

## The effect of leaf-lobing on the interception of direct solar radiation

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**Summary.** The extent to which leaf-lobing influences the interception of direct solar radiation by individual plants was studied by means of computer simulations. The morphology, size and orientation of *Ambrosia artemisiifolia* L. leaves were measured and used to construct a prototype *Ambrosia* plant upon which a computer simulation was based. The leaf geometries of this simulation were then varied, and daily integrated irradiances (DII) were calculated for each variant plant simulation. Data indicate that lobed *Ambrosia* leaves do not confer an advantage to light-interception based upon values of DII. Simulated plants identical in all respects to the prototype, but with simple, elliptic leaves, had equivalent DII values to the prototype. Simulations with leaves in which gaps between lobes were “filled-in” had reduced light-interception efficiencies compared to the prototype and to a simulation with elliptic-leaves. Light-interception was maximized when leaves on distal nodes were *Ambrosia*-like and leaves on proximal nodes were elliptic. The data are interpreted to indicate that lobing *per se* is not functionally advantageous to light-interception; however, gradients of leaf-lobing along the length of shoots may be very significant in terms of overall light interception.

**Key words:** Leaf-lobing – Light interception – Thermal load

Variations in the size, pigmentation, and orientation of leaves are often correlated with the quantity, spectral quality, and direction of light. A variety of studies have shown that these correlations are functionally significant in terms of the light reactions of photosynthesis and leaf temperature (Mooney 1972; Parkhurst and Loucks 1972; Ehleringer 1980; Ehleringer and Werk 1986; Lee 1986). Because transpiration and photosynthesis are tightly coupled through the conversion of radiant into thermal energy, the functional significance of variations in leaf morphology correlated with environmental differences may be very complex. For example, Vogel (1970) examined different leaf shapes for their capacity to convectively dissipate heat, and showed that this capacity increased as lobing became more prominent. However, leaf shape as defined by the extent of lobing may be important in other functional contexts, as for example, reducing self-shading and producing sunflecks deeper within a canopy (Horn 1971). The assessment of the importance of lobing is experimentally difficult because this variable cannot be isolated from other morphological features that are developmentally interdependent or that covary

through environmental induction. Nonetheless, it would be desirable to do so even from a heuristic perspective.

The present study attempts to evaluate the consequences of leaf-lobing on the capacity of an individual plant to intercept direct solar radiation, and to interpret these consequences in terms of self-shading. The approach taken here involves computer simulations. This approach has been applied to other biological contexts in which morphological complexity is experimentally refractive (Nobel 1980, 1986; Niklas 1988). Simulations allow each variable to be treated independently. They also provide a method to test various null hypotheses. For example, computer generated plants with lobed and nonlobed leaves, but which are identical in all other respects, can be used to study the affect of lobing on light-interception. If equivalent light-interception capacities can be shown for plants with lobed and nonlobed leaves, then lobed leaf morphologies need not be taken as *a priori* evidence for an adaptation that increases light-interception.

A series of computer simulations are presented in which total leaf area, leaf number, orientation, and phyllotaxy are held constant but leaf shape is varied. Additional simulations, designed to evaluate plants with varying leaf shapes along their shoots, are also presented. Morphometric data and leaf geometries of *Ambrosia artemisiifolia* L. are used to provide biological prototypes for these simulations. *Ambrosia* was selected because of its deeply lobed leaves, rapid growth, and variable leaf arrangement during shoot ontogeny.

### Material and methods

The morphology and orientation of leaves on shoots of *Ambrosia artemisiifolia* L. were examined to provide a biological prototype for computer simulated plants. *Ambrosia* leaves are once or more commonly twice pinnatifid, narrowly to broadly ovate or elliptic in outline, and petiolate. Typically, they are planar or they modestly curve out of a single plane. These characteristics are ideally suited for computer simulations of deeply lobed, flattened leaves, and of nonlobed leaves with an elliptic to ovate outline.

