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EFFECT OF NONRANDOM LEAF ORIENTATION ON REPRODUCTION IN *LACTUCA SERRIOLA* L.

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Abstract.—The cauline leaves of an annual, *Lactuca serriola* L., are naturally oriented vertically with the lamina perpendicular to the east and west. Previous physiological data indicated that this nonrandom leaf orientation should reduce water loss without substantially reducing photosynthesis and could thus influence plant growth and reproduction (Werk and Ehleringer, 1984, 1985). The effect of leaf orientation on flower and seed production was tested experimentally using potted *L. serriola* grown outdoors. Leaves of half the plants were forced to remain approximately horizontal while the other plants were allowed to orient naturally. The plants with horizontal leaves lost water more rapidly than the plants with naturally oriented leaves. Above-ground weight, below-ground weight, seed weight, and the number of seeds per flower were not significantly affected by leaf orientation. Flower production was a linear function of plant size for both treatments with plants with natural leaf orientation having a significantly greater slope. These results indicate that the nonrandom leaf orientation observed in *L. serriola* is a morphological character which can enhance reproduction.

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The cauline leaves of *Lactuca serriola*, the compass plant, orient so that they are in a vertical plane with the lamina perpendicular to the east and west (Werk and Ehleringer, 1984). Dolk (1931) questioned the adaptive significance of this morphological trait but Geiger (1966 pp. 391-393) suggested that it was related to midday heat avoidance. We demonstrated earlier (Werk and Ehleringer, 1984) that this orientation does indeed reduce the midday radiative heat load, but physiological data suggest that the indirect reduction of water loss may in fact be more important than heat avoidance (Werk and Ehleringer, 1985). *L. serriola* offers the rare opportunity to examine the effect of a single trait, leaf orientation, on the growth, survival, and reproductive success of individuals.

The leaf orientation observed in *L. serriola* results in a redistribution of the diurnal interception of solar irradiance. Noon solar irradiance incident on the leaf is limited to diffuse light while peak interception occurs early in the morning and late in the afternoon. A leaf oriented vertically, facing east-west, as in *L. serriola*, experiences approximately an 18% reduction of daily integrated solar irradiance when compared to a horizontal leaf. By comparison, the solar

irradiance intercepted by a leaf oriented vertically but facing north-south instead of east-west would be reduced by approximately 65% when compared to a horizontal leaf. Although vertical leaf orientation is usually associated with a decrease in intercepted irradiance, the magnitude of the reduction and the daily pattern of light interception depend greatly on the compass direction of the leaf (Ehleringer and Werk, 1986). While the leaf orientation observed in *L. serriola* results in an 18% reduction in integrated solar irradiance compared to horizontal leaves, 10% of the irradiance on a horizontal leaf occurs at a photon flux density of $1.8 \text{ mmol m}^{-2} \text{ s}^{-1}$ or more while *L. serriola* leaves never intercept more than $1.65 \text{ mmol m}^{-2} \text{ s}^{-1}$. Since photosynthesis becomes light saturated at less than $1.8 \text{ mmol m}^{-2} \text{ s}^{-1}$ in *L. serriola* (Werk and Ehleringer, 1985), the reduction in daily integrated solar irradiance which can be utilized is about 8%. Thus the reduction in usable solar irradiance is quite small while the diurnal redistribution is large. The potential for photosynthesis is not changed greatly by the east-west orientation of *L. serriola* leaves, but we suggest that the reduction in water loss is significant.

L. serriola has a strong response of leaf

TABLE 1. Leaf orientation experiment. *L. serriola serriola* was used in 1982; both *L. serriola serriola* and *L. serriola integrifolia* were used in 1983. Values are the mean \pm SE.

	1982		1983	
	Horizontal (<i>N</i> = 6)	Natural (<i>N</i> = 6)	Horizontal (<i>N</i> = 29)	Natural (<i>N</i> = 26)
Number of seeds/flower	15.0 \pm 2.00	19.0 \pm 0.40	16.0 \pm 0.60	17.1 \pm 0.40
Seed weight (mg)	0.5 \pm 0.04	0.5 \pm 0.01	0.7 \pm 0.03	0.8 \pm 0.02
Number of flowers/plant	67.0 \pm 2.00	132.0 \pm 16.0	134.0 \pm 7.10	151.0 \pm 9.30
Above-ground weight (g)	11.4 \pm 1.50	9.0 \pm 1.20	6.8 \pm 0.31	6.6 \pm 0.27
Below-ground weight (g)	4.5 \pm 0.70	3.8 \pm 0.02	2.4 \pm 0.13	2.3 \pm 0.13

conductance to water vapor both under laboratory conditions (Werk and Ehleringer, 1985) and natural field conditions (Werk and Ehleringer, 1986). The diurnal pattern of vapor concentration deficits results in a pattern of midday or midday and afternoon stomatal closure in *L. serriola* growing naturally. The pattern of light interception by *L. serriola* matches the pattern of stomatal opening that results from this humidity response.

