

## Non-random leaf orientation in *Lactuca serriola* L.

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**Abstract.** Leaf shapes and leaf orientation of *Lactuca serriola serriola* and *Lactuca serriola integrifolia* were studied. Leaf shapes in *L. serriola serriola* differed greatly from those of *L. serriola integrifolia*, but leaf surface areas were similar. In exposed habitats, leaf orientation of cauline leaves of both forms was non-random, with leaves almost vertical and tending to orient with their lamina normal to the east and west. In the shade, cauline leaves oriented randomly. An experiment demonstrated that the orientation of leaves did not change significantly once they were fully expanded. The leaf orientation in *L. serriola* affected the diurnal distribution of solar irradiance intercepted by a leaf. Peak solar radiation fluxes are incident on the rosette leaves at midday, but on the cauline leaves the peak solar radiation flux occurs early in the morning and again late in the afternoon. The significance of this unusual leaf orientation is discussed in relation to water loss and carbon gain.

**Key-words:** *Lactuca serriola*; Asteraceae; prickly lettuce; compass plant; leaf orientation.

### Introduction

*Lactuca serriola* L. is a common weedy annual species found in disturbed and ruderal sites. It is a cosmopolitan species, at times dominant in communities (Mucina, 1978), and is found at midlatitudes throughout Europe, Britain, North Africa, West Asia, and North America (Prince & Carter, 1977; Prince, Marks & Carter, 1978). Its seeds do not have a primary dormancy and so germination occurs during any favourable period from autumn through spring (Marks & Prince, 1979, 1981, 1982). Individuals which germinate in winter grow as rosettes until spring.

Stems begin to elongate from the rosettes between May and July and flower from July through September (Prince *et al.*, 1978; Marks & Prince, 1979). Leaves are produced on the stems as the rosette leaves die. These cauline leaves have very steep angles and are maintained so that their lamina face east–west. As a consequence, *L. serriola* has been called a ‘compass plant’ because with its leaves configured in this way it appears to point north–south. No study to date has quantified the leaf orientation of *L. serriola*.

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The compass plant phenomenon attracted some attention around the turn of the century but its significance has not been understood (Stahl, 1881; Bay, 1894; Mayer, 1912; Karsten, 1918; Stocker, 1926; Schanderl, 1930, as cited by Dolk, 1931). Dolk (1931) studied mechanical aspects of leaf orientation in *L. serriola* and related leaf orientation in *L. serriola* to maximizing sunlight interception. Geiger (1966) suggested that the vertical orientation served to minimize the amount of solar radiation intercepted. These conflicting conclusions suggest that effects of non-random vertical leaf orientation were not well understood. This led Dolk (1931) to say, ‘It is better not to speculate about this as it is quite possible that the north–south direction has no ecological significance at all.’ We will argue otherwise.

The cauline leaves of *L. serriola* have two different forms with any single plant always having the same form. Two leaf-form varieties of *L. serriola* are recognized: *L. serriola* forma *integrifolia* with unlobed leaves and *L. serriola* forma *serriola* with deeply lobed leaves (Prince & Carter, 1977). Leaf form and the type of lobing are genetically controlled, although significant phenotypic variation exists (Lindqvist, 1958).

The two leaf forms seen in *L. serriola* are of interest because leaf shape greatly influences leaf energy exchange through its effect on heat and mass transfer (Gates, 1980). Previous studies on lobed and unlobed leaves in different species have suggested that lobed leaves may be better suited to hot, high irradiance environments (Parkhurst *et al.*, 1968; Vogel, 1968; Parkhurst & Loucks, 1972; Gottschlich & Smith, 1982). On this basis, one could hypothesize that the lobed leaf-form variety would be more successful in hotter, more arid habitats.

The effect of leaf lobing on *L. serriola* energy balance is complicated by leaf size and vertical orientation. If lobed leaves are significantly larger than unlobed leaves, there may be no difference in convection coefficients between leaf forms. Orientation of *L. serriola* leaves may be important in reducing differences between lobed and unlobed forms. Vogel (1970) showed that the convection coefficient did not change with angle in lobed leaf models but increased significantly in vertical unlobed leaf models.

