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LOCAL VARIATION IN INTERGRADING ABIES GRANDIS–A. CONCOLOR POPULATIONS IN THE CENTRAL OREGON CASCADES.

II. STOMATAL REACTION TO MOISTURE STRESS

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ABSTRACT

Seasonal and daily patterns of xylem pressure potential (P) (measured with a pressure chamber) and stomatal opening (measured by an infiltration technique) were determined for four sapling populations, one of *Abies grandis* and three intermediate to *A. concolor*, in contrasting habitats in the central Oregon Cascades. Unexpectedly, populations east of the Cascade crest show higher P values (i.e., less moisture stress) than those from the west slope, where precipitation is greater and vegetation more mesic. Differences in daily and seasonal patterns of stomatal closure also occur among the populations studied. East-side trees show little daily variation in stomatal opening during daylight, but close somewhat in late season, even with little seasonal change in P. In contrast, stomata of low-elevation west-side saplings close considerably during each day, and the maximal daily opening decreases as P decreases. A high-elevation west-side population shifts from "constant-daily-opening" to "daily-closure" behavior as the summer progresses. On the west side, stomata of a low-elevation population close more rapidly as P decreases than those of high-elevation trees. Determination of leaf-resistance equivalents of infiltration pressures allows calculation of the magnitude of the possible effect of different stomatal patterns on water loss and on photosynthesis predicted from a mathematical model. Assumption of an east-side (constant-daily-opening) pattern by a low-elevation west-side tree would increase calculated transpiration and photosynthesis by 1.6 to 1.7 times. Such phenotypic differences in stomatal behavior of populations should be considered in modeling plant processes.

Introduction

In the central Oregon Cascades, populations intermediate between *Abies grandis* and *A. concolor* are widespread (Lacaze and Tomassone 1967; Daniels 1969; Hamrick and Libby 1972). The degree of intermediacy varies in relation to topography and inferred climatic patterns (Zobel 1973). The great habitat variability in the study area and the marked morphological response to it lead one to expect comparable differences in some physiological characteristics of these intermediate populations.

The reaction of stomata to environment is of particular interest because it may greatly modify rates both of transpiration and of photosynthesis; thus, the reaction is an important link in adaptation of a plant to its habitat. The reaction of stomata to plant-moisture stress varies among northwestern conifers adapted to different habitats (Lopushinsky 1969) and might be expected to vary within wide-ranging species also.

This paper describes variation in plant-moisture stress and stomatal reaction to moisture stress of native sapling firs in four contrasting environments in the central Oregon Cascades. Although these populations vary in their resemblance to *A. concolor*, for convenience they all will be called "grand fir" in this paper.

Site description

The populations studied were "intensively" sampled for morphology by Zobel (1973). Their location and site characteristics are given in table 1. Two populations occur west of the Cascade crest: (*a*) Delta is on a river terrace at low elevation between Blue River and McKenzie Bridge and represents "typical" *Abies grandis;* and (*b*) Lookout is in the H. J. Andrews Experimental Forest, on a sparsely forested rocky slope at high elevation, and shows a small amount of *A. concolor* morphology. The other two populations occur on Black Butte, a large

TABLE 1

ATTRIBUTES OF SAMPLING SITES AND TREES

			BLACK BUTTE	
	DELTA	LOOKOUT	BBN	BBS
Latitude (N)	44°10′	44°12′	44°24′	44°24′
Longitude (W)	122°17′	122°07′	121°38′	121°38′
Location from Cascade crest	39 km west	27 km west	18 km east	18 km east
Elevation (m)	350	1370	1570	1640
Topographic position	River terrace	Rocky slope	Slope	Slope
Aspect and slope	Flat	120°, 70%	350°, 61%	102°, 36%
Estimated precipitation (cm)	178	280	134	143
% full sunlight	13	35	12.5	36.5
Stand basal area (m^2/ha)	38.0	11.3	45.0	16.0
Stand dominants (and maximum age in years)	*Pseudotsuga* (ca. 400); *Libocedrus* (ca. 140)	*Pseudotsuga* (85); *Abies grandis*	*Pinus ponderosa* (225); *Pseudotsuga* (170); *A. grandis* (148)	*P. ponderosa* (128)

isolated volcanic cone east of the main Cascade range: (*a*) BBN is on a densely forested north slope and morphologically is very similar to the Lookout population; and (*b*) BBS is in open forest on a slope facing ESE. It resembles *A. concolor* considerably more than the other populations do (in periderm color and extent of stomata on the upper needle surface), but most trees are more like *A. grandis* than like *A. concolor*. There is considerable morphological variability within populations, especially the intermediate ones (ZOBEL 1973). These populations were chosen to represent variation in morphology and apparent moisture conditions of the habitat both east and west of the Cascade crest.

Percentage of full sunlight (table 1) at each sampling site was computed by dividing average energy received by eight to 12 ozalid paper sensors (FRIEND 1961) placed beside or in tops of fir saplings in each stand by energy received at two or three sensors placed in the open nearby. Data were taken at all sites on the same 2 clear days in late July.

