# Influence of Water Relations and Temperature on Leaf Movements of *Rhododendron* Species[1]

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## ABSTRACT

*Rhododendron maximum* L. and *R. Catawbiense* L. are subcanopy evergreen shrubs of the eastern United States deciduous forest. Field measurements of climate factors and leaf movements of these species indicated a high correlation between leaf temperature and leaf curling; and between leaf water potential and leaf angle. Laboratory experiments were performed to isolate the influence of temperature and cellular water relations on leaf movements. Significant differences were found between the patterns of temperature induction of leaf curling in the two species. Leaves of the species which curled at higher temperatures (*R. catawbiense*) also froze at higher leaf temperatures. However, in both cases leaf curling occurred at leaf temperatures two to three degrees above the leaf freezing point. Pressure volume curves indicated that cellular turgor loss was associated with a maximum of 45% curling while 100% or more curling occurred in field leaves which still had positive cell turgor. Moisture release curves indicated that 70% curling requires a loss of greater than 60% of symplastic water which corresponds to leaf water potentials far below those experienced in field situations. Conversely, most laboratory induced changes in leaf angle could be related to leaf cell turgor loss.

Leaf measurements can be functionally grouped into three basic categories. Movements in azimuth are often associated with solar tracking leaves (4, 29). Changes in leaf angle (in comparison to horizontal) are found in nyctinasty, thigmotrophic movements, leaflet cupping, as well as changes in angle related to water stress or light intensity (23). Curling of leaves is frequently found in dry climate grasses or in evergreens of cold habitats. Leaf movements in one species may include several of these categories as in desert solar tracking species (5) or in *Rhododendron* (16).

Previous studies on leaf movements in desert or mediterranean species have indicated that $\Psi_p$[2] can be the proximate cause of alterations in leaf angle (*e.g.* 4, 5, 8, 23). Leaf cupping in *Lupinus* was associated with leaf $\Psi_p$ (4). Also, a preliminary study of leaf movements in *Rhododendron maximum* indicated that water relations may influence leaf orientation (16) but other microclimatic factors were also important.

Leaf curling in response to cold temperature has been attributed to intercellular freezing (7, 9, 13, 16). In this case, the mechanism of leaf curling is a cellular dehydration due to symplastic water leaving the cells and freezing in the intercellular spaces. As a consequence, the cells shrink in volume, or the

mesophyll space is reduced by ice pulling cells closer, causing leaf curling (13). Similarly, in hot climates, leaf curling is a response to reduced turgor often associated with specific epidermal cells (4, 8, 22). Therefore, it is generally agreed that the leaf curling response is due to reduced cellular turgor as a result of cellular water deficits.

There are several species within the evergreen *Rhododendrons* which exhibit diurnal and seasonal leaf movements (7, 9, 10, 16). There is both a curling motion and alterations in leaf angle (16). Most *Rhododendron* species which exhibit leaf movement are subcanopy evergreen species of temperate forests (7, 9, 10) with relatively large leaves (40–100 cm$^2$). The majority of *Rhododendron* species are montane or of noncontinental distribution in the northern hemisphere. Although this genus has a worldwide distribution (3), and several species exhibit leaf movements, I have found few studies which evaluated the cause of leaf curling (7, 9-11, 16). Leaf orientation is particularly important in *R. maximum* because the photosynthetic apparatus is susceptible to damage from high irradiance (14). Second, *Rhododendron* is one of the evergreen species with large leaves which can survive in mountain regions of the eastern United States. The capacity to change leaf orientation may be the mechanism by which these leaves survive the winter conditions.

The purpose of this study was several-fold. First, I wished to separate the specific influences of temperature and cellular water relations on leaf movements in order to be able to predict field leaf orientation from microclimatic conditions. Second, I will compare the dynamics of leaf curling between two *Rhododendron* species growing in similar habitats. Third, I felt that a study on the individual influences of temperature and water relations on leaf curling would enhance our knowledge of the ecophysiological significance of leaf movements in response to winter conditions in subcanopy environments. My approach to studying the mechanism behind leaf movements in *Rhododendron* was to first make field correlations between climate factors and leaf position or leaf curling. I also studied the specific relationships between leaf orientation (position and curling) and leaf temperature or cell water relations in laboratory experiments using detached leaves.