The purpose of this study was to characterize the leaf orientation in *Lactuca serriola* for both leaf-form

varieties and to relate leaf orientation to environmental and physiological parameters.

## Methods

To compare leaf sizes and shapes in the two forms of *L. serriola*, leaves were collected from plants growing in a wide variety of habitats in and around Salt Lake City, Utah. Leaf areas were determined with an area meter (model LI-3100, Li-Cor, Inc.). Leaf size parameters (area, length, width) were compared using an ANOVA (Sokal & Rohlf, 1969). Leaf width was measured as the maximum width of the leaf.

Leaf orientation was measured in terms of the angle from horizontal and the azimuth (compass direction) the lamina faced. Angles were measured with a clinometer to the nearest  $5^\circ$  and azimuths were measured to the nearest  $5^\circ$  with a compass. Since the abaxial and adaxial leaf surfaces of *L. serriola* are morphologically similar (Werk, unpublished data), and because solar radiation regimes are symmetric around the north-south axis, leaf azimuths are reported as being  $0-180^\circ$  east of north, which is equivalent to  $0-180^\circ$  west of south. Thus, a leaf lamina facing  $10^\circ$  west of south is reported the same as a leaf lamina facing  $10^\circ$  east of north, since this is the direction its lower surface faces. Mean angles and azimuths were calculated trigonometrically as described by Zar (1974). Angular dispersion is used as a measure of the variance about the mean angle. Angular dispersions range from 0 to 1 with maximum dispersion being defined by a perfectly uniform distribution of angles around the circle (and an undefined mean angle) (Zar, 1974). Distributions of leaf azimuths were divided into eight classes of  $22.5^\circ$  each and compared to a uniform distribution using the Chi-squared test. All field measurements were made on leaves on intact plants growing naturally in and around Salt Lake City, Utah, latitude  $41^\circ$  N.

In an experiment to test whether leaves would orient with respect to limited direct sunlight, plants were grown from seed in pots in six different locations which received differing amounts of direct solar radiation. The hours during which each treatment received direct solar radiation were as follows: (1) 500-1900; (2) 830-1900; (3) 500-1200; (4) 500-800; (5) 1000-1200; (6) 1130-1230. After the plants had produced more than 10 cauline leaves each, the leaf orientations were recorded.

An experiment to test the effects of reorienting plants on changes in leaf orientation was also conducted on plants grown in pots. The protocol involved measuring the orientation of fully expanded cauline leaves on growing stems, and then rotating the pots  $90^\circ$ . This meant that leaf lamina orienting east-west originally were then facing north-south. After 17 d the pots were returned to their original orientations and the orientation of the leaves was remeasured. In addition the orientation of any new

leaves which had emerged and expanded in that period was recorded. Mean angle and azimuth of leaves which had expanded before the pots were rotated were compared to the mean angle and azimuth of these leaves after the plants had been repositioned for 17 d and to those of the newly emerged leaves.

All plants used in the orientation experiments were grown outside on the roof of the Biology Building at the University of Utah, Salt Lake City. Fisheye photograph analysis of the roof where the plants were grown indicated that the pots were shaded for less than 1 h after sunrise and for approximately 2 h before sunset. This slight shading was due to a wall around the roof, and so upper leaves were somewhat less shaded than lower leaves. The shading did not prevent the leaves from orienting, but may have increased the dispersion of the leaf azimuths. The plants were grown in a uniform potting soil and watered daily.

Leaf temperatures were measured on plants growing in the field. Measurements were done on adjacent leaves of one plant using 36-gauge thermocouples with one of the two leaves being held horizontal while the other was left with its natural orientation. Measurements of humidity, air temperature, and photon flux were made simultaneously with leaf temperatures and recorded using a datalogger (CR21, Campbell Scientific).

The photon flux incident on both sides of horizontal leaf and a vertical leaf facing east-west was measured using photon flux sensors (400-700 nm) (Biggs *et al.*, 1971).

The predicted photon flux incident on leaves with different orientations was calculated using a simple computer model. The calculations were done assuming very clear conditions (transmission coefficient = 0.8) on the summer solstice, latitude  $40^\circ$ . Diffuse light was calculated as 10% of the direct beam irradiance.

