

Plant Moisture Stress: Evaluation by Pressure Bomb

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Abstract. The recently developed technique for determining the water stress of a plant by measuring the pressure necessary to force water back to the cut surface of a severed twig is adaptable to both field and laboratory experiments. We have designed and operated an efficient portable system weighing less than 18 kilograms. Sampling variation within and among Douglas fir trees varies from less than ± 1 atmosphere under low stress conditions to ± 10 atmospheres under high stress conditions. In the measurement of plants of comparable height and similar exposure, the variation is reduced to a minimum. Values in internal water stress of Douglas fir vary from 3 to more than 40 atmospheres. Both duration and magnitude of stress are important ecologically. Pressure-bomb measurements are used to demonstrate a relation between plant distribution and internal water stress.

Scholander *et al.* (1) demonstrated that a pressure bomb could be used to evaluate the status of water within vascular plants. The simplicity of this technique, compared to other methods of measuring plant water stress, encouraged us to design an instrument that could be used efficiently in both laboratory and field situations. We took measurements with this instrument under a variety of environmental conditions to determine standards for the collection and preparation of samples.

Internal water stress, the key measure for many phases of research related to plant response, is most difficult to predict (2) because the status of a plant's moisture is dependent upon soil moisture stress, atmospheric stress, and the plant's ability to control water losses. For clarity we express the water status of plants as internal water stress rather than water potential or diffusion pressure deficit. The units of internal water stress are positive atmospheres rather than negative bars, dynes per square centimeters, ergs per cubic centimeter, or centimeters of water. Stress or water potential is a true scalar potential and "as for any other scalar potential in physics, the 'driving force' is (minus) the gradient of the potential, and bears no relation to its absolute value, which includes a constant of integration which we may assign at will" (3). Philip concluded that "the most convenient datum of water potential for plant physiological purposes is the potential of pure water under atmospheric pressure; and convenience is the only pertinent criterion." The less familiar terms, as Slatyer (4) has pointed out, "will not be accepted generally until the parameters they describe can be shown to be necessary to a fuller understanding of plant water relationships."

Within the vascular system of a plant the water column is generally

under tension. This tension results from the demands of the leaves for replacement of water lost to the atmosphere and from the inability of the roots to take up water rapidly enough from a progressively drying soil. When a twig is severed, the water column is broken and water withdraws into the twig a short distance. To measure the original tension, the twig can be placed in a bomb with the cut end protruding through a seal; pressure exerted on the leaves forces the water column back to the cut surface. The pressure at which water is observed is assumed to be the tension on the water column before it was severed.

To find what relation, if any, exists between pressure-bomb measurements of water stress in the twigs and a standard method of measuring water stress in the leaves of a plant, we made comparisons from 5 to 20 atm on Douglas fir (*Pseudotsuga menziesii*) by modifying Slatyer's (5) vapor equilibration technique and found agreement within the precision of the methods, which is about ± 1 atm. The relation at higher stresses has yet to be determined.

Our system is simple in operation. After a twig is cut from a plant, the bark and phloem are stripped back a short distance from the cut surface, and the exposed xylem is slipped through a rubber stopper and inserted into the cover that is screwed to the body of the bomb (Fig. 1). With the bleeder and flow-regulating valves closed and the gauge shutoff valve open, pressure is applied through the pressure regulator. The regulating valve is then opened, and the pressure is gradually increased. When water first appears on the cut surface, the regulating valve is closed. Finally, the pressure reading is recorded, and the bleeder valve is opened to vent the system and prepare it for the next sample. If pressures ex-

Table 1. Maximum variation in pressure-bomb readings on Douglas fir under different conditions of atmospheric stress (AS) and soil-moisture stress (SMS). Numbers represent values in atmospheres.

Low AS, low SMS	High AS, low SMS	High AS, high SMS
	Within a branch	
± 0.5	± 0.5	± 1.0
	Shaded versus exposed branch	
± 0.5	± 1.0	± 1.5
	Within a tree	
± 1.0	± 1.5	± 2.5
	Among trees	
± 1.0	± 3.0	± 10.0

ceed 1000 lb/in.² (68 atm), the gauge shutoff valve is closed, and the less accurate regulator gauge is used. The entire procedure takes less than 30 seconds, and twigs may be severed for at least 5 minutes without an increased reading.

