

Reprinted from BOTANICAL GAZETTE
Vol. 136, No. 1, March 1975

©1975 by The University of Chicago. All rights reserved.
Printed in U.S.A.

LOCAL VARIATION IN INTERGRADING ABIES GRANDIS-ABIES CONCOLOR
POPULATIONS IN THE CENTRAL OREGON CASCADES. III. TIMING OF
GROWTH AND STOMATAL CHARACTERISTICS
IN RELATION TO ENVIRONMENT

DONALD B. ZOBEL

Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331

ABSTRACT

Temperature, humidity, and timing of growth were observed for a population of *Abies grandis* saplings and three populations intermediate between *A. grandis* and *A. concolor*. The typical *A. grandis* population, which experienced the greatest moisture stress, had a more favorable temperature regime and less evaporative stress than populations on the other sites and began growth earlier. Two intermediate populations east of the Cascades, which never experienced severe plant moisture stress, grew in a cooler environment with drier air and started growth later. A third intermediate population experienced both high moisture stress and cool temperatures. For the typical *A. grandis* population, daily and seasonal stomatal closure in summer appears to be necessary to prevent fatal desiccation, but assimilation lost due to stomatal closure can probably be made up during the mild weather of other seasons. East-slope intermediate populations, without severe moisture stress, maintain open stomata, which would maximize assimilation during the short growing season; this is possible due to abundant soil moisture. The third intermediate population, in a cool habitat where soil water is limited, probably maximizes assimilation early in the season by maintaining open stomata but closes them more in late season to avoid fatal water deficits. Large numbers of adaxial stomata, characteristic of *A. concolor* and some intermediate populations, may provide an advantage in habitats where the season suitable for assimilation is short.

Introduction

Comparative study of related populations in different environments is a powerful tool for determining the possible adaptive importance of particular plant characteristics. The *Abies grandis*-*A. concolor* species complex in the central portion of the Oregon Cascades is quite amenable to this type of investigation. Here a strong environmental gradient from a maritime to a continental type of climate coincides with major changes in morphology and ecology of the populations of this species complex.

Abies grandis grows in maritime environments from California to British Columbia and recurs in a large area of the northern Rocky Mountains. *Abies concolor* grows farther south, with one variety in the southern Rocky Mountains and a second primarily in the interior mountains of California. Between the ranges of *A. grandis* and the California variety of *A. concolor* are extensive intermediate populations, which have apparently developed by introgression (DANIELS 1969; HAMRICK and LIBBY 1972). The populations in the central part of the Oregon Cascades include the border between typical *A. grandis* and the intermediate populations of the central and eastern Oregon mountains. Typical *A. grandis* grows in the river valleys of the Western Cascades Province. Scattered upper-slope populations in the Western Cascades, disjunct from those of the valleys, show morphological evidence of intergradation. East of the crest of the Cascades occurs the third entity of the complex in this area, extensive populations of variably intermediate trees. These intermediates are the climax dominants for a large forest zone (FRANKLIN and DYRNESS 1973).

This area where biological and environmental variation coincide was chosen to study how the morphology of these fir populations, their physiological response, and their environment are related. Variability in morphology, moisture stress, and stomatal closure patterns of these populations has been documented (ZOBEL 1973, 1974). This paper reports measurements of temperature and humidity at the study sites and the timing of growth of the populations. The adaptive significance of the population variability reported previously is discussed in the context of the study-site environments.

Environments of the study populations

Two study populations are in the Western Cascades Province with a wet, primarily maritime, climate: "Delta" is typical *Abies grandis* growing on a river terrace, whereas "Lookout" is on a rocky slope 14 km ENE and 1,020 m higher than Delta. The other two populations are on Black Butte, in the more arid region east of the Cascade crest, one on a densely forested north slope (BBN) and the other in a sparse forest of *Pinus ponderosa* on the southeast face of the butte (BBS). Although these latter three populations resemble *A. grandis* more than they do *A. concolor*, the morphological resemblance of some trees to *A. concolor* is obvious in all of them, especially BBS. More detailed site and stand characteristics are presented elsewhere (ZOBEL 1973, 1974).

A supplementary site, McRae Creek, is near the upper limit of low-elevation, stream-bottom grand fir populations, at 560 m, 9.5 km NNE of Delta.

It was used only for study of timing of growth and measurement of winter temperatures.

TEMPERATURE

METHODS.—At each site instruments were located in the type of habitat occupied by fir seedlings 1–3 m tall, the size used for earlier studies. At Lookout, a second thermograph was located under a forest canopy 20 m from the Lookout instruments. It is called Lookout (Shade). Air temperature at 1 m (under an insulated A-frame shield) and soil temperature at –20 cm were recorded on one 30-day thermograph at each site. Maximum-minimum thermometers were used to record winter minimum temperatures. Air temperature charts were digitized and average day and night temperatures computed. The average soil temperature for each day was taken from the charts.

Temperatures for each site were summarized by computing a monthly and a growing season Temperature Growth Index (TGI) by the method of CLEARY and WARING (1969). This index weights average day air and soil temperature by their effect on growth of *Pseudotsuga menziesii* seedlings in a controlled environment and is useful in local

comparisons of vegetation and environment in Oregon (WARING 1969; WARING, REED, and EMMINGHAM 1972; ZOBEL et al. 1974). The growing season was defined as the period from 5% elongation of lateral fir twigs to the second fall frost at the site.

