OPTIMAL LEAF SIZE IN RELATION TO ENVIRONMENT*

BY D. F. PARKHURST† AND O. L. LOUCKS

Department of Botany, University of Wisconsin, Madison, Wisconsin

I. INTRODUCTION

The physical laws governing heat and mass transfer between plants and environment have begun, over the last two decades, to be applied to the explanation of ecological problems. This paper describes a model, based on these laws, for understanding the general features of the plant geographical problem of leaf size variation with environment.

The physiological processes governing the growth of leaves on a given plant individual are certainly influenced by the physical environment during their ontogeny (Milthorpe 1959; Humphries & Wheeler 1963; Whitehead 1962; Milthorpe & Newton 1963). Even so, leaf size and shape are controlled largely by heredity, as shown by the ranges of sizes and shapes which sometimes occur when several species coexist in a given environment.

The variation of leaf size with climate, evidently the result of evolutionary convergence, was noted by Theophrastus (Hort 1948) and has been discussed ever since (e.g. von Humboldt 1850; Bailey & Sinnott 1916; Bews 1927; Cain & Castro 1959; Gentry 1969). In spite of this long consideration of the problem, few physical explanations have been given (Richards 1964).

Here the principle of optimal design is used, which may be stated as follows: 'Natural selection leads to organisms having a combination of form and function optimal for growth and reproduction in the environments in which they live.'

This is not to say that every organism is perfectly adapted to its present environment, but rather that the plants in any given environment will tend to become adapted to it. When a particular environment is so unsuitable for a species that none of its propagules can become established, the optimality principle is not applicable; differential survival is required for its operation.

The principle was formalized by D'Arcy Thompson as early as 1917 (Thompson 1966) and has been developed further by Rashevsky (1960) and Rosen (1967). It has been applied to plant physiognomic problems by Rashevsky (1943a, b; 1944), Opatowski (1944a, b; 1945; 1946), Esser (1946a, b), and Howland (1962).

Stated in other words, the fundamental axiom is simply that in a given population in a given environment, those genotypes having phenotypes closest to optimum for growth and reproduction in that environment will tend to survive and reproduce most often. Thus, by natural selection, the form and function of the members of the population may be expected to approach or reach an optimum condition (or series of conditions throughout the life cycle).

In engineering, the goal is often to produce at minimal cost some object or process for a particular function. Such a design goal can most easily be fulfilled when one can write an explicit function

† Present address: C.S.I.R.O., Division of Atmospheric Physics, Aspendale, Victoria, 3195, Australia.
Optimal leaf size

\[
\text{cost} = f \left( \text{design variables} \right)
\]

In biology, by analogy, one may attempt to understand or explain a given form or process of an organism by 'designing' an organism to fill the same role. The procedure used is to choose some cost variable thought to be of most importance to the survival of the organism, and to minimize that cost. If the resulting design is sufficiently similar to typical forms of the actual living organism, it is likely that one understands reasonably well the factors which have influenced its evolution.

Alternatively, if the design is not similar to the actual living organism, three explanations seem possible. First, the organism in question may not have been in the given environment long enough for evolution of optimality. Similarly, the environment may not have remained constant long enough. Third, it may be that not all the important variables affecting the living organism have been considered in the design (i.e. the cost variable was not correctly chosen).

In general, a lack of similarity between the design and the real organisms will be due to some combination of the three explanations, but it is most likely that one's understanding of the processes important to the evolution of the organism is not complete enough. Indeed, such negative results will sometimes be the major profit to be gained from the optimality principle, because they will demonstrate just how poorly understood the processes are.

These arguments should apply equally well to any sub-unit of a sexually-reproducing organism, such as an organ or organ system, provided that optimization of that sub-unit does not in some way increase the cost for the organism as a whole.

The principle of optimal design may seem teleological at first, but the only 'end' considered in applying it is that organisms will tend to become adapted to reproduce in their environment. The principle is a corollary to the theory of organic evolution, and, as such, is mechanistic rather than teleological. In Mayr's words (1968), the question is 'why—how come?' rather than 'why—what for?'.

The principle of optimal design can be applied to leaves in relation to their role as photosynthesizing organs by considering combinations of the following.

1. The vascular system affects both the mechanical strength of the leaf and the distribution of water, minerals, metabolites, and hormones within it. Size, density, and geometrical distribution of vascular elements would be important.

2. The coupling of a leaf to the temperature, momentum, water vapour, and carbon dioxide of the surrounding air depends on leaf size. Both the mechanical strength and the conducting capacity of the vascular system must vary with leaf size as well (Howland 1962).

3. In a deeply lobed leaf the lobes may be coupled individually to the air (cf. Cain & Castro 1959). If so, then the shape of the leaf helps to determine its effective size (Parkhurst et al. 1968; Parkhurst 1968; Vogel 1970). Shape in a broader sense, i.e. whether the organ is flat or cylindrical, influences the ability of the organ to orient selectively to light, and may change the proportion of tissue which carries out photosynthesis.

4. Stomatal size, shape, and distribution partially control transfer of water vapour, carbon dioxide of the surrounding air depends on leaf size. Both the mechanical strength and the conducting capacity of the vascular system must vary with leaf size as well (Howland 1962).

5. The absorptance*, emittance, reflectance, and transmittance of the leaf determine its relation to radiation in each portion of the electromagnetic spectrum. The spatial

* Gates (1965) has commented on the low absorptance of most leaves to near-infrared radiation, which is plentiful in the leaf environment but would serve only to raise leaf temperatures to undesirable levels. This low absorptance is one aspect of optimality in leaves.
distribution of chloroplasts within the leaf also helps control how efficiently light is used in photosynthesis.

(6) Internal structure, such as arrangement of palisade and spongy mesophyll tissue, affects diffusion of gases and dissolved substances, and determines in part the relative proportions of photosynthetic and non-photosynthetic tissues.

(7) Non-photosynthesizing external structures and secretions such as hairs and waxes increase the intrinsic (energy-consuming) costs of the leaf, but may decrease costs related to the environment.

In compound leaves, the leaflet may be the physiological unit to be designed, and the above considerations would therefore apply to a leaflet. In plants without leaves (e.g. stem succulents), the considerations should apply as well to whatever anatomical unit acts as the major photosynthesizing organ. In this paper, the term 'leaf' is used in a physiological, not morphological, sense.

The word 'size' applies here to the effective size of single leaves or leaflets, and has little to do with the total leaf area of a plant individual. This distinction must be made because there may be situations in which available water or nutrients might limit the total leaf area of a plant, but need not affect leaf size in doing so.

II. A MODEL TO PREDICT OPTIMAL LEAF SIZE

The principle of optimal design is here used to predict leaf sizes in various environments. To apply the principle to a specific problem, one makes an educated guess at cost functions for whatever structure (or function) is being considered. The particular form of the structure yielding the minimum cost indicates the form toward which natural selection would lead in a population having an environment similar to the one used as a basis for the design, and responding to the set of selection pressures included in the cost function. As stated earlier, if the resulting design is similar to the observed structure, then apparently the major selection pressures are understood.

According to Rosen's (1967) formulation, the cost of any structure of an organism has an intrinsic (metabolic) component and an extrinsic (environmental) one. An extrinsic cost is best thought of as a reduced fecundity relative to the maximum fecundity possible in the environment considered. The model discussed here is based on extrinsic costs.

The simplest model would be one predicting leaf size as an extremum problem of a single variable, that is, one for which $d \text{(cost)}/d \text{(leaf size)} = 0$ at the actual size found to occur in a given environment.

Considering the main function of leaves to be photosynthesis, one might first think of three simple variables which could be optimized, namely carbon dioxide uptake, water loss, and leaf temperature.

(a) Transfer resistances

To consider these three variables further, it is useful first to review the concept of transfer resistances (Holmgren, Jarvis & Jarvis 1965). These resistances are defined by the equations*

$$ q_x = -c_p \rho \frac{T - T_w}{r_a}, $$ \hspace{1cm} (1)

* All symbols used in this paper are defined in Table 1.
Optimal leaf size

\[ E = \frac{C(T) - U.C(T_a)}{r_a + r'_s}, \text{ and} \]

\[ p = \frac{[\text{CO}_2]_{\text{air}} - [\text{CO}_2]_{\text{leaf}}}{r_a + r''_s + r'''_n} \cdot f(T) \cdot g(I). \]

The two stomatal resistances \((r'_s \text{ and } r''_s)\) are related as discussed by Holmgren et al. (1965). The boundary layer resistances \((r_a)\) are related by the equation

\[ r_a = r_a \left( \frac{D'}{D_h} \right)^{2/3} = r_a \left( \frac{D''}{D_h} \right)^{2/3}. \]

The 2/3 power is often omitted in the literature, but is necessary because the transfer through the boundary layer is convective, and not purely diffusive.

The relation between the boundary layer resistance \(r_a\) and the convection coefficient \((h_c)\) is

\[ h_c = \frac{C_p \rho}{r_a}. \]

Equations (1) and (5) may be combined to yield

\[ q_c = h_c (T - T_a) \]

which is in fact the defining equation for \(h_c\), a parameter often used by heat-transfer physicists (Kreith 1965). The coefficient \(h_c\) can be calculated from the equation describing heat convection in wind-tunnel laminar flow (Parkhurst et al. 1968):

\[ h_c \propto \left[ \frac{\text{wind speed}}{\text{leaf dimension}} \right]^h. \]

Some recent field work (Hunt, Impens & Lemon 1968) has indicated that convection coefficients may be higher in the field than in wind tunnels. However, G. I. Pearman, H. L. Weaver, and C. B. Tanner (unpublished) have shown that the relation (7) holds for discs between 2 and 12 cm diameter, over a variety of surfaces outdoors. They found \(h_c\) to be about 50% higher outdoors than in wind tunnels (for a given mean wind speed), but the dependence on size was unchanged. Thus, large leaves have smaller convection coefficients and higher values of the resistances to heat and mass transfer through leaf boundary layers than do smaller leaves. The basic optimality arguments are continued below.