Leaves from ten plants growing in full-sun conditions and ten plants growing in partial shade (within a hedgerow) were sampled. Plants with cotyledonary scars were selected since the plastochron index (PI) of each plant could be calculated, as well as the plastochron index for each leaf (LPI), using the formulae

**Table 1.** Morphometric data and orientations for leaves from an *Ambrosia* plant used to create computer simulations. Outlines of leaves from each of the six leaf pairs are shown in Fig. 5

Node No.	LPI	Lamina				Total Leaf Area (mm <sup>2</sup> )	Petiole Length (p) (mm)	Internodal			Height of Leaf (H) (mm)	l:D	Rotation Angle (θ) (°)	Deflection Angle (φ) (°)	
		Area (A) (mm <sup>2</sup> )	Perimeter (P) (mm <sup>2</sup> )	Length (l) (mm)	Width (W) (mm)			l:W	L:W	l:p					Distance (D) (mm)
1	-0.148	159.6	163.7	25	8.2	159.6	0	3.05	3.05	-	0	171	0.146	0	20
2	+0.852	1316	797.5	71	32	1328	9	2.22	2.50	7.89	18	153	0.464	90	45
3	+1.852	1751	965.5	78	60	1777	21	1.30	1.65	3.71	20	133	0.586	0	60
4	+2.852	1602	881.5	72	48	1641	30	1.50	2.13	2.40	21	112	0.643	90	65
5	+3.852	909.3	553.9	51	39	947	31	1.31	1.10	1.65	24	88	0.580	0	65
6	+4.852	207.3	184.7	20	21	242.1	29	0.95	2.33	0.69	30	58	0.345	90	65
		5945.2													

$$PI = n + \frac{\text{Log } L_n - \text{Log } 30}{\text{Log } L_n - \text{Log } L_{n+1}}$$

$$LPI = PI - a,$$

where  $n$  is the serial number of the leaf just longer than 30 mm (the reference length used in this study),  $L_n$  is the length of leaf  $n$ , which is longer than 30 mm,  $L_{n+1}$  is the length of the leaf  $n+1$  (which is just shorter than 30 mm, and  $a$  is the serial number (counting from the cotyledonary scar) of any leaf (see Erickson and Michelini, 1957; Maksymowich, 1973, pp 5-7).

Young plants have a pseudodecussate leaf arrangement; however, older plants show a spiral phyllotaxy. LPI values were calculated as equivalent for each leaf in a pair.

Leaf size (length, width), number, arrangement, orientation (rotation, deflection, and pitch angles) and petiole lengths were measured on plants in the field. Lamina surface area and perimeter length were measured from photocopies of detached leaves whose outlines were digitized into an IBM PCXT equipped with the planimetry program of SECTION (Niklas and Boyd 1987). Data are presented in terms of LPI.

The geometries of *Ambrosia* leaves and nonlobed leaves (described below), along with data on leaf orientation, petiole lengths, and height from ground level, were used to construct simulated plants. Simulations were evaluated for their capacity to intercept direct solar radiation by means of the software described by Niklas (1988), heretofore referred to as PHYLLO. This program provides the option to specify the geometry, size, opacity, and orientation of each leaf on a single-stemmed plant, as well as petiole length, internode distances between leaves, and phyllotaxy. The program accepts the digitized outlines of real leaves, or generates elliptic shaped leaves with various ratios of major to minor axes.

PHYLLO contains a solar calendar that simulates the diurnal trajectory of the sun for any day of the year, at any specified latitude. The program automatically calculates the projected surface areas of unobstructed portions of all leaves and integrates the quantity of direct irradiance intercepted by leaf surfaces per day. This quantity is called the daily integrated irradiance (DII). It should be noted that all simulations involved computer generated plants with identical total leaf area. Therefore, DII can be given in units of W-h, rather than W-m<sup>-2</sup> (DII is normalized with respect to total leaf area, Table 2). The only exception to this involved simulations in which gaps in lobed leaves

were "filled-in" resulting in an increase in total leaf area (simulation IV, Tables 2, 3). However, comparisons among the light-intercepting capabilities of computer generated plants are based on percentage differences in their DIIs compared to the DII of the *Ambrosia*-prototype simulation (see Table 3). It is also important to note that an ambient light intensity of 400 W was used in each simulation. An increase in ambient light intensity would proportionately increase the magnitude of DII but not percentage differences among DIIs computed for simulations. Provided that ambient light intensity, day of year, and latitude are held constant, percentage DII can be used to compare the capacity of different simulated plant geometries to intercept direct solar radiation (see Niklas 1988; Niklas and Owens 1989).