Precipitation data (table 1) are derived as follows: (*a*) Delta: 18- and 10-year means were averaged from Blue River and McKenzie Bridge Ranger Stations, 7 km west and 11 km east of the plot, respectively; (*b*) Lookout: estimated from an isohyetal map of Oregon (SOIL CONSERVATION SERVICE 1964); (*c*) Black Butte plots: increase in precipitation with elevation was computed for several central Oregon locations from the isohyetal map. A weighted-average gradient (.13 cm m^{-1}) was used to adjust the map precipitation value for the elevation of the plot above the generally flat terrain surrounding the butte. This estimate is crude, at best. Basal area (table 1) was determined by the Bitterlich method, averaging readings taken with each of 10 1971 sample trees as a sample point.

Vegetation types which include the populations are: (*a*) Delta: *Pseudotsuga/Corylus cornuta–Symphoricarpos mollis/Polystichum munitum* community (HAWK 1973); (*b*) Lookout: not similar to any unit previously described—very scattered *Pseudotsuga* and younger grand fir share dominance; *Libocedrus decurrens* and shrubby *Quercus garrayana* are present. Between the trees there is a large variety of shrub and herb species, many of them associated with meadows at the same elevation. *Abies* reproduction is primarily uphill from *Pseudotsuga* trees or in clumps of *Quercus* or other shrubs; (*c*) BBN: *Abies grandis/Castanopsis/Chimaphila* community (SHERMAN 1969); and (*d*) BBS: *Pinus ponderosa/Arctostaphylos-Ceanothus/Pteridium* community (SHERMAN 1969), at the southern limit of grand-fir reproduction on Black Butte.

Delta soils are loam to sandy loam of the Haflinger series, cobbly loam phase (HAWK 1973), with considerable stoniness below 45 cm. Lookout soils are stony, and the bedrock is shallow, where not exposed. Black Butte soils are all structureless loamy sands (SHERMAN 1969). Rooting appears to be fairly deep, and there is little or no runoff. The surface soil dries rapidly following precipitation or snowmelt, especially at BBS, and appears to act as a mulch, reducing water loss from deeper layers. Sampling in mid-August 1970 showed soil-water contents below 15 cm as well within limits of "available water" defined by SHERMAN (1969), and in some cases nearly at field capacity. The surface soil was dry and powdery. It apparently dries rapidly and thoroughly enough to discourage seedling establishment, as attempts to establish seedlings by both sowing and planting required midsummer watering for even modest success.

A fifth population was sampled only for stomatal aperture in 1971. These trees at 1,450 m in the Ochoco Mountains, 100 km east of Black Butte, bear considerable resemblance to *A. concolor* (Zobel 1973).

Sampling years varied. July-August rainfall in 1969, 1970, and 1971 was 11%, 1%, and 100%, respectively, of the 10-year average on the west side and 50%, 120%, and 30%, respectively, of the average on the east side, based on data from the nearest weather stations, McKenzie Bridge (west side) and Sisters (east side). The latter is in a zone of considerably less rainfall than the Black Butte stands, where summer rainfall normally is from thundershowers; thus, data from Sisters may not reflect conditions on Black Butte.

Methods

Xylem pressure potential.—Seasonal patterns of plant-water potential were estimated in 1969 and 1970 by measuring five trees per site on 4–6 days each summer.

Water potential of trees was estimated as pressure potential of the xylem sap (*P*) with a pressure chamber (Scholander et al. 1965). The *P* should differ from sap-water potential by the solute potential of the xylem sap, which is usually small (Boyer 1967). Values of *P* are negative, so that a lower (more negative) *P* means greater plant-moisture stress.

Measurements were made on saplings 1–3 m tall. Occasionally, larger trees were measured for comparison, and if there was little difference from saplings, all data were used in site averages. At BBS, five small seedlings and one 10-m tree were also measured in late August 1971.

Only branches with considerable current-year growth were used. The most deeply shaded branches were sampled, since the shaded condition varied less with time and place than the condition of the most exposed twigs. In a preliminary study, shaded twigs showed significantly less stress than unshaded twigs. Variation in *P* within the crown (Hinckley and Ritchie 1970; Hinckley and Scott 1971) was minimized by sampling only shaded twigs of small trees. One twig per tree was sampled unless a measurement did not fit the general pattern at that site and time. If repeated readings differed considerably, the less negative *P* was used.

Sampling for seasonal changes in *P* was done just before dawn, a time when *P* should be highest and should best reflect the soil-moisture status of the area (Waring and Cleary 1967; Klepper 1968). When the predawn *P* was not the highest measured that day (as often found at Delta), the higher *P* was used as the maximum daily *P*. During the summers of 1969 and 1970, *P* was also determined just following stomatal aperture measurements, usually five times between 0630 and 1600 hours (standard time). In 1971, it was measured on 10 trees before dawn and at the approximate time of greatest water stress (lowest *P*) on that site, determined from previous sampling. Sampling was confined to clear or nearly clear days, with one exception, noted later.

Where feasible, the same trees were reused, at least during 1 year. The trees at BBN have few live branches and some new trees were selected in midseason. Most trees used in 1969 were not reused in 1970, to avoid excessive depletion of their crowns (removal of about one-fourth of their year-old foliage would be "excessive"). In 1971, with only two whole-twig samples for *P* each day, most sample trees from 1969 and 1970 were reused.

