

Effects of Leaflet Orientation on Transpiration Rates and Water Potentials of *Oxalis montana*

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Abstract- The leaflets of *Oxalis montana* (wood sorrel) show reversible leaflet movements with leaflets moving from a horizontal position to a vertical one in response to direct solar radiation. We studied the possibility that this response was (1) hydropassive, resulting from decreased water potential caused by higher transpiration rates in direct sunlight and (2) a mechanism to reduce water loss under conditions of high radiation. Using a lysimeter technique, the transpiration rate of *O. montana* with vertical leaflets was found to be higher than the transpiration rate of plants with leaflets in a horizontal position. The water potential of leaves with leaflets in a vertical orientation was significantly lower than the water potential of leaves with horizontal leaflets. These results do not support the hypothesis that leaflet movement is a mechanism to reduce water loss, but they are consistent with a hydropassive response, one where leaflet movement results from lower leaf water potential brought about by increased transpiration.

Introduction

Oxalis montana is a herbaceous perennial common in the temperate forests of central New England to Wisconsin, and north into Canada. It has a scaly, woody underground

trifoliate leaves of *Oxalis* fold downward, in response to direct sunlight, from a horizontal position in the shade, to a vertical position (Figure 1.) Similar



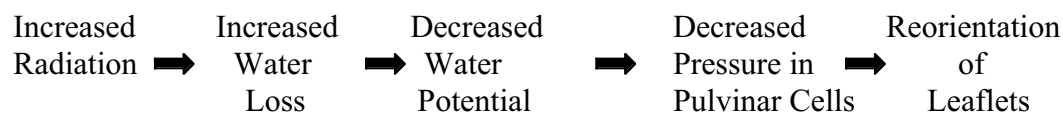
Figure 1 Leaflets Horizontal

Leaflets Vertical

rhizome that sends up clover shaped leaves in the spring, which persist for the summer then die back in the fall. In the Adirondacks of New York *Oxalis montana* covers large parts of the forest floor, forming thick blankets of leaves and flowers in the shade of the canopy. The leaves of *Oxalis* are dissected into three leaflets, which show movement in response to direct solar radiation. The small

responses have been reported for *Oxalis regnellii*, a species from Europe (Pedersen et al. 1993), and *O. oregana* a species from western North America (Bjorkman and Powles, 1981.)

Leaflet movements such as those shown by the various species of *Oxalis* are generally attributed to the action of a pulvinus, a group of cells at the base of the organ that exhibits movement. Pulvinar cells can effect movement as they swell or shrink in response to changes in internal water pressure, cell turgor pressure. The changes in the pressure of pulvinar cells could be the result of changes in solute concentration in these cells or changes in leaf water potential. We hypothesized the downward movement of the leaflets was “hydropassive” and involved decreases in leaf water potential resulting from increased transpiration in direct sunlight.



Lowered leaf water potentials generally result in stomatal closure and reduced transpiration rates. Thus we expected that vertically oriented leaves would not only have lowered leaf water potentials but that they would also exhibit reduced transpiration rates when compared with leaves that were horizontal.

Methods and Materials

The experiments were conducted on plants taken from Cranberry Lake Biological Station in Cranberry Lake, NY. Samples of soil containing *O. montana* were taken from the forest floor and placed in pans. Care was taken to disturb the roots as little as possible and to keep the soil and plants intact upon removal. The rhizomes and roots of *O. montana* are generally in the top 15cm of soil (the organic horizon), and so are easily removed intact. All other plants were removed from the soil samples and the plants were well watered. They were left in the lab for at least 24 hours before any experiments were performed. The

plants all appeared healthy and responded in a typical fashion when exposed to full sunlight.

The basic experiment design consisted of measuring the xylem pressure potential and transpiration rates in three replicate samples of *Oxalis* (each with approximately 50 leaves) during a 90 minute period in the shade (no direct sunlight, Photosynthetic Photon Flux Density <100 μmol m⁻² sec⁻¹.) The plants were then moved into direct sunlight where the leaves reoriented to the vertical position over the course of 90 minutes. When greater than 90% of the leaves had attained the vertical position, water potential and transpiration rates were again monitored during a 90-minute period.

We used a pressure bomb to measure the xylem pressure potential (assumed to be a good estimate of leaf water potential) of leaves and a lysimetry technique (repeated

weighing of the pans containing *Oxalis* with a triple beam balance) to measure transpiration. Since water loss (weight loss) could be the result of either transpiration or direct evaporation from the soil and leaf litter surface we had to estimate the amount of direct evaporation and subtract it from the total weight loss. To do this we used a sample in which all of the *Oxalis* leaves had been removed and therefore all weight loss was due to evaporation from the soil and litter. The amount of evaporation from the leafless sample was subtracted from the total weight change of the samples to estimate transpiration. Weighings were made every 15 minutes for a total of 90 minutes on three replicate samples which had been in the shade for an extended period of time and therefore had horizontal leaflets, plus a sample in which all of the *Oxalis* leaves had been removed. During this 90-minute period the xylem pressure potential of 15 leaves with horizontal leaflets was measured. The samples were then put into full sunlight. When over 90 percent of the leaves had leaflets in the vertical position, they were weighed every 15 minutes for 90 minutes and the xylem pressure potential of another 15 leaves with vertical leaflets was measured with the pressure bomb. Xylem pressure potential readings were also taken for *Oxalis* leaves in the field, comparing plants with horizontal leaflets to those with vertical leaflets.

