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An Examination of the Leaf Quaking Adaptation and Stomatal Distribution in *Populus tremuloides* Michx.

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ABSTRACT

The leaves of quaking aspen (*Populus tremuloides* Michx.) have a flattened petiole that allows them to quake (oscillate and roll) under low wind velocities. It was hypothesized that this adaptation might enable the plant to respond to windy conditions that would increase transpirational losses. No effects of wind with or without leaf quaking on stomatal resistance were observed under controlled conditions in the field. If wind and leaf quaking affect stomatal resistance, such effects must be small in comparison to those caused by other factors such as leaf water potential and ambient humidity.

Aspen leaves are hypostomatal with stomata evenly distributed over the abaxial surface. This observation casts serious doubt on the hypothesis that quaking is an adaptation to increase bulk air flow through amphistomatal leaves.

Some species of *Populus* have a flattened petiole that allows the leaf to quake (oscillate and roll) in the wind. At least three hypotheses have been proposed to explain the adaptive significance of leaf quaking. First, quaking may increase convective heat transfer between leaf and air by reducing the boundary layer and causing turbulent air flow close to the leaf surface (3, 4). This function seems insignificant because exaggerated leaf quaking, as in *Populus tremuloides*, can at most account for a 6% change in the rate of convective heat transfer (13).

A second hypothesis is that quaking may lessen wind damage by decreasing stress on the branches during strong winds (15). A related hypothesis is that quaking may tend to increase bulk air flow through the canopy which, in turn, would prevent severe depletion of CO_2 within the canopy during periods of photosynthesis. These hypotheses are difficult to test experimentally, but are certainly reasonable.

A third hypothesis is that leaf quaking may cause bulk flow of air through the leaves to enhance gas exchange. Wooley's (19) theoretical calculations for corn suggested that such an effect would be negligible, but Shive and Brown (15) reported that oscillation of amphistomatal leaves of cottonwood (*Populus deltoides* Marsh.) caused bulk flow of oxygen through the mesophyll cells. They also showed that changes in the boundary layer were insufficient to account for increases in oxygen flux.

Our original hypothesis was that leaf quaking might provide a mechanism by which the plant might "sense" low wind velocities that would be sufficient to remove the boundary layer of air adjacent to the leaf and increase transpiration. Such a mechanism would cause an increase in R_S[2], thereby reducing excessive water

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[2] Abbreviation: R_S, stomatal resistance.

loss. If the stomata respond to changes in humidity conditions or increased water deficits resulting from removal of the boundary layer, an increase in R_S should be observed in leaves subjected to wind but held still. Alternatively, if quaking causes a change in R_S due to mechanical disturbance (5), one would predict that an increase in R_S would be observed only in leaves allowed to flutter in the wind. Our experiments were designed to test the separate effects of wind with and without leaf quaking on R_S of *P. tremuloides* in the field. We also examined stomatal densities and distributions on the leaves of this species.

MATERIALS AND METHODS

R_S of *P. tremuloides* Michx. leaves was measured with a LI-COR LI-20S Diffusive Resistance Sensor (Lambda Instruments, Lincoln, NB). The porometer was calibrated according to Kanemasu (6), with care taken to keep the temperature of the calibration plate above the dew point of the air (9). RH of the calibration chamber was maintained between 85 and 95%. To minimize differences between leaf temperatures and the temperature of the porometer cup during readings in the field, the sensor cup was covered with aluminum foil to reflect sunlight; the cup was also kept out of direct sunlight between measurements.

Portable wind screens were constructed by attaching 12 mil transparent plastic sheets to the top half of wooden frames. Each frame was 2 m high × 1 m wide, with a 20 cm × 3.3 m base for holding the frame perpendicular to the ground. Two frames were positioned at the sides of a *P. tremuloides* branch, and another 1-× 1-m wind screen was attached to the side frames in front of the branch. This arrangement eliminated ambient wind and prevented leaf quaking, but it permitted full sunlight to strike the leaves. Air temperatures within the enclosure remained within 2 C of the ambient air temperatures.

An electric fan, driven by a portable generator, was used to provide a wind speed of approximately 5 m/s for experimental treatments in the field. This wind speed was more than adequate to produce quaking in free hanging leaves and was assumed to be adequate to reduce the boundary air layer (4) in either quaking leaves or leaves which were held still in the wind.

To test the effect of wind without leaf quaking on R_S, a leaf holding device was built. The frame was constructed from two 20 × 25 cm pieces of Plexiglas, which was used to reduce absorption and reflection of sunlight. An area 10 × 15 cm was cut from the center of each piece. This area was covered with a monofilament nylon mesh to support the leaf. The opening in the bottom half of the frame was covered with a 1-mm^2 mesh, and that in the top was covered with a 1-cm^2 mesh. This device was mounted on a camera tripod so that it could be easily positioned to the experimental leaves. Two leaves at a time were sandwiched between the mesh filaments with their abaxial surfaces, covered by the 1-cm^2 mesh, positioned at a 45° angle to incident wind from the fan. Field trials in still air showed that the leaf holding device had no effect on R_S of aspen leaves.

