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LEAF SURFACE WETNESS AND GAS EXCHANGE IN THE POND LILY *NUPHAR POLYSEPALUM* (NYPHAEACEAE)¹

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As part of a continuing study of the effects of leaf surface wetness on gas exchange, the occurrence of leaf surface wetting by dewfall and associated effects on photosynthesis were evaluated for floating and aerial leaves of the pond lily *Nuphar polysepalum* Engelm. Because of nighttime radiation exchange with a cold sky, high humidity, and the presence of adaxial stomata, we predicted that pond lily leaves would be particularly susceptible to wetting events such as dewfall. A substantial reduction in net photosynthesis (up to 20%) occurred for leaves that were experimentally misted to simulate leaf wetting by dewfall. Aerial leaves remained below dewpoint temperatures for long periods on clear nights. However, floating leaves rarely approached dewpoint temperatures at night because minimum nighttime temperatures of leaves were up to 10°C warmer than air temperature. Thus, floating leaves of *N. polysepalum* did not experience dew formation primarily because of strong thermal coupling to a substrate (water) that was much warmer than air temperature at night. This coupling to a warmer substrate prevented a potentially strong inhibition of photosynthetic CO₂ exchange the following morning.

Leaf surface wetness is a common phenomenon for plants in a wide variety of habitats. There has been a long-standing interest in the interaction of leaf surfaces with liquid water. Past studies have considered relationships between leaf wetness and pathogen infection (Reynolds et al., 1989), pollutant deposition (Massman et al., 1994) and nutrient leaching (Tukey, 1970). Yet, there are few accounts of the frequency and duration of leaf surface wetness among native plants in natural habitats (Brewer, 1993).

The physiological significance of leaf wetness stems from the fact that CO₂ diffuses ≈10,000 times more rapidly through air than water (Weast, 1979). Many terrestrial plants commonly experience leaf surface wetness for extended periods due to rainfall, dewfall, cloud mist, and fog (Smith and McClean, 1989; Brewer, 1993). Increased water repellency of plant leaf surfaces may be an important adaptive avenue in terrestrial plant evolution, as suggested by Smith and McClean (1989) and Brewer, Smith, and Vogelmann (1991). High transport resistance to CO₂ diffusion through water may also have been important in the evolution of floating leaves of aquatic plants. Higher photosynthetic rates clearly are possible for aerial leaves compared to submerged leaves of such plants (Madsen and Sand-Jensen, 1991).

Floating and aerial leaves of aquatic plants may be particularly susceptible to leaf wetness. Incidence of dewfall may be particularly common because of their close proximity to water, high air humidity, and their exposure to cold nighttime skies (Brewer, Smith, and Vogelmann,

1991; Brewer and Smith, 1994). Also, functional stomata are typically restricted to the adaxial surface for floating leaves of many species (Hutchinson, 1975). Wave action due to wind may also be a frequent source of leaf wetness. Features such as a waxy cuticle (Sculthorpe, 1967), dense surface trichomes (Weir and Dale, 1960; Kaul, 1976), and surface roughness (Kaul, 1976) have been postulated as adaptations to prevent excessive wetting of leaves.

As part of a continuing study of the importance of leaf surface wetness to gas exchange physiology, we examined floating and aerial leaves of the yellow pond lily (*Nuphar polysepalum* Engelm.). The purpose of this study was to evaluate the susceptibility of floating and aerial leaves to leaf surface wetting. Because of high ambient humidity and high nighttime exposure to cold skies, we hypothesized that pond lily leaves would be especially susceptible to natural wetting events such as dewfall. Moreover, these leaves would be particularly susceptible to water film formation and curtailed CO₂ exchange because they are hyperstomatous (stomata only on the adaxial side of the leaf).

MATERIALS AND METHODS

Study site and plant material—Studies were conducted on *Nuphar polysepalum* Engelm. (yellow pond lily) in a small pond in the Stillwater Park area of the Medicine Bow Mountains in southeastern Wyoming, USA (41° N, 106° W). The pond is at an elevation of ≈2,900 m in a shallow basin surrounded by lodgepole pine (*Pinus contorta* Dougl. ssp. *latifolia* Engelm.). Water depth was typically less than 1.5 m, and the bottom was soft and covered with organic material. The ice-free period extended from early May through mid-October. Floating pond lily leaves emerged from the pond in late May and early June. By July, pond lilies floated in a single layer nearly covering the surface of the pond and aerial leaves were abundant. Flowering began in July and lasted until mid-August. By mid-August, leaf senescence had begun, followed by complete senescence in late September when most of the her-

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baceous vegetation surrounding the pond had died or was dormant.