If water is an important resource for growth and reproduction, then we would predict that compass plants with natural leaf orientation would have an advantage over plants that have leaves oriented such that light interception occurs mostly at midday. The east-west facing leaves, by intercepting most light during the early morning and late afternoon, would be more water conservative while not suffering a substantial reduction in photosynthetic potential.

Since leaf orientation is easily manipulated, we decided to study the effect of different leaf orientations experimentally. Because *L. serriola* is an annual, the effect of east-west orientation on reproduction and not just water loss was determined. In this study we test the hypothesis that the leaf orientation observed in *L. serriola* results in enhanced growth and reproduction when compared to plants with horizontal leaves.

MATERIALS AND METHODS

To determine the effect of leaf orientation on growth and reproduction, plants of both *L. serriola serriola* and *L. serriola integrifolia* were grown outdoors in pots. The pots were constructed of 15 cm diameter PVC pipe and were 75 cm deep. The depth of the pots was sufficient to allow the plants to root naturally. Two treatments were used. Plants in the control group were allowed to grow

and orient their leaves naturally. Plants in the experimental group were manipulated so that the cauline leaves were prevented from orienting vertically, east-west; emerging cauline leaves were restrained with fine wires attached to an adjacent rod. Once the leaves were fully expanded the restraints were removed since leaves would not reorient (Werk and Ehleringer, 1984). In general the leaves of the experimental plants were forced to orient in all directions with angles of 0–45° from horizontal. The wires did not damage the leaves, covered an extremely small surface area of the leaves, and had no effect on leaf shape or area.

The plants were watered periodically during the course of the growing season. Each plant received the same amount of water. Water loss was monitored by weighing entire pots. To avoid damage to the plants and pots due to excessive handling, only a subset of plants (*N* = 7) in each of the treatments was used for these measurements.

All plants were harvested at the same time. Flower production, above-ground dry weight, and below-ground dry weight were determined. During the weeks preceding the harvest, matured seeds were harvested from flowers to determine average number of viable seeds per flower and average seed weight. Above-ground biomass included stems, leaves, and flower stems. Below-ground biomass included all root material recovered by washing roots over a 0.5 cm mesh screen. Plant material was oven dried at 60°C.

We used *L. serriola serriola* in 1982 and both *L. serriola serriola* and *L. serriola integrifolia* in 1983.

RESULTS

Our results show that the leaf orientation observed in *L. serriola* reduces water loss

but does not reduce carbon gain significantly. From June 15 (the start of the treatment) through July 19, 1983, the experimental plants lost 42.2 ± 3.4 ($\bar{x} \pm \text{SE}$) g $\text{H}_2\text{O plant}^{-1} \text{ day}^{-1}$, while the plants with naturally oriented leaves lost only 36.8 ± 2.2 g $\text{H}_2\text{O plant}^{-1} \text{ day}^{-1}$ (Mann-Whitney $U_{[7,9]} = 174$, $P < 0.01$). From July 20–July 27 the experimental plants lost 28.9 ± 3.3 g $\text{H}_2\text{O plant}^{-1} \text{ day}^{-1}$, while the control plants lost 23.4 ± 3.2 g $\text{H}_2\text{O plant}^{-1} \text{ day}^{-1}$ ($U_{[7,7]} = 267$, $P < 0.01$).

The effects of modified leaf orientation are summarized in Table 1. Reproductive characters were never enhanced by horizontal leaf orientation. Mean number of seeds/flower, mean seed weight, and mean number of flowers/plant were always lower for the horizontal treatment but not statistically different from the natural treatment in pairwise comparisons (except number of flowers/plant in 1982, $P < 0.05$). Combining the probabilities of the independent comparisons (Sokal and Rohlf, 1981) between horizontal and natural treatments for number of seeds/flower, seed weight, and number of flowers/plant gives a significant reduction in reproductive output in the horizontal treatment ($X^2 = 21.3$, $d.f. = 9$, $P < 0.02$).

There was an approximately three-fold range in plant size within each treatment. This variation was apparent even before the plants bolted and when the plants were chosen randomly for the experimental or natural orientation treatments. This variation must be attributed to unknown differences between individuals. This large range in size also completely obscured any possible effect of leaf orientation on growth rate.

