

Why Do Rhododendron Leaves Curl?

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A physiological ecologist looks at the significance of temperature-sensitive leaf movements in Rhododendrons.

For more than two hundred years, the genus *Rhododendron* has been a focal point for scientists and horticulturists. During the mid-nineteenth and early-twentieth centuries, a fascination with the genus stimulated many botanists to visit its center of diversity in remote parts of Burma and China in search of new species. The renowned botanist J. D. Hooker of Kew noted the leaf curling and

drooping of *Rhododendron arboreum* in his *Himalayan Journals* of 1855, and explorers such as E. H. Wilson, F. Kingdon-Ward, and R. Farrar made frequent notes on the temperature-sensitive (thermotropic) leaf movements in rhododendron. In addition, both amateur and professional rhododendron enthusiasts have made countless reports of leaf curling in various rhododendron species.



Rhododendron maximum in winter. Photo by Rácz and Debreczy.

Leaf movements in plants were first categorized by Charles Darwin in 1880 in his groundbreaking book *The Power of Movement in Plants*. Darwin pointed out that many plant parts, and particularly leaves, move in response to a number of extrinsic (environmental) and intrinsic (physiological) factors. The most important extrinsic factors are light intensity (phototropic), light direction (heliotropic), water content (hydrotropic), and temperature (thermotropic). The most frequently observed case of thermotropic movements occurs in plants in hot, dry environments where leaves move upward and become vertical to avoid excessive light absorption. The thermotropic leaf movements of *Rhododendron* are unusual because these movements are in response to cold temperatures and the leaves become pendent rather than vertical.

Research on the thermotropic movements of rhododendron leaves began in 1899 with the work of Harshberger. In 1933, a Japanese scientist, Y. Fukuda, studied the leaf-curling patterns of *Rhododendron micranthum*, making the important observation that its leaves could be kept from curling if he covered them with snow, thereby insulating them from cold air temperatures. Based on these observations, Fukuda concluded that the thermotropic leaf movements were correlated with leaf rather than air temperature.

My research on thermotropic leaf movements of *Rhododendron* began in 1984 with three main questions: (1) What are the specific seasonal and daily patterns of leaf movements, and how are they affected by climatic factors? (2) What is the physiological cause of thermotropic leaf movements and how does it relate to the leaf ultrastructure? (3) What is the adaptive significance of leaf movements to rhododendrons in their native habitats?

Before I began my research project, I was well aware of the popular dogma concerning the significance of leaf-curling and drooping movements, which claimed that this phenomenon was an accurate air temperature sensor. Frequently, I heard the statement: "When I look out of my kitchen window, I

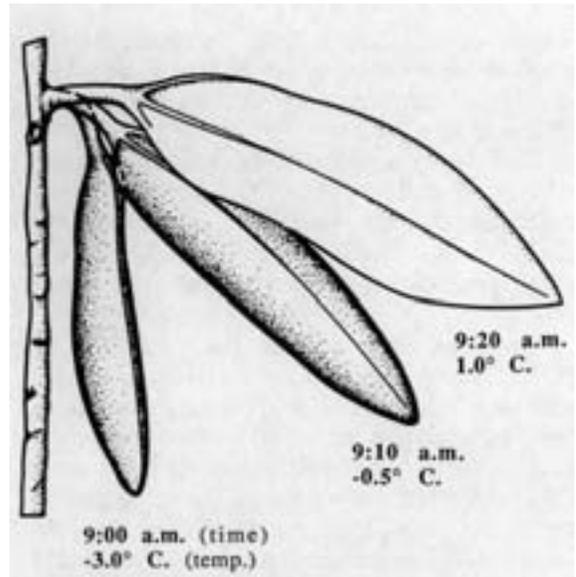


Figure 1. A diagrammatic representation of the leaf movements in *Rhododendron maximum*. Changes in leaf orientation move from curled and pendent at 9:00 a.m. to flat and more horizontal by 9:20 a.m.

know how cold it is by looking at my rhodo leaves." Most authors believed that this curling served one of two purposes: either it prevented water loss in a dry winter environment where the soil water was frozen and unavailable; or it protected the leaves from damage by repetitive freezing and thawing.

Six Possible Theories

My training in plant-stress physiology allowed me to propose six possible scenarios for the adaptive significance of thermotropic leaf movements in rhododendron. I will discuss each possibility in turn, along with supportive or contradictory evidence from my research program.

