

A simple model of light and water use evaluated for *Pinus radiata*

RODERICK C. DEWAR

School of Biological Science, University of New South Wales, Sydney, NSW 2052, Australia

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Summary An existing model of light and water use by crops (RESCAP) was adapted and evaluated for trees. In the model, growth on any given day is determined either by the amount of intercepted radiation (by means of the light utilization coefficient, ϵ) or by the maximum rate of water extraction by roots (a function of root biomass and soil water content). In either case, transpiration and growth are related by the water-use efficiency (q), which is inversely proportional to the daily mean saturation vapor pressure deficit (D). The model was applied to two *Pinus radiata* (D. Don) stands (control (C) and fertilized (F)) growing near Canberra, Australia, using data collected during the Biology of Forest Growth experiment (1983–1988). For both stands, predicted and measured soil water contents were in close agreement ($r^2 > 0.9$) over a 4-year period involving several wet–dry cycles. The parameter combination ϵ/qD was estimated to be 0.28 and 0.26 kg H₂O (MJ total)⁻¹ kPa⁻¹ for the C and F stands, respectively. Because of the close physiological link between water use and CO₂ uptake, the results suggest that tree growth may be realistically simulated by simple models based on conservative values for ϵ and qD .

Keywords: growth, light utilization coefficient, RESCAP model, water-use efficiency.

Introduction

A key objective of many forest models is the prediction of tree growth and water use at the stand scale. The physiology underlying the exchange of CO₂ and water vapor between the atmosphere and individual leaves is relatively well understood. However, a major challenge lies in applying this knowledge at the canopy scale (Jarvis 1995). Several detailed physiological models exist that explicitly represent leaf-scale fluxes of CO₂ and water and their variation within plant canopies (e.g., Wang and Jarvis 1990, McMurtrie et al. 1992, Sellers et al. 1992). However, two sets of observations indicate that the emergent behavior of growth and transpiration at the canopy scale may be more simply represented.

First, it is well documented for many crop and tree species that the amount of dry matter produced per unit of radiation intercepted by the canopy (i.e., the light utilization coefficient, ϵ) is approximately constant during vegetative growth when water supply is not limiting (e.g., Monteith 1977, Gallagher and Biscoe 1978, Linder 1985, Landsberg et al. 1996). Second, extensive growth data for crops (e.g., Tanner and Sinclair

1983) show that the amount of dry matter produced per unit of water transpired (i.e., the water-use efficiency, q) is approximately inversely proportional to the mean saturation vapor pressure deficit (D), whether water is limiting or not. Short-term gas exchange measurements suggest that this relationship may also apply to trees (Baldocchi et al. 1987, Baldocchi and Harley 1995, Cienciala and Lindroth 1995, Lindroth and Cienciala 1995).

Some progress has been made in understanding the physiological basis of these observations. The constancy of qD can be understood in terms of the conservative nature of the intercellular [CO₂] of foliage, although several empirical assumptions are needed to derive canopy-scale values of qD from the gas exchange properties of individual leaves (Bierhuizen and Slatyer 1965, Tanner and Sinclair 1983, Sinclair et al. 1984, Monteith 1990). The relationship between q and D is expected to be particularly strong for aerodynamically rough canopies, such as forests, for which transpiration is relatively insensitive to solar radiation (Jarvis and McNaughton 1986). More recently, the conservative nature of ϵ has been interpreted as the outcome of an optimal balance between photosynthesis and maintenance respiration (Dewar 1996). This interpretation leads to the theoretical prediction of ϵ as a function of several physiological and environmental factors, although further experimental work is needed to evaluate this as well as other interpretations (e.g., Landsberg et al. 1996). Models founded on the conservative quantities ϵ and qD are attractive because they summarize plant physiology directly at the canopy scale while remaining relatively simple.

