

Ecohydrology

Darwinian expression of
vegetation form and function

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Introduction and overview

This research monograph describes a search for the mechanisms by which natural selection influences vegetation form and function.

Here we summarize the work by describing, in non-mathematical terms, the discovered suboptimalities of the factors of net primary productivity, and how through increasing horizontal leaf area they lead to a productive gain which maximizes when the foliage density constrains the CO₂ supply to equal the light-stimulated CO₂ demand. We find a global maximum productivity over a range of horizontal leaf area that closely matches the range for observed species, thereby confirming our fundamental hypothesis that natural selection favors increased productivity.

Discovered dimensionless bioclimatic stability and optimality conditions are shown to yield the climax boundaries to the feasible habitat space.

A **Introduction**

The biophysical system

The physical interaction between a vegetation canopy and its atmospheric and soil environments is governed by both the plant structure and the biochemistry of the individual plants. The spacing of the individual plants; their height and diameter; the depth and shape of their crowns and root systems; the size, shape, number, color, texture and spatial arrangement of their leaves along with the associated pods, stems, twigs or shoots and branches, all contribute to the instantaneous vertical exchanges of momentum, mass and energy between canopy and atmosphere and/or to the extraction of moisture and nutrients from the soil. Plant biology modulates these fluxes through such transient mechanisms as stress-induced variability of leaf stomatal resistance to transpiration and to CO₂ assimilation, short-term changes in leaf attitude, and seasonal changes in the color and density of the foliage.

The question

Can we formulate this complex interaction in a way that is at once simple enough and yet sufficiently exact to reveal the principal natural selection pressures that determine the observed configurations and functionings of natural plant communities?

Background

The early work of Darwin (1859) on natural selection led to the concept of ecological optimality. This connection between natural selection and the principles of physics was recognized by Lotka (1922) who proposed that “natural selection tends to make the energy flux through the system a maximum, so far as is compatible with the constraints to which the system is subject . . .”, and further that “in the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient in directing available energy into channels favorable to the preservation of the species.”

Rosen (1967, p. 7) proposed a more general connection between natural selection and the environment. In his words “On the basis of natural selection, then, it may be expected that biological organisms, placed for a sufficiently long time within a specific set of environmental circumstances, will tend to assume characteristics which are optimal with respect to these circumstances.” Parkhurst and Loucks (1972, p. 505) refined this to the form commonly used today. That is “Natural selection leads to organisms having a combination of form and function optimal for growth and reproduction in the environments in which they live.”

Methodology

We seek to define, in terms of the key structural and behavioral parameters of a monocultural plant community, those conditions under which the reproductive potential of the individual plants is maximum for a given climate and soil. We assume the resulting community will prevail in the given environment. While our interest is in natural systems, primarily forests, we will also examine the behavior of crops to the extent that this may aid in generalization. We formulate our optimization arguments mechanistically in the belief that quantification is the key to understanding.

B Overview

Objective

We wish to find a set of general biophysical relations that define the optimum natural habitat for a given vegetation species and that alternatively will define the maximally productive stable (i.e., *climax*) vegetation community for a given climate and soil.



Plate 1.1. Hemlock and fir forest. Western hemlock (foreground) and Douglas fir (background) in the Olympic National Park, Washington. (Photograph by William D. Rich; Copyright © 2001 William D. Rich.)

Assumptions and organization

Here we consider only monocultures. We neglect the activities of insects and other animals (including man), omit the influence of disease and fire, and assume infinite nutrient and CO_2 reservoirs—leaving water and light as the limiting resources. We analyze the climate–soil–vegetation system as though it operated in its long-term temporal average and local spatial average states with a neutrally stable atmosphere and no lateral advection of energy or water from adjacent landscapes. Finally, we sever the feedback link from surface to atmosphere and consider the vegetation as a passive responder to climatic forcing.

We assume that the individual plants have arrived at their particular characteristics through a process of natural selection driven by the competition to survive in a given average environment and fine-tuned to the environment's local variabilities by adaptation. We deal here only with the natural selection and to do so analytically we assume that seed productivity is a surrogate for survival probability and is proportional to

the net primary productivity, NPP.[†] It is our thesis that the physical parameter values leading to maximum productivity in a given environment are those that we should find in a climax community[‡] and that the analytical expression of this optimum equilibrium may provide a useful means of coupling the vegetated land surface to the atmosphere in a slowly changing climate.

For pedagogical elegance the work is organized, beginning with Chapter 2, as the classical physical science textbook would be; understanding is developed analytically and in a reductionist manner from “first principles”, building gradually toward NPP in Chapter 10. However in this overview, in order not to lose sight of the forest for the trees, we omit mathematical detail and *begin* with the discussion of productivity.