To test our hypotheses, two separate experiments were performed. In the first, the combined effect of wind with leaf quaking on R_S was tested. The second tested the effect of wind without leaf quaking.

The protocol for experiment 1 was:

(a). Ten healthy, mature aspen leaves in full sunlight were selected and marked on each experimental and control branch on the same tree.

(b). Both branches were enclosed in wind screens for a 1-h period of calm.

(c). Beginning with the most distal leaf on the branch, R_S readings were taken from the leaves of the control and experimental branches respectively.

(d). The front of the wind screen was removed from the experimental branch and the leaves were subjected to 10 min of wind and quaking.

(e). The wind treatment was continued while R_S readings were taken from the experimental leaves following the same sequence as in step 3. This provided a wind treatment which varied between 10 and 25 min. Readings were then taken from the 10 leaves on the control branch.

The protocol for experiment 2 was:

(a). Leaves were selected, marked, and enclosed in wind screens as described in steps (a) and (b) for experiment 1.

(b). R_S readings were taken on the two most distal leaves of the control and experimental branches.

(c). The two experimental leaves were placed in the leaf holding device and treated with 15 min of wind without leaf quaking. The other leaves on the branch were protected from wind by a wind screen.

(d). R_S readings were taken from the two leaves just treated and from the corresponding control leaves.

(e). Steps (b) through (d) were repeated, taking two leaves at a time in an axial direction, providing before and after readings for the 10 experimental and control leaves.

Experiment 1 was repeated 11 times using trees from 10 different clones in the vicinity of Pocatello, ID. Because the diurnal patterns of R_S and water potential showed significant differences between the morning and the afternoon (Rushin and Anderson, in preparation), this experiment was repeated six times during morning hours and five times during the afternoon. Experiment 2 was done twice in the morning and twice in the afternoon on two aspen clones.

The data for the control and experimental branches in each experiment were each analyzed by a separate analysis of variance. The morning or afternoon replications (days) were treated as blocks in a randomized complete-block design with more than observation (individual leaf R_S values) per experimental unit (branch), with the before-after readings contributing the treatment sum of squares (17). Treatment effects were assumed to be fixed and block effects were assumed to be random; therefore, the experimental error mean square was used to test hypotheses concerning block or treatment effects (17). This statistical approach was used to take advantage of the pairing design. The questions asked statistically were as follows. Was there a significant change in R_S of control branches in either experiment 1 or experiment 2? Was there a significant change in R_S of branches subjected to treatment in either experiment?

Stomatal frequencies and distributions were determined with DUCO cement impressions (18).

RESULTS AND DISCUSSION

Mature leaves of quaking aspen were hypostomatal with stomata evenly distributed over the abaxial surface at a density of 9,105 ± 610 stomata/cm^2 (0.95 confidence interval). Therefore, all R_S values in this paper are from the abaxial surface.

The absence of stomata on the adaxial surface of the leaves of

Table 1. *Effect of Wind with Leaf Quaking on R_S of Populus Tremuloides*

Each value is the mean R_S of 10 leaves on that branch. Control and treatment branches were analyzed by separate ANOVAs (see under "Materials and Methods"). Because variances of morning vs. afternoon experiments were not homogeneous ($\chi^2 = 28.9$; $P < 0.005$), they were evaluated by separate ANOVAs.

Morning Repetitions

| Date | Stomatal resistance (s/cm) | | | |
| | Control branch | | Treatment branch | |
	Before	After	Before	After
July 7	4.2	2.4	2.9	3.3
July 8	3.6	5.2	3.0	5.9
July 14	3.8	4.6	3.8	3.7
July 23	1.6	3.1	1.9	4.7
August 30	4.6	5.2	4.4	4.6
September 1	4.1	4.1	4.3	3.7
Overall mean	3.7	4.1	3.4	4.3

ANOVA

Source	df	SS	F	df	SS	F
Blocks (day)	5	82.94	2.21[a]	5	32.98	0.57[a]
Treatment	1	6.03	0.80[a]	1	26.43	2.28[a]
Experimental error	5	37.49		5	57.85	
Sampling error	108	230.69		108	250.14	

Afternoon Repetitions

| Date | Stomatal resistance (s/cm) | | | |
| | Control Branch | | Treatment Branch | |
	Before	After	Before	After
June 13	10.3	10.7	7.9	6.4
June 20	7.3	6.3	20.3	9.8
July 7	4.2	2.5	2.9	3.3
August 30	6.9	7.0	10.7	11.9
September 1	8.6	9.0	13.7	13.1
Overall mean	7.5	7.1	11.1	8.9

ANOVA

Source	df	SS	F	df	SS	F
Blocks (day)	4	197.13	0.90[a]	4	1880.75	0.76[a]
Treatment	1	199.62	3.66[a]	1	122.77	0.20[a]
Experimental error	4	217.92		4	2459.24	
Sampling error	90	403.93		90	1957.96	

[a] Not significant.