## MATERIALS AND METHODS

**Species Description.** *Rhododendron maximum* L. and *R. catawbiense* L. are large shrubs which grow in the subcanopy of the eastern deciduous forest of the United States (15). Other *Rhododendron* species of similar morphology and habitat requirements are found in northwest United States, Japan, Soviet Union, Nepal, and China (3). The leaf size of *R. maximum* ranges to 150 cm$^2$ and averages 60 cm$^2$ (17) while that of *R. catawbiense* average 43 cm$^2$. Shoot growth rates are dependent upon a subcanopy light gradient (17) and leaf survivorship varies from 2.5 to 7 years old depending on the irradiance environment (17).

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[2] Abbreviations: $\Psi_p$, leaf turgor potential; $\Psi$, leaf water potential.

**Site Description.** Two research sites were selected to study leaf movements in the field. Both study areas were in one watershed (Poverty Creek) less than 1 km apart in the Jefferson National Forest of Virginia (longitude 80°, 22′, 59″; latitude 37°, 15′, 47″). The canopy vegetation at the first site (deciduous site) was dominated by deciduous trees such as *Acer rubrum* and *Quercus alba*. The canopy vegetation at the second site (Evergreen site) was dominated by evergreen trees such as *Tsuga heterophylla* and *Pinus virginiana*. Climatic conditions at these two sites were similar (16) except that the evergreen site had lower irradiance in all seasons in comparison to that of the deciduous site. Both study sites were near to Poverty Creek and had a slope of 0°. The dominant understory shrub at both research sites was *R. maximum*; however, occasional *R. catawbiense* were also present.

**Field Studies.** Seasonal midday measurements of leaf orientation (angle, curling), and microclimatic conditions were taken semiweekly during 1983 to 1985. Leaf angle was measured with a clinometer in relation to the gravitational vector (90° = vertical, 0° = horizontal). Leaf curling was measured on a relative scale based on the distance between the leaf margins. A flat leaf has the maximum distance between leaf margins ($D_{max}$). As the leaf curls the distance between margins at any time ($D_i$) is less than that of a flat leaf. Therefore the leaf curling index at any time is equal to ($D_{max} - D_i$) ÷ $D_{max}$. Diurnal cycles and seasonal midday values of the same measurements were also taken and reported elsewhere (16). Fifty leaves in four age classes (1, 2, 3, and 4 years old) were labeled in 1983 on three shrubs at each site for measurements of leaf angle and the leaf curling index.

Leaf water potential (Ψ) was measured (pressure chamber), on five leaves in each of the four age classes, immediately after the leaf orientation measurements. Microclimatic measurements were also taken concurrently with the leaf orientation measurements. Temperatures (air, leaf, soil) were recorded with 36 gauge thermocouples. Irradiance on a horizontal surface and at the angle of the leaf was measured with a quantum sensor (LICOR 195 S) and vapor pressure deficit was calculated from air and leaf temperature and RH (Vaisala humicap). Regression analysis was used to determine if significant relationships existed between leaf orientation, Ψ, and the measured microclimatic conditions.

**Laboratory Studies.** Leaf curling response to leaf temperature was examined in the laboratory by placing 10 leaves from three individuals, freshly cut in March from the two *Rhododendron* species (*maximum* and *catawbiense*), in a freezer box at −8°C. A 36 gauge copper-constantan thermocouple was inserted into each leaf. Data was recorded every minute, following insertion into the freezer box, with a Campbell Scientific (CR21) microdata logger. Every 3 to 5 min the curling percentage of the leaves was measured. The data were used to generate the relationship between leaf curling and temperature as well as indicating the time needed for curling induction. Each experiment was repeated five times on leaves which ranged in age from 10 months to 58 months old. The age of the leaves was determined by the method previously reported (17). The freezing point and super cooling point of leaves (13) was determined by the freezing exothermy method (1, 9, 13). Thermocouples (36 gauge) were inserted into leaves freshly cut in March from the field. The leaves were inserted into a test tube, stoppered, and placed in a freezer at −15°C. A stryofoam gasket kept the thermocouple-leaf surface off the wall of the test tube. The leaf temperature was recorded every 15 s to determine the super cooling point and the freezing point (13). Fifteen leaves were studied for each species, including all leaf age categories (10, 22, 34, 58 months).