Factors of productivity

We define the environment of a forest in terms of: the average length, m_τ , of its growing season for particular species; the climatic time averages[§] over this season of the insolation,^{††} I_0 , the precipitation, P_τ , and the daylight-hour atmospheric temperature, T_0 ; under the assumption that the reservoir of nitrogen and other nutrients in the soil, and that of CO_2 in the free atmosphere, remain non-limiting to production.^{§§} With these simplifications we recognize the principal productive needs for: *light* to keep the leaf stomates open for uptake of CO_2 , and to fuel its assimilation; *nitrogen* to nourish the formation of plant tissue; *water* to keep leaf stomates open by maintaining plant turgor, to transport the nitrogen from soil to plant, and to regulate plant temperature through evaporative cooling; and finally, the crown’s *turbulent flux capacity* to evacuate water vapor at a rate meeting the plant’s demand for water-borne nitrogen, and to supply atmospheric CO_2 at a rate meeting that demand for even the lowest leaf. We find biophysical bases for optimizing each of these.

We begin by assuming for the moment that the capacity of the turbulent flux to supply CO_2 to the leaves exceeds the light-driven demand of the leaves for CO_2 . Such demand-limited assimilation is illustrated by the classical experimentally-determined *photosynthetic capacity curve* for an isolated C_3 leaf at constant leaf temperature, T_l . This curve defines the rate of CO_2 assimilation, P , as a saturating function of the variable insolation, I , maximizing at the value P_s for large I . As sketched in Fig. 1.1, for the temperature $T_l = T_m$ producing maximum assimilation, the net photosynthesis is defined by two species-dependent parameters, the saturation rate of maximum carbon assimilation per unit of basal leaf area, P_{sm} , and the *saturation insolation*,

[†] The proportionality constant is likely to vary with species making uncertain those conclusions about interspecies competition that are based solely on NPP.

[‡] This neglects the fact that competitive advantage in a mixed community may shift with age leading possibly to a dominant stable species that is not “climax” in the globally optimum sense used here for the monoculture.

[§] Time-averaged quantities remain undifferentiated in notation because we write *all* our dynamic relationships in terms of climatic time-averages.

^{††} Insolation is the flux density of solar radiation on a horizontal surface.

^{§§} This crude assumption is an expedient that allows us to proceed and must be remembered when evaluating our results.

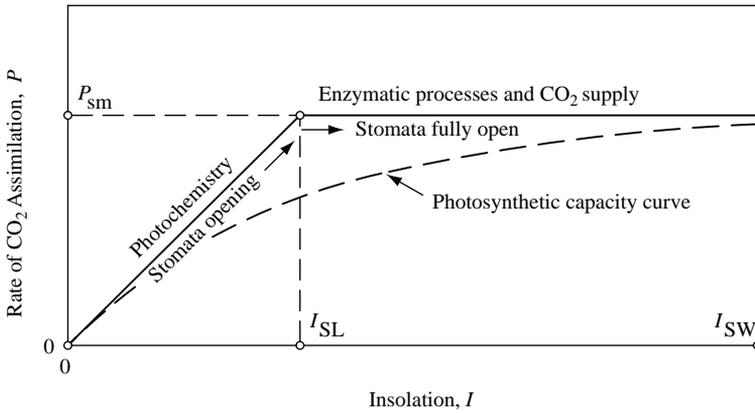


Fig. 1.1. Definition of the leaf light characteristic. Unit basal leaf area of C_3 species; water and nutrients non-limiting; optimal temperature; ambient CO_2 .

I_{SL} , at which the asymptotes of the photosynthetic capacity curve intersect. We call these asymptotes the leaf *light characteristic*, and show that provided water is not limiting, I_{SL} marks the insolation at which the stomates are effectively fully open. For maximum productivity and maximum efficiency of light utilization, the optimal bioclimatic state for a single leaf of the given species sets the climatic value, I_0 , of the insolation equal to I_{SL} , with $T_l = T_m$, as is shown in Fig. 1.2. We also show for isolated leaves that $I_{SL} = P_{sm}/\epsilon$ with ϵ constant over a wide range of species as is shown in Fig. 1.3. The relationship $P_{sm} = \epsilon I_{SL}$ is therefore the *biochemical assimilation capacity* for C_3 leaves.