The RESCAP (RESource CAPture) model (Monteith 1986, Monteith et al. 1989) combines ϵ and qD within a simple framework in which growth on a given day is either light-limited or water-limited. The type of limitation that applies depends on the availability of these resources and the plant's ability to capture them, equal emphasis being placed on the role of leaves in light interception and the role of roots in supplying water. RESCAP was originally developed for cereal crops. However, this simple, balanced approach to modeling light and water use appears to have received little attention from forest modelers.

The objective of this paper is to introduce a simplified version of RESCAP suitable for trees, and to evaluate it for *Pinus radiata* (D. Don) stands growing near Canberra, Australia, using data collected during the Biology of Forest Growth experiment (Benson et al. 1992). For this evaluation, the basic

assumptions for light and water use in RESCAP were combined with a simple soil water balance model appropriate to these stands.

Model assumptions

Light and water use in RESCAP

A list of symbol definitions and units is given in Table 1. The central assumption of the RESCAP model (Monteith et al. 1989) is that daily growth (G), defined as total (above- and below-ground) dry matter production, is either light-limited or water-limited. For either type of limitation, it is assumed that daily transpiration (T) is proportional to G ,

$$T = \frac{G}{q}, \quad (1)$$

where q , the water-use efficiency, is inversely proportional to daily mean saturation vapor pressure deficit of the atmosphere (D),

$$q = \frac{q_o}{D}, \quad (2)$$

Table 1. Definitions and units of symbols used in text (dm = dry matter, NPP = net primary productivity, VPD = vapor pressure deficit).

Symbol	Definition	Units
D	Daily mean atmospheric VPD	kPa
D_o	Empirical stomatal parameter (Leuning 1995)	kPa
d_s	Effective depth of rooting zone	m
E	Maximum rate of water extraction	kg H ₂ O m ⁻² day ⁻¹
E_{pen}	Penman evaporation rate	kg H ₂ O m ⁻² day ⁻¹
G	NPP (above- and below-ground)	g _{dm} m ⁻² day ⁻¹
G_L	Light-limited growth	g _{dm} m ⁻² day ⁻¹
G_w	Water-limited growth	g _{dm} m ⁻² day ⁻¹
I	Rainfall interception by canopy	kg H ₂ O m ⁻² day ⁻¹
I_{max}	Maximum rainfall interception	kg H ₂ O m ⁻² day ⁻¹
k	Light extinction coefficient	m ² ground (m ² leaf) ⁻¹
L_c	Projected leaf area index	m ² leaf (m ² ground) ⁻¹
P	Daily incident rainfall	kg H ₂ O m ⁻² day ⁻¹
q	Water-use efficiency	g _{dm} (kg H ₂ O) ⁻¹
q_o	Normalized water-use efficiency	g _{dm} (kg H ₂ O) ⁻¹ kPa
Q	Soil water content	kg H ₂ O m ⁻²
Q_{max}	Maximum soil water content	kg H ₂ O m ⁻²
Q_{min}	Minimum soil water content	kg H ₂ O m ⁻²
R (R_o)	Root biomass (initial value)	g _{dm} m ⁻²
s	Canopy water storage constant	kg H ₂ O (m ² leaf) ⁻¹ day ⁻¹
S_o	Daily incident (total) solar radiation	MJ m ⁻² day ⁻¹
T	Daily transpiration	kg H ₂ O m ⁻² day ⁻¹
ϵ	Light utilization coefficient	g _{dm} MJ ⁻¹
σ	Water extraction constant	m ² g _{dm} ⁻¹ day ⁻¹

with q_o , the normalized water-use efficiency, a constant. Light-limited growth (G_L) is calculated from the amount of radiation intercepted by the canopy. Using a Beer's law approach,

$$G_L = \epsilon S_o (1 - \exp(-kL_c)), \quad (3)$$

where ϵ is the light utilization coefficient, S_o is the daily incident (total) solar radiation, k is the canopy light extinction coefficient and L_c is the projected leaf area index (LAI) of the canopy.