Pressure volume curves (21, 27) were determined on leaves collected at both research sites. Six to 10 leaves from each age category (10, 22, 34, 58 months) were studied during the winter (February and March). This time period was selected because this is when most leaf curling occurs in the field. Monthly

pressure volume curve determinations are reported elsewhere (14). Several techniques (27) were used. The technique outlined by Tyree and Hammell (27) and Cheung *et al.* (2) was used to evaluate leaf turgor and osmotic potential relationships. In this technique the leaf was sealed in the chamber with the petiole protruding through a rubber stopper. The chamber was lined with moist paper and the petiole was wrapped with parafilm to inhibit water loss. As the pressure was incremented, the exuded water was collected on preweighed absorptant in a vial secured over the cut end. Secondary loss of water from the leaf in the chambers was minimal (less than 2% of the total). However, this technique prohibits measurements of leaf curling or leaf angle because the leaf is always in the chamber. An alternative bench top method (2, 12, 26) was used to evaluate the relationship between leaf curling and leaf Ψ components. The procedure for the bench top method was the following. The equilibrium pressure was measured, then the chamber was pressurized 100 p.s.i. over the equilibrium pressure. When the xylem fluid discontinued coming out of the petiole the chamber pressure was reduced slowly to prevent leaf freezing. The leaf remained out of the chamber for 20 min to equilibrate at the new water deficit. The leaf was then weighed to determine the mass of water lost, and the water potential, over pressurizing cycle was repeated. Leaf curling measurements (as in the field studies) were made just before each equilibrium pressure reading. Leaf-angle was also measured in these leaves by clamping the terminus of the petiole to a board. The angle of the leaf in relation to gravitational vertical could then be compared to protractor marks on the board. The petiole terminus was always held horizontal to gravity by the use of a level and a plumb bob.

In order to predict leaf movements in the field from laboratory-derived relationships, the angle of the branch must be taken into account. The mean branch angle for *R. maximum*, of canopy branches (16) was 68.7 ± 17° (1 SD; $n = 147$) for the deciduous site and 72.8 ± 13.1 ($n = 148$) for the evergreen site. Therefore the mean angular deflection of *R. maximum* canopy branches was 22.3 and 18.2° from vertical. It was necessary to adjust the laboratory derived leaf angle values by the mean field, branch deflection because the laboratory derived angles were determined from leaves with petioles clamped perpendicular to the gravitational vector.

## RESULTS

**Field Studies.** Midday leaf water potentials (midday Ψ) of *Rhododendron maximum* were similar between the two research sites (Fig. 1). However, during the winter months midday Ψ at the deciduous site was significantly lower than the evergreen site.
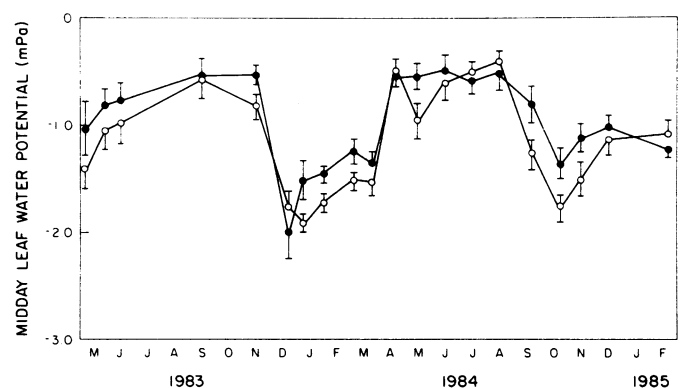


FIG. 1. Midday leaf Ψ of *R. maximum* in two sites. (●), Leaves under an evergreen canopy; (O), leaves under a deciduous canopy. ($n = 25$ per site, per date; error bars represent least significant differences at P ≤ 0.05).

