ELSEVIER

Forest Ecology and Management 104 (1998) 113–127

Forest Ecology and Management

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

N.C. Coops [a,*], R.H. Waring [b], J.J. Landsberg [c]

[a] *CSIRO Forestry and Forest Products, P.O. Box E4008, Kingston, ACT 2604, Australia*
[b] *Oregon State University, College of Forestry, Corvallis, OR 97331, USA*
[c] *CSIRO Land and Water, P.O. Box 821, Canberra, ACT 2614, Australia*

Received 4 February 1997; accepted 18 August 1997

Abstract

To evaluate the effects of spatial variation in climate and soils on forest productivity across broad regions requires an approach that can be widely applied and tested. Detailed physiological and micro-meteorological studies have recently lead to new insights that greatly simplify the prediction of above-ground net primary production (NPP), a variable closely related to conventional measures of forest growth, such as Mean Annual Increment (MAI) of stemwood. We applied these simplifications in a monthly time-step model driven by estimates of the fraction of light intercepted by green canopies, derived from near-infrared and red reflectances monitored from National Oceanographic and Atmospheric Administration (NOAA) weather satellites, and from equations utilising local temperature and rainfall records. Absorbed photosynthetically active radiation (APAR) was estimated from global solar radiation, derived from an established empirical relationship based on average maximum and minimum temperatures, and from a linear relation with the satellite-derived normalised difference vegetation index (NDVI) which represents the photosynthetic capacity of all vegetation within a cell for a given month and is often correlated with the fraction of PAR absorbed (fPAR). Monthly values of environmental constraints on productivity were expressed by modifiers calculated from the vapour pressure deficit (VPD) of the atmosphere, soil water deficit, or frost. This procedure leads to estimates of utilisable radiation (APARu). Gross primary production (GPP) was calculated by multiplying APARu by a constant canopy quantum efficiency (1.8 g C MJ^{-1}) and total NPP has been shown, in a number of studies, to approximate 0.45 ± 0.05 of GPP. 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. Above ground NPP (NPP_A) predicted by the model was compared with estimated above-ground NPP derived at eight contrasting forested sites in Australia and New Zealand. There was a linear relation between predicted NPP_A and measured wood production ($r^2 = 0.82$). The analysis also provided an assessment of the relative importance of various climatic variables upon production which varied extensively from site to site. © 1998 Elsevier Science B.V.

Keywords: Ecosystem remote sensing; AVHRR; Eucalypt forest; Net primary productivity (NPP); Fraction of photosynthetic active radiation (fPAR)

---

[*] Corresponding author.

PII S0378-1127(97)00248-X

1. Introduction

The global importance of forests has never been in question, but interest in them has been increasing in recent years because of their obvious commercial value, importance in maintaining regional biodiversity and the hydrologic integrity of catchments and, in part, because changes in composition and growth of forests reflect responses to longer term variation in climate and atmospheric properties. As a result of this interest the regional distribution of major forest (and other vegetation) types, has received increasing attention, with improved definition through satellite-derived data (Matthews, 1983; Prentice, 1990; Townshend et al., 1991; Running et al., 1994b). Seasonal and monthly photosynthetic activity, evapotranspiration, and growth have also been estimated (Running et al., 1994b; Prince and Goward, 1995), based on the current comprehensive satellite coverage of the Earth's surface.

Our understanding of how forests operate is improving as detailed physiologically-based process models are tested at sites where CO_2 and water vapour exchange have been continuously monitored throughout one or more years (Aber et al., 1996; Hollinger et al., 1994; Lloyd et al., 1995; Cienciala et al., 1997), and through experimental manipulations where most components of stand growth are assessed across a range of treatments (Benson et al., 1992; Ryan et al., 1996). A variety of closely related process models now exists which provide increasingly reliable estimates of gross photosynthesis (or gross primary production, GPP), autotrophic respiration, and the residual, net primary production (NPP). These include FOREST-BGC (Running and Coughlan, 1988; Running and Gower, 1991), BIOMASS (McMurtrie et al., 1992) and TREGROW (Weinstein et al., 1991). A major challenge remains to work out the magnitude and mechanisms by which NPP is differentially allocated above or below-ground, but even in this area considerable progress has been made (Runyon et al., 1994; Beets and Whitehead, 1996; Ryan et al., 1996, Landsberg and Waring, 1997).

Some simplifying principles have emerged from these detailed physiological studies and modelling efforts, as summarised by Landsberg and Waring (1997): (1) canopy photosynthesis can be estimated as a simple function of absorbed photosynthetically active radiation (APAR); (2) climatic constraints (frost, drought, and vapour pressure deficits) reduce the fraction of APAR (fPAR) that can be utilized for photosynthesis, so we can work with effective, or utilisable, radiation (APARu); (3) an estimate of gross photosynthesis (GPP) can be obtained by multiplying APARu by a constant canopy quantum conversion efficiency (1.8 g C MJ^{-1} APARu); (4) NPP for a wide range of forests is (approximately) a fixed fraction (0.45 ± 0.05) of GPP; and (5) the fraction of NPP allocated to roots increases with environmental limitations (drought, vapour pressure deficit (VPD) and soil fertility). Based on these principles, Landsberg and Waring (1997) developed a simplified model known as 3-PG (Physiological Processes Predicting Growth) which is designed to predict the growth, diameter distribution, and annual mortality for individual forest stands of known species composition. (See Section 2 for more detail and Landsberg and Waring (1997) for a complete description.)

In this paper, we use a modified version of 3-PG, with remotely-sensed data, to assess productivity at a range of forest sites in Australia and New Zealand where independent measures of stemwood production were also available. The analysis was limited to a single year (1987) to permit direct comparison with regional estimates of NPP generated by Prince and Goward (1995) but, since estimates of forest productivity are generally based on data collected over many years, at intervals of years, the modelled estimates of NPP are compared with long-term average values of forest productivity. Data from National Oceanographic and Atmospheric Administration (NOAA) weather satellites provided monthly estimates of landscape greenness derived from near-infrared and red reflectances, which are closely related to the fPAR that is absorbed by vegetation. The scale of analysis was, of necessity, broad (8×8 km), so there was no requirement (or possibility) for recognising species, size classes, or annual rates of mortality. Our objective in making this analysis was to provide a means of assessing forest production across regions, determining the major climatic limitations and, with multi-year coverage, accounting for the effects of extreme conditions that might greatly alter production and increase the danger of disturbance from fire, insects, and disease.

2. Development of the model

2.1. Physiological processes predicting growth (3-PG)

The simple process-based forest growth model called 3-PG, developed by Landsberg and Waring (1997) uses a monthly time step and requires values for total short-wave incoming radiation, monthly mean VPD, total monthly rainfall, an estimate of soil water storage capacity, and some estimate of fertility. The model generates a number of growth parameters that are directly relevant to forest managers, such as estimates of Diameter at Breast Height (DBH), stand volume and biomass and projected leaf area index (L^*).