Consider now an increasing *climatic insolation*, I_0 , which causes decreasing average soil moisture concentration, s_0 , when the other climatic variables remain fixed. With I_0 exceeding I_{SL} (and hence non-optimal), but not yet causing water-limitation due to a generous value of the fixed precipitation, the stomates remain fully open and the individual leaf continues to transpire at its climatically potential rate, $E_v = E_{ps}^\dagger$. However, at the particular climatic insolation, $I_0 = I_{SW}$ (which equals or exceeds I_{SL}), the declining average soil moisture concentration reaches a critical value, s_{oc} , at the end of the average interstorm period, causing the stomates to begin closing and transpiration to decline. This situation is illustrated in Fig. 1.4 where we define the evaporation function by its asymptotes which in this case we call the leaf *water characteristic* and which intersect at the *desiccation* or *water-critical* insolation, I_{SW} . We show how I_{SW} is estimated from the water balance (cf. Chapter 8). We also show that at constant temperature, the transpiration rate is an approximate surrogate for productivity of the same species (cf. Appendix E) allowing us to use the productivity, P , rather than the transpiration rate as the ordinate in Fig. 1.4, and making $P_{wm} = P_{sm}$. The range $I_{SL} \leq I_0 \leq I_{SW}$ is thus bioclimatically optimal for the isolated leaf because it maximizes leaf productivity (cf. Fig. 1.7).

[†] E_{ps} is the potential rate of evaporation from a wet, simple surface (cf. Appendix B).

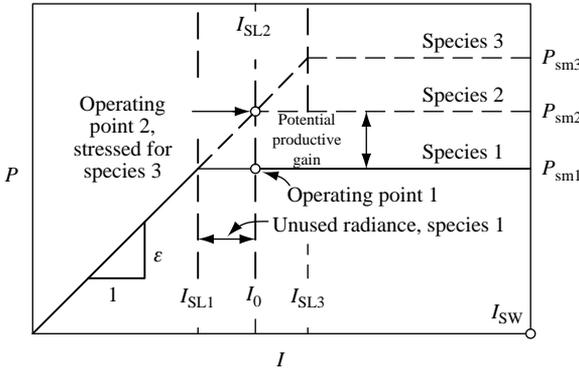
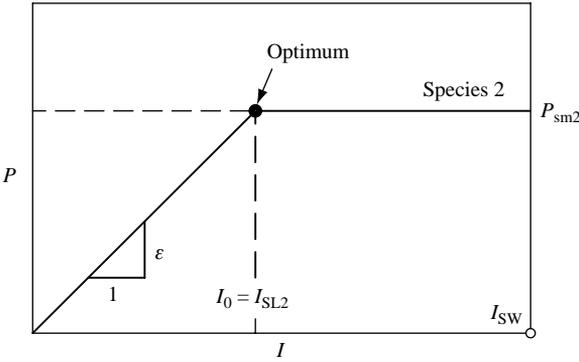


Fig. 1.2. Bioclimatic operating states under light control. Unit basal leaf area of C_3 species; water and nutrients non-limiting; optimal temperature; ambient CO_2 . (a) Suboptimal; (b) optimal.

(a)



(b)

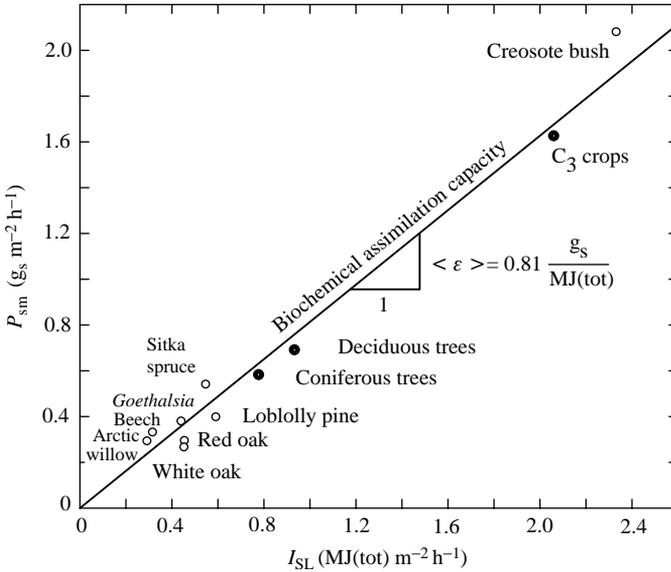


Fig. 1.3. Biochemical assimilation capacity of C_3 leaves. Data from Table 8.2.

