The results were very different, however, when individual root tips of loblolly pine and white spruce were removed from the seedlings growing in solution. Apical segments 4 to 8 cm long were removed from root systems, and their bases were sealed into pipettes so the volume of exudate could be observed. The root segments were immersed in nutrient solution during the experiments. All of the 75 root segments studied showed exudation, but the rate was very low, and the total volume exuded over a period of 72 hours was small compared with roots of angiosperms studied at the same time.

Since the roots used were of various sizes, some common basis was needed for comparison of exudation from various species, and the area of the absorbing surface was chosen as the most logical. The average volumes (in microliters per square centimeter of root surface) of exudate obtained in 72 hours were as follows: *Pinus taeda*, 1.0; *Picea glauca*, 2.0; *Betula populifolia*, 5.0; *Liriodendron tulipifera*, 17.0; *Acer saccharum*, 17.5; *Acer rubrum*, 27.5. It was interesting to note that *Acer saccharum* roots behaved like those of the two conifers. Entire root systems showed no exudation, but apical segments of roots showed relatively high exudation.

It usually is assumed that only growing roots exhibit root pressure, but it was found that fully suberized, nonelongating, apical segments of loblolly pine roots also show root pressure. It was slow in developing, and often no exudation occurred during the first 24 hours; but after 80 hours the total exudation from suberized root segments was about 2.5 times that from the unsuberized roots of similar size maintained under similar conditions.

The exudation observed by Dimbleby (*4*) and by White *et al.* (*5*) was from detached roots. The exudate collected from *Picea abies* and *Larix decidua* by Reuter and Wolffgang (*6*) apparently also came from detached roots. All three investigators apparently used roots which had been cut loose from the central axis of the plant. White *et al.* (*5*) used roots which were 0.5 to 1.0 cm in diameter and bore many smaller branches and root tips. The roots used in our study were approximately 1 to 2 mm in diameter and 4 to 8 cm long and were unbranched.

These results pose the interesting problem of why excised apical root segments show exudation although the entire root systems from which they are detached show no exudation. Failure of root systems to exhibit exudation might occur either because of failure to accumulate enough salt in the xylem to produce appreciable pressure or because of a high resistance to water flow through the root system.

The concentration of salt in the xylem solution of loblolly pine was very low, suggesting that it either has a limited capacity to accumulate salt or is unable to retain it in the xylem. However, the salt concentration in the xylem solution from white spruce was considerably higher than that of the solution in which the roots were immersed, indicating that there is no failure to accumulate salt in this species. White *et al.* (*5*) reported pressures of about 80 cm of water in roots of conifers. The resistance to flow in loblolly pine was not high, much larger volumes of water being moved through pine root systems under a pressure of 1 bar than through sugar maple root systems of similar size. The volume of solution pushed through white spruce root systems under 1 bar of pressure was approximately the same amount as that pushed through the sugar maple root systems. There seems to be no obvious explanation for the failure of the intact conifer root systems to show exudation when excised individual roots do show exudation.

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References and Notes

1. F. M. Eaton, *Am. J. Bot.* **30**, 663 (1943).
2. T. W. Daniel, *Plant Physiol.* **24**, 327 (1949).
3. A. D. Pitra, *Jahrb. Wiss. Bot.* **11**, 437 (1878).
4. G. W. Dimbleby, *Plant Soil* **4**, 141 (1953).
5. P. R. White, E. Schuker, J. R. Kern, F. H. Fuller, *Science* **128**, 308 (1958).
6. G. Reuter and H. Wolffgang, *Flora* **142**, 146 (1954).
7. B. S. Meyer, D. B. Anderson, C. A. Swanson, *Laboratory Plant Physiology* (Van Nostrand, New York, 1955).
8. Supported by contract AT-(40-1)-1827 with the AEC.
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Turgor Pressures in Phloem: Measurements on Hevea Latex

Abstract. *Hydrostatic pressures in laticiferous phloem tissues of* Hevea brasiliensis *trees exhibit a diurnal fluctuation, with minimum values occurring during the day. Pressure decreases with increasing height up the trunk, the gradient becoming greater under conditions of rapid transpiration. Sieve-tube turgor must be controlled independently if pressure-flow is to occur in the expected direction.*

A number of attempts have been made to measure hydrostatic pressures occurring within plants. For example, measurements were obtained by Marvin on maple sap (*1*), Scholander *et al.* on lianas (*2*), and Bourdeau and Schopmeyer (*3*) and Vité (*4*) on oleoresin exudation in *Pinus* species. No direct measurement on the phloem of actively growing plants appears to have been published, although various estimates based on determinations of osmotic pressure have been made (*5*).