Water-limited growth (G_w) is determined by the maximum rate of water extraction by roots (E). In RESCAP, E is calculated from the vertical distribution of root length density and extractable soil water content. This degree of resolution is appropriate for annual crops, where the rate of descent of the root system after sowing critically determines the seasonal pattern of water extraction (Monteith 1986, Robertson et al. 1993a, 1993b). For perennials with an established root system, it may be more appropriate to adopt a coarser resolution. In adapting the model for trees, a single-layer approximation is used in which E is a function of the root biomass (R) and soil water content (Q) within a homogeneous rooting zone of effective depth d_s ,

$$E = \sigma R(Q - Q_{min}), \quad (4)$$

where σ is a constant and Q_{min} is the minimum (non-extractable) soil water content to depth d_s . Although a multi-layer description of the rooting zone might be more realistic, the single-layer approximation must be evaluated, ultimately, in terms of its predictive success. Transpiration during water-limited growth is equal to E , and Equation 1 then determines G_w as

$$G_w = qE. \quad (5)$$

Daily growth is then taken as the lesser of the two limiting rates,

$$G = \min(G_L, G_w), \quad (6)$$

and daily transpiration is given by

$$T = \min\left(\frac{G_L}{q}, E\right). \quad (7)$$

Figure 1a shows the general dependence of G and T on soil water content.

Soil water balance

Following McMurtrie et al. (1990a), daily maximum rainfall interception by the canopy (I_{max}) is assumed to be proportional to canopy LAI,

$$I_{max} = sL_c, \quad (8)$$

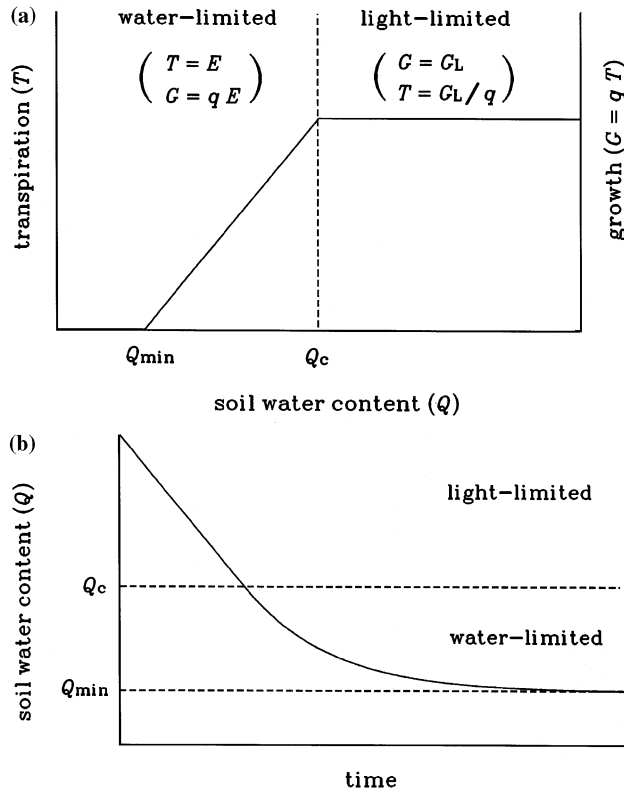


Figure 1. (a) Schematic relationship between transpiration (T), growth (G) and soil water content (Q) assumed in the model. The vertical axes are calibrated in terms of water or dry matter, related by water-use efficiency (q). In the water-limited phase ($Q_{\min} < Q < Q_c$), T and G are determined by the maximum rate of water extraction by roots (E , Equation 4). In the light-limited phase ($Q > Q_c$), T and G are determined by intercepted radiation (G_L is light-limited growth, Equation 3). The critical water content (Q_c , given by $Q_c = Q_{\min} + G_L/q\sigma R$) is a function of canopy LAI, root biomass, solar radiation and vapor pressure deficit; the value of Q_c therefore changes on a daily basis. (b) Hypothetical soil drying curve predicted by the model with no rainfall input and Q_c held fixed. Soil water content declines at a constant rate (G_L/q) in the light-limited phase, and exponentially (with rate constant σR) in the water-limited phase.