Leaf surface characteristics—Morphological and anatomical characteristics known to influence leaf wettability were measured for both floating and aerial leaves. These characteristics included leaf surface wettability and water droplet retention. We also measured stomatal density (stomata/mm²). The degree of water repellency of the leaf surface was determined by measuring the contact angle (θ) of a 5- μ l droplet placed upon the leaf surface with a micropipette (Adam, 1963). The angle, θ , is formed by the line drawn through the point of contact between the droplet and the leaf surface and tangent to the droplet (Brewer, Smith, and Vogelmann, 1991). For all leaves, θ was measured on horizontally positioned leaves. Five replicates were measured for each of 15 leaf surfaces on both floating and aerial leaves. Leaves with $\theta < 110^\circ$ are generally considered wettable, while $\theta > 130^\circ$ are considered nonwettable (Crisp, 1963).

Droplet retention was measured by placing a 0.05-ml droplet on a horizontal leaf surface and measuring the angle of leaf inclination at which the droplet first began to move. Angular values $>60^\circ$ indicate a tendency to retain droplets. Five replicates per leaf surface were measured for 15 leaves of both aerial and floating leaves. Stomatal counts were made using surface impressions (enamel) of adaxial and abaxial leaf surfaces (Neill, Neill, and Frye, 1990). Stomatal density was estimated by counting the number of stomata within a micrometer grid (0.15×0.15 mm²). Five replicates on 15 leaves were counted for both floating and aerial leaves.

Microclimate and leaf temperature—During the growing seasons (May through September) of 1990, 1991, and 1992, micrometeorological data (air temperature, water temperature, relative humidity, net radiation, photosynthetic photon flux density) and leaf temperatures were measured every minute and averaged over 15-min intervals using a data logger (Campbell Scientific model CR21X). Wind speed was measured at 0.1 m and 1.0 m above the pond surface with a cup anemometer system designed to measure low wind speeds (<2 m/sec) with 0.1 m/sec accuracy and a stall speed of ≈ 0.14 m/sec (RIMCO R/AMI 6). All other micrometeorological measurements for ambient conditions (except water temperature) were made at 0.5 m above the pond surface. Photon flux density of photosynthetically active wavelengths (PFD) was measured with a LI-COR 190SB quantum sensor oriented horizontally. Ambient air temperatures were measured with a thermocouple that was shaded from direct solar radiation, while ambient water temperatures were measured at a depth of 10 cm.

Leaf temperatures were measured to ± 0.1 C with fine wire (36 ASW gauge, 0.012 mm diameter) copper-constantan thermocouples carefully threaded into the blades of floating and aerial leaves. Care was taken to avoid surface wetting of floating leaves due to the positioning of the thermocouples. Leaf temperatures were averaged from measurements on four floating leaves (positioned on the pond surface) and four aerial leaves (≈ 10 cm above the pond surface).

Ambient relative humidity was measured with an Ome-

ga HX-92 Humidity Transducer and converted to vapor pressure using air temperature measurements at the same location above the pond (Campbell, 1977). To establish a water vapor profile above the pond surface, relative humidity and air temperature were also measured at 2-cm intervals from the pond surface to a height of 1 m above the pond. Using data for air temperature and relative humidity, vapor pressure and dew point temperatures were calculated according to Monteith and Unsworth (1990). The leaf-to-air difference in water vapor pressure (LAVD) for floating and aerial leaves was computed from measurements of leaf temperature, air temperature, and ambient relative humidity, and by assuming that the air inside the leaf was saturated at leaf temperature (Nobel, 1983).

Photosynthesis and leaf conductance—Net photosynthetic CO₂ assimilation (A) and leaf conductance to water vapor (g) were monitored during cloud-free periods (to avoid low light effects on photosynthesis) on three consecutive days during July 1992. A and g were measured for floating and aerial leaves with a closed-flow infrared gas analyzer system (LI-COR Inc., Lincoln, NE, model 6200), which also monitored leaf temperature and PFD. Measurements were made on portions of individual leaves (leaf area of 20 to 25 cm²) that were sealed inside a 1.0-liter cuvette.