In the investigation described here, hydrostatic pressures in the phloem tissue of trees of *Hevea brasiliensis* were measured with simple capillary manometers similar to those developed by Bourdeau and Schopmeyer (*3*). It is assumed that this hydrostatic pressure is largely the result of pressure within the latex vessels. A small hole is bored in the bark down to the wood and a hypodermic needle fitted to a sealed glass capillary (10 to 12 cm long) is inserted into the hole. Latex flows in rapidly and the pressure is estimated from the difference between the initial and final lengths of the air column in the capillary. Maximum pressure is usually attained within 10 minutes.

Figure 1 illustrates the pressures observed when measurements were made at 3-hour intervals for 1½ days at two heights (50 and 950 cm above ground) on the trunk of a large untapped seedling tree. Five fresh manometers were used for each reading; the maximum pressure observed (rather than the mean) has been taken as the best estimate of the true pressure. During the 1st day, which was fine and sunny, pressure fell to a minimum by 1500 (3 p.m.) and then rose again to become more or less constant during the night. On the 2nd day, the

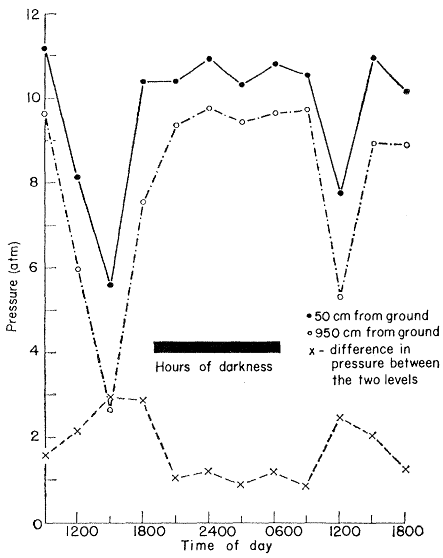

Fig. 1. Diurnal changes in hydrostatic pressure recorded at two heights on the trunk of a tree of *Hevea brasiliensis*.

pressure fell steadily until midday, but recovered again after a heavy rainstorm at 1220. This diurnal fluctuation in pressure has been amply confirmed in several experiments, although it is highly sensitive to weather conditions.

Hydrostatic pressure at the lower level on the tree is always greater than that at the upper position (Fig. 1). We have detected no direct influence of girth size on observed hydrostatic pressure and therefore conclude that this height effect is not an artefact occasioned by the smaller volume of laticiferous tissue at the high level. As a consequence of the "head" of latex, which has a specific gravity close to one, it might be expected that the pressure at the lower point would exceed that at the higher by approximately 1 atmosphere. At night, the observed difference does, in fact, approach this figure. It may be supposed that this hydrostatic pressure difference is counterbalanced by a corresponding difference in osmotic pressure; otherwise water would be lost from the vessels at the base of the trunk, owing to the excess pressure.

During the day, pressure falls more rapidly near the top of the tree than near the ground, so that the pressure difference between the two levels increases. Reduction in turgor pressure of the latex vessel system during the daylight hours is most probably brought about by loss of water to the xylem, although contraction of the wood under transpirational tension may have an effect, by relieving the pressure within the encircling bark (which may be thought to be under a peripheral, elastic, tension at night). In either case, the production of a steeper pressure gradient during the day would seem to reflect a considerable tension gradient in the xylem under conditions of rapid transpiration. The difference in pressure between the two levels reaches a maximum of 2.9 atmospheres; this figure is of the same order as estimates published previously for xylem tension gradients during active transpiration (*6*).