The 3-PG model essentially consists of two major parts:(1) Biomass production: net radiation (required for the Penman–Monteith equation), is calculated from incoming solar radiation and standard empirical relationships that take into account albedo. GPP is calculated from APARu and the canopy quantum efficiency coefficient, and total NPP obtained as a simple fraction of GPP. Initial values of stem, foliage and root mass are provided and L^*, the key parameter determining radiation interception and photosynthesis, is calculated from specific leaf area values (White and Running, 1994). APARu is obtained by reducing APAR by an amount determined by a series of modifiers derived from constraints imposed by: (a) stomatal closure, caused by high day-time atmospheric VPDs (see Landsberg and Waring, 1997); (b) soil water balance, which is the difference between total monthly rainfall, plus available soil water stored from the previous month, and transpiration, calculated using the Penman–Monteith equation with canopy conductance modified by L^* of the forest (Kelliher et al., 1995); and (c) the effects of sub-freezing temperatures using a frost modifier calculated from the number of frost days per month. The modifiers take values between 0 (system ‘shutdown’) and 1 (no constraint) (see Landsberg, 1986; McMurtrie et al., 1994; Runyon et al., 1994). They are multiplicative, except in the case of VPD and soil moisture, when the factor causing the greatest constraint is applied. (2) Carbon allocation: the model uses the well defined self-thinning relationship based on the $-3/2$ power law (Drew and Flewelling, 1977) as the basis for a population sub-model (which was not utilised in this study), and equations based on differentiation of allometric relationships to determine the allocation of carbon to foliage and stems after the fraction of total NPP allocated to roots has been determined from an evaluation of constraints of photosynthesis and the inherent soil fertility. Stem diameter (DBH) conventionally is the independent variable in the allometric equations. DBH and L^* are updated at the end of each month. Soil fertility was included in the version of 3-PG described by Landsberg and Waring (1997), but only applied in a few test cases by assuming that trees would allocate increasing proportions of NPP to roots on progressively less fertile soils, up to a maximum of about 0.6 of NPP.

2.2. The 3-PGS model

We have modified the original 3-PG model to allow remotely sensed observations to be utilised as inputs to it. The modified model is called 3-PGS, the S symbolising the use of satellite data in the model framework. In this paper we compare above-ground NPP ($\mathrm{NPP_A}$) predictions made with 3-PGS for forest sites in Australia and New Zealand with actual NPP values as derived from standard forest inventory data collected by forest managers. The analysis was limited to a single year (1987) and was restricted to comparisons of $\mathrm{NPP_A}$. The biomass partitioning procedures in 3-PG were not used and leaf fall, root decomposition and self-thinning routines were not implemented.

The fraction of PAR absorbed by the forest canopies (fPAR) was estimated from a satellite-derived reflectance index—the normalized difference between reflectances measured in the near-infrared and red wavelengths, termed the normalised difference vegetation index (NDVI). This spectral vegetation index has been shown, both empirically and theoretically, to be related to the fPAR absorbed in vegetation canopies (Kumar and Monteith, 1982; Sellers, 1985, 1987). Although there are several possible limitations to such an inference it appears that an approximation to absorbed PAR, integrated over the diurnal cycle can be derived from the NDVI measurement and incoming solar radiation (Prince and Goward, 1995). We obtained monthly estimates of NDVI for 8 × 8 km areas from the NOAA Advanced Very High Resolution Radiometer (AVHRR) satellite Pathfinder dataset (see Section 3.5).

3. The project

3.1. Site data

We were able to obtain long-term forest inventory data from either agencies or private firms in New South Wales, Victoria, Tasmania, and New Zealand (see map: Fig. 1), covering areas which were large enough to include stands of reasonably homogeneous forest at least 8 × 8 km—approximating the resolution of the NOAA AVHRR satellite dataset. Whilst there can be extensive variation in species composition, growth rates, soil fertility and terrain within each cell we attempted to minimise this by centering the cell (i) over the largest number of field measurement sites possible, (ii) where the terrain was relatively uniform and (iii) over areas (as far as possible) completely covered by forest. We toured these areas and evaluated the forests visually, with forest officers from each region. Table 1 provides information about the location, elevation, and dominant species present at the eight selected forest sites.

In all cases data from representative survey plots were available within the chosen 8 × 8 km areas. In the case of pine and eucalyptus plantations, much more detailed data bases on forest growth were available, but their spatial extent was much smaller than that of the native eucalypt forest and there was concern that these plantations did not completely occupy the pixels of the NOAA AVHRR satellite pathfinder dataset. This issue is addressed in Section 3.5.

3.2. Soil data

An estimate of the maximum available soil water storage capacity was required for each site. This is

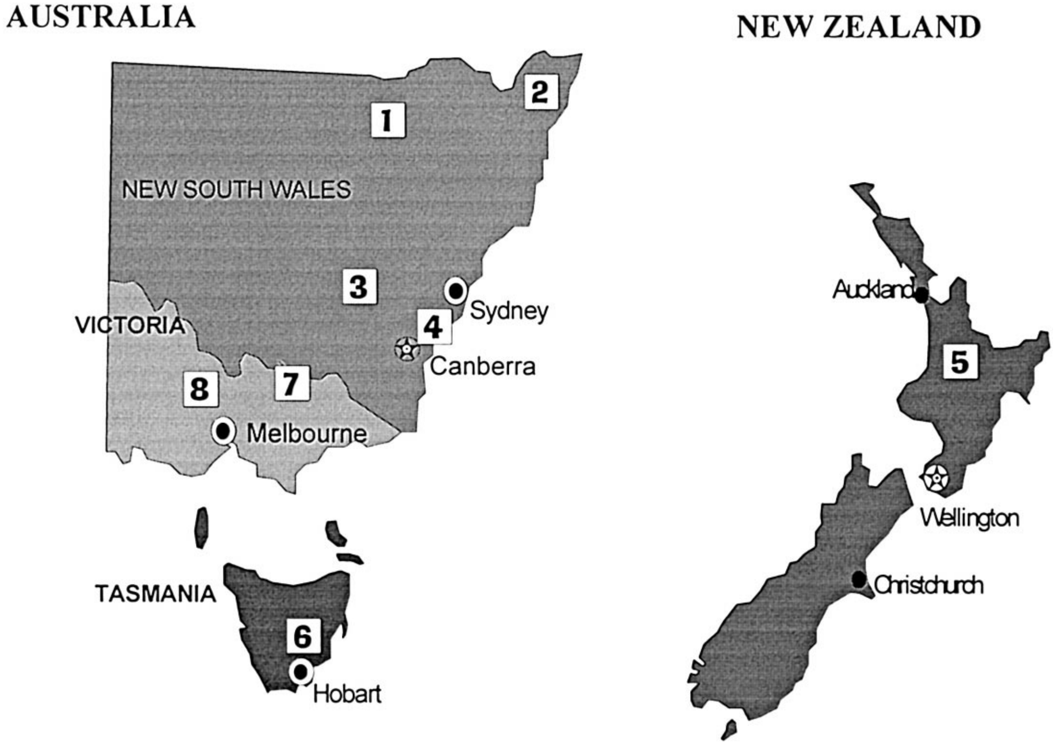

Fig. 1. Map indicating locations of the eight forest sites in Australia and New Zealand. 1: Pilliga, 2: Lorne, 3: Tumut, 4: Kioloa, 5: Haupapa, 6: Picton, 7: Tarra Bulga, 8: Wombat.