Evolutionary Relict Theory. This theory is the hardest to support or refute because it is based on a long-term evolutionary perspective. Theoretically, thermotropic leaf movements could have evolved in response to climatic conditions in the geological past, perhaps during the ice ages of the Pleistocene. Current interglacial conditions differ from those that led to the evolution of these leaf movements.

Thus thermotropic leaf movements in rhododendron are a relict and have no adaptive significance to plants under the current climatic conditions.

This theory is plausible because *Rhododendron* is an ancient genus, with a fossil history extending through several glacial and interglacial periods. In addition, this species is long-lived and clonal, two characteristics that reduce the rate of evolutionary change.

One argument against the evolutionary relict theory is that those rhododendron species that demonstrate cold tolerance are those species with the leaf movements. For example, *R. ponticum* and *R. macrophyllum* show little if any leaf movement in the same garden in Virginia, and these two species are not cold hardy. On the other hand, two extremely hardy species, *R. maximum* and *R. catawbiense*, show prominent leaf movements. In addition, my experiments on the physiological causes of leaf movements clearly indicate that they require no metabolic energy and that they occur *after* complete turgor loss. Since

these movements do not require energy, there is no reason why evolutionary processes would select against them.

Mechanical Theory. The leaves simply droop to protect themselves from mechanical damage due to the accumulated weight of rime, ice, and snow. Rhododendron leaves are subject to a considerable buildup of ice, up to 1.5 centimeters thick, during winter months. Even under these conditions, however, the leaves are tenaciously held to the branches, and I have never observed them damaged by ice buildup. Quite clearly mechanical protection is not a likely explanation for the adaptive significance of thermotropic leaf movements.

Desiccation Theory. Many reports suggest that thermotropic leaf movements are a mechanism to prevent desiccation during cold periods. In fact, until recently this has been the main explanation for the significance of rhododendron leaf movements. According to this theory, the action of curling is thought to reduce the transpiring leaf area by creating a moist microsite around the stomata of the lower leaf surface to reduce water loss and protect against desiccation.

Several lines of evidence can be brought against this theory. First, the leaf stomata are not open during cold periods. In fact, they *cannot be induced* to open during the cold months. When stomata are closed, the internal leaf water is unaffected by changes in atmospheric humidity. Therefore, leaf curling can have no impact on the leaf's water balance. The fact that there is only a very small evaporative demand placed on the leaf during cold weather further suggests that very little water is conserved by the leaf-curling behavior.

Second, the waxy cuticular layer on the upper surface of the leaf is relatively thick and effectively inhibits the flow of water through the epidermal cells. Theoretically, tension placed on the cuticle layer by curling could induce fissures in this cuticle and actually increase the loss of water from the epidermis.

Third, I have taken many thousands of rhododendron leaf-water potential measure-

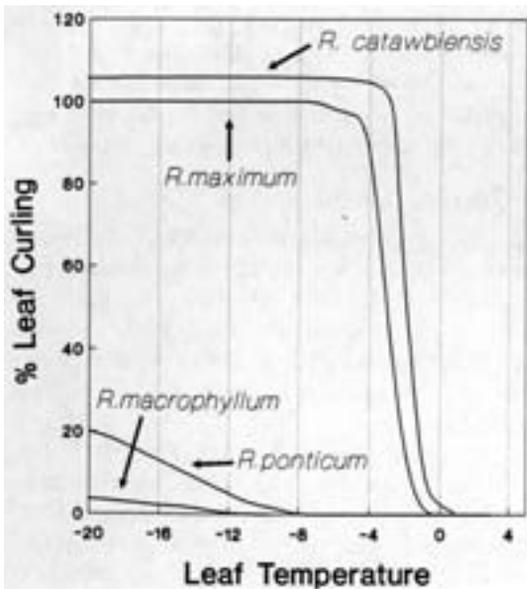


Figure 2. The relationship between leaf curling and leaf temperature for four *Rhododendron* species growing in a common garden.