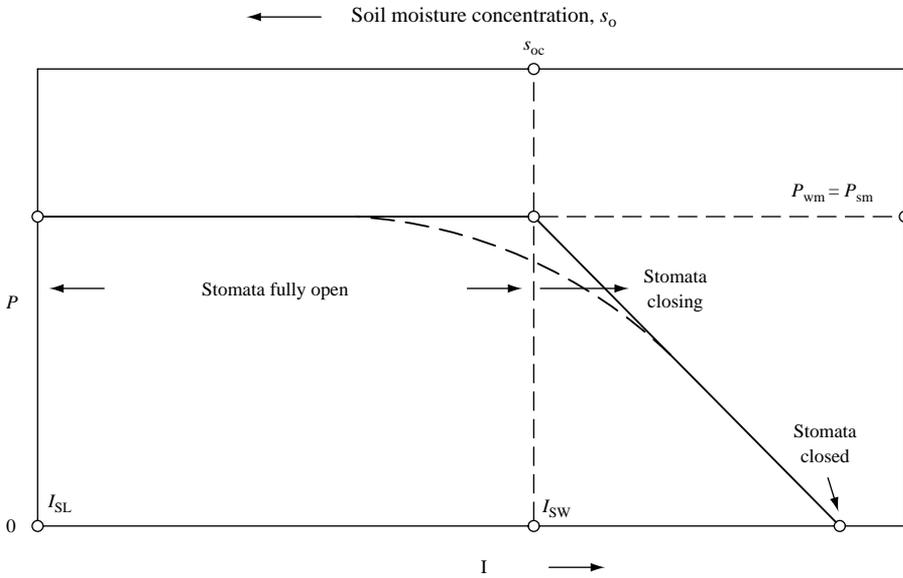


Fig. 1.4. Definition of the leaf water characteristic. Unit basal leaf area; light and nutrients non-limiting; ambient CO_2 ; fixed species, soil, precipitation and temperature.

To proceed toward canopy production, we must expand P_{sm} from isolated leaf to full canopy. Expanding in the vertical direction we multiply first by the leaf area index, L_t , to incorporate the total basal leaf area per unit of crown basal area, and next by the so-called *carbon demand function*, $f_D(\beta L_t)^\dagger$ (cf. Chapter 10) to average the leaf assimilation rate induced by a decaying insolation over the crown depth. This function is based upon our following proposed conditions for *optical optimality* in multilayers:

The reflection coefficient of the photosynthetically active component, PAR, of the incident radiation is small and nearly invariant over the range of vegetated latitudes, thus the incident light is used optimally for photosynthesis when *in the time average*:

- (1) the upper leaf surfaces are in full sunlight and the crown basal area is in full shadow at the average solar altitude, h_\otimes ; by including scattering we show (cf. Chapter 3) that this mandates an important geometrical relation between the solar altitude and the leaf angle, resulting in $\beta = \kappa, \ddagger$ as is sketched for a pair of opaque leaves in Fig. 1.5 and as is verified from observations of full crowns of translucent leaves in Fig. 1.6; and
- (2) the insolation at the lowest leaf is the minimum for leaf metabolism (i.e., the so-called *compensation intensity*, I_k); we show that its relative value, I_k/I_0 , is a species constant (cf. Appendix H) that fixes the value of the *insolation*

[†] βL_t is called the (horizontal) *momentum absorption index*, or the *horizontal leaf area index*, since β is the cosine of the leaf angle, θ_L , with the horizontal.

[‡] κ is the light extinction coefficient.

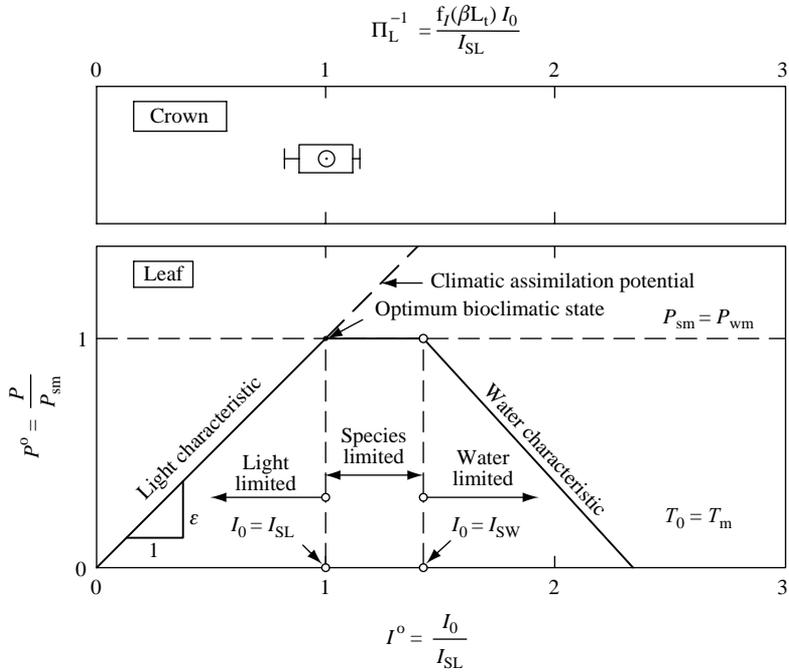


Fig. 1.7. Optimal bioclimatic state and the supporting evidence. Data from Table 9.1. Eight communities from desert shrub to rainforest. Plotted circle shows mean, box shows \pm one standard deviation, and bar shows range (fixed C_3 species, soil and precipitation; ambient CO_2 ; nutrients non-limiting).

