Plant, Cell and Environment (1986) **9**, 681–683

SHORT COMMUNICATION

Field water relations of a compass plant, *Lactuca serriola* L.

K. S. WERK & J. EHLERINGER Lehrstuhl Pflanzenökologie der Universität Bayreuth, D-8580 Bayreuth, FRG and Department of Biology, University of Utah, Salt Lake City, UT 84112, U.S.A.

Received 13 February 1986; accepted for publication 5 June 1986

Abstract. Field water relations of *Lactuca serriola serriola* and *L. serriola integrifolia* were examined. Leaf conductance to water vapour was high early in the morning and declined rapidly during the midday hours. Leaf water potentials decreased to their minima early in the morning and remained low all day. Afternoon recovery of leaf conductance occurred occasionally. Leaf conductance was shown to have a linear response to vapour concentration difference. No differences were seen between *L. serriola serriola* and *L. serriola integrifolia*. The pattern of diurnal gas-exchange activity appeared to be complemented by the pattern of intercepted solar irradiance which results from the compass plant leaf orientation observed in *L. serriola*.

Key-words: Lactuca serriola; water-use efficiency; leaf orientation; water relations.

Midday reductions in photosynthesis and leaf conductance have been observed in numerous species (Schulze & Hall, 1982). This phenomenon has been shown to be related to the direct response of stomata to humidity (Farquhar, 1978; Schulze & Hall, 1982; Hall, Schulze & Lange, 1976). Under hot and dry climatic conditions, restrictions of gas exchange to early morning and late afternoon by reducing midday conductance should lead to maximizing carbon uptake for a set amount of water lost (Cowan & Farquhar, 1977; Cowan, 1982). Stomatal restrictions of gas-exchange activity during midday periods when irradiances are high can lead to potential damage to the photosynthetic apparatus if excessive leaf temperatures result or if photoinhibition occurs. Various leaf movements can result in a reduction in light interception and have been related to the avoidance of such damage (Forseth & Ehleringer, 1982; Powles & Björkman, 1981; Ludlow & Björkman, 1984). Changes in photosynthetic capacity and in carboxylation efficiency associated with midday stomatal closure have also been investigated with respect to their influence on minimizing photoinhibitory damage (Tenhunen *et al.*, 1984). In contrast to active leaf movements, it is possible that certain static leaf orientations can serve as a morphological means of both avoiding excessive midday water loss and midday exposure to conditions aggravating photoinhibition, yet without substantially reducing the overall daily amount of solar radiation incident on the leaf (Ehleringer & Werk, 1986).

Correspondence: Dr K. Werk, Lehrstuhl Pflanzenökologie der Universität Bayreuth, D-8580 Bayreuth, FRG.

Lactuca serriola is known as a compass plant because its cauline leaves are vertically oriented in a north–south plane so that the laminae are normal to the east and west (Werk & Ehleringer, 1984; Dolk, 1931). The importance of this east–west leaf orientation appears to be related to the resulting diurnal pattern of solar irradiance interception. Early morning and late afternoon irradiance is enhanced while midday irradiance is reduced (Werk & Ehleringer, 1984) the diurnal pattern of leaf temperature and leaf to air vapour concentration difference (ΔW) in *L. serriola* is also affected by this leaf orientation (Werk & Ehleringer, 1984). Compared to horizontal leaves the temperature of vertical east–west facing leaves is reduced during the midday hours as a result of the reduction in irradiance. Since transpiration in *L. serriola* increases with increasing leaf temperatures, especially at leaf temperatures above 30 °C (Werk & Ehleringer, 1985), the leaf orientation observed is expected to substantially reduce the water lost under field conditions.

We studied the field water relations of *L. serriola* to determine whether the observed leaf orientation is consistent with the hypothesis that it is a morphological means of improving daily water-use efficiency by reducing midday water loss while emphasizing morning and afternoon activity. Two leaf forms of *L. serriola* exist, one lobed and the other unlobed. No differences in leaf orientation (Werk & Ehleringer, 1984), or photosynthetic characteristics (Werk & Ehleringer, 1985) have been observed. This study investigates the field water relations of both leaf forms.