Table 1
Locations, elevation and dominate species at the eight sites used in 3-PGS model

Location	Longitude (°)W	Latitude (°)S	Elevation (m)	Dominant species
Pilliga region, NSW	149.16	30.75	266	*Callitris glaucophylla*
Lorne State forest, NSW	152.63	30.58	228	*E. pilularis*
Tumut region, NSW	148.5	35.25	1100	*Pinus radiata*
Kioloa State forest, NSW	150.3	35.57	125	*E. maculata*
Haupapa region, NZ	176.42	38.50	580	*Pinus radiata*
Picton region, Tasmania	146.81	43.08	400	*E. obliquia*
Tarra Bulga region, Vic	146.56	38.43	101	*E. regnans*
Wombat State forest, Vic	144.21	37.45	700	*E. obliqua*

dependent on the water holding characteristics of the soils and the rooting depth of the trees. Values between 50 and 250 mm have been reported in the literature. The 3-PG model allows the soil water modifiers to be calculated with coefficients representing four different soils types: sand, sandy loam, clay loam and clay. For each of the eight forest areas the soil type was determined and an approximate value for the maximum water storage capacity made on the basis of soil series information (Australian Society of Soil Science, 1985), local knowledge, and field evaluations by RHW and JJL. Information about the soils of each study area is given in Table 2.

3.3. Meteorological data

Meteorological data were averaged over each of the 8 × 8 km cells encompassing each study site. Mean monthly rainfall and temperature estimates were derived for each site from the ESOCLIM package (Hutchinson, 1984) using the mean elevation of the cell. These monthly estimates were then scaled by actual 1987 meteorological conditions as recorded by the nearest meteorological climate station. The number of frost days for each month were taken directly from the nearest climate station. Climatic conditions for 1987 in the study areas are given in Table 3.

Incoming solar radiation was not recorded at these stations so procedures were written into 3-PGS by which radiation could be estimated from empirical relationships (Goldberg et al., 1979). We used a technique first developed by Bristow and Campbell (1984) and later incorporated into a more general model by Hungerford et al. (1989), which relates diurnal air temperature amplitude to atmospheric transmittance. Site elevations are specified and clear sky transmissivity calculated for each site, assuming a clear sky transmissivity at mean sea level of 0.65 which increases by 0.008 per meter of elevation. Final atmospheric transmittance is calculated as an exponential function of the diurnal temperature amplitude of the site (Bristow and Campbell, 1984). A model of potential radiation was used to calculate direct and diffuse radiation which accounts for latitudinal differences (Garnier and Ohmura, 1968; Buffo et al., 1972; Swift, 1976; Hungerford et al., 1989).

Table 2
Soil and satellite inputs at the eight sites used in 3-PGS model

Location	Soil type	Est. water holding capacity (mm)	NDVI 1987 minimum	NDVI 1987 maximum
Pilliga	Sand	20	0.36	0.46
Lorne	Clay Loam	136	0.52	0.64
Tumut	Clay Loam	200	0.38	0.67
Kioloa	Sand	84	0.36	0.61
Haupapa	Sand	440	0.44	0.67
Picton	Clay	170	0.15	0.66
Tarra Bulga	Clay Loam	150	0.37	0.60
Wombat	Clay Loam	136	0.37	0.64

Table 3
1987 climatic conditions at the eight forest sites used in 3-PGS model

1987						
Location	Yearly rainfall (mm)	Minimum temperature in coldest month (°)	Maximum temperature in warmest month (°)	Average daily solar radiation (MJ m^{-2} day^{-1})	Total no. of frost days	Maximum daily VPD (mbar)
Pilliga	485	2.9	35.7	18.7	12	36.8
Lorne	1322	7.5	28.2	11.5	0	15.1
Tumut	1225	−2.6	25.6	23.4	120	21.9
Kioloa	886	5.3	24.8	12.5	0	13.3
Haupapa	1153	2.9	21.5	16.7	9	12.0
Picton	2526	−1.2	20.7	18.6	50	14.3
Tarra Bulga	1141	1.9	23.6	17.0	26	16.6
Wombat	1090	2.7	22.7	18.1	29	15.7

The final estimate of incoming solar radiation was then calculated as the above atmosphere radiation reduced by the atmospheric transmittance. The procedure accounts for clouds, water vapour, pollutants and other factors that reduce clear sky transmissivity. Daily incoming solar radiation is then computed by multiplying incoming solar radiation by day length (computed as the time between sunrise and sunset which is date and latitude dependent). PAR is assumed to be approximately 0.5 of the incoming solar radiation. The coarse spatial resolution of the satellite data allowed the assumption that site surfaces were flat. In situations where finer scale analyses are of interest, models exist to account for radiation on different slopes and aspects, as well as the effects of shading from adjacent slopes (Hungerford et al., 1989).

To assess the accuracy of the predicted incoming solar radiation estimated from minimum and maximum temperature we selected three sites where radiation data as well as appropriate temperature data were available for periods of at least three years: Kioloa State Forest, NSW, Haupapa region on the North Island of New Zealand and Canberra, ACT (Table 4). The results of the comparison are shown in Fig. 2, which indicates that the values of incoming solar radiation calculated from temperature data provide very good estimates of measured values (Table 5) with the predicted values explaining over 90% of the actual recorded incoming solar radiation at the sites with an average standard error of 1.0 MJ m^{-2} day^{-1}.

3.4. Forest growth data

Two major vegetation types dominate across the eight sites. Most of the native forests are dominated by eucalypts of various types, with the exception of the Pilliga, where cypress white pine (*Callitris glaucophylla*) is the dominant species, with scattered eucalypts still present. Native forests sometimes have a wide range of age classes within stands, as a result of their inherent ecology or because of different disturbance histories. Forest growth estimates therefore vary considerably with stand age and by site quality across the range of study sites, but plantations of *Pinus radiata* and *Eucalyptus regnans* are of uniform age and spacing, and therefore better

Table 4
Sites used for comparison of actual versus solar incoming radiation as estimated from minimum and maximum temperature

	Elevation (m)	Dates of comparison	Minimum temperature in coldest month (°)	Maximum temperature in warmest month (°)
Canberra	571	3-yr average (temperature); 80-yr average (radiation)	−2.1	29.5
Haupapa	400	1987 (temp. and rad.)	2.9	21.5
Kioloa	20	1987 (temp. and rad.)	5.9	23.8