insolation, $\hat{I}_l = f_l(\beta L_l)I_0$. We assume all leaves in the crown to have the same light characteristic making the crown-average \hat{I}_{SL} equal the isolated leaf I_{SL} , whereupon the *optimal bioclimatic state* for the canopy becomes $I_{SL} = \hat{I}_l = f_l(\beta L_l)I_0$. This is supported in Fig. 1.7 by observations over a range of communities from desert shrub to rainforest (cf. Chapter 9). Together with Fig. 1.3, it defines the *climatic assimilation potential*, $P_{sm} = \epsilon f_l(\beta L_l)I_0$, fixing the maximum CO_2 assimilation rate for given climate and species. The uppermost leaves in the canopy will reach their desiccation moisture state, I_{SW} , first and at the lower canopy-average radiance, $\hat{I}_{SW} = f_l(\beta L_l)I_{SW}$. Comparison of the relative magnitudes of \hat{I}_l , I_{SL} , and \hat{I}_{SW} , in all their permutations, defines the range of natural habitats in water and light space and reveals the boundaries of this space as *climax conditions* which compare favorably in Fig. 1.8 with observations from the same wide range of communities (cf. Chapters 8 and 9).

Expanding crown productivity in the horizontal direction we multiply by the fraction of the ground surface covered by crown basal areas (i.e., the canopy cover, M). Being a canopy property, M depends upon the collective action of the individual plants in satisfying their individual water needs and is not maximized by Dawkins’s “selfish gene”. We show that the canopy demands water over the full growing season at the time-averaged rate ME_v , where $E_v \equiv k_v^* E_{ps}$ is the canopy transpiration rate (cf. Chapter 6),

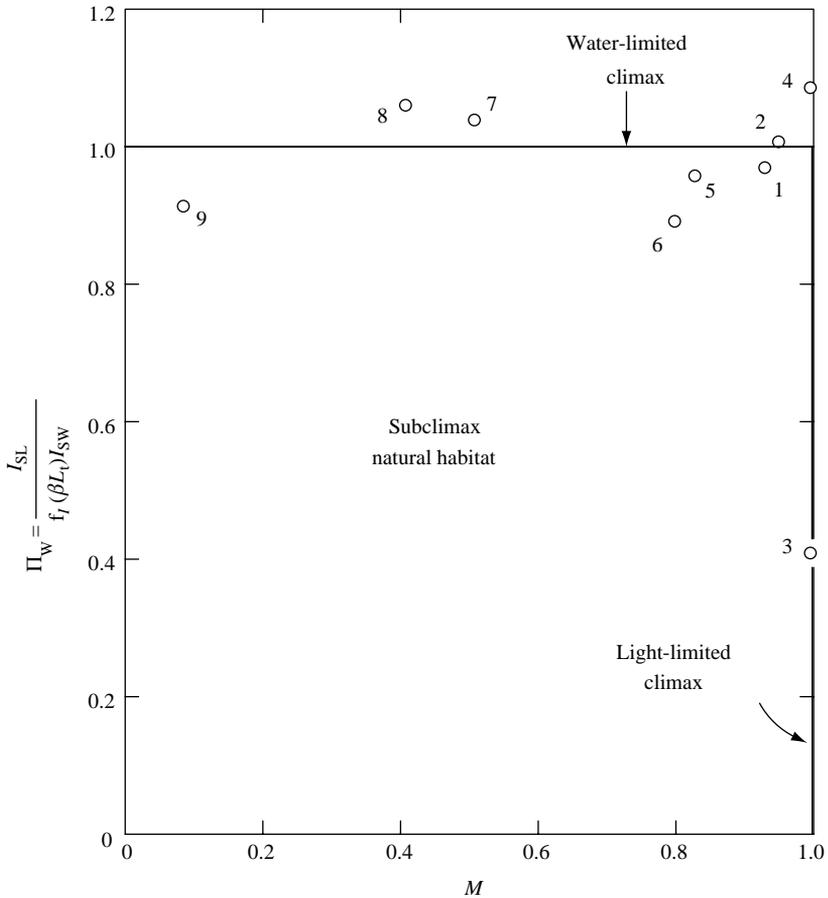


Fig. 1.8. Climax conditions as bounds to natural habitat. Data from Table 9.2.
 1, Beech; 2, oak; 3, *Goethalsia* (rainforest); 4, Sitka spruce; 5, ponderosa pine;
 6, loblolly pine; 7, pinyon-alligator juniper; 8, pinyon-Utah juniper; 9, creosote bush.

and k_v^* is the *canopy conductance* (cf. Chapter 6). In order to maintain the water balance, M will be less than 1 when E_v exceeds the climatically available water supply, and such a vegetation community is termed *water-limited*. Otherwise $M = 1$ and the community is *light-limited* with an excess of water. We recognize that the proportionality between soil-to-plant nitrogen flux and the flux of water, when coupled with the sensitivity of CO_2 assimilation to nitrogen availability, provides a degree of productivity-motivated selection pressure to maximize the plant transpiration rate, E_v . This may be accomplished by maximizing k_v^* , through minimizing the normalized canopy resistance, r_c/r_a (at given temperature) as is shown in Fig. 1.9 (cf. Chapter 7).[†] For given β we find this minimization to favor tapered crowns when L_t is large. For

[†] We show that the open-stomate condition of the optimal bioclimatic state allows approximation of the canopy flux resistance, r_c/r_a , as being independent of stomatal resistance. We then use the canopy-average eddy viscosity to derive r_c/r_a in terms of β and L_t .