## Results

The two leaf forms of *Lactuca serriola* growing in the field differed significantly in leaf shape (Fig. 1). Leaf lobing is controlled genetically (Lindqvist, 1958) but leaves of each form spanned a wide range of surface areas, with larger leaves normally occurring on plants in more mesic sites. The largest leaves were seen on plants which were adjacent to irrigated areas. Statistically, lobed leaves had the same leaf area as unlobed leaves ( $F = 2.09$ ,  $P > 0.1$ ). This is possible because lobed leaves are wider than unlobed leaves ( $F = 40.3$ ,  $P < 0.001$ ). The slope of the linear regression of leaf width on leaf length was greater for lobed leaves than for unlobed leaves ( $F = 392$ ,  $P < 0.001$ ). This indicated that for any given leaf length, lobed leaves were wider than unlobed leaves and have similar surface areas.

A survey of cauline leaves on lobed and unlobed

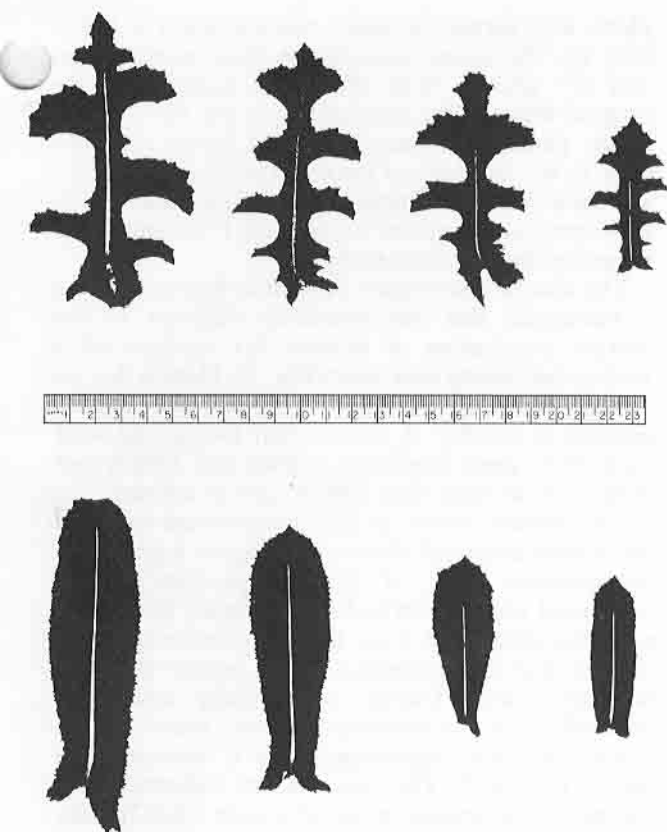


Figure 1. Examples of leaf shape in *Lactuca serriola serriola* (lobed) and *L. serriola integrifolia* (unlobed). Leaves of both forms were collected from various populations in Salt Lake City, Utah, during August 1982.

*Lactuca* plants growing in open habitats revealed the striking pattern that had been qualitatively described before. Leaves were almost vertical and usually faced east-west. There did not appear to be a difference between the way lobed and unlobed leaves oriented. The mean lobed leaf angle was  $78.26^\circ$  from horizontal with a very small dispersion of 0.03. Unlobed leaves had a mean angle of  $80.27^\circ$  from horizontal with a dispersion of 0.01. The distributions of leaf azimuths indicated non-random orientation (Fig. 2). Lobed leaf azimuths were distributed significantly different from uniform ( $\chi^2 = 100.03$ ,  $P < 0.001$ ), as were unlobed leaf azimuths ( $\chi^2 = 146.88$ ,  $P < 0.001$ ). Leaf azimuths of both varieties were centred around  $90^\circ$  (lamina facing east-west).

