derived from NDVI measurements and incoming solar radiation (Prince and Goward 1995).

NDVI values for each of the six sites were extracted from the monthly 1990 Pathfinder dataset. The maximum NDVI values for each site for 1990 are given in table 4. To predict *f* PAR from NDVI we used the equation developed by Goward *et al.* (1994), relating OTTER ground measured *f* PAR and satellite AVHRR NDVI measurements. The equation is:

$$f\mathrm{PAR}\ (\%) = (121\,\mathrm{NDVI}) - 4.0 \qquad (1)$$

where NDVI is the atmospherically corrected NDVI from the Pathfinder dataset.

3. Results

3.1. *Normalized Difference Vegetation Index*

The pathfinder maximum NDVI (8 km × 8 km spatial resolution) values for the OTTER sites are shown in figure 4. Comparison of these values and the 1 km NDVI values presented in Goward *et al.* (1994) indicate that both the seasonal trends as well as maximum NDVI values were similar. Table 4 also shows the *f* PAR values collected at each of the OTTER sites as presented in Goward *et al.* (1994) and supplemented by data provided by Law *et al.* (1999) for site 5. There is a strong correlation between the Pathfinder NDVI data and the field measured *f* PAR data with an explained variance of 93%. This relation is more significant than the one originally reported by Goward *et al.* (1994) using a single AVHRR scene due to more representative field *f* PAR values collected by Law *et al.* (1999) at site 5 than those collected as part of OTTER (as discussed by Goward *et al.* (1994)).

3.2. *Model predictions of gross photosynthesis and above-ground net primary production*

A combination of simulations run with the 3-PGS model are presented in table 5. For ease of comparison, independent estimates of P_G (as modelled by Williams *et al.* (1997)) and $\mathrm{NPP_A}$ (measured) values from table 3 are listed again. In its default run

Table 4. Maximum values of NDVI recorded in mid-summer from 8 km × 8 km area around OTTER transect sites, along with *f* PAR data acquired by Goward *et al.* (1994).

Site Site name	1 Cascade Head	2 Corvallis	3 Scio	4 Santiam Pass	5 Metolius	6 Juniper
f PAR	0.96	0.94	0.99	0.61	0.53[a]	0.22
Maximum NDVI 1990	0.72	0.69	0.64	0.49	0.51	0.20

[a] Data from Law *et al.* (1999) were substituted for OTTER site 5, because the latter was subjected to reduced overstorey leaf area index associated with blowdown and subsequent logging.

Table 5. Comparison of 3-PGS modelled predictions of NPP_A and P_G under fixed (Case I) and variable (Case II) assumptions of α and θ with observed or calculated values (table 3).

Site	Quantum efficiency (molC/mol APAR)	Available soil H_2O storage (mm)	3-PGS modelled NPP_A (Mg $ha^{-1} yr^{-1}$)	Observed NPP_A (Mg $ha^{-1} yr^{-1}$)	3-PGS model P_G (Mg $ha^{-1} yr^{-1}$)	Calculated P_G (Mg $ha^{-1} yr^{-1}$)
CASE I						
1	0.04	226	10.3	10.5	31.5	28
2	0.04	226	8.1	11.6	18.0	33.3
3	0.04	226	10.3	17.5	22.9	48.1
4	0.04	226	5.7	5.1	12.7	17.6
5	0.04	226	3.6	2.7	13.5	13
6	0.04	226	2.7	1.2	9.5	6
CASE II						
1	0.04	500	11.2	10.5	33.2	28
2	0.04	226	8.1	11.6	25.1	33.3
3	0.05	500	15.6	17.5	47.3	48.1
4	0.04	500	5.7	5.1	19.1	17.6
5	0.04	116	3.2	2.7	12.0	13
6	0.04	100	1.9	1.2	7.1	6

3-PGS predictions of P_G were compared with estimated P_G at each of the OTTER sites. With fixed values of quantum efficiency (α) of 0.04 mol C/MJ APAR and available soil water storage (θ) of 226 mm, predicted and estimated gross photosynthesis (P_G) differed substantially at the upper limits, and the regression equation has a large negative intercept (figure 1).