where s is a storage constant. The canopy interception rate is then taken as the lesser of I_{\max} and daily incident rainfall (P),

$$I = \min(I_{\max}, P). \quad (9)$$

The reduction in canopy transpiration due to wet foliage was incorporated using the method described by McMurtrie et al. (1990a) (see Discussion), but was found to have a negligible effect on the predicted water balance of the two *P. radiata* stands to which the model was applied; this feature is therefore ignored here. Similarly, understory evapotranspiration was estimated to be a minor component of water balance for these stands (Myers and Talsma 1992) and is also ignored. The daily rate of change of soil water content is then given by

$$\frac{dQ}{dt} = P - I - T, \quad (10)$$

with drainage occurring at field capacity ($Q = Q_{\max}$). Figure 1b shows a hypothetical soil drying curve obtained from Equation 10 with $P = I = 0$ and with L_c , R , S_o and D held fixed. Initially, growth is light-limited and soil water content decreases at a constant rate (given by G_L/q). Below a critical value (Q_c , which is a function of L_c , R , S_o and D and is therefore fixed in this example), growth becomes water-limited and soil water content declines exponentially with a rate constant given by σR (see Equation 4). In reality, the value of Q_c will change on a daily basis because of variations in incident radiation and vapor pressure deficit, and on longer time-scales because of variations in leaf area and root biomass.

Materials and methods

The model was evaluated using data collected during the Biology of Forest Growth (BFG) experiment (1983–88) on the effects of fertilization and irrigation on *P. radiata* stands growing near Canberra, Australia. In 1983, trees were 10 years old and stocking density was approximately 700 ha^{-1} . Experimental treatments applied were irrigation (I), solid fertilizer (F), irrigation plus solid fertilizer (IF), irrigation plus liquid fertilizer (IL); a control (C) stand received no treatment. Data from the C and F stands were used to evaluate the present model (soil water content in the I, IF and IL stands being maintained at, or close to, field capacity). The F treatment was applied in two doses in September and October 1983, with a total addition of 400 kg ha^{-1} of nitrogen and 200 kg ha^{-1} of phosphorus. A detailed description of the site and experiment is given in Benson et al. (1992).

Raison et al. (1992) estimated the pattern of leaf area development in each stand from 1983 to 1987. Their data correspond well with leaf areas predicted for these stands by the BIOMASS model (McMurtrie and Landsberg 1992, McMurtrie et al. 1992); BIOMASS was therefore used to extrapolate the leaf area data to 1988 to cover the period over which soil water contents were measured (Myers and Talsma 1992). Projected LAI (L_c) was approximately 2 before treatment, increasing to maximum values of 5 and 5.5 for the C and F stands, respectively (Figure 2). The linearly interpolated LAI data were used in conjunction with measured daily incident solar radiation (S_o) to calculate light-limited growth (G_L , Equation 3), and in conjunction with measured daily incident rainfall (P) to calculate rainfall interception (I , Equation 9).

Following the method described by McMurtrie et al. (1990a), the mean daily vapor pressure deficit (D) was calculated using a sinusoidal pattern of temperature over a 24-h cycle, with the assumption that air is saturated at the daily minimum temperature. No root biomass data were available to estimate the maximum water extraction rate (E , Equation 4) directly. As the simplest reasonable hypothesis, it was assumed that the ratio of root biomass to LAI remained constant throughout the experiment; the sensitivity of the model to this assumption is discussed below.

Myers and Talsma (1992) measured soil water content to a depth of 2 m at 2-week intervals in each stand. Their data for the C and F stands were compared with soil water contents