Aerial leaves were positioned at their natural height and orientation to the sun. For wet leaves, gas exchange was measured after carefully blotting both leaf surfaces with absorbent filter paper until dry (Smith and McClean, 1989) prior to sealing them in the chamber. Floating leaves were lifted off the water surface, blotted dry, oriented in a horizontal position, and then measured. Measurements were initiated within 15 sec of placing the leaves in the cuvette, and CO₂ depletion was measured over the next 15 to 30 sec. Upon completion of each measurement, the cuvette was flushed with air. To protect against occult moisture, the parts of the cuvette in contact with previously wet surfaces were carefully dried prior to subsequent measurements so that internal humidity values were normal and constant. Fans in the cuvette maintained leaf temperature within approximately ± 2 C of air temperature. The initial concentration of CO₂ in the cuvette was within 5 μ l/liter of ambient CO₂ levels (350 μ l/liter) and did not decrease more than 25 μ l/liter during the measurement interval. Vapor pressure of air in the chamber was maintained within $\pm 5\%$ of ambient by regulating the amount of flow diverted through the desiccant.

Measurements of A and g were made on five floating and five aerial leaves at each 1-hr measurement interval during the day from 0600 to 1800 hr. The same leaves were not typically resampled at each measurement interval. Differences between floating leaves and aerial leaves were compared with a Student's t -test for each measurement interval. In addition, to assess the effects of leaf surface wetness on gas exchange, both aerial and floating leaves were experimentally wetted by spray misting, and A and g were measured several times before wetting and while leaves dried naturally outside the measurement cuvette. Immediately before measurements on artificially wetted leaves, moisture was quickly blotted from the wet leaf surfaces with tissue paper before placing the leaves