Stomatal reaction to xylem pressure potential.—Preliminary sampling for stomatal aperture in 1969 used only two needles from each of five trees, but indicated a possible population difference in rate of stomatal closure with decrease in *P*. Sampling in 1970 was done on five trees per plot, and *P* determinations were made immediately following measurements of stomatal opening, five times each sample day, 2 hr apart, starting well after sunrise (0630–0730). Each sampling took about 1 hr. These results showed population differences in diurnal patterns of stomatal closure. In 1971, sample size was increased to 10 trees, to try to confirm the diurnal patterns, and pressure-chamber readings were decreased to two—before dawn and in midday. Number of sample days was reduced from 4–6 to 1–3 per site because of weather and the emphasis on diurnal changes.

Stomatal aperture of conifers can be determined only indirectly. The pressure-infiltration technique of Fry and Walker (1967), which works satisfactorily with grand fir (Lopushinsky 1969), was used in this study. "Infiltration pressures" (*IP*), determined by the instrument, are related to the transpiration rate of conifer seedlings, and therefore presumably to stomatal aperture. The technique depends on a subjective decision about when a needle is "infiltrated," so that comparison of exact *IP* values among investigators is not possible. Infiltration pressures were determined while pressure automatically increased at .07 bar sec^{-1}. The instrument would not stand high pressures, so that all high *IP*s could only be recorded as "above 2.76 bars." At this *IP* transpiration of Douglas-fir is very small (Fry and Walker 1967).

The *IP* was usually determined on year-old needles, since the current-year twigs at some sites were still expanding during the study periods. Preliminary measurements indicated that year-old foliage had higher *IP*s than new foliage in 71% of 152 single-needle comparisons. In 1970 and 1971, one needle from each of five branches throughout the shaded crown of the tree was sampled each time. The five *IP* values were averaged to give a single-tree value for that time. Shaded needles had slightly, but significantly, lower *IP* values (0.1 bar) than unshaded needles in a preliminary experiment.

Differences in *IP* within the crown, found in other species (HINCKLEY and RITCHIE 1970; HINCKLEY and SCOTT 1971), showed no consistent pattern from tree to tree. Since most trees were small, the sampling pattern used should yield an approximate average *IP* for the shaded part of the crown.

To compare the daily *IP* patterns between sites, the standard deviation (V_{IP}) of *IP* values for each tree on each sample date was computed. The mean V_{IP} was then determined for each sample date on each site.

To look at nighttime patterns of stomatal opening, three trees each on the west and southeast sides of Black Butte were sampled about every 2 hr from late afternoon to the following midmorning on September 9–10, 1970. Three trees near the Delta site were sampled similarly on August 27–28, 1970.

INFILTRATION-PRESSURE–LEAF-RESISTANCE RELATIONSHIPS.—Three trees per site were sampled at BBS and BBN on July 23, 1971; at Lookout and Delta on August 3; and at all sites except BBN on September 8, 1971. Twigs were cut from 1–3-m trees and placed with their bases in water in a dark and humid environment for transport to the laboratory. The relationship between *IP* and transpiration was usually determined within 24 hr of excision. Pieces of twig with year-old foliage were cut from the foliage samples and the cut ends sealed. Twigs were hung vertically in a 1.3–1.4 m sec^{-1} airstream, in a controlled-environment room. Water loss was measured by weighing at the beginning and end of 10-min periods, 15–30 min apart. The *IP* of two needles per twig was determined immediately after each period. Temperature and humidity in the airstream were measured periodically with a psychrometer. Leaves were assumed to be at air temperature, and light intensity was about 1,200 ft-c. Leaf area was determined on dried needles with a photoelectric planimeter (GEPPERT 1968). Boundary-layer resistance was small, 0.11 sec cm^{-1} (calculated as in SLATYER 1967, pp. 242–243, 248, for largest needles used and wind of 1.4 m sec^{-1}). Therefore, leaf resistance (r_L) was estimated by dividing vapor-pressure deficit (g cm^{-3}) by rate of water loss (g cm^{-2} sec^{-1}). Because of the variability of the data, and possibly great mesophyll resistance in grand fir (HODGES 1967; LOPUSHINSKY 1969), stomatal resistance was not calculated separately from leaf resistance.

Water loss was computed for two Delta trees (using their stomatal *IP* patterns of July 18, 1970 and August 31, 1970) and two BBS trees (for September 15, 1970) by use of (*a*) the *IP*-r_L relationships determined in 1971 and (*b*) vapor-pressure deficit (*VPD*) patterns of 1 late summer day each at Delta and BBS. Computations were made for each half-hour period from 0645 to 1545, and summed to give a 9-hr total. (In some cases the *IP*-r_L relationship had to be extrapolated below measured *IP* values.) Environmental data taken for several weeks in 1971 indicated that the BBS day was somewhat less humid than average for late August but certainly not exceptional, whereas the Delta day was representative for the site and season.

Photosynthesis of one Delta tree was calculated for both its measured stomatal pattern and a hypothetical pattern. Rates were predicted from a mathematical model of photosynthesis (LOMMEN et al. 1971, fig. 3) using (*a*) temperature patterns of the same days used to estimate water loss and (*b*) the *IP*-r_L relationships for resistance to water loss of the tree used. Although resistance to CO_2 is not the same as to water, the daily pattern of changes in resistance should be similar.