The lowest midday $\Psi$ reached in the winter was between $-1.8$ and $-2.5$ MPa while summer midday $\Psi$ was above $-1.0$ MPa. This region of southwestern Virginia commonly has a dry period in August-September (17). Such a dry period, as reflected in the midday $\Psi$, occurred in 1984 but not in 1983.

During 1983 to 1985, midday $\Psi$ was related to site temperature relationships (air, leaf, soil). The best relationship was between leaf temperature (Fig. 2) and midday $\Psi$. This is consistent with a low temperature driven reduction in $\Psi$ (1, 24). There was no site specific difference in the relationship between midday $\Psi$ and leaf temperature.

Average midday leaf angle was linearly related to the midday $\Psi$ (Fig. 3). There was no difference in the association of midday $\Psi$ and leaf angle when the data are separated by site. However, a majority of leaf angles measured at the deciduous site were more vertical (closer to 90°) than those at the evergreen site, and a majority of midday $\Psi$ values at the deciduous site were lower than those at the evergreen site during the winter (Figs. 2 and 3). On the other hand, there was no relationship between midday $\Psi$ and leaf curling in field populations (data not shown). Previous studies demonstrated that leaf curling of *R. maximum* was closely linked to leaf temperature (16). Zero to 100% leaf curling in field plants occurred between $-2$ and $-4$°C.

**Laboratory Studies.** Leaf curling increased as leaf temperature decreased in both *R. maximum* and *R. catawbiense* (Fig. 4) in
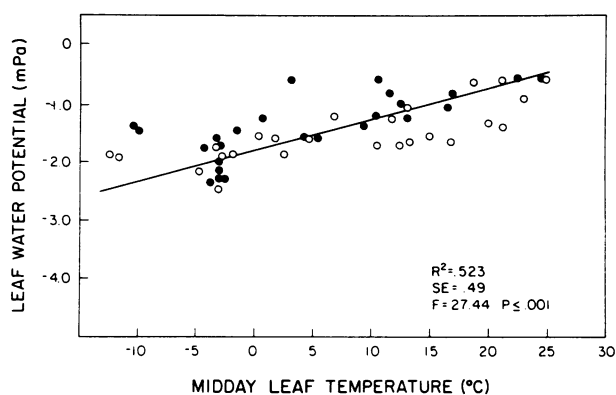


FIG. 4. Relationship between leaf temperature and leaf curling in two *Rhododendron* species, points are averages of 10 measurements. Error bars represent 2 SE.
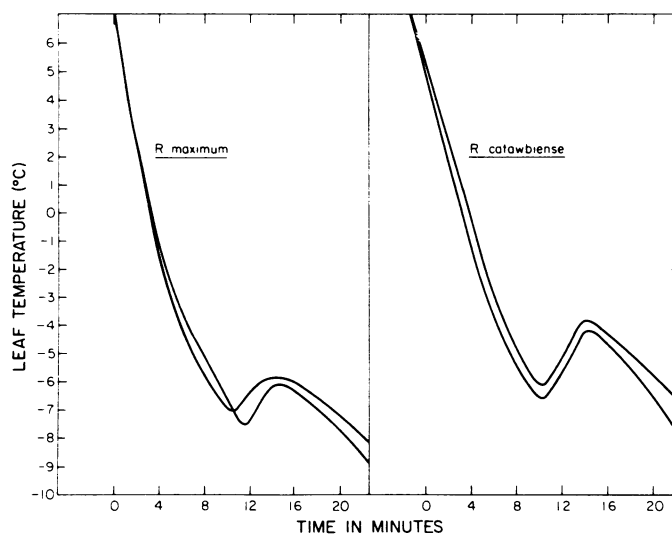


FIG. 5. Representative freezing point determinations (two even-aged leaves) for two *Rhododendron* species.