When cauline leaves on plants growing under a canopy of *Populus fremontii* (LAI  $\approx 6$ ) were surveyed, it appeared that the leaves of *L. serriola* required direct solar radiation in order to orient. Leaf angles and azimuths from plants in shade environments were different from those in open environments. The mean leaf angle in the shade was  $47.83^\circ$  with a high dispersion of 0.55. Leaf azimuths

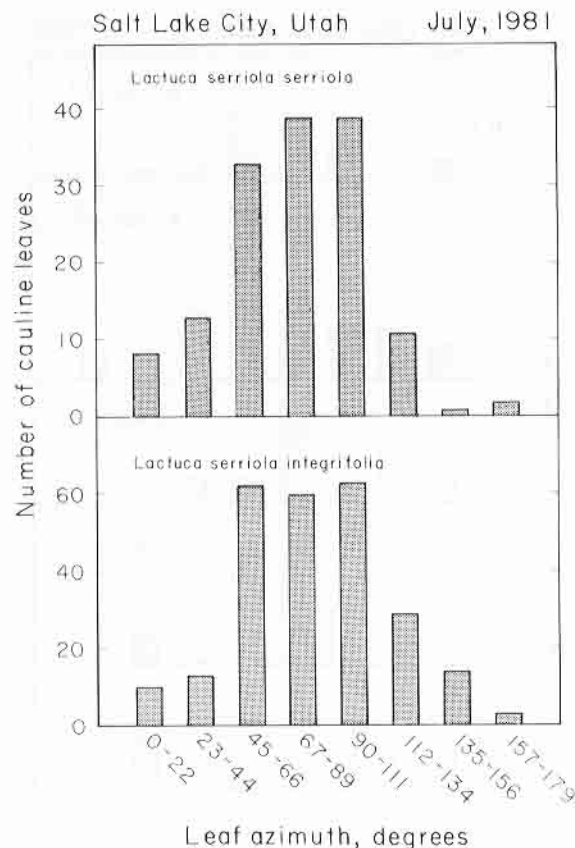


Figure 2. Distributions of azimuths of cauline leaves of (a) *L. serriola serriola* (lobed) and (b) *L. serriola integrifolia* (unlobed) growing in the open. Leaf azimuths are expressed in degrees east of north (equivalent to degrees west of south). All measurements were done on leaves of intact plants growing naturally in and around Salt Lake City.

were distributed uniformly around the compass ( $\chi^2 = 4.4$ ,  $P > 0.5$ ) (Fig. 3).

Leaves on the experimental plants grown in different locations had non-random distributions in

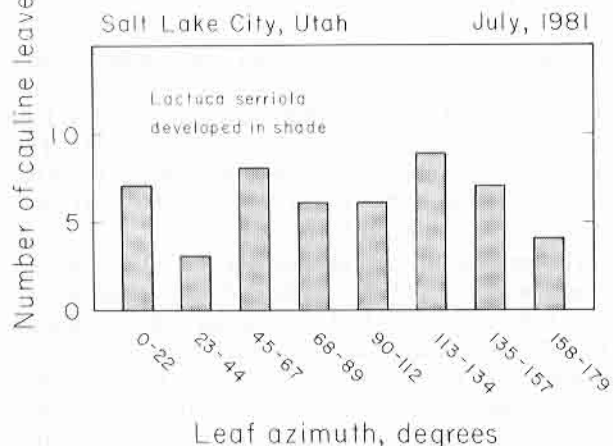
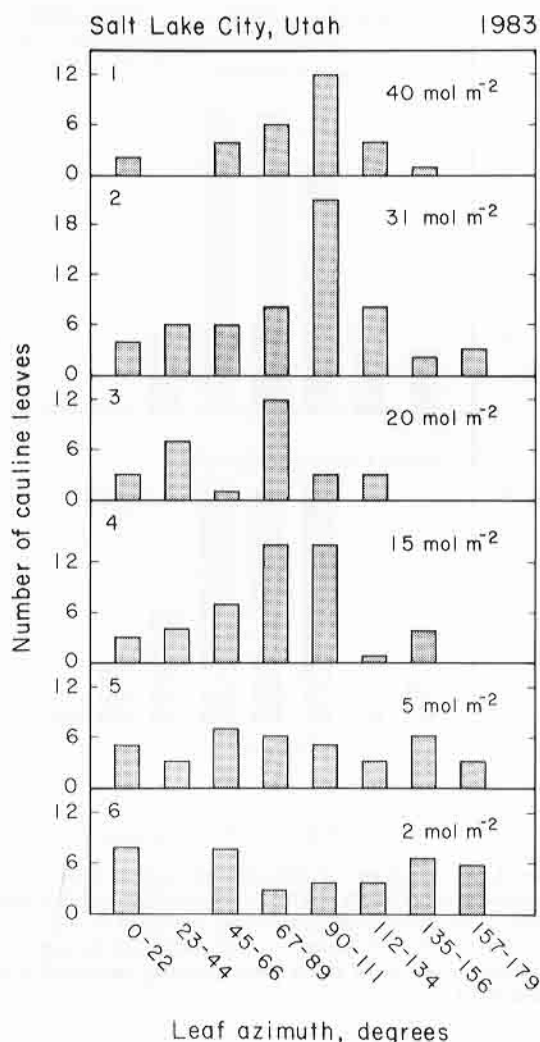


