

Adaptive Significance of Evergreen vs. Deciduous Leaves: Solving the Triple Paradox

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Patterns in the dominance of evergreen vs. deciduous plants have long interested ecologists, biogeographers, and global modellers. But previous models to account for these patterns have significant weaknesses. Bottom-up, mechanistic models – based on physiology, competition, and natural selection – have often been non-quantitative or restricted to a small range of habitats, and almost all have ignored belowground costs and whole-plant integration. Top-down, ecosystem-based models have succeeded in quantitatively reproducing several patterns, but rely partly on empirically derived constants and thresholds that lack a mechanistic explanation. It is generally recognized that seasonal drought can favor deciduous leaves, and that infertile soils can favor long-lived evergreen leaves. But no model has yet explained three great paradoxes, involving dominance by 1) evergreens in highly seasonal, boreal forests, 2) deciduous larch in many nutrient-poor peatlands, and 3) evergreen leaf-exchangers in nutrient-poor subtropical forests, even though they shed their leaves just as frequently as deciduous species. This paper outlines a generalized optimality model to account for these and other patterns in leaf longevity and phenology, based on maximizing whole-plant carbon gain or height growth, and building on recent advances in our understanding of the quantitative relationships of leaf photosynthesis, nitrogen content, and mass per unit area to leaf life-span. Only a whole-plant approach can explain evergreen dominance under realistic ecological conditions, or account for the boreal paradox, the larch paradox, the leaf-exchanger paradox, and expected shifts in shade tolerance associated with leaf phenology. Poor soils favor evergreens not merely by increasing the costs of nutrient acquisition, but also by depressing the maximum rate of photosynthesis and thus the seasonal contrast in photosynthetic return between leaves adapted to favorable vs. unfavorable conditions. The dominance of evergreens in western North America beyond the coastal zone of mild winters and winter rainfall appears related to the unusually long photosynthetic season for evergreen vs. deciduous plants there. Future models for optimal leaf phenology must incorporate differences between evergreen and deciduous plants in allocation to photosynthetic vs. non-photosynthetic tissue, rooting depth, stem allometry, xylem anatomy, and exposure to herbivores and leaching, and analyze how these differences interact with the photosynthetic rate, transpiration, and nutrient demands of leaves with different life-spans to affect rates of height growth in specific microsites.

Keywords evergreens, deciduous trees, optimality models, leaf longevity, phenology

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1 Introduction

As long recognized (Grisebach 1872, Warming 1896, Schimper 1898) and now confirmed by satellite imagery (DeFries et al. 2000), evergreen broad-leaved trees dominate tropical rain forests and cloud forests in relatively aseasonal regions of the Americas, Africa, Madagascar, Australasia, and the Pacific (Fig. 1A). Evergreen, leathery-leaved shrubs and trees characterize temperate forests throughout much of the southern hemisphere, as well as Mediterranean scrub, slightly wetter sclerophyll forests, and even wetter temperate rain forests in areas of winter rainfall on the west sides of continents at mid-latitude. Evergreen, needle-leaved conifers dominate many boreal forests at high latitudes in the northern hemisphere. By contrast, deciduous broad-leaved trees characterize temperate forests at mid-latitudes in eastern North America, eastern Asia, and northwestern Europe (Fig. 1B). Tropical and subtropical areas with pronounced dry seasons but little thermal seasonality are mostly covered by seasonally deciduous forests and savannas.

What factors determine these broad patterns of community dominance by evergreen vs. deciduous plants? What advantages do evergreen or deciduous leaves provide in different climates or on different soils? These two questions have attracted much attention over the past 35 years. Ecologists are generally agreed that long-lived, evergreen leaves offer a potentially longer photosynthetic season than deciduous leaves, and reduce the amount of nutrients that must be absorbed each year from the soil. Deciduous leaves reduce transpiration and respiration during drought, and often have higher rates of photosynthesis per unit leaf mass. These respective advantages and disadvantages explain, at least in qualitative terms, why tropical rain forests with little seasonality in temperature or rainfall are dominated by evergreen trees; why seasonally dry forests and savannas in the tropics and subtropics are dominated by deciduous trees, as are cold temperate forests with frozen, effectively dry winters and warm, moist, productive summers; and why nutrient-poor bogs, peatlands, and sandy forests are usually dominated by evergreen trees and shrubs.

But there are other striking, seemingly contradictory patterns that previous models have been unable to explain. Why are boreal forests dominated by evergreens, when they are exposed to intense thermal seasonality and winter drought? Why do deciduous larches often dominate nutrient-poor bogs and swamps within the boreal zone? And why do evergreen leaf-exchangers dominate nutrient-poor sites in the seasonally dry subtropics, when they shed their leaves just as frequently as deciduous competitors on adjacent, more fertile sites?

I propose that existing models for the advantages of evergreen vs. deciduous leaves have been unable to provide satisfactory explanations for global patterns and the three paradoxes just mentioned because those models are non-quantitative, limited in scope to a small range of ecological communities, or – most importantly – because they ignore belowground costs and whole-plant integration. In this paper I present an alternative approach, based on economic analyses of how leaf longevity and phenology affect whole-plant growth and competitive ability, drawing implications for patterns in the ecological dominance of evergreen vs. deciduous plants. Based on recent photosynthetic data, I show that a whole-plant perspective is required to demonstrate an energetic advantage of evergreen vs. deciduous leaves in many circumstances, and that adopting such a perspective helps account for several previously unexplained patterns.

2 Review of Previous Cost/Benefit Models

Since 1966, nearly 40 key papers have addressed the adaptive significance of evergreen vs. deciduous leaves (Monk 1966, Mooney and Dunn 1970, Small 1972, Schlesinger and Chabot 1977, Schulze et al. 1977, Miller 1979, Miller and Stoner 1979, Chabot and Hicks 1982, Goldberg 1982, Sarmiento et al. 1985, Field and Mooney 1986, Woodward 1987, Arris and Eagleson 1989, 1994, DeLucia et al. 1989, Schlesinger et al. 1989, Waring and Franklin 1989, Gower and Richards 1990, Kikuzawa 1991, 1995, Hollinger 1992, Sobrado 1991, 1993, 1997, Prentice et al. 1992,

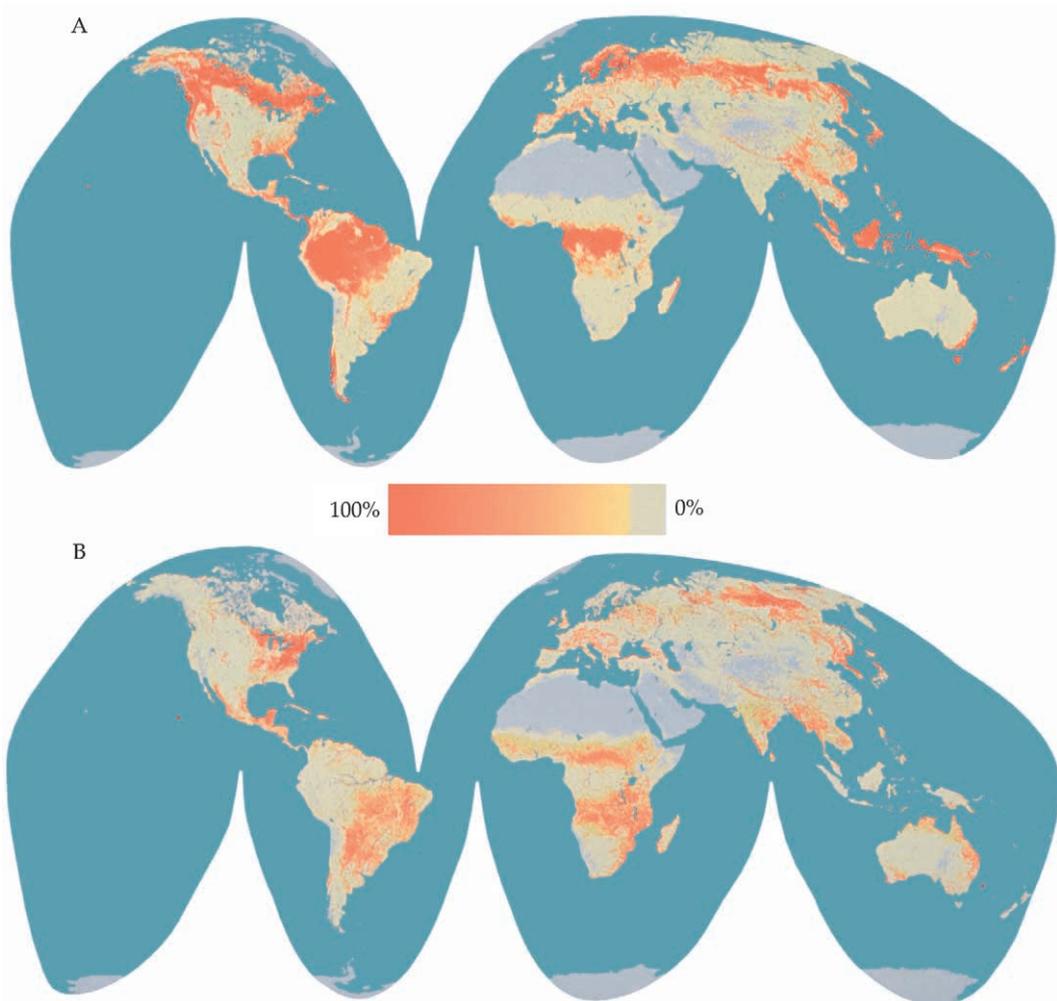


Fig. 1. Percent coverage by (A) evergreen and (B) deciduous trees based on analysis of satellite data (after DeFries et al. 2000). Note evergreen dominance of tropical and temperate rain forests, sclerophyll woodlands, Mediterranean scrub, temperate forests in the southern hemisphere, and most boreal forests, and deciduous dominance of tropical dry forests, savannas, steppes, cool temperate forests in the northern hemisphere, and larch swamps in central Siberia. The algorithm used by DeFries et al. (2000) misclassifies some areas of Mediterranean scrub and sclerophyll forests – especially in southeastern and southwestern Australia, and western North America – as dominated by deciduous trees, when they actually have an evergreen (but often sparse) canopy of trees and shrubs.

Reich et al. 1992, Piggott and Piggott 1993, Aerts 1995, Neilson 1995, Montague and Givnish 1996, Salleo et al. 1997, Zobel and Singh 1997, Damesin et al. 1998, Kloeppe et al. 1998, Lei and Koike 1998, Walters and Reich 1999, Namikawa et al. 2000). Several have proposed models to account for the distribution and/or dominance

of plants with one or the other leaf phenology. Broadly speaking, such models can be grouped into two categories based on their approach. *Bottom-up models* (e.g., Small 1972, Miller and Stoner 1979, Chabot and Hicks 1982, Kikuzawa 1991, Reich et al. 1992, Reich 1995, Montague and Givnish 1996) attempt to deduce from fun-

damental physiological constraints on leaf (and, occasionally, root) function whether competition would favor evergreen or deciduous plants in specific environments. *Top-down models* (e.g., Specht 1981, Arris and Eagleson 1985, Woodward 1987, Prentice et al. 1992, Neilson 1995, Haxeltine et al. 1996) use a “rule-based” approach, in which hydrological or nutrient-cycling constraints on stand function (e.g., evapotranspiration balancing with precipitation) – combined with rule-of-thumb parameters for the potential distributional limits of various growth forms, and inferences regarding which growth forms would outcompete others based on empirical data on growth rates – are used to predict the distribution of evergreen and deciduous communities. Top-down models have achieved considerable success in accounting for the distribution of different vegetation types at continental and global scales, and have even been incorporated in complex models (e.g., Foley et al. 1996, 1998, Kutzbach et al. 1996, Doherty et al. 2000, Levis et al. 2000) to predict responses of global climate and vegetation to shifts in atmospheric CO₂ levels or solar input. Their weakness is that some key parameters (e.g., thermal limits for broad-leaved deciduous trees) are derived from the actual distributions of particular growth forms and vegetation types – which these models then “predict”. Ultimate physiological and selective bases for these critical parameters are not sought. By contrast, bottom-up models aim to deduce the mechanistic and evolutionary foundations of critical differences between evergreen and deciduous plants, and then use these differences to understand observed plant distributions – but often do so in non-quantitative fashion. Bottom-up models thus provide deeper but less precise explanations of ecological patterns. The following review therefore focuses on these fundamental models, with just a few comments on current top-down models.

2.1 Bottom-up Models

Several bottom-up papers discuss one or more qualitative advantages of various leaf habits without incorporating them in an explicit cost-benefit model. Monk's (1966) classic paper pointed to the nutrient-conserving advantage of evergreen

leaves, whose elemental stocks must be replaced less frequently than those of annually shed deciduous leaves. Monk focused on the ecosystem effects of evergreen foliage, arguing (essentially in group-selection terms) it would reduce overall nutrient losses by involving year-round leaf fall and more slowly decomposing litter than that derived from deciduous foliage. Small (1972) had the crucial insight that evergreen leaves could give *individual* plants a competitive advantage, and showed how such leaves produced a greater photosynthetic return from a given amount of nitrogen over their lifetimes, even though they had a lower instantaneous photosynthetic rate per unit leaf mass than deciduous leaves. Many authors subsequently adopted Small's perspective (e.g., Schlesinger and Chabot 1977, Chabot and Hicks 1982, Goldberg 1982, Tyrrell and Boerner 1987, DeLucia et al. 1989, Schlesinger et al. 1989, Aerts 1990, 1995, Eckstein et al. 1999), but very few (Hollinger 1992, Montague and Givnish 1996) explicitly considered the associated allocation of energy to roots. Different levels of leaf nutrient conservation should strongly affect such root costs, which in turn should critically affect a plant's overall rate of growth and competitive ability (Givnish 1979, 1986a,b, Mooney and Gulmon 1979).

Mooney and Dunn (1970) advanced the first explicit, albeit qualitative cost-benefit model for leaf phenology, arguing – in the context of Californian chaparral – that leaves should be shed if their own expected respiratory loss during the hot, dry summer would exceed their own cost of replacement. They argued that the relatively short length of the unfavorable summer drought (at least on deep soils with substantial capacity for water storage) and relatively mild winters favored evergreen dominance in Mediterranean scrub with cool, moist winters and hot, dry summers. Summergreen deciduous species would be at a disadvantageous in such areas, given their shorter photosynthetic season and the dry conditions that limit carbon uptake during much of it. Based on these principles, Miller and his colleagues (Miller and Mooney 1974, Miller 1979, Miller and Stoner 1979) constructed the first – and, in many ways, the best – quantitative cost-benefit models for leaf phenology. They predicted that, in California, wintergreen shrubs should

dominate coastal sage with intense summer drought, evergreen shrubs should dominate inland chaparral, and summergreen shrubs and trees should dominate higher elevations with colder, longer winters. The Miller models are highly unusual for including the effects of belowground allocation on whole-plant growth via impacts on the length of the photosynthetic season and delivery of water and nutrients to the foliage. They predicted that evergreens should dominate winter-rainfall areas where the supply of absorbable nitrogen falls below $4 \text{ g m}^{-2} \text{ yr}^{-1}$.

Chabot and Hicks (1982) presented a cost-benefit model for optimizing the net carbon gain of evergreen vs. deciduous leaves, based on the annual rates of net photosynthesis per unit area of leaf cohorts during the favorable and unfavorable periods, the metabolic costs of manufacturing leaf tissue, and tissue losses caused by various agents:

$$\text{Net income} = \sum P_{fi}F + \sum P_{ui}U - C - W - H - S \quad (1)$$

where P_{fi} is daily carbon gain per unit area of leaves of age i during the favorable season; P_{ui} is the same for leaves during the unfavorable season; F is the length of the favorable season; U is length of the unfavorable season; C is the initial cost of producing a unit of leaf area in grams of photosynthate; W is the loss of leaf tissue and productivity due to stress during the unfavorable period, summed over leaf life-span; H is the similar loss due to herbivory; and S is photosynthesis stored but not transported.