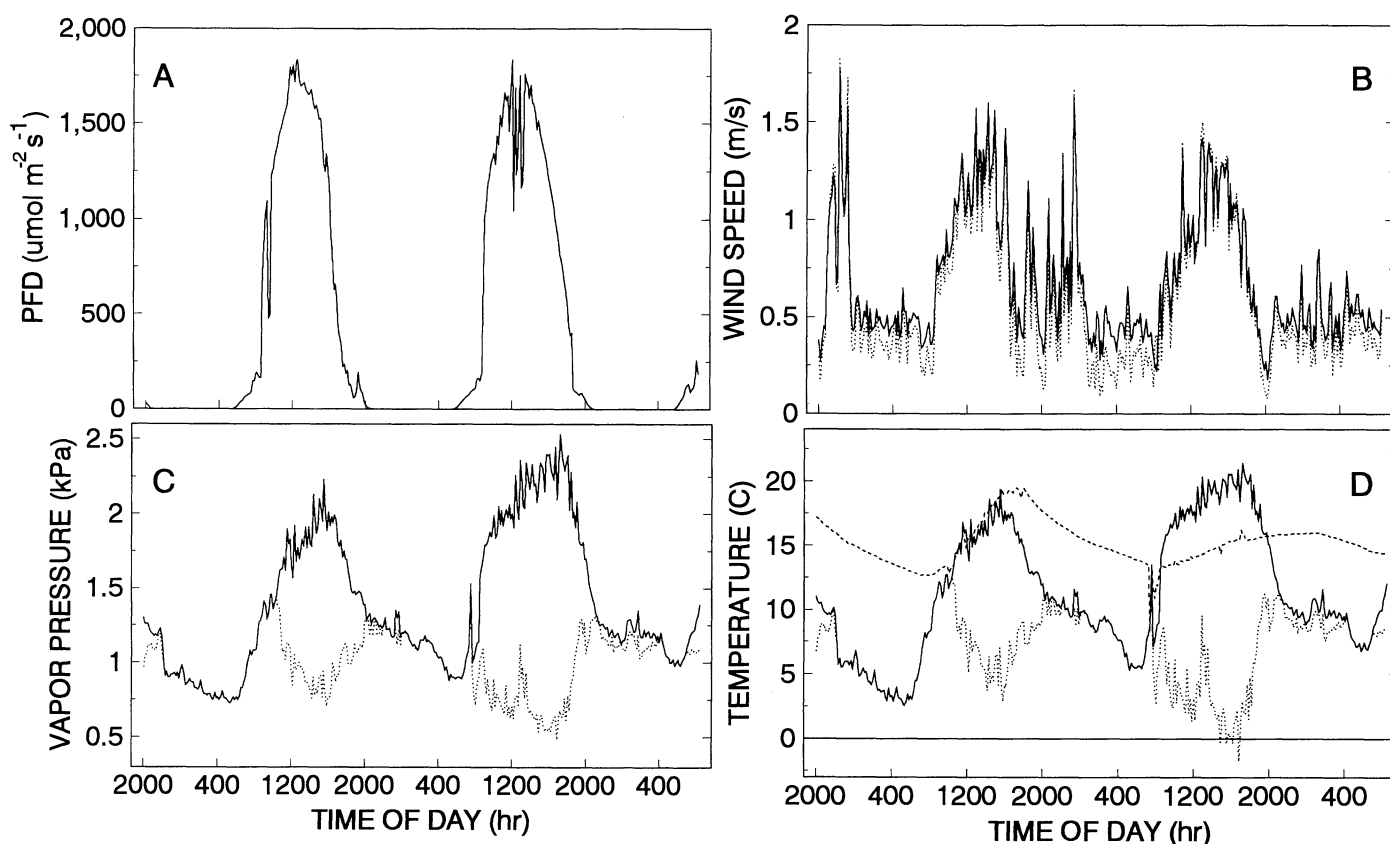


Fig. 1. Diurnal variations in microclimate for pond lily leaves in a small subalpine pond. (A) Photosynthetic photon flux density (PPFD; $\mu\text{mol m}^{-2} \text{sec}^{-1}$) incident 0.5 m above the surface of the pond. (B) Wind speed (m/sec) at 0.1 m (dotted line) and 1.0 m (solid line) above pond. (C) Diurnal variation in saturation vapor pressure (solid line) and ambient vapor pressure (dotted line) in kPa. (D) Temperatures (C) for air (solid line), water (dashed line), and dewpoint (dotted line).

in the gas exchange cuvette in order to estimate stomatal conductance. Control leaves (not misted) were also measured to account for the effects of blotting and handling the leaves (Smith and McClean, 1989).

RESULTS

Leaf surface characteristics—Floating leaves were usually flat on the surface of the pond with much of the leaf blade in contact with the water. Aerial leaves typically projected 10 to 25 cm above the pond surface and varied in leaf orientation. At sunrise, aerial leaves were often covered with a film of water on both surfaces and moisture often persisted until ≈ 1000 hr for shaded leaves. The basal lobes of floating leaves (up to one-third of the leaf blade), which projected at a steep angle from the pond surface, were also covered with dew. In contrast, the exposed adaxial (top) surfaces of floating leaves were virtually dry at dawn.

Both floating and aerial leaves of *N. polysepalum* are considered wettable on adaxial leaf surfaces (θ approximately 30°), despite a waxy cuticle. For small droplets, both floating and aerial leaves also had high droplet retention (retention angle up to 70°). However, leaves exhibited low retention for large droplets because these droplets tended to coalesce and roll off the leaf surface when leaves moved as a result of wind or the action of moving water. Typically, surface moisture on floating and

aerial leaves generated from splashing or rainfall was spread out in a patchy distribution across the leaf surface. In contrast, surface moisture resulting from dewfall generally formed a monolayer of droplets covering the entire leaf surface. Stomata were found only on adaxial leaf surfaces and there was no statistical difference ($P > 0.05$) in the number of stomata for aerial ($589 \text{ stomata mm}^{-2} \pm 18$; mean \pm SE) and floating leaves ($601 \text{ stomata mm}^{-2} \pm 20$). In the leaves examined, stomata were fairly evenly distributed across the leaf blade.

Microclimate—Although several other periods were sampled, results from one representative sampling period (16–19 July 1992) are presented. In most areas of the Rocky Mountains, morning skies are clear but cloud activity increases during the early afternoon (Fig. 1A). At this site, PPFD typically approached $2,000 \mu\text{mol m}^{-2} \text{sec}^{-1}$ during clear mornings while patchy clouds or even thunderstorms developed by 1300–1400 hr (PPFD 300–800 $\mu\text{mol m}^{-2} \text{sec}^{-1}$). The maximum diurnal variation in water temperature was 8.0°C compared to as much as 17.0°C for air temperature at 0.5 m above the surface of the pond (Fig. 1D). Minimum air temperatures (as low as 2.5°C) occurred between 2400 hr and 0600 hr. Minimum water temperatures were never lower than 11.0°C and occurred during the early morning (0700–0800 hr).