Figure 3. Distribution of azimuths of cauline leaves of *L. serriola integrifolia* growing in the shade. Conditions as in Fig. 2.



**Figure 4.** Distributions of azimuths of cauline leaves on potted plants grown in six different locations. Daily total solar radiation incident on an average vertical leaf within a uniformly distributed canopy is presented in mol m<sup>-2</sup> of photons (400–700 nm). Treatments 1–4 are statistically different from uniformly distributed ( $P < 0.01$ ). Treatments 5 and 6 are not different from uniform ( $P > 0.05$ ).

the four treatments receiving the most direct sunlight. The two treatments receiving less than 10 mol m<sup>-2</sup> of photons (400–700 nm) per day had uniform distributions of leaf azimuths (Fig. 4). The chi-squares for each of the treatments were: (1) 30.9,  $P < 0.01$ ; (2) 40.3,  $P < 0.01$ ; (3) 32,  $P < 0.01$ ; (4) 34.5,  $P < 0.01$ ; (5) 3.7,  $P > 0.5$ ; (6) 10.8,  $P > 0.1$ .

The results of the experiment in which potted plants were turned 90° indicated that once leaves were fully expanded, leaf orientation did not change (Fig. 5). The mean azimuth for these leaves was originally 82.6°. Seventeen days after the pots had been turned, the mean azimuth for the same leaves was 80.2°. These differences were not statistically significant ( $t = 1.2$ , d.f. = 120,  $P > 0.2$ ). The distribution of new leaves which expanded after the

plants were turned 90° had a mean azimuth of 179.5° (Fig. 6). The mean azimuth for these newer leaves was 97° greater than the mean azimuth of the original leaves. This corresponds to the 90° rotation of the plants. The mean angles of leaves remained close to 85° throughout the experiment (84.7°, 82.7°, and 86.8° for the original leaves at the beginning of the experiment, original leaves after 17 d, and newly expanded leaves, respectively).

The diurnal distribution of photon flux incident on a horizontal leaf was markedly different to the diurnal distribution of photon flux incident on a vertical leaf facing east–west (Fig. 7). Photon flux on a horizontal leaf followed a parabolic distribution, peaking at midday. A vertical leaf facing east–west received its peak irradiance at 0800 and 1600 h and received little more than diffuse light at midday.

The diurnal course of leaf temperature followed the diurnal course of photon flux. Figure 8 presents a representative day of leaf temperature for a horizontal and vertical leaf with azimuth 90°. In the early morning when more light was incident on the vertical leaf its temperature was higher than the horizontal leaf. During the midday while the horizontal leaf was intercepting much more light its temperature was approximately 5°C warmer than the vertical leaf. The temperature difference was completely eliminated in the afternoon when the sky became overcast.

## Discussion

The leaf shapes of the lobed and unlobed forms of *L. serriola* differ greatly. Despite these differences, surface areas of individual leaves of the two forms are not different on average. This information suggests that the lobed form should have larger convection coefficients, and thus have a potential advantage in arid habitats. Unfortunately, no trend has emerged in the data we have collected and to date no complete demographic study looking for regional or geographical clines in the two forms of *L. serriola* along temperature or aridity gradients has been done.

The data clearly demonstrate that leaf orientation in both forms of *L. serriola* is non-random and appears to be controlled by the pattern of direct solar radiation received. In fully exposed plants, the cauline leaves are held vertically, oriented with the lamina facing east–west. Leaves on the lobed variety orient the same way as leaves on the unlobed variety.