Four different leaf-types were examined: Referring to Fig. 1, the outlines of real *Ambrosia* leaves; elliptic-type leaves with equivalent lamina areas to their prototypes but with two different aspect ratios l:W and L:W; and simple leaves formed by digitizing the tips of lobes on real *Ambrosia* leaves. The aspect ratio l:W is the ratio of lamina-length to lamina-width; L:W is the ratio of total leaf length (petiole + lamina) to lamina-width. These two ratios were measured from *Ambrosia* leaves with different LPIs (see Table 1), and were used to evaluate the influence of leaf length and width on light-interception isolated from the effect of leaf-lobing. Simple leaves were used to examine the consequences of the reduction of lamina area (caused by lobing) on light-interception. Simple leaves have the equivalent aspect ratios and roughly the same primary and secondary venation patterns as their prototypes. Therefore, their architectural "cost" in terms of vasculature is nearly equivalent to real leaves, but they have significantly larger leaf areas (see Table 2).

Five simulations, designated by roman numerals, were performed (Table 2). Referring once again to Fig. 1, Simulation I is based on leaf outlines from a real *Ambrosia* plant (shown in Fig. 4; data given in Table 1); simulation II used elliptic leaves with leaf areas and l:W values equivalent to the real leaves shown in Fig. 4; Simulation III used elliptic leaves with leaf areas and L:W values equivalent to their prototypes; simulation IV used simple, nonlobed leaves whose outlines span the tips of lobes on real leaves; and simulation V used *Ambrosia* leaves on the top three distal nodes and elliptic leaves on the bottom three nodes of the simulated plant. The leaf areas and l:W values of leaves used in this "composite" simulation, regardless of their shapes, are equivalent to their prototypes.

**Table 2.** Morphometrics of simulated leaves and simulated plants used to calculate daily integrated irradiances (DII). Data for *Ambrosia*-type plant simulation not given since they are identical to those presented in Table 1

Node No	$l:W^a$	$l$ (mm)	$W$ (mm)	Simulated Lamina Area (mm <sup>2</sup> )	$p^a$	$\theta^a$ (°)	$\phi^a$ (°)	$H^a$ (mm)
<i>Elliptic-type Leaf Simulation II</i>								
1	3.05	24.89	8.16	159.5	0	0	20	171
2	2.22	60.98	27.47	1315.6	9	90	45	153
3	1.30	53.83	41.41	1750.7	21	0	60	133
4	1.50	55.31	36.87	1601.7	30	90	65	112
5	1.31	38.94	29.73	909.3	31	0	65	88
6	0.95	15.83	16.65	207.3	29	90	65	58
				5944.1				
<i>Elliptic-type Leaf Simulation III</i>								
1	3.05	24.89	8.16	159.5	0	0	20	171
2	2.50	64.72	25.89	1316.0	9	90	45	153
3	1.65	60.65	36.76	1751.0	21	0	60	133
4	2.13	65.91	30.94	1601.6	30	90	65	112
5	2.10	49.30	23.48	909.2	31	0	65	88
6	2.33	24.80	10.64	207.2	29	90	68	58
				5944.5				
<i>Simple-type Leaf Simulation IV</i>								
1	3.05	25	8.2	174.5	0	0	20	171
2	2.22	71	31	1729.7	9	90	45	153
3	1.30	78	60	2677.0	21	0	60	133
4	1.50	72	48	2239.5	30	90	65	112
5	1.31	51	39	1371.7	31	0	65	88
6	0.95	20	21	334.9	29	90	68	58
				8527.3				
<i>Composite-type Leaf Simulation V</i>								
1	3.05	25 <sup>a</sup>	8.2 <sup>a</sup>	159.6 <sup>a</sup>	0	0	20	171
2	2.22	71 <sup>a</sup>	31 <sup>a</sup>	1316 <sup>a</sup>	9	90	45	153
3	1.30	78 <sup>a</sup>	60 <sup>a</sup>	1751 <sup>a</sup>	21	0	60	133
4	1.50	55.31 <sup>b</sup>	36.87 <sup>b</sup>	1601.7 <sup>b</sup>	30	90	65	112
5	1.31	38.94 <sup>b</sup>	29.73 <sup>b</sup>	909.3 <sup>b</sup>	31	0	65	88
6	0.95	15.83 <sup>b</sup>	16.65 <sup>b</sup>	207.3 <sup>b</sup>	29	90	68	59
				5944.9				