Wind speeds measured at 1 m above the pond surface typically averaged $\approx 30\%$ ($\bar{X} = 0.7 \text{ m sec}^{-1}$) higher than

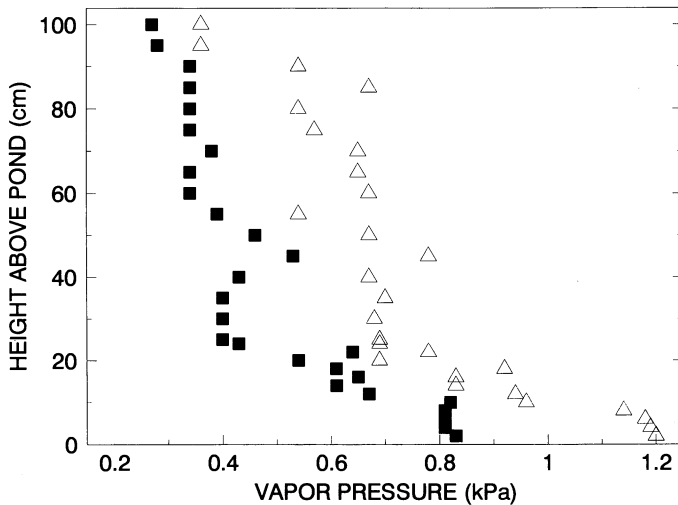


Fig. 2. Vapor pressure gradient (kPa) above pond surface under different wind conditions. Vapor pressure gradient from 1 cm to 100 cm above the pond under calm conditions typical of the morning (open triangles; wind <1 m/sec; air temperature 18.5 C) and slightly windy conditions typical during the afternoon (solid squares; wind velocity to 5 m/sec; air temperature 23.0 C).

wind speeds only 10 cm above the surface ($\bar{X} = 0.6$ m sec $^{-1}$; Fig. 1B). Wind speeds within 1.0 cm of the pond surface were <0.1 m sec $^{-1}$ (virtually still air). The lowest winds occurred in the early morning hours (2400 to 0500 hr) corresponding to the coolest air, leaf, and water temperatures.

In general, the air 0.5 m above the pond became saturated with water vapor by about midnight (Fig. 1C). The vapor pressure gradient above the pond (Fig. 2) was steepest under calm conditions (wind <1 m/sec; air temperature 18.5 C). During periods of higher wind (≈ 5 m/sec; air temperature 23.0 C), vapor pressure was generally lower (e.g., at 8 cm, vapor pressure = 0.81 kPa in windy vs. 1.14 kPa in calm conditions). In both calm and windy conditions, the highest values for vapor pressure were recorded within the first 5 cm of the pond surface. Thus, vapor pressure was considerably higher in the region inhabited by floating (kPa = 1.2 at pond surface) vs. aerial leaves (kPa = 0.83–0.96 at ≈ 10 –25 cm above the pond surface; Fig. 2).

Plant temperatures, dewpoint, and LAVD—On clear, still nights aerial leaf temperature fell as much as 3.5 C below air temperature when floating leaves were as much as 10 C warmer than aerial leaves (Fig. 3A). Also, aerial leaf temperatures were never above air temperature at night, and floating leaves only occasionally fell below air temperature during the early morning (Fig. 3A; ≈ 0600 –0630 hr). The difference in temperature for aerial and floating leaves was greatest during the coldest part of the night.

At night, the susceptibility to leaf wetting by dew was also quite different for aerial and floating leaves (Fig. 3B). By 2000 hr, aerial leaf temperatures were very near or below dewpoint until early morning (0700–0800 hr) for all days sampled. At the same time, floating leaves were always above dewpoint temperature, except for very short intervals (minutes) on any night sampled (Fig. 3B).