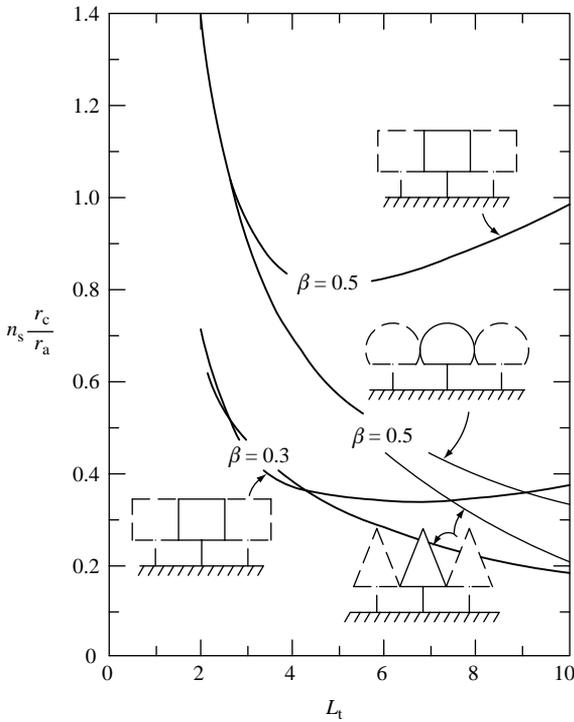


Fig. 1.9. Effect of crown shape on canopy resistance. Homogeneous multilayers with $M = 1$; r_c = canopy resistance; r_a = atmospheric resistance; $n_s = \frac{\text{stomated leaf area}}{\text{projected leaf area}}$.

water-limited canopies this transpiration maximization requires reduction of M and thus a larger investment in root mass by the individual plant with an associated loss in its seed productivity. This tradeoff of seed production for transpiration rate in order to gain seed production through added nitrogen flux is of indeterminate advantage to the plant. However with the plentiful water of light-limited situations no tradeoff is required, and rapid nitrogen recycling is fostered by this mechanism. Can this be the selection pressure leading to tapered crowns in nitrogen-poor soils?

There is much evidence (cf. Figs. 3.15 and 3.18) that β is heavily dependent upon h_{\otimes} . For a given deciduous species having cylindrical crowns, optical optimality in combination with the minimum resistance can determine both L_t and β as is shown in Fig. 1.10, and the range of L_t so determined is that observed (cf. Chapter 7). For evergreen species we show empirically that the needles are normal to the radiation beam (cf. Fig. 3.18). Under extreme temperature conditions these β vs. h_{\otimes} relations appear to be biased by the need to control the reflection of the near infrared (NIR) component of radiation (cf. Fig. 3.15).

Returning now to the productivity, we next incorporate the temperature sensitivity of leaf photosynthesis by multiplying by the function $g(\hat{T}_l)$ where \hat{T}_l is the crown-average leaf temperature. We show in Fig. 1.11, albeit for only three communities, that the local growing season average atmospheric temperature, T_0 , equals T_m , the species-dependent leaf temperature yielding maximum CO_2 assimilation (cf. Chapter 9). We infer that \hat{T}_l is approximately equal to T_0 by demonstrating growing season average

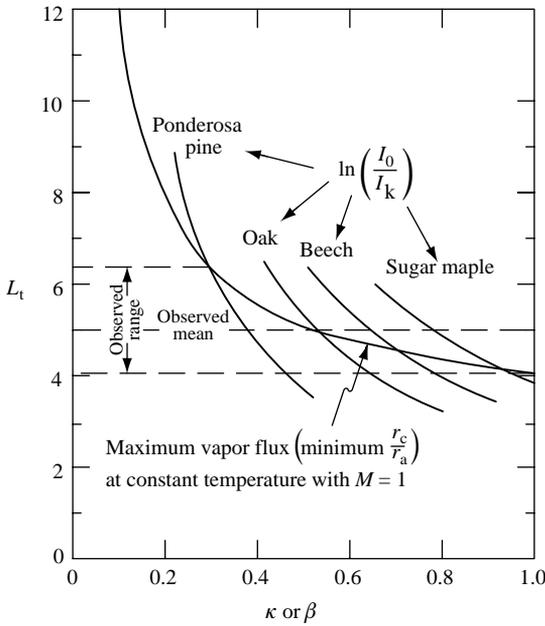


Fig. 1.10. Foliage parameters for maximum vapor flux. Homogeneous cylindrical multilayers with $M = 1$.

