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High-Latitude Rainforests and Associated Ecosystems of the West Coast of the Americas

Climate, Hydrology, Ecology,
and Conservation

With 83 Illustrations



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6. Constraints on Terrestrial Primary Productivity in Temperate Forests Along the Pacific Coast of North and South America

R.H. Waring and W.E. Winner

When residents of the temperate forest regions along the Pacific Ocean of North and South America exchange places, their first impression is that the climates of the two continents are similar but out of phase. The second impression is that the forests, although predominantly evergreen in both places, differ in form. Broadleaf, broad-crowned trees are common in the south; whereas narrowleaf, narrow-crowned trees occur in the north. In both regions, the climates are moderated by the Pacific Ocean. This maritime influence allows considerable photosynthesis by evergreen species beyond the normal growing season (Alaback, 1991; Waring & Franklin, 1979).

To assess the implications of current or changing climate in either region requires a model that accounts for how various climatic factors affect growth-related processes. To generalize for the myriad combinations of topography, climate, and soils present, we attempt to interpret environmental factors in an operational sense (Mason & Lagenheim, 1957) as they directly initiate a response that impairs or improves a plant's ability to: 1) capture light and carbon dioxide for photosynthesis; 2) maintain favorable water relations; 3) sequester nutrients; and 4) grow and maintain structure.

A general ecosystem model developed by Running and colleagues at the University of Montana incorporates these operational principles and allows reliable predictions of the growth of coniferous forests throughout

much of the western United States (Running, 1994; Running & Coughlan, 1988; Running & Gower, 1991). We extracted basic relationships from this model that couple photosynthesis and growth to the availability of light, water, and nutrients and tested the ability of a simplified model to predict forest growth across a steep climatic gradient in Oregon (Runyon, Waring, Goward, & Welles, 1994; Waring et al., 1993).

In this chapter, we present the logic behind the simplified model and summarize the results of field comparisons. Extrapolation of some components of the simplified growth model provides insights into how a changing climate associated with continued accumulation of CO₂ and other greenhouse gases in the earth's atmosphere might alter forest productivity in the Pacific Northwest and in the temperate forest region of Chile.

General Model Principles

The forest-growth component of the FOREST-BGC ecosystem model accumulates daily estimates of photosynthesis and subtracts the cost of maintenance respiration accumulated throughout a year. The remaining carbon resource is distributed above and below ground, based on the relative availability of nitrogen for leaf growth and an integrated measure of drought stress (Running & Gower, 1991).

Photosynthesis

The absorption of visible light by leaves, branches, and whole canopies has received much study in the last two decades. A number of models estimate light interception and maximum rates of photosynthesis for individual strata of leaves in canopies (Wang & Jarvis, 1990). In mild climates, photosynthesis is a linear function of light absorption by the canopy (Wang, McMurtrie, & Landsberg, 1992).

More complex simulation models allow for variation in the rates of photosynthesis as a function of leaf nitrogen content (or the primary photosynthetic enzyme), soil-water availability, humidity deficits, ambient temperature, and carbon dioxide concentrations (McMurtrie, Comins, Kirschbaum, & Warg, 1992; Raupach, 1989). The data requirements for such models, however, are rather demanding and thus limit their application. We sought a simplified model that generalized responses for whole canopies and assumed thresholds common for a wide range of species (Running & Coughlan, 1988).

Water Relations

Water relations of plants are a function of the supply of water in the soil and the demand from transpiration, balanced against limitations in the

rate of transport through the vascular system. Under cloudy and cool conditions, plants have little difficulty in maintaining good water relations. Increasing transpiration beyond certain rates, however, causes some portions of a plant's vascular system to fail and lose hydraulic efficiency. When this happens, stomata begin to close, limiting both transpiration and photosynthesis (Tyree & Sperry, 1988). The threshold when stomata begin to close differs among species. Most temperate forest species in the Pacific Northwest close their stomata completely when the humidity deficit of the atmosphere exceeds 2.5 kPa, as shown in Figure 6.1.

Soil drought can also lead to partial or complete stomatal closure. Under drying conditions, roots extract water from the surface soil downward. Once tree roots have extracted most of the available soil water, tensions increase in the plant's vascular system during the night, when no transpiration is occurring (Waring & Cleary, 1967). As predawn tensions increase, the ability of stomata to open during the day is progressively restricted until complete closure occurs, as shown in Figure 6.2.

