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Conifers and broadleaf species: stomatal sensitivity differs in western Oregon

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Increasing stomatal closure was exhibited by two conifer and six broadleaf species as vapor pressure deficit increased. Conifers were more sensitive to high vapor pressure deficit than were the broadleaved species. One shrub, snowbrush (*Ceanothus velutinus* Dougl. ex Hook.), exhibited no stomatal closure as vapor pressure deficit increased. These traits, when interpreted in terms of known soil moisture depletion patterns, help explain why broadleaved species initially colonize disturbed areas in western Oregon, but are later replaced by long-lived conifers.

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Une diminution de l'ouverture des stomates s'est manifestée chez deux essences conifériennes et chez six essences feuillues suivant l'élévation du déficit de tension de vapeur. Comparativement aux essences feuillues, les essences conifériennes étaient plus sensibles aux forts déficits de tension de vapeur. Chez une essence arbustive, le *Ceanothus velutinus* Dougl. ex Hook., l'élévation du déficit de tension de vapeur ne s'est pas traduit par la fermeture des stomates. Ces traits particuliers, quand interprétés en termes de patterns de déperdition en humidité du sol, permettent d'expliquer pourquoi les essences feuillues colonisent initialement les zones perturbées dans l'ouest de l'Oregon, qui, part la suite font place aux essences conifériennes à long cycle de vie.

[Traduit par le journal]

Introduction

The native forests of the Pacific Northwest region of North America are dominated by several species of massive, long-lived, coniferous trees that accumulate exceptional amounts of biomass (Waring and Franklin 1979). Many of the 25 coniferous species represent the largest and longest lived of their genera. In contrast, the hardwood flora is impoverished and occurs primarily on the wettest sites and in early successional stages, contributing less than 1% of the total standing biomass (Franklin and Dyrness 1973; Waring and Franklin 1979). This is a reversal of the normal temperate zone successional sequence, in which conifers are replaced by hardwood species and remain dominant only on infertile, cold, or droughty sites (Franklin and Dyrness 1973).

Winter temperatures in the Pacific Northwest are one factor in that reversal. Waring and Franklin (1979) point out that, whereas the climate of the Pacific Northwest is considered temperate at lower elevations, winters are milder and summers drier and less humid than are typical of temperate zones. The mild winters allow the evergreen conifers to maintain significant photosynthetic rates throughout the winter. Carbon assimilation between October and May may account for more than 50% of the annual total (Emmingham and Waring 1977). During the same period, deciduous species are unable to assimilate carbon. Mild winter temperatures may partially explain eventual conifer dominance, but do not explain why the broadleaved species flourish in early successional stages and on wet sites.

A study was started in the summer of 1977 to characterize the stomatal responses of nine common species in the Cascade Mountains of western Oregon. This paper addresses the question of whether differences in stomatal response patterns can partially explain the unusual distribution of species observed in the Pacific Northwest.

Methods and materials

The study sites were in the H. J. Andrews Experimental Forest in the western Cascade Mountains 70 km west of Eugene, Oregon (44° N, 122° W). Two watersheds 4 km apart and at elevations between 500 and 1000 m were selected. In one watershed, measurements were made in two sites: in a 15-year-old clearcut, and beneath a 450-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) canopy. In the second watershed, a 3-year-old clearcut was sampled. All three sites had deep soils and were located on steep slopes.

Six areas, along a transect with aspects ranging from south to west, were sampled in both the 15-year-old clearcut and beneath the old-growth canopy. In the 3-year-old clearcut, 12 sample areas were selected across a southwest-facing slope.

