Environmental limits of an endemic spruce, *Picea breweriana*[1]

R. H. WARING, W. H. EMMINGHAM, AND S. W. RUNNING

Forest Research Laboratory, School of Forestry, Oregon State University, Corvallis, Oregon 97331

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Brewer spruce (*Picea breweriana* Wats.) persists as a relict in protected physiographic situations in southwestern Oregon and northwestern California, where a cool, montane, temperate zone inland from the Pacific Ocean is moderated in summer by maritime air masses. We attempted to uncover the reasons for its survival. We surveyed the species distribution and geologic and floristic associations, then studied effects of environment on growth and survival of two widely distributed species, *Pseudotsuga menziesii* (Mirb.) Franco and *Abies magnifica* Murr. var. *shastensis* Lemm., for a common basis for comparison. The survey included 130 plots along a 250-km transect. Brewer spruce was encountered along 70 km of the transect. Brewer spruce ranked well with other conifers in tolerance to soil moisture stress, cold temperatures, low light, and heavy, deep snow. Although sensitive to high evaporative demand, it appears to compete well with sparse vegetation in infertile or unbalanced soils developed from ultrabasic materials.

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L'épinette de Brewer (*Picea breweriana* Wats.) subsiste à l'état reliqual dans des situations physiographiques protégées au sud-ouest de l'Oregon et au nord-ouest de la Californie, où une zone montagneuse fraîche, située à l'intérieur des terres par rapport au Pacifique, est tempérée par des masses d'air maritime pendant l'été. Nous avons tenté de déceler les causes de la survie de cette épinette. Nous avons inventorié la distribution de l'espèce et ses associations floristiques et géologiques; puis afin d'avoir une base de comparaison, nous avons étudié les effets du milieu sur la croissance et la survie de deux espèces largement distribuées, *Pseudotsuga menziesii* (Mirb.) Franco et *Abies magnifica* Murr. var. *shastensis* Lemm. L'inventaire a porté sur 130 parcelles distribuées le long d'un transect de 250 km. L'épinette de Brewer a été retrouvée dans ce transect sur une distance de 70 km. Elle se compare aux autres conifères en ce qui concerne les déficits en eau du sol, les températures froides, les faibles intensités lumineuses et les neiges abondantes et épaisses. Bien que sensible aux fortes évaporations en eau, elle semble apte à entrer en compétition avec la végétation éparse des sols infertiles et instables formés à partir de matériaux ultrabasiques.

[Traduit par le journal]

Introduction

Knowledge of the natural distribution and ecological behavior of any rare organism helps one gain a clue to historical events and selection pressures operative upon more widely distributed plants and animals. As part of a study of vegetation in the Siskiyou Mountains of southwestern Oregon and northwestern California, we became interested in interpreting the scattered distributional pattern of an endemic spruce, *Picea breweriana* S. Wats. Within the region, Brewer spruce occupies a wide range of soil and topographic conditions and is found in association with more than a dozen other conifers.

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In this paper, we describe the geographic distribution of the spruce and offer through observations of its physiological behavior and ecological associations a plausible explanation of its present environmental restrictions. To be able to compare environments both with and without the spruce, we examine the responses of more widely distributed conifers.

History and Geographic Distribution

Brewer spruce is distinct both morphologically and genetically from other representatives of the genus in the Pacific Northwest (Daubenmire 1968). In a comprehensive study of the genus, Wright (1955) concluded that Brewer spruce is related only distantly to other spruces in North America and finds its closest living associates in China in the form of *P. brachytyla*