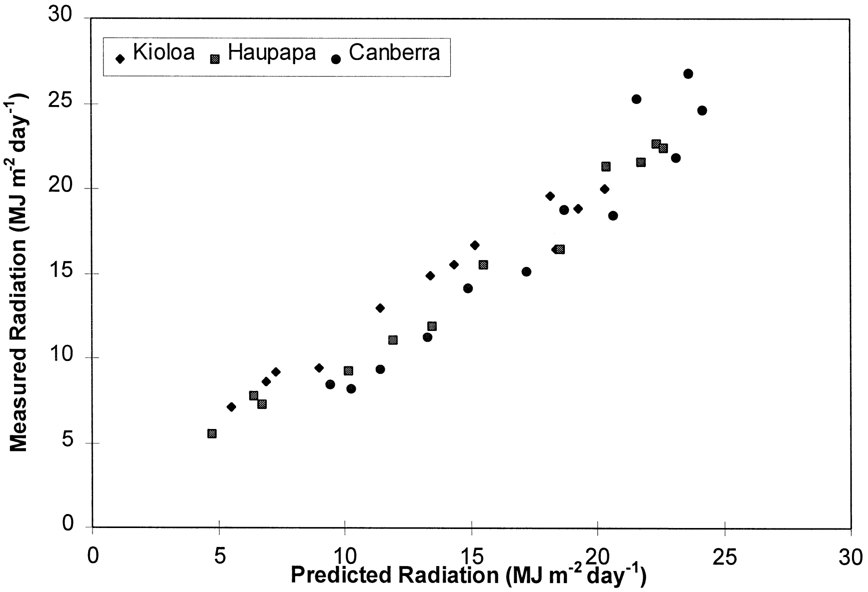

Fig. 2. Calculated versus measured incoming solar radiation for each month (MJ m^{-2} day^{-1}) for three test sites in Australia and New Zealand.

estimates of growth are available from them. The maximum current annual volume increment (CAI) for most native eucalypt forest occurs around 20 yrs after establishment; by 40 yrs, the CAI has usually decreased to less than half of the maximum; and by 100 yrs, CAI is less than 15% of maximum (West and Mattay, 1993). Pine plantations show a similar, but less marked reduction in average volume growth rates (CAI) with age (Lewis et al., 1976).

We were interested in predicting the basic capacity of sites to grow forests, and the way this might change with climate or management over time so we chose, in all but one case (Pilliga), to base our analysis on mean annual increment (MAI) for stands that had reached ages of between 20 and 40 yrs, when the periodic MAI is almost stable. In the Pilliga area, where slow growing cypress pines develop high populations that require 'release' by thinning, we analysed growth on research plots thinned to different densities where growth in height and basal area were recorded over a period of 16 yrs after release and volume increment could be calculated accurately by applying a cylindrical taper coefficient of 0.38 (Knott, 1995). At most of the sites with native eucalypts, measurements of the height and age of dominant trees were available. From these

Table 5
Relationship between measured and predicted solar incoming radiation as estimated from minimum and maximum temperature. Daily radiation represents averages for each month and the correlation coefficient (r^2) reference the three separate regression equations and their standard errors (SE) for data presented in Fig. 2

Radiation (MJ m^{-2} day^{-1})	Measured minimum radiation	Predicted minimum radiation	Measured maximum radiation	Predicted maximum radiation	r^2	S.E.
Canberra	8.20	9.40	26.80	23.20	0.90	1.12
Haupapa	5.56	4.74	22.68	22.38	0.97	0.80
Kioloa	7.09	5.54	20.01	20.30	0.91	1.08

Table 6
Forest mensuration data for the eight sites used in 3-PGS model

	Growth data provided	Time interval (yr)	No. of plots	Max. height (m) at 100 yrs	Site index height at 20 yr (m)	MAI m^3 ha^{-1} yr^{-1} (at age 20–40)	MAI kg^3 ha^{-1} yr^{-1} (at age 20–40)
Pilliga	CAI	16	6	17–18	NA	2.2	1300
Lorne	CAI	6	6	25–26	10	6	3500
Tumut (P)	MAI	30	18	32–33	25	17	7650
Kioloa	CAI	7	3	30–35	23	8	4800
Haupapa (P)	CAI	30	NA	40–41	28.5	30	13 500
Picton	CAI	5	4	55–60	30	13	7700
Tarra Bulga (P)	MAI	30	NA	40–41	27.5	27	12 150
Tarra Bulga (E)	MAI	30	NA	58–60	30.5	17	10 200
Wombat	CAI	16	5	30–38	12.4	7	4400

CAI: Current Annual Increment; MAI: Mean Annual Increment (P): Pine plantations; (E): Eucalyptus plantation; NA: indicates information about the growth of the stand was provided by field personnel based on a variety of field harvest and growth plots.

data we estimated the height at 20 yrs and, for fully-stocked stands, derived good estimates of MAI averaged over the age range 20–40 yrs using published tables and graphs (West and Mattay, 1993). At the Lorne site the ages of the trees were not precisely known, but the stands were composed of large diameter trees that appeared to have reached maximum height. In this case we selected an appropriate site index (height over age) curve and from that, and the reference height at 20 yrs, were able to estimate MAI between 20–40 yrs for fully stocked stands. Table 6 summarises mensurational data collected at each site. The range of field estimates of forest stand growth within each location is summarised in Table 6 by the range of maximum heights achieved at 100 yrs. From these mean values we derived MAI estimates for fully stocked stands between the ages of 20–40 yrs for all but the Pilliga site.

3.5. Satellite dataset

The current AVHRR sensor on board the NOAA series of weather satellites is a simple scanning radiometer producing data in five spectral channels from the visible, near-infrared and thermal regions of the spectrum (Kidwell, 1988). The orbit of the NOAA satellites allows a daily orbital overpass to produce full Earth coverage every day. The extensive data archive accumulated from these sensors has become one of the most significant data sets relating to the biosphere. A great deal of work has been done to ensure that the AVHRR data are accurate and consistent, to provide continuity of comparable data providing interannual information on biosphere functioning. Ten-day summaries of the daily observations are created using a procedure, known as compositing, which attempts to minimise the effect of cloud contamination and atmospheric attenuation on the imagery (Holben, 1986). The result has been the NOAA AVHRR Land Pathfinder data set (Agbu and James, 1994), which produces composites of a number of key variables from the satellite data including NDVI, surface temperatures, and albedo.

The 1987 Pathfinder dataset contains a number of errors as documented by NOAA. First, there is no Rayleigh correction applied to the data and second, the incident solar angle had not been corrected for solar zenith angle before being used to calculate the reflectance in the visible AVHRR bands. To overcome the lack of the Rayleigh correction we followed the procedure used by Prince and Goward (1995) and limited the NDVI to between 0.05 and 0.65. Because no raw radiances are used from the Pathfinder data set in the model the solar angle corrections were unnecessary. The maximum and minimum NDVI for each site for 1987 are given in Table 3. To predict fPAR from NDVI we used the equation originally developed by Goward and Huemmrich (1992) and modified by Prince and Goward (1995) to account for errors within the 1987 Pathfinder dataset. The equation:

$$\text{Fraction of PAR absorbed} = 1.67I - 0.08$$

where I is the NDVI from the Pathfinder dataset.