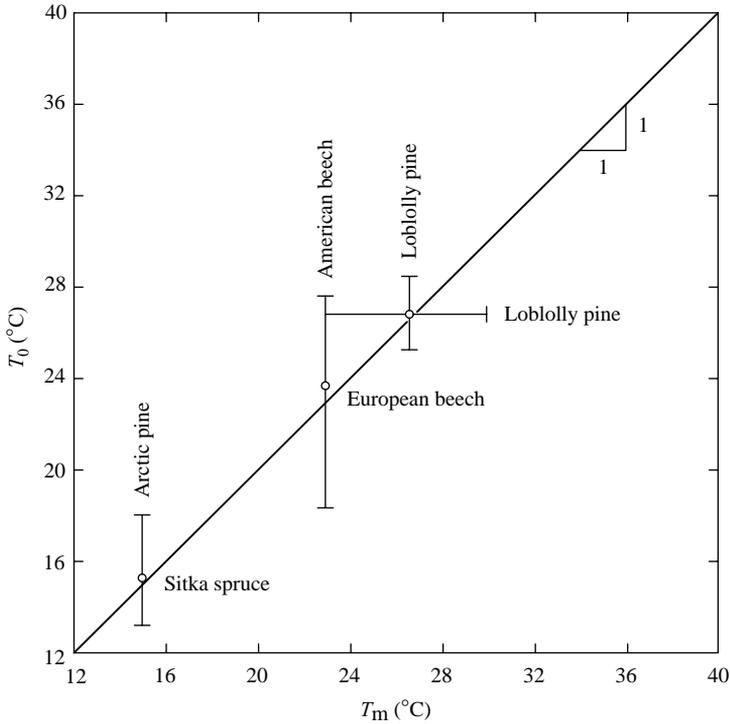


Fig. 1.11. Limited test of habitat heat proposition.

Bowen ratios on the order of 10^{-1} for a wide range of communities (cf. Table 9.2), and therefore that nominally $g(\widehat{T}_l) \approx g(T_0) = g(T_m) = 1$.

Finally, in order to get the potential (i.e., carbon demand-limited) annual production for a given species, we multiply by the average length of the growing season, m_τ , and to convert the *gross* primary productivity calculated in $g(\text{CO}_2)$ into *net* primary productivity, NPP, measured in grams of (above-ground) solid matter, g_s , we multiply by the widely accepted nominal empirical conversion factor, $\vartheta = 0.50 \text{ g}_s \text{ g}^{-1}$.

Potential productive gain

We can now write the product of the above productivity factors in the convenient form (cf. Chapter 10)

$$\frac{\text{NPP}}{p_D} = \frac{\text{NPP}}{g(T_0)P_{sm}Mm_\tau} = f_D(\beta L_t). \tag{1.1}$$

We show p_D to be the productive demand of a unit basal area of the monolayer, $L_t = 1$, for the given species, making $\frac{\text{NPP}}{p_D}$ the potential (contingent upon adequate CO_2 supply) productive *gain* for this species resulting from the canopy structure. The independent variable, βL_t , is a species parameter (cf. Appendix H), and $\frac{\text{NPP}}{p_D}$ is the maximum for a given species due to our use of both optical optimality and bioclimatic optimality in deriving the demand function, $f_D(\beta L_t)$. Equation 1.1 is plotted as Curve (a) in Fig. 1.12 where we see it to be monotonically increasing.

Picking a form for the vertical gradient of CO_2 concentration within the crown and calculating the eddy momentum diffusivity from a “big leaf” model of the crown, we use the flux–gradient relation to find the downward CO_2 supply function,

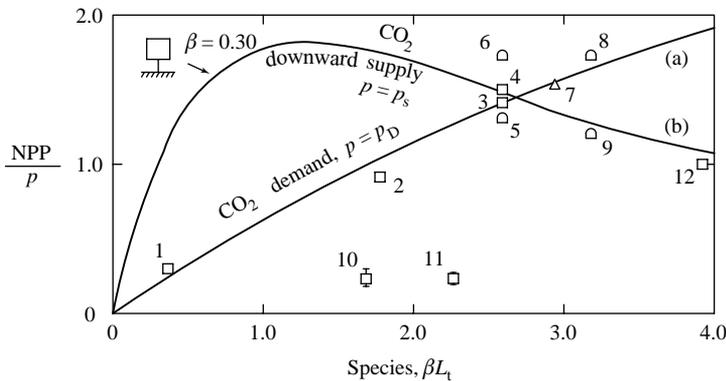


Fig. 1.12. Productive gain of C_3 multilayer canopies. Curve (a) = canopy CO_2 demand compared to monolayer demand; curve (b) = canopy downward CO_2 supply compared to monolayer supply. Data points: 1, Creosote bush; 2, ponderosa pine; 3, loblolly pine; 4, oak; 5, rainforest (Ghana); 6, rainforest (Congo); 7, red spruce; 8, beech (Tennessee); 9, beech (Eastern Europe); 10, pinyon-alligator juniper; 11, pinyon-Utah juniper; 12, sugar maple. Symbol shape indicates crown shape.