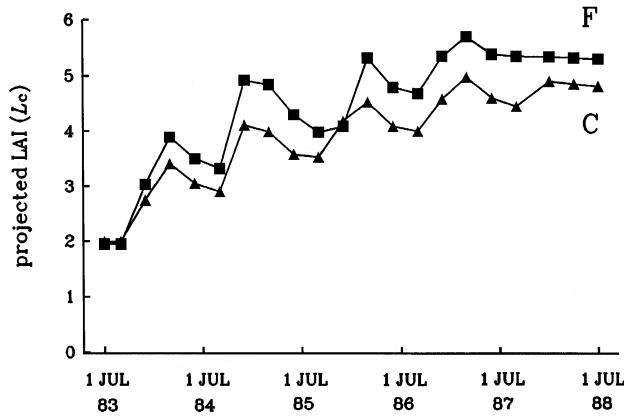


Figure 2. Seasonal changes in projected leaf area index estimated by Raison et al. (1992) for control (C, \blacktriangle) and fertilized (F, \blacksquare) *P. radiata* stands; the last three data points for each stand were estimated by the BIOMASS model (McMurtrie et al. 1990a) and reflect the summer drought of 1987–88. The interpolated data (lines) were used to estimate light-limited growth (G_L , Equation 3) on a daily basis.

predicted by numerical integration of Equation 10 from July 1, 1984 to July 1, 1988 on a daily timestep, assuming a rooting zone of effective depth $d_s = 2$ m. Using previous estimates for *P. radiata* stands, the light extinction coefficient was set to $k = 0.5$ (McMurtrie et al. 1992) and the storage constant was set to $s = 0.5$ mm day $^{-1}$ (McMurtrie et al. 1990a). For each stand, Q_{\max} was set equal to the maximum observed soil water content. As discussed by McMurtrie et al. (1990b), a run-off of 50 mm from the C stand was assumed to occur following the single rainfall event of 130 mm that broke the summer drought of 1984–85.

The remaining parameters of the model determine daily transpiration (T) according to Equation 7. With the ratio R/L_c constant, T depends on three independent parameter combinations: ϵ/q_0 , the ratio of the light utilization coefficient to the normalized water-use efficiency; σR_0 , the initial value of the rate constant for water extraction on July 1, 1984; and Q_{\min} , the minimum soil water content. These parameters determine different characteristics of the soil drying curve, as the hypothetical example in Figure 1b illustrates. For each stand, the values of σR_0 and Q_{\min} were adjusted to obtain the best fit to the observed soil water contents in the water-limited phase of the first drying cycle. The value of ϵ/q_0 , which determines water use on light-limited days, was then adjusted to obtain the best agreement between predicted and measured soil water contents over the entire simulation period. Note that ϵ and q_0 cannot be estimated separately by this procedure.

Results

The model gave good agreement with measured soil water contents over a 4-year period involving several wet–dry cycles, for both the C and F stands ($r^2 = 0.93$ and 0.96 , Figures 3a and 3b, respectively; the goodness of fit did not vary significantly with season). The fitted values of σR_0 and ϵ/q_0 (Table 2) are

