

Plant Gas Exchange at High Wind Speeds¹

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ABSTRACT

High altitude *Rhododendron ferrugineum* L. and *Pinus cembra* L. seedlings were exposed to winds at 15 meters per second for 24-hour periods. Wind-sensitive stomata of *Rhododendron* seedlings immediately initiated a closing response which resulted in decreased photosynthesis and an even greater reduction in transpiration. Stomatal aperture and transpiration rates of *P. cembra* were only slightly reduced by high speed winds. However, photosynthesis was substantially reduced because of changes in needle display to available irradiation.

Most available information concerning rates of photosynthesis and transpiration at elevated wind speeds has been limited to comparatively slow rates of air movement (2, 6, 11, 12). The influence of wind speeds in excess of 10 m/sec on plant gas exchange has received little attention. Tranquillini (15) investigated the response of transpiration and photosynthesis of several high altitude species to stepwise increases in wind velocity from 0.5 to 20 m/sec. However, when the plants were exposed to winds in excess of 10 m/sec, they had already been exposed to lesser winds for a minimal period of 12 hr. Therefore, the response of these plants at higher wind speeds cannot be clearly separated from the possible residual effect of long exposures at slower speeds. Changes in stomatal aperture were only inferred from the gas exchange behavior.

This research was designed to investigate directly the effect of high wind speeds on photosynthesis, transpiration, and stomatal aperture in two species. Seedlings of *Rhododendron ferrugineum* and *Pinus cembra* native to Austrian treeline areas were used. These studies were conducted at wind speeds of 15 m/sec. Such velocities can occur at the vegetation layer above timberline in areas where the foehn is common (Caldwell, unpublished data).

MATERIALS AND METHODS

Seedlings of *R. ferrugineum* L. and *P. cembra* L. were excavated from their natural sites of establishment above 2000-m elevation on the Patscherkofel Mountain near Innsbruck, Austria. These plants were immediately potted and grown in a uniform garden in the treeline environment at 1950-m elevation for a period of 4 months (July 1–October 30, 1968). The plants were then brought into a greenhouse (20 C average day temperature, 15 C night), in the Klimahaus Laboratory (13) to prevent them

from becoming photosynthetically inactive (1). The plants remained in this greenhouse until they were used in the experiments during the next 2 to 3 months.

Stomatal aperture was determined for seedlings which had been exposed to high wind speeds in a large, fully climatized wind tunnel (13). Leaves were individually removed from plants in the wind tunnel and immediately observed for stomatal aperture. Stomatal opening of *Rhododendron* leaves was determined by an infiltration method of Oppenheimer and Engelberg (9) as modified by Lingl (7). Stomatal aperture of *P. cembra* was measured with an infiltration porometer on individual needles (4). For simultaneous measurements of photosynthesis and transpiration, three to five plants were placed in a smaller wind tunnel designed for gas exchange measurements (14). Both wind tunnels were programmed for the following conditions: air temperature, 20 C; soil temperature controlled in the small wind tunnel at 10 C and varied between 10 C and 20 C in the large wind tunnel; dew point, 10 C; CO₂ concentration, 300 ± 10 μl/liter; and total short wave irradiation (Xenon arc lamp) at the leaf surface, 0.4 cal cm⁻² min⁻¹ (measured with a Stern pyranometer). Leaf and needle temperatures were measured with fine wire thermocouples inserted into the tissue. Plants in both wind tunnels were exposed at a base wind speed of 0.5 m/sec until they were in equilibrium (approximately 6–10 hr). Wind velocity was then elevated abruptly to 15 m/sec for a 24-hr period before being returned to the base rate for 3 additional hr.

RESULTS AND DISCUSSION

Throughout these experiments leaf and needle temperatures never deviated more than 0.5 C from the ambient air temperature. Therefore, the effects of increased wind speed in this study did not include changes in plant temperature caused by increased convective heat exchange.