Chabot and Hicks (1982) made a major contribution by showing that evergreen leaves have lower nitrogen concentrations; that plants need only replace the difference between their initial and final nutrient content upon abscission (ignoring losses to herbivores); and that both evergreen and deciduous leaves retranslocate roughly half of their N and P before abscission. However, their model was never used to address the relative magnitudes of phenological costs and benefits or how they vary with environmental conditions, so it is not clear whether the trade-offs discussed can actually favor evergreen or deciduous foliage, given the actual relationship of photosynthetic rate to leaf longevity (see next section). Further, by focusing on returns per unit area – not per unit leaf or plant mass – their model invites

spurious comparisons of the absolute growth by plants of different sizes. Competition should favor plants that maximize energetic return per unit investment, not per unit leaf area (Givnish 1988). Finally, Chabot and Hicks ignored belowground costs associated with absorbing water and nutrients, even though such costs are unavoidably tied to – and must be balanced against – the energetic benefits of any leaf trait affecting photosynthesis (Givnish and Vermeij 1976, Givnish 1979, 1984, 1986a,b, 1988, Mooney and Gulmon 1979).

Kikuzawa's (1991, 1995) model for optimal leaf longevity (Fig. 2) is, in many ways, the logical successor to that of Chabot and Hicks. As a first step, Kikuzawa asked how long should leaves be held in an aseasonal environment to maximize the net rate of photosynthetic gain per leaf mass, given an initial investment in leaf construction and linearly declining rates of leaf photosynthesis and respiration with leaf age. Kikuzawa argued that natural selection should maximize the rate of carbon gain per leaf mass, and that optimal leaf longevity is given by the abscissa at which a line through the origin is tangent to the cumulative returns curve (Fig. 2). He predicted that leaf longevity should increase with leaf construction cost and the rate of photosynthetic senescence, and decrease with peak photosynthetic rate.

This model is widely cited but deeply flawed. Structural leaf carbohydrates – cellulose and similar compounds, involving almost all the carbon invested in leaf biomass – are not retranslocatable. They are sunk capital. As such, investments in leaf biomass should not be abandoned until their net marginal return falls to zero – as ecologists from Horn (1971) to Ackerly (1999) have argued. To the extent that the Kikuzawa model might be applied to a retranslocatable resource, such as leaf nitrogen, more realistic and precise models already exist (e.g., Field 1983, Hirose and Werger 1987, Reich et al. 1992). These models all predict that the resource should be re-allocated among leaves so as to maintain constant marginal return (e.g., $\partial A/\partial N = \lambda$), provided that the costs of retranslocation are zero or small¹). The Kikuzawa model ignores the connection between maximum photosynthetic rate and the rate at which photo-

¹) Selection for constant marginal return should result in leaves being shed slightly before their net marginal rate of return falls to zero (Givnish 1984).

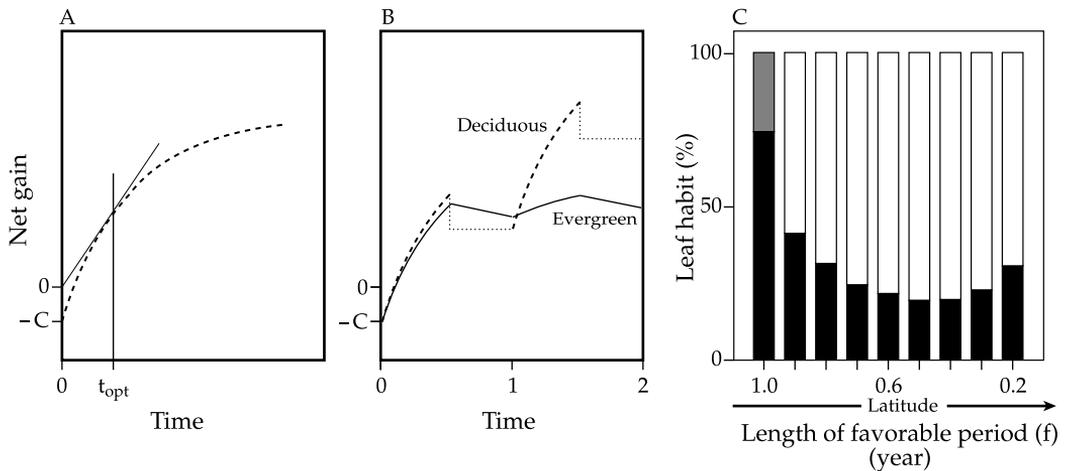


Fig. 2. Kikuzawa's model for optimal leaf longevity and phenology. (A) In an aseasonal environment, photosynthesis is assumed to decline linearly with leaf age, so that cumulative returns (curve) increase at an ever-decreasing rate. At time zero, cumulative returns are negative, reflecting leaf construction costs. According to this model, optimal leaf longevity maximizes cumulative returns per unit time, and is given by the abscissa of the point on the cumulative returns curve tangent to a line through the origin. (B) In a seasonal environment, net photosynthetic returns from evergreen leaves become negative during the unfavorable season, causing the cumulative returns curve to decline. When favorable conditions return, photosynthesis again becomes positive, at a rate dependent on total leaf age, including times of unfavorable conditions and dormancy. Deciduous leaves, which must be rebuilt each year, are favored if they result in greater net return on an annual basis. Evergreen leaves that live about one year are favored in the case shown. (C) Results of Kikuzawa's simulations, showing proportion of cases in which plants with randomly assigned physiological parameters would grow faster by being deciduous (white) or evergreen (black), plotted as a function of the length of the unfavorable season. Evergreens with leaf life-spans less than one year are shown in gray. See text for critique.

synthesis declines with leaf age, caused by the rates at which new leaves are produced and overshadow older ones (Mooney et al. 1981, Field 1983, Williams et al. 1989, Reich et al. 1992, Ackerly 1999), and ignores belowground costs.

The Kikuzawa model is the only one which, when applied to seasonal environments, appeared to predict an increase in evergreenness at boreal latitudes. Indeed, Chabot and Hicks (1982) stated that "The most puzzling biogeographic pattern involves the bimodal distribution of evergreen tree species along temperature gradients either latitudinally or elevationally ... The relationship between leaf life span and carbon balance alone cannot account for this pattern." However, Kikuzawa's conclusion in the context of seasonal environments is invalid, because his model ignores interspecific competition. He asks only what leaf life span would maximize rates of return for a given set of parameters, not which parameters and

leaf life span would outcompete others overall. Chabot and Hicks (1982) argued that frequent frosts favored vesselless (and, perhaps coincidentally, evergreen) conifers at high latitudes and altitudes. While the winter incidence of cavitation is indeed lower in conifers than in angiosperms (Sperry and Sullivan 1992, Sperry et al. 1994), the presence of deciduous larch, birch, and aspen at many treelines around the northern hemisphere argues against the general validity of the hydraulic argument, and begs the question of why more tracheid-bearing conifers aren't deciduous. So the puzzle of boreal evergreenness remains.

Recently, Reich and his colleagues (Reich et al. 1991, 1992, 1997) have made crucial contributions to our understanding of the significance of leaf longevity and habit, showing that leaf lifespan is strongly and negatively correlated with maximum photosynthetic rate per unit time, leaf mass per unit area (LMA), and leaf nitrogen

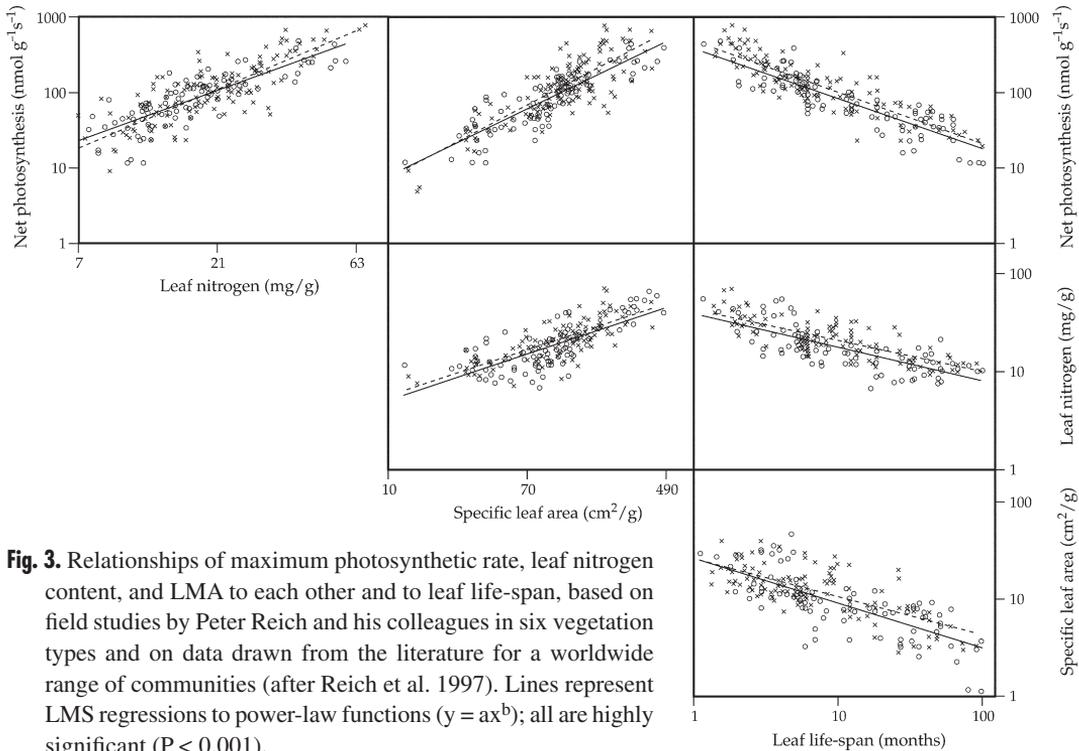


Fig. 3. Relationships of maximum photosynthetic rate, leaf nitrogen content, and LMA to each other and to leaf life-span, based on field studies by Peter Reich and his colleagues in six vegetation types and on data drawn from the literature for a worldwide range of communities (after Reich et al. 1997). Lines represent LMS regressions to power-law functions ($y = ax^b$); all are highly significant ($P < 0.001$).

content (Fig. 3). Long-lived leaves have low photosynthetic rates, low nitrogen concentrations, and high mass per unit area. Reich et al. (1992) argued that these correlations arise partly because high rates of leaf photosynthesis result in rapid growth, shading older leaves and favoring rapid retranslocation of leaf nitrogen and, ultimately, early leaf demise; and partly because long-lived leaves must be sufficiently tough and nutritionally unattractive to withstand herbivore attack over long periods. Interestingly, Reich et al.'s data show that photosynthetic rate scales as roughly the $-2/3$ power of leaf longevity, which varies roughly 400-fold across biomes and plant lineages (Fig. 3). If leaf senescence were caused solely by overtopping, photosynthesis per unit leaf mass should simply scale as the inverse of leaf longevity: as the rate at which new leaves can be constructed from photosynthate doubles, the time that leaves can remain productive until they are shaded maximally by new leaves should roughly halve. Reich et al. (1992, 1997) do not comment on this interesting issue, to which I shall return in the next section.

Reich et al. (1992, 1997) demonstrated that LMA and leaf nitrogen content are both strongly correlated with photosynthetic rate per unit leaf mass across species and biomes. Givnish (1979, 1986a) predicted such a pattern, with photosynthesis per unit leaf mass declining in thicker leaves of a given nitrogen content based on increased competition for photons and CO_2 within the mesophyll, and on the increased length of the diffusive pathway²). Herbaceous ephemerals have the highest levels of photosynthesis and leaf nitrogen and shortest leaf life-spans, while evergreen woody plants – especially conifers – have the lowest photosynthetic rates, leaf nitrogen contents, and longest leaf life-spans.

² Optimal leaf thickness, specific mass, nitrogen content, stomatal conductance, and photosynthetic rate should depend on the economic trade-offs discussed by Givnish and Vermeij (1976), Cowan and Farquhar (1977), Givnish (1979, 1986a,b, 1988) and Mooney and Gulmon (1979). Whatever the optimal leaf characteristics for a particular environment, the overtopping process itself should lead directly to a strong relationship of leaf productivity to leaf life-span, and thus of each leaf characteristic to leaf life-span. Leaf traits (and their interrelationships) favored by context-specific trade-offs should drive selection on leaf life-span as much or more than leaf life-span drives selection on leaf traits.

2.2 Top-down Models

Early top-down models (Specht 1972, 1981, Woodward 1987) assumed that the vegetation on a given site would develop so as to maximize the amount of water transpired, subject to the constraint that extractable ground water never falls to zero. Woodward (1987) used this approach to simulate global patterns of LAI, assuming that water-limited vegetation would support as large a ratio of leaf area to ground area as possible, consistent with the total amount of precipitation received. Vegetation with a lower LAI (and, hence, lower water usage and photosynthesis) would be outcompeted; vegetation with a higher than optimal LAI would exhaust the groundwater supply, reducing plant vigor and ultimately LAI. Woodward (1987) simulated distributions of evergreen and deciduous trees using a rule-based approach, adding assumptions about the physiological tolerances of various growth forms to thermal and moisture extremes. Prentice et al. (1992) refined this approach by including soil properties and month-by-month climatic data in their hydrological simulations, projecting the global distribution of biomes by asking how the different growth-forms characterizing those biomes should be distributed. Neilson (1995) modified this technique to simulate seasonal variation in LAI for graminoids and woody plants, incorporating additional rules (and associated parameter values) to obtain a unique combination of graminoid and woody LAIs under any given set of conditions.

Haxeltine et al. (1996) refined the method of Prentice et al. (1992) with a two-layered soil model, based on how competition between grasses and shrubs might determine savanna structure. According to Walter (1985), shallow-rooting grasses should outcompete savanna shrubs for water in the upper soil, while taller and deeper rooting shrubs should outcompete grasses for light and for water deeper in the soil profile. In areas with low precipitation and fine-grained, slowly infiltrating soils, grasses should dominate; in areas with higher rainfall and/or coarser, more permeable soils, shrubs should dominate.

Haxeltine et al. (1996) were able to simulate the quantitative mix of LAIs by different growth forms as a function of latitude, longitude, and

time of year, nearly replicating the original distributions of various vegetation types in Australia. Haxeltine and Prentice (1996) extended this approach to the global scale while adding elementary biogeochemical constraints. While the output from these simulations is remarkably like the observed distributions of various vegetation types, these models all depend on parametric values for the thermal and drought tolerances of various growth forms, which in turn are induced – to a greater or lesser degree – from current distributions and physiologies. These models do incorporate deductive, bottom-up elements, such as competition based on relative growth rate or stature. But they also include some unrealistic components, assuming that whole-plant respiration rates do not depend on growth form (the allometry of support tissue with plant height results in large systematic differences [Givnish 1984, 1986c, 1995]), that photosynthesis varies linearly with irradiance, and that all plant types have the same maximum evapotranspiration rate per unit ground area (Haxeltine et al. 1996).

The greatest promise may be held by models that contain elements of both the bottom-up, deductive, physiological approach and the top-down, feedback-dominated, ecosystem approach. Hollinger (1992) used just such a framework, combining data on leaf photosynthesis, transpiration, and nitrogen use by oaks in Californian savannas with calculations of water and nutrient availability in the rooting zone to predict that deciduous *Quercus lobata* should dominate areas with high resource densities, while evergreen *Q. agrifolia* should dominate drier, less fertile areas. But even this approach, based on maximizing canopy photosynthesis, falls a bit short – it is not clear what limits the soil area exploited by individual trees in a savanna, and the below-ground costs of roots used to obtain water and nutrients are ignored. Including rooting costs and constraints would likely have dramatic effects on plant growth at optimal LAI, the key feature of the Hollinger model.

3 Whole-Plant Model for Optimal Leaf Habit

In devising a whole-plant model for optimal leaf phenology, I asked how holding evergreen vs. deciduous leaves would affect a plant's net rate of energy capture and growth. I assumed that competition in a given environment favors plants whose form, physiology, and behavior tend to maximize whole-plant growth there, in terms of biomass or (under densely crowded conditions) height. Such plants should have the greatest resources with which to compete and reproduce (Givnish 1979, 1995).