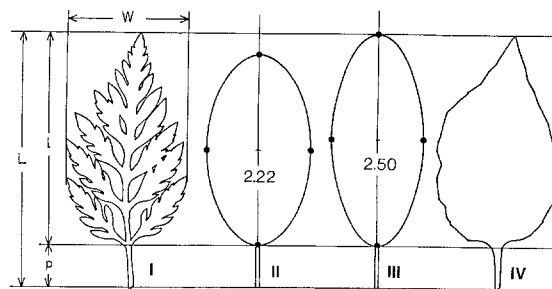
<sup>a</sup> Data taken from *Ambrosia* prototype (see Table 1)<sup>b</sup> Data taken from Elliptic-type Leaf Simulation II**Table 3.** Daily integrated irradiance of DII calculated for five computer simulations with various leaf-shapes and leaf areas (Table 2). All simulations computed DII for July 20th, 40° N latitude, with an ambient solar flux of 400 Watts

Type of Simulation	DII (W-h)	% DII of <i>Ambrosia</i> -simulation	% Total Leaf Area of Prototype
I. <i>Ambrosia</i>	187.71	100%	100%
II. Elliptic-type ( $l:W$ )	198.44	105.7	99.9
III. Elliptic-type ( $L:W$ )	186.95	99.6	99.9
IV. Simple-type	259.21	138.1	143.4
V. Composite	210.43	112.1	99.9

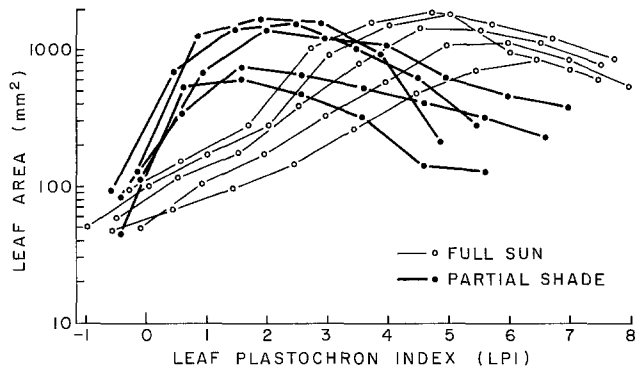
## Results

### Morphometrics

Linear regression analyses of morphological features of leaves reveal a number of significant correlations. Among those significant at the 1% level are leaf area ( $A$ ) and perim-



**Fig. 1.** Notation and representative geometries of four different types of leaf-simulations. An *Ambrosia* prototype (I), traced from the outline of a real *Ambrosia* leaf (see Fig. 5B), provides dimensionless ( $l:W$  and  $L:W$ ) ratios and absolute dimensions ( $L$ ,  $l$ ,  $p$ ) used to construct elliptic leaf-simulations (I–II) with two different aspect ratios ( $l:W=2.22$  and  $L:W=2.50$  for types I and II, respectively). Tips of lobes on prototype leaf (I) define the irregular outline of leaf-simulation type IV. Leaf types I and II–III have equivalent total leaf areas; types I and IV have equivalent primary and secondary venation “costs” but different total leaf areas ( $IV > I$ ).  $L$  = leaf length,  $l$  = lamina length,  $p$  = petiole length;  $W$  = lamina (leaf) width