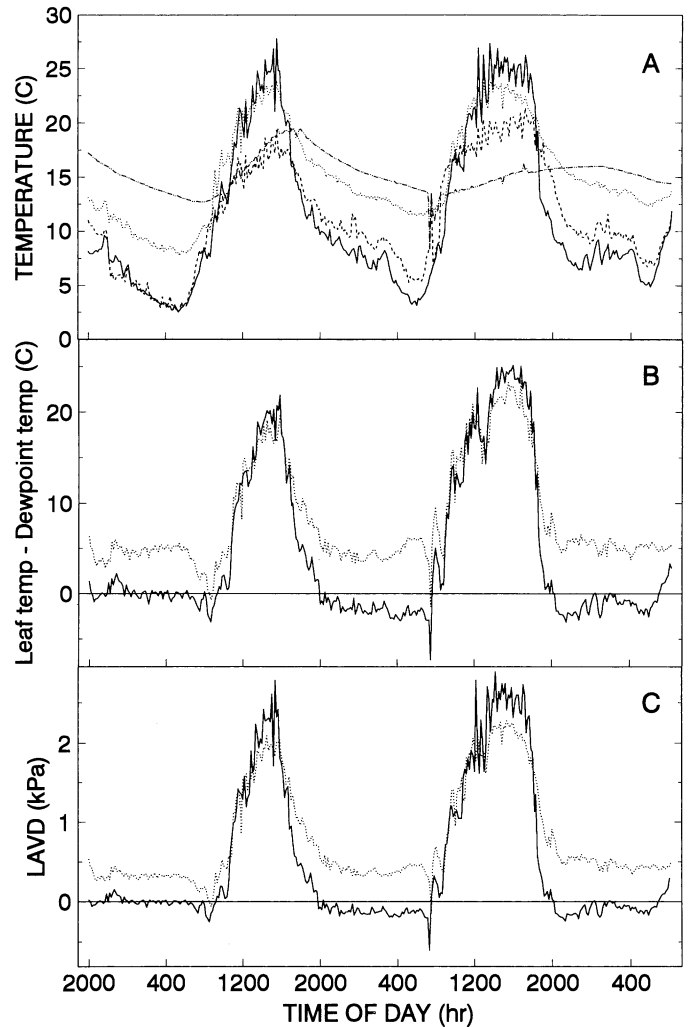


Fig. 3. Temperature and moisture regimes for pond lily leaves. (A) Air and leaf temperatures (C). Air (dashed line); water (dot-dash line); floating leaves (dotted line); and aerial leaves (solid line). (B) Deviation of leaf temperature from dewpoint temperature. The dotted line is floating leaf temperature minus dewpoint temperature; the solid line is aerial leaf temperature minus dewpoint temperature. Values above the "zero" line indicate leaf temperatures greater than the dewpoint temperature while values on or below the line indicate leaf temperature at or below dewpoint. (C) Leaf-to-air vapor pressure deficit (kPa). Floating leaf (dotted line); aerial leaf (solid line).

Diurnal patterns in LAVD were also different for floating and aerial leaves (Fig. 3C), especially at night. Only during the morning (0800–1100 hr) was LAVD similar for floating and aerial leaves. Under conditions of higher leaf and air temperature and wind speed, along with lower vapor pressure (Figs. 1–3), LAVD was as much as 30% higher for aerial leaves than floating leaves. By 1800 hr, LAVD for aerial leaves decreased to below LAVD for floating leaves, reflecting the rapid drop in leaf temperature at sunset. LAVD for aerial leaves remained lower than for floating leaves until morning.

Photosynthesis and leaf conductance—There were no statistically significant differences ($P = 0.05$ level) between floating and aerial leaves for A or g despite differences in leaf temperature and LAVD (Fig. 4). Stomatal conduc-

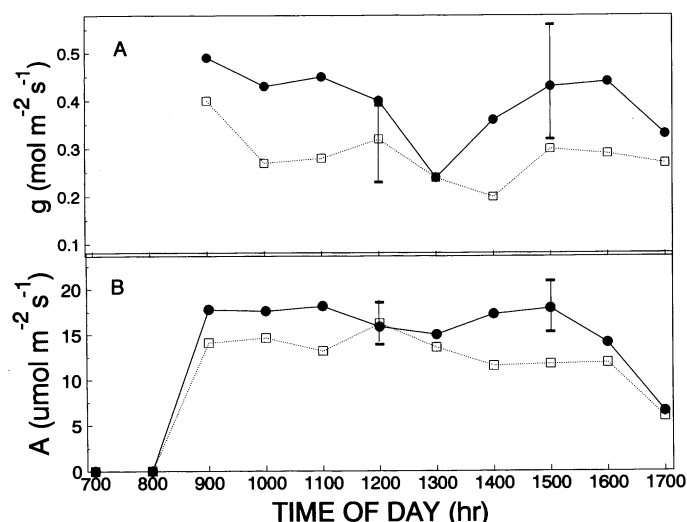


Fig. 4. Daily pattern in stomatal conductance to water vapor and net photosynthesis. For both panels, the solid line with closed circles represents aerial leaves and the dotted line with open squares represents floating leaves. (A) Stomatal conductance to water vapor, g ($\text{mol m}^{-2} \text{sec}^{-1}$). (B) Net assimilation, A ($\mu\text{mol m}^{-2} \text{sec}^{-1}$). $N = 5$; vertical bars represent the largest values of ± 1 standard error of the mean.

tance was highest early in the day (Fig. 4A), declined slightly in the early afternoon, and then rose again in the late afternoon. For all measurement intervals, g of floating leaves was slightly lower than for aerial leaves, although differences were not significant at the $P = 0.05$ level.