(b) Variables relating leaf size to the environment

Leaves contribute to the reproduction of a plant individual by photosynthesizing. One might therefore think that the optimal size for a leaf would be the size minimizing the resistance to CO\(_2\) uptake. Eqns (3), (4), (5) and (7) imply that this resistance would be a minimum for very small (zero-dimension) leaves. However, there are two reasons why CO\(_2\) resistance alone is not a logical variable to optimize. One reason is that \(r''_s\) is usually much smaller than \(r''_s + r'''_m\) (Holmgren et al. 1965), and thus even large relative changes in \(r''_s\) will not much affect the total resistance to photosynthesis.

Also, eqns (2) and (4) demonstrate that a decrease in leaf size (and thus in \(r_a\)) could increase transpiration rates under some conditions. An optimality argument must provide for maximum reproduction, however, and for a number of reasons high transpiration
Table 1. List of symbols used in the equations

<table>
<thead>
<tr>
<th>Variable</th>
<th>Dimensions</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>[CO₂]</td>
<td>g cm⁻³</td>
<td>CO₂ concentration</td>
</tr>
<tr>
<td>C(T)</td>
<td>g cm⁻³</td>
<td>Saturation water vapour concentration at temperature T</td>
</tr>
<tr>
<td>Dₙ</td>
<td>cm² min⁻¹</td>
<td>Molecular diffusivity of heat, taken as 12.8</td>
</tr>
<tr>
<td>D'</td>
<td>cm² min⁻¹</td>
<td>Molecular diffusivity of water vapour, taken as 15.9</td>
</tr>
<tr>
<td>D''</td>
<td>cm² min⁻¹</td>
<td>Molecular diffusivity of CO₂, taken as 9.95</td>
</tr>
<tr>
<td>E</td>
<td>g cm⁻² min⁻¹</td>
<td>Transpiration flux density</td>
</tr>
<tr>
<td>I</td>
<td>Arbitrary</td>
<td>Light intensity</td>
</tr>
<tr>
<td>Lₑ</td>
<td>cm</td>
<td>Effective convecting length of a leaf</td>
</tr>
<tr>
<td>Lₜ</td>
<td>cal g⁻¹</td>
<td>Heat of vaporization (water)</td>
</tr>
<tr>
<td>P</td>
<td>g cm⁻² min⁻¹</td>
<td>Net assimilation of CO₂ (flux density)</td>
</tr>
<tr>
<td>P'</td>
<td>(g cm⁻² h⁻¹)</td>
<td>Normalized net assimilation (defined in text)</td>
</tr>
<tr>
<td>R</td>
<td>Dimensionless</td>
<td>Water-use efficiency (P/E)</td>
</tr>
<tr>
<td>R'</td>
<td>cm² g⁻¹</td>
<td>Normalized water-use efficiency (P'/E)</td>
</tr>
<tr>
<td>Rₑ</td>
<td>min cm⁻¹ (s cm⁻¹)</td>
<td>r_s' + r_v' + r_m'</td>
</tr>
<tr>
<td>Rₜ</td>
<td>min cm⁻¹ (s cm⁻¹)</td>
<td>r_s + r_v</td>
</tr>
<tr>
<td>T</td>
<td>deg C (deg K)</td>
<td>Leaf temperature</td>
</tr>
<tr>
<td>Tₑ</td>
<td>deg C</td>
<td>Air temperature</td>
</tr>
<tr>
<td>U</td>
<td>Dimensionless</td>
<td>Relative humidity (as a fraction)</td>
</tr>
<tr>
<td>cₚ</td>
<td>cal g⁻¹ deg⁻¹</td>
<td>Specific heat of air, taken as 0.24</td>
</tr>
<tr>
<td>cₑ</td>
<td>cal g⁻¹ deg⁻¹</td>
<td>Specific heat of water vapour, taken as 0.446</td>
</tr>
<tr>
<td>f</td>
<td>Function relating P to T</td>
<td></td>
</tr>
<tr>
<td>g</td>
<td>Function relating P to I</td>
<td></td>
</tr>
<tr>
<td>hₑ</td>
<td>ly min⁻¹ deg⁻¹</td>
<td>Convection coefficient</td>
</tr>
<tr>
<td>qₑ</td>
<td>ly min⁻¹</td>
<td>Absorbed radiation flux density</td>
</tr>
<tr>
<td>qₑ</td>
<td>ly min⁻¹</td>
<td>Convective heat flux density</td>
</tr>
<tr>
<td></td>
<td>min cm⁻¹ (s cm⁻¹)</td>
<td>Transfer resistances: without ', heat; with ', water vapour; '”, CO₂; a, boundary layer; m, mesophyll; s, stomatal</td>
</tr>
<tr>
<td>t</td>
<td>Arbitrary</td>
<td>Time</td>
</tr>
<tr>
<td>ε</td>
<td>Dimensionless</td>
<td>Thermal emissivity of leaf, taken as 0.97</td>
</tr>
<tr>
<td>ρ</td>
<td>g cm⁻³</td>
<td>Density of air</td>
</tr>
<tr>
<td>σ</td>
<td>ly min⁻¹ deg⁻¹</td>
<td>Stephan–Boltzmann constant, 8.13 x 10⁻¹¹</td>
</tr>
</tbody>
</table>

Rates tend to reduce plant reproduction, at least whenever water uptake does not proceed at an equal rate (Kramer & Kozlowski 1960).

1. High drought stress often kills plants.

2. P can be reduced by low water potentials (sometimes drastically) through partial or complete stomatal closure, through increases in r_m, and probably through direct effects on biochemical reactions. Slavík (1965) showed, using a stoma-free liverwort, that some combination of the last two mechanisms can alone reduce photosynthesis, and Boyer & Bowen (1970) found direct effects in isolated chloroplasts.

3. Higher water loss by leaves often makes less water available to developing flowers and fruits, although in some species drought stimulates flowering (Zahner 1968).

4. At any place where water supply is seasonal, less stored water for the dry season results from a high water loss at a time when water is plentiful.

Thus leaf water status is at least as important as CO₂ uptake in determining the reproductive capacity of a plant. One might therefore expect optimal leaf size to be the size minimizing water loss (the second variable to be considered). However, under many environmental conditions a reduction in transpiration is accompanied by a reduction in CO₂ uptake because CO₂ and water move through the same boundary layer. Water loss, like CO₂ uptake, is too simple a variable to optimize.
One could then consider the third alternative, that is, that leaf size might change to optimize leaf temperature. As indicated symbolically in eqn (3), net photosynthesis is temperature dependent (Kramer & Kozlowski 1960), and perhaps natural selection would favour whatever leaf size yielded an average leaf temperature nearest the optimum for the enzyme system in a given species. The difficulty here is that enzyme systems can obviously change, since plants in different regions are known to have different temperature optima for photosynthesis (Kramer & Kozlowski 1960). Since changes in leaf size to optimize leaf temperature might often affect $P$ and $E$ adversely, enzyme systems would tend to evolve to fit leaf temperatures, rather than size evolving to fit the temperatures to the enzymes.

Carbon dioxide uptake, water loss, and leaf temperature are so interdependent that optimization of any one of them (by a change in leaf size) might adversely change the others. Perhaps a variable can be found which combines the important responses in a simple way.

(c) Water-use efficiency

The simplest solution to the dilemma that water loss and $\text{CO}_2$ uptake are closely coupled is to assume that a leaf will have minimum extrinsic cost when its size yields a maximum water-use efficiency ratio, $P/E$ (see Slatyer 1964). The main point of this paper, then, is to explore the consequence of that assumption.

The analysis may be simplified as follows: eqn (3) shows that $P$ depends in part on the $\text{CO}_2$ concentration at the chloroplast. This concentration is usually unknown; at least it differs from species to species due in part to photorespiration. One can circumvent this difficulty by defining

\[ P' = \frac{P}{[\text{CO}_2]_{\text{air}} - [\text{CO}_2]_{\text{leaf}}} = \frac{l}{r_s'' + r_s' + r_m'}. \]  

(8)

This will be termed the normalized net photosynthesis. Then any leaf size maximizing $P'$ will also maximize $P$, and this analysis therefore deals with the simpler $P'$.

To consider the dependence of the normalized water-use efficiency ratio ($P'/E$) on leaf size, one more equation is necessary, to describe the steady-state energy balance of leaves:

\[ q_s = q_c + \sigma \varepsilon T^4 + [L_0 + c_{pv} (T - T_0)]E^*. \]  

(9)

All the terms on the right-hand side of eqn (9) depend on the variable $T$. It is not possible to solve for $T$ explicitly, but with fixed values of $q_s$, $h_c$, $T_s$, $r'_s$ and $U$, the Regula Falsi algorithm yields a numerical solution.

The ratio of photosynthesis to transpiration (the water-use efficiency) depends on leaf size, through the convection coefficient $h_c$, in three ways. First, as noted above, higher values of $h_c$ are accompanied by lower boundary-layer resistances, and thus by higher $P'$ values. Second, $h_c$ affects leaf temperature, which controls the potential of the leaf to lose water (the numerator of eqn 2). Finally, the resistance through which the water loss occurs (the denominator of eqn 2) increases with a decrease in $h_c$. The net effect of a given change in $h_c$ may be either to increase or to decrease $P/E$, depending on the other variables.

It is often stated that because $r'_s$ is usually very much smaller than $r'_s$ in moving air,
variations in $h_c \left[ = \frac{c_p \rho}{r_s} \right]$ have little effect on $P$ and $E$. This ignores the direct effect of $h_c$ on leaf temperature and the resulting influences on $E$. In fact, as shown in Figs. 4 and 6, an order of magnitude increase in leaf size (and a decrease of $\sqrt{10}$ in $h_c$) can result in a 40% increase in transpiration and a 50% decrease in water-use efficiency. Cowan & Troughton (1971) have explored these relationships intensively in a different context.

(d) Optimal leaf size as a function of water-use efficiency

Predictions for leaf sizes can now be obtained by optimizing the water-use efficiency ratio for as many combinations of values as desired of the seven independent variables.

(1) Convection coefficient $(h_c)$
(2) Air temperature $(T_a)$
(3) Relative humidity $(U)$
(4) Absorbed radiation $(q_a)$
(5) Stomatal resistance $(r_i)$
(6) Mesophyll resistance $(r_m)$
(7) Stomatal distribution (whether hypo- or amphi-stomatous).

Variables 2 and 3 taken together specify the ambient absolute humidity, a more fundamental measure than relative humidity. Eqns (1)–(9) yield values for the three dependent variables $T$, $E$, and $P'$.

