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"SUN LEAVES" AND "SHADE LEAVES": DIFFERENCES IN CONVECTIVE HEAT DISSIPATION

Steven Vogel
Department of Zoology, Duke University, Durham, North Carolina

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Abstract. Temperatures of radiantly heated sun and shade leaves of white oak (*Quercus alba* L.) were measured in a low-speed wind tunnel. In either still air or a gentle updraft the difference between ambient and leaf temperature is about 20% less for the sun leaves than for the shade leaves. Consequently the former are more effective heat dissipaters.

In many large broad-leafed trees such as oaks and maples, leaves from the top of the tree or from an exposed southern position (so-called "sun leaves") differ markedly in structure from those of the interior of the crown or the northern periphery, the "shade leaves" (see, for example, Hanson 1917). In general, the sun leaves are smaller, thicker, hairier, and more deeply lobed than the shade leaves; in short, the sun leaves are more like those of plants characteristic of dry habitats. One inference is that leaves which develop in the sun are better adapted to withstand a scarcity of water. This supposition has proven difficult to reconcile with observations that sun leaves, with up to 12 times the number of stomata per unit area, have a greater capacity for transpiration than do shade leaves (Shields 1950). Under some seemingly normal circumstances, the more "xeromorphic" sun leaves do transpire more rapidly (Shields 1950). Perhaps there are factors other than the availability of water to which the structural differences between sun and shade leaves represent adaptations.

A broad leaf in bright sunlight and nearly still air may be 10°–20°C warmer than its surroundings (Platt and Wolfe 1950, Loomis 1965, Gates, Tibbals, and Kreith 1965); thus on a warm day it can approach its upper thermal limit of about 55–60°C. The differences in their locations on the tree should render the sun leaves more susceptible to overheating than the shade leaves; consequently the former should be better adapted to dissipate large amounts of heat. Indeed, the structural differences between the two appear appropriate for facilitating greater convective heat dissipation in sun leaves. The surface of a smaller, more deeply lobed leaf will be, on the average, a shorter distance from a free edge. Since the boundary layer thickness increases with distance from an edge, it will have a thinner boundary layer of heated air. A thicker leaf might also be capable of more rapid conduction of heat from the center of the blade out to an edge. Thus, under circumstances of equivalent input of radiant energy, sun leaves should remain cooler than shade leaves. This possibility was tested as follows.

Sun and shade leaves of the white oak (*Quercus alba* L.) were collected from trees along the roads on the Duke University campus and used within 2 hr. The initial attempts to heat a leaf with radiant energy heated the chamber more than the leaf, demonstrating the limited and highly selective absorptivity of leaves emphasized by Gates (1962). To circumvent this problem and to ensure a common absorptivity for sun and shade leaves, the upper surfaces of all leaves were sprayed with quick-drying flat black paint (Tester's Spray Pla #49). This coating increased leaf mass less than 10%.

Temperature measurements were made on single leaves in the working section of a low-speed vertical wind tunnel, with each leaf oriented as nearly horizontally as possible. The leaf was heated through a plexiglas window by a 650-w "movie light" (G.E. DVY) mounted outside the tunnel and controlled with a variable autotransformer. The lamp illuminated the leaf from about 45° above horizontal, so the leaf itself shaded a small bead thermistor in contact with the center of its undersurface. Tunnel air velocity was determined with a hot bead thermistor anemometer, the latter previously calibrated on a whirling arm. The supply voltage to the lamp was varied so that leaf temperature was recorded at a series of light intensities which heated the leaf to temperatures spanning a range of 25°–43°C (ambient = 23° ± 0.2°C). A steady state was established 60–90 sec after a change in the level of illumination.

No water was provided for leaves in the tunnel. Water loss during the measurements amounted to less than 1% of their weight; heat loss through evaporation was estimated to be less than 5% of convective dissipation. Thus any short-term physiological adjustments within the leaves were probably reduced to minor proportions.

Paired measurements of the temperature of sun and shade leaves at various levels of illumination are plotted in Fig. 1. Clearly the data do not fit the 45° line representing equal temperatures for the two morphological types; the difference between ambient and leaf temperature is about 20% less for the sun leaves than for the shade leaves in either still air or a gentle upward current.

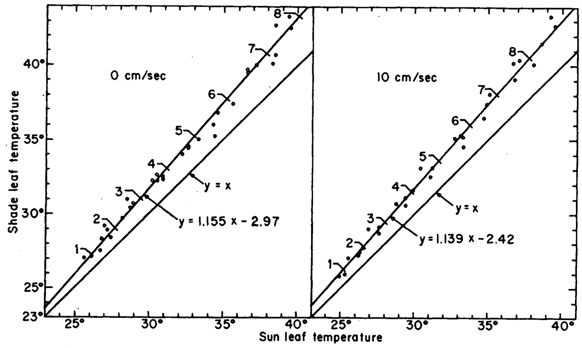

FIG. 1. Sun- and shade-leaf temperatures from measurements on five pairs of white oak leaves at 0 and 10 cm/sec air speed. The numbers marked on the linear regression lines indicate levels of illumination (arbitrary units), permitting comparisons between the two air speeds.

In short, the sun leaves are significantly better heat exchangers.

Gates et al. (1965) have estimated that a wind of 1 mph (44 cm/sec) will halve the difference between ambient and leaf temperature, and thus a problem of overheating will exist only under very nearly calm conditions. Whether a leaf on a tree ever simultaneously encounters both still air and full sunlight is questionable—at worst it should still be exposed to a "convective chimney" resulting from the free convection of neighboring leaves. Hence it is significant that the differences in heat dissipation noted above occur in a slight updraft as well as in still air. The 10 cm/sec air current cooled both sun and shade leaves about 17%; however, under natural circumstances, the temperature of the "convective chimney" itself would have to be considered.

Broad leaves exist in a bewildering variety of shapes. Perhaps certain of their features are adaptations directed toward increasing convective cooling. Knoerr and Gay (1965) found that heat loss by free convection in real leaves could reach twice that predicted by equations developed for free convection from flat rectangular plates. Measurements on model leaves (*unpublished data*) indicate that even shade leaves are better suited for convective heat dissipation than are circles of the same area. It is certainly incorrect to regard the problem of overheating as the sole factor to which leaf shapes represent adaptations. But the difference in heat dissipation between sun and shade leaves directs attention to what may be a definitive feature of large species characteristic of forest climax vegetation. Through ontogenetic control of leaf structure, an individual may first be a successful understory plant and later a proper part of the forest canopy.

The present measurements come from preliminary experiments in a more general study of the thermal and aerodynamic properties of leaves, which has been supported by NIH Biomedical Sciences Support Grant R-01-GM-1222 and NASA University Program Grant NGR 34-001-005.

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