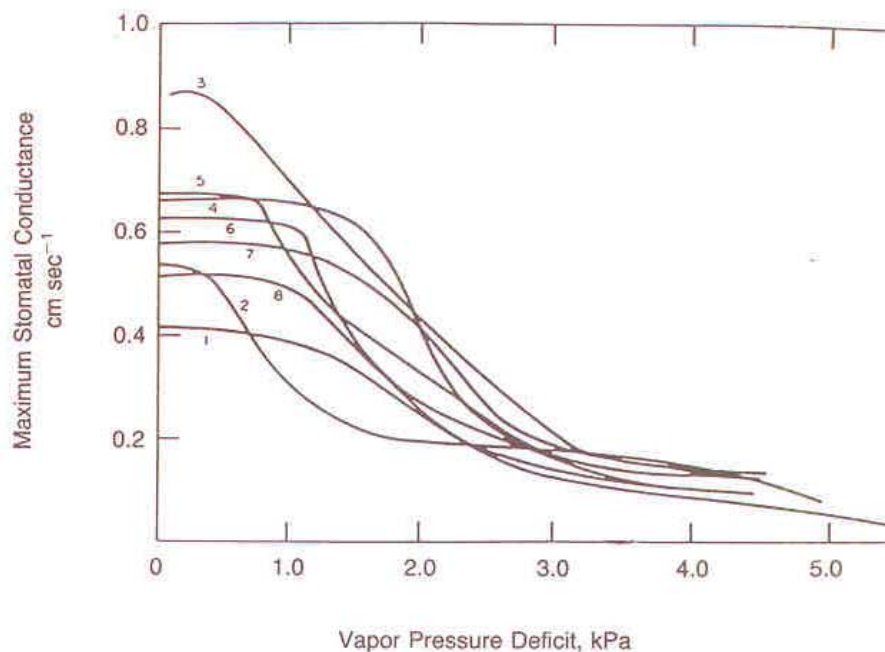


Figure 6.1. The maximum conductance of various species in the Pacific Northwest differ in relation to water-vapor deficits of the air, but most species close their stomata at high deficits. Conifers: 1) *Pseudotsuga menziesii*, 2) *Tsuga heterophylla*; deciduous trees: 3) *Cornus nuttallii*, 4) *Acer macrophyllum*; evergreen broadleaf trees: 5) *Castanopsis chrysophylla*; deciduous shrubs: 6) *Acer circinatum*; evergreen broadleaf shrubs 7) *Rhododendron macrophyllum*, 8) *Gaultheria shallon*. From Waring and Schlesinger (1985).

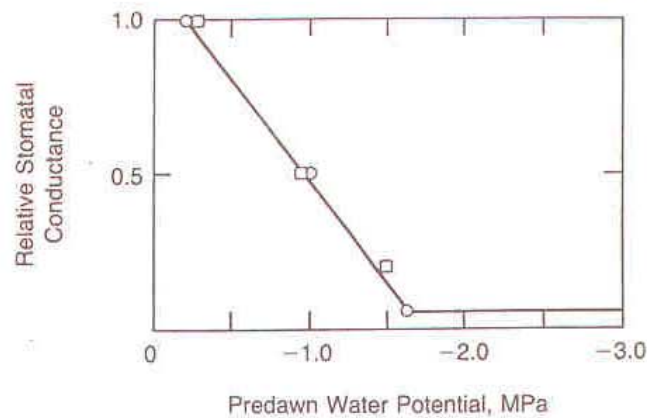


Figure 6.2. As soils dry, predawn water potentials in Douglas fir decrease. Maximum relative stomatal conductance during the day also decreases until complete closure is attained at -1.6 MPa. From Waring and Schlesinger (1985).