Net photosynthesis increased rapidly with increased light for both aerial and floating leaves and remained at approximately the same level until about 1500 hr (Fig. 4B). After that time, the rate of photosynthesis decreased as PFD fell to $<300 \mu\text{mol m}^{-2} \text{sec}^{-1}$. Throughout the day, photosynthesis was slightly higher for aerial leaves (usually $\approx 10\%$) compared to floating leaves, though differences were not significant at the $P = 0.05$ level. Daily fluctuations in LAVD appeared to account for little variation in g for either aerial or floating pond lily leaves (Fig. 5). In general, there was considerable variation between g and the corresponding values of LAVD.

Experimental misting of both floating and aerial leaves caused an average net decrease in photosynthesis compared to nonmisted control leaves. Compared to premisting levels, net photosynthesis decreased by 14% for misted floating leaves (reduced from 10.5 to 9.0 $\mu\text{mol m}^{-2} \text{sec}^{-1}$) and 20% for misted aerial leaves (reduced from 17.9 to 14.3 $\mu\text{mol m}^{-2} \text{sec}^{-1}$). Once leaf blades were dry, A recovered to premisting levels within ≈ 10 min. During the same time, net photosynthesis increased by $\approx 5\%$ for control leaves. We were unable to evaluate a response of experimental misting on stomatal conductance because of difficulty with moisture in the experimental chamber.

DISCUSSION

Susceptibility to leaf wetness—High humidity is common in wetland habitats. Higher humidity has been attributed to increased fog and dew in the vicinity of wetland areas (Priban, Ondok, and Jenik, 1986). When vapor pressure was high, small reductions in leaf temperature were

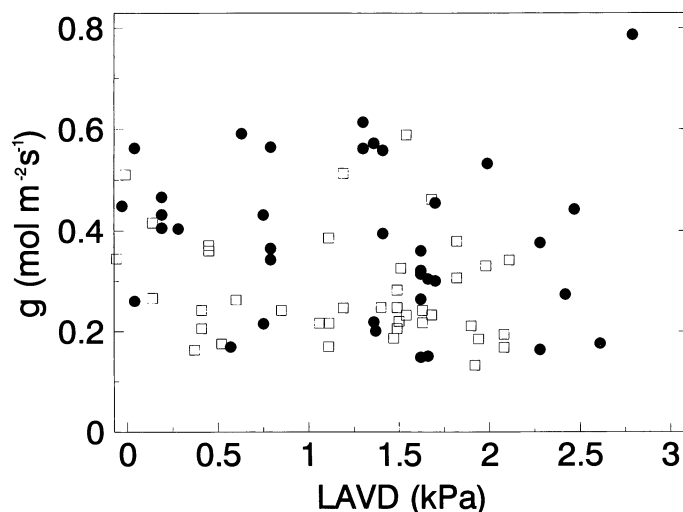


Fig. 5. Relationship between stomatal conductance ($\text{mol m}^{-2} \text{sec}^{-1}$) and leaf-to-air vapor pressure deficit (kPa) for floating (open squares) and aerial (solid circles) pond lily leaves.

sufficient to reach dewpoint temperatures. According to Monteith and Unsworth (1990), conditions that minimize convective heat exchange, such as low wind speeds (Fig. 2B), can decrease leaf temperatures below dewpoint even when relative humidity is much lower than 100%. For example, at night the air 0.1 m above the sampled pond surface (roughly the height of aerial leaves) was essentially still (wind speed $<0.5 \text{ m sec}^{-1}$; Fig. 1B). At such low wind speeds, convective heat exchange between a leaf and the air is greatly reduced, enhancing the influence of radiative heat exchange between the leaf and the cold night sky.

In the sampled pond, aerial leaves were frequently wet compared to floating leaves, and surface moisture from dewfall persisted well into the midmorning hours. Dew formation occurred during the nighttime and early morning hours when leaf temperature fell beneath the dewpoint temperature (Fig. 3). Thus, temperatures of aerial leaves on clear nights were depressed below air temperature by as much as 5 C and below dewpoint for many hours (up to 12 hr) (Fig. 3A, B). As a result, aerial leaves had surface wetness that often persisted late into the morning. In contrast, the temperature of floating leaves remained above the dewpoint temperature (Fig. 3B), much closer to the warmer water temperature. The high heat capacity of water results in considerable solar heat storage during a day. Moreover, close contact of floating leaves with the surface water ensures strong thermal coupling and leaf temperatures well above air temperature, especially at night.