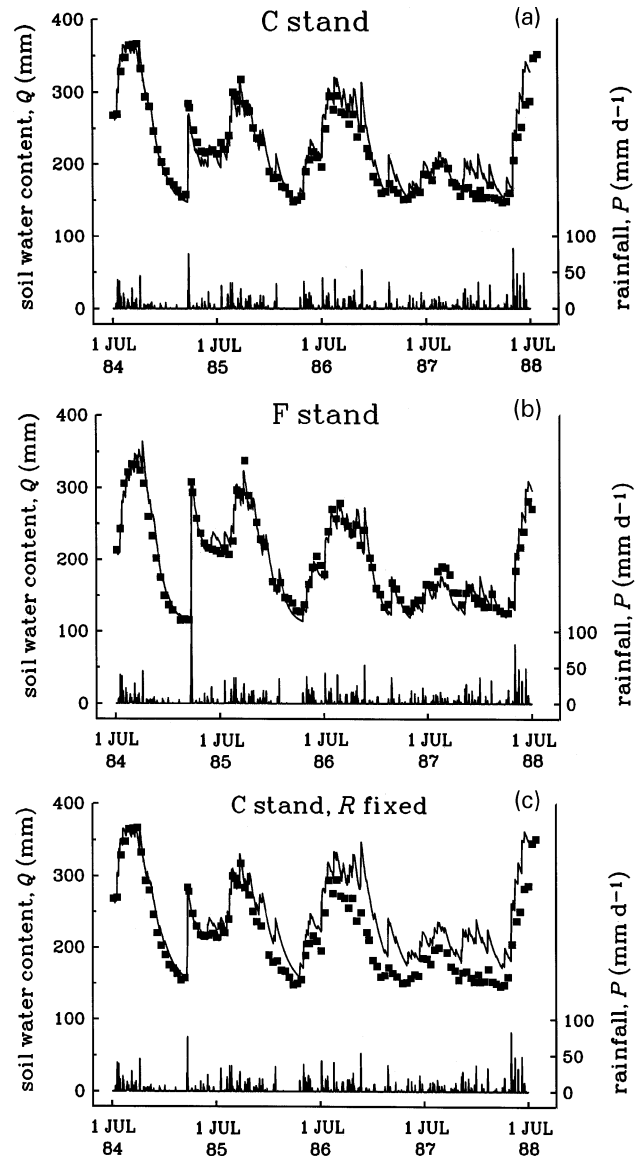


Figure 3. Predicted (upper line) and measured (\blacksquare) soil water contents in the top 2 m, and measured incident rainfall (lower plot), over a 4-year period for (a) the C stand, and (b) the F stand. Parameter values are given in Table 2. See Myers and Talsma (1992) for details of soil water measurements. (c) As for (a), but with root biomass (R) fixed at its initial value instead of proportional to leaf area; in this case, water use is significantly underestimated.

physiologically reasonable. The value of σR_0 for both stands (0.02 day $^{-1}$) compares with values of 0.015 day $^{-1}$ and 0.05 day $^{-1}$ for sorghum growing on a vertisol and alfisol, respectively (Monteith 1986). I am unaware of other estimates of this parameter for trees.

The value of ϵ/q_0 (0.26 – 0.28 kg H $_2$ O MJ $^{-1}$ kPa $^{-1}$) is intermediate between those reported by Monteith (1989) for temperate cereals (about 0.4 kg H $_2$ O MJ $^{-1}$ kPa $^{-1}$) and for C $_4$ cereals and tropical/sub-tropical legumes (about 0.17 kg H $_2$ O MJ $^{-1}$ kPa $^{-1}$). There are few published data on ϵ/q_0 for trees; most estimates of ϵ and q are on incomparable timescales, and

Table 2. Parameter values for the C and F stands, giving $r^2 = 0.93$ and 0.96 , respectively (Figures 3a and 3b). See Table 1 for parameter definitions.

Parameter	C	F
k ($\text{m}^2 \text{ground m}^{-2} \text{leaf}^1$)	0.5	0.5
s ($\text{kg H}_2\text{O m}^{-2} \text{day}^{-1} = \text{mm day}^{-1}$) ²	0.5	0.5
ϵ/q_0 ($\text{kg H}_2\text{O MJ}^{-1} \text{kPa}^{-1}$) ³	0.28	0.26
σR_0 (day^{-1}) ³	0.02	0.02
d_s (m) ⁴	2	2
Q_{\min} ($\text{kg H}_2\text{O m}^{-2} = \text{mm}$) ³	140	110
Q_{\max} ($\text{kg H}_2\text{O m}^{-2} = \text{mm}$) ⁵	365	365

¹ McMurtrie et al. (1992).

² McMurtrie et al. (1990a).

³ Best fit values.

⁴ Myers and Talsma (1992).

⁵ Maximum observed soil water content.

q_0 values are rarely quoted. An exception is the study by Baldocchi et al. (1987), who estimated short-term (half-hour) canopy values of ϵ and q_0 in a relatively well-watered oak-hickory forest (*Quercus* and *Carya* spp.) using eddy correlation techniques. Their estimates of ϵ (4–8% photosynthetically active radiation conversion efficiency, or about 1.75 – $3.5 \text{ g CO}_2 \text{ MJ}^{-1}$ total radiation) and q_0 ($10.9 \text{ g CO}_2 \text{ kg}^{-1} \text{ H}_2\text{O kPa}$) imply $\epsilon/q_0 = 0.16$ – $0.32 \text{ kg H}_2\text{O MJ}^{-1} \text{kPa}^{-1}$, with a mid-range value (0.24) comparable to the present estimate for *P. radiata*.