Results

XYLEM PRESSURE POTENTIAL.—In 1969, a moderately dry year, distinct differences occurred between sites. Black Butte populations had higher xylem pressure potential (*P*) (i.e., less moisture stress) in late summer than west-side populations, the opposite of the pattern anticipated. In 1970, an exceptionally dry summer on the west side, the differences between the west side and Black Butte increased (fig. 1), and Delta was drier than Lookout. Early September rains broke the drought on the west slope and increased *P* at Delta to early summer levels (fig. 1), but were very light on Black Butte. In 1971, general measurable rains occurred on the west side on July 10 (3 mm at Blue River), July 30–31 (2 mm), and August 22 (16 mm). All measurements of predawn *P* were at or above -7.5 bars. However, sampling missed the end of the longest west-side dry period (22 days).

Daily fluctuation of *P* in 1969 and 1970 was reduced as predawn *P* declined, averaging 8.0 bars when predawn *P* was above -10, but only 2.9 bars when predawn *P* was below -20 bars.

Differences in *P* associated with tree size were explored at BBS. Comparisons of predawn and early-afternoon *P* show a larger tree having *P* 2–3 bars higher and the smaller trees 1–7 bars lower than the average of 1–3-m trees. Even the smallest tree sampled (31 cm) did not show what could be considered high stresses (-13.8 bars at predawn and -20.3 bars in midafternoon).

STOMATAL CLOSURE PATTERNS.—Data taken in 1969 showed that stomata were more closed at a given *P* in the river-terrace population at Delta than in the high-elevation Lookout population. More extensive sampling in 1970 confirmed this finding

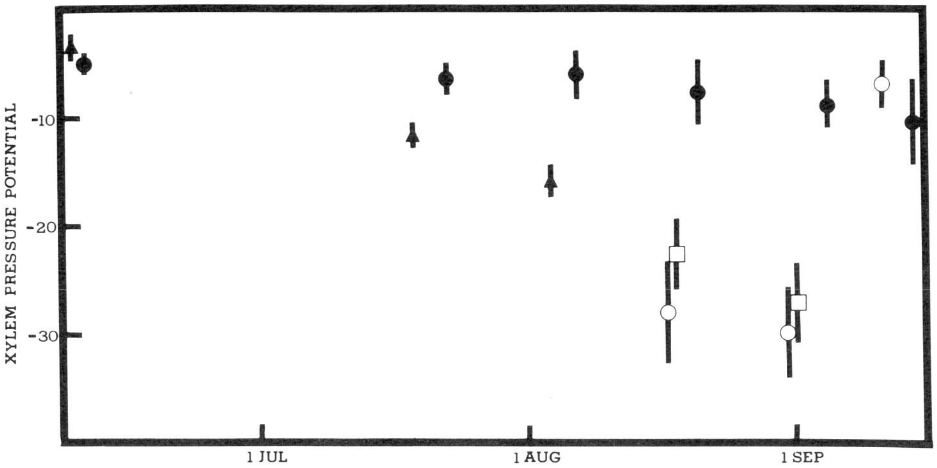

FIG. 1.—Predawn xylem pressure potential (P, in bars) of grand fir populations (n = 5) in 1970. Solid circles are averages for BBN and BBS. Triangles are averages for Delta and Lookout when they were similar. Open circles are for Delta, and squares for Lookout. Vertical bars given ± standard deviation.

(fig. 2). On Black Butte, P was high in both summers, and such a difference between BBS and BBN was not discernible.

In 1970 and 1971 the daily sequence of IP changes showed two contrasting patterns: (a) Daily closure—a strong daily stomatal closure (increased IP) is associated with the daily decrease in P in the early season, and a rapid increase in minimal daily IP with the seasonal decrease in P (e.g., fig. 3). "Closure" indicates a large increase in IP during the day; it does not imply that stomata always close completely. (b) Constant daily opening—little daily closure of stomata occurs (constant IP), despite diurnal changes in P, and a gradual seasonal increase in IP occurs, despite the small seasonal decrease in P (e.g., fig. 4).