Field water relations were studied on *L. serriola* growing naturally in Salt Lake City, UT, 41°N latitude. Diurnal courses of leaf water potential, leaf conductance, leaf temperature, and leaf to air ΔW were measured periodically from May to September in 1983 and 1984. Measurements were made on cauline leaves of both *L. serriola serriola* and *L. serriola integrifolia*. Water potential measure-

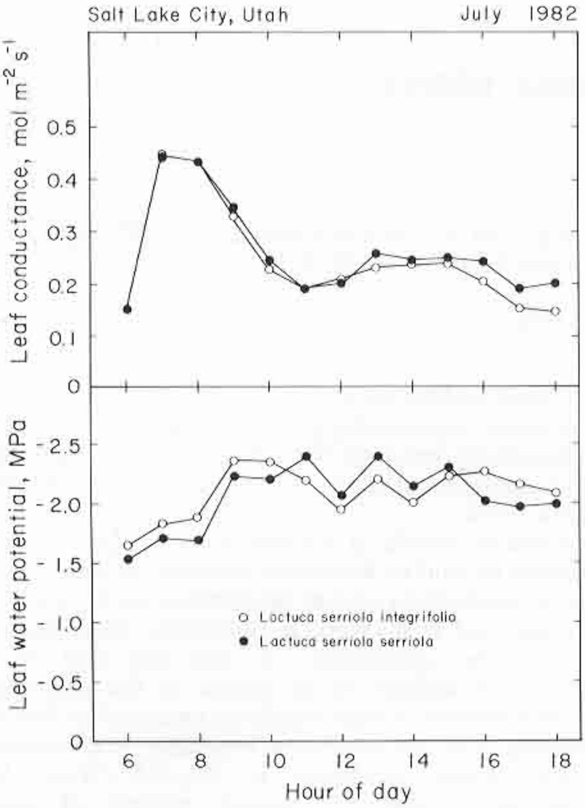

Figure 1. Diurnal course of leaf conductance and leaf water potential in *L. serriola serriola* (●——●) and *L. serriola integrifolia* (○——○) growing naturally in the field. Standard errors for leaf conductance ranged from 0.02 to 0.06, and from 0.02 to 0.15 for water potential. There were no significant differences between *L. serriola serriola* and *L. serriola integrifolia*. Sample sizes were five for each form.

ments were made on single leaves using a pressure chamber (PMS, Corvallis, OR). Leaf conductances were measured on individual leaves using an automatic porometer (Delta T Devices Mk II, Cambridge, U.K.). The porometer was calibrated in the field every 10–15 measurements using a series of calibration plates with known resistances to water loss. Leaf temperature was measured with a 36 gauge thermocouple and a Bat-9 thermocouple meter (Baily Instruments, Saddle Brook, NJ). For ΔW measurements air temperature and relative humidity were measured (Relative Humidity Probe HT-100, Weathermeasure, Sacramento, CA).

The field water relations of *L. serriola serriola* and *L. serriola integrifolia* were indistinguishable (Fig. 1). Leaf water potential dropped rapidly during the early morning hours but then remained relatively constant until sunset. This pattern was observed regardless of the diurnal response of leaf conductance.

The most common pattern of diurnal leaf conductance consisted of an early morning peak followed by a relatively low conductance for the rest of the day. Another rarer pattern was one of high morning and afternoon leaf conductance with midday closure (Fig. 2). This pattern of afternoon recovery was always correlated with a declining afternoon ΔW although the recovery was not usually very large. The more frequently observed pattern of high conductance in the morning only occurred when the afternoon ΔW remained high.

Field measurements confirmed that leaf conductance in *L. serriola* responded to ΔW. Using diurnal data collected in 1983, a strong correlation between leaf conductance and leaf to air ΔW was observed (Fig. 3). Over 37% of the variation in leaf conductance was accounted for by the ΔW under all light, temperature, and leaf water potential conditions.