The way the NDVI-derived estimates of the *f* PAR were used varied depending on vegetation type. At sites with native eucalypts the monthly estimates of *f* PAR were used to predict APAR for each site. In sites dominated by pine plantations concern about their areal extent, and the effect of surrounding pasture on the monthly NDVI responses altered our use of the NDVI response. In these cases (Tumut, Tarra Bungle, and Haupapa) we ran two simulations: (i) using the actual NDVI data, and the estimates of *f* PAR derived from them and (ii) assuming that these managed forest systems maintained a projected L^* above 5 throughout the year, resulting in $> 90\%$ of PAR being absorbed (Grace, 1987; Lang et al., 1991). On this basis we calculated PAR absorbed at these sites, assuming that the maximum monthly NDVI recorded for 1987 applied for every month throughout the year. This ensured that the effects of surrounding pasture and crops greening during the growing season and subsequent dying off and harvest did not influence the NDVI response of that site.

3.6. Summary of the modelling procedure

The 3-PGS procedures can be summarised as follows (Fig. 3): (1) estimates of total incoming radiation were derived from temperature data, and *f* PAR from NDVI for each month. From these two variables APAR was calculated; (2) if frost occurs, reduce APAR in proportion to the days per month below freezing; (3) calculate soil water balance as the difference between precipitation, storage capacity of the soil, and water transpired by the vegetation, carrying stored water from month to month. The soil water modifier is based on the ratio of currently available to total available water; (4) calculate the VPD modifier for each month from average values of VPD. (Either the soil water or the VPD modifier applies—whichever is the most severe in any month); (5) calculate monthly GPP by multiplying APARu by the canopy quantum efficiency (1.8 g C MJ^{-1} of APARu); (6) calculate NPP as $0.45 \times \mathrm{GPP}$; (7) the ratio APARu:APAR, determines the fraction of NPP allocated to roots, with the remainder available for above-ground growth.

4. Results

The model was run, following the procedure outlined above, for 1987. Rather than starting in January

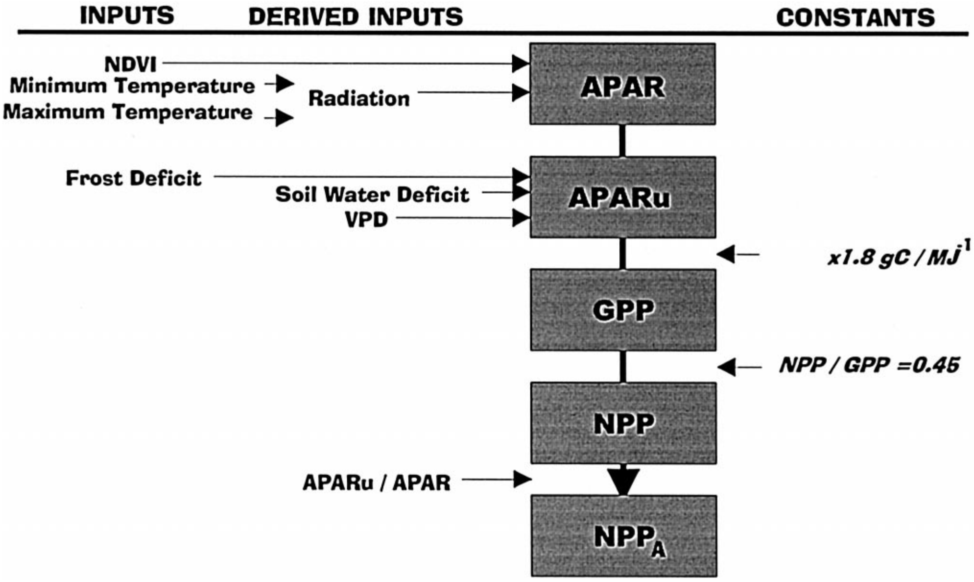

Fig. 3. Diagrammatic representation of the inputs, constants and sequence of calculations used in the 3-PGS model. (APAR = Absorbed Photosynthetically Active Radiation, APARu = Utilisable APAR, GPP = Gross Primary Productivity, NPP = Net Primary Productivity, $\mathrm{NPP_A}$ = above ground NPP).

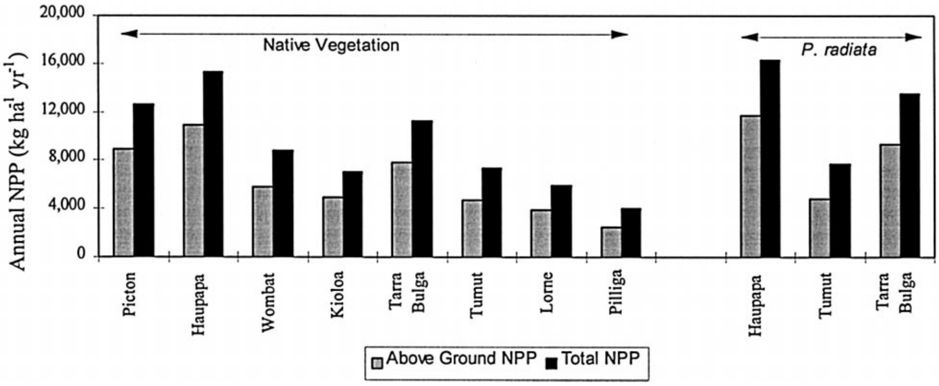

Fig. 4. Estimated Total and above ground NPP (NPP_A) for the eight forested sites in Australia and New Zealand response. In the cases of Tumut, Tarra Bungle, and Haupapa we ran two simulations: (i) using the actual NDVI data, and the estimates of fPAR derived from them and (ii) assuming that these managed forest systems maintained a projected L^* above 5 throughout the year, resulting in $> 90\%$ of PAR being absorbed. We calculated PAR absorbed at these sites using the maximum monthly NDVI recorded for 1987 applied for every month throughout the year.

with soils arbitrarily set at field moisture capacity, we initialised conditions by running the model for the full year, then repeating the run starting with the soil moisture reached at the end of the year in the initialisation run. The results reported are from the second run.

The regional estimates of NPP and NPP_A for the 8×8 km Pathfinder pixels are shown in Fig. 4. The simulations using 1987 data indicate the highest above-ground and total NPP values occur at Tarra Bulga Forest and Picton Forests in Tasmania, followed closely by the New Zealand pine forest at Haupapa. The lowest NPP recorded for the year occurred at Pilliga in Northern NSW, with Lorne State Forest, located in north Eastern NSW recording the next lowest estimate of NPP. Of the sites where NDVI was fixed for the year, significantly higher estimates of NPP were obtained at the Tarra Bulga and a slight increase at the Haupapa plantation site (possibly because cloud cover throughout the month of July may have artificially reduced the estimate of NDVI in 1987). At Tumut, the NDVI of the region did not fall significantly throughout the year, and as a result, there was little difference between estimates of APAR determined with a fixed maximum NDVI and the seasonal NDVI data.