![Fig. 1. Calculated leaf temperatures, as a function of convection coefficient ($h_c$) and absorbed radiation flux density ($q_a$). A hypostomatous leaf was assumed. $T_{st} = 20^\circ C$, $R_{stom} = 20$ s cm$^{-1}$, R.H. = 50%.

---

FIG. 1. Calculated leaf temperatures, as a function of convection coefficient ($h_c$) and absorbed radiation flux density ($q_a$). A hypostomatous leaf was assumed. $T_{st} = 20^\circ C$, $R_{stom} = 20$ s cm$^{-1}$, R.H. = 50%.
Fig. 2. Water vapour concentration difference between leaf and air, as a function of convection coefficient (h_c). \( T_{air} = 20^\circ C, R_{atom} = 20 \text{ s cm}^{-1}, \text{R.H.} = 20\% \).

Fig. 3. The dependence of the resistances to transfer of heat, water vapour and CO\(_2\) on convection coefficient (h_c). \( R'_{atom} = 20 \text{ s cm}^{-1}, R_{meso} = 10 \text{ s cm}^{-1} \).
A simple example of the insight to be gained from optimizing water-use efficiency is presented first. Certain of the independent variables are held fixed in the example: air temperature = 20°C; relative humidity = 50%; stomatal resistance = 20 s cm⁻¹; mesophyll resistance = 10 s cm⁻¹; and a hypostomatous leaf is assumed. These values are used in eqns (1)–(9) for multiple values of the convection coefficient and for two values of absorbed radiation, 0.6 and 0.8 ly min⁻¹. The last two values correspond to likely absorption by shade and sun leaves, respectively, in a southern Wisconsin oak forest. The shade value, 0.6 ly min⁻¹, is equivalent to blackbody radiation from a surface at 22°C.

The results of these calculations are presented in Figs. 1–6. Figs. 1 and 2 show that both leaf temperature, and water-vapour concentration difference between leaf and air, decrease with increasing convection coefficient for either radiation flux, but that they decrease much faster at the higher radiation level. However, the convective resistance to vapour transfer also decreases with $h_c$ (Fig. 3); the net effect is that transpiration rate increases with $h_c$ for the shade leaf and decreases with $h_c$ (i.e. with higher wind or with smaller leaves) for the sun leaf (Fig. 4). Results similar to these were first published by Raschke (1958).

Because the boundary layer resistance to convection of CO₂ from the air to the leaf surface also decreases with $h_c$ (Fig. 3), the normalized CO₂ uptake ($P'$) increases with $h_c$ as shown in Fig. 5. All these results are combined in Fig. 6. Not only is the water-use
Optimal leaf size

Fig. 5. Calculated normalized carbon dioxide uptake for a hypostomatous leaf, as a function of convection coefficient \( h_c \)—see text. \( R_{stom} = 20 \text{ s cm}^{-1} \), \( R'_{meso} = 10 \text{ s cm}^{-1} \).

Fig. 6. Calculated normalized water-use efficiency for a hypostomatous leaf, as a function of convection coefficient \( h_c \). \( T_{at} = 20^\circ \text{C} \), \( R''_{stom} = 20 \text{ s cm}^{-1} \), \( R''_{meso} = 10 \text{ s cm}^{-1} \), R.H. = 50\%.
efficiency higher for the shade leaf, but also the slopes of the curves (plotted against \( h_c \)) have opposite signs for the two leaves.

More specifically, the normalized water-use efficiency of shade leaves is higher when they are large, while that of sun leaves is higher when they are small. The difference in actual efficiency between the two radiation levels may be slightly exaggerated, because the two curves would be strictly comparable only if [CO₂] at the chloroplasts were the same for both leaves. In fact this concentration might be higher in the shade leaf (if its photosynthesis were light limited), so that \( P'/E \) shown in the Figure is likely to differ somewhat more than \( P/E \) between the two light regimes. For a given radiation level, however, \( P'/E \) and \( P/E \) will vary in the same fashion, and conclusions about the variation in efficiency with convection coefficient remain valid.

(e) General results

Examples of the calculated dependence of the three independent variables—leaf temperature, transpiration rate, and normalized water-use efficiency—on six independent variables are listed in Tables 2–4. These tables allow one to follow through more combinations of independent variables than were covered by the previous example (Figs. 1–6). The tables provide information of the following types.

Table 2. Calculated leaf temperatures (°C) as a function of the number of leaf surfaces bearing stomata (D), relative humidity (U), stomatal resistance (rs), air temperature (\( T_a \)), convection coefficient (hc), and absorbed radiation flux density (qa).

<table>
<thead>
<tr>
<th>D: 1</th>
<th>U: 20%</th>
<th>2</th>
<th>30</th>
<th>2</th>
<th>30</th>
<th>2</th>
<th>30</th>
<th>2</th>
<th>30</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ta</td>
<td>h_c</td>
<td>q_a</td>
<td>rs</td>
<td>( T_a )</td>
<td>h_c</td>
<td>q_a</td>
<td>rs</td>
<td>( T_a )</td>
<td>h_c</td>
</tr>
<tr>
<td>15</td>
<td>0.028</td>
<td>0.8</td>
<td>2</td>
<td>20%</td>
<td>20</td>
<td>21.9</td>
<td>2</td>
<td>21.9</td>
<td>15</td>
</tr>
<tr>
<td>1.2</td>
<td>26.0</td>
<td>32.1</td>
<td>28.1</td>
<td>32.4</td>
<td>22</td>
<td>31.2</td>
<td>25</td>
<td>31.8</td>
<td>21.1</td>
</tr>
<tr>
<td>0.089</td>
<td>0.8</td>
<td>15.9</td>
<td>17.5</td>
<td>17.2</td>
<td>17.6</td>
<td>14.5</td>
<td>17.4</td>
<td>16.9</td>
<td>17.6</td>
</tr>
<tr>
<td>1.2</td>
<td>19.5</td>
<td>21.6</td>
<td>20.8</td>
<td>21.7</td>
<td>17.8</td>
<td>21.4</td>
<td>20.1</td>
<td>21.6</td>
<td>20.1</td>
</tr>
<tr>
<td>35</td>
<td>0.028</td>
<td>2</td>
<td>30</td>
<td>36.3</td>
<td>36.0</td>
<td>37.2</td>
<td>26.4</td>
<td>35.4</td>
<td>35.5</td>
</tr>
<tr>
<td>1.2</td>
<td>36.7</td>
<td>46.1</td>
<td>42.0</td>
<td>46.9</td>
<td>31.7</td>
<td>44.6</td>
<td>39.8</td>
<td>46.1</td>
<td>39.8</td>
</tr>
<tr>
<td>0.089</td>
<td>0.8</td>
<td>31.9</td>
<td>35.5</td>
<td>35.4</td>
<td>35.9</td>
<td>29.3</td>
<td>35.2</td>
<td>25.2</td>
<td>35.8</td>
</tr>
<tr>
<td>1.2</td>
<td>35.1</td>
<td>39.5</td>
<td>38.5</td>
<td>39.8</td>
<td>32.0</td>
<td>39.0</td>
<td>37.6</td>
<td>39.7</td>
<td>37.6</td>
</tr>
</tbody>
</table>

(1) Leaf temperature (Table 2) may climb from 36.7°C to 46.1°C when stomatal resistance changes from 2 to 30 s cm⁻¹ (when air temperature is 35°C, convection coefficient is 0.028 ly min⁻¹ deg⁻¹, absorbed radiation is 1.2 ly min⁻¹, and relative humidity is 20%). This calculated temperature increase indicates that a leaf under those conditions could be cooled appreciably by transpiration provided its stomatal resistance remained low.

(2) Transpiration under the same conditions drops from 4.42 to 0.71 g dm⁻² h⁻¹ with the increase in stomatal resistance from 2 to 30 s cm⁻¹ (Table 3). The higher transpiration rate probably could not be maintained for long under arid conditions. Leaf water potential would drop, and stomata would close.

(3) Water-use efficiency is in general much higher at 95% relative humidity than at 20%, other factors being equal (Table 4). This is not surprising, because transpiration...
Table 3. Calculated leaf transpiration rates (g dm\(^{-2}\) h\(^{-1}\)) as a function of the number of leaf surfaces bearing stomata (D), relative humidity (U), stomatal resistance (r\(_s\)), air temperature (T\(_a\)), convection coefficient (h\(_c\)), and absorbed radiation flux density (q\(_a\))

<table>
<thead>
<tr>
<th>D:</th>
<th>1</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td>U:</td>
<td>20%</td>
<td>95%</td>
</tr>
<tr>
<td>T(_a)</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>h(_c)</td>
<td>0.028</td>
<td>0.028</td>
</tr>
<tr>
<td>q(_a)</td>
<td>0.8</td>
<td>0.8</td>
</tr>
<tr>
<td>r(_s)</td>
<td>2.56</td>
<td>2.56</td>
</tr>
<tr>
<td>1.2</td>
<td>1.87</td>
<td>1.87</td>
</tr>
<tr>
<td>0.089</td>
<td>0.39</td>
<td>0.39</td>
</tr>
<tr>
<td>1.2</td>
<td>0.93</td>
<td>0.93</td>
</tr>
<tr>
<td>35</td>
<td>0.52</td>
<td>0.52</td>
</tr>
<tr>
<td>0.089</td>
<td>0.46</td>
<td>0.46</td>
</tr>
<tr>
<td>1.2</td>
<td>0.53</td>
<td>0.53</td>
</tr>
</tbody>
</table>

Table 4. Calculated values of the normalized water-use efficiency (dm\(^3\) g\(^{-1}\)) for a hypostomatous leaf, as a function of relative humidity (U), stomatal resistance (r\(_s\)), air temperature (T\(_a\)), convection coefficient (h\(_c\)), absorbed radiation flux density (q\(_a\)), and mesophyll resistance (r\(_m\)) (values for an amphistomatous leaf are similar—though always slightly lower—and are not listed)

<table>
<thead>
<tr>
<th>r(_m)</th>
<th>2</th>
<th>30</th>
<th>2</th>
<th>30</th>
</tr>
</thead>
<tbody>
<tr>
<td>T(_a)</td>
<td>15</td>
<td>35</td>
<td>15</td>
<td>35</td>
</tr>
<tr>
<td>h(_c)</td>
<td>0.028</td>
<td>0.028</td>
<td>0.028</td>
<td>0.028</td>
</tr>
<tr>
<td>q(_a)</td>
<td>0.8</td>
<td>0.8</td>
<td>0.8</td>
<td>0.8</td>
</tr>
<tr>
<td>20</td>
<td>27.3</td>
<td>15.2</td>
<td>35.4</td>
<td>16.9</td>
</tr>
<tr>
<td>1.2</td>
<td>15.9</td>
<td>9.7</td>
<td>18.5</td>
<td>9.5</td>
</tr>
<tr>
<td>20</td>
<td>15.5</td>
<td>3.3</td>
<td>14.2</td>
<td>7.3</td>
</tr>
<tr>
<td>0.089</td>
<td>27.5</td>
<td>11.7</td>
<td>46.9</td>
<td>17.7</td>
</tr>
<tr>
<td>20</td>
<td>8.9</td>
<td>3.8</td>
<td>36.0</td>
<td>13.5</td>
</tr>
<tr>
<td>1.2</td>
<td>21.2</td>
<td>9.5</td>
<td>35.4</td>
<td>13.8</td>
</tr>
<tr>
<td>20</td>
<td>6.8</td>
<td>3.0</td>
<td>27.1</td>
<td>10.6</td>
</tr>
</tbody>
</table>

would be lower. High stomatal resistance increases water-use efficiency at the lower humidity level, especially when mesophyll resistance to CO\(_2\) transfer is high.