FIG. 2. Correlation between leaf midday temperature of *R. maximum* and leaf midday $\Psi$ in two field populations during 1983 to 1985. ($\bullet$), *R. maximum* leaves under an evergreen canopy; (O), leaves under a deciduous canopy. Each point is a mean of 25 $\Psi$ measurements and 25 leaf temperature measurements.
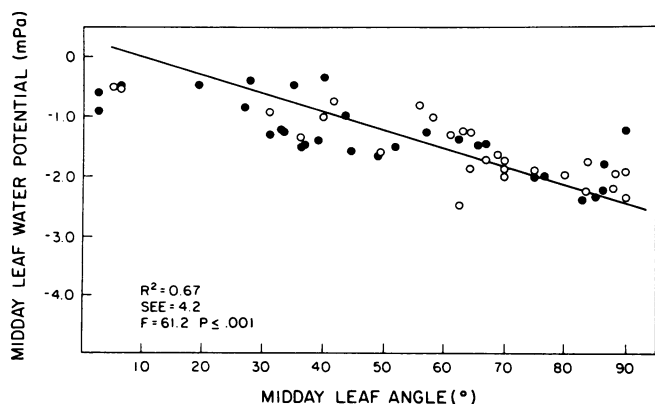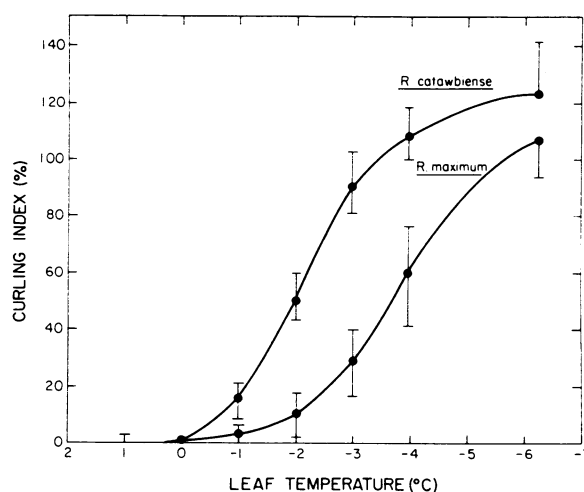


FIG. 3. Correlation between midday leaf angle of *R. maximum* and midday leaf $\Psi$ in two field populations during 1983 to 1985. ($\bullet$), *R. maximum* leaves under an evergreen canopy; (O), leaves under a deciduous canopy. Each point is a mean of 25 $\Psi$ measurements and 50 leaf angle measurements.

the laboratory studies with detached leaves. Leaves of *R. catawbiense* started to curl at higher temperature and curled to a greater extent than leaves of *R. maximum* below $-6.0$°C. The actual curling response occurred over 10 to 20 min in these laboratory experiments which was similar to the time course observed in field measurements of uncurling in *R. maximum* leaves (16). Also, the temperature-curling response for detached leaves of *R. maximum* was very similar to that of field leaves (16).

The average leaf freezing point of *R. maximum* leaves of various age was $-5.9 \pm 0.21$°C which was lower (Mann Whitney U test P < 0.01) than $-4.3 \pm 0.14$°C measured for *R. catawbiense*. Similarly, the supercooling points were lower for *R. maximum* $-6.9$°C $\pm$ 0.4 than that of *R. catawbiense* $-6.0 \pm 0.7$; however, not significantly (Mann Whitney U test P < 0.01, $n = 15$). In both cases the freezing point and supercooling point (Fig. 5) were below that which causes leaf curling (Fig. 4).