All species found in significant numbers on each area were measured. This analysis, however, is restricted to the nine species for which adequate data were obtained. These species included the following: a deciduous shrub, vine maple (*Acer circinatum* Pursh); four evergreen broadleaf shrubs, Oregon-grape (*Berberis nervosa* Pursh), snowbrush (*Ceanothus velutinus* Dougl. ex Hook.), salal (*Gaultheria shallon* Pursh), and Pacific rhododendron (*Rhododendron macrophyllum* G. Don); an evergreen broadleaf tree, golden chinkapin (*Castanopsis chrysophylla* (Dougl.) A.D.C.); a deciduous broadleaf tree, Pacific dogwood (*Cornus nuttallii* Aud. ex T. & G.); and two evergreen needle-leaf trees, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.).

Measurements were taken at each site about five times daily at intervals of 3–4 weeks from June 22 to October 11, 1977. Of the 21 days on which measurements were taken, 16 were clear throughout, 3 were mostly clear, and 2 were overcast. Daily maximum temperatures ranged from 16 to 35°C. Measured vapor pressure deficits (Δw) varied from 0.1 to 5.4 kPa.

A null-balance porometer (Beardsall *et al.* 1972) and an aspirated diffusion porometer (Turner and Parlange 1970) were used to assess stomatal behavior on selected conifer and broadleaf species throughout. Measurements by the two porometers agreed within 10%. Porometers consist of a chamber within which transpiring foliage is temporarily placed; temperature and humidity within the chamber are monitored. The null-balance porometer measures the flux of dried air required to offset the increase in humidity owing to transpiration. The

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TABLE 1. Regression equations relating stomatal conductance to vapor pressure deficit for each major species on two clearcuts. Coefficients followed by the same letter were not significantly different ($\alpha = 0.05$) as determined by covariance analysis ($R^2 = 0.80$)

Species	Intercept	Slope	*n*
Western hemlock	−0.69*a*	−0.28*a*	253
Douglas-fir	−0.70*a*	−0.26*a*	312
Salal	−0.90*b*	−0.23*b*	274
Golden chinkapin	−0.86*b*	−0.21*b*	135
Pacific dogwood	−0.70*a*	−0.20*b*	248
Pacific rhododendron	−0.91*b*	−0.15*c*	289
Vine maple	−1.18*c*	−0.15*c*	285
Oregon-grape	−1.13*c*	−0.13*c*	95
Snowbrush	−0.87*b*	+0.03*d*	127

TABLE 2. Average predawn water potential of conifers and broadleaved species in summer of 1977. Means followed by the same letter are not significantly different by the Student–Newman–Keuls test

Species	ψ_p (MPa)
Golden chinkapin	−0.25*a*
Pacific dogwood	−0.27*a*
Pacific rhododendron	−0.29*a*
Salal	−0.33*a*
Vine maple	−0.34*a*
Snowbrush	−0.34*a*
Western hemlock	−0.44*b*
Douglas-fir	−0.51*b*

aspirated diffusion porometer measures the time required for humidity inside the chamber to increase to a reference value. Either variable (dry-air flux or time) can be used to determine the water vapor flux from leaf to chamber and calculate the conductance through stomata.

Both calculations also require an accurate estimate of the leaf surface area in the chamber. The aspirated porometer used to sample broadleaved species sampled exactly 5 cm^2 of projected leaf area. Because leaves on all broadleaved species were hypostomatous, sampling was concentrated on the abaxial surfaces. Measurement of adaxial surfaces yielded low values ($<0.01\ \mathrm{cm\ s^{-1}}$). Abaxial measurements were averaged with a constant adaxial leaf conductance for each species to give conductance for the total leaf area.

The conifer foliage sampled by the null-balance porometer varied in leaf area. Therefore, repeated measurements of transpiration were obtained from 10 to 20 cm^2 (all-sided) of foliage throughout the day, after which the foliage was collected and brought to the laboratory for leaf area determination. Projected surface areas were determined using a LI-COR optical planimeter (model LI-3000). To obtain estimates of total surface area, projected surface values were multiplied by 2.36 and 2.14 for Douglas-fir and western hemlock, respectively (Gholz *et al.* 1976). Air temperature was measured with a ventilated thermistor, and dewpoint temperature with a shielded lithium chloride sensor. Instantaneous measurements of air temperature and dewpoint temperature were then used to calculate the vapor pressure deficit of the atmosphere (Δw) (Campbell 1977).