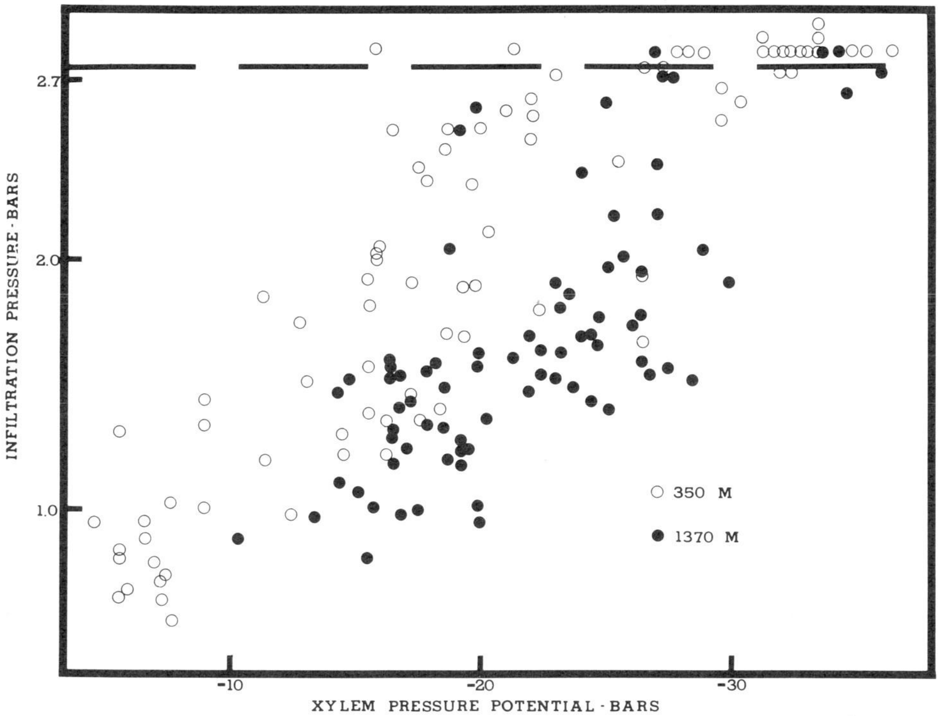

FIG. 2.—Relationship of stomatal infiltration pressure (IP) to xylem pressure potential (P) at Delta (350 m) and Lookout (1,370 m) sites in 1970. Data in which IP decreased following P increase in late afternoon are omitted from this figure. The broken horizontal line is at 2.76 bars, the upper limit of measurable IP.

Trees at Delta showed a daily-closure pattern (figs. 5*D*, 6*E*). Black Butte trees showed a constant-daily-opening pattern (figs. 5*A*, 5*B*, 6*B*, 6*C*). High-elevation, west-side trees at Lookout varied considerably. Generally, early-season stomatal patterns showed constant daily opening, while in late season stomata showed daily closure (figs. 5*C*, 6*D*). The Ochoco Mountain population was similar to the Black Butte populations (fig. 6*A*). In 1971, when all sites had similar *P* values, the same type of population differences in stomatal-closure pattern occurred as in 1970, when *P* varied greatly with the site (cf. figs. 5, 6).

Comparisons of yearly average V_{IP} values showed Delta had significantly larger daily variation in *IP* than Lookout, and Lookout V_{IP} was larger than Black Butte, in both 1970 and 1971 (*t*-test, .01 level).

The most stomatal closure between sampling dates at Lookout took place in 1970 from mid-July

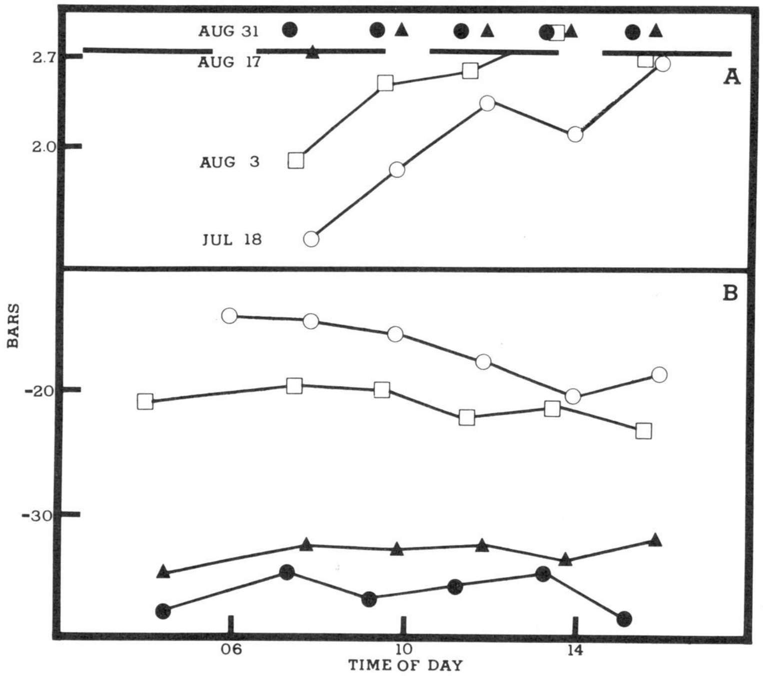

FIG. 3.—Daily pattern of *A*, infiltration pressure (*IP*) and *B*, xylem pressure potential (*P*) for one tree at Delta, 1970. The broken horizontal line in *A* is at 2.76 bars, the upper limit of measurable *IP*. Symbols in *B* represent the same dates that they do in *A*.

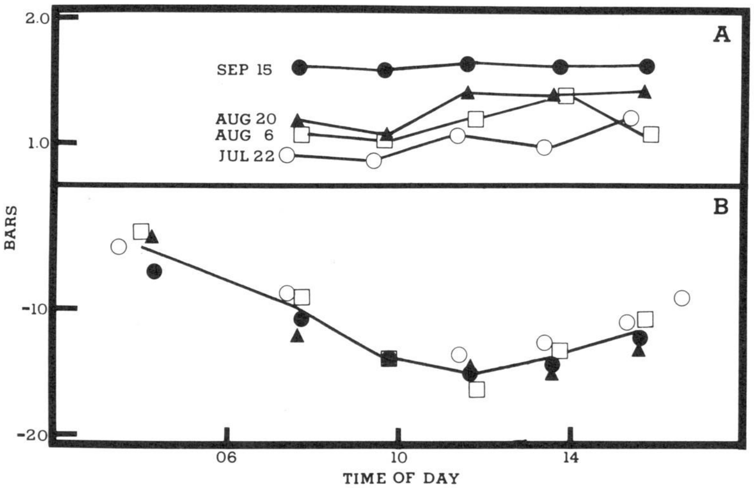

FIG. 4.—Daily pattern of *A*, infiltration pressure (*IP*) and *B*, xylem pressure potential (*P*) for one tree at BBS, 1970. The *P* varied little during the season; the line represents an average for all dates. Symbols in *B* represent the same dates they do in *A*.