Proportional allocation to reproduction is usually plant-size dependent (Samson and Werk, 1986). It is thus inappropriate to compare proportional allocation when there is a wide range in plant size in the samples. Since absolute reproductive weight is frequently a linear function of plant dry weight, differences in reproductive allocation can be determined by comparing the slopes of these relationships (Samson and Werk, 1986). Reproductive output of the plants in each of the leaf-orientation treatments was compared using this method. Since the number of seeds/flower and seed weight were very

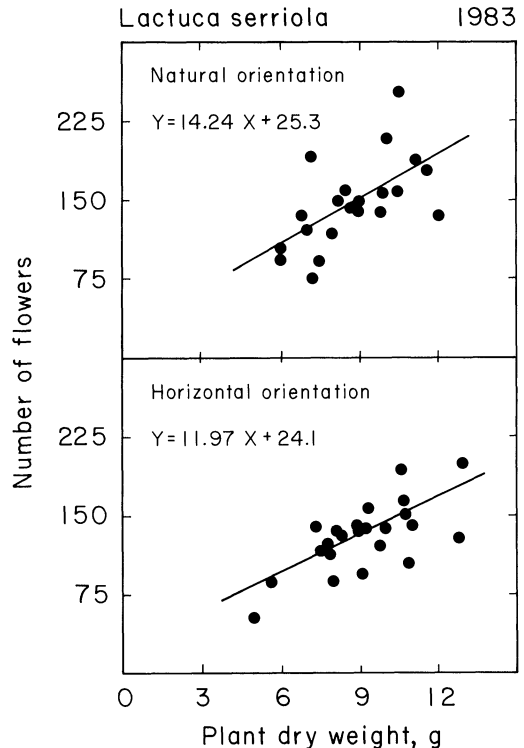


FIG. 1. Number of flowers produced as a function of plant dry weight for each treatment in the leaf orientation experiment. Both regressions are statistically significant ($P < 0.01$). The slopes of the two treatments are statistically different ($F_{[1,40]} = 5.02$, $P < 0.05$).

similar between treatments, reproduction was expressed in terms of the number of flowers/plant.

Reproduction in relation to plant size was significantly decreased by the horizontal-leaf treatment (Fig. 1). The linear regressions of flower production on plant dry weight were: $Y = 14.24X + 25.3$ ($r = 0.60$, $P < 0.01$) for the natural-orientation group, and $Y = 11.97X + 24.1$ ($r = 0.69$, $P < 0.01$) for the horizontal group. The slopes of the two lines are significantly different ($F_{[1,40]} = 5.02$, $P < 0.05$). Thus at the end of the growing season the control plants were producing more flowers/plant weight than the plants with horizontal leaves.

DISCUSSION

Many aspects of leaf orientation have been investigated in the past. Several researchers have examined the effects of leaf orientation on particular aspects of light or temperature

regimes, physiology, carbon gain, or water use efficiency (e.g., Medina et al., 1978; Mooney and Ehleringer, 1978; Shaver, 1978; Ehleringer and Forseth, 1980; Nobel, 1980; Powles and Björkman, 1981; Forseth and Ehleringer, 1983; Werk and Ehleringer, 1984). In this study we have been able to experimentally examine the link between compass plant leaf orientation and reproductive output.

Plants in both treatments were watered equally, but the plants with horizontal leaves lost water at a higher rate; they probably experienced lower water potentials earlier than the control plants. Since photosynthesis and leaf conductance decrease in *L. serriola* in response to increasing drought (Werk, unpubl.), the plants with horizontal leaves probably had lower rates of photosynthesis than those with east-west orientation at the end of the growing season. This difference in carbon-gaining capacity probably accounts for the reduction in flower and seed production by the plants with horizontal leaves. Most of the biomass accumulation by *L. serriola* in this experiment occurred early in the season, both before bolting (before the experimental manipulation) and before water potentials would have begun to decrease. It is thus not surprising that there were no significant differences in plant biomass between treatments. The difference occurred after vegetative growth was complete and flower production was underway. The natural east-west facing vertical leaf orientation led to greater reproductive output on a per plant weight basis.

The leaf orientation observed in *L. serriola* has been demonstrated to affect the diurnal pattern of solar irradiance and thus the diurnal pattern of leaf temperature (Werk and Ehleringer, 1984). This in turn reduces transpirational water loss and probably enhances carbon gain at the end of the growing season. This study has demonstrated that leaf orientation ultimately affects reproductive output. These experimental results suggest that the nonrandom, east-west, vertical, leaf orientation observed in *L. serriola* is indeed adaptive and functions as a morphological means of enhancing water con-

servation and improving reproduction in arid habitats.

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