Below-freezing air temperatures and cold soil temperatures also restrict the uptake of water and the degree that stomata open. Conifers in the Pacific Northwest show some differences in sensitivity to cold soil temperatures only up to about 10°C , as shown in Figure 6.3. All the

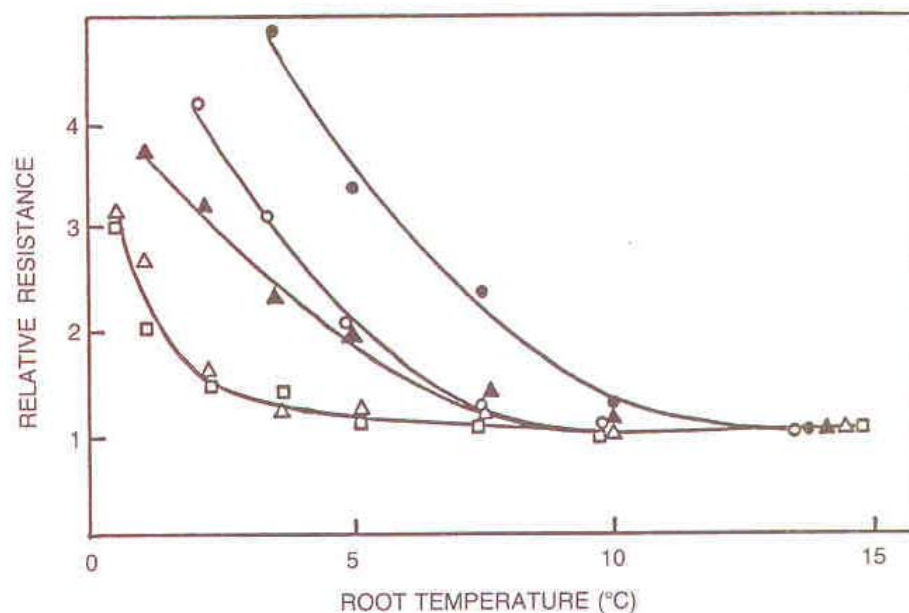


Figure 6.3. Five species of Northwest conifers—*Abies amabilis* (□), *A. procera* (△), *Thuja plicata* (▲), *Tsuga heterophylla* (○), and *Pseudotsuga menziesii* (■)—show differences in their relative resistance to water uptake when root temperatures are only below 10°C .

interacting factors that limit stomata opening were combined into a simulation model by Running, Waring, and Rydell (1975) to predict daily transpiration. Models with both hourly and daily resolution have been compared and proved in close agreement (Running, 1984). The equations and defined thresholds that apply for this water balance model underlie the current FOREST-BGC ecosystem simulator.

Nutrition

In the Pacific Northwest, nitrogen is generally the most common element limiting growth. Because of its organic origin, nitrogen is concentrated in the upper soil horizons. When drought occurs, roots must extract water from lower horizons, causing the concentration of nitrogen in the sap stream to decrease significantly even if water uptake is not affected (Goulden, 1991; Stark, Essig, & Baker, 1989). The resulting decrease in the flux of nitrogen to leaves limits further growth of foliage much more than it does photosynthesis. When nutrients are not readily available, canopy development is restricted and the ability to absorb solar radiation is reduced. Generally, there is also an increase in the proportion of carbon allocated to root growth (Mooney, 1972; Running & Gower, 1991; Waring & Schlesinger, 1985).

Once physiological thresholds are established, as shown in Table 6.1, constraints on the utilization of intercepted photosynthetically active radiation (IPAR) can be calculated in units of MJ m^{-2} for each climatic variable when requisite data are available. Such an analysis was performed across a steep climatic gradient in Oregon at 44°N latitude; see Figure 6.4. In the coastal zone, where deciduous and evergreen forests both grow (sites 1 and 1A, Figure 6.4), climatic constraints other than cloud

Table 6.1. Criteria for Sequentially Reducing Intercepted PAR Based on Physiological Thresholds Applicable to All Major Tree Species in Oregon. From Runyon et al., 1994

Freezing Temperatures

- If less than -2°C , assume no radiation utilized for 24-hour period
-

Soil Drought

- If predawn water potential less than -1.5 MPa , assume no radiation utilized for 24-hours
 - If predawn water potential is between -1.0 and -1.5 MPa , assume half radiation utilized
-

Vapor-Pressure Deficits (VPD)

- If VPD exceeds 2.5 kPa , assume no radiation utilized for hour period
 - If VPD is between 1.5 to 2.5 kPa , assume half radiation utilized for hour period
-