The representativeness of the single soil temperature sampling point was checked in mid-August 1970, with 15–20 thermometer measurements at the base of 5–10 young firs.

RESULTS.—Trees at the low-elevation site at Delta experience temperature conditions much more favorable for growth than the populations at Lookout and Black Butte. Comparisons between sites for individual months indicate that Delta almost always has the highest TGI (table 1). The TGI at Lookout is similar to that at Delta in midsummer but is less in June and September, when air temperatures are well below those at Delta (fig. 1). The lower annual TGI at Lookout and especially at Black Butte (table 2) is also strongly influenced by their shorter growing season and by their lower soil temperature (fig. 1). Lookout (Shade) is considerably cooler than Lookout and is similar to BBS; BBN is slightly cooler than BBS (table 2). The difference between Lookout and Lookout (Shade) is

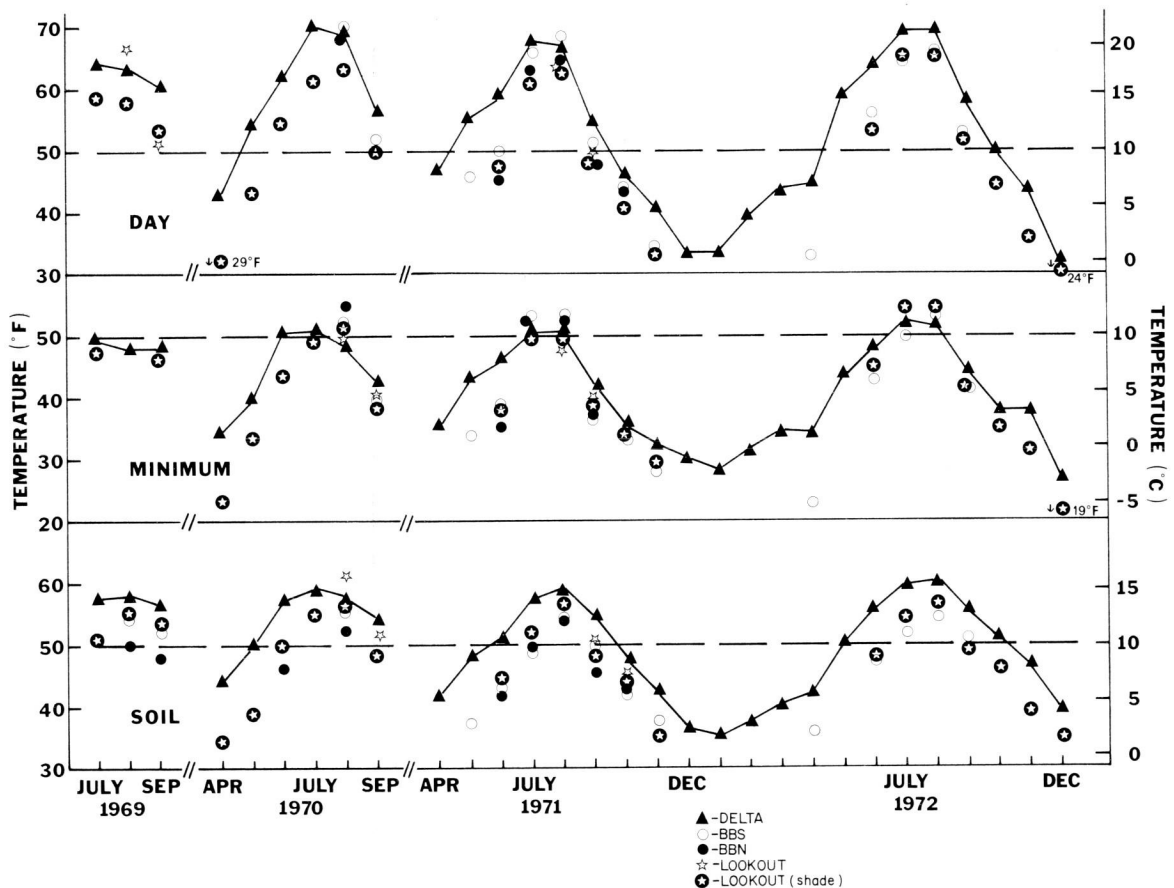


FIG. 1.—Average day air, minimum air and soil temperature for each month at Delta, Lookout, Lookout (Shade), BBS, and BBN. Months with data missing for 6 or more days are excluded.