The assumption that root biomass increased in proportion to leaf area was important in obtaining close agreement between predicted and measured soil water contents throughout the 4-year period. When the rate constant for water extraction was held fixed at its initial value (σR_0), predicted soil water contents were consistently higher than measured values, particularly during the last two years of the simulation (Figure 3c), as a result of the underestimation of water use on water-limited days.

Discussion

Alternative approaches

McMurtrie and Landsberg (1992) and McMurtrie et al. (1992) applied a more detailed model of canopy photosynthesis and water use (BIOMASS, McMurtrie et al. 1990a) to the same stands. They also obtained a good fit between predicted and measured soil water contents over the same 4-year period. In their simulations, the canopy was represented by three layers, each divided into sunlit and shaded fractions, and the soil was represented by two layers. Calculations of leaf CO_2 exchange were based on the detailed physiological model of Farquhar and von Caemmerer (1982) together with the empirical stomatal conductance model of Ball et al. (1987). It was assumed that conductance was unaffected by soil water deficit until plant-available water declined to 40% of that at field capacity; below that point, conductance was assumed to decline linearly with plant-available soil water (McMurtrie et al. 1990a).

My results indicate that water use by these *P. radiata* stands can also be predicted successfully by a simpler scheme. Light-limited growth is calculated directly from intercepted radiation, rather than by integrating leaf-scale photosynthesis through the canopy. The effects of soil and air water deficits are expressed directly in terms of transpiration and growth and their relationship in terms of water-use efficiency, rather than in terms of stomatal conductance explicitly. The canopy and soil are each represented as a single layer, rather than several layers. Given that about 85% of the fine root system in these stands was found in the A horizon (0–40 cm depth), the apparent success of a single-layer soil model with effective depth $d_s = 2 \text{ m}$ may reflect the importance of water extraction by the remaining 15% of the root system during summer droughts (Myers and Talsma 1992).

Root/foliage allocation

The present simulations used measured (and BIOMASS-estimated) leaf areas as inputs to evaluate the basic assumptions of the RESCAP model. Clearly, it is desirable to predict L_c from the model itself, on the basis of additional assumptions for growth allocation. RESCAP places equal emphasis on the role of leaves in light interception and the role of roots in supplying water, so that root/foliage allocation plays a key functional role in the RESCAP approach.

The assumption that R/L_c was constant resulted in approximate co-limitation of growth by light and water over the 4-year simulation; the proportion of days on which predicted growth was water-limited was 54 and 49% in the C and F stands, respectively. A more functional approach, and one that fits naturally into the RESCAP model, would be to assume that root/foliage allocation is a positive function of G_L/G_w , the ratio of light- to water-limited growth on any given day. By incorporating the role of roots in nutrient uptake, this approach could be extended to include nutrient-limited growth. Experimental studies (e.g., Linder 1985, Dalla-Tea and Jokela 1991) and theory (Dewar 1996) suggest that nutrient limitations on forest productivity may operate primarily through allocation to foliage growth and light interception, rather than through the efficiency of light utilization (ϵ).

Validity of $q \propto 1/D$

The assumption that vapor pressure deficit is the main determinant of water-use efficiency is expected to be valid more often for forests than for crops. For aerodynamically rough canopies that are well coupled to the atmosphere, transpiration is relatively insensitive to solar radiation (Jarvis and McNaughton 1986), as is the case for *P. radiata* canopies (Kelliher et al. 1990).