As mentioned earlier the model utilises the approach of Landsberg and Waring (1997) in that the allocation of NPP below-ground is strongly influenced by limitations to growing conditions imposed by frost, atmospheric vapour pressure and available soil water. The effect of this dynamic allocation procedure can be seen in the model estimates shown in Fig. 4 at the sites with low total NPP, such as Pilliga and Lorne. More of the available carbon was allocated to the root system at these sites, over 38% of total NPP going to the roots at Pilliga and 33% of NPP being assigned to roots at Lorne. In the most productive stands, where the environmental conditions are more favourable the allocation was reduced, with Picton allocating less than 29% of total NPP to the roots and Haupapa less than 28%.

Not all above-ground production goes to stems (wood production), but branches and foliage usually represent less than 25% of the total biomass for trees between the age of 20 and 40 (Pastor et al., 1984). The above-ground biomass values predicted by the model were converted into stem volume estimates although the density of wood, particularly in eucalyptus species, is highly variable, and generally increases rapidly between age 10 to 30. Tables are available which summarise average wood densities for Australian species, but values range from less than 300 kg m^{-3} to more than 900 kg m^{-3} (dry mass/fresh volume) (Kingston and Risdon, 1961) and age is not recorded as a variable making estimation of wood densities for specific locations difficult. For the managed forest sites (pine and eucalypt plantations) wood density values were provided by regional forest officers, and we applied these values

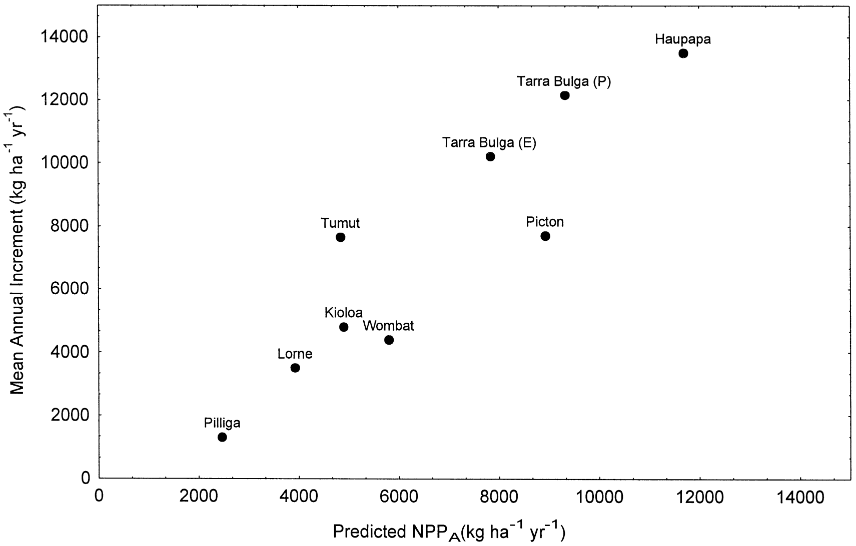

Fig. 5. Relationship between NPPA as predicted using 3-PGS and Mean Annual Increment as derived from forest inventory data for the eight sites in Australia and New Zealand. Haupapa and Tumut pine plantation results were derived by setting NDVI to a constant maximum for 1987 (NDVI = 0.65). Two Tarra Bulga results are compared (i) using the actual 1987 NDVI data (equivalent to a native forest plantation), and (ii) setting NDVI to a constant maximum for 1987 (for the pine plantation comparison).

to covert MAI (m^3 ha^{-1} yr^{-1}) to mass units (kg ha^{-1} yr^{-1}). Where we lacked information, we used the average values provided by Kingston and Risdon (1961).

Fig. 5 shows the relationship between the estimated NPP$_A$ from the 3-PGS model and actual NPP$_A$, constructed from mensurational data collected in the field. We emphasise again that growth is MAI projected for fully stocked stands between the ages of 20 to 40 yrs that are present within the area assessed from the NOAA satellite images. The relationship between the predicted NPP$_A$ and estimated (as derived from field data) is generally good with an overall error of about $\pm 20\%$. Biases in the relationship indicate that the MAI estimated by the 3-PGS model are slightly higher in low production areas and slightly lower in high production areas than those estimated from field data.

5. Discussion

5.1. Choice of independent variable

There are two main reasons for choosing to estimate the mean annual production between ages 20 to 40 yrs for fully stocked stands, rather than using actual 1987 growth increments.

(i) The 3-PGS model utilises monthly 1987 NDVI data to estimate the fPAR absorbed and provide values of the radiation term needed in the hydrologic component of the model. The NDVI values, however, provide an estimate of the absorption of radiant energy by all vegetation in the observed cell, which encompasses both overstorey and understorey plants. This is particularly the case in Australian native forest environments where the L^* of the overstorey canopy is much lower than in typical northern hemisphere forests (Landsberg and Gower, 1997). As a result, the NDVI of the pixel reflects the total vegetation present, regardless of its position in the canopy. Any estimate of NPP derived from satellite analyses represents the photosynthetic capacity of all vegetation and subsequently provides an estimate of MAI of the forest at maximum stocking. Actual production of the forest depends on age, stocking and species composition. The use of the 1987 NDVI data provides realistic estimates of the constraints that need to be applied to the data and the use of the corresponding meteorological data allows constraints imposed by the environmental conditions to match the NDVI constraints in the model. This, we feel, allows us to demonstrate the general soundness of the modelling approach, before extending the analyses to include decades of satellite and weather data.

(ii) The use of this model to provide NPP estimates for forests at or near their peak production provides valuable information: almost regardless of the kind and age of vegetation present it essentially represents an index of the productive capability of the site (Goward et al., 1985). If, over time, climate or management change the capacity of the site, the cause should be identifiable by assessing whether or not the NDVI pattern matches changes in weather patterns or is independent, and therefore likely to represent other causes (e.g., pollution, erosion, compaction, sustained outbreaks of insects and pathogens).

5.2. Physiologically-based models driven by satellite data

In this project we used remotely sensed observations as inputs to the 3-PGS model to derive the fraction of PAR absorbed by the canopies, thus providing constraints to the model with respect to the NPP accumulated by the forest stands. We have shown that, at relatively coarse scales, incoming solar radiation can be accurately modelled from commonly available meteorological variables such as temperature coupled with basic geographical information about the site. From the model output it is possible to identify the constraints imposed on potential growth by vapour pressure deficit, soil water balance and frost. These constraints can be compared to provide an indication to the key factors restricting vegetation growth of the area. The satisfactory correspondence between values of NPP_A obtained from 3-PGS, and estimated by conventional forestry measurement techniques, indicates that the model provides a sound and useful framework for regional modelling.

There are, however, some key areas where the original forestry data, the modelling procedure and the use of field data for development and validation can be improved.

