EVIDENCE FOR ERROR IN PRESSURE-BOMB ESTIMATES OF STEM XYLEM POTENTIALS[1]

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Abstract. The hydrostatic component of water potential was measured concurrently in stems and needles of five species of conifers (*Pinus contorta, P. jeffreyi, Pseudotsuga menziesii, Abies amabilis,* and *A. procera*). In Douglas-fir and the true firs pressure-chamber measurements of potentials were up to 4 bars more negative in stems than in needles. The difference appears to be due to filling of non-vascular xylem tissue with fluid during measurement. This tissue seems to function as a water reservoir, enabling needles to maintain relatively high turgor levels during periods of rapid transpiration.

INTRODUCTION

Dixon (1914) and more recently Scholander et al. (1965) described a simple technique for assessing water status of excised plant stems. The stem is placed in a sealed chamber with the cut end protruding through a rubber stopper at the neck. Pressurized nitrogen gas is introduced into the chamber, and the pressure at which water emerges from the exposed xylem face is recorded. In Boyer's (1968) notation, this balancing pressure is related to water potential by:

$$\Psi_w = P + \Psi_s^{xylem},$$

where Ψ_w is total water potential, P is the hydrostatic component, and Ψ_s^{xylem} combines the osmotic and matric components. The pressure chamber does not estimate Ψ_s^{xylem} (Boyer 1968), but this component is reported to not normally exceed −3 bars in the transpiration stream (Scholander et al. 1966, Boyer 1967, 1968). Thus chamber measurements of P have been successfully used as field estimates of water potential (Klepper 1968, Waring and Cleary 1967, 1969).

However, using *Rhododendron roseum,* Boyer (1967) found differences between P in stems measured with the pressure chamber and Ψ_w measured with a thermocouple psychrometer that were too large to attribute to Ψ_s^{xylem}. He suggested that this difference resulted from filling pith with sap during pressure application causing erroneously low (more negative) values. Kaufman (1968) using similar techniques found even greater differences than those reported by Boyer (1967). With *Quercus alba* and *Q. rubra* these approached 15 bars; agreement was slightly better between branch and needle potential values of five other species. He attributed these differences to the filling of large empty vessels during the pressure measurement, supporting Boyer's observation.

The magnitude of these errors and our current use of the pressure-chamber technique prompted us to investigate this problem.

MATERIALS AND METHODS

Modification of a pressure chamber like the one described by Waring and Cleary (1967) to allow measurement on individual needles made direct comparisons of stem $P(P_s)$ and needle P (P_n) possible. The underside of the rubber stopper was hollowed out to within 0.3 cm of the upper surface leaving a peripheral rim of 0.5 cm thickness. The stopper was split radially to the center hole so that it could be opened sideways and the needles inserted without damage. A dissecting microscope was used to observe the minute vascular bundle at the detached needle end.

Two seedlings each of 2-year-old lodgepole pine (*Pinus contorta* Dougl.), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and Douglas-fir (*Pseudotsuga menziesii* Franco) and two 6-year-old Pacific silver fir (*Abies amabilis* Dougl. Forbes) and noble fir (*A. procera* Rehd.) were put through soil drying and rewetting schedules in a controlled environment room. Measurements of P_n and P_s from the same stem were compared over a wide range of water-stress levels. It was necessary to remove the fascicle sheath of pine needles and excise the vascular bundle extension to within 0.3 mm of the fascicle base. True fir and Douglas-fir needles were detached and placed directly in the chamber with 1.0 mm of the basal end protruding from the stopper. Detached needles were stored in a humid chamber for up to 5 min before measurement, during which time no more than a 0.20 bar decrease in P_n ever occurred.

RESULTS

In both species of pine $P_s \cong P_n$ throughout the range of water-stress levels (Fig. 1), but in the other species P_s was always more negative than P_n. Examination disclosed that the pith in pines was very reduced in size or lacking, whereas in the other species it generally occupied the entire center of the stem, having a radius of from 0.3 to 0.5 times the xylem