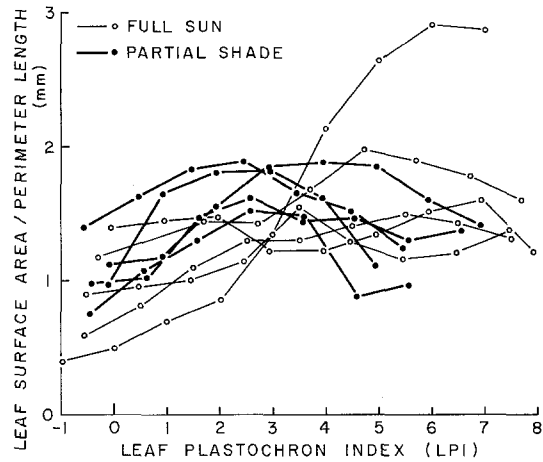
**Fig. 2.** Semi-log plot of leaf area versus leaf plastochron indices (LPI) for *Ambrosia artemisiifolia* growing in full sun and partial shade. Reference leaf-length used to compute LPI is 30 mm. Data for leaves from each plant are graphed as interconnected points. Largest leaf areas recorded for five full sun plants and five partially shaded plants are roughly equivalent. However, maximum leaf areas for partially shaded plants are achieved at lower LPI than for full sun plants

eter length,  $P$  ( $r=0.956$ ,  $n=94$ ); leaf length ( $L$ ) and the ratio of leaf area to perimeter length,  $A/P$  ( $r=0.595$ ); and leaf area,  $A$ , and the ratio of total leaf length to leaf width,  $L:W$  ( $r=-0.345$ ). The mean plastochron indices of plants growing in shaded and full-sun conditions ( $7.90 \pm 0.79$  and  $7.82 \pm 0.85$ ,  $n=10$ ) do not differ significantly, indicating that the mean age of plants growing in full sun and partial shade are comparable. PI correlates significantly with the maximum value for  $A/P$  ( $r=0.548$ ,  $n=20$ ; significant at the 2% level), and with the maximum leaf area ( $r=0.858$ ). Therefore, older plants with higher PI values have larger and less lobed leaves.

However, these correlations do not adequately reflect the morphometric variations within plants and between plants growing under the two different ambient light conditions. Leaf area changes as a function of leaf plastochron index LPI (Fig. 2), increasing and then decreasing toward higher LPI. This reflects the increase in leaf area resulting from lamina expansion and leaf maturation, and the decrease in leaf area toward the base of stems resulting from herbivory, leaf senescence, and juvenile, small leaves produced during the establishment phase of seedling development. The maximum leaf areas for partially shaded and full-sun plants differ significantly ( $1133 \pm 536 \text{ mm}^2$  and  $1653 \pm 371 \text{ mm}^2$ , respectively). Similarly, the LPI of leaves with maximum leaf areas are lower for partially shaded plants ( $1.0 \leq \text{LPI} \leq 2.5$ ) than for full-sun plants ( $4.5 \leq \text{LPI} \leq 5.0$ ). Therefore partially shaded plants have leaves with smaller leaf areas than do full-sun plants, but achieve maximum leaf area earlier in their development.

The extent of leaf-lobing, expressed by the dimensional ratio  $A/P$  does not appear to differ significantly between plants growing under the two ambient light conditions (Fig. 3).  $A/P$  equals  $1.24 \pm 0.32 \text{ mm}$  and  $1.62 \pm 0.56$  for full-sun and shaded plants, respectively. There is a slight tendency for full-sun plants to have lower ratios (=greater lobing); however, some of least lobed leaves were recorded for full-sun plants (Fig. 3).