There are several sources of variation in readings obtained with the pressure bomb. These fall into two classes, those attributed to variation in plant material and to the method itself. Table 1 shows variation in sampling Douglas fir under a range of environmental conditions. The values are the ranges around a sample mean where the sample size is between 3 and 6. Sampling variation is small under both low atmo-

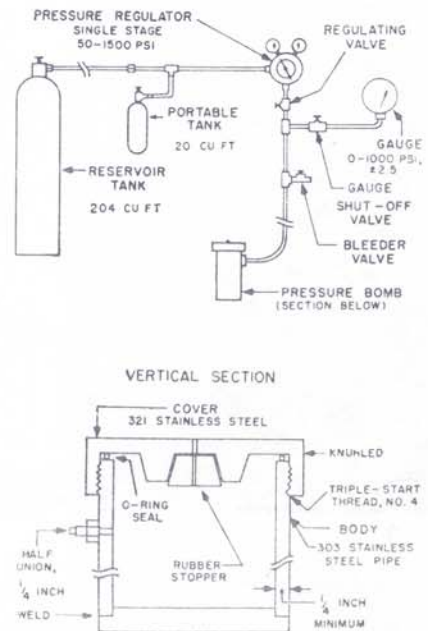


Fig. 1. Pressure bomb system. Connections to reservoir tank and pressure bomb are made of high-pressure flexible hose; all others are rigid high-pressure tubing and fittings.

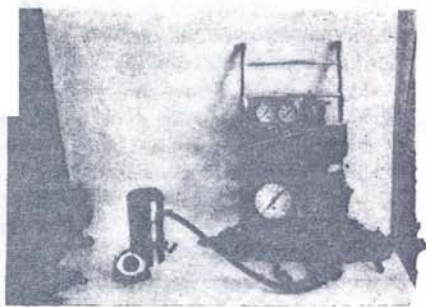


Fig. 2. Portable bomb and pressure apparatus.

spheric stress and low soil-moisture stress. Variation under high atmospheric stress and low soil-moisture stress is almost entirely a function of stand microclimate. Trees exposed to the same degree show close agreement regardless of their size. Differences in stresses between completely shaded and fully exposed trees may be as much as 6 atm.

When soil moisture is in critical supply, the size of the tree as an index to the depth of rooting is all-important. For example, 25-m trees in the same stand have been recorded at 20-atm stress, but 1-m trees were at nearly 40 atm. Comparison of trees of the same size is absolutely essential, then, in comparing environments. Variation among trees of the same size is generally less than ± 2 atm.

Possible errors in the method itself are of two types—those related to the rate of pressure increase and those related to sample preparation. Abnormally high readings occur when the pressure is increased too rapidly and when equilibrium within the sample is not reached. If the pressure is increased very slowly, high readings also

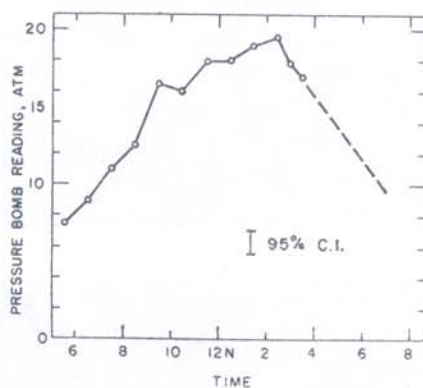


Fig. 3. Diurnal change in water stress on a Douglas fir (25 m) with adequate soil moisture. Confidence interval (95 percent) is 1.4 atm.

may be recorded. This phenomenon is not easily explained, but has been observed a number of times. Both errors can be avoided by standardizing the rate of increase at about 10 lb/in.² (0.68 atm) per second. A faster rate may be applied to within 100 lb/in.² (6.8 atm) of the reading.

The length of xylem extending from the bomb can also be a source of variation. With 50 cm of stem extending from the bomb, a value 10 atm high has been recorded. Such a high reading may reflect the increased volume of stem available for the water to occupy in tissue under no pressure or tension. The amount of stem inside the bomb is not critical. For maximum reproducibility the length of stem exposed should be held to a minimum (less than 2 cm).

The pressure bomb is filled directly from the nitrogen gas reservoir tank when the system is operated near a vehicle or in the laboratory (Fig. 1). From 10 to 50 determinations (with the number depending upon the size of the bomb and the stress of the plant material) can be made with one filling of the portable tank (Fig. 1).

The pressure bomb is constructed of stainless steel because of this material's high strength and resistance to oxidation. We have made the bomb in two sizes (inside dimensions): one 10.2 cm in diameter and 25.4 cm deep, and the other 6.4 cm in diameter and 12.7 cm deep. The larger bomb is more versatile for general use; the smaller bomb, because of its lighter weight (3.4 compared to 9.1 kg) and smaller volume, is ideal for extensive field work and for use on very small samples. The portable pressure apparatus weighs 14.5 kg (Fig. 2).

The cover on the bomb was specially designed for a rubber stopper to permit rapid insertion of a sample from any woody species. For herbaceous material, a compression gland (1) is probably necessary to avoid crushing the vascular system.