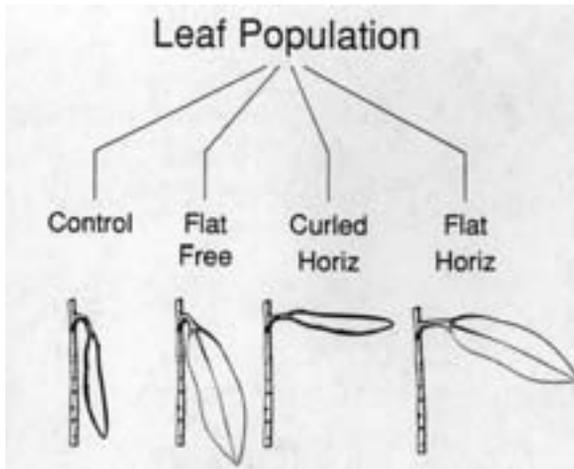


Figure 3. A diagrammatic representation of leaf treatments used to determine the adaptive significance of leaf movements in the genus *Rhododendron*.

ments during the winter and the summer in Virginia. These data provide no indication of water stress during the winter months. I have found that leaf-water potentials (an index of the energy in water in the leaf) are directly related to temperature. When I measure the water potential of a leaf on a cold day, then let the leaf warm up and measure again, the warmed measurement will be larger than the cold measurement even though there has been no change in the leaf-water content. This means that the low water potentials measured by other workers in the winter are not the result of desiccation, but rather the direct influence of temperature on the leaf water.

As a final point, the desiccation theory depends upon a limited availability of water from the soil as a consequence of its being frozen. The evidence does not support this notion because leaf movements in *rhododendron* begin months before the soil freezes. Also, the fact that leaf curling can be repetitively stimulated on detached leaves indicates no influence of the roots on the leaf curling or uncurling processes. The observation that curling fails to occur when the leaf is covered with snow further contradicts the desiccation theory. If leaf curling were dependent upon desiccation, the presence of snow on the leaf

should have no impact on the response of the leaf to the lack of water moving up from the root zone.

Heat Balance Theory. The thermotropic leaf movements of many desert plants, in which the leaves move upward into a vertical position, serve the purpose of reducing leaf temperature by reducing the total quantity of light absorbed by the leaf. Thermotropic leaf movements in *rhododendron* are different because these movements occur in response to cold rather than hot temperatures. Leaves that are horizontal and flat have a greater exposure to the sky than those that are pendent and curled. Energy budget calculations made with a model *rhododendron* leaf indicate that a horizontal leaf could have a leaf temperature 3 to 6 degrees Centigrade lower than the air temperature while the pendent and curled leaf temperature will match the air temperature. Temperatures between -25 and -35 degrees C. are usually considered lethal to Appalachian *rhododendrons*. Air temperatures in the mountains frequently reach -15 to -17 degrees C., suggesting that leaf temperatures could come close to the lethal values if leaf curling did not occur.

Interpreting the heat balance data is further complicated by the type of canopy trees shading the *rhododendron* plant. The presence of a thick deciduous canopy or a moderate evergreen canopy would cut down on heat loss. One might compare the canopy to a blanket for the subcanopy plants. In several wild *rhododendron* populations, with and without a forest canopy cover, I forced leaves to remain flat and horizontal during the winter months. Repetitive measurements of leaf temperature throughout several nights at all sites never found more than a 4 degree C. difference between leaves with or without curling and drooping movements. Actually, only the leaves on plants without an overhead canopy showed more than a one degree difference between the flat horizontal leaves and the night air temperature. This small effect of leaf movement on leaf temperature is not likely to be significant in preventing leaf damage due to freezing. In general, the canopy over the

rhododendron plants has a strong ameliorating effect on winter nocturnal leaf temperatures, and leaf movements have little to no effect in most of the wild rhododendron habitats on the East Coast.

Photoinhibition Theory. A very active field of research in plant-stress physiology is the influence of multiple environmental factors on plant physiology. One of the first case studies involved the interaction of cold temperatures and bright light on leaf physiology. These studies demonstrated that leaf cell membranes are susceptible to damage by intense radiation when they are cold. The membranes most susceptible to damage are those in the chlorophyll-rich chloroplasts. In particular, the membranes supporting photosystem-2 (a group of proteins that captures light energy and converts it to chemical energy) are most susceptible. The damage occurs during cold leaf temperatures when there are no outlets for the light energy captured by photosystem-2. In this situation the protein-membrane association between photosystem-2 and the chloroplast membranes is disturbed, resulting in a physiological dysfunction termed *photoinhibition*.