Consider two plant species similar in all regards, with the same total dry mass in leaf tissue. Following Chabot and Hicks (1982), assume that these plants face two seasons: one "favorable", and the other "unfavorable" as a result of very low or high air temperatures, low rainfall or soil moisture availability, or low irradiance. Such conditions are unfavorable for plant growth because they 1) increase the energetic cost of roots needed to replace the water inevitably lost during photosynthesis, while maintaining photosynthetic capacity; or 2) decrease the amount of photosynthesis associated with a given amount of water loss and attendant belowground costs (Givnish 1979, 1986a,b, 1988). To determine where vegetation should be dominated by plants with evergreen vs. deciduous leaves, we need to know the relative advantages of each kind of leaf, and how such advantages affect a plant's net energetic return along various environmental gradients.

In weighing these advantages, we must keep in mind a key finding by Reich et al. (1992, 1997): photosynthesis, LMA, and leaf N content are all more closely related to leaf longevity than to the dichotomy between evergreen and deciduous leaves. Deciduous leaves held for one month vs. six months differ more from each other in absolute terms than evergreen leaves held for one year vs. three years. However, with the exception of some plants in relatively aseasonal tropical forests, evergreen leaves are generally long-lived and deciduous leaves short-lived. Furthermore, even in such a habitat, it seems unlikely that an evergreen would have leaves with shorter lives

than those of co-occurring deciduous plants that shed their leaves in response to drought. Short-lived leaves have low LMA (Reich et al. 1992), so the hypothetical evergreen's soft, thin leaves should be even more sensitive to drought – and thus be even more likely to be shed – than deciduous species in the same habitat.

Thus, in the following, I focus on the respective advantages of evergreen, long-lived leaves vs. deciduous, short-lived leaves, recognizing that fertile, productive conditions in aseasonal environments can favor evergreen plants with short-lived leaves, and that the deciduous habit is logically incompatible with leaves that survive longer than a year.

3.1 Energetic Advantages of Evergreen Leaves

The major advantages of evergreen leaves are 1) a longer photosynthetic season, 2) lower amortized costs of leaf construction, 3) lower amortized costs of replacing leaf nutrients, and 4) tougher laminae that can better endure frost, drought, and/or herbivore attack. These advantages are detailed below.

First, evergreen leaves potentially can conduct photosynthesis over a longer period each year than deciduous leaves, including part or all of the unfavorable season (Bell and Bliss 1977, 1979, Mooney and Dunn 1970, Waring and Franklin 1989). In cold temperate forests or taiga, evergreens cannot photosynthesize year-round, usually ceasing activity after the ground freezes and water becomes unavailable to replace transpiration (Schulze et al. 1967, Troeng and Linder 1982, Sakai and Larcher 1987, Jurik et al. 1988, Day et al. 1989, 1991, Kappen 1993). In areas with milder winters, photosynthesis during brief warm spells can occur (Schulze et al. 1977, Reynolds et al. 1980, Lassoie et al. 1983, Cropper and Gholz 1993), although photoinhibition and acclimatory changes can also limit gas exchange (Jurik et al. 1988, Öquist and Malmberg 1989, Öquist and Huner 1991). But usually evergreens can begin photosynthesizing earlier in the spring than deciduous species, and continue later in the fall (Schulze et al. 1977, Lassoie et al. 1983, Jurik et al. 1988, Gower and Richards 1990).

The same is true in seasonally arid environments, where evergreens can photosynthesize – albeit at reduced rates – for some time into the dry season after deciduous plants have dropped their leaves (Mooney et al. 1975, Sobrado 1991, 1993, Reich 1995).

Second, evergreens have a lower amortized cost of constructing the carbohydrate skeletons of leaves, provided that their leaves are held for more than a year. If an evergreen holds its leaves for, say, three years, then it must replace only about a third of its leaf canopy each year. This reduces the average annual carbon cost of leaf construction ($\text{g C g}^{-1} \text{ leaf yr}^{-1}$) accordingly. This carbon-skeleton cost advantage of evergreen leaves should be independent of environmental conditions.

Evergreens also have a lower amortized cost of replacing nutrients, and this advantage should be context-dependent (Miller and Stoner 1979, DeLucia et al. 1989, Schlesinger et al. 1989, Gower and Richards 1990). Mineral nutrients (e.g., N, P, K) are incompletely withdrawn from leaves (whether evergreen or deciduous) before they are shed, and the fraction not retranslocated must be replaced when new leaves are produced (Chabot and Hicks 1982). The more frequently that leaves are shed, the higher should be the energetic costs associated with capturing the nutrients needed to manufacture new leaves. This gives plants with evergreen foliage an ecological advantage, especially on nutrient-poor sites. Short-lived deciduous leaves also generally have higher concentrations of nitrogen and phosphorus (Chabot and Hicks 1982, DeLucia et al. 1989, Reich et al. 1997, Walters and Reich 1999, Kloeppel et al. 2000), presumably adapted to the more humid, brighter, or more moderate conditions present during the favorable season, and co-adapted to the thinner leaf cross-sections and higher stomatal conductances such conditions favor (Givnish and Vermeij 1976, Cowan and Farquhar 1977, Givnish 1979, 1986a,b, Cowan 1986). The higher nutrient content of deciduous leaves further increases the nutrient-cost advantage of evergreens. This advantage should be greater the more infertile the substrate. Indeed, Aerts et al. (1991) found that fractional root allocation was roughly twice as high in deciduous *Molinia* as in evergreen *Erica* and

Calluna coexisting in the same heathland habitat, that root allocation increased in all species at low nutrient supply rates, and that the increase was especially marked in deciduous *Molinia*. Givnish and Montague (1996) found that saplings of deciduous *Larix laricina* devoted 41.0% of their biomass to roots, vs. only 21.5% for evergreen *Picea mariana* in the same habitat, and had a higher root:needle biomass ratio (3.18 vs. 0.88). Such within-habitat differences are key determinants of the competitive success of evergreen vs. deciduous plants. Differences between species in different habitats are *not* relevant competitively and can run in exactly the opposite direction as a result of the frequent restriction of evergreens to poorer soils. Gower et al. (2001) show, for example, that the fraction of net primary productivity allocated to roots averages 19% for deciduous boreal forests, vs. 36% for evergreen boreal forests.

Finally, evergreen leaves often have to be tougher, with greater thickness and/or allocation to mechanical tissue, at least in part to withstand frost or drought during the unfavorable season without suffering irreparable damage (Chabot and Hicks 1982). Thicker leaves should also be favored by the higher root costs associated with water losses during the dry or cold unfavorable period (Givnish 1979, 1984). Tough leaves, together with low levels of leaf nutrients and high levels of chemical defenses, should also help deter leaf consumption by herbivores (Coley 1983, 1988, Coley et al. 1985, Reich et al. 1992) – an important consideration for long-lived leaves, or for the only leaves exposed to consumers during unfavorable periods – but they do so at the cost of increased internal self-shading and competition for carbon dioxide. Given the relatively high cost of replacing leaves lost to herbivores in nutrient-poor environments (Janzen 1974), thick tough leaves with low photosynthetic capacity should be favored there. The presence of mechanical and chemical defenses (including those against UV: Day 1993) seem likely to increase the construction cost per unit dry mass of evergreen leaves, but the actual difference from deciduous leaves is slight (ca. 6%) and related almost exclusively to differences in LMA and leaf size (Chapin 1989, Villar and Merino 2001). This effect is almost surely dwarfed by the

higher belowground costs associated with putting more nitrogen per unit leaf mass into deciduous leaves.

3.2 Energetic Advantages of Deciduous Leaves

The potential advantages of deciduous leaves are 1) a higher photosynthetic rate per unit leaf mass, 2) lower root costs during the unfavorable season, and 3) no leaf respiration during the unfavorable season. Deciduous leaves should have higher rates of photosynthesis per unit leaf mass during favorable conditions than evergreens, given their higher leaf nitrogen content and specific leaf area, higher intrinsic photosynthetic capacity, and the reduced internal competition for light and carbon dioxide. Leaves that are adapted only to moister or more moderate conditions during the favorable season should have thinner cross-sections, higher stomatal conductance, and higher nitrogen concentrations— and hence, higher mesophyll photosynthetic capacity per unit leaf mass— compared with evergreen leaves, which must also be adapted to drier, less productive, and/or more physically stressful conditions during the unfavorable season. This advantage of deciduousness should be context-specific: whole-plant growth during the favorable season is likely to be optimized by thicker, less productive leaves when that season is drier or more nutrient-poor, reducing the likely photosynthetic edge of deciduous leaves. The photosynthetic advantage of deciduous leaves per unit leaf mass may be enhanced at the canopy level because evergreens in the same habitat, by retaining several leaf cohorts, may suffer greater self-shading among branches. The

greater total leaf mass of evergreens may partly compensate for their low rates of photosynthesis per unit leaf mass; conversely, juvenile evergreens that have not achieved maximum LAI are likely to be at a competitive disadvantage (Schulze et al. 1977).

Deciduous plants greatly reduce their transpiration during the unfavorable season, which may reduce or eliminate the additional root costs (Givnish 1979, 1986a,b) imposed by harsher conditions which would otherwise have to be borne. Generally, optimal allocation to roots should increase, and whole-plant net growth per unit leaf mass should decrease, as soils become dry, very wet, or unusually cold. Dry conditions require investment in massive amounts of roots in order to replace a given amount of water loss; the marginal cost of transpiration, $\partial A/\partial E$, would thus be high (Givnish 1986b). Absorption of water and nutrients becomes less efficient in soils below 10° C or in anaerobic soils, so that more root tissue would have to be built or more root respiration sustained in order to support the same functions. When soil temperatures drop below freezing, water absorption essentially ceases, making winters effectively dry seasons in cold temperate forests, taiga, and tundra transpiration (Schulze et al. 1967, Troeng and Linder 1982, Sakai and Larcher 1987, Jurik et al. 1988, Day et al. 1989, 1991). Obviously, deciduous plants show no leaf respiration during the unfavorable season.

3.3 Whole-Plant Model for Optimal Leaf Phenology

The benefits and costs just outlined can be captured in a simple model for expected whole-plant growth per year per gram of leaf biomass in evergreen vs. deciduous plants:

$$G_e = f(A_{ef} - R_{ef} - bE_{ef}) + (12 - f)(A_{eu} - R_{eu} - bE_{eu}) - C/T_e \quad (2a)$$

$$G_e = G_{ef} + G_{eu} - C/T_e \quad (2b)$$

$$G_d = f(A_{df} - R_{df} - bE_{df}) - (12 - f)R_{du} - C \quad (3a)$$

$$G_d = G_{df} + G_{du} - C \quad (3b)$$

Growth by an evergreen (G_e) is simply its expected growth rate during the favorable season, times the length f of that season in months, plus its average growth rate during the unfavorable season times its length $12 - f$, minus the above- and belowground cost C of producing a gram of leaf tissue, amortized over the number of years T_e a leaf is held. In this simple model, growth per unit leaf mass ($\text{g g}^{-1} \text{mo}^{-1}$) during each season is photosynthesis A minus leaf respiration R and the root costs associated with the average transpiration rate E during that season. Givnish (1986b) argued that the constant b measuring the costs of transpiration might be approximated by $\partial A/\partial E$ – the marginal cost of transpiration – incorporating both root costs and depression of photosynthesis caused by running leaves at lower water potentials. The marginal costs of transpiration, as well as the average rates of photosynthesis and leaf respiration, are likely to vary between the favorable and unfavorable seasons. Growth by a deciduous plant is its expected growth rate during the favorable season, times the length of that season, minus root respiration during the unfavorable season and the annual cost of producing a gram of leaf tissue. For simplicity, allocation to stem tissue and storage, as well as differences in rates of herbivory and the longevity of different leaf cohorts, and root costs of deciduous plants during the unfavorable season, have been ignored in Eqs. 2 and 3, so as to focus attention on the major impacts of leaf phenology on the overall productivity of the leaf-root system. I will later explore some implications of potential differences between evergreen and deciduous plants in stem allocation and rate of herbivory.

Evergreen plants should be favored if their growth rate per unit leaf mass exceeds that for deciduous plants:

$$G_e > G_d \quad (4)$$

otherwise, deciduous leaves should be favored. In making this comparison, three terms must be considered: growth during the favorable season G_{ef} , growth during the unfavorable season G_{eu} , and amortized leaf construction costs (see Eqs. 2 and 3). Generally, deciduous plants will have an advantage in the first term ($G_{df} > G_{ef}$), and evergreen plants an advantage in the last; exceptions

might arise if evergreens hold individual leaves, on average, for less than a year (but see below). Evergreen plants can obtain a net advantage or disadvantage from the second term, depending on how harsh conditions are – and how greatly photosynthesis is reduced and/or root costs increased – during the unfavorable season.

Based on these considerations, deciduous leaves should be favored when the cost of capturing nutrients for new leaves is small, and when the seasonal difference in the net rate of whole-plant return from leaves adapted to the favorable vs. unfavorable seasons is large. Under these conditions, deciduous leaves entail a relatively small disadvantage in nutrient costs (C is small in the third term), while enjoying a relatively large advantage in growth during the favorable season ($G_{df} \gg G_{ef}$ in the first term), and little disadvantage during the unfavorable season (G_{eu} small, so $G_{eu} - G_{du} \approx G_{eu}$ is small in the second term). Conversely, infertile soils should favor evergreens, as should low seasonal variation in whole-plant return per unit leaf mass. If there is little contrast in the net whole-plant return per unit leaf mass between leaves adapted to the favorable vs. unfavorable seasons, then deciduous leaves will clearly be disadvantageous: they do not gain carbon during the unfavorable season, have higher leaf construction costs, and have little or no offsetting photosynthetic advantage during the favorable season. Even if deciduous leaves have a big advantage in photosynthetic rate during the favorable season, they can be a disadvantage overall if associated with high root costs during the favorable season (as might occur if transpiration rates are high or soil moisture is low), or if the costs of nutrient acquisition are high.

As we shall see, this version of the whole-plant model accounts qualitatively for most global patterns in the distribution and dominance by evergreen vs. deciduous plants. However, it is not fully quantitative, to the extent that it is not possible (at least currently) to separate the belowground costs associated with transpiration (included in term 1) and nutrient capture (included in term 3). For those who wish a more operational version of the model, it can be recast in terms of a simple exponential model for growth in plant leaf mass:

$$dL/dt = p(A - R) \cdot L/C - L/T \tag{5a}$$

$$= L \cdot [p(A - R)/C - 1/T] \tag{5b}$$

$$\therefore L(t) = L(0) \cdot \exp ([p(A - R)/C - 1/T]t) \tag{6a}$$

$$L(t) = L(0) \cdot \exp (\alpha t) \tag{6b}$$

where L is total leaf mass, p is the fractional allocation of energy to leaves / (leaves + roots), A is photosynthetic rate per unit leaf mass, R is the corresponding rate of leaf respiration, C is the construction cost of leaf carbohydrate skeletons, and T is leaf longevity. If one assumes that plant allocation to leaves vs. roots remains constant with plant size, then the growth rates of the leaf and root pool are characterized by the same exponential coefficient α , and the average value of α can then be compared for evergreen and deciduous plants of arbitrary leaf longevity to see which is favored. Note that if plants do not reinvest current photosynthate into new leaf and root tissue until the next growing season, they forego compound interest in the short term and Eq. 6 must be replaced by the corresponding difference equation:

$$L(t) = L(0) \cdot \alpha^t \tag{7}$$

The instantaneous rate of new photosynthetic production $p(A - R)/C$ should scale like photosynthesis times the fractional allocation to leaves, given that leaf respiration R is roughly 7% of the maximum photosynthetic rate (Givnish 1984). Leaves should be shed as enough leaves are added overhead to reduce the marginal return of the lowermost leaves to zero (Field 1983, Reich et al. 1992, Ackerly 1999). This implies that photosynthesis times fractional leaf allocation should scale like the inverse of leaf longevity – a conclusion supported by a dimensional analysis of Eqs. 5 and 6.