A second 3-PGS simulation was undertaken, this time replacing the default available water holding capacity values with more realistic values of θ and α and site 3 was increased from 0.04 to 0.05 mol C/MJ APAR. Figure 2 shows the predictions of 3-PGS P_G were much improved when compared to field-based observations, with a near 1:1 agreement between predicted and estimated P_G with an r^2 of >0.92.

The capability of 3-PGS to allocate above- and below-ground NPP correctly, once realistic values of α and θ were supplied, is shown in figure 3. Considering that species-specific allometric relations were applied in deriving NPP_A values for each

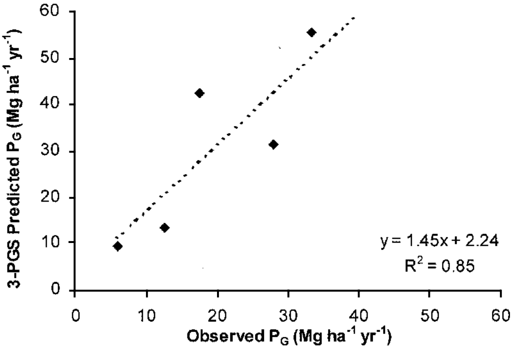

Figure 1. Gross photosynthesis (P_G) in dry mass equivalent predicted with 3-PGS using a fixed quantum efficiency (0.04 mol C/MJ APAR) and available soil water storage (226 mm) at all six sites on the Oregon transect showed a good correlation with measured values, but not a 1:1 relationship.

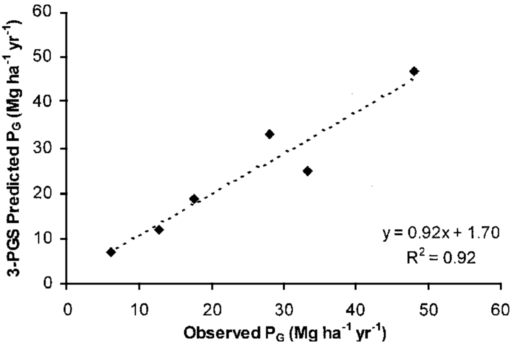

Figure 2. Gross photosynthesis (P_G) predicted with 3-PGS was in nearly 1:1 agreement with measured values when quantum efficiency was raised to 0.05 mol C/MJ APAR at the most productive site (5) and available soil water storage was set at appropriate values in reference to measured predawn water potentials reported by Runyon *et al.* (1994).

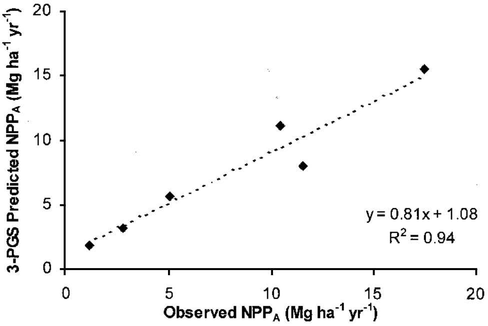

Figure 3. Predicted above-ground net primary production (NPPA) with 3-PGS closely agreed with measured values at the six Oregon transect sites when the quantum efficiency was raised to 0.05 mol C/MJ APAR at the most productive site (site 3) and available soil water storage values were adjusted to approach values associated with measured predawn water potentials at the end of summer drought (Runyon *et al.* 1994).

of the six sites, the 1:1 agreement between 3-PGS predictions and those measured is extremely encouraging ($r^2 = 0.93$).

4. Discussion

4.1. *Modelling*

The benefits of ecosystem modelling include the capability of extending traditionally point-based data acquired at scattered locations across landscapes, and to incorporate generalized biophysical and physiological principles into predictable and scalable relationships. Models such as 3-PGS owe a debt to those who have previously developed fully fledged ecosystem models that combine water, carbon and nutrient cycling. A few models like FOREST-BGC (Running and Coughlan 1988, Running and Gower 1991) and PnET (Aber and Federer 1992, Aber *et al.* 1995) have been successfully tested across regions. One of the most helpful aspects of these models is their ability to generate predictions of maximum L under any specified environment. In drought-prone areas, model simulations quickly provide limits on reasonable values of soil water storage capacity (Running 1994).