TABLE 1
TEMPERATURE GROWTH INDEX (TGI) CALCULATED FOR
EACH STUDY SITE, BY MONTH AND YEAR

Site and year	May	June	July	Aug.	Sept.
Delta:					
1969.....	NA	NA	19.1	19.2	16.8
1970.....	12.8	18.7	22.1	21.5	15.7
1971.....	13.7	15.3	21.7	21.7	14.8
1972.....	15.2	NA	NA	22.7	14.5
Lookout (Shade):					
1969.....	NA	NA	15.0	15.5	14.0
1970.....	3.6	11.5	17.6	19.2	9.7
1971.....	NA	NA	17.0	18.7	9.7
1972.....	NA	NA	18.0	19.0	10.6
Lookout:					
1970.....	NA	NA	NA	22.9	12.3
1971.....	NA	NA	NA	20.9	10.9
Black Butte S:					
1970.....	NA	NA	NA	20.5	11.8
1971.....	2.5	9.4	16.1	19.1	11.9
1972.....	NA	NA	16.9	17.6	10.5
Black Butte N:					
1970.....	NA	NA	NA	18.2	NA
1971.....	NA	6.5	15.5	18.9	9.0

NOTE.—NA = insufficient data.

partly due to the unrepresentative soil temperature used for calculation of TGI at the Lookout area (table 3). There, the thermograph site was much less sheltered than the bases of most fir saplings.

The pattern of July-August minimum temperatures, which are not reflected in TGI, differs from that of day and soil temperatures (fig. 1). As a result of temperature inversions which occur fairly regularly in late summer, Delta is cooler than the other sites in many cases.

Winter air temperature minima at the sites were not particularly low but were lower on Black Butte than at Delta or McRae Creek. Minima at BBS were 3 F (−16 C). McRae Creek, at the upper limit of grand fir on alluvial habitat, had minima of about 20 F (−7 C), similar to the 17 F (−9 C) at Delta. During the intense cold spell of December 1972, however, the minimum reached 1 F (−17 C) at Delta and −6 F (−21 C) at Lookout (Shade).

Absolute maxima in 1970 and 1971 averaged 97 F (36 C) at Delta, 89 F (32 C) at Lookout (Shade), 95 F (35 C) at Lookout, and 87 F (31 C) at BBS and BBN. In 1972 they were 103 F (39 C) at Delta, 97 F (36 C) at Lookout (Shade), and 93 F (34 C) at BBS.

EVAPORATIVE STRESS

METHODS.—Vapor pressure deficits (VPD) at Delta and Black Butte were compared with those at Lookout. Simultaneous measurements of temperature and relative humidity in 1971 were made with a hygrothermograph (with a hair humidity sensor) in an instrument shelter placed on the ground near the thermograph. The shelter was a 40-cm cube with metal louvers and a two-layered plywood top, similar to that described by VOGEL and

JOHNSON (1965). To describe evaporative stress of the environment, VPD was calculated for each hour and summed for each day and night. For site comparisons, VPD was used only for those days with data from both sites; days for which both sites had 100% relative humidity were excluded. Daylengths were defined by those of the fifteenth of each month. Only three hygrothermographs were available: two were at Lookout and BBS from July 15 to October 1, 1971; the third was at BBN until August 1, when it was moved to Delta. Clock malfunction considerably reduced the length of the BBS record.

RESULTS.—Delta was much more humid than Lookout during the last half of the 1971 growing season (table 4). Dew was common at Delta, keeping the humidity high near the ground. Compared with Lookout, BBS and BBN were considerably drier at night, and BBS was also drier during the day. On the least humid days, however, Lookout was as dry as or drier than BBS, and much drier than BBN.

COMPARISON OF POPULATION ENVIRONMENTS

The environments of the study sites differ in several ways. Delta has more equitable temperature conditions and less evaporative stress than the other sites, but moisture stress is extreme in the dry years, with xylem pressure potential (P) averaging

TABLE 2
TEMPERATURE GROWTH INDEX (TGI) FOR GROWING
SEASON AT EACH STUDY SITE

SITE	1970		1971	
	Growing season	TGI	Growing season	TGI
Delta.....	May 15–Sept. 14	79	May 2–Oct. 17	93
Lookout (Shade)	May 31–Sept. 13 ^a	53	June 14–Sept. 26 ^a	51
Lookout...	May 31–Sept. 13	63 ^b	June 14–Sept. 26	57 ^b
BBS.....	May 30–Sept. 13	NA	June 9–Sept. 26	54
BBN.....	May 28–Sept. 13	NA	June 13–Sept. 29	48

NOTE.—NA = insufficient data.

^a Growth initiation date is for trees in the open.

^b 20–30 days estimated from Lookout (Shade), using a regression relationship ($r^2 = .99$).

TABLE 3

COMPARISON OF SOIL TEMPERATURE IN AUGUST AT THERMOGRAPH WITH AVERAGE OF THERMOMETER MEASUREMENTS UNDER GRAND-FIR TREES AND SAPLINGS

SITE	THERMOMETER READINGS		THERMOGRAPH
	Mean	Range within site	
Delta.....	57.9 (14.4)	3.6 (2.0)	57.0 (13.2)
Lookout.....	58.8 (14.8)	6.3 (3.5)	64.6 (18.2)
BBS.....	57.0 (13.2)	1.8 (1.0)	57.0 (13.2)
BBN.....	50.9 (10.5)	2.7 (1.5)	52.0 (11.2)

NOTE.—Temperatures in F, with C in parentheses.

TABLE 4
SUMMATION OF VAPOR PRESSURE DEFICIT AT DELTA AND
BLACK BUTTE AS PERCENTAGE OF THAT AT
LOOKOUT FOR SAME PERIODS IN 1971

	SITE		
	Delta	BBS	BBN
Day.....	37 (37)	135 (32)	93 (23)
Night.....	17 (32)	190 (27)	151 (21)

NOTE.—No. of days in each comparison shown in parentheses.