These results will be further interpreted in Section III.

Other means may be used to look at the results of this model, that is, of the assumption that leaves in a given environment might evolve such that their water-use efficiencies reach the maximum possible in that environment. One may consider the environmental m-dimensional hyperspace* (habitat space) as two subspaces—one in which water-use efficiencies would be greatest for large leaves and the other in which they would be greatest for small leaves.

As before, let the normalized water-use efficiency be denoted by R' and let the effect of leaf size be considered through its part in the determination of convection coefficient,

* Habitat space is presumably a subspace of the n-dimensional niche hyperspace (Hutchinson 1965).
Then the two subspaces could be defined mathematically according to whether $\frac{\partial R'}{\partial h_e}$ is negative or positive, respectively.

An example of this approach is presented in Fig. 7, for a hypostomatous leaf with fixed values of stomatal resistance (20 s cm$^{-1}$) and mesophyll resistance (10 s cm$^{-1}$), assuming a convection coefficient of 0.032 ly min$^{-1}$ deg$^{-1}$. Relative humidity, air temperature, and absorbed radiation—three variables in the environmental hyperspace—are shown along the three axes. The surface shown in the Figure is the locus of points where $\frac{\partial R'}{\partial h_e} = 0$. Everywhere above the surface $\frac{\partial R'}{\partial h_e} < 0$ (i.e. water-use efficiency increases with increasing leaf size), and everywhere below the surface $\frac{\partial R'}{\partial h_e} > 0$ (water-use efficiency increases with decreasing leaf size).

In Fig. 7, three general features are of interest. First, the subspace where efficiency increases for larger leaves (or low wind speeds) is the one in which absorbed radiation is low. Conversely, the efficiency is greatest for small leaves (and high wind speeds) when absorbed radiation is high. This is consistent with the general tendency for sun leaves to be small and lobed, while shade leaves are large and less lobed (Clements 1904; Graner 1942; Shields 1950; Blackman 1956; Talbert & Holch 1957; Richards 1964).

Second, the range of radiation-absorption levels for which efficiency increases with increasing leaf size (decreasing convection coefficient) is much smaller at lower air temperatures than at high air temperatures. Let us recall the assumption that natural
selection for leaf size tends to maximize the water-use efficiency. This assumption, along with the results in Fig. 7, thus implies that small leaves will be selected for in cold climates, regardless of radiation levels. Also, at the higher temperatures, large leaves would be at an advantage where there is little light, and small leaves where light is intense, because water-use efficiency is thereby increased. The relationships between leaf size and climatic temperatures will be discussed further in the final section.

The third feature of Fig. 7 seems less consistent with reality. The model predicts that the lower the relative humidity (at high air temperatures), the wider the range of radiation levels under which large leaves would tend to evolve. The surface (representing neutral leaf size) does not slope very steeply along the humidity axis, however. Furthermore, in hot, dry environments foliage is seldom if ever dense enough to cast deep shade. Thus the environment in the upper-left-front corner of the Figure does not occur in nature; the model still predicts small leaves in hot, dry environments.

In this section, a specific model has been suggested for predicting natural selection of leaf size in various environments. The assumption made is that water-use efficiency (CO₂ assimilated/water transpired) would in the long run become optimal through selection for leaf size. The results are generally consistent with observed leaf sizes. More detailed comparisons will be made in the final section.

III. FACTORIAL DESIGN AND SIMULATED EXPERIMENTS

In the previous section the interactions of a number of plant and environment factors with leaf temperature, transpiration, and water-use efficiency were described mathematically by means of eqns (1)-(9). Some results calculated from those equations were presented in Tables 2-4 and were discussed briefly. Those results are considered in more detail here, especially as they relate to the potential evolution of leaves in their role of photosynthesizing organs.

Eqns (1)-(9) form a complex system from which no explicit solution for leaf temperature can be obtained. When leaf temperature is calculated numerically, transpiration rate and water-use efficiency may be obtained directly. Because of the complexity, the sensitivity of each response variable to variations in the independent variables is difficult to grasp directly from the equations. Neither is it easy to calculate how the independent variables interact to determine the responses. Furthermore, no adequate procedure is available for presenting the relationships graphically.

One can circumvent these difficulties by using the system of equations (the model) to produce synthetic ‘data’ and analysing them by the methods of the 2ᴺ Factorial Design, a technique used in statistical experimental design (Davies 1967; Simpson, Roe & Lewontin 1960).

(a) Definitions

In such a design, a ‘response’ (a dependent variable) is measured for each possible combination of N factors (the independent variables) each at one of two allowable levels. There are 2ᴺ such combinations. The iᵗʰ factor is denoted by Fᵢ, and its ‘main effect’ is defined as the difference between the mean response for the 2ᴺ⁻¹ factor combinations including Fᵢ at its high level, minus the mean response for the 2ᴺ⁻¹ factor combinations including Fᵢ at its low level (Davies 1967).

An example of a main effect is that of air temperature (Tₐ) on the response variable leaf temperature. In the 2⁶ factorial experiment using the synthetic data of Table 2, this
main effect is the mean calculated leaf temperature in the bottom four rows (all combinations of variables in which \( T_a = 35^\circ \)) less the mean calculated leaf temperature in the top four rows (all combinations in which \( T_a = 15^\circ \)). This amounts to \( 37-0^\circ - 21-5^\circ \), or \( 15-5^\circ \).

'Interactions' among two or more independent variables can also be calculated (Davies 1967). A two-factor interaction between the factors \( F_1 \) and \( F_2 \) is defined as \( \frac{1}{2} \) the mean response when both \( F_1 \) and \( F_2 \) are at their high levels or both are at their low levels, minus \( \frac{1}{2} \) the mean response when \( F_1 \) is at its high level and \( F_2 \) is at its low level or vice versa. In Table 2, the interaction between \( T_a \) and \( D \) (the number of leaf surfaces bearing stomata) is \( \frac{1}{2} (29-15^\circ - 29-32^\circ) \), or \(-0-085^\circ \ C\).

An \( F_1-F_2 \) interaction near zero implies that the effect of \( F_1 \) on the response is nearly independent of \( F_2 \). A large interaction implies that the effect of \( F_1 \) depends strongly on the value of \( F_2 \). By the definition, the foregoing two statements would remain correct if \( F_2 \) and \( F_1 \) were interchanged in them.

Ordinarily, main effects and interactions calculated in a \( 2^N \) experiment are tested for statistical significance by an analysis of variance. Such a procedure is not valid for synthetic data such as are treated here, because there is no source of random variation. The calculated effects are as reliable (and only as reliable) as the equations producing them.

(b) Two simulated experiments

The data in Tables 2-4 represent the results of one generated experiment. In it, leaf temperature, transpiration rate, and water-use efficiency were calculated as the seven independent variables took on the 128 possible combinations of levels listed in Table 5(a) (seven variables each at two possible levels).

| Table 5. (a) Factors, symbols, and levels used in the simulated Expt I (resistance levels enclosed in parentheses were those used for an amphistomatous leaf, while those not so enclosed were used for a hypostomatous leaf): (b) levels of convection coefficient used in Expt II—all other levels were as in (a) |
|---|---|---|---|---|
| Factor | Symbol | Units | Low level | High level |
| (a) Absorbed radiation | \( Q \) | ly min\(^{-1}\) | 0-8 | 1-2 |
| Air temperature | \( T \) | deg C | 15 | 35 |
| Relative humidity | \( U \) | – | 0-2 | 0-95 |
| Stomatal distribution | \( D \) | leaf side(s) | 1 | 2 |
| Stomatal resistance | \( S \) | s cm\(^{-1}\) | 2 (1) | 30 (15) |
| Mesophyll resistance | \( M \) | s cm\(^{-1}\) | 4 (2) | 20 (10) |
| Convection coefficient | \( H \) | ly min\(^{-1}\) deg\(^{-1}\) | 0-028 | 0-089 |
| (b) Convection coefficient | \( H \) | ly min\(^{-1}\) deg\(^{-1}\) | 0-28 | 0-89 |

The levels of the independent variables for the above experiment (denoted Expt I) were chosen to represent reasonable values occurring in nature with wild (uncultivated) plant species. The levels of convection coefficient (\( H \)) were calculated by using the equations for wind-tunnel laminar flow (Parkhurst et al. 1968) for leaves of 10 cm and 1 cm linear dimensions (low and high levels respectively) in a wind of 180 cm s\(^{-1}\) (4 mile h\(^{-1}\)).

Convection under field conditions is not yet fully understood (Section IIa). It is not known how closely the theory developed for convection in wind-tunnel flow approximates to field conditions, so a second synthetic experiment (Expt II) was performed.
using levels of convection coefficients listed in Table 5(b). These are ten times higher than
in Expt I, and they approach the high values calculated from the data of Hunt et al.
(1968). Convection coefficients in nature are probably between these two limits for the
leaf sizes and wind speed chosen. Levels of all other variables are the same in both
experiments.