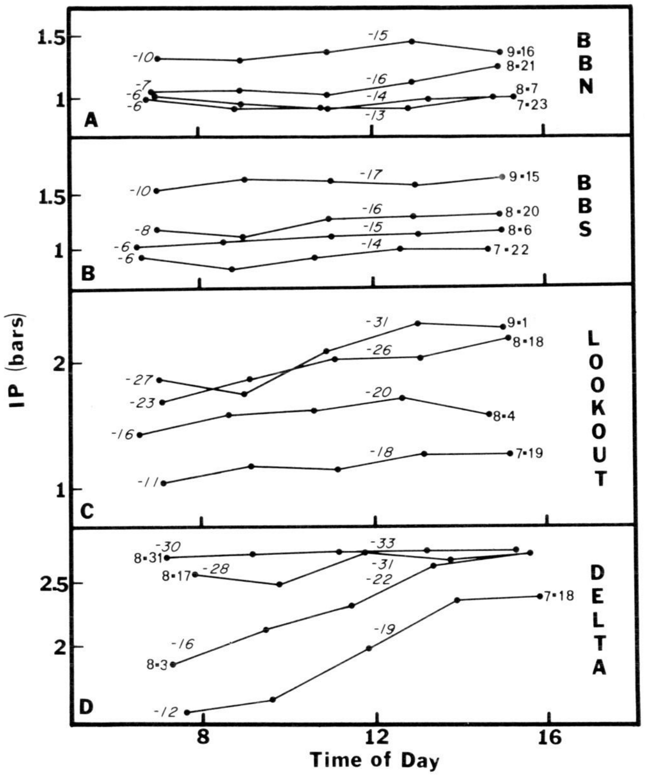

FIG. 5.—Daily patterns of average infiltration pressure (n = 5) at all sites in 1970. Negative numbers with each line give the average predawn P, and the average midday P (in bars) for each sample day. Note that the IP scale differs for the various samples.

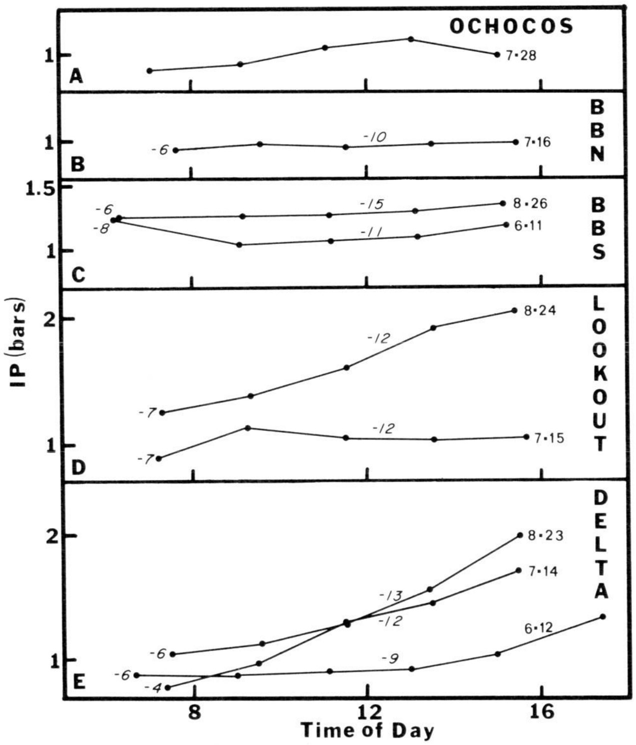

FIG. 6.—Daily patterns of average infiltration pressure (n = 10) at all sites in 1971. June 12 at Delta was a uniformly overcast day. Negative numbers with each line give the average predawn P and the average midday P (in bars) for each sample day. Note that the IP scale differs for the various samples.

to mid-August. At Black Butte it occurred after mid-August (fig. 5). Average daily *IP* ($\overline{IP}$) in populations with relatively constant daily stomatal opening increased as predawn *P* ($P_{\max}$) decreased in 1970. Simple linear regressions were significant: Lookout: $\overline{IP} = 8.9 + .0567\ P_{\max}$, $r^2 = .69$ for $P_{\max} = -9.0$ to -27.2 bars; pooled Black Butte data: $\overline{IP} = 9.5 + .0664\ P_{\max}$, $r^2 = .38$ for $P_{\max} = -4.8$ to -11.7 bars.

The *IP* at a sampling time varied considerably among trees within some populations. The midday range in *IP* within the west-side sites sometimes exceeded 1 bar when *P* was high; some trees had closed their stomata considerably when the closure of others was just beginning. Stomatal *IP* within the Black Butte populations was generally more homogeneous; the range in *IP* among trees at a given time seldom exceeded a half-bar. Despite the variation in absolute *IP*, the closure patterns at a site fairly consistently followed the site average (figs. 5, 6); exceptions usually involved only a single tree for a given sample date.