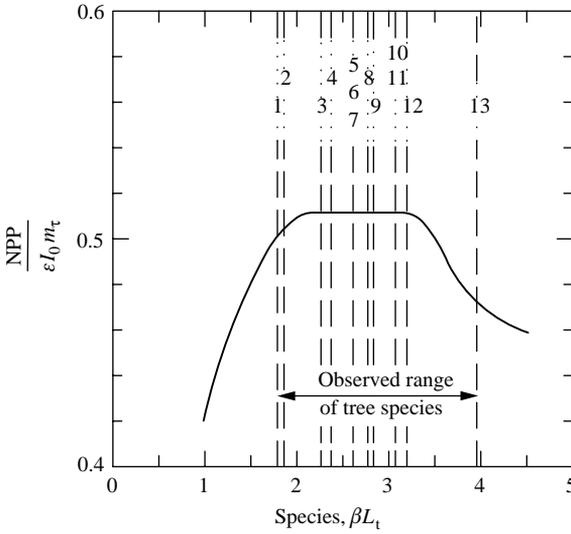


Fig. 1.13. Evidence for maximization of light-limited productivity of trees. Observed range from Baker's I_k/I_0 (1950, Table 12, p. 143) using $\kappa = \beta$; Table 3.9. 1, Ponderosa pine; 2, Scots pine; 3, Northern white cedar; 4, tamarack; 5, lodgepole pine; 6, Douglas fir; 7, red oak; 8, hackberry; 9, Engelmann spruce; 10, Norway spruce; 11, Eastern hemlock; 12, beech; 13, sugar maple.

$NPP/p_S = f_S(\beta, L_t)$ for cylindrical crowns shown as Curve (b) in Fig. 1.12 for the commonly observed value $\beta = 0.30$. Here p_S is the carbon supply analog of p_D which we assume to equal p_D for the $L_t = 1$ monolayer. With this critical assumption, comparison of the supply and demand functions shows a *critical absorption index*, $\widehat{\beta L_t}$, separating the region ($\beta L_t \leq \widehat{\beta L_t}$) in which the atmosphere can supply the entire CO_2 demand from that ($\beta L_t > \widehat{\beta L_t}$) in which a growing fraction of the CO_2 demand must be met from below by decaying plant matter. We show that for tapered crowns (i.e., cones or hemispheres) the atmospheric CO_2 supply is monotonically increasing with βL_t so that these crown shapes can meet the CO_2 demand at all βL_t without local recycling. Limited observations seem to support our derivation of this optimum productivity as shown by the plotted points on Fig. 1.12.

Maximization of species potential productivity

Fundamental to all this work is the assumption that the dominant selective pressure is to maximize the individual plant's reproductive potential as expressed through maximization of annual biomass production with its proportional seed production. By substituting the climatic assimilation potential, $P_{sm} = \varepsilon f_I(\beta L_t) I_0$,[†] in the denominator of Eq. 1.1[‡], for non-limiting water supply, $M = 1$, and with $g(T_0) = 1$, we write

$$\frac{NPP}{\varepsilon I_0 m_\tau} = f_D(\beta L_t) f_I(\beta L_t), \quad (1.2)$$

[†] We find $\langle \varepsilon \rangle = 0.81 \text{ g}_s \text{ MJ}(\text{tot})^{-1}$.

[‡] Without the need here to have the denominator on the left-hand side of Eq. 1.1 represent monolayer productivity we are free to extract from P_{sm} its dependence upon species through $f_I(\beta L_t)$ and to move this function to the right-hand side in Eq. 1.2.

the species-dependence of the potential (i.e., light-limited) NPP is now all on the right-hand side. Equation 1.2 is plotted as the solid line in Fig. 1.13 and shows a broad global maximum over a particular range of βL_t . The range of observed tree species is indicated by the spread of the vertical dashed lines at the respective species-constant βL_t . Their clustering in the range of the global maximum NPP is taken as confirmation of our fundamental assumption.

Extreme climates call for extreme βL_t in order to conserve heat (large βL_t) or water (small βL_t) leading to locally optimal NPP that are smaller (due to CO_2 or water limitation respectively) than this global, light-limited maximum. While the above development of productivity and its underlying optical and bioclimatic optimalities is at the heart of this work, we also present and evaluate applications of these ideas to natural habitats and to ecotone location, and we discuss their potential use to assess some of the apparent consequences of global climate change.