P. tremuloides is contrary to Shive and Brown's (15) hypothesis that leaf quaking is an adaptation to enhance bulk flow of air through amphistomatal leaves. Parkhurst (12) suggested that bulk air flow is much reduced through hypostomatal leaves. It is possible that, during quaking, pressure differences across the leaf surface might allow for an appreciable amount of air movement in and out of open stomata on the abaxial surface.

Parkhurst (12) suggested several possible adaptive values for stomata being located exclusively on the underside of leaves. One is that the upper surface of the leaf is more likely to be blocked by dust, rainwater, etc. than the lower surface. Another is that the stomata on the bottom of the leaf would humidify the still air underneath the plant canopy, causing a decrease in the vapor pressure gradient between the leaf and air. The CO_2 concentration in the air underneath the canopy would be reduced, but the proportional increase in absolute humidity would be much greater.

Table II. *Effect of Wind without Leaf Quaking on R_S of Populus tremuloides*

Each value is the mean R_S of 10 leaves on that branch. Data were analyzed as explained in Table I and under "Materials and Methods."

Morning Repetitions

Date	Stomatal resistance (s/cm)			
	Control branch		Treatment Branch	
	Before	After	Before	After
August 30	4.8	5.3	4.6	4.4
September 1	4.1	4.1	5.5	4.9

ANOVA

Source	df	SS	F	df	SS	F
Blocks (day)	1	9.20	0.87[a]	1	4.87	0.67[a]
Treatment	1	0.72	0.07[a]	1	1.75	0.24[a]
Experimental error	1	10.63		1	7.25	
Sampling error	36	77.51		36	84.20	

Afternoon Repetitions

Date	Stomatal resistance (s/cm)			
	Control branch		Treatment branch	
	Before	After	Before	After
August 30	6.8	7.2	9.7	12.1
September 1	9.1	9.3	11.3	14.9

ANOVA

Source	df	SS	F	df	SS	F
Blocks (day)	1	50.24	0.98[a]	1	47.59	0.34[a]
Treatment	1	0.81	0.02[a]	1	87.23	0.63[a]
Experimental error	1	51.14		1	138.39	
Sampling error	36	106.55		36	1059.72	

[a] Not significant.

This would provide a favorable environment for gas exchange. A third possible adaptive value is that the stomata on the underneath side of the leaves would typically be shaded from direct sunlight and cooler than those on the exposed leaf surfaces. Because saturated water vapor pressure varies exponentially with tissue temperature, evaporation from leaves having stomata in direct sunlight could be significantly greater than from those having stomata shaded from the sun.

None of the above suggestions seem to explain the hypostomatal condition in *P. tremuloides*. Mature aspen leaves tend to hang vertically in still air, and the bottom side of a leaf is about as likely to receive direct sunlight as the top side. Also, quaking aspen trees do not form a canopy with still air underneath. Wind easily moves through the trees as the leaves quake.

Under field conditions, we were unable to detect any effect of wind treatment with or without leaf quaking on R_S (Tables I and II). There was no significant change in R_S of either control or treatment branches over the time that the wind treatment was applied. Similar results were observed in morning and afternoon experiments, but R_S values tended to be higher and were much more variable during the afternoons (Tables I and II). Our hypotheses predicting increases in R_S with wind treatment in both experiments 1 and 2 were rejected. If wind and leaf quaking cause a change in R_S, it must be small in comparison to effects of other

factors such as light, leaf water potential, and humidity, and therefore its ecological significance would be questionable.

There are reasons to believe that R_S might increase under windy conditions. When the boundary layer about the leaf is reduced by wind, one would predict an initial increase in transpiration (11), followed by an increase in R_S due either to water deficits in the leaf tissue (10) or increased evaporation from the guard cells (7, 16). There is also the possibility that wind might cause an increase in R_S through mechanical disturbance of the leaf (5). Studies with various plant species have shown that wind speeds that would be sufficient to cause leaf quaking in *P. tremuloides* increased R_S, either immediately (1) or after several hours of treatment (1, 2, 8, 14).

Our results seem to concur with those of Fluckiger et al. (2) who found no significant change in R_S of mature leaves of the European aspen, *P. tremula*, when treated with intermittent wind gusts in a greenhouse. Furthermore, they did observe significant increases in R_S after 2 to 5 h of continuous wind at a velocity of 6 m/s (2). It is possible that *P. tremuloides* would also show an increase in R_S when subjected to several hours of wind. If leaf quaking is part of a special wind-sensing mechanism, one would expect R_S to change more rapidly.

An increase in R_S with wind and leaf quaking would restrict bulk movement of air through the leaf tissue. Therefore, our results are what would be expected if bulk flow was important in *P. tremuloides*. As we have indicated, the presence of stomata on only one leaf surface suggests that bulk flow of air through the leaves (15) would be minimal. We conclude that the most reasonable hypothesis to account for leaf quaking in aspen is that it serves as an adaptation to help prevent branches from breaking in strong winds.

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