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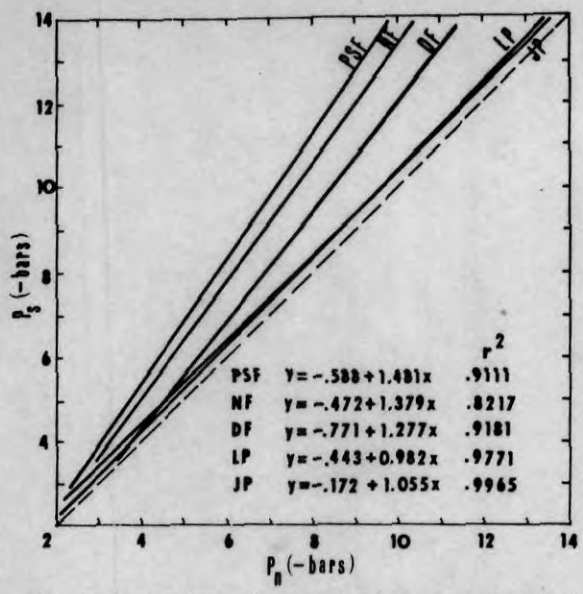

FIG. 1. Regressions of mean hydrostatic potential of three needles (P_n) versus hydrostatic potential of the stem to which the needles were attached (P_s) measured with a pressure chamber. Data are for Pacific silver fir (PSF-32 points), noble fir (NF-25 points), Douglas-fir, (DF-13 points), lodgepole pine (LP-22 points), and Jeffrey pine (JP-14 points).

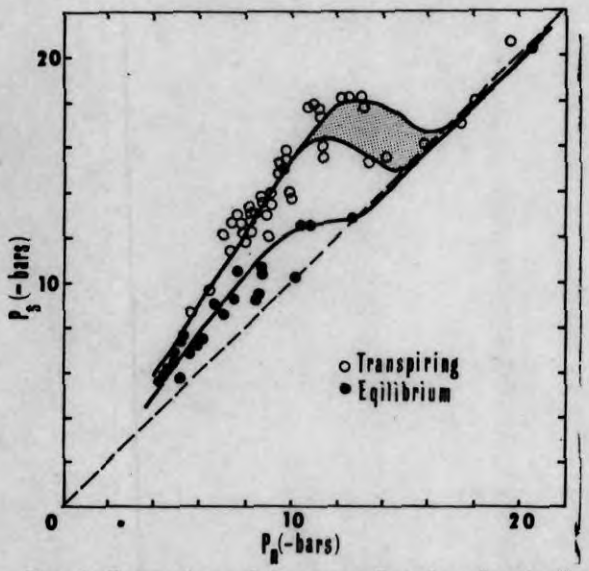

FIG. 2. Comparison of P_s versus P_n values for Pacific silver fir measured during periods of active transpiration (open circles) and immediately following 8-hr dark periods (solid circles), during which plant water potential was allowed to equilibrate with soil matric potential. Dehydration of pith occurs in shaded area.

radius. This supported the observations of Boyer (1967) and Kaufman (1968). As these non-conducting tissues dehydrated during transpiration the difference between P_s and P_n increased. When P_s dropped to below about −18 bars in the true firs P_n suddenly decreased to equal P_s (Fig. 2). We interpret this as the point at which pith tissues are no longer hydrated. Beyond this point P_n and P_s measurements seem to remain equal.

We compared P_n and P_s in the true firs during times of active transpiration and immediately following 8-hr dark periods when seedling water stress was approximately in equilibrium with soil matric potential (Fig. 2). During transpiration ($P_s - P_n$) was considerably greater than at equilibrium, indicating that during the dark period the non-conducting xylem tissue had partially rehydrated. Furthermore, during days of high transpiration rates P_s often decreased during the day by as much as 10 bars below morning levels, while concurrent P_n values typically changed by only 4 bars over the same period.

Discussion

This study suggests that non-conducting stem xylem tissues of these true firs and Douglas-fir act as reservoirs for water. These reservoirs seem to allow needles to transpire rapidly without undergoing abrupt turgor changes by constantly resupplying them with water. This could have considerable adaptive significance.

In addition to the osmotic error reported by other investigators, our experiments indicate that a substantial discrepancy may exist between pressure-bomb estimates of stem xylem potential and actual needle-pressure potentials. The magnitude of this discrepancy varies with species and increases with decreasing water potentials. Thus, pressure-chamber data are not a valid basis for species comparisons unless this error is accounted for. Stem stress values currently reported for species with large non-vascular xylem components are probably considerably more negative than concurrent foliar stress levels.

The direct measurement of needle potentials has several advantages. First, the discrepancy between P_s and P_n is eliminated. It is possible to use smaller and lighter chambers that consume less gas and are superior for field use to those used for measuring stem potentials. Reproducibility is excellent with standardized procedures. Since relatively small amounts of tissue are required for determinations the method is especially valuable for use with seedlings. Finally, it may provide a substitute for the laborious psychrometer technique after appropriate calibration and when high accuracy is not required.

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