Leaf orientation in *L. serriola* is a growth response. As a leaf develops, it twists and bends near its base in such a way as to adjust orientation. The plant rotation experiment demonstrated that once fully expanded, leaves cannot reorient. Plants growing in the shade have a random distribution of leaves. Leaves not exposed to direct solar radiation in the morning and afternoon also do not orient in any particular direction. This suggests that there may



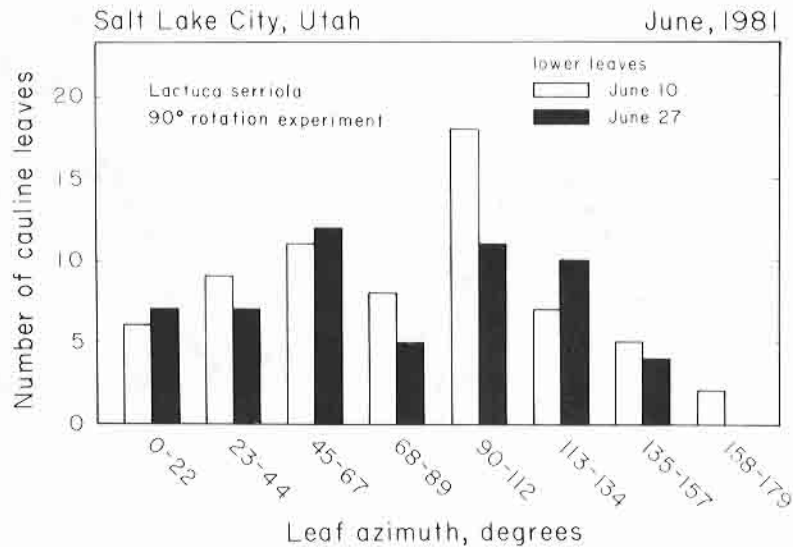


Figure 5. Distributions of azimuths of cauline leaves on potted plants before and 17 d after the pots were turned 90°.

be some minimum threshold level of direct solar radiation which is required to produce the non-random leaf orientation.

How does the pattern of non-random leaf orientation seen in *L. serriola* relate to the solar radiation environment? One direct consequence is an altered distribution of when solar radiation is intercepted diurnally. Instead of receiving a peak irradiance at noon each day, as the rosette leaves would, cauline leaves of *L. serriola* intercept very little light at midday (Fig. 7). More light is intercepted early in the morning and late in the afternoon by *L. serriola* leaves than by horizontal leaves. Dolk (1931) suggested that this maximizes the amount of sunlight intercepted each day. In

actuality, the orientation which would maximize the amount of solar radiation intercepted by a leaf varies with both latitude and solar declination. During the summer, leaves facing south with low leaf angles receive the most solar radiation over the course of the day (Table 1). All steeply angled leaves experience reduced solar radiation loads at noon in the summer, but only leaves facing east and west also receive increased loads in the morning and afternoon. This is an important distinction between leaves with random azimuths and leaves with specific azimuths.

Nobel (1980) demonstrated that cladodes of the platyopuntia *Opuntia chlorotica* preferentially faced north-south. During the winter, when these cacti are