Recall that, across species and biomes, photosynthesis scales roughly as the $-2/3$ power of leaf longevity (Fig. 3):

$$A(T) = 10^{(2.64 - 0.64 \cdot \log_{10} T)} \mu\text{mol g}^{-1} \text{s}^{-1} \tag{8}$$

where T is measured in months (Reich et al. 1992). Based on the argument just given, this

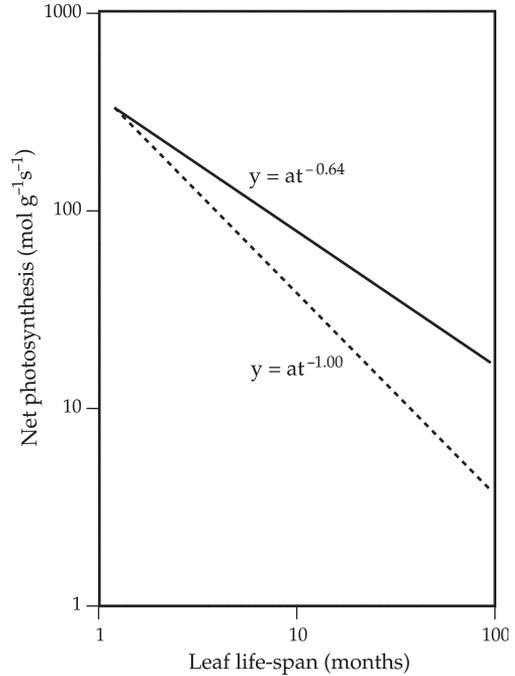


Fig. 4. Deviation of the observed relationship of maximum photosynthetic rate to leaf life-span (Reich et al. 1992) from with that expected (dashed line) if leaf life-span scaled simply as the inverse of photosynthesis. The rate of leaf production – and thus of the overtopping and adaptive death of older leaves – should scale roughly as net photosynthesis *times* the leaf allocation ratio. Thus, the difference between the slopes of the lines shown suggests that the proportional allocation of biomass to leaf tissue scales roughly as the -0.36 power of leaf longevity. Infertile or dry conditions that result in lower photosynthetic rates thus also favor lower fractional allocation of energy to leaf tissue.

implies that fractional leaf allocation varies as roughly the -0.36 power of leaf longevity. This makes sense: longer-lived leaves on less productive, highly infertile sites are associated with heavier allocations belowground. Leaves at a given photosynthetic rate have a much greater longevity than expected if one focuses on leaf performance only (Fig. 4). Their greater longevity is caused by reduced allocation to leaf production, apparently involving up to an eight-fold variation in leaf allocation fraction across plants and biomes. Allometric differences in support alloca-

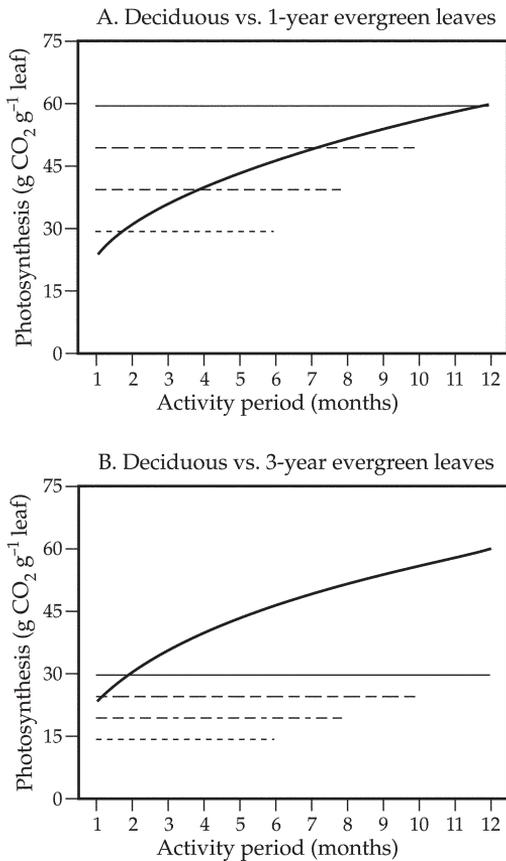


Fig. 5. Sample calculations showing the traditional, foliocentric view of the energetic returns from evergreen vs. deciduous leaves as a function of the effective lengths of their growing seasons. Calculations involve evergreen leaves held for (A) one year or (B) three years, and assume that leaves photosynthesize continuously at the maximum rates specified by Eq. 8 with 12-hr photoperiods; nighttime respiration is 7% of the photosynthetic rate. In each panel, the heavy curve shows carbon uptake as a function of growing-season length for deciduous leaves. Photosynthesis by evergreens is shown by horizontal dashed and fine lines whose height represents the total photosynthesis expected over the evergreen season considered, and whose rightmost extension specifies the length of that season. For one-year evergreens, note that for each growing-season length shown, there is a deciduous growing-season length below which evergreen leaves show a higher return, and above which deciduous leaves should be favored. By contrast, three-year evergreens appear only rarely to have an advantage, and then only if the deciduous growing season is exceedingly short.

tion might help account for the greater leaf longevity of taller, woody plants relative to shorter herbs at a given photosynthetic rate observed by Reich et al. (1997). These possibilities need to be explored empirically.

If we use the photosynthetic rates per unit leaf mass for leaves of different longevities documented by Reich et al. (1997), and the leaf construction costs ($C \approx 2 \text{ g CO}_2 \text{ g}^{-1} \text{ leaf}$) measured by Baruch and Goldstein (1999), we can now present sample calculations to ask how much longer an evergreen's effective photosynthetic season must be than that of a deciduous plant for the evergreen to have an advantage (Figs. 5, 6). These calculations show explicitly how leaf longevity and root vs. leaf allocation might affect the competitive balance between evergreen and deciduous species.

For evergreens that hold individual leaves for just one year, there are several plausible combinations of evergreen vs. deciduous growing-season

lengths that can yield an advantage for evergreens in the traditional terms of total photosynthesis minus leaf construction costs (Fig. 5A). Here we equate the effective length of the evergreen growing season as that which, if multiplied by the instantaneous photosynthetic rate projected from the Reich et al. (1997) equation from leaf longevity, equals the yearly total of photosynthesis, with a zero rate assumed over the remainder of the year (including part of the unfavorable season). But note that the deciduous growing season required to favor evergreens under even these conditions must be quite short; for example, only four months long when the evergreen growing season is eight months. And it becomes nearly or completely impossible to favor evergreens by these traditional standards if evergreens hold their leaves for 3 years or longer (Fig. 5B): the deciduous growing season must then be only one month long. The small size of carbon skeleton construction costs, and the fact that they are merely

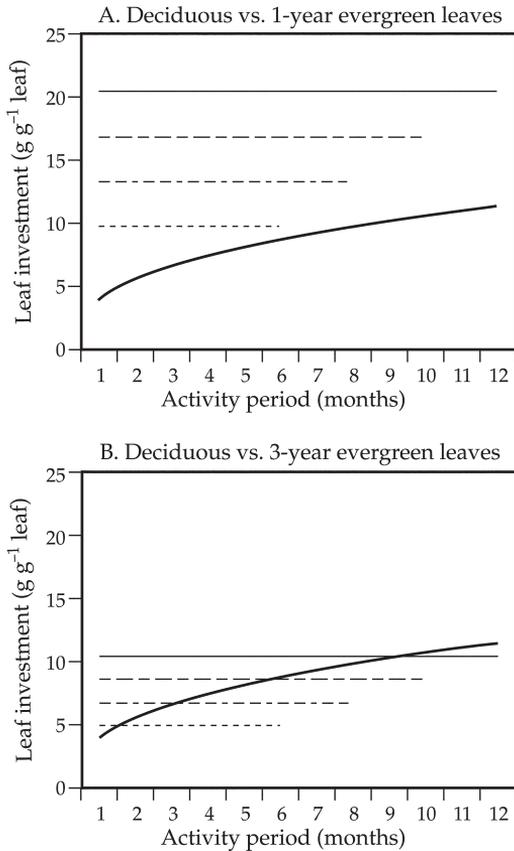


Fig. 6. Sample calculations showing the expected annual rate of new leaf production by evergreen vs. deciduous leaves as a function of the effective lengths of their growing seasons. Calculations involve evergreen leaves held for (A) one year or (B) three years, and make the same assumptions as Fig. 5. The fraction p of biomass allocated to new leaf production was arbitrarily set to 0.4 for deciduous plants and 0.7 for evergreen plants, for examples that reflect the lower root costs thought to be associated with nutrient uptake by evergreens (see text). The rate of new leaf production was set equal to α (Eqs. 6, 7) evaluated on a yearly basis. In each panel, the heavy curve shows carbon uptake as a function of growing-season length for deciduous leaves, while evergreen photosynthesis is shown by horizontal dashed lines as in Fig. 5. For one-year evergreens, note that the growing seasons for both kinds of leaves would have to be less than six months for deciduous plants to have an advantage. For three-year evergreens, evergreen or deciduous leaves can each be favored by plausible combinations of the lengths of deciduous and evergreen growing seasons – contrary to the folio-centric model in which it was almost impossible to find conditions favoring multi-year evergreens (see Fig. 5).

subtracted from the total photosynthetic income, means that small increases in their value are unlikely to overturn the apparent disadvantage of evergreens.

However, if we now incorporate the leaf allocation fraction in our exponential model, and assume that deciduous plants have a lower such fraction – in line with their higher nutrient costs – a quite different picture emerges. In the example worked in Fig. 6, the leaf allocation fraction p for deciduous species was assumed to be 0.4, while that for evergreen species was 0.7. Evergreens which hold their leaves for one year can outproduce deciduous plants for a wide range of growing season growths, and – depending on the relative lengths of the evergreen and deciduous growing seasons – evergreens holding their leaves for 3 years can also sometimes outcompete deciduous plants (Fig. 6). This model was run for a variety of evergreen and deciduous growing season lengths, leaf vs. root allocations, and ever-

green leaf longevities to predict the circumstances under which evergreens or deciduous species are favored (Fig. 7). Evergreen leaves are more likely to be favored the longer the evergreen growing season relative to that for deciduous plants, the higher the leaf allocation ratio of evergreen vs. deciduous plants, and the greater the leaf longevity of evergreens. Because poor soils favor a greater evergreen advantage in leaf allocation ratio and longer evergreen leaf lifetimes, they should favor evergreen leaves. Poor soils may also favor evergreen leaves by creating a smaller difference in evergreen vs. deciduous growing seasons: reduced photosynthetic capacity in deciduous leaves should lead to less potential variation in their potential rate of return at different times of year, favoring a longer “favorable” season for deciduous species and a lower photosynthetic advantage over evergreens during that time (see below). Strong seasonality in potential rates of net photosynthetic return should favor

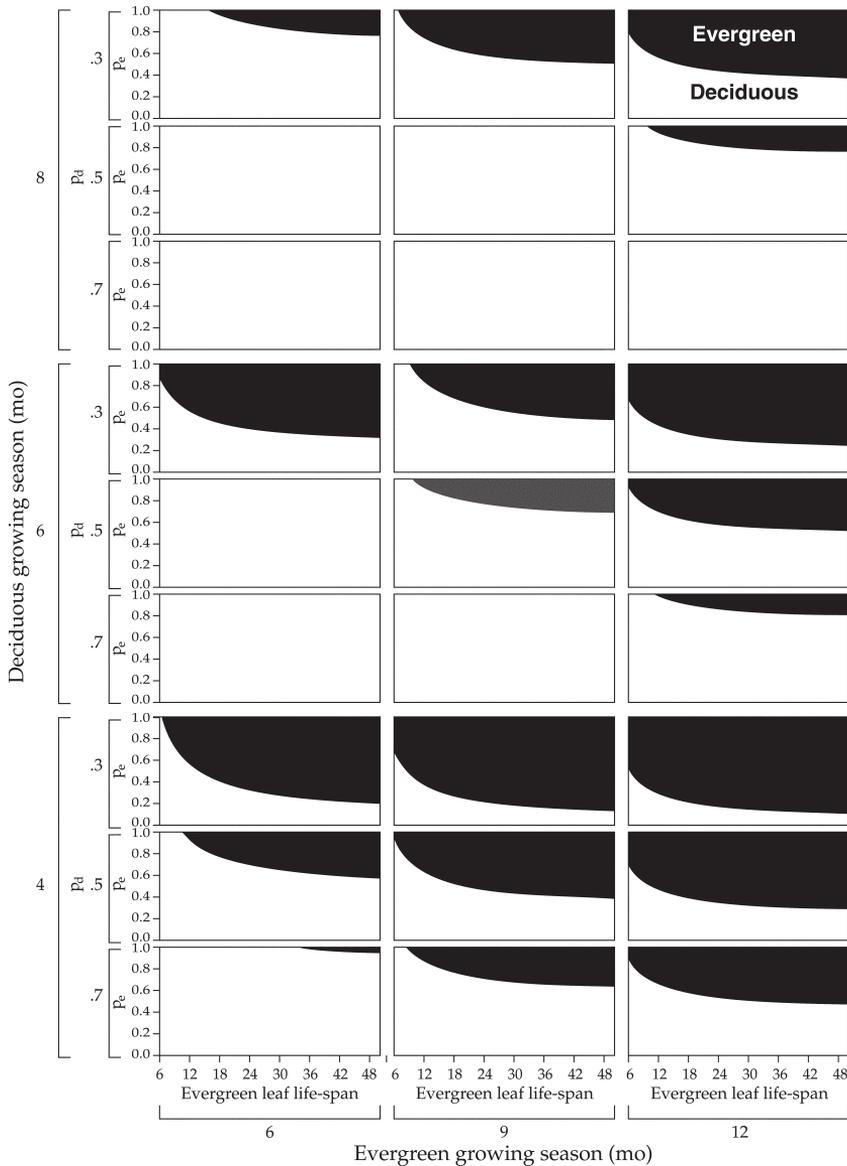


Fig. 7. Optimal leaf phenology (black = evergreen, white = deciduous) as a function of the growing-season lengths and proportions of biomass allocated to leaves by evergreen and deciduous leaves, as well as the life-span of evergreen leaves. Calculations are based on a simplified version of the model presented in the text, and ask which leaf phenology shows a greater net production G of new leaf tissue per gram of existing leaves. For deciduous plants, $G_{dec} = p_{dec}[A(t) - R(t)]t - 2$, assuming that deciduous leaves flush en masse at the beginning of the growing season and persist to the end of the growing season, so that all leaves have longevity t . For evergreens, $G_{dec} = p_{ev}[A(t) - R(t)]n_{ev} - 24/t$, where n_{ev} is the effective length of the evergreen growing season (see text) and t is leaf longevity. This equation assumes that evergreen leaf production and death occur continuously, with a loss of $2 \cdot 12/t$ grams of fixed CO_2 per gram of initial leaf tissue. $A(t)$ is given by Eq. 8; R is assumed to be $0.07A$ (see text). Note that evergreen leaves are more likely to be favored the longer the evergreen growing season relative to that for deciduous plants, the higher the leaf allocation ratio of evergreen vs. deciduous plants, and the greater the leaf longevity of evergreens.

deciduous species, by decreasing the advantages of evergreens in leaf allocation ratio and/or the effective length of the evergreen growing season (calculated based in part on photosynthetic rates during the colder, drier, or darker unfavorable season). No such predictions could be made if belowground costs were not included: evergreens with long-lived leaves simply could not be favored using previous, leaf-based models, given the rates of photosynthesis as a function of leaf longevity documented by Reich et al. (1997).