The pattern of leaf conductance in *L. serriola* in the field was more conservative than expected. Werk & Ehleringer (1984) predicted that the leaf orientation observed in *L. serriola* should lead to both early morning and late afternoon activity. This pattern was observed (Fig. 2) but only rarely since ΔW normally remained quite high during the

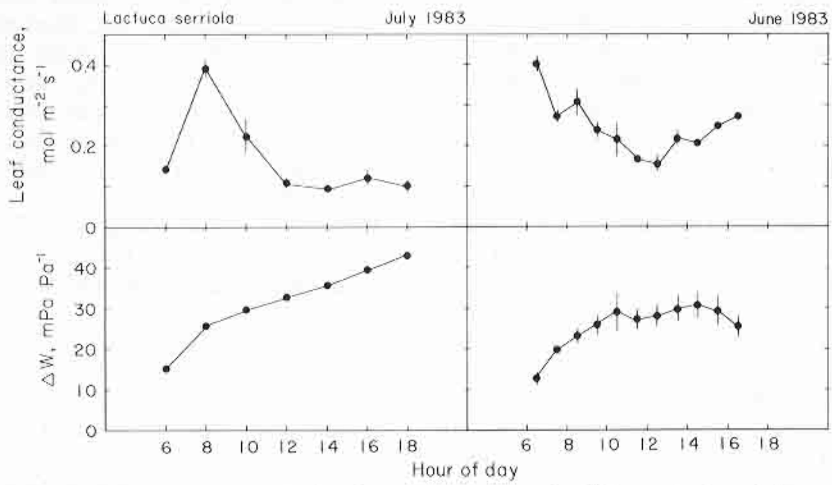

Figure 2. Diurnal course of leaf conductance and leaf to air vapour concentration difference in *L. serriola* growing naturally in the field during June 1983 and July 1983. Sample sizes were eight in June and 16–23 in July. Vertical bars represent ± one standard error.

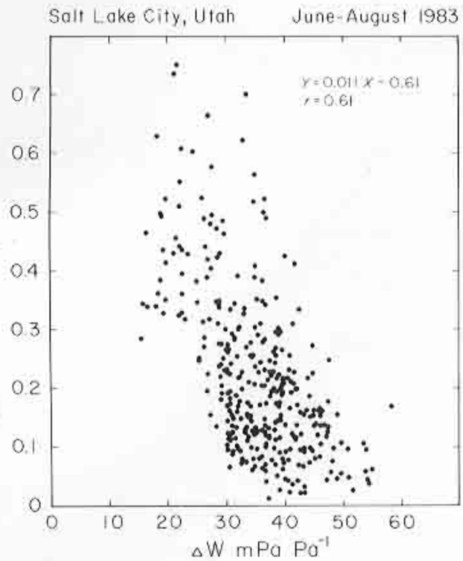

Figure 3. Relationship of leaf conductance to leaf to air vapour concentration difference (ΔW). Measurements were made on individual leaves of plants growing naturally in the field during June–August 1983. Measurements were made throughout the day from just after sunrise to just before sunset.

afternoon. *Lactuca serriola* is known to have a strong stomatal response to ΔW from laboratory measurements (Werk & Ehleringer, 1985) and this response was also apparent under field conditions (Fig. 3).

The prediction that *L. serriola* would be most active during the early morning and the afternoon was based on the assumption that ΔW would recover in the afternoon by the time the east–west facing vertical leaves of *L. serriola* would be intercepting high irradiances. Since the ΔW only rarely decreased significantly in the afternoon in Salt Lake City, where the research was carried out, *L. serriola* was most active in the morning. Our data suggest that both the morning and afternoon periods would be utilized by *L. serriola* growing in more humid environments where there is a larger decrease in afternoon ΔW. It is clear that the east–west leaf orientation alone is insufficient to take advantage of low ΔW in the early morning and late afternoon. A strong humidity response is also required to ensure that stomatal opening is reduced when ΔW remains high during the afternoon. The east–west leaf orientation does appear to enhance the benefits of a stomatal humidity response.