—29 bars before dawn in late summer 1970 (ZOBEL 1974). Black Butte sites, in contrast to Delta, are much cooler and have more evaporative stress, but average predawn P remains at —10 bars or wetter. At Lookout, all the conditions quantified in this study are relatively adverse: temperatures are almost as cool and the air nearly as dry as at Black Butte, and plant moisture stress is similar to that at Delta (ZOBEL 1974).

Environments at BBS and BBN, as quantified by the temperature and moisture indexes, are within the range of those occupied by populations of the *Abies grandis*-*A. concolor* complex in the Siskiyou Mountains of the California-Oregon border (fig. 2) (WARING 1969 and unpublished data). Delta and Lookout, on the other hand, are somewhat drier than any other stands measured in the Siskiyou or Western Cascades which include the fir complex (WARING 1969; ZOBEL et al. 1974). Lookout has a combination of environmental indexes quite unlike any others measured in these forests. This environmental comparison (fig. 2) reflects the zonal nature of the east-side communities including the fir (BBS and BBN), compared with the relative restriction of the fir populations to peripheral habitats in the Western Cascades. Most of the other stands (fig. 2) represent vegetation types of considerable importance in the regions sampled, none of which occupy cool-dry environments like that of Lookout.

Timing of growth

METHODS.—The course of twig and leader elongation and the cessation of cambial cell divisions were determined. Elongation was measured in 1970 and 1971 on three (occasionally two) lateral shoots of nine firs at each site, except at McRae Creek where three trees were measured. Most trees measured were 1–3 m tall, but one or two larger trees were included at each site. Terminal shoot elongation was followed only on 1–2-m trees. Measurements were made to the nearest millimeter, from insect pins placed in the twigs before growth initiation and were expressed as a percentage of total seasonal elongation. Data from twigs growing less than 20 mm a season were not used.

Cessation of cambial cell division was determined

by the method of WOLTER (1968). During the 1969, 1970, and 1971 growing seasons, pins were periodically placed through the bark into the cambial region of four trees at each site. Disruption of normal cambial differentiation by pin placement should result in abnormalities in xylem cells developing at that time, allowing one to determine whether xylem differentiation was then occurring. Blocks of bark and wood containing the pins were collected in late fall and stored in alcohol until sectioning. Cross sections adjacent to points of pin insertion were stained and examined for xylem abnormalities and their location relative to the cambial zone. Occasional trees larger than saplings (8–25 cm diameter at breast height [dbh]) were used.

RESULTS.—Seasonal elongation patterns of lateral branches at Delta and McRae Creek contrasted sharply with those at Lookout, BBS, and BBN (fig. 3). The time lag in the three intermediate populations—compared with the growth curve of typical *Abies grandis* at Delta—was about 16 days at 5% growth and 12 days at 30% growth in 1970, and 38 and 30 days in 1971. In 1972 the midseasonal time lag approached that in 1971. The latter 2 yr had a heavy late snowpack, which may account for the longer delay in growth at these higher elevation

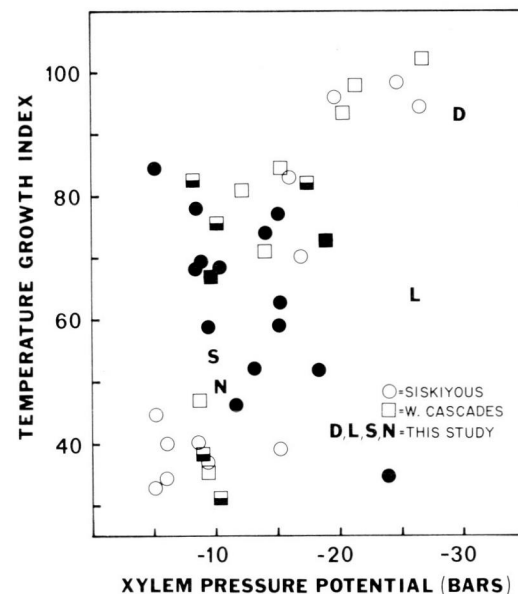


FIG. 2.—The distribution of the *Abies grandis*-*A. concolor* complex in the Siskiyou and central Cascade Mountains in relation to indexes of temperature and plant moisture stress. The open symbols represent vegetation types where the complex is absent. Half-filled symbols represent a "trace" of grand fir; filled symbols represent more. Letters are the study sites, D = Delta, L = Lookout, S = BBS, and N = BBN. Siskiyou data are from single stands in 1967 (WARING 1969 and unpublished). Western Cascade data are from communities represented by one stand in which environmental indexes were determined; data represent the maximum TGI and moisture stress measured (DYRNESS, FRANKLIN, and MOIR 1973; ZOBEL et al. 1974).