4 Ecological Predictions

The whole-plant model for leaf habit (eqs. 2–4) generates several ecological predictions: 1) infertile soils favor evergreen leaves; 2) deciduous leaves are favored by high seasonality in the net return from leaves adapted to different seasons, which is especially likely when favorable thermal, moisture, and light conditions are positively correlated across seasons; 3) soil infertility can reduce seasonal variance in net leaf returns and favor evergreens and/or leaf-exchangers even under highly seasonal climatic conditions; 4) greater soil depth, rooting depth, and soil permeability can favor evergreens in seasonally arid areas; 5) greater leaching and insect herbivory during the rainy season, combined with soil water storage, can favor leaf flushing during the dry season in subtropical dry forests and savannas; 6) leaf shedding by canopy dominants can favor contrarian phenologies in understory plants, with leaves active during well-lit but cold or dry conditions; 7) the greater relative length of the evergreen vs. deciduous growing seasons helps favor evergreens in western North America and some boreal sites; 8) evergreens should often have greater shade tolerance than deciduous species within habitats, but less shade tolerance when comparisons are made across habitats; 9) early leafing in deciduous trees of cold temperate forests should help confer shade tolerance, and is favored by productive conditions; 10) fire favors deciduous trees early in boreal succession, while intense herbivory may favor heavily defended evergreens; and 11) deciduous larches are favored by greater supplies of nitrogen and phosphorus,

higher water tables, and slower soil warming in peatlands with intermediate levels of groundwater cation input. I discuss these predictions in detail below, focusing first on the direct and indirect effects of soil fertility, and then on the effects of climatic variation on a biome-by-biome basis, from tropical rain forests to tundra.

4.1 Effects of Soil Fertility Across Biomes

Low nutrient availability on sandy or peaty soils should favor evergreen leaves. Several other models (e.g., Small 1972, Chapin 1980, Chabot and Hicks 1982, Gray 1983, Tyrrell and Boerner 1987, Schlesinger et al. 1989, Aerts 1990, Reich et al. 1992, Yin 1993, DeLucia and Schlesinger 1995, Reich 1995, Namikawa et al. 2000) have made this claim, based on the notion that increased leaf longevity increases nitrogen use efficiency (NUE) – the ratio of photosynthesis to nitrogen uptake. However, these models are based on a fallacy: competition is not likely to maximize NUE, but the difference between the benefits and costs associated with a particular NUE. The data of Field and Mooney (1986), Reich et al. (1997), and Cornelissen et al. (1997) show that instantaneous NUE would be maximized by the greatest leaf nitrogen content – and hence, the *shortest* possible leaf longevity – because maximum photosynthetic rates increase at a faster than linear rate with leaf N content. These data also show that NUE over the lifespan of a leaf should be maximized by the *longest* possible lifespan, but the papers advancing such an argument (e.g., Monk 1966, Small 1972, Sheriff et al. 1995) ignore the great short-term disadvantage this entails in low absolute rates of carbon uptake. The issues involved are analogous to those involving water use efficiency (WUE) – the ratio of photosynthesis to transpiration – high values of which Shantz (1927), Mooney (1972), Parkhurst and Loucks (1972), and many aridland ecologists have argued are adaptive under dry conditions. Givnish and Vermeij (1976) and Cowan (1977) showed, however, that water use efficiency is maximized as leaf conductance goes to zero, minimizing both photosynthesis and transpiration. High water or nitrogen use efficiency is hardly adaptive if it results in low absolute photo-

synthesis and growth relative to other species in the same environment. In spite of the manifest shortcomings of cost/benefit ratios rather than differences, many ecologists remain enamored by them, and fail to appreciate that selection is unlikely ever to favor the optimization of either NUE or WUE, calculated either on an instantaneous basis or over a leaf's lifespan.

Infertile soils were first linked to evergreenness indirectly by Beadle (1954) and Loveless (1961), who recognized a correlation of sclerophylly with soils poor in phosphorus in Australia. Much debate has ensued as to whether sclerophyllous leaves – with thick cross-sections, thick cell walls, and abundant mechanical tissue – are primarily an adaptation to drought or soil poverty (e.g., Schlesinger and Chabot 1977, Chabot and Hicks 1982, Salleo et al. 1997), or to both in terms of their effects on whole-plant growth (Givnish 1979) or herbivory (Coley 1983, Reich et al. 1992). After controlling for phylogenetic effects via independent contrasts, Cunningham et al. (1999) found that leaves become thicker, denser, and narrower along gradients of decreasing rainfall and soil phosphorus in Australia, consistent with the worldwide correlations of SLA (Specific Leaf Area), photosynthetic capacity, and leaf longevity documented by Reich et al. (1992, 1997). Dry Australian conditions favored more sclerified vasculature (presumably to resist wilting and cell damage) and higher leaf N content (to adapt to brighter, more open conditions). Infertile conditions, on the other hand, favored thick epidermides (to resist leaching or herbivory), lower leaf N content, and higher ratios of defensive tannins and phenols to leaf nitrogen.

The boreal paradox – Infertile soils may partly account for the puzzling dominance of boreal forests by evergreen trees. The high precipitation/evaporation ratio at boreal and low-arctic latitudes leads to leaching and the formation of highly infertile, acid podsoils with low rates of nitrogen fixation (Walter 1985, Oechel and Lawrence 1985). I propose that leaching and its direct and indirect effects are key factors promoting the dominance of evergreens at high latitudes; these effects have been overlooked by previous models that focus on climate rather than substrate, and on leaves rather than whole-plant integration (e.g., see Chabot and Hicks 1982, Arris and

Eagleson 1989, 1994, Kikuzawa 1991, 1995, Neilson 1995). Indeed, when tundra is artificially fertilized, dominance shifts from evergreen cushion shrubs to deciduous graminoids (Fox 1992). Fertilization also leads to the competitive dominance of a deciduous grass (*Molinia caerulea*) over the evergreen shrubs (*Calluna vulgaris*, *Erica tetralix*) that usually dominate temperate heathlands (Aerts et al. 1991), and a much larger enhancement of growth by deciduous herbs and shrubs than by evergreens in boreal forest (Nams et al. 1993). Natural fires in boreal forests, which lead to short-lived spikes in soil nutrients, often lead to temporary dominance by birch, aspen, or larch, which are then slowly replaced by later-successional conifers (see Schulze et al. 1977, Foster 1983, Oechel and Lawrence 1985, Foster and King 1986, Kenkel 1987, Landhausser and Wein 1993). A global map of precipitation minus evapotranspiration (Fig. 8) shows a concentration of putative leaching at boreal latitudes and in tropical rainforests. Note the area of low leaching running through central North America, in the rain shadow of the Rocky Mountains, and characterized by prairies, aspen woodlands, and (now) wheat fields, all dominated by deciduous plants.

The high P/E ratio in tropical rainforests leads to severe leaching, especially at higher elevations and on older land surfaces (Walter 1985, Whitmore 1984, Terborgh 1992, Tanner et al. 1998). Such leaching should favor shallow rooting in nitrogen-fixing legumes; such plants and their symbionts require access to relatively large amounts of phosphorus, given that nitrogenase has two phosphorus atoms per molecule, and the higher photosynthetic energy throughput associated with N₂-fixation (Givnish 1989). The shallow rooting of legumes, in turn, may make them especially likely to become deciduous during short dry seasons. This may help explain Sobrado's (1991, 1993) observation that deciduous trees in tropical seasonal forests in Venezuela – two-thirds of those studied being legumes – are more shallowly rooted and have higher photosynthetic rates than co-occurring evergreen species. Givnish (1999) argued that competition for soil phosphorus by N-fixing tropical leguminous trees should favor shallow rooting and lead to a high incidence of deciduousness, especially when

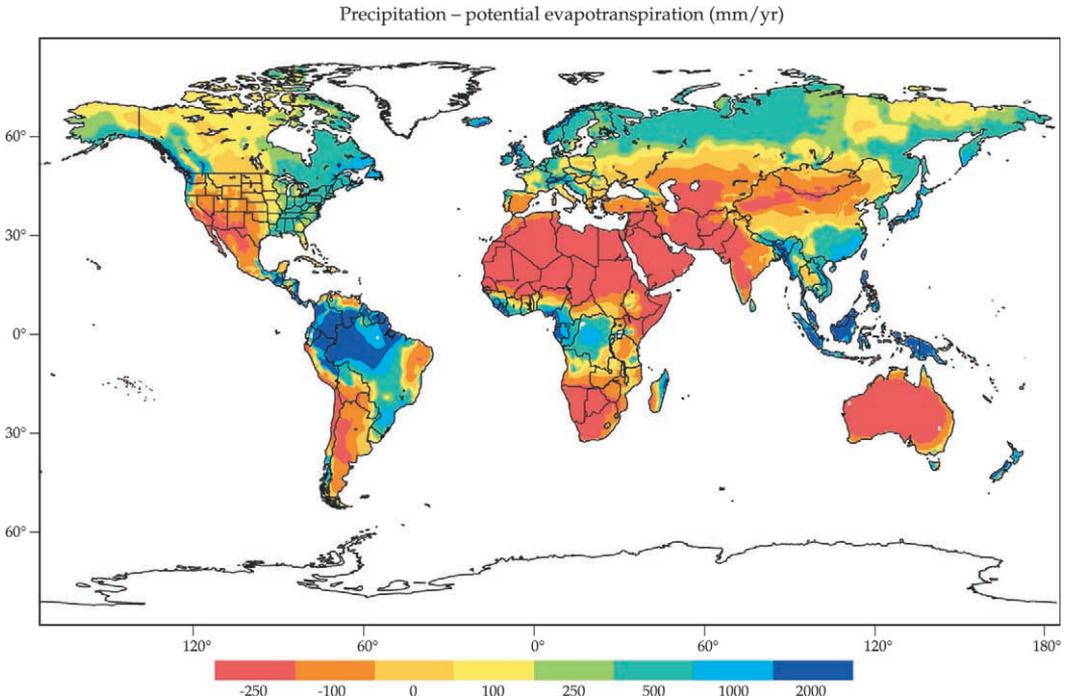


Fig. 8. Global map of annual precipitation minus evapotranspiration, an index of leaching. Note high values in regions of tropical rain forests, temperate rain forests, and boreal forests. Map generated by Aurelie Botta from climatic data of New et al. (1999), using an algorithm developed by Navin Ramankutty to calculate evapotranspiration from the Penman equation.

such rooting is combined with a well-illuminated position high in the canopy, which in turn should be favored by the high leaf nitrogen levels associated with N_2 -fixation. Fixers retranslocate low amounts of N but high amounts of P, as expected (Killingbeck 1993, Vogel and Dawson 1993). Sobrado (1997) showed that the greater vulnerability of deciduous trees to embolism during the tropical dry season is not due to differences in xylem structure, but to their rooting more shallowly than evergreen trees.

Soil infertility and the leaf-exchanger paradox – In general, soil infertility should reduce the maximum rate of photosynthesis by reducing the optimal level of leaf nitrogen (Mooney and Gulmon 1979). Thus, soil poverty should reduce the absolute difference in net photosynthetic rates between seasons and favor dominance by evergreens (see Eqs. 2–3). This previously overlooked effect may help account for the boreal paradox (see above) and the puzzling behavior of evergreen leaf-

exchangers (sensu Reich 1995), species that hold their leaves for about a year, replacing them just before or after they drop last year's foliage. In an edaphic mosaic of subtropical woodlands in the Sierra Madre Occidental of northwestern Mexico, Goldberg (1982) showed that evergreen, leaf-exchanging oaks dominated open microsites over acid, hydrothermally altered substrates, while deciduous trees (mainly the legumes *Lysiloma divaricata*, *Acacia cochliacantha*, *Coursetia glandulosa*) dominated closed stands over adjacent unaltered, more fertile substrates. She argued that infertile microsites favored evergreen oaks because their leaf phenology conserved nutrients better, allowing them to survive. However, this argument can not be valid, because the oaks are leaf-exchangers that replace their leaves once a year – just as frequently as the co-occurring deciduous species. How can evergreen leaf-exchangers gain an advantage on poor soils, if they shed their leaves just as frequently as deciduous competi-

tors? Poor soils should reduce maximum photosynthetic capacity and thus the absolute magnitude of the seasonal variation in net photosynthetic return. Eqs. 2–4 show that evergreen leaf-exchangers can gain an edge under these circumstances when combined with the longer growing season of leaf-exchangers. More generally, semi-arid subtropical habitats and other seasonal environments with low average rates of photosynthesis and plant growth that favor leaf death (*sensu* Field 1983, Hirose and Werger 1987, Reich et al. 1992, Ackery 1999) in about 12 months are likely to favor leaf-exchanging plants if soil poverty minimizes the seasonal variance in photosynthetic rate, and if leaf drop coincides with seasonal drought. Indeed, leaf-exchanging oaks are common in Florida sand scrub (Menges and Hawkes 1998), and evergreen leaf-exchangers occur on sandstone in tropical seasonal forest in Panama, where deciduous species dominate adjacent slopes on limestone (R. B. Foster, pers. comm.). Soil infertility also favors increased root allocation (Mooney and Gulmon 1979, Tilman 1988, Aerts et al. 1991, Montague and Givnish 1996), which should reduce the additional allocation to roots that induced during the dry season and be an additional factor favoring the evergreen habit. Selection to satiate foliovores may play an important role in *synchronizing* leaf exchange within a narrow time window (see Coley 1983 and below).

4.2 Effects of Climatic Seasonality

Tropical and subtropical forests and savannas – Aseasonal conditions in tropical rain forests clearly favor the evergreen habit. Leaf flushing in such habitats appears to be under endogenous control (Reich 1995), and may be timed to coincide with drier conditions so as to satiate or avoid invertebrate leaf predators (Janzen 1974, Coley 1983, Murali and Sukumar 1993) or maximize light capture (Van Schaik et al. 1993). The long-term persistence of lineages in climatically stable rain- and cloud-forest areas might help account for the long leaf lifetimes that Rogers and Clifford (1993) found associated with early-divergent angiosperms. But I would also argue that the low hydraulic conductivity of narrow xylem elements in basal angiosperms – and gymnosperms

– should favor evergreens by limiting transpiration and hence photosynthesis, reducing the seasonal contrast in potential photosynthetic rate (see below).

Substantial variation in the net whole-plant return from leaves adapted to different seasons favors deciduousness (eqs. 2–4). The greater the length and intensity of the dry season in tropical communities, the greater should be the dominance of deciduous plants. Such habitats undergo little thermal seasonality, so there is likely to be a much greater energetic return from leaf-root systems during the wet season than in the dry season. In other words, plants should be raingreen, as they usually are in seasonally droughted tropical dry forests and savannas (Fig. 1; Walter 1971, 1985, Reich and Borchert 1984). As a general rule, a strong summer concentration of rainfall favors deciduousness in tropical and subtropical communities, but the following two instructive exceptions also conform to theory.

In savannas of central Venezuela, the dominant deep-rooting shrubs *Bowdichia*, *Byrsonima*, *Casearia*, and *Curatella* are evergreen leaf-exchangers that shed their leaves a few days or weeks before new flushes of leaves are expanded (Sarmiento et al. 1985). These species tap the permanent groundwater table in the deep, well-drained soils of the vast plains along the lower Orinoco, are relatively isolated from the six-month seasonal drought, and retain relatively high leaf water potential and stomatal conductance year-round (Sarmiento et al. 1985). So, even though rainfall is strongly seasonal, shrubs that tap water stored in deep soil profiles experience low seasonality in moisture and temperature and are, as expected, evergreen. Conversely, the other dominant growth-form of the Orinoco savannas – shallow-rooted grasses, often with the C₄ photosynthetic pathway – experience a strong seasonality in moisture, and are deciduous (Walter 1971, 1985, Sarmiento et al. 1985). Remarkably, many llanos shrubs expand their leaves at the end of the dry season, at the very height of the annual drought. Sarmiento et al. (1985) argued that this behavior minimizes the leaching of nutrients from soft, newly expanded leaves, and showed that mature leaves are more resistant to leaching and that these shrubs have an adequate water supply year-round for photosynthesis and leaf expansion.

sion. Leaf expansion during times of low rainfall and atmospheric humidity might also reduce leaf consumption by herbivorous insects (Murali and Sukumar 1993, Givnish 1999) or mechanical damage to soft young leaves by torrential rains.