The physiological basis for $q \propto 1/D$ may be understood at the leaf scale in terms of the conservative nature of the ratio c_i/c_a of intercellular to atmospheric $[\text{CO}_2]$ (e.g., Sinclair et al. 1984). However, because stomata close in response to increasing vapor pressure deficit, the ratio c_i/c_a is not strictly constant as D varies. Future applications of RESCAP might consider the modified assumption $q \propto (1/D + 1/D_0)$, where D_0 is an empirical constant, as suggested in the Appendix on the basis of a recent

model for stomatal conductance (Leuning 1995). This modification takes into account the stomatal response to D and its effect on c_i/c_a , and implies that q approaches a non-zero value as D increases.

A central assumption in RESCAP is that q has the same value whether water is limiting or not. The physiological basis for this assumption at the leaf scale is that the c_i/c_a ratio is independent of water supply. McMurtrie et al. (1992) observed this to be the case for the *P. radiata* stands in the BFG experiment. In the context of Leuning's (1995) stomatal model (Appendix), one interpretation is that bimodal (i.e., patchy) stomatal closure occurs when the supply of water is limiting, resulting in a proportional decline in stomatal conductance and photosynthesis.

Applicability of the model to other stands

The reduction in canopy transpiration caused by wet foliage was ignored in the present application. Following McMurtrie et al. (1990a), this effect may be incorporated into Equation 10 by replacing T with $\max(0, 1 - I/E_{\text{pen}})T$, where E_{pen} is the Penman rate of evaporation from a wet surface (Monteith 1965). The value of I/E_{pen} , the fraction of the day during which the canopy is wet, was estimated to be small for these *P. radiata* stands, but may be significant when rainfall occurs as frequent showers. Understorey evapotranspiration was also ignored, but can be a major component of the water balance of open stands (Kelliher et al. 1990, Whitehead and Kelliher 1991). These components of water balance may need to be included when applying RESCAP to other stands.

Conclusion

In view of the close physiological link between water and CO_2 uptake, the results of this study suggest that stand growth may be realistically simulated by relatively simple models based on conservative values for the light utilization coefficient (ϵ) and the normalized water-use efficiency (q_0). The physiological basis for this approach can be explored with more detailed models that explicitly represent leaf-scale fluxes of CO_2 and water; both approaches are useful and complementary.

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Appendix—Leaf-scale water-use efficiency

Let A_{leaf} , T_{leaf} and g denote net leaf CO₂ exchange, transpiration and stomatal conductance for CO₂, respectively. For a leaf that is well coupled to the atmosphere (i.e., boundary layer conductance much greater than g), the leaf-scale WUE is

$$q_{\text{leaf}} = \frac{A_{\text{leaf}}}{T_{\text{leaf}}} = \frac{g(c_a - c_i)}{1.6gD} = \frac{c_a}{1.6D} \left(1 - \frac{c_i}{c_a} \right), \quad (\text{A1})$$

where c_i and c_a are the intercellular and atmospheric [CO₂], respectively. Leuning (1995) proposed a stomatal conductance model that combines the correlation between g and A_{leaf} (Ball et al. 1987) with the hyperbolic function of Lohammer et al. (1980) describing stomatal response to humidity deficit:

$$g = a_1 \frac{A_{\text{leaf}}}{c_a} (1 + D/D_o)^{-1}, \quad (\text{A2})$$

where a_1 and D_o are empirical constants (the parameters g_o and Γ in Leuning's model have been set to zero for simplicity). With $A_{\text{leaf}} = g(c_a - c_i)$, Equation A2 implies that

$$\frac{c_i}{c_a} = 1 - \frac{1}{a_1} \left(1 + \frac{D}{D_o} \right), \quad (\text{A3})$$

and substituting this expression into Equation A1 gives

$$q_{\text{leaf}} = \frac{c_a}{1.6a_1} \left(\frac{1}{D} + \frac{1}{D_o} \right). \quad (\text{A4})$$

From this analysis it may be seen that the assumption $q \propto 1/D$ of RESCAP is equivalent, at the leaf scale, to neglecting the stomatal response to humidity deficit and its effect on c_i . The effect of including the humidity response is that q_{leaf} approaches a non-zero value (rather than zero) as D increases.