Since leaf area decreases toward higher LPI due to the destruction of lamina in older leaves and because of juvenile leaf morphologies, an analysis of younger leaves in their expansionary phase of development was conducted. These



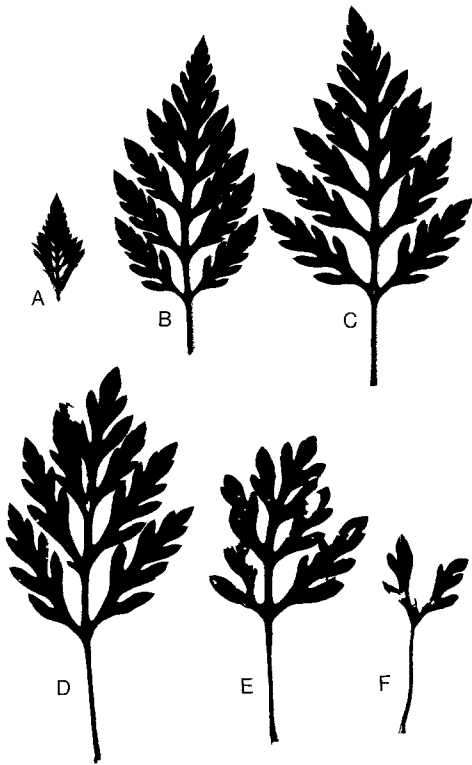
**Fig. 3.** Dimensional ratio of leaf area to perimeter length plotted against leaf plastochron indices of five plants growing in full sun and five growing in partial shade. In general, leaf area:perimeter length increases and then decreases as LPI increases

leaves correspond to those with LPI values for which leaf area increases or has reached a maximum value (see Fig. 2). When LPI is linearly regressed against morphological features for these leaves a number of correlations surface: (1) for both shaded and full-sun plants,  $L:W$  decreases as LPI increases ( $r=-0.798$  and  $-0.843$ , respectively); (2) leaf area increases with LPI ( $r=0.645$  and  $0.975$ ); (3) the ratio of lamina length to leaf width,  $l:W$ , decreases as LPI increases ( $r=-0.861$  and  $-0.899$ ) and (4) the ratio of leaf area to perimeter length increases ( $r=0.996$  and  $0.984$ ). All of these correlations reflect the fact that as leaves expand they first lengthen and then widen due to the development of laminae.

#### Computer simulations

All computer simulations were based on leaves from a single prototype plant of *Ambrosia* found growing under full-sun conditions. This plant had a total of twelve leaves (Fig. 4), arranged in a pseudodecussate phyllotaxy (=internodes between leaves in a pair had not elongated). Therefore, the plant had the appearance of having six leaf pairs, with each alternate pair of leaves rotated  $90^\circ$  with respect to the leaf pair above and below it. Data for petiole lengths, lamina lengths and widths, leaf areas, perimeter lengths rotation and deflection angles, and various dimensionless ratios are given in Table 1. The rotation angle ( $\theta$ ) of the first leaf-pair was arbitrarily set at  $0^\circ$ ; pseudodecussate leaf-arrangement results in the alternation of  $90^\circ$  and  $0^\circ$  for the rotation angles of the remaining leaf-pairs. The deflection angle ( $\phi$ ) measures the angle between the axis of a leaf and the vertical stem.

Five simulations, designated by roman numerals I to V, were performed. The dimensions, aspect ratios, and orientations for the leaves used in simulations II-V are given in Table 2. Note that leaf orientations and the height of leaf-pairs are identical in all simulations, and are based on the *Ambrosia* prototype. Using the DII and the total leaf area calculated for the *Ambrosia* simulations as baselines, Table 3 indicates that elliptic leaves based on the ratio of lamina length to lamina width ( $l:W$ ) of total leaf length to lamina width ( $L:W$ ) yield nearly equivalent or larger



**Fig. 4 A–F.** Photocopies of six leaves removed from a single *Ambrosia artemisiifolia* plant growing in full sun. The dimensions and orientations of leaves are given in Table 1, and were used to construct the *Ambrosia* prototype simulation (Simulation I). Variant simulations (II–V) are based on this prototype. LPI increases from A–F. Leaves D–F show signs of lamina damage due to herbivory. For further details, see text

values of DII despite having equivalent total leaf areas (99.9%) to the prototype. The percentage DII of simulations III and II are 99.6% and 105.7% that of the prototype's DII. Simulation IV yields a 38.1% increase in DII compared to the prototype. However, this simulation has 43.4% more leaf area than the prototype. Since the percentage gain in DII is less than the percentage gain in leaf area, this simulation is less efficient than either of the two elliptic type leaves or the *Ambrosia* simulation (Table 3, I–III). Finally, simulation V has a 12.1% higher DII than the *Ambrosia* simulation, despite an equivalent total leaf area. Therefore, acropetal lobed leaves and basipetal non-lobed leaves appear to maximize DII.