A broad range of leaf surface wettability has been reported for native plants. Some leaves become covered by a film of water while other types repel surface water by forming droplets (Brewer, Smith, and Vogelmann, 1991; Brewer, 1993). Both floating and aerial leaves of *N. polysepalum* were very wettable ($\theta < 30^\circ$) according to the classification of Crisp (1963), despite the presence of a waxy surface cuticle. Large droplets tended to have a high contact area with the leaf surface, and 50–90% of the leaf surface was often covered by a film of water after rain or

dewfall. As a result of leaf wetting events such as splashing or flooding, for example, a patch of water covering 25 mm² could potentially cover as many as 15,000 stomata on a pond lily leaf. Although small dew droplets persisted to late morning on shaded leaves, most large droplets coalesced and then rolled off the leaf surface at the deep notch where the petiole was attached. Thus droplet retention was low for large droplets. Furthermore, moisture tended to evaporate from the dark green leaf surfaces when they were exposed to direct sunlight.

Photosynthesis and leaf conductance—Avoidance of leaf surface wetness may be particularly important in aquatic plants, because stomata in some species may never close. Wagner (1973, as cited by Ziegler, 1987) reported stomata which were permanently open in *Nymphaea alba* L., *Nuphar lutea* L. and *Lemna minor* L. In *N. lutea* and *N. alba*, the guard cells of the stomata had chloroplasts and mitochondria but lacked a substomatal cavity required to allow subsidiary cells to bend. Hence, the guard cells in these species were disabled by the fixed position of the subsidiary cells. Moreover, the stomatal pore is often partially occluded by a waxy cuticle, thus hindering the entry of water into the pore.

The decline in photosynthesis for both leaf types with wet surfaces was similar to the patterns of lowered photosynthetic performance reported for other subalpine species (Smith and McClean, 1989; C. A. Brewer and W. K. Smith, unpublished data). Recovery of *A* to premisting levels occurred quickly after leaf surfaces had dried. Because of the rapid recovery to premisting levels, it is unlikely that the reduction in photosynthetic CO₂ uptake was due to stomatal closing and opening. The decline in photosynthetic uptake of CO₂ appears to be due to physical blockage of stomata by water. Stomata covered with water experience a considerable resistance to CO₂ uptake due to the slow diffusion of CO₂ through water compared to air (Weast, 1979; Smith and McClean, 1989). As a result of dewfall, small droplets and films of water could cover a substantial area of adaxial leaf surfaces on aerial leaves.

The interpretation of seemingly passive stomata in the water lilies is supported by the lack of a response to LAVD. Even though LAVD was quite different for floating and aerial leaves throughout the day (Fig. 3C), we found no apparent threshold value of LAVD that led to changes in stomatal conductance (Fig. 5). Both leaf types exhibited the same range of stomatal conductance, although aerial leaves had higher leaf temperatures and were positioned in a drier microenvironment. Moreover, *g* did not respond to PFD, wind velocity, water temperature, or air temperature (data not shown). Stomata that are insensitive to LAVD may be a consequence of evolution in an environment with high humidity and water availability, coupled with relatively low short-term variation in the microenvironment close to the surface of the pond (e.g., Fig. 1).

Leaf wetting events such as rainstorms, wind-driven splashing of water on leaves, fog, mist, and dewfall may have important effects on photosynthetic gas exchange in water lilies. In fact, the effects of dewfall may have a potentially greater effect on photosynthetic uptake of CO₂ in the subalpine environment because dew persists

throughout the morning, the time of day when plant water status and sunlight are often optimal for *A* and *g* due to high tissue water potential, as well as optimal air temperatures and light availability (Schulze and Hall, 1982). Although floating and aerial leaves of *Nuphar polysepalum* have relatively high water repulsion and low droplet retention, floating leaves had an additional mechanism for avoiding excessive wetting from dewfall (and therefore, the negative effects of water films on photosynthetic gas exchange), primarily because they were coupled to a warm substrate (i.e., water). The example provided by water lilies may be a dramatic illustration of dewfall avoidance that results from the thermal properties of a substrate, in this case water. Other species with close contact with other warm substrates (e.g., soil) have also been shown to benefit by having warmer leaf temperatures (Smith et al., 1983). Close proximity to the soil in terrestrial plants may also prove to be important for avoiding dew deposition during the night.

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