Xylem pressure potential was determined before dawn from a twig cut at 1–3 m from one plant of each species growing at each sampling area. Predawn water potential approximates soil water potential in the zone where roots are most actively extracting water (Waring and Cleary 1967). Predawn water potentials were compared among species using analysis of variance, with species as treatments in a completely randomized design, on all data collected throughout the summer. Means were compared using the Student–Newman–Keuls (SNK) test (Steel and Torrie 1980).

Regression analysis was used to relate stomatal conductance (g) to vapor pressure deficit (Δw) for each species, based on the demonstrated importance of Δw in previous studies (Running 1976; Whitehead and Jarvis 1981). Stomatal conductance may be further constrained by light, low temperatures, high CO_2 concentrations, or low water potentials (Whitehead and Jarvis 1981). We also attempted to relate stomatal conductance and daily maximum stomatal conductance to predawn water potential, using Δw and time of day as covariates (Steel and Torrie 1980). In both cases, it was necessary to logarithmically transform the conductance data to obtain homogeneity of variance across the range of the data (Steel and Torrie 1980). Regression lines were compared using covariance analysis (Neter and Wasserman 1974).

Diurnal variation in stomatal conductance was described for each species, using data from all sample dates, as a function of time, using regression analysis. It was again necessary to logarithmically transform the data to homogenize variance across the range of the data. Regression lines were again compared using covariance analysis (Neter and Wasserman 1974).

Results

Regression coefficients of equations relating log stomatal conductance to vapor pressure deficit (Δw) are presented in Table 1. The equations fitting the Douglas-fir and western hemlock data were not significantly different ($\alpha = 0.05$) (slope nor intercept). When compared with the broadleaved species, however, the conifers had higher intercepts than did all of the broadleaved species except Pacific dogwood. Moreover, the conifers had steeper slopes than did all of the broadleaved species.

Further differences were found among the broadleaved species, but the most striking difference was between snowbrush and the other broadleaved species. Whereas slopes of the Δw response curves were significantly different from zero for all other species, snowbrush showed no response to Δw.

We could demonstrate no significant effect of predawn xylem water potential (ψ_p) on stomatal conductance through regression analysis, even when Δw and time of day were included as covariates. Nonetheless, it did appear that ψ_p, had some effect on conductance values, if only at the most negative water potentials observed. Because 1977 was a wet year, however, the effect of drought was inconsequential when the data were analyzed as a whole.

Predawn water potentials, when compared over the entire sampling period, were significantly different among species. The differences, as tested by the SNK, were not significant either among broadleaf species or between conifer species (Table 2). The conifers were, however, significantly more negative (−0.48 MPa) than the broadleaf species (−0.31 MPa).

Diurnal curves relating log stomatal conductance to time of day and time of day squared are presented in Fig. 1. Of the species examined, snowbrush had highest conductance from early morning until late afternoon, with a peak at 1200 Pacific Standard Time (PST), 2–3 h later than most of the other eight species studied. The other species, with the exception of western hemlock, demonstrated remarkably similar conductance patterns with peaks at 0900–1000. Before 0800 and after 1800, conductance of western hemlock exceeded that of all other species.