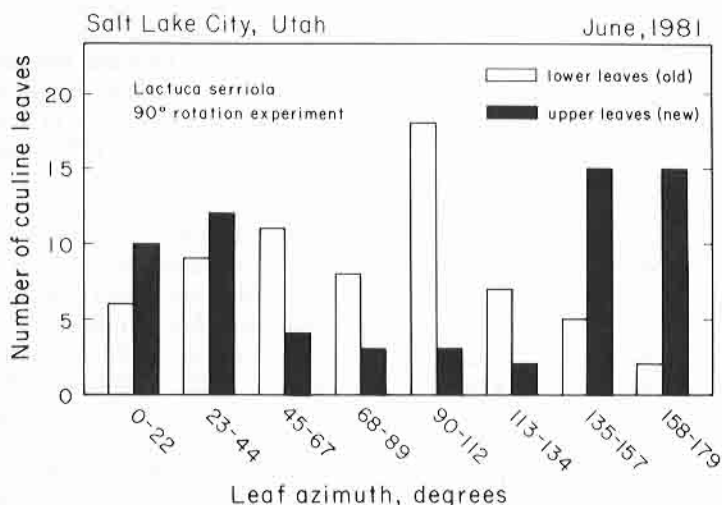
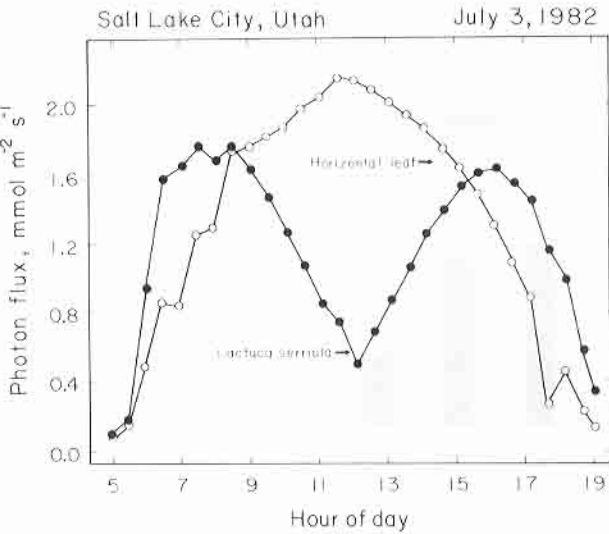


Figure 6. Distribution of azimuths of cauline leaves on potted plants before the pots were turned 90° and of azimuths of cauline leaves which emerged after the pots were turned. The pots were returned to their original positions when the second set of measurements were made.

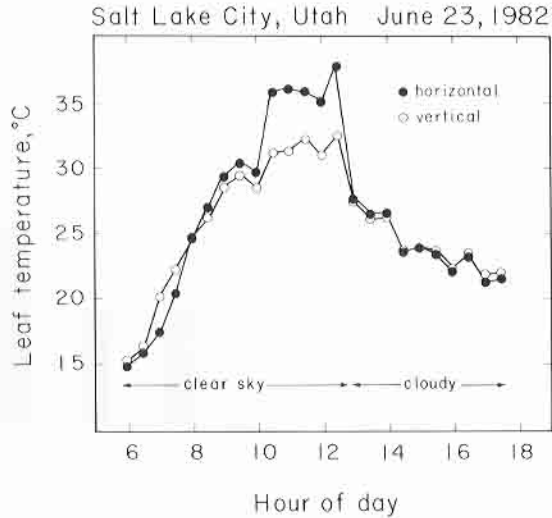


**Figure 7.** Diurnal course of photon flux (400–700 nm) incident on a horizontal leaf and on a vertical leaf facing east–west such as a cauline leaf of *L. serriola*. Measurements are the sum of photon flux incident on both sides of the leaves.

most active, this orientation results in more solar radiation being intercepted. It is important to point out that *L. serriola*'s leaf orientation neither maximizes nor minimizes the daily total amount of solar radiation received, but instead results in a dramatic change in the diurnal distribution of the solar radiation intercepted (Fig. 7). Gibbs & Patten (1970) suggest that the east–west orientation of the cladodes of *Opuntia engelmannii* prevents overheating while maintaining high daily total solar radiation received, because of the reduction of midday heating.

**Table 1.** Calculated photon flux in  $\text{mmol m}^{-2} \text{s}^{-1}$  incident on leaves. The transmission coefficient was assumed to be 0.8. Diffuse light was calculated as 10% of the direct beam normal irradiance. Data presented represent photon flux for the summer solstice at 40° latitude. Daily totals are in  $\text{mol m}^{-2} \text{d}^{-1}$

Solar time	Leaf orientation		
	Horizontal	Vertical, azimuth = 90°	Angle = 15°, azimuth = 180°
5	0.01	0.13	0.03
6	0.33	1.1	0.41
7	0.81	1.56	0.85
8	1.29	1.65	1.26
9	1.72	1.50	1.73
10	2.05	1.18	2.10
11	2.26	0.73	2.34
12	2.33	0.21	2.43
13	2.26	0.73	2.34
14	2.05	1.18	2.10
15	1.72	1.50	1.73
16	1.29	1.65	1.26
17	0.81	1.56	0.85
18	0.33	1.1	0.41
19	0.01	0.13	0.03
Daily total	69.5	57.3	71.5



**Figure 8.** Diurnal course of leaf temperature of a horizontal and a vertical leaf facing east–west on a single *Lactuca serriola* plant.