Pressure volume curves performed on different aged leaves of *R. maximum* from both sites, taken over the season were not significantly different (Fig. 6). Also, pressure volume curves done by the bench top or enclosed technique yielded similar results (data not presented). The leaves lost turgor ($\Psi p = 0$) between
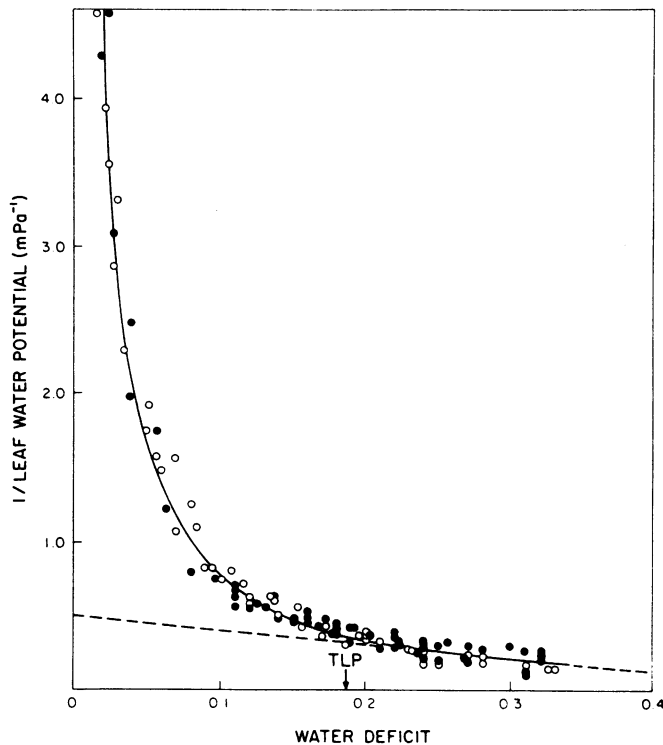
FIG. 6. Pressure-volume curves for 12 leaves of *R. maximum* from two research sites. Leaves used were from 1 to 5 years old. The symbols refer to the composition of the canopy over the *R. maximum* leaves (●, evergreen canopy present; ○, deciduous canopy present). TLP, turgor loss point; (---), osmotic regression line $(1/\Psi = WD [-0.096] + 0.051;$ $R^2 = 0.99)$.
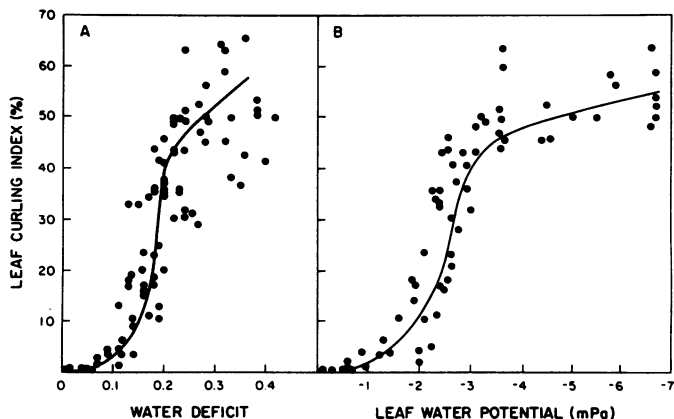


FIG. 7. A, Relationship between leaf curling index and leaf water deficit in detached leaves of *R. maximum*; B, relationship between leaf curling index and leaf $\Psi$ in detached *R. maximum* leaves. Ten leaves were used for each panel from two rsearch sites ($n = 20$ leaves).

0.18 and 0.20 water deficit (1-RWC) which corresponds to a $\Psi$ of $-2.94$ MPa ($\pm0.15$; 1 SD). Osmotic potential at full turgor averaged $-1.92$ MPa ($+0.19$).

Leaf curling index was related to water deficit and $\Psi$ of *R. maximum* as derived from bench top pressure volume curves (Fig. 7). There was no difference in these relationships between leaves from the two research sites. A linear relationship could be derived from the comparison of leaf curling index and leaf water deficit; however, below a leaf water deficit of 0.2 an exponential relationship (exponential regression model; $R^2 = 0.52$, P < 0.001) was observed. There was also an exponential relationship (exponential regression model; $R_2 = 0.56$, P < 0.001) between leaf

curling index and $\Psi$ until a $\Psi$ of approximately $-3.00$ MPa was reached (Fig. 7). At $\Psi$ values below $-3.00$ MPa the rate at which the leaf curling index increased with lowering $\Psi$ was reduced in comparison to that above $-3.00$ MPa.

Leaf curling index was exponentially related (exponential regression model; $R^2 = 0.53$; P < 0.001) to leaf turgor potential (Fig. 8). However, the maximum curling percentage of all leaves measured at the turgor loss point was 45% or less curled.