For a given stomatal shape, size, and density, a hypostomatous leaf has stomatal and
mesophyll resistances twice as great as an amphistomatous one (Gale & Poljakoff-
Mayber 1968). The calculations include this effect—whenever \( D \) was at its 'low' level (a
hypostomatous leaf), the resistance values were doubled in the equations.

The model allows one to investigate three separate dependent response (or 'yield')
variables—leaf temperature, transpiration rate, and photosynthesis/evaporation ratio
(actually \( P'/E \)—Sect. II c). The first two responses are not dependent on mesophyll
resistance, and are thus involved in \( 2^6 \) experiments while the \( P'/E \) ratio was calculated for
\( 2^7 \) combinations of levels.

(c) Leaf temperature

The main effects and interactions of the independent variables, as they affect calculated
leaf temperature, are shown in Fig. 8(a, b) for Expts I and II respectively. Also shown
there are the grand means of calculated leaf temperature for each experiment. The
'grand mean' response is defined as the mean of the \( 2^N \) response values.

The leaf temperature response in Expt I is an example of the usefulness of the factorial-
design technique for analysing a complex system of equations. In particular, the technique
will be seen to provide a measure of the relative importances of various controlling
factors and of their interactions.

Fig. 8(a) shows that at the levels chosen for the independent variables, leaf temperature
varies most with air temperature (cf. Linacre 1964; Priestley 1966); as air temperature
changes from 15 to 35°C, the mean leaf temperature (averaged over all combinations of
the other five independent variables) increases by \( 15.5°C \). That is, the range of variation
in leaf temperature is \( 78\% \) as great as the range of variation in air temperature. The
former range is not as wide as the latter because of increased cooling by thermal radi-
ation and transpiration at the higher temperature.

The main effects of the other factors are all less than half as big as the air temperature
effect, and all but one of the main effects are larger than any of the interactions. (Inter-
actions are indicated in the figures by the appearance of more than one capital letter
beneath a vertical column in the bar graphs.) After air temperature, absorbed radiation
(\( Q \)) has the largest effect on leaf temperature. This factor is followed by stomatal resis-
tance—which partially controls evaporative cooling, convection coefficient (\( H \)), and
relative humidity (\( U \)). Next in size come several interactions, such as the one between \( H \)
and \( Q \).

The \( H-Q \) interaction (calculated from Table 2 as the mean of the leaf temperatures
listed in the first, fourth, fifth, and eighth horizontal rows, minus the mean of the values
in the remaining four rows) is \(-2.3°C \). This interaction may be interpreted as follows.
Suppose that when \( Q \) is at its high level, leaf temperature varies an average of \( \Delta T \) degrees as
\( H \) changes from its high level to its low level. Then the \(-2.3°C \) interaction means that,
when \( Q \) is at its low level, leaf temperature varies \((\Delta T+4.6)\) degrees as \( H \) changes from its
high level to its low level.

The factor having the smallest main effect on leaf temperature is \( D \), the stomatal dis-
tribution. In addition, \( D \) enters into no large interactions with other variables. The model
predicts, then, that little information would be lost by ignoring this factor in other theoretical or experimental studies in which leaf temperature is the major response variable.

The dependence of leaf temperature on the factor levels used in Expt II is shown in Fig. 8(b). Because the convection coefficients here are ten times higher, the leaf is very closely coupled to the air, and the air temperature effect is more than twenty times larger than any other effect or any interaction. If convection coefficients in the field are somewhere between those in Expts I and II, the relative main effects and interactions will be between those shown in Fig. 8(a, b).

(d) Transpiration

The calculated transpiration responses in Expts I and II are shown in Fig. 9(a, b). Regardless of the size of convection coefficient $H$ (low in Expt I and high in II), the greatest effects are those of stomatal resistance ($S$) and relative humidity ($U$). The $S-U$ interaction is third highest in both experiments.

Interestingly, in neither experiment is the main effect of convection coefficient ($H$) as large as the effects of several other variables. The convection coefficient, it should be remembered, increases with wind speed and decreases with leaf size. In Expt I, changing $H$ from its low level to its high level does lead to appreciable interactions of $H$ with other factors. In Expt II, however, even the low level of $H$ is high enough so that the change from low to high level does not cause much change in evaporation, either directly or indirectly through interactions with other factors.

In other words, the effect of convection coefficient (and thus of wind speed and leaf size) on transpiration rates is swamped by the effects of stomatal resistance, air tempera-
Fig. 9. (a) Main effects and factor interactions on calculated transpiration rates in Expt I, a simulated 2⁵ factorial design. Symbols are as in Fig. 8(a). (b) Main effects and factor interactions on calculated transpiration rates in Expt II, a simulated 2⁶ factorial design. Symbols are as in Fig. 8(a).

ture, absorbed radiation, etc. These other variables would therefore have to be carefully accounted for in an experiment designed to detect effects of wind speed on transpiration. This may explain why experiments and field measurements attempting to relate transpiration and wind speed have yielded such variable results (Renner 1910; Maximov 1929; Martin & Clements 1935; Pyykkö 1966; Wilson & Loomis 1967).

Fig. 10. (a) Main effects and factor interactions on calculated normalized water-use efficiencies (R') in Expt I, a simulated 2⁷ factorial design. M is the mesophyll resistance to CO₂ transfer; other symbols are as in Fig. 8(a). (b) Main effects and factor interactions on calculated normalized water-use efficiencies (R') in Expt II, a simulated 2⁸ factorial design. Symbols are as in Fig. 8(a).
(e) Water-use efficiency

In Section II, a 'normalized' net photosynthesis ($P'$) was defined as the actual net photosynthesis (in g dm$^{-2}$ h$^{-1}$) divided by the (often unknown) CO$_2$-concentration difference between the chloroplasts and the free air (in g dm$^{-3}$). Then the normalized water-use efficiency ($R'$) was defined as $P'/E$, where $E$ is the leaf's transpiration flux density (also in g dm$^{-2}$ h$^{-1}$). The dependence of this efficiency on the seven independent variables in Expts I and II is shown in Fig. 10(a, b).

In each case, the greatest effect is an increase in water-use efficiency due to changes in humidity level. In Expt I (with relatively low convection coefficients), the absorbed radiation and its interaction with humidity are the next most important effects, due to the dependence of evaporation on leaf temperature and of that in turn on radiation flux density. In Expt II, however, the leaf is more closely coupled with the air, making stomatal resistance and air temperature the second and third most important factors.

Several main effects were qualitatively the same in both cases. First, calculated water-use efficiency increased with increased stomatal resistance, as was also predicted by Slatyer (1964). This may explain why stomatal resistances of wild plants such as oak trees are usually higher than those of crop plants, which have been bred for high CO$_2$ assimilation in less severe environments (e.g. with irrigation).

Second, the water-use efficiency increased with decreasing mesophyll resistance ($M$). We recall the assumption that plants having higher water-use efficiencies will tend to survive and reproduce more often than those with lower efficiencies (other factors being equal). The optimality principle then implies that mesophyll resistances will tend through natural selection to become as low as is consistent with the structure and chemistry of leaves otherwise adapted to the environment concerned.

Third, on average, and except for shady conditions, water-use efficiency increased with convection coefficient. In Expt I, for example, the average efficiency nearly doubled for a $\sqrt{10}$ increase in $h_v$.

Fourth, hypostomatous leaves were generally more efficient than amphistomatous ones. (The main effect of $D$ on $R'$ is negative, but is too small to be shown, Fig. 10.) This occurs because the former have less area for CO$_2$ and water exchange than for heat exchange. The resulting balance is favourable to the efficiency in any high radiation situation.

Fifth, higher radiation absorptance led to lower water-use efficiency, in part because the calculations were made under the assumption that CO$_2$, and not light, was limiting. Probably in nature there is some radiation level at which $P'/E$ reaches a maximum, dropping off at lower radiation due to light limiting photosynthesis, and dropping off at higher radiation due to heating and resulting increased transpiration. The fact that photosynthetic energy is not a constant fraction of the total radiative energy absorbed would make this optimum difficult to predict.

(f) Advantages of the factorial approach

Use of the $2^N$ factorial design with synthetic data produced from a system of equations (apparently a new approach) is helpful in several ways. Firstly, it provides a means to judge the sensitivity of the system responses to the variables affecting them. For example, as noted earlier, leaf temperatures depend strongly on air temperature, but weakly on whether the leaf is amphi- or hypo-stomatous.

Secondly, the relative effects of single variables and of interactions among two or more variables are made easily comparable. This is especially important in a field like ecology,
whose textbooks have traditionally lamented the complexities of environmental interac-
tions (e.g. Oosting 1956, p. 82). For example, in both experiments, stomatal resistances
interact strongly with relative humidity in their effects on transpiration.

Thirdly, results involving many variables are easily graphed; their effects and inter-
actions can be visualized together on a single graph (e.g. Figs. 8–10). The factorial ap-
proach should be compared with the more usual ‘sectional’ approach (e.g. Fig. 1) in
which sections are cut through the n-dimensional hyperspace representing plant–
environment interactions. Such graphs can represent at most three variables, but at least
they do show curvature (which is lost in the factorial approach). Both approaches require
arbitrary choices—factor levels on the one hand, or levels at which to cut sections, on the
other. In general, they give somewhat different information, and thus complement one
another.

IV. DISCUSSION AND CONCLUSIONS

'The experimental study of selection in plant populations should obviously
be complemented, where feasible, with investigations of mechanisms of
adaptation, and we may expect to see much more effort in this field in the
next decade or so.' (Heslop-Harrison 1964).

The previous sections have dealt with a model for predicting the probable direction
of natural selection of leaf sizes in various environments. The model is based on the
principle of optimal design (Rosen 1967) which states that natural selection leads to
organisms with optimal form and function for growth and reproduction in a particular
environment. The principle was applied under the simplifying assumption that, as a
first approximation, the water-use–efficiency ratio is the property which tends to reach an
optimum. This assumption is justified if one pictures a breeding population differing in
leaf size from plant to plant. Then the individuals having a leaf size allowing more
efficient use of water will tend to produce more offspring.