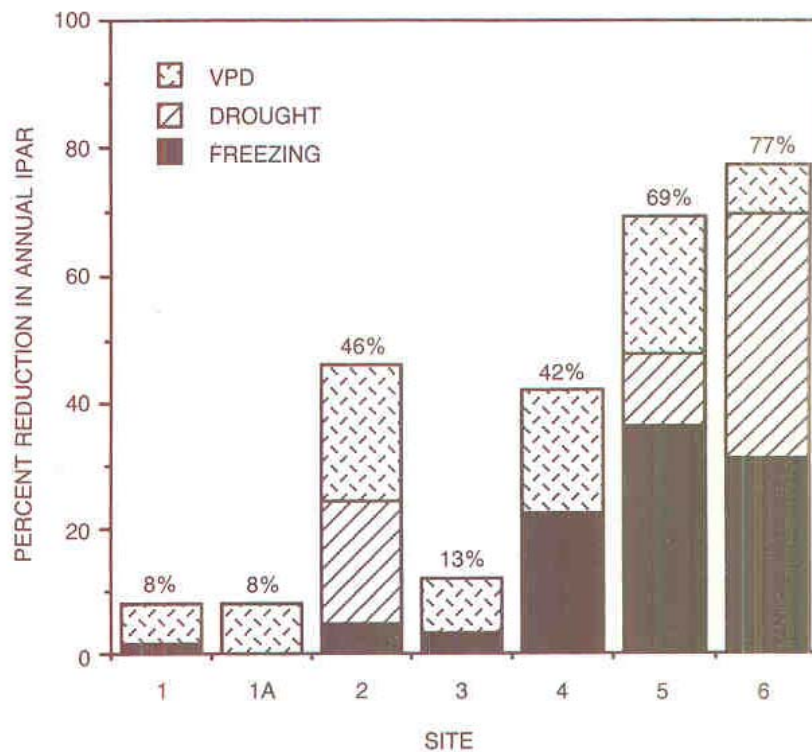


Figure 6.4. The fraction of intercepted radiation not utilized by various forests aligned along a transect (44°N latitude) from coastal rainforests (site 1) across a central valley (site 2) up and over the Cascade Range (sites 3–6) indicate that freezing temperatures, drought, and excessive vapor-pressure deficits constrain photosynthesis to different extents. From Runyon et al. (1994).

cover limit the utilization of intercepted light by less than 10% annually. In the central valley (site 2), a dense coniferous forest mixed with oak uses only about 50% of the annual intercepted PAR, due to limitations from frost, drought, and extreme humidity deficits. To the east of the valley, in the foothills of the Cascade Mountains, precipitation increases and climatic constraints limit IPAR less than 15% annually. In the subalpine zone (site 4) and other sites (sites 5 and 6) in the rainshadow of the Cascade Mountains, 50% to more than 75% of the intercepted radiation is not utilized, due to unfavorable climatic conditions during the year.

Respiration

As trees age, the amount of respiring tissue accumulates. The sapwood, which contains living cells, converts completely to inactive heartwood after a specific number of years (Pothier, Margolis, & Waring, 1989). For

young stands of conifers, the maintenance cost of sapwood as a percentage of total annual carbon uptake is generally small, ranging from 5% to 20%, as shown in Figure 6.5. Once height growth slows or ceases, new limb production stops. Additional above-ground growth is restricted to the elongation of previously formed limbs, diameter growth, and the replacement of foliage. The total stand leaf area decreases as the forest opens (Ryan & Waring, 1992). The reduction in leaf area counterbalances to a large extent the increase in sapwood volume associated with increasing tree height. Branch length increases as a consequence of slowed height growth and canopy opening. The hydraulic conductivity for water movement is reduced in such branches and makes stomata more sensitive to humidity deficits (Waring & Silvester, 1994; Yoder et al., 1994). For these reasons, old-growth forests exhibit photosynthetic rates 20% to 30% less than younger stands (Ryan, 1991; Ryan & Waring, 1992; Yoder et al., 1994).