Leaf angle from the horizontal increased with decreasing leaf $\Psi$ (Fig. 9) for detached leaves as well as field plants (Fig. 3). Unlike the situation with leaf curling, most of the change in leaf angle (40°) occurred before the turgor loss point. Following turgor loss only slight (7°) change in leaf angle occurred.

Leaf angle and leaf curling were predicted from field $\Psi$ values and laboratory derived associations between $\Psi$ and leaf position. Predicted values were significantly different from observed values for leaf curling ($\chi^2 = 2909$). However, leaf angle adjusted for branch deflection, as predicted from the laboratory association with $\Psi$ was similar to that of field measurements ($\chi^2 = 622$; P < 0.01).

## DISCUSSION

Leaf movement of *Rhododendron maximum* and *R. cataw-biense* were found to be related to both temperature and leaf water potential in field and laboratory studies. The autocorrelation between leaf temperature and leaf water potential prohibited the field evaluation of the specific influences of temperature or water potential on leaf curling or leaf angle. At constant temper-
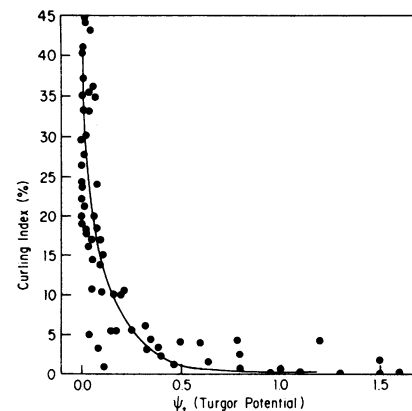


FIG. 8. The relationship between leaf curling index and leaf turgor potential in detached *R. maximum* leaves.
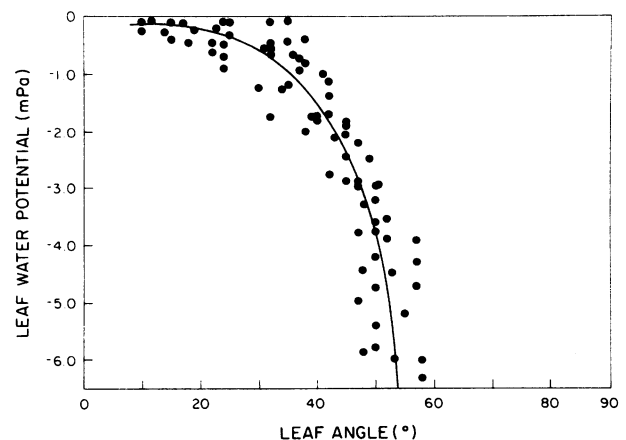


FIG. 9. The relationship between leaf $\Psi$ and leaf angle of detached *R. maximum* leaves ($n = 20$ leaves from two research sites).

ature, the leaf angle of detached leaves was related to leaf water potential, and this relationship could be used to predict field leaf angle from leaf water potential measurements *in situ*. Leaf angle has been shown to be controlled by leaf water potential in many other species (*e.g.* 4–6, 8, 22).

There have been many studies which have evaluated the causes of leaf curling in response to drought or low temperatures (21). In general, the cause for leaf curling is reduced turgor potential either by desiccation or by freezing induced desiccation of the symplasm (10, 13, 22). To separate the direct influences of desiccation or intercellular freezing on tissue water relations, the curling response must be investigated at constant temperature during desiccation and at constant tissue hydration during temperature variation.

The relationshp between leaf curling and leaf water potential was inadequate to predict leaf curling of *in situ R. maximum* leaves. Leaves in the field never experienced leaf water potentials below −3.0 MPa; therefore, they had positive turgor during all measurements. The laboratory relationships between leaf curling and leaf water potential, turgor potential, or water deficit would predict little to no leaf curling under field conditions; however, significant curling of *in situ* leaves occurred.