It remains to test the model using available published data. For environments and
plant types in which agreement is good, the model may be taken as a possible indication
of the way in which evolution in leaf size has proceeded. In situations where agreement is
poor, the model must be modified to account for the lack of agreement. As stressed in
Section I, this process of modification often leads to increased understanding of the
phenomenon being modelled. As Kac (1969) stated, a major role of models in science
is ‘to pose sharp questions’. In the present leaf-size problem, hypotheses about the
physiology of certain unusual plant forms result from the modifications which will be
made—these hypotheses will be discussed later.

(a) Comparison of the model with records of leaf size

The main trends to be expected in the natural selection of leaf size are summarized in
Fig. 11. These results, from the model discussed in the previous two sections, predict that
large leaves will have an advantage only when air temperatures are high and radiation
(light) levels are low.

Leaf sizes have been recorded for vegetation of different microclimates in only a few
studies (Brown 1919; Cain et al. 1956). Cain et al. measured the areas of single leaves or
leaflet s of several hundred species in a Brazilian rainforest, and listed the species by
their life forms. Fig. 12 shows the mean leaf size (square root of leaf area) for each life-
form class. Most of the means in Fig. 12 are based on the flora in each life form, i.e. each
species contributes equally to the mean regardless of whether it was represented by one or by many individuals. However, Cain et al. listed importance values for the two tallest strata of trees, and for those strata a mean leaf size has been calculated, weighted by the importance of each species concerned.

The four height classes of trees (A–D in Fig. 12) are discussed first. There is a general
tendency for the taller trees (whose leaves would absorb more radiation) to have smaller leaves, the trend being reversed only between the lowest two strata. The tendency is consistent with the qualitative observations of Richards (1964). The third stratum of trees is represented by only three species, and the 95% confidence interval for the mean leaf size in that stratum is very wide (Fig. 12). One cannot be very confident that the mean estimated from such a small sample is representative, and that the true mean leaf size for trees in the third stratum is different from the mean size in the fourth stratum.

The tendency for the tallest tree stratum to have smaller leaves than the second stratum was accentuated when the means were weighted by species importance. This is good evidence for the fit of the model, since one would expect a positive correlation between the importance of a species in a given environment and the degree to which it was adapted for growing there.

Leaf sizes for other life forms are also shown in Fig. 12. The lianas (vines) provide little information for testing the model, because they grow in all the vertical levels of the forest, and Cain et al. (1956) did not state at what heights the liana leaves were collected. The three classes of ground herbs had quite variable leaf sizes, as shown by the wide confidence intervals of the estimates of their means. The chamaephytes included one species of monocotyledon and one of Selaginella, the hemicyryptophytes included five species of ferns and one grass, and the cryptophytes one grass and one other monocoty-ledonous species.

When grouped together, the three types of herbs had a mean leaf size of 8.5 cm, a size slightly larger than the mean leaf of the second storey tree. Interestingly, of the five fern species included, only one had a simple leaf—with an area of 403 cm². The other four had pinnate, bipinnate, or bipinnatifid leaves which may well have had a single boundary layer for the whole leaf rather than for each leaflet. If so, then physiologically the leaves of these ground herbs would be much larger than the sizes indicated in Fig. 12.

Table 6. Mean leaf widths (based on numbers of individuals per species \times leaf width of species) as a function of altitude and vegetation layer, on Mt Maquiling, the Philippines (after Brown 1919)

<table>
<thead>
<tr>
<th>Altitude (m)</th>
<th>200ᵃ</th>
<th>450ᵇ</th>
<th>700ᶜ</th>
<th>1100ᵈ</th>
</tr>
</thead>
<tbody>
<tr>
<td>First storey species</td>
<td>4.9ᵉ</td>
<td>4.4ᶠ</td>
<td>3.9ᵉ</td>
<td>3.1ᵉ</td>
</tr>
<tr>
<td>Second storey species</td>
<td>5.9ᵉ</td>
<td>5.0ᶠ</td>
<td>3.9ᵉ</td>
<td></td>
</tr>
<tr>
<td>Third storey species</td>
<td>4.7ᵖ</td>
<td>6.1ᶠ</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undergrowth species</td>
<td>2.5ᵉ</td>
<td>3.3ᶠ</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All species</td>
<td>4.5</td>
<td>4.7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

ᵃ Selectively lumbered dipterocarp forest;ᵇ virgin dipterocarp forest;ᶜ mid-mountain forest;ᵈ mossy forest;ᵉ erect woody plants taller than 1 m;ᶠ erect woody plants taller than 2 m;ᵍ all plants shorter than 1 m.

One other set of quantitative leaf-size data is available for comparison with the model. Brown (1919) studied the vegetation and the environment of Mt Maquiling, the Philippines, in great detail. Mean leaf widths, calculated from his data, are given in Table 6 and are used here as an indication of the effective leaf size. The means include only the widths of simple leaves, and not those of compound leaves. They are weighted by species density, since Brown conveniently listed numbers of individuals in each leaf width class. The general trends in the environmental factors measured by Brown were, from low
altitude to high altitude: (1) decreasing air temperature; (2) decreasing light intensity*; (3) increasing relative humidity; (4) increasing precipitation; and (5) increasing fractional soil moisture.

The first three trends would also describe the changes occurring from higher to lower strata of vegetation at a given altitude.

With these environmental trends in mind, one can compare Brown's data (Table 6) with the results of the model. The most striking trend in the data is the reduction of leaf size with increasing altitude, in both first- and second-storey species. This is exactly the trend predicted by the model, in view of the decreasing air temperatures which Brown reported.

Also, the width of the leaves in the three tree strata in the virgin rainforest stand (450 m altitude) follows the same trend as that noted for the data of Cain et al. (1956) being greater in each of the more shaded storeys. Once again, this is consistent with the model, and with the data reported in Section II (e) for sun and shade leaves in the same species.

Other climates, too, have leaf sizes consistent with the predictions. Both desert and Mediterranean vegetation, for example, have mostly small leaves (Pyykkö 1966); radiation intensities are high in both climates. Small leaves also predominate in cold and alpine climates.

It would be surprising if the simple model considered so far agreed perfectly with natural leaf sizes, and indeed it does not. For example, in Brown's (1919) stand at 200 m elevation, the third-storey trees had a smaller mean leaf size than the first- or second-storey trees. However, it is difficult to say how the selective cutting and resulting canopy opening in that stand might have altered the leaf size patterns. In addition, leaf sizes in the woody 'undergrowth' layers of both the low elevation rainforest stands were smaller than those of any other storey, a result not consistent with the predictions of the model.

There are two other growth forms in which leaf size seems to contradict the results of the model. The succulent habit, occurring in many arid and semi-arid regions, is usually accompanied by larger photosynthesizing surfaces (leaves or stems) than non-succulent plants in the same habitats. The model predicts small leaves in such environments (Fig. 11). Another difference from the expected occurs in the cushion plants of arctic and alpine regions (Rauh 1939). Although individual leaves of such plants are usually very small, the dense cushion surface as a whole probably has its own boundary layer (K. Raschke, personal communication). Thus the cushion apparently acts as a large surface, physiologically, in an environment for which small surfaces are predicted instead. These apparent contradictions are considered in Section IV(e).

(b) Limits to leaf size

It has been emphasized that the leaf-size model considered so far is a first approximation only—that it is based on the simple assumption that leaves would be selected for, whose size maximized the ratio of net photosynthesis to water loss. The agreement of this simple model with the leaf sizes actually occurring in nature has been remarkably good. Within some vegetation types or microhabitats agreement is not good, however, indicating the need for other variables to be considered.

* Measured as the difference between water evaporated from a black atmometer cup and a white one. This would give a highly non-linear measurement of integrated light intensity, a measurement which would depend strongly on the temperature of the cups.
A major shortcoming of the water-use-efficiency model has been its failure to predict specific optimal sizes. Instead, it predicts only probable trends in evolution of leaf size to larger or smaller sizes, with no limits placed on how large or how small a leaf might eventually be expected to become. The first refinement to be made, then, will be to suggest factors which might limit final sizes. Stated in another way, the model so far has assumed the total 'cost' of a leaf is equal to its environmental cost only, with no contribution from intrinsic (metabolic) costs. The question is: what intrinsic costs contribute to the total cost?

One intrinsic cost which may act to limit large sizes in leaves is lack of strength. Geometrically similar cantilevers (e.g. leaves held horizontally by a petiole) become less economical as they get bigger (Howland 1962), i.e. the strength of a larger structure is proportionately lower, and less able to support the structure.

Other factors limit how small leaves are likely to become. Leaves have veins supplying them with water, minerals, and other substances. Poiseuille's Law (Rose 1966) states that the flow of a fluid through a tube is proportional to the fourth power of the tube diameter. This implies that xylem elements become very inefficient as they get smaller. The restriction of water flow can be considered an intrinsic cost, and it will tend to place a lower limit on vein size.

For a given vein size, however, the blade size should be large, in order to increase the ratio of photosynthetic tissue to non-photosynthetic tissue (since the latter represents a metabolic cost to the plant). Therefore, not only is it inefficient for vein size to be very small, but it is likewise inefficient for blade size to be small relative to the amount of vein supplying the blade. These factors, if they could be put into the same units as the water-use efficiency, might well predict limits on the large and small sizes attained in the natural selection of leaves.

In areas where dew is an important part of plant water budgets, another limit to small leaf size may act. Calculations show that for many reasonable combinations of radiation level, air temperature, and humidity, dew deposition reaches an absolute maximum at specific convection coefficients in the range from about 0.005-0.05 ly min⁻¹ deg⁻¹. To include dew as a factor in the model, one would have to know what fraction of the dew deposited actually penetrated into the plant.

(c) Dependence of net photosynthesis on light and temperature

So far, it has been assumed for the calculations that light, and leaf temperatures, influence the water-use efficiency only through their effects on transpiration rates. Of course, net photosynthesis is in reality a function of both factors (as was expressed symbolically in eqn 3). To what degree will consideration of these relationships improve the agreement of the model with observed leaf sizes?