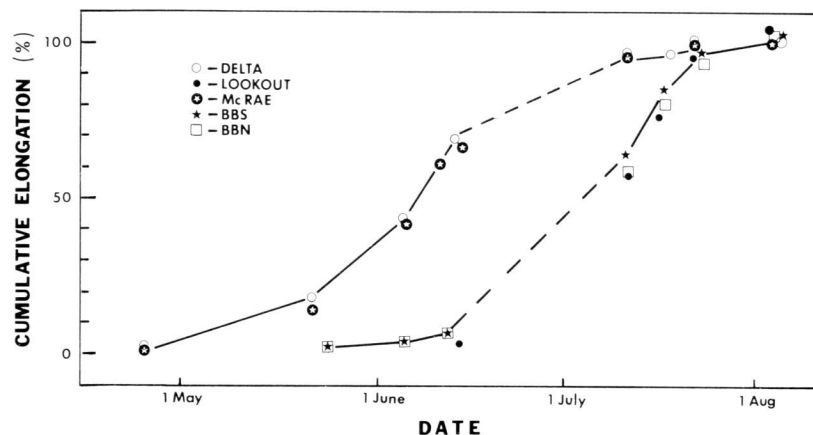


FIG. 3.—Cumulative elongation of lateral twigs of grand fir on the study sites, 1971. Number of twigs in the average is Delta (26), McRae Creek (6), Lookout (22), BBS (27), and BBN (21).

sites. At all sites, elongation of terminal shoots trailed the laterals by several days. In 1971 this lag was about 2 wk during early growth but gradually diminished. In 1970 the terminal lag was only 0–9 days. The terminal lag at Black Butte and Lookout generally was greater and persisted later in the season than at Delta and McRae Creek.

Temperatures associated with growth initiation (i.e., 5% elongation) were lower at Black Butte than at Delta (table 5). The relationship between TGI and twig elongation also varied with site. In 1971 during the time that laterals elongated from 5% to 65% Delta accumulated 18.1 TGI units, but Lookout, BBS, and BBN accumulated only 11.9, 10.5, and 9.2. Differences among sites in degree-hours during that period were even greater.

WOLTER'S (1968) method of determining the end of xylem growth gave disappointing results. The fir responded to the pin wound by forming resin ducts several cells thick. The wound also appeared to stimulate formation of xylem cells after their formation has ceased away from the wound. The injury extended considerably beyond the point of wounding, both vertically and horizontally, in contrast to WOLTER'S (1968) results with red pine. These features made it difficult to determine how much of the xylem outside the wound would have been produced without wounding, the exact radial location of the wound, and sometimes even if a given wound

response was caused by that pin or an adjacent one placed earlier or later. These data, originally collected to define the end of the growing season, could be interpreted only in a very general way.

There was little evidence of growth at any site after about September 1. Growth cessation at a given site varied widely between trees, differing by a month in several cases. The larger trees often stopped growth after the smaller ones.

Year-to-year differences in time of growth cessation appeared at Lookout but not at Black Butte. Data for Delta were too fragmentary to interpret. In 1970 Lookout trees had ceased cambial activity by August 4, with their predawn xylem pressure potential at -15.4 bars. In 1969 one of two, and in 1971 three of four Lookout trees were still growing in early August.

Environmental differences between sites are associated with differences in the growth patterns of the populations. The period of growth of the typical grand fir at Delta and McRae Creek begins earlier than that of the intermediate populations (fig. 3). That the cool-site populations begin elongation at colder temperatures (table 5) helps to compensate for the shorter and cooler growing season, however, and indicates that some adaptive differences may exist in the populations' responses to temperature (or other early season cues). Further compensation for the shorter growing season comes from the low

TABLE 5

AIR AND SOIL TEMPERATURES ASSOCIATED WITH GROWTH INITIATION OF LATERAL TWIGS AT DELTA AND BLACK BUTTE

SITE AND YEAR	AIR				SOIL
	Mean day	Mean night	Maximum	Minimum	
Delta 1970	54.9 (13.7)	51.3 (10.7)	68.4 (20.2)	39.6 (4.3)	48.9 (9.4)
Delta 1971	53.4 (12.0)	50.9 (10.5)	63.4 (17.5)	42.4 (5.8)	46.6 (8.2)
BBS 1971	47.8 (8.8)	44.9 (7.2)	58.3 (14.7)	37.4 (3.0)	42.1 (5.6)
BBN 1971	43.3 (6.3)	39.4 (4.2)	49.9 (9.9)	32.9 (0.5)	41.4 (5.2)

NOTE.—Temperatures in F with C in parentheses and are averages for 7 days centered on the interpolated data for 5% elongation.

moisture stress experienced by the Black Butte trees which should allow high metabolic rates even in late summer. At Lookout (and probably Delta) plant moisture stress apparently caused an early halt to cambial activity in the driest year. Such levels of moisture stress are severe enough to reduce photosynthesis of pot-grown grand fir significantly (PURITCH 1973).

Stomatal distribution and environment

A major morphological difference between *Abies grandis* and *A. concolor* is the number of stomata on the adaxial (upper) side of the needle. *Abies grandis* has few or no adaxial stomata; when present they are localized at the needle tip. On *A. concolor* needles, however, stomata are numerous on the adaxial surface. Number of stomatal rows on the abaxial (lower) surface varies little (HAMRICK 1966).