In subtropical forests of the Indian Himalayas, the dominant trees are also evergreen leaf-exchangers, despite a heavy concentration of rainfall during the summer monsoon and relatively low thermal seasonality (Singh et al. 1994). Zobel and Singh (1997) argued that evergreenness was favored by low seasonal variation in irradiance, reflecting a combination of low latitudes, sunny winters, and cloudy summers. The wet, warm summers are also made less favorable by the high incidence of invertebrate herbivores and diseases preying on leaves (see Murali and Sukumar 1993), and leaves must be tough enough to withstand the monsoon itself. As with shrubs of the Venezuelan llanos, the leaf-exchanging trees of the Himalayas tend to expand their leaves before the rainy season. Van Schaik et al. (1993) argued that leaf flushing in tropical and subtropical communities often coincides with seasonal peaks in irradiance except when water availability is insufficient (e.g., Barone 1998), and that the concentration of leaf production into one or a few discrete flushes may help satiate specialized herbivores (Janzen 1974, Coley 1983). D. H. Janzen (pers. comm.) indicates that most so-called “evergreen” species (e.g., *Hymenaea courbaril*) in Costa Rican dry forests actually are leaf-exchangers that flush en masse during the dry season.

Mediterranean scrub, sclerophyll forests, temperate rain forests – Winter rainfall in Mediterranean scrub and wetter areas of sclerophyll woodlands and temperate rain forests on the west sides of continents results in negative correlations of rainfall with temperature and light availability. This, in turn, leads to relatively low seasonality in the net potential return from photosynthesis, at least on deep soils with substantial water storage, favoring dominance by evergreens. Evergreen shrubs dominate Mediterranean scrub in North and South America, South Africa, Australia, and the Mediterranean littoral; sclerophyll woodland is dominated by evergreen pines in North America and by evergreen *Eucalyptus* and *Banksia* in Australia; and temperate rain forests are dominated by evergreen conifers in North America, *Euca-*

lyptus in Australia, and *Nothofagus* in southern South America. In Australia, sclerophyll woodlands occur not only in areas of moderate winter rainfall in the southwest and southeast, but also in areas of uniform or summer-weighted precipitation along the Pacific coast near Sydney. Mild temperatures and abundant rainfall there apparently favor evergreens much the same as they do in southern China and along the Gulf Coast of the United States (Walter 1985), at the southern extremes of temperate deciduous forests.

The Mooney-Miller paradigm posits that leaves in Mediterranean scrub should be shed if their respiratory loss during summer exceeds their cost of replacement (Mooney and Dunn 1970, Miller 1979, Miller and Stoner 1979). This criterion, however, is incomplete when viewed in terms of whole-plant growth (eqs. 2–6). It overlooks the higher photosynthetic rates ($G_{df} > G_{ef}$) which would be possible if leaves were active only for a shorter, more favorable period, the savings that deciduous plants might make in root costs of water uptake during the unfavorable season, and the cost of ultimately replacing evergreen leaves ($C/T > 0$). Simulations by Mooney et al. (1975) demonstrate that chaparral shrubs on deep soils show low seasonal variance in photosynthetic rate (Fig. 9), consistent with the conditions favoring evergreen leaves in the whole-plant model. Like the models of Miller, Mooney, and their colleagues, my whole-plant model predicts that the low thermal seasonality but limited winter rainfall – and hence a strong winter concentration of available moisture – near the coast on the west sides of continents favors dominance by wintergreen, shallow-rooted, deciduous plants, as seen near San Diego (Mooney and Dunn 1979, Miller and Mooney 1974, Miller and Stoner 1979). Drought-deciduous sage is also found in inland chaparral in early succession and on thin soils (Wells 1962, Harrison et al. 1971, Mooney 1977); reduced access to soil-water storage, as a consequence of shallow rooting, shallow soils, or low total rainfall, favors wintergreen species in winter-rainfall regions with mild winters (Mooney and Dunn 1970, Mooney 1977). Given the low sensitivity of C_3 photosynthesis to temperature, photosynthesis in chaparral may be more limited by photoperiod than temperature during winter (Mooney et al. 1975). Within

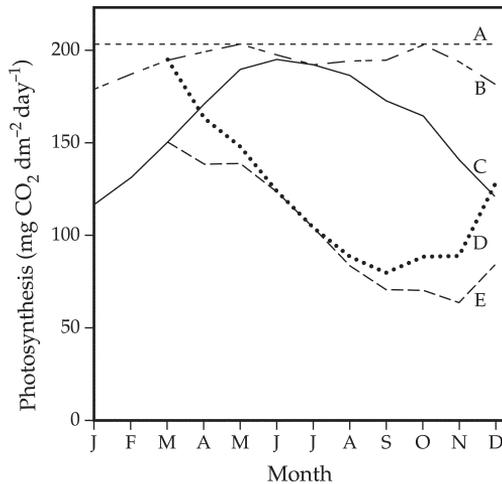


Fig. 9. Calculated annual course of photosynthesis by the evergreen *Heteromeles arbutifolia* in California chaparral with (A) no environmental limitations; (B) seasonality in temperature; (C) seasonality in temperature and photoperiod; (D) seasonality in temperature and water availability; and (E) seasonality in temperature, photoperiod, and water availability (actual conditions). After Mooney et al. (1977).

winter-rainfall regions, the incidence of evergreenness drops from a maximum of 75% (California) or 100% (Chile) in areas of relatively high rainfall, to quite low levels in areas with nine or ten months of drought (Mooney and Dunn 1970). Gill and Mahall (1986) showed that some details of the Mooney-Dunn model (e.g., deciduous species flushing leaves much earlier than evergreens and avoiding drought by shedding leaves early) were incorrect. But overall these results can be seen as validating general aspects of the cost-benefit model: in an inland chaparral on thin soil, where evergreen and deciduous shrubs had nearly equal biomass, Gill and Mahall found that both groups of plants had comparable rates of growth. Presumably, as soil depth or rainfall decreases, the magnitude of net summer carbon gain should fall, decreasing the relative advantage of evergreen shrubs; at some point on the continuum from typical chaparral to coastal sage (or thin-soiled chaparral microsites), the net growth of drought-deciduous shrubs should just equal that of evergreen shrubs, and then exceed it on even droughtier sites.

Heavy winter rainfall, summer droughts ameliorated by coastal fogs, and mild winters were invoked by Waring and Franklin (1989) to explain the dominance of evergreen conifers in the coast-hugging Pacific Northwest. Summergreen deciduous plants – like California walnut and elderberry in chaparral, and alders and cottonwoods along the Columbia River – are favored along streamsides in temperate areas with winter rainfall, presumably because year-round moisture availability and low thermal seasonality make summer substantially more favorable for plant growth (Mooney and Dunn 1970, Miller and Stoner 1979, Waring and Franklin 1989). Where Mediterranean scrub and temperate forests intergrade in southern France, evergreen sclerophyll shrubs dominate south slopes while summergreen trees dominate north slopes; summer drought is the proximal factor excluding soft-leaved deciduous trees from the sun-baked south-facing slopes (Pigott and Pigott 1993). In a similar transitional zone in northern Italy, penetration of the interior by evergreen species is limited by winter cold, while summer drought reduces the performance of deciduous species near the coast (Tretiach 1993, Tretiach et al. 1997).

Temperate deciduous forests – Winter-deciduous trees dominate the temperate deciduous forests of eastern North America, east Asia, and northern Europe, where cold winters with frozen soils, short winter daylengths, and abundant warm-season precipitation make the spring, summer, and fall much more favorable than winter for net whole-plant growth. The Coriolis effect results in warm ocean currents offshore eastern North America and east Asia, while the Gulf Stream bears warm water to the northwestern coast of Europe. In each case, the resulting abundance of summer rain favors deciduous dominance in mid-latitude areas with winters cold enough to make them effectively dry seasons.

Dominance by summer- or raingreen trees creates the possibility that understory plants may show a complementary, “contrarian” leaf phenology (to maximize light capture) or be evergreen (to adapt to reduced seasonality in photosynthetic rates, resulting from the negative correlation of light with moisture and temperature, induced by phenology of the canopy dominants). In northern Japan, the understory shrub *Daphne kamtschatica*

is the only woody plant to shed its leaves in summer, and apparently does so to reduce the cost of maintaining sun-adapted leaves in the shade; the closely related species of the open alpine, *D. miyabeana*, is evergreen (Lei and Koike 1998). In the southeastern United States, the understory shrub *Aesculus sylvatica* has a vernal photosynthetic phenology, with leaves emerging early in spring and then dropping soon after canopy closure (DePamphilis and Neufeld 1989). Evergreen shrubs (especially *Rhododendron* and *Kalmia*) frequently occur under deciduous canopies in the southern Appalachians (Whittaker 1956, Nilsen 1992), though most shrubs in such forests are deciduous (Whittaker 1956). Forest herbs in temperate deciduous forests show a great diversity of leaf phenologies; several species – especially spring ephemerals, winter annuals, and wintergreen species, but also early summer and dimorphic species to a lesser extent (Givnish 1987) – have phenologies that ensure some or most of their light capture occurs when the canopy is predictably open and temperatures near the ground are compatible with photosynthesis. As expected, spring ephemerals dominate on rich soils while evergreen forest herbs dominate on infertile microsites (Givnish 1982, 1987, Foster 1998).

In the eastern United States, dominance shifts from deciduous trees to needle- and broad-leaved evergreens on the Atlantic and Gulf coastal plains, both characterized by infertile sands and peats (see Chabot and Hicks 1982). In the southern Appalachians, evergreen pines replace broad-leaved deciduous trees on dry, nutrient-poor ridges (Whittaker 1956); in Japan and Sweden, evergreen conifers replace deciduous trees on poorer microsites (Fulton and Prentice 1997, Namikawa et al. 2000). At temperate latitudes in Great Britain and western Europe, evergreen broad-leaved plants like *Ilex* and *Hedera* are common mainly in the most maritime, equable climates on the west and south coasts of England and Ireland (Tansley 1939). The much greater area of ocean in the southern hemisphere leads to low thermal and moisture seasonality throughout much of that region, favoring evergreen dominance, as observed (Fig. 1).

Length of the favorable season – Chabot and Hicks (1982), Kikuzawa (1991, 1995), and

models presented in this paper all assume specific lengths for the so-called “favorable” and “unfavorable” seasons, without reference to detailed climatological, hydrological, photosynthetic, or rooting-depth data. There are many ways to define these seasons and incorporate temporal variation within a season in performance by plants with a specific leaf phenology; two plausible approaches have important ecological implications.

First, for moist temperate areas with a cold winter, the length of the growing season for deciduous plants with soft, easily damaged leaves should correspond roughly to the time between the latest date when the average minimum air temperature is 0° C in the spring, and the earliest such date in the fall. The length of the growing season for evergreens should correspond roughly to the time between the latest date when the average air temperature is 0° C in the spring, and the earliest such date in the fall, when the ground remains unfrozen and water available. The difference between these growing seasons (Fig. 10) creates a “shoulder” of conditions favorable for evergreen but not deciduous plants. One might expect evergreen photosynthesis to be positive during the “shoulder” and then fall to zero during the remainder of the unfavorable period, unless there is a prolonged thaw providing the roots with access to liquid water (e.g., see Schaberg et al. 1995, 1998). If the length of the “shoulder” varies little with latitude, its length relative to the deciduous growing season might increase with increasing latitude, and help favor evergreens at high temperate and boreal latitudes.

Jenny Dahm (unpubl.) examined this idea using the witness trees noted by surveyors when they crisscrossed northern Wisconsin on a mile-by-mile grid in the 1830’s; David Mladenoff and the Laboratory for Landscape Ecology at the University of Wisconsin have recently computerized witness-tree data and several environmental variables across the state. Dahm found a strong positive relationship of the percentage of evergreen witness trees per township (36 miles²) to both the average percent sand in mapped soils and the relative length of the evergreen vs. deciduous growing season. At a global scale, support for the existence of relatively longer evergreen growing seasons at high latitudes is equivocal, with support greatest in Eurasia (Fig. 11). However, the

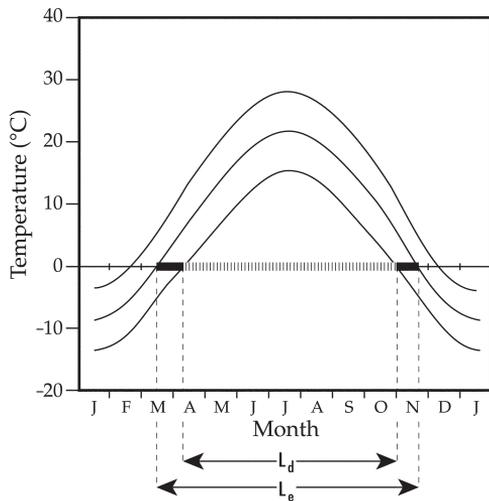


Fig. 10. Schema showing the length of the “shoulder” of the evergreen growing season relative to that for deciduous plants. Average daily maximum, mean, and minimum temperatures are plotted vs. time of year. The length of the thermal growing season for deciduous plants (S_d) on well-watered sites at mid to high latitudes should correspond to the interval between the average time of the last spring frost (average minimum temperature $< 0^\circ\text{C}$) and the first autumn frost. For evergreens in similar habitats, their growing season (S_e) should correspond to the time between when the average mean temperature first exceeds 0°C in the spring and when it last is above freezing in the fall. Under these assumptions, the length of the “shoulder” of the evergreen growing season – the amount by which it exceeds the deciduous growing season, shown in black – is $L_e - L_d$. The relative amount by which the evergreen growing season exceeds that for deciduous plants is $(L_e - L_d)/L_d$.

relative length of the evergreen vs. deciduous growing season is quite high throughout much of western North America; the relatively mild winters of this region provide a new explanation for the dominance by evergreen plants well outside the maritime region within about 250 km of the Pacific coast considered by Waring and Franklin (1989), and extending beyond the area marked by a strong concentration of rainfall in winter.

Second, the photosynthetic periods for deciduous species in cold temperate forests might instead be viewed as being set not by mean temperature, but by the shifting probability distributions of minimum temperature as a function of date. Earlier leaf flushing and/or later abscission brings with it a greater probability of frost damage to tender emerging leaves (requiring their replacement, as well as the nutrients within them) or to old leaves prior to nutrient retranslocation (Lockhart 1983). In deciduous plants, the timing of leaf emergence and abscission is directly coupled to growing-season length. Natural selection should thus *roughly* favor times of leaf emergence and abscission in deciduous plants that maximize the expected whole-plant return per unit leaf mass per season, minus the average cost of leaves and/or nutrients that must be replaced due to untimely frosts. For evergreen leaves, the length of the photosynthetic season is not coupled to the timing of leaf emergence and abscission, but young leaves still are at risk of frost damage. Consequently, the timing of leaf emergence for evergreens should be much later than that for deciduous plants in the same habitat, in order to minimize the likelihood of leaf loss at little or no cost to growing-season length. Indeed, evergreen needle- and broad-leaved species in the eastern United States generally leaf out much later in the spring than co-occurring deciduous trees and shrubs; as expected, leaf-shedding often occurs at about the same time in both groups, in mid-fall coincident with the approach of frost-induced drought.