Nighttime stomatal behavior varied considerably; it was probably influenced by *P*. Stomata on three Delta trees sampled were closed all night ($P_{\max}$ averaged -26 bars). In only one of these had stomata opened appreciably by 1000 hr the next morning. The *IP* of trees sampled near BBS increased rapidly after dark, but then began to decrease before midnight. By 0200, values were similar to those the previous afternoon. During this decrease, *P* was low and virtually constant (average $P_{\max} = -4.7$). On the west slope of Black Butte, *IP* of only one tree decreased after closure during the dark period, and almost all stomatal opening occurred after dawn ($P_{\max}$ averaged -9.3 bars).

INFILTRATION-PRESSURE–LEAF-RESISTANCE RELATIONSHIPS.—The effect of *IP* on transpiration is not linear in *Pseudotsuga* (FRY and WALKER 1967). To determine the significance of patterns of *IP*, its relationship to water loss or leaf resistance (r_L) was investigated.

As *IP* increases, so does r_L. Individual trees showed a variety of patterns of r_L with increasing *IP* (for September data, see fig. 7). The variation within the three-tree samples at each site was large in all cases.

Calculated gas exchange varies considerably with environment and stomatal pattern. The BBS environment results in water loss about three times that of the Delta environment. If Delta trees were to assume a constant-daily-opening stomatal pattern (with *IP* remaining constant once it has reached its minimum value), water loss and photosynthesis in both environments would be 1.6–1.7 times what they are with a daily-closure pattern.

Discussion

PATTERNS OF XYLEM PRESSURE POTENTIAL.—The difference in the seasonal patterns of xylem pressure potential between east-side and west-side sites was

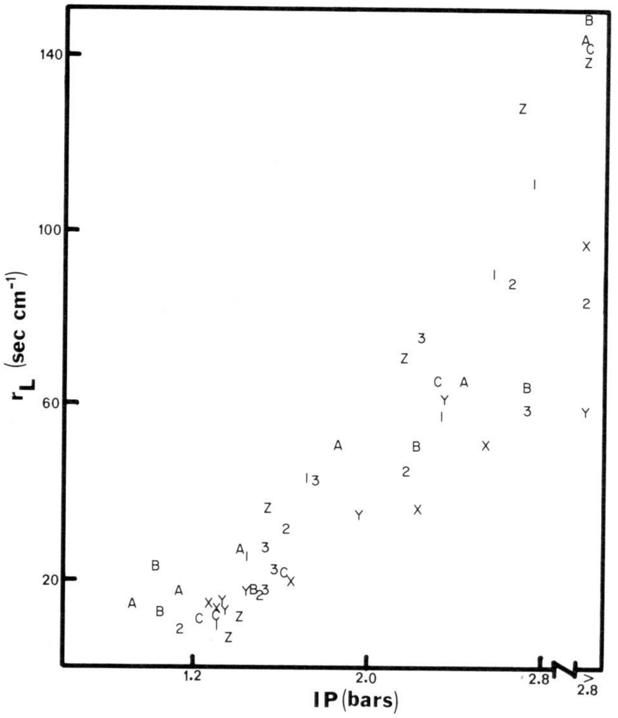

FIG. 7.—Relationship of leaf resistance to transpiration (r_L) and infiltration pressure (*IP*) of three trees each from BBS, Delta, and Lookout, collected September 8, 1971. *A*, *B*, *C* represent Delta twigs; *X*, *Y*, *Z* are from BBS; and 1, 2, 3 are from Lookout.

the reverse of that anticipated from regional environment and vegetation. Nature of soils on the sample sites may be responsible for this discrepancy. The deep soils on Black Butte appear to dry only superficially even in dry years, but the surface layer of soil dries rapidly and completely. This dry surface soil may be a strong barrier to seedling establishment. However, once a seedling has its root system below the zone of rapid drying, water stress apparently is of minor importance compared with that in dry years on the west side, even for trees shorter than 0.5 m. There has been no evidence of sapling death from drought. Similar situations probably occur elsewhere in the recent volcanic soils east of the Cascade crest (C. T. YOUNGBERG 1972, personal communication). At the west-side areas, the soil-water reservoir is limited by shallow soil (Lookout) and high stone content (Delta). Vegetation cover at Delta is much greater than on the other sites, increasing the rate of soil-water depletion. Some saplings (no sample trees) up to several meters tall died at both west-side sites during the dry summer of 1970, almost surely as a result of drought.

A high predawn P in late summer, as found at Black Butte, is apparently common for conifers on the volcanic soils just east of the central Oregon Cascades (MASON and TIGNER 1972; STEVEN KEYS and D. B. ZOBEL, unpublished data).

STOMATAL BEHAVIOR.—The differences in stomatal closure patterns described here are within what many might consider, for all practical purposes, a single species. The existence of such differences should suggest caution to those who model plant processes, as modeling may often involve extrapolation from one provenance to another, or even farther. In the simple models used here, the assumption of the wrong pattern of stomatal opening led to errors of 60%. Population differences in physiology are difficult to define; however, failure to compensate for them, or to demonstrate their absence, could easily cause larger errors in modeling gas exchange. Some modelers (e.g., LOMMEN et al. 1971) also ignore the effect of moisture stress on stomatal closure, which would lead to further errors.