In the study populations, the number of rows of adaxial stomata increases from 0.5 near Delta to 2.8, 3.4, and 4.7 near Lookout, BBN, and BBS, while the length of the adaxial needle surface occupied by stomata increases from 4% at Delta to 11%, 15%, and 41% at the other sites (ZOBEL 1973). Populations with the most adaxial stomata are those in the cooler, less humid environments; except for Lookout, they experience less moisture stress. This pattern fits the more general pattern within Oregon, the central and eastern Oregon populations having more adaxial stomata than those west of the Cascades (LACAZE and TOMASSONE 1967; DANIELS 1969).

The relationship between environment and the extent of adaxial stomata in the entire species complex was determined by comparing the stomatal data of LACAZE and TOMASSONE (1967), DANIELS (1969), and HAMRICK and LIBBY (1972) with climatic attributes of the populations they sampled. Most of the populations studied are not close to weather stations, but BAKER (1944) provides a uniform source of climatic data. The extent of adaxial stomata was compared with (1) the amount of precipitation in July and August, a measure of the availability of water in summer; and (2) the "period during which the mean temperature exceeds 42° F," a measure of the growing season. Whether from natural populations (DANIELS 1969) or from nursery seedlings (LACAZE and TOMASSONE 1967; HAMRICK and LIBBY 1972), the data sets showed a similar pattern and were combined (fig. 4). *Abies grandis* populations—with a few adaxial stomata—are limited to 3–11 cm of July–August rainfall but exist in all but the shortest growing seasons. Intermediate populations are limited to areas with less than 9 cm and shorter growing seasons (110–210 days); with a given growing season, they occupy somewhat drier locations than typical *A. grandis*. Populations of *A. concolor*—with many adaxial stomata—grow more nearly throughout the range of

environments: southern Rocky Mountain populations receive up to 25 cm of late summer rain, in contrast to California populations with almost none. The few *A. concolor* populations with 6–8 cm rain in July and August are from Nevada and Utah. *Abies concolor* grows throughout the range of growing seasons. The study populations in the central Oregon Cascades, considered to be typical *A. grandis* at Delta and *A. grandis*-like intermediates at the other sites, fit within the general pattern (fig. 4).

Stomatal behavior and environment

The reaction of abaxial stomata of the study populations to plant moisture stress, as indicated by the pressure infiltrometer, varied considerably (ZOBEL 1974). Stomatal closure at Delta and Lookout was related to moisture stress, although at a given stress stomata were more open at Lookout. Delta stomata closed somewhat each day, even with low predawn stress. As the stress increased during dry summers, the stomatal opening in early morning decreased. This pattern contrasted with the Black Butte populations, which never experienced great moisture stress. Their stomata remained open to about the same extent all day, even with a large diurnal change in moisture stress. However, they do close slightly as the summer progresses, although the predawn stress changes little. Lookout stomata seem to have a closure pattern intermediate between the two types: they display a constant opening during the day—like Black Butte—early in the season but shift toward daily closure in late summer.

Thus the stomatal closure pattern seems to be correlated to a great degree with the predawn plant moisture stress, which is largely a function of soil moisture. At Delta and Lookout some stomatal closure is probably necessary to prevent fatal desiccation in dry years. However, the populations which experience the greatest evaporative stress—at Black Butte—do not close their stomata during the day and close them very little as the season progresses. Abundant soil moisture available to trees of the size studied apparently removes the need to limit transpiration.

Adaptive significance of stomatal differences

Some effects of plant moisture stress on grand fir metabolism in the laboratory are known. Photosynthesis of potted 5-yr-old *Abies grandis* remained high until xylem pressure potential reached -10 bars (PURITCH 1973). At -20 bars it was above 60% of the maximum and was still above 20% even at -30 bars; it stopped at -42 bars. The most extreme midday xylem pressure potential (P) reached in the Black Butte populations in two dry summers (1969–1970) was -17 bars, and it often was above -15 (ZOBEL 1974); the latter value corresponds to 80% of the maximum photosynthetic rate in PURITCH's (1973) trees. In contrast, at Look-