The relationship between leaf curling and leaf temperature from laboratory studies on detached leaves was the same as that found for *in situ* leaves in a previous study (16). Therefore, leaf curling may be related to internal redistribution of water as a sequence of intracellular freezing rather than bulk leaf turgor potential. If such a redistribution of water is the cause of leaf curling, then this occurs at temperatures above the leaf freezing point. The freezing point and the supercooling point of leaves from both *R. maximum* and *R. catawbiense* were several degrees below the temperature which caused 100% leaf curling. Also, the influence of temperature on the water potential of the symplastic water (at the temperature causing curling, −1 to −4°C) are not likely to cause turgor loss at the osmotic concentrations of these cells when fully hydrated (18, 28). In the event that the leaf temperature directly caused cell turgor loss, the influence of turgor on leaf curling could not explain the magnitude of leaf curling. Therefore, leaf curling in *Rhododendron* may be a response to intercellular freezing, which occurs above the leaf freezing point, causing a change in the ratio of symplastic to apoplastic water. However, the resultant loss of turgor alone cannot explain the magnitude of leaf curling. The curling response may relate to the interaction between intercellular freezing and the unusual vascular anatomy of leaves (ET Nilsen, unpublished data).

Seasonal and diurnal changes in leaf orientation are suggested to have ecophysiological significance. In the case of desert species, or species of other arid or hot environments, vertical leaf orientation serves to improve water use efficiency and net photosynthetic gain during periods of water stress (*e.g.* 5, 26) or the vertical leaf angles and leaf curling reduces the energy load on the leaves which maintain a favorable leaf temperature (18). The adaptive significance of leaf movements in *Rhododendron* cannot be equated with that for plants in hot or arid environments. First, leaf angle was not immediately related to photosynthesis because the stomata were closed during the winter (16) particularly during the time of mimimum leaf angle and maximum leaf curling. Second, the subcanopy environment is characterized by low irradiance and cold temperatures which are opposite to the conditions stimulating leaf movement in species of arid or hot climates.

Many authors have suggested that leaf curling in response to freezing temperatures serves to protect the leaves from dessication (7, 9–11, 21). However, the leaves of *R. maximum* are not losing water during the winter months because the stomata are closed, there is little evaporative water loss through the cuticle,

and there are only small decreases in leaf water potential (16). More likely, one could speculate that the curling and angle changes of leaves in winter relate to the susceptibility of the chloroplasts to damage during cold temperatures and high irradiance (*e.g.* 20). Several studies have shown that photoinhibition of electron transport and Chl photooxidation is enhanced at cold temperatures (19, 20, 25). In particular, there is evidence that photooxidation and photoinhibition are likely with *R. maximum* in the absence of leaf movement. First, the leaves are subjected to the highest most prolonged radiation during the winter because the forest canopy is absent. Second, our studies on acclimation to irradiance environments indicate photoinhibition and damage to chloroplast membranes under moderate or high irradiance (Lipscomb, 1986; ET Nilsen, DA Stettler, unpublished data). Leaves which are prevented from moving during the winter suffer photooxidation of Chl and reduced quantum yield in comparison to control leaves (ET Nilsen, Y Bao, unpublished data).

In conclusion, these field and laboratory studies indicate that changes in bulk-leaf $\Psi$ can cause some leaf curling and leaf drooping in *R. maximum*. The leaf angle of *R. maximum* is probably controlled by petiole hydration. Pressure volume curves of bulk leaf water potential do not accurately address the water relations of the petiole because the petiole is not receiving the pressure of the chamber and thus is not necessarily in equilibrium with the leaf water deficit. Also, the heavy cuticle over the leaf epidermis is minimal over the petiole (22). Therefore, water balance of the large parenchyma cells characteristic of these petioles (22) is controlled by xylem water availability and the atmospheric to petiole vapor pressure deficit. However, bulk-leaf $\Psi$ is not the proximate cause of leaf curling in field populations. This does not rule out internal leaf $\Psi$ gradients as the cause of leaf movements. Such gradients, established by changing cation distribution or intercellular freezing, have been found to be the major cause of leaf curling in leaves (23). Further studies on leaf cytology are in progress in an effort to precisely identify the physiological cause of leaf movements.

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