Time of leafing, shade tolerance, and xylem morphology – Deciduous tree species in a given habitat can differ rather dramatically in their timing of leaf emergence and abscission. Certain species (e.g., *Acer saccharum*, *Carpinus caroliniana*) flush their leaves as much as two to three weeks earlier than others (e.g., *Fraxinus americana*, *Nyssa sylvatica*) (Lechowicz 1984). Similar differences in times of leaf abscission exist and, in general, early leafers are often late shedders; oaks are notable as exceptions, tending to have late dates of both leaf emergence and abscission (Lechowicz 1984). Lechowicz (1984) showed that early leafers tend to be diffuse-porous, with narrow xylem vessels that are safe but inefficient – that is, highly resistant to

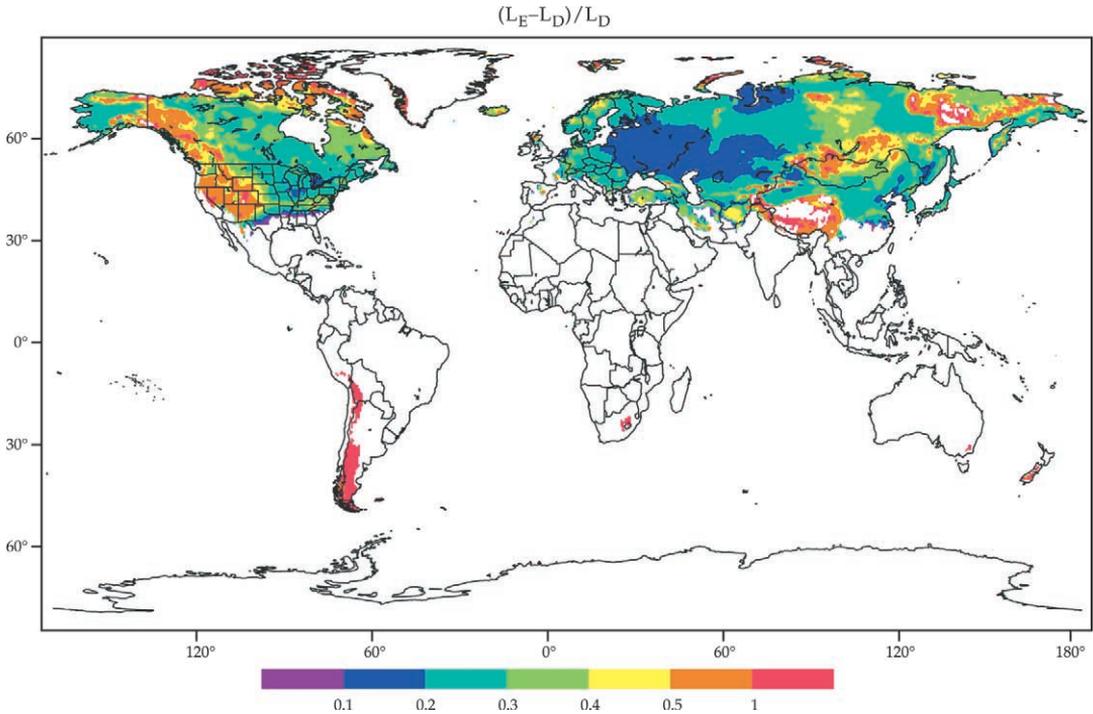


Fig. 11. Global map showing the additional length $(L_E - L_D)/L_D$ of the evergreen growing season relative to that for deciduous plants in cool climates. Map generated by Aurelie Botta, using climatic data of New et al. (1999).

frost-induced cavitation, but with a low hydraulic conductance per unit of wood cross-section. By contrast, late leafers tend to be ring-porous, with wide xylem vessels that have a high conductance but are more susceptible to cavitation (Zimmermann 1983, Sperry and Sullivan 1992, Sperry et al. 1994, Tyree et al. 1994, Davis et al. 1999).

Lechowicz (1984) asserted there was no relationship between time of leafing and shade tolerance, but Givnish (1990) found a significant tendency for early leafers to be more shade-tolerant. Generalizing the results for *Lonicera* and *Rhamnus* by Harrington et al. (1989), I hypothesized that early leafing provides saplings with a few days or weeks of intense photosynthesis while the canopy overhead is open and soil conditions are highly favorable, and that this “spring carbon subsidy” can enable those saplings to endure microsites that are shadier in midsummer. Given that irradiance levels during summer may be close to (or even below) the whole-plant compensation point (Givnish 1988, 1995), a few

days or weeks of photosynthesis early in spring may provide a large fraction of total yearly carbon capture for early-leafing saplings. Based on various measures of shade tolerance (e.g., Baker 1949, Barden 1983, Kobe et al. 1995), shade tolerance across deciduous woody species in the Great Smoky Mountains is positively correlated with the earliness of leafing and negatively correlated with the number of vertically superimposed leaf layers (Givnish 1990 and unpubl. data). Most highly shade-tolerant species (e.g., *Acer saccharum*, *Aesculus lutea*, *Carpinus caroliniana*) leaf early and have monolayered canopies (sensu Horn 1970), at least as juveniles; most late leafers have multilayered crowns and are shade-intolerant (e.g., *Carya ovata*, *Nyssa sylvatica*, *Robinia pseudo-acacia*, *Quercus coccinea*). Not surprisingly, many early-leafers are mainly found in cove forests on moist, fertile sites, where the canopy is quite dense; shade-intolerant species are often found in open forests and heaths on xeric ridges (Whittaker 1956). While the connec-

tion of shade intolerance to late leafing seems understandable, it is remarkable that late leafing characterizes the deciduous species that inhabit (evergreen-dominated) xeric ridges, given that early spring is the one time of year when such sites are predictably moist. Differences between habitats in the timing of frosts doesn't seem to be the reason, given that cold air drainage is likely to be most important in the early-leafing coves. However, the effective cost of replacing leaves lost to early frosts should be greater on dry, infertile ridges than in moist, fertile coves – in terms of both the greater allocation to roots required to replace nutrients and the longer period of photosynthesis required to replace carbon skeletons. This should favor late, safe leafing on less productive sites. Late leafing may confer one other advantage. Wider vessels should facilitate higher conductance and thus higher rates of photosynthesis, *at least across species within habitats*. Indeed, experimentally induced reductions in xylem conductance do decrease leaf conductance (Sperry 2000), and leaf conductance and photosynthetic rate are generally closely correlated within species (Wong et al. 1979). Sobrado (1993) found that deciduous tropical trees had higher photosynthetic rates and hydraulic conductivities than evergreens in the same habitat. It would be interesting to see if these trends hold in temperate forests as well. Across temperate habitats, I predict that the correlation of late leafing with dry, infertile habitats should result in a negative correlation of photosynthetic rates with time of leafing, the opposite of the trend expected within habitats.

The longer period for amortizing leaf construction costs in evergreens, as well as the greater length of photosynthetic activity under open or partly open deciduous canopies may often give evergreens greater shade tolerance than deciduous plants *in the same habitat* (see Givnish 1988, King 1994, Hunter 1997, Lusk and Contreras 1999, Walters and Reich 1999). Examples conforming to this hypothesis abound, including species of *Abies*, *Picea*, *Rhododendron*, *Taxus*, and *Tsuga*. Several *Pinus*, however, appear to be exceptions as they are replaced by deciduous *Quercus* during succession in the southern United States. However, *Pinus* establishes on bare mineral soil, which they then make more mesic until

Quercus invades about 20 years later (Billings 1938), so this example may reflect a secular change in the environment. Because the infertile conditions that favor evergreens also favor greater allocation to unproductive roots, evergreens should have lower shade tolerance than deciduous plants when comparisons are made *across habitats*.

Boreal forests: coexistence of evergreen and deciduous species – As noted previously, leaching and (in some areas, at least) the length of the evergreen “shoulder” favor evergreens in boreal forests. In the transition zone from temperate deciduous forests to boreal forests, evergreen and deciduous species frequently co-occur in the same stand (Oechel and Lawrence 1985). It seems unlikely that this coexistence is mediated simply by a rough equality of growth rates: over time, even a small average difference in growth would lead to dominance by evergreen or deciduous trees. Schulze et al. (1977) argued that, in boreal and transitional forests, deciduous species should gain an edge in early succession because it takes evergreens several years to accumulate a full set of leaf cohorts (e.g., Gower et al. 1993). Equations 2–6 overlook this important effect – which could help mediate landscape-scale coexistence of evergreen and deciduous species – because they represent an equilibrium model in which rates of leaf production and abscission are assumed to have come to steady-state; an altered version of the model could, however, incorporate the Schulze effect. As argued in the preceding paragraph, differences between evergreen and deciduous trees in shade tolerance could also maintain both phenologies in boreal successional sequences. Local differences in soil fertility – induced by substrate differences, or nutrient pulses after fire – could also allow both evergreen and deciduous species to coexist in boreal landscapes. Within forest stands at a given point in time, the advantage of the deciduous and evergreen habits should also be partly frequency-dependent, perhaps allowing both to coexist in areas where their yearly productivities under full illumination are nearly equal. Photosynthesis by an evergreen tree during early spring and late fall should be greater if it is surrounded by deciduous trees, and lower if it is instead surrounded by other evergreens. As a result, both evergreens and

deciduous species should enjoy an advantage at low densities, promoting stable coexistence at local scales. The needlelike leaves of evergreen conifers may be adaptive partly because they increase light penetration to lower, older leaf cohorts, while the broader leaves in deciduous trees may elevate leaf temperature and photosynthesis in midsummer (Sprugel 1989).

In boreal landscapes, positive feedback between plants and soil may help create and maintain patches dominated by plants with differing leaf phenologies. Evergreen trees, especially conifers, often bear leaves that are heavily defended by tannins and phenols. These compounds also complex with soil cations after being released from decomposing leaves, leading – at least on sandy, poorly buffered soils – to decreased soil pH and cation levels. The low N concentrations of live and dead evergreen leaves also result in low rates of leaf composition and N mineralization (Gower and Son 1992, McInnes et al. 1992, Reich et al. 1992, 1997). All of these conditions should, in turn, favor continued or increased dominance by evergreens, leading to positive feedback and the formation and growth of patches dominated by evergreens. Conversely, deciduous plants may also help favor themselves on poorly buffered soils, by casting less tannic, more nutrient-rich foliage (Chabot and Hicks 1982). Aerts et al. (1991) and Aerts (1995) envisioned another feedback loop, with the longer leaf lifetime and slower leaf decomposition of evergreens allowing them to immobilize nutrients and draw soil concentrations below those needed for survival by faster-growing deciduous plants.

Herbivory might also shift the balance between evergreen and deciduous plants. McInnes et al. (1992) showed that heavily defended, evergreen *Abies balsamea* and *Picea alba* became dominant in boreal forests exposed to heavy herbivory by moose on Isle Royale. Conversely, sites protected from moose became dominated by lightly defended deciduous birches and maples with soft, N-rich leaves. McInnes et al. (1992) showed that nitrogen mineralization rates below evergreens on heavily browsed plots were depressed below the controls, suggesting that browsing was also indirectly favoring evergreen plants by lowering soil fertility. The role of herbivores in facilitating dominance by evergreens may be species-

and context-specific, however. In transitional forests in Wisconsin, white-tailed deer often wreak havoc on sapling survival of *Tsuga canadensis*, a slow-growing, fairly strongly defended evergreen conifer that remains vulnerable to predation year-round for long periods (Waller and Alverson 1997). Exclusion of grazers favors evergreen *Calluna* over shorter, deciduous graminoids in heathlands (Alonso et al. 2001).

Tundra – Low temperatures and short growing seasons are likely to result in low rates of nitrogen mineralization in many arctic tundra communities, which – if acting alone – would favor evergreens. But other factors appear to favor the deciduous habit, including (i) prolonged winter darkness, (ii) winter drought, (iii) ice blasting, and (iv) sodden soils that are slow to warm in spring. Experimental studies by Read and Francis (1992) suggest that the first of these factors is not likely to be important, at least if winter temperatures are less than 10° C; furthermore, respiration for plants below snow cover should be close to nil. Winter drought (and the possibility for severe photoinhibition) as well as ice blasting are most likely to be important for plants occupying exposed microsites; ice blasting is an important cause of needle damage, desiccation, and death for many conifers near treeline (Hadley and Smith 1986). Overall, evergreens should thus be favored on well-drained but protected and/or more infertile substrates (e.g., cushion plants like *Diapensia*, *Empetrum*, *Loiseluria*, *Phyllodoce*, and *Phlox* in well-drained snowbank communities and fell fields). Deciduous plants should be favored on less protected, more sodden, or more productive substrates (e.g., sedges in muskeg, poorly drained snowbank communities, and sites swept clear in winter; broad-leaved herbs in nutrient-flush alpine meadows).

The larch paradox – Finally, let us turn to one last, enduring ecological paradox: the deciduous habit of larches (*Larix*) at high latitudes in nutrient-poor peatlands in the northern hemisphere, where evergreen plants are expected to dominate and often do. Extreme conditions that impose leaf mortality during the unfavorable season – such as ice blasting, fire, and excessive heat or cold that cannot be survived – clearly favor the deciduous habit. This may be the primary cause of the extensive dominance of *Larix dahurica* and



Fig. 12. Aerial view of the Crandon Lake peatland in northern Wisconsin during autumn, showing central ombrotrophic area dominated by black spruce, and peripheral minerotrophic area dominated by larch (yellow). Northern white cedar, another evergreen, dominates the narrow band at the highly minerotrophic margin of the peatland abutting the uplands.

L. gmelinii in central Siberia. Larch swamps there have the most extreme winters outside Antarctica, with January conditions frequently descending below -40 to -60°C (Walter 1985, Vygodskaya et al. 1997), the supercooling limit for spontaneous ice formation in buds, leaves, and other sensitive, saturated tissues (Arris and Eagleson 1989, Greller 1989). Larch buds have a special “freeze-drying” ability that removes moisture from live tissue as conditions cool, allowing them to survive exposure to much lower air temperatures than other higher plants (Gower and Richards 1990). Larch dominance of Siberian peatlands is not a result of high seasonal variance in photosynthetic activity; rates of summer photosynthesis and growth by larch in those wetlands are quite low, apparently reflecting nitrogen limitation (Schulze et al. 1995, Hollinger et al. 1998).

Larches are highly efficient at retranslocating leaf N, resorbing an average of 75% before

leaf loss, compared with roughly 50% for most other deciduous and evergreen trees (Chapin and Kedrowski 1983, Matyssek 1986, Tyrrell and Boerner 1987, Gower et al. 1989, del Arco et al. 1991, Negi and Singh 1993). This unique feature reduces larch’s nutrient needs and tends to favor its having a deciduous habit (Gower and Richards 1990). Furthermore, winter loading by high winds, ice, and snow should force evergreens to build more massive stems and branches and give deciduous plants an advantage in mechanical efficiency. Indeed, larches allocate less to stem tissue at a given height than do nearby evergreen competitors (Gower et al. 1987, Montague and Givnish 1996).

Gower and Richards (1990) argued that larches do well in nutrient-poor peatlands because they have advantages in nitrogen retranslocation and mechanical efficiency. But these advantages do not explain regular shifts in dominance from

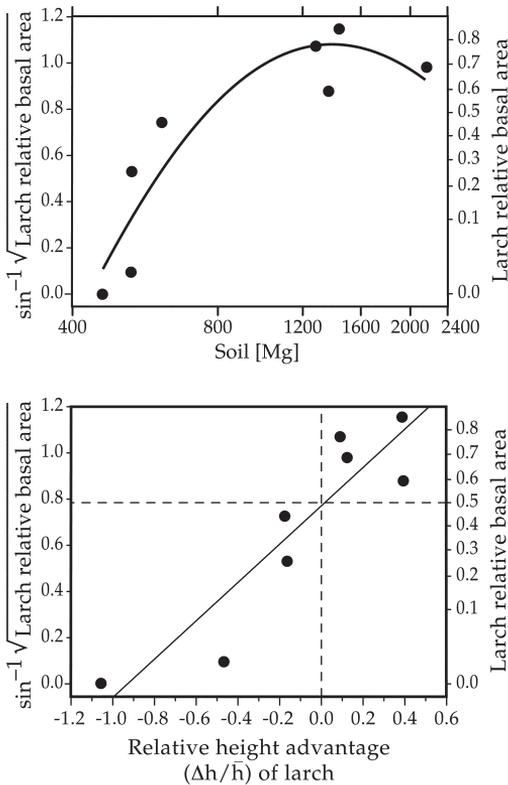


Fig. 13. Relative basal area of larch (*Larix laricina*) at two study sites in northern Wisconsin as a function of (A) the soil concentration of magnesium and (B) height relative to black spruce (*Picea mariana*) (after Montague and Givnish 1996). Curves represent non-linear least mean squares regressions, significant at the levels of $P < 0.01$ and $P < 0.002$, respectively. The vertical dashed line at $\Delta h/h = 0$ indicates the point at which neither larch nor spruce has a height advantage; at that point, the abundance of larch predicted by the linear regression is very close to 50% (horizontal dashed line), as expected.

deciduous larch to evergreen *Picea* or *Thuja* along peatland gradients. Studies in Minnesota (Heinselman 1963, 1970, Glaser et al. 1981, 1990, Glaser 1987, Wright et al. 1992), Wisconsin (Montague and Givnish 1996), and Ontario (Vitt and Bayley 1984, Jeglum and He 1995) have shown that *Larix laricina* replaces *Picea mariana* in moving from extremely infertile, ombrotrophic bogs to more fertile, minerotrophic fens. Even

more remarkably, in some extremely rich fens, dominance reverts to *Picea* or *Thuja* (Fig. 12). Most previous studies that compare larch photosynthesis, growth, and nutrient use with those of co-occurring evergreen trees (e.g., Schulze et al. 1977, 1986, Tyrrell and Boerner 1985, 1987, Gower et al. 1989, Gower and Richards 1990) have done so only in single stands where these species coexist in roughly equal numbers. Such studies can not evaluate the context-specific advantages of *Larix* vs. evergreen competitors along environmental gradients.