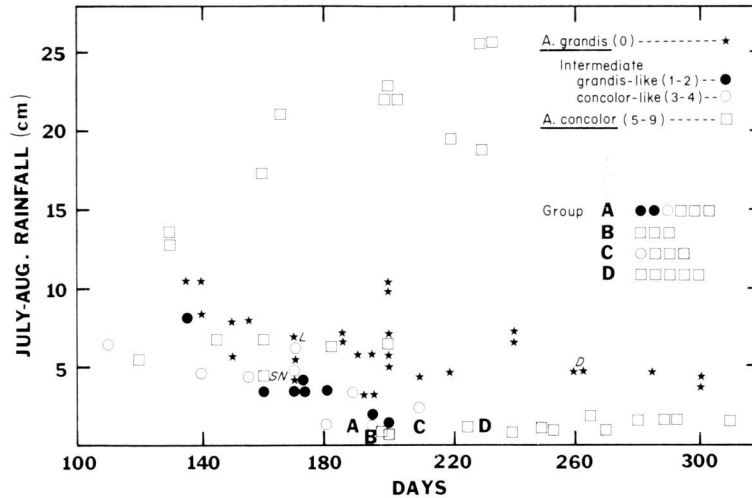


FIG. 4.—Relationship of extent of adaxial stomata of populations of the *Abies grandis*–*A. concolor* complex to summer rainfall and growing season (days with mean temperature above 42 F). Stomatal characteristics of seedlings in common garden studies (LACAZE and TOMASSONE 1967; HAMRICK and LIBBY 1972) and of native trees (DANIELS 1969) are used. All “extent of stomata” data are reduced to four groups: *A. grandis* (0) = 0%–9% of the range encountered, *A. grandis*-like intermediates (1-2) = 10%–29%, *A. concolor*-like intermediates (3-4) = 30%–49%, and *A. concolor* (5-9) = 50% of the range and greater. Environmental data are from BAKER (1944). Groups A, B, C, and D represent multiple data points at a single area; their coordinates are indicated by the bold-faced letters on the figure. The italic letters represent the Cascade study sites, D = Delta, L = Lookout, N = BBN, and S = BBS.

out and Delta the midday P was above -15 bars only in early summer of 1 yr. It averaged -26 at Delta and -24 at Lookout in July-August 1970, values that allowed only about 45% of maximum photosynthesis in the laboratory (PURITCH 1973). Photosynthetic models using the field stomatal closure and environmental patterns (ZOBEL 1974) also lead to the conclusion that photosynthesis during dry summers was probably reduced much more at Delta and Lookout than on Black Butte.

Transpiration in the laboratory declined much more rapidly than photosynthesis as P decreased, dropping to 20% of the maximum rate at approximately -22 bars (PURITCH 1973). Stomata at Delta closed rapidly as P declined from -10 to -25 bars (ZOBEL 1974), the pattern approximating the decline in transpiration in PURITCH's seedlings.

Given the stomatal reactions of the study populations and the environments they experience, and assuming the trees do not react in a drastically different way from the potted trees, adaptive relationships between the stomatal reactions and the environmental situations were suggested. Delta trees must close their stomata to minimize summer water loss or experience fatal desiccation. The assimilation lost due to stomatal closure can be made up during the relatively mild weather in other seasons. Winter photosynthesis is significant for Douglas-fir in western Washington (HELMS 1965) in a climate similar to that at Delta (FRANKLIN and DYRNESS 1973) and so may be appreciable in *Abies* at Delta. In contrast, the Black Butte populations have a shorter growing season and winter temperatures much less favorable for photosynthesis than at

Delta. Foliage of many trees yellows considerably during winter and early spring. They must maximize summer assimilation and can afford the water loss from open stomata because soil water is adequate to prevent extreme moisture stress, even late in the growing season. Lookout trees must cope with both the problem of moisture stress and that of a season for assimilation limited by both cold and drought. Their stomata seem to open all day early in the growing season, maximizing photosynthesis while sacrificing soil water. Late-season stomatal closure is probably necessary for survival. Even late in the summer, however, stomatal closure at a given moisture stress is less than at Delta.

It seems paradoxical that the fir populations have more adaxial stomata in the more arid environments, since amphistomatous needles should have higher transpiration rates than those with only abaxial stomata. Occurrence of the intermediate study populations, with more adaxial stomata, in drier areas than *A. grandis* may simply reflect the historical development of the species complex (HAMRICK and LIBBY 1972) superimposed on the regional climatic pattern of the western United States. However, the following hypothesis seems to provide an adaptive rationale for this situation and fits the stomatal distribution-environment patterns both in my study area and throughout the range: Adaxial stomata provide an adaptive advantage to populations with short effective growing seasons, which may be limited by either temperature or drought. The additional stomata, when open, should allow greater assimilation rates, which would be of the most benefit where the favorable season

for assimilation is short. In the study populations in the central Cascades, the trees with the most adaxial stomata had the shorter growing seasons (table 2, fig. 3). In some parts of its range (central and southern California) *A. concolor* populations experience long warm seasons, but only in combination with dry summers (fig. 4); drought intensifies well before the end of the warm season (TAPPEINER and HELMS 1971), probably greatly reducing assimilation. On the other hand, most *A. concolor* populations with wet summers (the southern Rocky Mountains) have relatively short growing seasons (fig. 4); those from Arizona and New Mexico experience warm seasons of over 200 days (fig. 4), but their early summer coincides with the driest part of the year, perhaps shortening the season of maximal assimilation somewhat. Although conifer seedling moisture stress readings taken in east-central Arizona show no increase in moisture stress during the presummer dry season, they were made at elevations above those where *A. concolor* is most important (JONES 1972). Although it must be recognized that July–August rainfall does not necessarily reflect the plant moisture stress the populations experience and that other environmental patterns may be selecting for stomatal distribution, the hypothesis presented does seem to agree with the available data.

A similar relationship of adaxial stomata to apparent growing season seems to exist within western North American *Abies* in general when one compares their taxonomic descriptions (SARGENT 1933) with their geographic (LITTLE 1971) and elevational ranges (LIU 1971). *Abies bracteata*, at relatively low elevations in the California coast ranges, has no

adaxial stomata. *Abies magnifica*, *A. procera*, and *A. lasiocarpa* all are stomatiferous on both needle surfaces; all generally occur farther inland or at higher elevations than *A. grandis* or *A. bracteata*, at a given latitude, and thus probably experience shorter growing seasons. A partial exception to this general trend is *A. amabilis*, which has no adaxial stomata. It grows together with *A. procera* and *A. lasiocarpa* in the Cascade Range where it usually follows these species in succession (FRANKLIN and DYRNESS 1973). In British Columbia, the range of *A. amabilis* is for the most part coastward and at lower elevations than that of *A. lasiocarpa*, following the general relationship noted above.