Above-Ground Growth and Utilized Light

When the resource-constrained light-absorption model is applied to forests still growing in height, a linear correlation with estimated annual

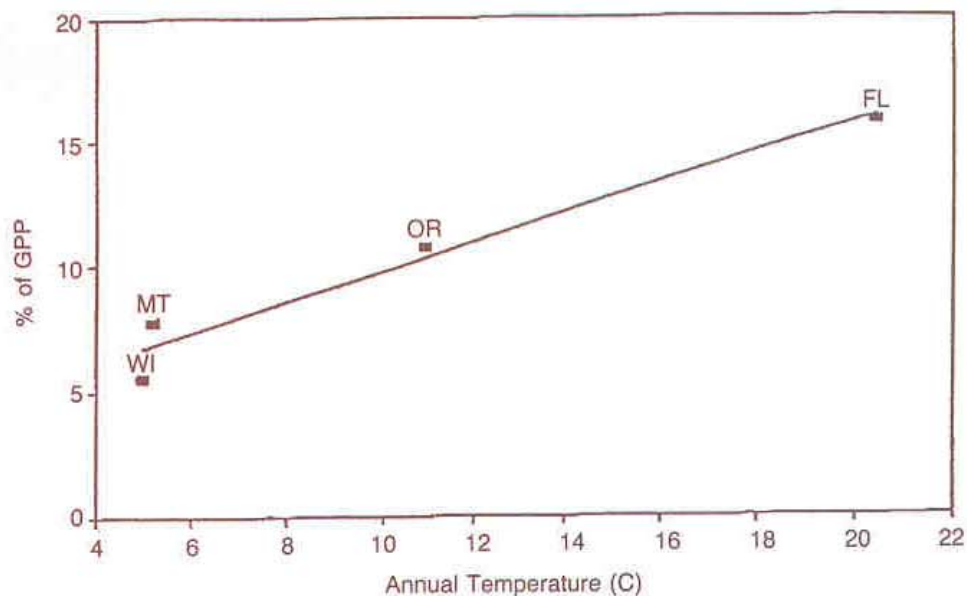


Figure 6.5. The percentage of total gross primary production (GPP) required for maintaining live cells in sapwood increases linearly with annual temperature according to measurements made on pine forests in the States of Wisconsin (WI), Montana (MT), and Florida (FT) and in Douglas-fir and western hemlock forests in Oregon (OR). From M.G. Ryan et al. (1995).

utilized light and above-ground growth was observed across a broad range of environments, as shown in Figure 6.6. No specific threshold for soil-temperature responses was established eliminate because most species in the Pacific Northwest have considerable tolerance for cool soils, perhaps reflecting their boreal origins (Waring & Franklin, 1979). Old-growth forests (1, Figure 6.6), because of reduced photosynthetic capacity and increased maintenance respiration, grow much less than younger stands with similar leaf area (Waring & Franklin, 1979).

Effects of Climatic Change on Forest Growth in the Pacific Northwest

From a sequential analysis of the factors constraining photosynthesis (Table 6.1), climatic warming combined with increased drought should