(i) The coarse spatial resolution of the AVHRR Pathfinder dataset effectively limits the predictions of the 3-PGS model to areas, in the order of 8 × 8 km. Whilst this is adequate for global or continental analysis (Prince and Goward, 1995) it obviously limits the application of the results at landscape scales. Future research in this area is likely to introduce two alternatives: (a) using currently available technology, landscape studies could be initiated using full resolution AVHRR data (with a near nadir spatial resolution of 1.1 km), combined with for example, Landsat Thematic Mapper (TM) or Multi Spectral Scanner (MSS) data. This would provide ‘snapshots’ of the forest with very high spatial resolution (30 or 80 m respectively) to be obtained at specific intervals. The utilisation of this higher spatial and spectral resolution remotely-sensed imagery should allow, at very least, basic discrimination of forest age classes (e.g., Cohen et al., 1995) and structure (e.g., Wu and Strahler, 1994), which could then be utilised as inputs to the 3-PGS model. By combining the monthly composites of NDVI from the AVHRR with high resolution maps of the region derived from Landsat data, 3-PGS could be applied at a landscape scale combined with a number of key spatial variables such as current forest age class, and some basic quantitative soil information, such as fertility and water holding capacity. (b) In the longer term the launch of the Earth Observation System (EOS), scheduled for the year 2000, will provide data from a new sensor (Moderate Resolution Imaging Spectro-radiometer, (MODIS)) with a near nadir spatial resolution of 250 m, which will allow weekly 1 km spatial resolution estimates of biome specific net photosynthesis of the global terrestrial biosphere (Running et al., 1994a).

(ii) The predictions of NPP for large 8 × 8 km areas makes it difficult to validate the results on the basis of forest plot data because of the difficulty of making a spatial estimate from sufficient plots to encompass field variability. We have attempted to do this in this paper, but it is worth noting the need for forest managers to develop procedures to sample at spatial scales in their inventory data collection techniques. Data on the extent, size and spatial distribution of the forests, and their condition within specified areas are immensely important for the validation of models of this type, and indeed for good estimates of forest productivity over large areas.

(iii) Both 3-PG and 3-PGS use a monthly time step, which has disadvantages with respect to modelling the water balance of forests. Improvements could be effected by introducing a daily time step version of the model, although this would require significantly more meteorological information (particularly rainfall) at each site, as well as a more accurate estimates of rooting depth of the species, and would lose some of the advantages of the simplified formulation of these models.

(iv) The comparison of model output with actual forest growth information has highlighted differences in the way managers and landscape modellers measure the forest. Typically forest managers in Australia measure tree DBH or basal area of the forest stand in plots. This provides conventional inventory information, but these data are difficult to utilise for biomass estimation because they do not usually include estimates of forest age, height or composition, or these estimates are poor. As a result, while there is a wide variety of forest growth information available, much of it is difficult to analyse and utilise in a comparison with NPP_A estimates for a forest. Similarly the density of the wood is a key factor in estimating the total biomass of the stand. The Kingston and Risdon (1961) tables are invaluable, but they provide no information about variations caused by growing conditions or the way wood density changes as the trees age.

6. Conclusions

In this paper we combine general physiological principles into a model that can be driven, almost entirely, from readily available monthly weather records and monthly satellite-derived images of changing greenness across landscapes. Minimal information is required on soils and vegetation. With one year's data, we demonstrate the potential to obtain a reasonable estimate of a region's present productive capacity. The opportunity exists to expand the analyses to include decades of data, and thereby evaluate longer-term implications of climatic variation and other factors affecting forest productivity.

Acknowledgements

We are very grateful to the many people and forestry organisations in Australia who provided us with forest growth information, and in some cases, tours of the forest estate. We thank: Fiona Hamilton [*Wombat*] *Victorian Department of Conservation and Natural Resources*; Mike Welch [*Tumut*], John Mills, Phil Carter, Jude Harrison [*Lorne*], Garry King [*Pilliga*] and Mark Watt [*Kioloa*], *State Forest of NSW*, Drs. Mick Brown [*Picton*] *Forestry Tasmania*, and David Whitehead [*Haupapa*] Landcare NZ and Henry Lieshout and Phil Whiteman [*Tarra Bulga*] AMCOR for providing valuable forest plot information and site advice. We also wish to acknowledge Drs. Sam Goward, Phil Ryan, and Steve Running for useful discussions in the development of the model. We thanks Drs. John Raison, Trevor Booth, Miko Kirchbaum and David Whitehead for discussion on methods and results and two anonymous reviewers for valuable comments on this manuscript. Part of this research (NCC) was undertaken within CSIRO Multi-Divisional Project 31 on the Spatial Prediction of Forest Productivity. RHW acknowledges with thanks support for a CSIRO McMaster Fellowship, support on sabbatical from his own department and a grant from the Forestry and Forest Products Research and Development, Australia. Additional information on this research is available at http://www.ffp.csiro.au/nfm/mdp/.

References

Aber, J.D., Reich, P.B., Goulden, M.L., 1996. Extrapolating leaf CO_2 exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. Oecologia 106, 257–265.

Agbu, P.A., James, M.E., 1994. The NOAA/NASA Pathfinder AVHRR Land Data set User's Manual. Goddard Distributed Active Archive Centre. NASA Goddard Space Flight Centre, Greenbelt, USA.

Australian Society of Soil Science, 1985 (Queensland Branch). Identification of Soils and Interpretation of Data. Australian Society of Soil Science, Queensland Branch, Brisbane, Australia, VII, +251 pp.

Beets, P.N., Whitehead, D., 1996. Carbon partitioning in *Pinus radiata* stands in relation to foliage nitrogen status. Tree Physiol. 16, 131–138.

Benson, M.L., Landsberg, J.J., Borough, C.J., 1992. The biology of forest growth experiment: an introduction. For. Ecol. Manage. 52, 1–16.

Bristow, K.L., Campbell, G.S., 1984. On the relationship between oncoming solar radiation and daily maximum and minimum temperature. Agric. For. Meteorol. 31, 159–166.

Buffo, J., Fritschen, L., Murphy, J., 1972. Direct solar radiation on various slopes from 0° to 60° north latitude. Res. Pap. PNW-142 Portland, OR, US. Department of Agriculture Forest Service, 74 pp.

Cienciala, E., Running, S.W., Lindroth, A., Grelle, A., Ryan, M.G., 1997. Analysis of carbon and water fluxes from the NOPEX boreal forest. Comparison of measurements with FOREST-BGC simulations. Journal of Hydrology, (in review).

Cohen, W.B., Spies, T.A., Fiorella, M., 1995. Estimating the age and structure of forests in a multi-owenership landscape of Western Oregon, USA. Int. J. Remote Sensing 16, 721–746.

Drew, T.J., Flewelling, J.W., 1977. Some recent Japanese theories of yield-density relationships and their applications to Monterey pine plantations. For. Sci. 23, 517–534.

Garnier, B.J., Ohmura, A., 1968. A method for calculating the direct shortwave radiation income on slopes. J. Appl. Meteorol. 7, 796–800.