Montague and Givnish (1996) hypothesized that *Picea* should outgrow *Larix* on highly infertile sites (based partly on lower nutrient-acquisition costs), and that *Larix* should outgrow *Picea* on more fertile sites (based on a reduced disadvantage in energy allocation to roots, and an increased leaf N concentration and photosynthetic capacity of its thin, highly productive needles). Indeed, the relative abundance of *Larix* across two patterned peatlands in northern Wisconsin was strongly correlated to its local advantage in height, which increased with soil cation concentration (Fig. 13). In the hydrologically stable peatland at Crandon Lake, we observed the expected cross-over in rates of height growth with increasing fertility: *Picea* outgrew *Larix* on highly infertile sites, but *Larix* growth increased more rapidly with site fertility and exceeds that of *Picea* on the relatively fertile sites it dominates (Fig. 14). *Larix* had needle nitrogen concentrations that averaged 75% more than those of spruce, and the absolute amount by which *Larix* N leaf content increased over the gradient was twice that seen for *Picea*. In seedlings and small saplings, *Larix* allocated roughly 40% to roots, versus roughly 25% in the less nutrient-demanding *Picea*. This study appears to have been the first to quantify the growth rates of evergreen and deciduous competitors along a gradient and relate them to shifts in the relative abundance of such competitors.

Interestingly, at every point along the gradient at Crandon Lake, biomass growth by *Picea* is two to three times that by *Larix* (Montague and Givnish 1996). *Larix* achieved its context-specific advantage in height growth because it allocates less to foliage, stem, and branches at a given height, and thus requires less biomass to achieve a given increment in height growth. *Larix* has a

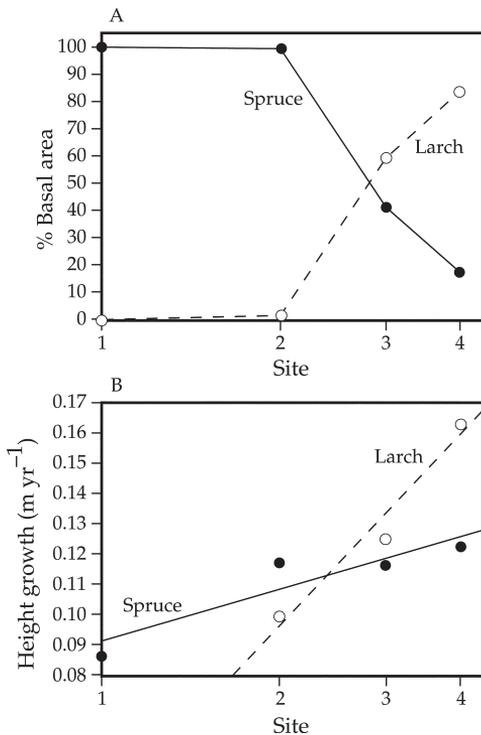


Fig. 14. (A) Relative basal areas of larch and black spruce and (B) their rates of height growth along a transect from ombrotrophic to minerotrophic sites at Crandon Lake (adapted from Montague and Givnish 1996). Lines in (B) represent LMS regressions of growth rate vs. position. Spruce's growth rate exceeds larch's under ombrotrophic conditions (sites 1 and 2), but increases more slowly toward more fertile conditions (sites 3 and 4). As a result, spruce has an advantage in height growth at sites 1 and 2, where it dominates, while larch has a growth advantage at sites 3 and 4, where it dominates. The cross-over point in species' growth rates occurs between sites 2 and 3, as expected.

more slender stem at a given height, probably because it is deciduous and exposed to less severe wind and ice-loading during winter. *Picea* has more leaf mass at a given height because it retains several annual leaf cohorts. *Larix* seedlings occur on wetter microsites than *Picea*, and *Larix* height growth is reduced less by shallow water tables.

Based on these results, I propose a general model (Fig. 15) to account for the paradoxical shift from evergreen to deciduous to evergreen

dominance, along gradients of increasing mineral supply in boreal peatlands. Five primary factors are involved:

- 1) Cation availability – Extremely base-poor, rain-fed microsites should favor evergreen species, based on their lower costs of nutrient acquisition and longer growing season. Greater cation supplies decrease the energetic advantage of evergreens in acquiring such nutrients. Cation supply rate should increase sharply with soil pH in moving from ombrotrophic bogs, to minerotrophic fens, to calcareous, extremely minerotrophic, rich fens (Glaser 1987, Foster et al. 1988a,b, Wright et al. 1992).
- 2) Nitrogen and phosphorus availability – Cation supply may indirectly cause supplies of N and P (the two nutrients most likely to limit growth) to peak in mid-gradient and favor deciduous *Larix* there. Cations help buffer the acidification of peatland soils and groundwater by humic acids and cation exchange by *Sphagnum* (Clymo 1963, 1983, Gorham et al. 1984, 1987). Nitrogenase activity and N₂-fixation by soil microbes peaks between pH 5.4 and 6.5, falling toward lower and higher pH in bogs and rich fens, respectively (Waughman and Bellamy 1980, Malmer 1986). Intermediate pH is also associated with *Alnus* and *Myrica* (Tilton 1978, Waughman and Bellamy 1980, Kenkel 1987), which harbor the N₂-fixing actinomycete *Frankia* and cast N-rich foliage. High soil N content should accelerate nitrate and/or ammonium production, by lowering peat C: N ratio and stimulating peat decomposition (Malmer 1986).

Phosphorus is derived mainly from groundwater flow, and so is present in higher concentrations in less acid peats. P availability drops sharply below pH ~ 4.5 as iron and aluminum become mobile and precipitate P (Gorham et al. 1987). In rich and extremely rich fens, P availability also declines (Tamm 1956, Sjörs 1961, Malmer 1986), perhaps as a result of its co-precipitation with CaCO₃ as CO₂ degases from groundwater that has percolated through calcareous material (Boyer and Wheeler 1989).

Greater supplies of N and P at intermediate pH should favor *Larix* by decreasing its nutrient acquisition costs (which appear relatively high given its deciduous habit, consistent with its much

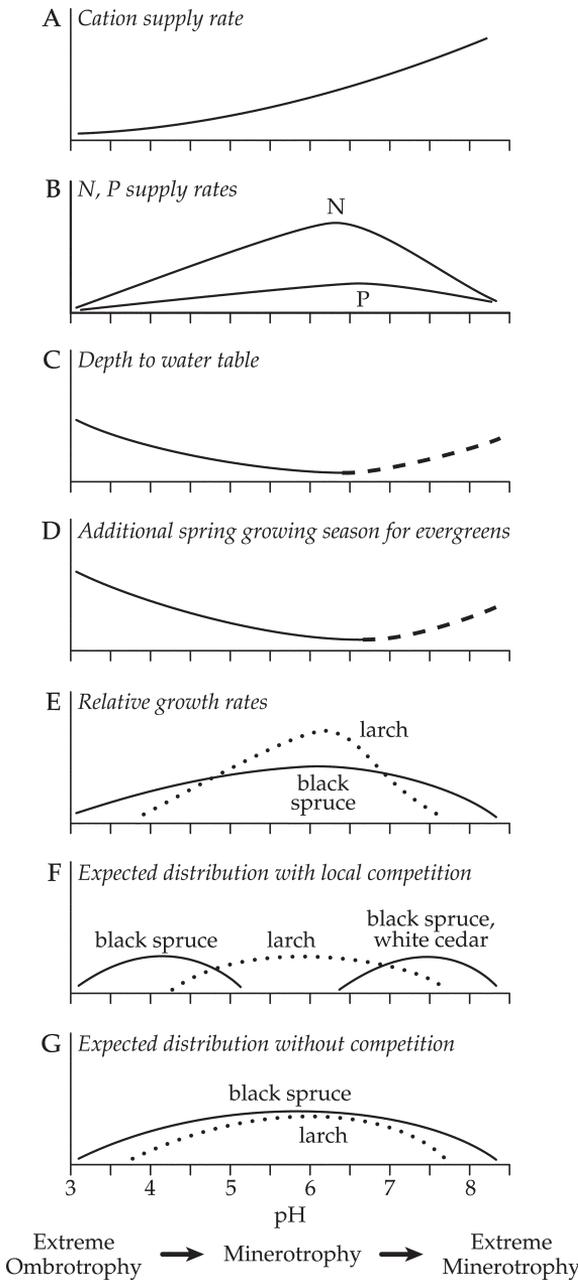


Fig. 15. Conceptual model for the causes of the differential distribution of black spruce vs. larch along a gradient from extremely ombrotrophic to extreme minerotrophic peatlands. (A) With increasing groundwater input, pH and the supply rate of most mineral cations should increase. Plant absorption of cations with a low supply rate relative to demand (e.g., K^+) may result in a reversed gradient in the standing crop of such cations in the soil and groundwater (see Montague and Givnish 1996). (B) Supply rates of nitrogen and phosphorus should peak at intermediate pH, reflecting the optimal conditions for N_2 -fixation, and the declines in P availability at low pH (due to co-precipitation with Fe) and high pH (due to co-precipitation with Ca). (C) Increased rates of N and P supply should accelerate peat decomposition, creating the wettest conditions at intermediate pH. (D) Shallow water tables retard the warming of peat in the spring, inhibiting root function and truncating the additional photosynthetic period for evergreens before deciduous trees leaf out. Dashed line represents the expected but as yet undocumented trend under highly ombrotrophic conditions. (E) As a consequence of greater N and P supplies and the relatively shorter growing season for evergreens in the middle of the gradient, larch should have an advantage in height growth at intermediate pH. Under extremely ombrotrophic or extremely “minerotrophic” conditions at low and high pH, respectively, the lower supplies of N and P and the longer growing season for evergreen species should favor a higher rate of height growth in evergreen black spruce or (at high pH) northern white cedar. Extreme nutrient shortages may make it impossible for larch to obtain enough minerals to support its more mineral-demanding deciduous habit. (F) Under crowded conditions, competition should restrict each species to where it has an advantage in height growth, leading to spruce dominance under ombrotrophy, larch dominance under moderate minerotrophy, and spruce or white cedar dominance under alkaline, extreme minerotrophy. (G) Under less crowded conditions, each species should expand its range toward the full set of conditions it can physiologically tolerate in the absence of competition.

higher allocation to roots than *Picea* [see above]), and by increasing its leaf concentrations of N and P and its photosynthetic rate. The paradoxical shift in dominance from deciduous *Larix* to evergreen *Thuja* or *Picea* in the most calcareous peatlands (Heinselman 1963, Vitt and Bayley 1984, Glaser 1987, Glaser et al. 1990, Wright et al. 1992) may reflect the decreased availability of N and P there (Fig. 15).

- 3) Peat decomposition and water-table depth – Minerotrophy fosters shallow water tables in peatlands: lower C: N ratios lead to more rapid peat decomposition at a given oxygen level, and groundwater flow may increase oxygenation (Heinselman 1963, 1970, Glaser 1987, Wright et al. 1992). As a result, peat should accumulate more slowly and decompose closer to the water table under minerotrophic conditions. Shallow water tables should – paradoxically – reduce nutrient availability to plants under the most minerotrophic conditions, by reducing the aerated rooting zone and slowing peat decomposition and nutrient release deep in the profile (Ponnampertuma 1984, Lieffers 1988).
- 4) Growing-season length – Shallow water tables inhibit warming of the upper peat layers (Lieffers and Rothwell 1987a, Lieffers 1988). Cold or anoxic soil conditions inhibit water and nutrient absorption in trees generally and in *Larix* and *Picea* specifically (Kozłowski 1982, 1986, Lieffers and Rothwell 1986, Lieffers and MacDonald 1990, MacDonald and Lieffers 1990). So shallow water tables may favor *Larix* by reducing the spring “shoulder” during which evergreen competitors can absorb water and photosynthesize before larch budbreak.

Perhaps to take advantage of mineral-rich groundwater, fulfill its greater requirement for nutrients, and survive on sites with seasonally higher water tables, *Larix* roots more deeply than *Picea* on a given site and allocates more heavily to root vs. leaf tissue (Lieffers and Rothwell 1987a,b, Montague and Givnish 1996). *Larix* deeper rooting exacerbates the problem of slow soil warming in spring, further favoring its deciduous habit. The shallow rooting of *Picea* exposes it to warm soil conditions earlier and further favors its evergreen habit. Differences in rooting depth thus appear co-adapted to leaf habit. Such differences might affect the physiological ability of *Picea* and *Larix*

seedlings to tolerate different water table depths even before local competition for light or rooting space occurs.

- 5) Initial stocking density – Competition based on differences in height growth should be less important in sparsely covered sites hit by heavy mortality or establishment failure. Under these conditions, the range over which *Larix*, *Picea*, or *Thuja* are distributed should approach the range of conditions each can tolerate physiologically (Fig. 15).

This model may also help account for the deciduous habit of bald cypress (*Taxodium distichum*) and pond cypress (*T. ascendans*). These trees typically dominate wet, minerotrophic peatlands along the southern Atlantic Coastal Plain, and are usually replaced by evergreen conifers and angiosperms in pocosins and other more nutrient-poor systems. The two remaining genera of deciduous conifers – *Ginkgo* and *Metasequoia* – occur in upland, minerotrophic sites in temperate areas of east Asia and probably are adapted to avoid winter drought, like many of the broad-leaved angiosperms occurring at the same latitude, and like montane and Siberian larches (Gower and Richards 1990, Kloeppe et al. 2000).

The *Picea-Larix* model illustrates how we must go beyond differences in leaf-level performance to account for the distribution of deciduous vs. evergreen species. We need to incorporate differences in allocation to photosynthetic vs. non-photosynthetic tissue, rooting depth, and stem allometry, and analyze how these differences interact with the photosynthetic rate, transpiration, and nutrient demands of leaves with different life-spans to affect rates of height growth in specific microsites. The discussion of constraints on leaf phenology in tropical forests and savannas points to the critical importance of herbivores and/or leaching from young leaves in determining optimal leaf phenology in certain contexts. Future models should incorporate all of these features, as well as the impacts of plants on their local environments that have been captured in several state-of-the-art top-down models.

The expected shift in dominance from evergreen spruce to deciduous larch with increasing supply rates of nitrogen and phosphorus not only

accounts for the last of our three paradoxes, it may have important implications for global change. *Larix* and *Picea* today dominate a greater area of the earth's surface than other tree genera, occupying vast areas of patterned peatlands in North America and Eurasia. Increased burning of fossil fuels is increasing the rates of deposition of nitrogen oxides produced by combustion. A consequence of this increased deposition at boreal latitudes might be a general increase in the competitive ability of larch, caused both by the direct effects of fertilization and the indirect effects of increased rates of peat decomposition caused by fertilization. Increased rates of peat decomposition favorable to larch are also likely to ensue from warming caused by elevated levels of atmospheric carbon dioxide (Gorham 1991). But increases in the coverage of boreal peatlands by larch might significantly increase global albedo at high latitudes, especially in winter when snow would show through its deciduous canopies. Increases in boreal albedo, in turn, might reduce the expected warming due to elevated CO₂ levels, which is expected to be greatest at such latitudes (Bonan et al. 1995, Eugster et al. 2000). There are many questions, at a variety of levels, that would need to be resolved to justify and test this prediction, but this final possibility illustrates the extraordinary variety of levels at which optimal leaf phenology can have important ecological consequences, from the level of individual leaves and plants to the entire biosphere.

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