Consider light first. Its effects on leaf temperature are included via the variable $q_a$, so only the direct effects of light on photosynthesis need be discussed. The use of the normalized CO₂ uptake ($P'$, see Section II) allowed light to be ignored, since light does not affect $P' (=1/resistance to CO₂ uptake)$ when stomatal resistance is held constant. Thus the trends in leaf size predicted by optimizing $P'/E$ are independent of light levels, provided light is not so limiting that the resistance of CO₂ uptake has a negligible effect on net photosynthesis. Stated in another way, the trends predicted on the basis of the normalized water-use efficiency will be correct if CO₂ partially limits photosynthesis. Light will influence levels of water-use efficiency ($P/E$), but will have little effect on the trends in $P/E$ as leaf size varies. If actual optimal sizes could be predicted by cost
functions of the form: total cost = extrinsic cost + intrinsic cost, the addition of light dependencies to the model might shift the absolute size predictions to some small extent.

Net photosynthesis rates depend also on leaf temperatures (Leopold 1964). Because the latter are strong functions of leaf size (through convection coefficients; see Fig. 1), the temperature effect is probably a more critical factor to build into the leaf-size model than light. The following analysis proves interesting.

Let the water-use efficiency be denoted by $R = P/E$ (net photosynthesis/transpiration) and consider the rate of change of $R$ with changes in convection coefficient $h_c$ (here denoted $h$ for simplicity). Then:

$$\frac{\partial R}{\partial h} = \frac{\partial R}{\partial E} \frac{\partial E}{\partial h} + \frac{\partial R}{\partial P} \frac{\partial P}{\partial h}.$$  \hfill (10)

From the definition of $R$, $\frac{\partial R}{\partial P} = E^{-1}$ and $\frac{\partial R}{\partial E} = -P E^{-2}$. But $P$ and $E$ each depend on $h$ through two separate mechanisms, i.e. through temperature effects and transfer-resistance effects. Thus:

$$\frac{\partial E}{\partial h} = \frac{\partial E}{\partial T} \frac{\partial T}{\partial h} + \frac{\partial E}{\partial R_s} \frac{\partial R_s}{\partial h}.$$  \hfill (11)

and

$$\frac{\partial P}{\partial h} = \frac{\partial P}{\partial T} \frac{\partial T}{\partial h} + \frac{\partial P}{\partial R_s} \frac{\partial R_s}{\partial h}.$$  \hfill (12)

Combining eqns (1)–(9) and (10)–(12) yields:

$$\frac{1}{R} \frac{\partial R}{\partial h} = \left[ \left( \frac{1}{P} \frac{\partial P}{\partial T} - \frac{1}{E} \frac{\partial E}{\partial T} \right) \frac{\partial T}{\partial h} \right] + \left[ \frac{1}{h} \left( r_a^{'} \frac{\partial E}{\partial R_s} - \frac{r_a^{''}}{P} \frac{\partial P}{\partial R_s} \right) \right].$$  \hfill (13)

Suppose all factors remain constant other than those explicitly appearing in eqns (10–13). Then the proportional change in water-use efficiency with a change in convection coefficient (the left-hand side of eqn 13) is the algebraic sum of effects of $h$ on leaf temperature and effects of $h$ on transfer resistances. The latter effects are described by the second brackets in eqn (13) and will not be considered further here, because they are part of the earlier, simple form of the model.

The first set of brackets contains the temperature effects. It implies that the proportional derivative of $R$ by $h$ increases with the derivative of leaf temperature by $h$, times the difference between the proportional change in photosynthesis with temperature and the proportional change in transpiration with temperature. Because water vapour concentration within a leaf is roughly an exponential function of leaf temperature (Slayter 1964; Dilley 1968), it can be shown that $\frac{1}{E} \frac{\partial E}{\partial T}$ increases with $T$. On the other hand, $\frac{1}{P} \frac{\partial P}{\partial T}$ is large and positive at low temperatures, zero at the temperature optimum for net photosynthesis, and large (negatively) at high temperatures (Leopold 1964). What are the net results?

At temperatures higher than the optimum for photosynthesis, the rates of change of both $P$ and $E$ with leaf temperature will be additive in their effects on the proportional change in $R$. If $(\partial T)/(\partial h)$ is negative, as is usually true for a sunlit leaf, the effect will be
that $R$ will increase as $h$ increases (as leaf size decreases). At low leaf temperatures, the $P$ and $E$ effects on $(\partial R)/(\partial h)$ will be in opposite directions, and the $P$ effect may well dominate, so that water-use efficiency ($R$) increases with increasing surface size. This is a conservation-of-heat effect.

The rate of change of net photosynthesis with leaf temperature may be especially large in plants where photosynthesis is limited at low temperatures by carbohydrate accumulation, presumably due in turn to low rates of respiration and growth (Warren Wilson 1966; Neales & Incoll 1968). The probable existence of such a phenomenon emphasizes the need for including the leaf-temperature influence on $P$ in a general leaf-size model which will apply in cold climates.

(d) Fluctuating environments

So far we have assumed for each calculation that conditions remained constant. Of course most of the independent variables in the model vary from minute to minute, day to day, and season to season. The average efficiency of water use defined by

$$R = \frac{\int_0^t P(t) \, dt}{\int_0^t E(t) \, dt}$$

(14)

(where $t$ is some time period long enough to cover fluctuations of interest) is the variable to be optimized by natural selection in the fluctuating environment.*

As mentioned before, no unique optimal leaf size is predicted by the constant-conditions model. In some environments where small leaves would be optimal at midday, large leaves would be optimal early and late in the day, and it seemed possible that these effects might average over the period of a day to predict some specific leaf size. However, when $R$ (eqn 14) was evaluated using air temperature and humidity data recorded in a Wisconsin oak woodland, combined with diurnal radiation and stomatal resistance curves, again only trends (not specific sizes) were predicted. This emphasizes that the intrinsic costs previously mentioned must be important in the evolution of leaf size.

In regions where dew is an appreciable fraction of the water economy of plants, the integrals in eqn (14) defining $R$ would have to be evaluated over periods of at least 24 h. In such a period, the negative evaporation occurring at night would be included. Dew deposition is a function of leaf size, of course, since size would affect both leaf temperature and the ability of water vapour to pass through the leaf boundary layer. One would have to account for the fact that the deposition of dew involves different surfaces and transfer resistances from the loss of water by transpiration.

Because night-time respiration rates depend on leaf temperature, net photosynthesis should also be averaged over periods of 24 h or more, at least in principle.

A model based on the assumption that natural selection in leaf size would tend to optimize $R$ (eqn 14) leads to an interesting speculation. Eqns (1)–(9) can be used to calculate $R$. Three of the independent variables in those equations are plant parameters subject to change by natural selection, namely convection coefficient ($h_c$), stomatal resistance ($r'_s$), and mesophyll resistance ($r''_m$). It was stated in Section II that natural selection would probably tend to minimize $r''_m$ to the lowest value consistent with the chemical and physical properties of a leaf, because a decrease in $r''_m$ is always accompanied by an increase in water-use efficiency.

* An average water-use efficiency defined by $\frac{1}{t} \int_0^t (P/E) \, dt$ would not be appropriate. What matters is the total CO$_2$ assimilation during the period $t$, divided by the total water loss. The average value of the ratio is meaningless.
The size of a fully expanded leaf makes a constant contribution to the convection coefficient of that leaf. On the other hand stomatal resistance varies from hour to hour and day to day. We have already assumed that leaf size would evolve for which $\bar{R}$ over the life of a leaf was a maximum. A similar hypothesis is that stomatal control mechanisms may have developed which change $r_s$ throughout a day in such a way that $\bar{R}$ is greatest. It must be emphasized that this suggestion is pure speculation, but it provides a testable prediction of the stomatal movements in nature. One might argue that stomatal opening varies simply in response to water and carbohydrate levels within the leaf, but some recent evidence indicates that metabolic processes are involved (Salisbury & Ross 1969). It is certainly possible that plants carry a genetic programme allowing for diurnal variations in stomatal opening which increase overall water-use efficiency.

Environmental fluctuations in the longer term should also be considered. The implicit assumption that leaf size would become adapted to common, or ‘average’, conditions may be criticized. Indeed it is almost a platitude that plants should evolve to fit extremes rather than means. This may be true for plant features related to life versus death (e.g. fire-resistant bark), but is less likely to be true for features related to reproduction. The following points may be made.

(1) Common conditions (average ± normal variation) are responsible for most of the photosynthesis in most populations, and plants must be able to use them efficiently to reproduce.

(2) Plants need not reproduce in extreme years. Perennials can survive using carbohydrate reserves, then reproduce when conditions return to normal. Populations of annuals pass through unfavourable years as seeds.

(3) If conditions remain ‘extreme’ for long, then those conditions become the new average, and a new set of species will take over. Thus, it seems reasonable to base a model for leaf size on normal conditions.

(e) Reconsideration of apparent differences between real and predicted leaf sizes

Now that certain refinements have been added to the original, very simple model, the apparent disagreements between the model and leaves occurring in nature can be reconsidered. Herbs growing under forest canopies seem to have highly variable leaf sizes, as in the studies of Cain et al. (1956) and of Brown (1919). The same is true of herbs in Wisconsin forests, where Dicentra, with highly dissected leaves, often grows within a few decimetres of Sanguinaria, with large rounded leaves. Furthermore, the average leaf sizes in the ground vegetation layers of Brown’s (1919) study were smaller than leaf sizes in some of the tree strata above them.

It was suggested above that in the herbs discussed by Cain et al. (1956), each compound leaf of the ferns may have acted as a single physiological unit, with one boundary layer. If so, those leaves would have effective sizes much larger than the values used in the means of Fig. 12. No similar interpretation is available for Brown’s (1919) data, however, since Table 6 is based on widths of simple leaves only. Experimental work is required to determine the form of the boundary layer over a compound leaf.

Several explanations for the apparent special nature of the ground-layer species can be posed. For example, light may limit photosynthesis to such an extent on the forest floor that CO₂ is not limiting. If so, leaves might be selected for, which minimized evaporation rather than optimizing water-use efficiency.
On the other hand, water might be so constantly available there, and the evaporation stress so low, that the relative change in 'cost' for a change in leaf size would be negligible. If so, leaf sizes might change simply by genetic drift, an idea consistent with the variability noted above.

Herb species may have evolved or migrated recently (Bailey & Sinnott 1916), and their leaf sizes then would not yet have evolved to equilibrium with their present environment. Climatic change could be similarly involved in the Wisconsin forests, but is unlikely to be a factor in the tropical rainforest.