Results

The transpiration rates of plants in the shade with horizontal leaflets were very low, often below the level that our technique could measure. Hence, some of the samples from the shade showed a slight negative transpiration (i.e. weight gain.)

Transpiration rates from plants in the sun with vertical leaflets were consistently

much higher than for plants in the shade with horizontal leaflets (Fig. 2). A non-parametric Sign Test comparing means, revealed that the transpiration rate from plants with vertical leaflets was significantly greater than that from plants with horizontal leaflets ($p=0.05$, $n=9$, 9 greater than/0 less than.)

The mean xylem pressure potential of vertical leaflets from laboratory samples were significantly lower than the xylem pressure potential for horizontal leaflets (t-test $p=0.05$, $t=14.83$, $df=88$ Fig 3.) A similar pattern was found in the field (t-test $p=0.05$, $t=8.425$, $df=23$ Fig 3.)

Figure 2

Average Water Transpired Per Leaf During a 90 Min Period

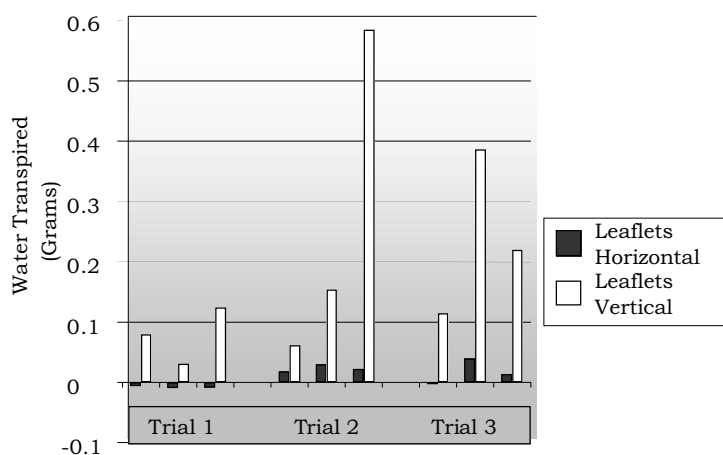
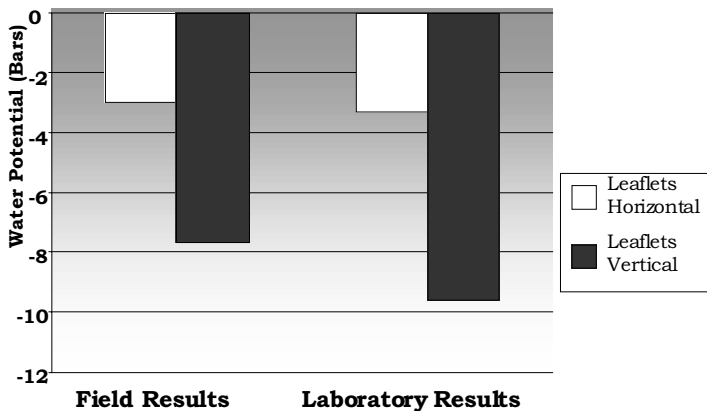


Figure 3

Mean Xylem Pressure Potential of Leaves with Horizontal and Vertical Leaflets



Discussion

Plants with vertically oriented leaflets had a significantly lower xylem pressure potential than those with horizontally oriented leaflets. This is consistent with a “hydropassive” mechanism controlling pulvinar movement. However the observation that transpiration was consistently and substantially higher in the samples with vertically oriented leaves does not support the hypothesis that leaflet movement is a means to reduce transpiration. However plants suffering excessive water loss and lowered water potential generally exhibit stomatal closure and reduced transpiration and this was not the case; transpiration rates for plants with vertical leaves was vastly greater than for plants with horizontal leaves. This suggests that the stomatal conductance of leaves in the vertical position was increased not decreased as would be expected if the plants were experiencing excessive water loss. Thus it is possible that the loss of turgor in the pulvinar region comes about not so much from sunlight increasing leaf temperature and thereby increasing transpiration, but rather from sunlight

increasing stomatal conductance and thereby increasing transpiration.

Literature Cited

Pedersen, M., R. Dalløkken, A. Johnsson, and J. Mæhle. 1993. Short period leaf movements in *Oxalis regnellii*. *Psilogia Plantarum* 89: 277-284.

Bjorkman, O. and S.B. Powles. 1981. Leaf movement in the shade species *Oxalis oregana*. I. Response to light level and light quality. Annual Report of the Director, Department of Plant Biology, Stanford California. Carnegie Institute of Washington Year Book, 80:59-62.