Xylem pressure potential affected stomatal behavior in this study, as might be expected from the rapid stomatal response of other species to changes in water potential (RASCHKE 1970). However, there is considerable evidence that these population differences are not completely determined by differences in the site environments. The contrasting stomatal-closure patterns found in 1970 were repeated in 1971, a summer with high P at all sites. One Delta tree in a distinct microenvironment maintained both a high P and a daily stomatal-closure pattern all summer in 1970. A uniformly cloudy day (June 12, 1971, fig. 6) resulted in a delayed and reduced increase in IP in all Delta trees, but the pattern was still present. The apparent shift from little daily IP change early in the season to more daily closure late in the season at Lookout was maintained in 1971, with no decrease in P between the dates. Low humidity may also cause stomatal closure (LANGE et al. 1971); however, in the present study the least humid sites—on Black Butte (ZOBEL 1974)—were also those where stomata closed the least.

Stomatal closure influences P (HINCKLEY and RITCHIE 1970), as well as being influenced by P. When stomata reopened late in the day, apparently as a result of higher P allowed by earlier stomatal closure, the data points were not included in the IP-P relationships or calculations of daily variability in IP.

Stomatal effects on plant processes have often been demonstrated (e.g., CALDWELL 1970; WAGGONER and TURNER 1971). Stomatal closure by dry-site *Pseudotsuga* in southern Oregon may reduce seasonal transpiration to 30% of its value on sites where stomata do not close (REED and WARING 1974). In this study, calculated transpiration and photosynthesis of Delta grand fir for 2 days was only about 60% of what it would have been had they a stomatal pattern like that of the east-side trees.

SOURCES OF VARIATION IN STOMATAL BEHAVIOR.—It cannot be determined from this study whether these stomatal patterns have a genetic basis, with stomatal control systems differing in sensitivity to the environment, or whether they represent the effects of different environments on the same control system. There is some field evidence for stability of these stomatal patterns with changing environment, as discussed above. Intraspecific variation in stomatal closure patterns has been reported in *Erica* and *Calluna* (BANNISTER 1971), although these differences are not necessarily genotypic, either.

HAMRICK and LIBBY (1972), in their study of genetic variation in *Abies concolor* seedlings, found that local habitat (i.e., elevational) variation in growth and phenological characteristics was greater than that in morphology. Needle morphology differs considerably from BBN to BBS populations, with BBS trees having more and longer rows of adaxial stomata (ZOBEL 1973). There is little evidence of a parallel difference in stomatal behavior, a more clearly adaptive character. However, little difference in selective pressure for stomatal behavior probably exists for trees of the size used, since P remained high in both habitats. Seedlings might be exposed to greater differences in moisture stress, since BBS and BBN differ in aspect and shading. The change in stomatal reaction from Delta to Lookout to BBS does parallel that in morphology, with Lookout somewhat intermediate between the others in both respects.

Determination of the degree of genetic control over stomatal-closure patterns might be of considerable importance. Discovery of strong genetic control should limit the movement of provenances in forestry, for example.

EFFECT OF SAMPLE PROCEDURES.—Results of a study of this nature are greatly influenced by place, time, and method of sampling. This study included summer periods of 3 weeks without rain (1971) to about 9 weeks without rain (1970), reflected in the P values at west-side sites. Choice of particular sample areas may also affect conclusions. Vegetation at Delta and Lookout sites represents the drier end of the ranges of grand fir in their respective zones. Grand fir trees within 100 m of the Delta site, on a lower terrace with denser forest and more mesic ground-cover species, could conceivably have much different levels of P. Sampling drier environments in a study of adaptation to water stress is certainly preferable to sampling wetter areas, but the P values given should not be accepted as average values reached by similar saplings in all habitats in one section of the study area.

Determination of r_L-IP relationships has numerous probable and possible sources of error: (*a*) whether shoots cut hours before transpire at rates near those in nature is questionable at best; (*b*) variation in growth-chamber environment was greater than desirable, so that vapor-pressure deficits may have changed between times of measuring individual branches; (*c*) low water-loss rates may result from exhaustion of twig water (considerable cortical shrinking occurred during measurements) as well as changes in leaf resistance; (*d*) leaf area may decrease during drying; (*e*) leaf resistances may be caused by factors not assessed by the IP method, such as mesophyll resistance and wax in stomatal pores and on leaf surface (HANOVER and REICOSKY 1971; JEFFREE, JOHNSON, and JARVIS 1971), or variable numbers and behavior of adaxial stomata.

In favor of the analysis done here is the use of field-grown twigs to determine the r_L-IP relationship. Morphology and physiology of cultured seedlings, usually used for this type of determination, depend considerably on the conditions of growth. Such preconditioning effects reversed the relative transpiration rates of two provenances of *Pseudotsuga* (RUETZ 1968; UNTERSCHUETZ 1970). The errors mentioned above should preclude use of the actual rates calculated with the simple models of transpiration and photosynthesis in this investigation. However, no obvious differences occur between populations in the r_L-IP relationship; thus, the differences in rates depend primarily on the variability in the daily patterns of IP. The relative differences in calculated gas exchange are probably not much affected by the deficiencies in technique cited above.

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