Discussion

There are a number of adaptive features favoring the conifers

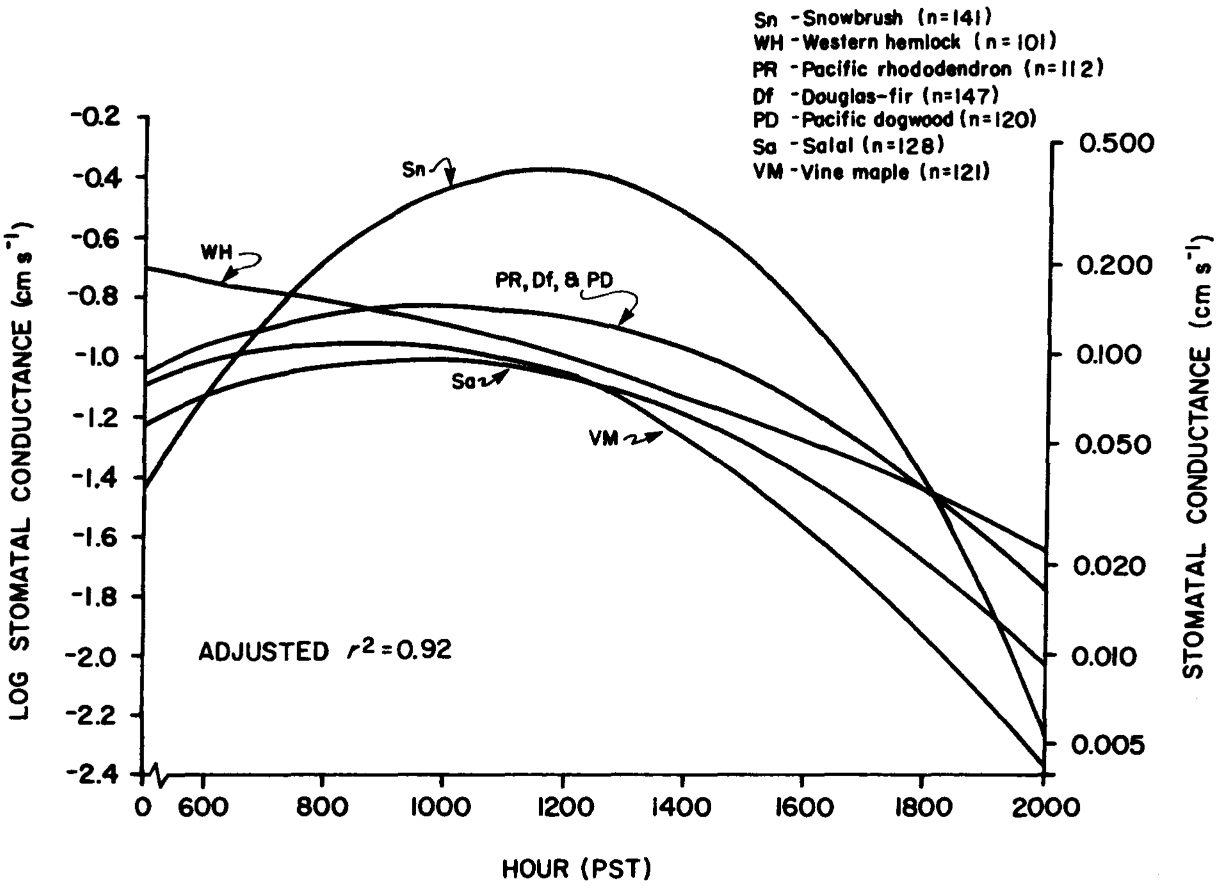

FIG. 1. Diurnal conductance regression lines for selected species growing in 15-year-old clearcut.

over the hardwoods in the Pacific Northwest; they are able to store more water in their sapwood, have lower nutrient requirements, and are able to grow to larger sizes than the hardwood species (Waring and Franklin 1979). Furthermore, because they carry their leaves through the winter, the conifers are able to utilize warm winter days for photosynthesis (Emmingham and Waring 1977). These adaptive advantages are apparently overcome, however, by the broadleaved species when growing on sites with high moisture availability, such as riparian zones and recent clearcuts (Franklin and Dyrness 1973).