Bailey & Sinnott (1916) studied the climatic distribution of entire and non-entire leaves. They concluded that the climatic trends in this character were more marked in woody dicotyledons than in other plants, and attributed the difference to 'the fundamental differences between these growth forms, herbaceous plants [being] less subject to or react[ing] differently toward prevailing environmental influences'. It may be true that herbs in general have some unknown differences in physiology from woody plants.

It seems unacceptable to argue that herbs are less closely coupled to the environment than are woody plants, however. The latter may be coupled to the regional climate through their heat and mass transfer mechanisms, but herbs are presumably coupled just as closely to the forest floor microclimate. It is the leaf-size predictions for microclimates, not for macroclimates, which seem to disagree with sizes occurring in nature.

It appears, in summary, that the water-use-efficiency model does not apply as well to herbs as to woody plants. The reasons are obscure, but further investigation of the differences from predicted leaf sizes could follow any or all of the above lines.

The desert succulents are another growth form which seems to disagree with the model. They have large photosynthesizing surfaces in a climate where non-succulent plants have very small leaves and where the model predicts that small leaves should occur. The succulents are often classified as 'drought-enduring xerophytes' (Kozlowski 1964), and are able to store relatively large amounts of water. It might possibly be argued that efficient use of water is not a criterion in natural selection of size in succulents.

Regardless of their endurance of drought, however, the succulents must still assimilate carbon to reproduce, and they must do so in an environment where water is seldom if ever plentiful. It seems likely, therefore, that water-use efficiency is a factor in natural selection of the succulents. Slatyer (1964) has pointed out that the crassulacean acid metabolism occurring in many succulents gives them a much higher water-use efficiency than other plants growing in the same environments. In its extreme form, acid metabolism allows for CO₂ uptake at night (when transpiration rates are lower) and for photosynthesis of the stored carbon in the light of the following day (with closed stomata during the day).

Plants which take up their CO₂ at night are effectively shade plants, and the model predicts they should have large photosynthesizing surfaces. It may be concluded that the more highly developed the acid metabolism in a desert plant, the more likely are its surfaces to be large. It may turn out that some large succulents (saguaro, for example) do not in fact take up CO₂ during the night, and then some other explanation will have to be found for the large surfaces.* For the time being, however, the model poses an interesting hypothesis against which experimental data may be tested.

The large surfaces of arctic and alpine cushion plants have already been noted as another growth form which is inconsistent with the first-approximation model. The examination of the dependence of photosynthesis on tissue temperature (Section IVc)

* Since this was written Despain, Bliss & Boyer (1970) have found saguaro to have crassulacean acid metabolism.
may provide an explanation. If leaf temperature decreases with increasing convection coefficient, as is likely for a sunlit leaf (cf. Warren Wilson 1957), then \( \frac{\partial T}{\partial h} \) is negative. Then \( \frac{1}{P} \frac{\partial P}{\partial T} \) of eqn (13) is likely to be positive in the arctic, and greater in magnitude than \( \frac{1}{E} \frac{\partial E}{\partial T} \). Thus \( \frac{1}{R} \frac{\partial R}{\partial T} \) will be negative, which implies that water-use efficiency increases with increasing surface size.

In other words, the water-use-efficiency model predicts for cold environments that when net photosynthesis is strongly limited by temperature (i.e., \( \frac{1}{P} \frac{\partial P}{\partial T} \) large and positive), then large surfaces are at a selective advantage. When \( \frac{1}{P} \frac{\partial P}{\partial T} \) is small, however, small surfaces are at an advantage. Another hypothesis arises—that the cushion form is likely to be best developed in plant species whose photosynthetic enzymes are poorly adapted to low temperatures. Again, this may prove to be wrong, but it provides a framework for comparison with experimental data on the physiological ecology of arctic-alpine plants. The analysis of eqn (13) supports the observations of Spomer (1964) that the cushion form is more closely related to cold temperatures than to moisture stress. As with compound leaves, experimental work is needed to determine the boundary layer resistance of cushion forms.

(f) General conclusions

This paper has been concerned with a general model to predict the trends in leaf size likely to be selected for in any given terrestrial environment. It has been based on the simple assumption that a leaf size is optimal if it has the greatest efficiency of water use (g CO\(_2\) assimilated per g water lost). In view of the simplicity of the model, its predictions are remarkably good for the arctic, the desert, and different strata in the tropical rainforest.

Any botanist could doubtless cite numerous examples of particular plant species in particular regions with leaf sizes disagreeing with the predictions of the model. Indeed, several such examples were discussed in Section IV(e). Some special cases can apparently be explained by simple refinements to the model which consider unusual physiological features of the plants concerned.

Other apparent disagreements between the model and real leaf sizes are not so easily explained. It may be that the species concerned have not been in the particular environment long enough for selection to have occurred, or it may be that the environment is changing rapidly. Alternatively, the model may be too simple. For example, net photosynthesis may sometimes be relatively more important than water loss, or vice versa.

Furthermore, other factors (in addition to the seven independent variables used in the model) must at times directly influence water-use efficiency. For example, spines, arising by selection under heavy grazing, probably affect the convection coefficient of the surfaces bearing them, and so change the efficiency.

Similarly, the model does not preclude leaf size being modified by factors other than water-use efficiency. Thus very windy environments may select for small leaves which are not so easily torn or removed by wind. Or, in environments where radiation frosts can occur any time during the growing season, small leaves (e.g. conifer needles) will be less coupled to sky temperature than broad leaves, and will probably suffer less frost damage.
(Parkhurst 1968). In other words, the model is very general and a knowledge of local conditions and local species will be useful to anyone applying it in specific places.

Even though other factors play a part, water-use efficiency seems to be such an important factor in evolution of leaf size that many plant individuals have the genetic ability to produce different sizes of leaves (or photosynthesizing surfaces) in different micro-environments. Thus many plants produce larger, less dissected leaves in the shade than in sun (Section II). Similarly, some species grow as cushions in the cold, but at higher temperatures their shoots elongate, exposing the small leaves (Sperner 1964).

Federov (1966) wrote: ‘Nevertheless these leaf characters [such as size] have no distinct adaptive significance in the tropics, as is the case in fact with many other specific distinguishing features.’ Federov attributed leaf sizes in tropical rainforest to genetic drift, in spite of the clear tendencies reported by Cain et al. (1956).

Heslop-Harrison (1964) also discussed leaf characters such as size: ‘Differences between sun and shade leaves of the same genotype are a direct consequence of the morphogenetic effects of light, and it is widely supposed that the characteristic features are in some way adaptive, although the direct evidence is slight.’

The water-use-efficiency model not only demonstrates one way that the differences in size and shape between sun and shade leaves are adaptive; it also provides evidence that leaf size does have adaptive significance in the tropics (and in other environments). The model may serve as a working hypothesis for comparison with the leaf sizes occurring in nature. Where agreement is good, water-use efficiency may perhaps be assumed to have played a part in leaf evolution. Where agreement is poor, the disagreement will indicate that some factor other than water must be considered, and the model may help suggest what other factors to consider.

Finally, the results of the work may be useful to plant breeders, who should be able to improve water-use efficiencies of crop species by producing plants with a given total leaf area divided into smaller units. Also, when crops are grown under glass or plastic, the ventilation rate should be high (because high air speeds have effects similar to small leaves). Exceptions would include crops such as coffee, with its large leaf adapted to shade, and tobacco, when production of large leaves is desirable. With further development, the model should also be helpful to palaeobotanists wishing to reconstruct past climates from fossil floras.

Acknowledgments

Many have helped with this work. We especially thank two: W. R. Gardner who provided the original germ of the ideas developed here, and Jennifer Parkhurst who assisted in editorial work. Support was provided primarily by a U.S. National Science Foundation grant, GB/3548, to O. L. Loucks.

Summary

The principle of optimal design (Rosen 1967) can be stated as follows. ‘Natural selection leads to organisms having a combination of form and function optimal for growth and reproduction in the environments in which they live.’ This principle provides a general framework for the study of adaptation in plants and animals.

The efficiency of water use by plants (Slatyer 1964) can be defined as grams of carbon dioxide assimilated per gram of water lost. Leaf temperatures, transpiration rates, and
water-use efficiencies can be calculated for single leaves using well-established principles of heat and mass transfer. The calculations are complex, however, depending on seven independent variables such as air temperature, humidity and stomatal resistance. The calculations can be treated as artificial data in a $2^N$ factorial design experiment. This technique is used to compare the sensitivity of the system response variables to changes in the independent variables, and to their interactions.

The assumption is made (as a first approximation) that the optimal leaf size in a given environment is the size yielding the maximum water-use efficiency. This very simple assumption leads to predictions of trends in leaf size which agree well with the observed trends in diverse regions (tropical rainforest, desert, arctic, etc.). Specifically, the model predicts that large leaves should be selected for only in warm or hot environments with low radiation (e.g. forest floors in temperate and tropical regions).

There are some plant forms and microhabitats for which observed leaf sizes disagree with the predictions of the simple model. Refinements are thus proposed to include more factors in the model, such as the temperature dependence of net photosynthesis. It is shown that these refinements explain much of the lack of agreement of the simpler model.

One of the main roles of mathematical models in science is ‘to pose sharp questions’ (Kac 1969). The present model suggests several speculative propositions, some of which would be difficult to prove experimentally. Others, whether true or not, can serve as a theoretical framework against which to compare experimental results. The propositions are as follows.

1. Every environment tends to select for leaf sizes increasing the efficiency of water utilization, that is, the ratio of CO$_2$ uptake to water loss.
2. Herbs are physiologically different from woody plants, in such a way that water-use efficiency has been more important in the evolution of the latter.
3. The stomatal resistance of a given leaf varies diurnally in such a way that the water-use efficiency of that leaf tends to be a maximum.
4. The larger the photosynthesizing surface of a desert succulent, the more likely it is to exhibit acid metabolism, with stomata open at night and closed during the day.
5. In arctic and alpine regions, the plant species whose carbohydrate metabolism is most severely limited by low temperatures are most likely to evolve a cushion form of growth.

In addition to providing these testable hypotheses, the results of the model may be useful in other ways. For example, they should help plant breeders to alter water-use efficiencies, and they could help palaeobotanists interpret past climates from fossil floras.

**REFERENCES**


Optimal leaf size


(Received 27 August 1971)