Plants with solar tracking leaves can attain high rates of photosynthesis at almost any time of the day, including the early morning and late afternoon (Ehleringer & Forseth, 1980). This allows a considerable amount of carbon gain to occur during periods of the day when water loss is reduced. However, Forseth & Ehleringer (1983) demonstrated that solar trackers must either possess a mechanism such as paraheliotropy, to avoid high radiation loads during periods of water stress, or have the physiological capability to operate at moderately large negative water potentials. The leaf orientation observed in *L. serriola* may actually represent a system that is a compromise between the ability to exploit early morning and late afternoon irradiance fully with the avoidance of large heat loads during midday, and the lack of ability to utilize midday irradiance during periods of abundant water when midday ΔW's are also low. Since midday periods with low ΔW's are relatively rare, the compass plant leaf orientation observed is probably an effective way of increasing the carbon gain while limiting the amount of water lost.

References

Cowan, I.R. (1982) Regulation of water use in relation to carbon gain in higher plants. In *Encyclopedia of Plant Physiology* (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), New Series Vol. 12b, Physiological plant ecology II, pp. 589–613. Springer-Verlag, Berlin.

Cowan, I.R. & Farquhar G.D. (1977) Stomatal function in relation to leaf metabolism and environment In *Integration of Activity in Higher Plants*, (ed. D.H. Jennings), Vol. 31, pp. 471–505. Society of Experimental Biology Symposium University Press, Cambridge.

Dolk, H.E. (1931) The movement of the leaves of the compass-plant Lactuca scariola. *American Journal of Botany*, **18,** 195–204.

Ehleringer, J. & Forseth, I. (1980) Solar tracking by plants. *Science*, **210,** 1094–1098.

Ehleringer, J. & Werk, K.S. (1986) Modifications of solar-radiation absorption patterns and implications for carbon gain at the leaf level. In *On the Economy of Plant Form and Function*, (ed. T.J. Givnish). Columbia University Press.

Farquhar, G.D. (1978) Feed-forward responses of stomata to humidity. *Australian Journal of Plant Physiology*, **5,** 787–800.

Forseth, I.N. & Ehleringer, J. (1982) Ecophysiology of two solar tracking desert winter annuals. II. Leaf movements, water relations and microclimate. *Oecologia*, **54,** 41–49.

Forseth, I. N & Ehleringer, J. (1983) Ecophysiology of two solar tracking desert winter annuals. IV. Effects of leaf orientation on calculated daily carbon gain and water use efficiency. *Oecologia*, **58,** 10–18.

Hall, A.E., Schulze, E.-D. & Lange, O.L. (1976) Current perspectives of steady state stomatal responses to environment. In *Water and Plant Life* (eds O.L. Lange, L. Kappen & E.-D. Schulze), Vol. 19, Ecological studies, pp. 169–188. Springer-Verlag, Berlin.

Ludlow, M.M. & Björkman, O. (1984) Paraheliotropic leaf movements in Siratro as a protective mechanism against drought-induced damage to primary photosynthetic reactions: damage by excessive light and heat. *Planta*, **161,** 505–518.

Powles, S.B. & Björkman O. (1981) Leaf movements in the shade species *Oxalis oregana* II. Role in protection against injury by intense light. *Carnegie Institute of Washington Yearbook*, **80,** 63–66.

Schulze, E.-D. & Hall, A.E. (1982) Stomatal response, water loss and CO_2 assimilation rates of plants in contrasting environments. In *Encyclopedia of Plant Physiology* (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), New Series, Vol 12b, Physiological plant ecology II, pp. 181–230. Springer-Verlag, Berlin.

Tenhunen, J.D., Lange, O.L., Gebel, J., Beyschlag, W. & Weber, J.A. (1984) Changes in photosynthetic capacity, carboxylation efficiency, and CO_2 compensation point associated with midday stomatal closure and midday depression of net CO_2 exchange of leaves of *Quercus suber*. *Planta*, **162,** 193–203.

Werk, K.S. & Ehleringer, J. (1984) Non-random leaf orientation in *Lactuca serriola* L. *Plant Cell and Environment*, **7,** 81–87.

Werk, K.S. & Ehleringer, J. (1985) Photosynthetic characteristics of *Lactuca serriola* L. *Plant Cell and Environment*, **8,** 345–350.