The 3-PGS model is much less comprehensive than the ecosystem simulation models mentioned above as it does not include heterotrophic respiration or mineral cycling. It has, however, the advantage of not requiring calculation of autotrophic respiration through the assumption of a constant ratio of NPP/P_G for temperate forests. Ryan *et al.* (1997) indicated that boreal forests may also show a nearly constant ratio of NPP/P_G but the value is much lower (about 0.3) due to restricted photosynthesis in the spring.

For real progress in constructing more realistic allocation models, year-round eddy-flux studies of CO_2 exchange, combined with detailed curvette measurements, are required (Arneth *et al.* 1998, Law *et al.* 1999). Although it is possible to increase greatly the detail in the canopy photosynthetic component in 3-PGS, we prefer to keep the model as simple as possible and balanced in the amount of detail included in all the major processes (Landsberg and Coops 1999). In this sense, we are most limited by our inadequate knowledge of how various environmental factors affect root allocation.

4.2. *Remote sensing*

In this paper we made the assumption that over a 8 km × km area, tree cover could be quite variable but *f*PAR inferred from satellite-derived measurements of NDVI would be similar, regardless of the present mix of vegetation. We realize, of course, that considerable topographic variation occurs in mountainous regions and that a more desirable scale for analysis would be 1 km^2 or less. With the launch of the next generation of NASA's Earth Observing System (EOS), spectral and spatial resolution will be much improved, and data products should be more readily available to both scientists and the public (Running *et al.* 1994).

In driving 3-PGS, we relied on meteorological data acquired at the sites. The OTTER study demonstrated that incoming solar radiation (total and PAR), ambient air temperatures and vapour pressure deficits could all be obtained from measurements acquired with sensors on NOAA weather satellites with surprisingly good accuracy (Goward *et al.* 1994). Climatic variables derived through remote sensing provide an important means of validating extrapolations of meteorological variables from scattered recording stations.

The most difficult variable to assess is the available water storage capacity of the soil. Nemani and Running (1989) used NDVI measurements from satellites and an ecosystem simulation model to provide reasonable constraints on the amount of water stored in soils in drought-prone regions. Nemani *et al.* (1993) combined NDVI with thermal infrared estimates of surface temperature to develop a drought index that further aids in modelling NPP and P_G from space globally (Prince and Goward 1995).

One might hope to obtain remotely sensed estimates of canopy quantum efficiency from satellite sensors through a correlation with chlorophyll concentrations and content (Waring *et al.* 1985). Unfortunately, assessment of canopy biochemistry requires fine-resolution spectrometry and rigorous attention to atmospheric corrections. To date, only aircraft have carried such fine-resolution spectrometers (Matson *et al.* 1994, Smith and Curran 1995, Martin and Aber 1997), however the successful launch of EO-1 in 2000 offers significant new potential to predict canopy quantum efficiency from satellite sensors.

4.3. *Applications*

In this paper we combined general physiological principles into a model that can be driven, almost entirely, from readily available monthly weather records and satellite-derived images of changing greenness across landscapes. Minimal information is required on soils and vegetation and when detailed field-based data are available the model can be utilized to help provide valuable information on the available soil water holding supply. Using one year's data, we obtained excellent agreement with field measurement of forest growth collected as part of the OTTER project and related studies. These comparisons indicate that 3-PGS should be able to provide reasonable estimates of forest productive capacity across the Pacific Northwest, USA. The opportunity exists to expand these analyses to include decades of data, and thereby evaluate longer term implications of climatic variation and other factors affecting forest productivity.

Acknowledgments

We wish to acknowledge Drs Sam Goward, Phil Ryan and Steve Running for useful discussions in the development of the model. We thank Drs John Raison, Trevor Booth and David Whitehead for additional discussions and Drs Miko Kirschbaum and Mike Battaglia who provided valuable comments on the manuscript.

Part of this research (N. Coops) was undertaken at the Department of Forest Science, Oregon State University, Oregon whilst Dr Coops was on leave from CSIRO Forestry and Forest Productions, Australia. R. H. W. acknowledges with thanks support for a CSIRO McMaster Fellowship, support on sabbatical from his own department and a grant from the Forestry and Forest Productions Research and Development Corporation, Australia. A component of the research reported in this article was supported by funds from the National Aeronautics and Space Administration (NASA), Grant Number NAG5-7506. Additional information on this research is available via the Internet (http://www.fsl.orst.edu/bevr/or http://www.ffp.csiro.au/nfm/mdp/).

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