The quantity of light absorbed by the leaf during the winter is the critical determinant of the potential for photoinhibition. Irradiance conditions under a canopy of leafless trees are higher in the winter than in the summer, which means that rhododendron plants experience the highest radiation of the year during the coldest weather. Under these conditions, leaf drooping and curling act to reduce the quantity of light impinging on the leaf during the coldest temperatures, thereby preventing or limiting photoinhibition.

I tested the possibility of cold-induced photoinhibition by high light in my leaf manipulation studies. My measurements of leaf photosynthesis decreased by as much as 50 percent in leaves prevented from moving during the winter. In addition, diagnostic techniques using the interaction between light intensity and photosynthesis clearly pointed to photoinhibition as the root cause of the decrease in photosynthesis.

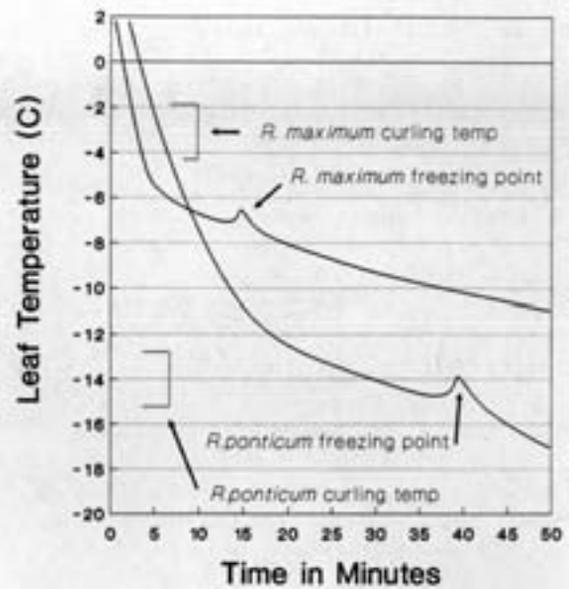


Figure 4. Thermal emission (freezing point) and the temperature range for leaf curling of *Rhododendron maximum* and *Rhododendron ponticum*.

During this leaf manipulation study, it was significant that leaf curling had little influence on the potential for photoinhibition. Rather, it was the drooping of the leaves that protected the leaves from photosynthetic damage. Indeed, leaf angle and leaf curling should be treated as distinct phenomenon. Leaf curling responds directly to temperature, while leaf angle responds to the water potential of the petiole. To be accurate, one should separate these movements in terms of both their physiological cause and their adaptive significance.

Freezing damage theory. Along with many others, Jacob Levitt has demonstrated that most of the damage caused by leaf freezing is a result of ice crystals piercing cellular membranes, followed by too rapid a rate of rewarming after freezing. The field of cryogenics has clearly demonstrated that tissues are best preserved by rapid freezing and slow rewarming. Leaf freezing points of rhododendron in the Appalachian mountains are -8 degrees C. on the average. Of course there is variability

between species and times of the year, but this amounts to a range of less than 2 degrees C. Winter temperatures in these mountains are normally -10 degrees C. or lower. Consequently, the rhododendron leaves freeze on most evenings. Daily temperature is normally near -2 degrees C., so the leaves also thaw daily. *Rhododendron* is one of the few evergreen genera on the East Coast that has the capacity to tolerate frequent freeze and thaw cycles. Energy budget models (as well as our field measurements) indicate that horizontal flat leaves will thaw more rapidly than the pendent curled leaves. In particular, leaf curling will reduce the leaf area exposed to light and thereby slow the rate of thaw, protecting the leaf from freezing damage.

Summary

Our research on leaf movements in *Rhododendron* over the past five years has answered several questions. Leaf curling and leaf drooping are distinct behaviors with different responses to climatic factors and possibly different adaptive significances. Leaf angle is controlled by the hydration of the petiole, as affected by water availability from both the soil and the atmosphere and by air temperature. In contrast, leaf curling is a specific response to leaf temperature, and the leaf hydration state has little effect. The physiological cause of leaf curling is not well understood, but the mechanism must lie in the physiology of the cell wall or regional changes in tissue hydration.

The thermotropic drooping of rhododendron leaves most likely serves to protect them from membrane damage due to high irradiance and cold temperatures during the long Appalachian winters. In addition, the thermotropic leaf curling in *Rhododendron* may serve to prevent damage to cellular membranes during the process of daily rethawing that often occurs during the early morning. Our initial results with species comparisons indicate that leaf movements may be an important factor determining cold hardiness in *Rhododendron* species.

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