The diurnal variation in turgor pressure suggests a passive reflection of changes in xylem tension. It is of interest to consider what effect such changes in turgor of the phloem tissue might have on translocation. The latex vessel system and sieve tubes are closely associated elements of the phloem tissue in *Hevea* (*7*) and, in the absence of any active mechanism controlling sieve-tube turgor, one might expect the pressures in the two systems to be similar. For a simple form of Münch's pressure-flow hypothesis to operate in sieve tubes, a turgor gradient is required from crown to base in an actively growing tree. At no time does a significant gradient exist in this direction in our measurements. Thus if pressure-flow does operate, sieve tube turgor must be controlled by a separate mechanism.

A number of workers have observed gradients in the concentration of sieve-tube exudate (*5*, *8*), generally in the direction required for pressure-flow, but because of the probable loss of turgor due to transpiration, such determinations cannot be accepted as proof of the existence of turgor-pressure gradients. Direct measurement of sieve-tube turgor might be possible by the use of micromanometers in conjunction with the aphid-stylet technique (*9*), but the technical difficulties involved need no emphasis.

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References and Notes

1. J. W. Marvin, in *The Physiology of Forest Trees*, K. V. Thimann, Ed. (Ronald, New York, 1958), p. 96.
2. P. F. Scholander, B. Ruud, H. Leivestad, *Plant Physiol.* **32**, 1 (1957).
3. P. F. Bourdeau and C. S. Schopmeyer, in *The Physiology of Forest Trees*, K. V. Thimann, Ed. (Ronald, New York, 1958), p. 313.
4. J. P. Vité, *Contrib. Boyce Thompson Inst.* **21**, 37 (1961).
5. A. Frey-Wyssling, in *Deformation and Flow in Biological Systems*, A. Frey-Wyssling, Ed. (North-Holland, Amsterdam, 1952), p. 322; M. Zimmerman, *Plant Physiol.* **32**, 399 (1957).
6. O. Renner, *Ber. Deut. Botan. Ges.* **30**, 576 (1912); H. H. Dixon, *Transpiration and the Ascent of Sap in Plants* (Macmillan, London, 1914); M. Nordhausen, *Jahrb. Wiss. Botan.* **60**, 307 (1921); F. M. Eaton, *Plant Physiol.* **16**, 545 (1941).
7. W. Bobilioff, *Anatomy of* Hevea brasiliensis, C. Yampolsky, trans. (Orell Fussli, Zurich, 1923); H. Gunnery, *J. Rubb. Res. Inst. Malaya* **6**, 8 (1935).
8. B. Huber, E. Schmidt, H. Jahnel, *Tharandt. Forstl. Jahrb.* **88**, 1017 (1937).

J. S. Kennedy and T. E. Mittler, *Nature* **171**, 528 (1953).

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Circadian Rhythmicity in the Sensitivity of Two Strains of Mice to Whole-Body Radiation

Abstract. *When male mice of the Swiss-Webster and C_3H strains are maintained on a light-dark cycle in which the light begins at 7 a.m. and ends at 7 p.m., they are more sensitive to whole body x-irradiation (800 to 900 roentgens) given at 2 a.m. than at any other time in the cycle tested.*

The last 10 years have witnessed a considerable renewal of interest in the old observation that organic functions, typically executed once a day in the native state, continue to be executed with a nearly 24 hour rhythmicity in environments of constant light (or dark) and temperature (*1*). Halberg (*2*), and Pittendrigh (*3*, *4*) among others have emphasized the fact that these rhythms, typically assayed by "superficial" phenomena such as locomotory activity or leaf movement, are only reflections of an underlying rhythmicity that pervades the whole metabolic system. Daily—or circadian—rhythmicity, as it is now called, applies to enzyme systems, drug sensitivity, temperature tolerance, sensitivity to ultraviolet light, and other less easily assayed parameters of organisms, as demonstrated by several investigators. It has been emphasized repeatedly that the rhythmicity is an innate, inherent feature of physiological systems (*4*). Thus, circadian rhythmicity not only persists indefinitely with the period of about a day (hence, circadian) in constant conditions of light and temper-