Stomata of *Rhododendron* leaves reacted immediately to the onset of high wind speeds with a pronounced decrease in aperture. Stomatal closure continued for several hours of exposure at 15 m/sec until reaching an equilibrium aperture after approximately 8 to 12 hr following the initiation of the higher wind speed. *Rhododendron* stomata exhibit this sensitive, though less pronounced, closing response to wind speeds as low as 1 m/sec (15). This closure is initiated at leaf water deficits which appear to be much less than those required to cause hydropassive stomatal closure under still air conditions (15). Simultaneously measured rates of photosynthesis and transpiration of *Rhododendron* seedlings are shown for two representative experiments in Figure 1. These gas exchange rates closely parallel the observed stomatal behavior pattern. However, under any circumstance at high wind speed, transpiration underwent a consistently greater reduction than photosynthesis. If stomatal diffusion resistance is considered in relation to the other diffusive resistances involved in transpiration and photosynthesis, the greater reduction in transpiration would be reasonable.

Total diffusive resistance for transpiration has been considered as the sum of stomatal diffusion resistance, r_s , and boundary

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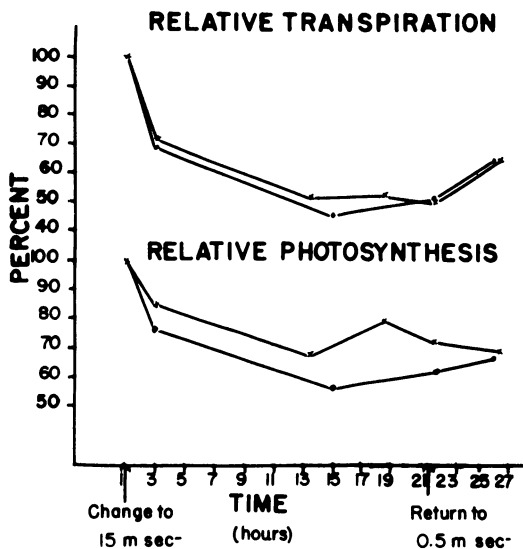


FIG. 1. Simultaneously measured rates of transpiration and photosynthesis for *Rhododendron ferrugineum* L. seedlings at a wind speed of 15 m/sec. Before and after this exposure at high wind speed, the seedlings were exposed to an air flow rate of 0.5 m/sec. Each pair of lines represents a separate trial using three to five seedlings.

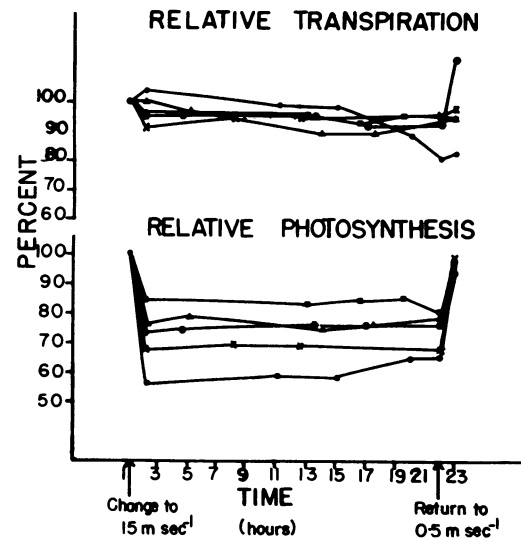


FIG. 2. Simultaneously measured rates of transpiration and photosynthesis for *P. cembra* L. seedlings at a wind speed of 15 m/sec. Before and after this exposure at high wind speed, the seedlings were exposed to an air flow rate of 0.5 m/sec. Each pair of lines represents a separate trial using three to five seedlings.

layer resistance, r_a , whereas the total diffusive resistance for photosynthesis includes an additional mesophyll resistance, r_{me} , encountered between the intercellular spaces and the site of carboxylation in the chloroplast (3, 5, 16). Since r_{me} is usually of sizable magnitude (3, 5, 16), changes in stomatal diffusion resistance are proportionately much more important for transpiration than for photosynthesis. Therefore, transpiration should undergo a greater reduction than photosynthesis when r_s is increased. The decrease in r_a caused by increasing wind speed was apparently not sufficient to offset the increase of r_s . Other possible effects of wind on plant gas exchange such as enhancement of transpiration due to reduction of air pressure at the leaf surface, by a mechanical "pumping" action of leaves caused by leaf flutter, or due to ventilation through amphistomatous leaves have been considered to be insignificant (17).