The ability of the hardwoods to "out compete" the conifers on sites with high soil moisture availability may be related to the more conservative water use patterns of the conifers. As demonstrated by the slopes of the regression equations in Table 1, stomatal conductance of both the conifers and the broadleaved species was significantly reduced in response to increasing vapor pressure deficit. Thus when Δw increased, as during the temperature rise on a typical sunny afternoon, stomatal conductance declined. Conductance of the conifers declined much more rapidly than that of the broadleaved species, however. For example, at 1.0 kPa, conifer conductance had already been reduced by 46%, whereas conductance of the broadleaved species had been reduced by only 34%. The exception to these general statements was snowbrush. Snowbrush showed no significant decrease in conductance in response to Δw.

The differences in stomatal sensitivity help to explain the species differences in diurnal conductance curves (Fig. 1). Western hemlock, the species most sensitive to Δw, reached its daily conductance maximum earliest in the day, soon after sunrise. On the other hand, snowbrush, the species least sensitive to Δw, reached its daily maximum latest in the day, at around noon.

These differences in stomatal sensitivity may be related to the ability of narrow, needlelike leaves to dissipate heat more readily than do broader leaves when leaves are exposed to high radiant flux. The smaller width of conifer needles reduces boundary layer thickness and thereby permits more rapid heat dissipation (Gates 1968; Campbell 1977). This is particularly important when stomata are closed and sensible heat transfer provides the only means of heat dissipation. Narrower leaves would be less prone to damage caused by high leaf temperatures (Gates 1968; Whitehead and Jarvis 1981). Kramer (1983), however, points out that leaves are rarely damaged by the temperature rise associated with midday stomatal closure. The tendency to close stomata might also be detrimental for broader than for narrower leaves in terms of the daily carbon balance of the leaf. The higher temperatures of broader leaves would lead to lower CO_2 assimilation rates (Salisbury and Ross 1975) and more rapid turnover of pigments and enzymes (Penning de Vries 1975). Whatever the detrimental effects of high temperatures, the broadleaved species seem to be constrained by their leaf morphology to maintain more open stomata under high Δw than the conifers, thus minimizing the increase in leaf temperature associated with stomatal closure.

The high stomatal conductance of snowbrush has been previously reported (Conard and Radosevich 1981) and is not unusual among nitrogen-fixing plants (Schulze and Hall 1982). Further, the relative insensitivity of stomatal conductance in snowbrush has been observed, although to a lesser extent, in other nitrogen-fixing species (Schulze and Hall 1982). Perhaps nitrogen fixation, with its substantial drain on plant photosynthate (Gutschick 1978), encourages adaptations to maximize photosynthesis, including high stomatal conductance and low stomatal sensitivity.

The lesser sensitivity of broadleaved species to vapor pressure deficit may be compensated for by greater sensitivity to deficient soil moisture. Although this effect could not be demonstrated with data collected in the summer of 1977, it was evident in data collected on the same sites with the same instruments in the drier summer of 1974 (Running 1976; S. W. Running and R. H. Waring, unpublished data). Similarly, red alder and black cottonwood (Pezeshki and Hinckley 1982) demonstrated greater stomatal sensitivity to water potentials and lesser stomatal sensitivity to vapor pressure deficits than Douglas-fir (Running 1976).

The differences in stomatal sensitivity discussed above would tend to favor one species over another under particular conditions by causing differences in partitioning of finite soil water or by differential reductions in photosynthesis owing to partial stomatal closure. These differences in stomatal responsiveness might therefore strongly influence species distributions.