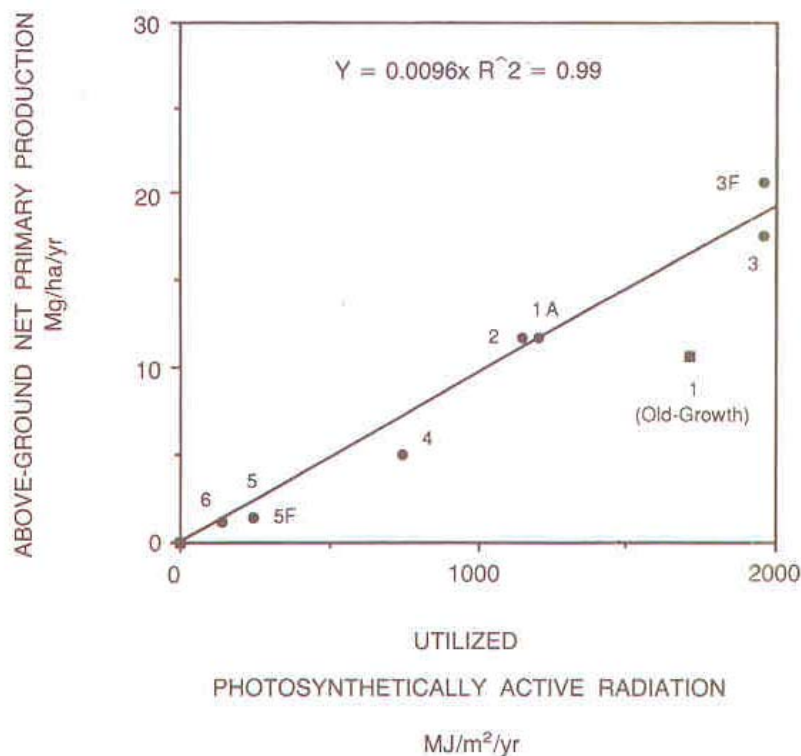


Figure 6.6. Estimated aboveground Net Primary Production correlates well with estimates of photosynthetically active radiation that can be utilized by a range of vegetation across a steep climatic gradient in western Oregon. Letters (A) refer to a deciduous forest of alder, and (F) indicate stands that were fertilized with nitrogen. The old-growth stand (1) was excluded from the regression. It utilized 30% less PAR than indicated. Deducting an additional 100 MJ m^{-2} for increased maintenance respiration compared to an adjacent 120 year-old stand brings the calculated production in line with that observed. From Runyon et al. (1994).

lead to a reduced fraction of IPAP being utilized by forests in the Pacific Northwest. Slower-growing species better adapted to drought should invade and replace more mesic types of forests as the total area occupied by forests contracts in comparison to the current distribution (Franklin & Dyrness, 1973). The transition could be abrupt, spurred by outbreaks of insects, disease, and fire across much of the region (Waring, Savage, Cromack, Jr., & Rose, 1992; Waring & Schlesinger, 1985).

Application of the Light Utilization Model in Chile

In the last 2 decades, much of the native forests of Chile have been logged and the land replanted with introduced species such as *Pinus radiata* (Lara, 1985). The pine forests are planted very densely and absorb >95% of all visible light, as do coniferous species composing forests on the west side of the Cascade Range in the states of Oregon and Washington (Runyon et al., 1994; Waring & Franklin, 1979). Read and Hill (1985) reported that in 21 sampled native Chilean forests, >30% of the light penetrated to the forest floor. The temperate forest region in Chile has a milder climate, with more uniform distribution of rainfall, than the Pacific Northwest (Alaback, 1991; Lawford, 1995). The milder climates result in an extra month of growing season (Goward, Dye, Kerber, & Kalb, 1987). During the growing season, however, the climate is much cooler than at a comparable latitude in the Pacific Northwest. The mild and moist climate in the mid-coastal zone of Chile permits plantations of *Pinus radiata* to produce wood volumes from 22–24 m³ ha⁻¹ yr⁻¹. On the other hand, second-growth stands of the fastest-growing native species (*Nothofagus obliqua* and *N. alpina*) produce only 12–14 m³ ha⁻¹ yr⁻¹ (Schmidt & Lara, 1985).

Why might native species in Chile form more open canopies than introduced species and generally grow more slowly? One possibility is that most of the native flora is less than perfectly adapted to the current climate as a result of being derived from subtropical stock (Axelrod, Kalin-Arroyo, & Raven, 1991; Raven & Axelrod, 1974). Related genera in New Zealand derived from subtropical origin exhibit a temperature optimal for photosynthesis of 27°C, as compared to 20°C for Pacific Northwest conifers (refer to Table 6.2). Even presumably well-adapted, relatively fast-growing species from Chile such as *Nothofagus obliqua* and *N. alpina* have temperature optima of 23°C, which is well above mean monthly temperatures during the growing season recorded within most of the current range of these species (Alaback, 1991; Read & Busby, 1990; Read & Hill, 1985).

We infer that cool soil temperatures provide a much greater constraint on the growth of most Chilean tree species than equivalent temperatures do on Northwest conifers (Figure 6.3). Unfavorably cool soil temperatures can restrict stomatal opening, photosynthesis, the growth of roots,

Table 6.2. Optimum Temperature for Photosynthesis Compared with Actual Mid-summer Temperatures for Five Genera of Native New Zealand and North American Tree Species. From Hawkins and Sweet, 1989