In contrast to *Rhododendron* seedlings, stomata of *P. cembra* seedlings were virtually unaffected by 24-hr exposures at 15 m/sec. By using the infiltration porometer of Fry and Walker (4), it was possible to obtain a quantitative approximation of the change in stomatal aperture after wind speed was increased. For the purpose of calculating change in stomatal aperture, a stomatal pore length of 15μ was assumed for *P. cembra*. The exact pore length is not critical when merely calculating change in stomatal aperture. The average change in stomatal aperture for mature needles for this group of 16 seedlings, with three needles per individual, was only 0.02μ . Young needles from the current year's flush were somewhat more responsive and showed an average 0.07μ change in stomatal aperture. To estimate what these changes in stomatal aperture might represent in terms of change in stomatal diffusion resistance, it is necessary to evaluate the diffusive resistances encountered by gaseous diffusion through stomatal pores. If the stomatal diffusion resistance is taken as the sum of the resistance through the stomatal pores according to Fick's equation and the diffusive resistances into and away from the end of the stomatal pores according to Stefan's law, r_s could be represented as

$$r_s = \frac{1}{Dna} \left(L + \frac{\pi r}{2} \right) \quad (1)$$

where D is the diffusion coefficient of the gas; n , the number of



FIG. 3. A: Conformation of *P. cembra* seedlings at 0.5 m/sec wind speed; B: the same seedlings at 15 m/sec; C: simulated high wind speed conformation of these seedlings using thread. Wind speed is 0.5 m/sec.

stomata on the leaf surface; a , the cross sectional area of one stoma; L , the length of a stomatal tube; and r , the radius of the stomatal tube (8). If D and n are taken as constants and L as 15μ , which is representative of conifer stomatal pore lengths (8), there would be a 5.6% change in stomatal diffusion resistance for old needles and a 24% change for new needles. Although new needles represent only 10 to 15% of the total leaf area of these seedlings, these new needles have been found to exhibit higher rates of transpiration (10) and are probably more photosynthetically active. Therefore, the significant increase in r_s for new needles should effect an appreciable increase in the composite value of r_s for the entire seedling. The influence of high wind speed on the boundary layer resistance, r_a , could not be quantified in this study.

The gas exchange behavior of five groups of *P. cembra* seedlings at 15 m/sec is shown in Figure 2. Transpiration was little affected by exposure to 15 m/sec winds. The slight decrease in transpiration suggests that an increase in r_s , although slight, was able to offset decreases in r_a . For photosynthesis there was an abrupt decrease immediately following initiation of the high wind speed. Once this level of photosynthesis was established, it remained constant over the entire 24-hr exposure period. When the plants were returned to the base wind speed rate, there was a nearly complete recovery of photosynthetic rate in all five trials. At high wind speed, photosynthesis underwent a much greater reduction than transpiration. This would not be expected if changes in r_s and r_a were the only principal effects of high wind speed. If, however, the needle display to the available irradiation were substantially changed when the plants were subjected to high wind speeds, this might result in lower levels of irradiation avail-

able for photosynthesis of some needles. The effect of this decreased available irradiation for transpiration would be less important because needle and air temperatures were constant and nearly identical in these experiments. Figure 3A shows the normal conformation of seedlings at low wind speed. At high wind speed there is a definite change in conformation of the seedling, as shown in Figure 3B. When this high wind speed conformation was simulated by binding the seedlings as shown in Figure 3C, photosynthesis was reduced as at high wind speeds with little change in transpiration in a pattern identical to Figure 2.

Gas exchange at higher wind speeds is apparently little different than at lower wind speeds for plants such as *Rhododendron*. For *Rhododendron*, which characteristically grows in protected ravines and depressions, the sensitive stomatal closure which occurs at wind speeds as low as 1 m/sec is only further enhanced at 15 m/sec. For *P. cembra*, which thrives on wind swept ridges, the stomata are little affected by high wind and the principal influence of high speed wind is the reduction of available irradiation for photosynthesis caused by changes in conformation of the seedlings.

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