It is difficult to explain, however, what benefit is accrued to the conifers by more rapid stomatal closure in response to Δw without considering soil moisture limitations. If soil moisture were unlimited, the more conservative conifers would be outgrown by the less conservative broadleaved species. In fact, this is what occurs on sites with wetter soils: riparian zones, recent clearcuts, and sites near the Pacific coast (Franklin and Dyrness 1973). On the other hand, the summer drought that commonly occurs in the Pacific Northwest means that a finite quantity of soil water must be apportioned among species through the summer. As mentioned above, this seems to be a minor difficulty on recent clearcuts, where soil moisture is high relative to transpirational demand and broadleaf species grow rapidly. As the broadleaf stand develops, however, soil moisture progressively declines. Even if there were no differences in stomatal sensitivity to predawn water potential the depletion of soil moisture would shorten the period of summer photosynthesis, which would be far less damaging for the conifers than for the broadleaved deciduous species. If, on the other hand, the broadleaved species were more sensitive to predawn water potential than the conifers, then the conifers would be favored to an even greater extent over the broadleaved species as soil water potentials fell. These sequences of events could explain the emergence of conifers through dense broadleaf cover on former clearcuts in the Oregon Cascades (Franklin and Dyrness 1973), as well as the tenaciousness of broadleaved species in riparian zones and in areas of high summer rainfall in the Pacific Northwest.

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BEARDSALL, N. F., P. G. JARVIS, and B. DAVIDSON. 1972. A null-balance diffusion porometer suitable for use with leaves of many shapes. J. App. Ecol. **9**: 677–690.

CAMPBELL, G. S. 1977. An introduction to environmental biophysics. New York, Springer-Verlag.

CONARD, S. G., and S. K. RADOSEVICH. 1981. Photosynthesis, xylem pressure potential, and leaf conductance of three montane chapparal species in California. For. Sci. **27**: 627–640.

EMMINGHAM, W. H., and R. H. WARING. 1977. An index of photosynthesis for comparing forest sites in western Oregon. Can. J. For. Res. **7**: 165–174.

FRANKLIN, J. R., and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.

GATES, D. N. 1968. Transpiration and leaf temperature. Ann. Rev. Plant Physiol. **19**: 211–238.

GHOLZ, H. L., F. K. FITZ, and R. H. WARING. 1976. Leaf area differences associated with old-growth forest communities in the western Oregon Cascades. Can. J. For. Res. **6**: 49–57.

GUTSCHICK, V. P. 1978. Energy and nitrogen fixation. Bioscience, **28**: 571–575.

KRAMER, P. J. 1983. Water relations of plants. Academic Press, New York.

NETER, J., and W. WASSERMAN. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, IL.

PENNING DE VRIES, F. W. T. 1975. The cost of maintenance processes in plant cells. Ann. Bot. **39**: 77–92.

PEZESHKI, S. R., and T. M. HINCKLEY. 1982. The stomatal response of red alder and black cottonwood to changing water status. Can. J. For. Res. **12**: 761–771.

RUNNING, S. W. 1976. Environmental control of leaf conductance in conifers. Can. J. For. Res. **6**: 104–112.

SALISBURY, F. B., and C. W. ROSS. 1978. Plant physiology. 2nd ed. Wadsworth Publishing Co., Belmont, CA.

SCHULTZE, E. D., and A. E. HALL. 1982. Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. *In* Encyclopedia of plant physiology. New series. Vol. 12B. Water relations and carbon assimilation. *Edited by* O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler. Springer-Verlag. Berlin, Heidelberg, New York.

STEEL, R., and J. TORRIE. 1980. Principles and procedures of statistics—a biometrical approach. 2nd edition. McGraw-Hill, New York.

TURNER, N. C., and J. Y. PARLANGE. 1970. Analysis of operation and calibration of a ventilated diffusion porometer. Plant Physiol. **46**: 175–177.

WARING, R. H., and B. D. CLEARY. 1967. Plant moisture stress: evaluation by pressure bomb. Science (Washington, D.C.), **155**: 1248–1254.

WARING, R. H., and J. R. FRANKLIN. 1979. Evergreen coniferous forests of the Pacific Northwest. Science (Washington, D.C.), **204**: 1380–1386.

WHITEHEAD, D., and P. G. JARVIS. 1981. Coniferous forests and plantations. *In* Water deficits and plant growth. Vol. VI. *Edited by* T. T. Kozlowski. Academic Press, New York. pp. 49–152.