Species	Optimum Temperature, °C	Mid-Summer Temperature, °C	Difference, °C
New Zealand			
<i>Agathis australis</i>	27.0	22.2	4.8
<i>Dacrycarpus dacrydiodes</i>	27.0	17.9	9.1
<i>Dacrydium cupressinum</i>	27.0	16.8	10.2
<i>Nothofagus solandri</i>	27.0	17.0	10.0
<i>Podocarpus totara</i>	27.0	21.5	5.5
Mean	27.0	19.1	+7.9
North America			
<i>Larix decudua</i>	17.0	19.0	-2.0
<i>Pinus radiata</i>	23.0	21.0	2.0
<i>Pseudotsuga menziesii</i>	21.0	20.2	0.8
<i>Sequoia sempervirens</i>	19.0	17.0	2.0
<i>Tsuga heterophylla</i>	18.0	20.2	-2.2
Mean	19.6	19.4	+0.2

and the uptake of nutrients (Dulucia, 1987; Kramer, 1983). The largest species of *Agathis* (*A. australis*) is very sensitive in its stomatal response to modest humidity deficits when soil temperatures are as high as 15°C. When soils are artificially warmed to 25°C, stomata remain open to much increased humidity deficits (2.5 kPa versus 1.5 kPa; Silvester, University of Waikato, personal communication). Seasonal variations in the maximum observed stomatal conductance also mirror changes in soil temperature (Silvester, personal communication). *Pinus radiata* is sensitive to soil temperatures up to 15°C (Babalola, Boersma, & Youngberg, 1968; Kaufmann, 1977). We might expect many Chilean tree species, given their subtropical origin, to be physiologically constrained at soil temperatures below 20°C.

If native tree species of Chile exhibit similar sensitivity to humidity deficits as *Agathis* in New Zealand at current soil temperatures, then the thresholds at which photosynthesis should be set in our model would be reduced by more than half that assigned for species in the Pacific Northwest (Table 6.1). Other processes, such as maintenance respiration and root growth initiation at the start of the growing season, may also be restricted by cooler temperatures, but these effects are likely to be less important than reductions in photosynthesis, given the generally cool temperatures observed throughout most of the year (Alaback, 1991).

The strong maritime influence in Chile buffers against extremely cold temperatures, allowing plantations of eucalyptus and Monterey pine to be established at the lower elevations in the Andes. In the Pacific Northwest,

subfreezing winter temperatures occur sufficiently often to prevent successful plantation of these species, even along the Pacific coast. One might expect in the temperate-forest region of Chile that Northwest conifers such as Douglas fir would not experience sufficient cold temperatures to meet their chilling requirements. This is not the case, however, because young Douglas fir can be observed growing more than a meter in height a year, side by side with eucalyptus and Monterey pine in the Andes at 41°S latitude (Waring, personal observation with photographic evidence available).

Effects of Climatic Change on the Temperate Forests of Chile

If global warming were to increase the growing-season temperature in Chile, native tree species might be expected to respond far differently from species in the Pacific Northwest. We speculate that an increase in temperature would improve the ability of Chilean trees to take up water and nutrients from soils and increase their tolerance to atmospheric humidity deficits. Although a decrease in summer precipitation in Chile is not predicted in climate models (Revkin, 1988), if drought were to occur, it should be less extreme than in the Pacific Northwest, because Chilean forests receive at present from 10% to 25% of their annual precipitation during summer months, whereas forests in the Pacific Northwest receive only 3% to 15% of annual precipitation during the same interval (Alaback, 1991). Other factors may contribute to changes in forest composition, but to assess these requires different kinds of models that account for competition, reproduction, dispersal, introduction, and extinction of species.

Conclusions

With an environmentally constrained light-absorption model, we quantified the influence of frost, drought, and humidity deficits upon photosynthesis and growth across a steep climatic gradient in Oregon. When account was made for reduced utilization of intercepted light due to partial or complete stomatal closure, the solar conversion efficiency was similar for all types of Pacific Northwest coniferous forests. Because Northwest conifers are derived from boreal stock, they show little restriction on water uptake or growth once soil temperatures exceed 10°C. In contrast, the native species of Chilean forests are derived mainly from subtropical stock and thus are likely to be restricted in their performance at soil temperatures below 20°C. If climatic warming occurs in Chile, improved growth of native species is predicted from our model. The opposite prediction applies to the Pacific Northwest forests, because drought is expected to have more impact.

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