Goldberg, B., Klein, W.H., McCartney, R.D., 1979. A comparison of some simple models used to predict solar irradiance on a horizonal surface. Solar Energy 23, 81–83.

Goward, S.N., Huemmrich, K.F., 1992. Vegetation canopy PAR absorption and the normalised difference vegetation index: an assessment using the SAIL model. Remote Sensing Environ. 39, 119–140.

Goward, S.N., Tucker, C.J., Dye, D.G., 1985. North American vegetation patterns observed with the NOAA-7 advanced very high resolution radiometer. Vegetatio 64, 3–14.

Grace, J.C., 1987. Theoretical ratio between one-sided and total surface area for pine needles. N.Z. J. For. Sci. 17, 292–296.

Holben, B.N., 1986. Characteristics of maximum value composite images from temporal AVHRR data. Int. J. Remote Sensing 11, 1417–1434.

Hollinger, D.Y., Kelliher, F.M., Byers, J.N., Hunt, J.E., McSeverny, T.M., Weir, P.L., 1994. Carbon dioxide exchange between undisturbed old-growth temperate forest and the atmosphere. Ecology 75, 134–150.

Hungerford, R.D., Nemani, R.R., Running, S.W., Coughlan, J.C., 1989. MTCLIM: a mountain microclimate simulation model. United States Department of Agriculture Research Paper INT0414, 52 pp.

Hutchinson, M.F., 1984. A summary of some surface fitting and contouring programs for noisy data. Consulting Report No. ACT 84/6. CSIRO Division of Mathematics and Statistics. CSIRO, Canberra.

Kelliher, F.M., Leaning, R., Raupach, M.R., Schulze, E.D., 1995. Maximum conductance for evaporation from global vegetation types. Agric. For. Meteorol. 73, 1–16.

Kidwell, K.B., 1988. NOAA Polar Orbiter Data TIROS-N, NOAA-6, NOAA-7, NOAA-8, NOAA-9, NOAA-10, NOAA-11 User's Guide. National Oceanic and Atmospheric Administration.

Kingston, R.S.T., Risdon, C.J.E., 1961. Shrinkage and density of Australian and other southwest Pacific woods. CSIRO Division of Forestry Products. Technical Paper, 13. Melbourne, Australia, 65 pp.

Knott, J., 1995. White cypress pine thinning trials of the western region. Research Paper, 27. Research Division, State Forests of NSW, Sydney.

Kumar, M., Monteith, J.L., 1982. Remote sensing of plant growth, in: Smith, H. (Ed.), Plants and the Daylight Spectrum, Academic Press, London, pp. 133–144.

Landsberg, J.J., 1986. Physiological Ecology of Forest Production. Academic Press, Sydney, 198 pp.

Landsberg, J.J., Gower, S.T., 1997. Application of Physiological Ecology to Forest Management. Academic Press, San Diego, CA, 354 pp.

Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance, and partitioning. Forest Ecology and Management 95, 209–228.

Lang, A.R.G., McMurtrie, R.E., Benson, M.L., 1991. Validity of surface area indices of *Pinus radiata* estimated from transmittance of the sun's beam. Agric. For. Meteorol. 57, 157–170.

Lewis, N.B., Keeves, A., Leech, J.W., 1976. Yield regulations in South Australian *Pinus radiata*. Bull. No. 23, Woods and Forests Department, South Australia.

Lloyd, J., Grace, J., Miranda, A.C., Meir, P., Wong, S.C., Miranda, H.S., Wright, I.R., Gash, J.H.C., McIntyre, J., 1995. A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties. Plant, Cell Environ. 18, 1129–1145.

Matthews, E., 1983. Global vegetation and land use: new high-resolution data bases for climate studies. J. Clim. Appl. Meteorol. 22, 474–487.

McMurtrie, R.E., Comins, H.N., Kirschbaum, M.U.F., Wang, Y.P., 1992. Modifying existing forest growth models to take account of effects of elevated CO_2. Aust. J. Bot. 40, 657–677.

McMurtrie, R.E., Gholz, H.L., Linder, S., Gower, S.T., 1994. Climatic factors controlling the productivity of pine stands: a model-based analysis. Ecol. Bull. 43, 173–188.

Pastor, J., Aber, J.A., Melillo, M., 1984. Biomass prediction using generalized allometric regressions for some Northeast tree species. For. Ecol. Manage. 7, 265–274.

Prentice, K.C., 1990. Bioclimatic distribution of vegetation for general circulation model studies. J. Geophys. Res. 95, 11811–11830.

Prince, S.D., Goward, S.M., 1995. Global primary production: a remote sensing approach. J. Biogeography 22, 815–835.

Running, S.W., Coughlan, J.C., 1988. A general model of forest ecosystem processes for regional applications: I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol. Modelling 42, 125–154.

Running, S.W., 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., Justice, C.O., Salomonson, V., Hall, D., Barker, J., Kaufmann, Y.J., Strahler, A.H., Huete, A.R., Muller, J.-P., Vanderbilt, V., Wan, Z.M., Teillet, P., Carneggie, D., 1994a. Terrestrial remote sensing science and algorithms planned for EOS/MODIS. Int. J. Remote Sensing 15, 3587–3620.

Running, S.W., Loveland, T.R., Pierce, L.L., 1994b. A vegetation classification logic based on remote sensing for use in global biogeochemical models. Ambio 23, 77–81.

Runyon, J., Waring, R.H., Goward, S.N., Welles, J.M., 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. Ecol. Appl. 4, 226–237.

Ryan, M.G., Hubbard, R.M., Pongracic, S., Raison, R.J., McMurtrie, R.E., 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiol. 16, 333–344.

Sellers, P.J., 1985. Canopy reflectance, photosynthesis and transpiration. Int. J. Remote Sensing 68, 1335–1372.

Sellers, P.J., 1987. Canopy reflectance, photosynthesis, and transpiration: 2. The role of biophysics in the linearity of their interdependence. Remote Sensing Environ. 21, 143–183.

Swift, L.W., 1976. Algorithm for solar radiation on mountain slopes. Water Resour. Res. 121, 108–112.

Townshend, J., Justice, C., Li, W., Gurney, C., McManus, J., 1991. Global land cover classification by remote sensing: present capabilities and future possibilities. Remote Sensing Environ. 35, 243–255.

Weinstein, D.A., Beloin, R.M., Yanai, R.D., 1991. Modelling changes in red spruce carbon balance and allocation in response to interacting ozone and nutrient stresses. Tree Physiol. 9, 127–146.

West, P.W., Mattay, J.P., 1993. Yield prediction models and comparative growth rates for six eucalypt species. Aust. For. 56, 211–225.

White, J.D., Running, S.W., 1994. Testing scale dependent assumptions in regional ecosystem simulations. J. Veg. Sci. 5, 687–702.

Wu, Y., Strahler, A.H., 1994. Remote estimation of crown size, stand density and biomass on the Oregon Transect. Ecol. Appl. 4, 299–312.