Cauline leaves of a herb such as *L. serriola* do not have the problem of thermal storage, characteristic of thick cactus cladodes. However, leaves could still overheat under intense radiation loads, high air temperatures, and still air conditions. Additionally, increased radiation loads and associated increased leaf temperatures may result in significantly increased transpiration rates. We have demonstrated that the leaf orientation seen in *L. serriola* reduces midday radiation loads and leads to a reduction in midday leaf temperature (Fig. 8). This also means that midday vapour pressure deficits will be greatly reduced in *L. serriola*. The noon leaf-to-air vapour pressure deficits for the horizontal and vertical leaves described in Fig. 8 were 5.15 kPa and 3.94 kPa, respectively.

If one considers the trade-off of water loss and carbon gain imposed by gas exchange through stomata, the leaf orientation observed in *L. serriola* may greatly increase the ratio of carbon gained to water lost. Vertical leaves facing east–west receive high light levels early in the morning when vapour pressure deficits (VPD) and air temperatures are lowest. As a result, high rates of photosynthesis could be achieved while transpiration rates would be lower. During the heat of midday when the VPD is high, the amount of light striking these leaves is reduced. This would tend to decrease both transpiration and photosynthesis rates. Midday reductions in photosynthesis and stomatal conductance to water vapour are frequently observed in plants with horizontal leaves under high irradiance and high VPD conditions (Shulze & Hall, 1982). Leaves of *L. serriola* experience reduced solar radiation levels at midday and thus have a lower risk of thermal damage or photoinhibition than if the leaves were horizontal (Powles & Bjorkman, 1981). Late in the afternoon when the VPD is lower, *L. serriola* leaves

are once again receiving high irradiance. High rates of photosynthesis can then be achieved during a period when transpiration rate is again reduced.

Several previous studies have related steep leaf angles to reductions in leaf temperature and transpiration (Medina, Sobrado & Herrera, 1978; Shaver, 1978), but have not considered leaf azimuth and the diurnal distribution of irradiance intercepted by leaves. Several species appear to have leaf orientations similar to those observed in *L. serriola* (e.g., *Silphium laciniatum*, *Artostaphylos uva-ursi*, *Quercus laevis*, and *Aster linosyris*, in arid habitats (Geiger, 1966; personal observation)). The advantage of the leaf orientation observed in these plants may not be simply the reduction in light and heat loads, but rather a more efficient diurnal use of incident light. With most plants that become light saturated at light intensities well below full noon sunlight, any excess light above saturating levels only results in a heat load and increased transpiration rates. Leaves of 'compass plants' receive approximately 80% of the daily integrated solar irradiance received by horizontal leaves during the summer (Table 1). This 20% difference is mostly due to the 'compass plants' receiving low levels of solar irradiance during the midday hours when horizontal leaves are receiving in excess of  $2 \text{ mmol m}^{-2} \text{ s}^{-1}$  of photon flux. Stomatal conductance to water vapour in *L. serriola* growing in the field during the early summer is vapour pressure sensitive. Conductance is high early in the morning and late afternoon but low during midday (Werk & Ehleringer, unpublished data) corresponding to the times of day when incident light levels are high and leaf-to-air vapour pressure deficits are reduced. Thus, compass plants may not lose much potential photosynthesis, but gain considerably in being able to photosynthesize during periods of the day when water-use efficiency would be highest.

Forseth & Ehleringer (1982) demonstrated that one of the major benefits of leaves which solar track (maintain their leaves perpendicular to the sun) is that they intercept large amounts of sunlight early in the morning before the plants become water stressed. The solar trackers are able to gain significantly more carbon than plants with horizontal leaves before having photosynthetic rates reduced by water stress. We propose that the leaf orientation observed in *L. serriola* and other 'compass plants' conveys a similar advantage. During periods of low water availability or high VPD, *L. serriola* and other 'compass plants' would appear to have an advantage because of their ability to attain high rates of photosynthesis early in the morning.

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