## Discussion

The objective of this paper was to provide a heuristic basis for evaluating the influence of leaf-lobing on the interception of direct solar radiation isolated from all other morphological variables in leaf shape and shoot morphology. This involved computer simulations, since the morphometrics of leaf and stem development of real plants are interdependent and therefore developmentally refractive (Chazdon 1985, Chazdon and Fletcher 1984, Larson 1980). The results presented from admittedly simplistic simulations indicate that lobing does not in itself confer an advantage to whole plant light-interception. Rather, the results indicate that the gradient in leaf-lobing along the length of a shoot may

be much more significant. Consequently, the morphometry of leaf development, particularly the relative rates of leaf expansion and elongation, is important to an understanding of light-interception.

Horn (1971) suggested that lobing of sun leaves facilitates the penetration of light deeper into the canopy of trees where lobed shade leaves are more prevalent (see also Nobel 1983, Vogel 1968). Similarly, Vogel (1970) demonstrated that lobed sun leaves are more efficient at convective heat dissipation than shade leaves, and that lobing decreases the dependence of heat dissipation on leaf orientation to the direction of wind. A gradient in leaf-lobing on the shoots of herbaceous plants may confer similar advantages to light-interception and convective heat dissipation. However, unlike the mature sun and shade leaf morphologies of arborescent species, the morphometry of leaf development may be much more significant for herbaceous species. The extent to which *Ambrosia artemisiifolia* leaves appear lobed is dependent upon the stage of leaf development, quantified in this context by leaf plastochron indices (LPI). LPI values provide the means to draw comparisons among leaves that are equivalent developmentally but often dramatically dissimilar in shape and size. Data indicate that juvenile leaves appear to be deeply lobed because leaf laminae have not fully expanded. The apparent reduction in the lobing of older, more basipetal leaves is the result of a shift in the relative rates of lobe elongation and expansion favoring the latter. Shaded plants produce leaves that undergo this shift sooner than leaves produced by plants growing in full sun. Analyses based on LPI values indicate that plants growing in full sun protract the expansion of leaf laminae over more LPI than do shaded plants. Thus, significantly different gradients in leaf lobing occur between sun and shaded plants, even though the final leaf morphologies may be quite similar. Computer simulations indicate that these gradients may be advantageous. The acropetal, juvenile leaves of *A. artemisiifolia* are likely to experience higher thermal loads than more basipetal leaves or leaves on shaded plants. Similarly, an acropetal gradient of increasing leaf-lobing permits direct light to pass between lobes to be intercepted by basipetal, less lobed leaves. This gradient effectively increases leaf area indices along the length of shoots toward their base, as inferred by Horn (1971). Computer simulations indicate that the more abrupt gradient in leaf-lobing observed for shaded plants is advantageous in a potentially light-limited habitat in which thermal loads are inferred to be minimal or less significant.

Perhaps counterintuitive, simulations indicate that the reduction in photosynthetic surface area incurred by lobing of leaves increases the overall efficiency of light-interception. It might be anticipated that the addition of laminar leaf surfaces between the gaps of lobes would increase efficiency. However, when the increase in light-gathering is normalized against the increase in total leaf area, overall light-interception efficiency is seen to be reduced. This has a potential bearing on treatments of the "cost" of leaves (ratio of supporting, vascular tissue to photosynthetic tissue). An acropetal, lobed leaf (with a high "cost") is actually more beneficial than an unlobed leaf (with a proportionately lower "cost") provided a gradient in leaf lobing results during shoot ontogeny. This suggests that estimates of the cost of leaves based upon the performance of individual leaves are naive when viewed in the context of whole plant performance.

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