The interpretations given in this section are based on information about stomatal distribution and behavior—only two of the characteristics which influence water relations and assimilation in trees—in relation to only two crude environmental indexes. The populations studied may differ in other ways which at least potentially affect moisture stress. Differences in cuticle thickness, needle surface waxes, hypodermal development, and mesophyll resistance may compensate for (or reinforce) the differences discussed here; however the stomatal differences studied are probably of much greater adaptive significance than these factors.

Acknowledgments

W. B. CRITCHFIELD and J. L. JENKINSON, U.S. Forest Service, and W. K. FERRELL, Oregon State University, read the manuscript; their comments were very helpful. Unpublished data provided by R. H. WARING are appreciated.

LITERATURE CITED

- BAKER, F. S. 1944. Mountain climates of the western United States. Ecol. Monogr. 14:224–254.
- CLEARY, B. D., and R. H. WARING. 1969. Temperature: collection of data and its analysis for the interpretation of plant growth and distribution. Can. J. Bot. 47:167–173.
- DANIELS, J. D. 1969. Variation and intergradation in the grand fir-white fir complex. Ph.D. diss. University of Idaho. 235 pp.
- DYRNESS, C. T., J. F. FRANKLIN, and W. H. MOIR. 1974. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. Coniferous Forest Biome Bull. 4, Coniferous Forest Biome, U.S./IBP. University of Washington AR-10, Seattle.
- FRANKLIN, J. F., and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service Gen. Tech. Rep. PNW-8. 417 pp.
- HAMRICK, J. L., III. 1966. Geographic variation in white fir. Master's thesis. University of California, Berkeley. 143 pp.
- HAMRICK, J. L., and W. J. LIBBY. 1972. Variation and selection in western U.S. montane species. I. White fir. Silvae Genet. 21:29–35.
- HELMS, J. A. 1965. Diurnal and seasonal patterns of net assimilation in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, as influenced by environment. Ecology 46:698–708.
- JONES, J. R. 1972. Moisture stresses in Arizona mixed conifer seedlings. USDA Forest Service Res. Paper RM-86. 8 pp.
- LACAZE, J.-F., and R. TOMASSONE. 1967. Contribution à l'étude de la variabilité infraspécifique d'*Abies grandis* Lindl. Caractéristiques juvéniles. Ann. Sci. Forest. Paris 24:277–325.
- LITTLE, E. L., JR. 1971. Atlas of United States trees. Vol. 1. Conifers and important hardwoods. USDA Forest Service Misc. Pub. 1146.
- LIU, TANG-SHUI. 1971. A monograph of the genus *Abies*. Department of Forestry, National Taiwan University, Taipei. 608 pp.
- PURITCH, G. S. 1973. Effect of water stress on photosynthesis, respiration, and transpiration of four *Abies* species. Can. J. Forest Res. 3:293–298.
- SARGENT, C. S. 1933. Manual of the trees of North America (exclusive of Mexico). Houghton Mifflin, Boston. 910 pp.
- TAPPEINER, J. C., II, and J. A. HELMS. 1971. Natural regeneration of Douglas fir and white fir on exposed sites in the Sierra Nevada of California. Amer. Midland Natur. 86:358–370.
- VOGEL, T. C., and P. L. JOHNSON. 1965. Evaluation of an economical instrument shelter for microclimatological studies. Forest Sci. 11:434–435.

- WARING, R. H. 1969. Forest plants of the eastern Siskiyou; their environmental and vegetational distribution. *Northwest Sci.* **43**:1-17.
- WARING, R. H., K. L. REED, and W. H. EMMINGHAM. 1972. An environmental grid for classifying coniferous forest ecosystems. Pages 79-91 in *Proceedings—research on coniferous forest ecosystems—a symposium* (Pacific Northwest Forest and Range Experiment Station, U.S. Forest Service, Portland, Ore.).
- WOLTER, K. E. 1968. A new method for marking xylem growth. *Forest Sci.* **14**:102-104.
- ZOBEL, D. B. 1973. Local variation in intergrading *Abies grandis*-*A. concolor* populations in the central Oregon Cascades: needle morphology and periderm color. *BOT. GAZ.* **134**:209-220.
- . 1974. Local variation in intergrading *Abies grandis*-*A. concolor* populations in the central Oregon Cascades. II. Stomatal reaction to moisture stress. *BOT. GAZ.* **135**:200-210.
- ZOBEL, D. B., W. A. MCKEE, G. M. HAWK, and C. T. DYRNESS. 1974. Correlation of forest communities with environment and phenology on the H. J. Andrews Experimental Forest, Oregon. Pages 48-56 in R. H. WARING and R. L. EDMONDS, eds. *Integrated research in the coniferous forest biome*. Coniferous Forest Biome Bull. 5 (Proceedings of the AIBS symposium on coniferous forest ecosystem), Coniferous Forest Biome, U.S./IBP. University of Washington AR-10, Seattle.