The diurnal pattern of internal water stress has great importance physiologically. Each point in Fig. 3 represents an average of four measurements collected from the upper crown of a 25-m tree. Water stress can reach 20 atm even with soils near field capacity if the radiation load is sufficiently high. Stress may fluctuate rapidly, with up to 5 atm increase or decrease per hour, depending upon the atmospheric stress. Haze or partial cloud cover account for the temporary

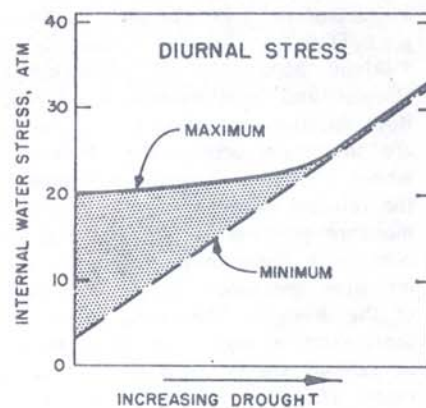


Fig. 4. Trend of internal water stress with increasing drought. Maximum values depend upon atmospheric stress and range within shaded portion of the diagram.

plateaus and for the abrupt decrease after 2:30 p.m. With water readily available, we found in other experiments that the minimum value was approached by 8:00 p.m.

By anatomical inspection, we have found that no cell divisions occur under conditions where there is no diurnal shift in water stress (Fig. 4). In Douglas fir this value is very close to 25 atm. If drought continues, the stress can increase to at least 40 atm without permanent injury to the plant. With precipitation of 3 cm or more, the diurnal pattern almost immediately returns to that in Fig. 3.

Our specific objective in construct-

Table 2. Siskiyou vegetation in relation to internal water stress at peak of drought (1 September 1966). Abbreviations: BO, black oak (*Quercus kelloggii*); DF, Douglas fir (*Pseudotsuga menziesii*); ES, Englemann's spruce (*Picea engelmannii*); IC, incense cedar (*Libocedrus decurrens*); JP, Jeffrey pine (*Pinus jeffreyi*); MH, mountain hemlock (*Tsuga mertensiana*); PP, ponderosa pine (*P. ponderosa*); SF, Shasta fir (*Abies magnifica* var. *shastensis*); SP, sugar pine (*P. lambertiana*); WF, white fir (*A. concolor*); WP, white pine (*P. monticola*); Y, yew (*Taxus brevifolia*).

Stand No.	Elevation (m)	Vegetation*	Minimum stress (atm)
1	2040	MH-SF	3.0
2	1400	ES-DF-WF	6.5
3	1920	SF-(WP)	7.0
4	1680	WF-DF-(SP)	11.0
5	760	DF-Y-(WF)	12.5
6	1500	WF-PP-DF	14.0
7	1280	PP-DF	17.5
8	2130	MH-(SF)	19.0
9	1700	JP-IC-(DF)	19.0
10	790	DF-BO-PP	28.0

* Stand composition, listed in decreasing order of density. Species in parentheses make up less than 5 percent of total number of trees.

ing a pressure bomb was to evaluate a heretofore unmeasurable moisture gradient in the eastern portion of the Siskiyou Mountains of southwestern Oregon and northwestern California. Both duration and magnitude of stress are important ecologically. However, where a summer drought is common, the relation between vegetation and a moisture gradient is demonstrated by comparing the minimum internal water stress measured during the peak of the drought. The stress values for representative vegetation types shown in Table 2 are averages from three or more Douglas or Shasta fir trees (*Abies magnifica* var. *shastensis*), 1 to 2 m in height. In the same stand, other species of conifers in the same size class gave similar water stresses. Hardwoods and evergreen shrubs generally were under more stress.

Obviously, the moisture gradient is not closely related to elevation. Trees growing on very shallow soil near timberline may be under considerable stress (stand 8), while nearby trees on deeper soils are experiencing little stress (stand 1). Soils developed on serpentinite or peridotite (stand 9) are generally shallow and are characterized by higher stress values. White fir (*Abies concolor*) occurs over a wide range of elevations and temperature patterns, but was not found on sites where stress reached 25 atm. Black oak (*Quercus kelloggii*), many shrubs, and herbaceous species appear restricted to the drier sites (stands 10 and 7). The ground vegetation appears very sensitive to the entire moisture gradient, which is not surprising when one considers their more restricted root systems.

Our data represent a portion of 1500 measurements with the pressure bomb. Measurement and sampling techniques should be standardized, and more detailed comparisons with other methods of measuring water stress with different species should be made.

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References and Notes

1. P. F. Scholander, H. T. Hammel, E. D. Bradstreet, E. A. Hemmingsen, *Science* 148, 339 (1965).
 2. R. O. Slatyer and W. R. Gardner, *The State and Movement of Water in Living Organisms* (Cambridge Univ. Press, London, 1965), pp. 113-129.
 3. J. R. Philip, *Annu. Rev. Plant Physiol.* 17, 245 (1966).
 4. R. O. Slatyer, *ibid.* 13, 351 (1962).
 5. ———, *Australian J. Biol. Sci.* 11, 349 (1958).
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