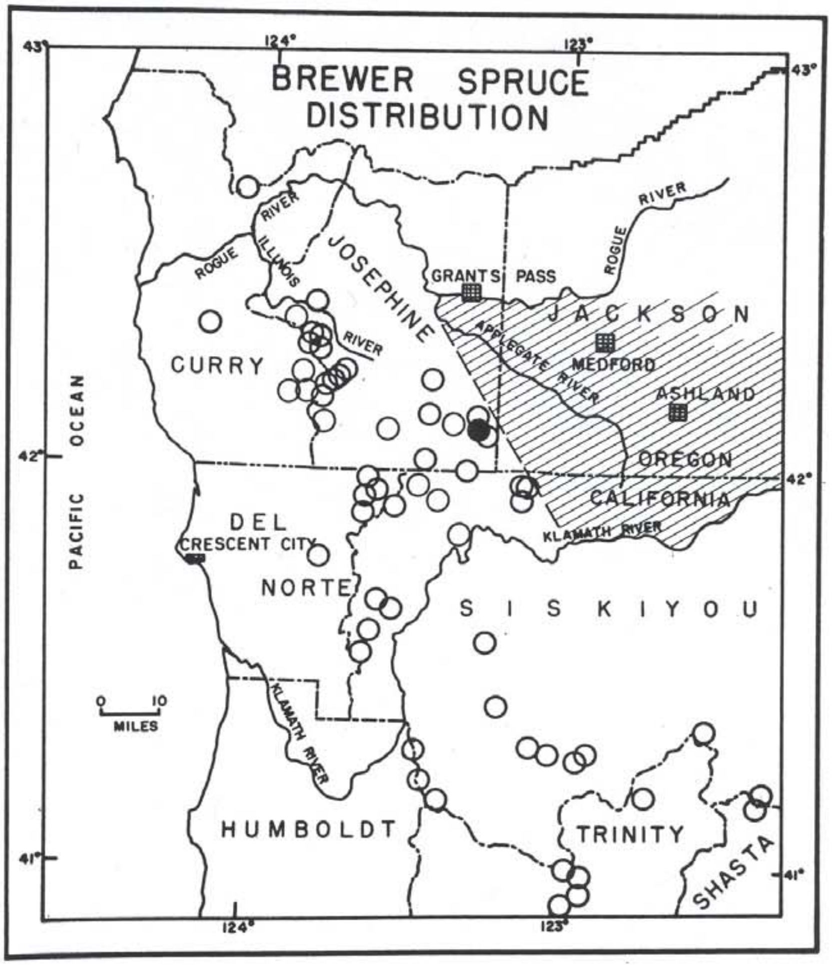

FIG. 1. Present distribution of *Picea breweriana* in southwestern Oregon and northwestern California. The darkened circle indicates where measurement of environment and species' response were concentrated. The shaded area represents the eastern Siskiyou region where environments are unfavorable for the species.

(Franch.) Pritz. Recent protein analyses by E. Von Rudloff substantiate Wright's conclusion.[2] This suggests that Brewer spruce may have migrated across the boreal route from a source of origin in northeastern Asia considerably before other North American spruces had evolved. *Picea chihuahuana* Martinez, endemic to Mexico, reputedly has a similar history (Gordon 1968).

Fossils of Brewer spruce, or a closely related taxon, appear in Miocene deposits in northeastern Oregon laid down at least 15 million years ago (Chaney *et al.* 1944). From the Pliocene, the spruce has been recorded from beds located in Idaho, eastern Oregon, California, and Nevada. With the final uplifting of the Cascade Mountains during the Pliocene epoch, the species became restricted, first to the western slope of the Cascade Mountains and finally to its limited range today (Fig. 1). The range map was derived from all verifiable herbarium records at the University of California, the California Academy of Science in San Francisco, Oregon State University, unpublished records of reliable botanists, and extensive field reconnaissance by the authors.

The northern limit of the species is on Iron Mountain at 1200 m elevation. Its western limit is at Snowcap Mountain, also at 1200 m elevation, 22 km inland from the Pacific Ocean and 18.5 km inland from the nearest Sitka spruce (*P. sitchensis* (Bong.) Carr.). Its eastern limit, described by Haddock (1938), is among the Castle Crags at the west base of Mt. Shasta. The southern limits, about 220 km south of its

[2]Personal communication from Dr. E. von Rudloff, National Research Council of Canada, Prairie Regional Laboratory, Saskatoon, Saskatchewan, Canada.

northern extension, is in the Salmon-Trinity Alps near Derrick at 1350 m elevation and on Red Mountain at 2300 m. According to Matthews,[3] the best development of the species is on Grayback Mountain, not far from Oregon Caves National Monument in Oregon, and near Black Butte in northeastern Del Norte County in California. At the latter location, the species is reported to reach 52 m in height and 1.35 m in diameter at breast height. Some of the trees live to an age of 900 years.

Brewer spruce occurs at elevations from 560 m to 2300 m; it is generally at higher elevations as one progresses inland. Annual precipitation ranges from over 250 cm in Curry and Del Norte counties to about 125 cm near its eastern limits. Precipitation occurs mainly between November and June so that the growing season, which begins near the end of June and extends into September, is practically rain-free.

In the winter, snow cover may accumulate to 6 m and is usually high in moisture content.

This climate and the diversity of environments associated with the Klamath Mountain province, of which the Siskiyou mountains are the most northern representatives, provide a refuge for many endemics (Whittaker 1961).

Floristic Associates

In Table 1, the changing composition of the forest from west to east is presented along a 70-km transect in which the spruce was encountered. The sample was drawn from 130 survey plots distributed across a 250-km transect of southwestern Oregon (Waring, unpublished). One of the most striking features of the vegetation is the richness of the evergreen component, with 15 conifers and 21 broadleaf evergreen trees and shrubs associated with Brewer spruce. Many of these species occur on the same site. For example, Brewer spruce grows with eight other conifers within an area 30 m square at the eastern limit of the transect (stand 21).

Two families, Fagaceae and Ericaceae, are of major importance. In Fagaceae, the genera *Castanopsis*, *Lithocarpus*, and *Quercus* are well represented. The ericaceous genera include *Arbutus*, *Chimaphila*, *Vaccinium*, *Arctostaphylos*, *Gaultheria*, *Kalmiopsis*, *Rhododendron*, *Pyrola*, *Ledum*, and *Sarcodes*.

The transect indicates a reduction in the richness of these two families progressing eastward toward the limits of Brewer spruce. In the western Siskiyou Mountains, *Picea breweriana* is found in stands with a complete understory of evergreen shrubs; forests immediately to the east of the spruce's limits, however, have only a trace of evergreen shrubs. This distinction led Waring (1969) to recognize a separate floristic subregion within the Siskiyou province of the Klamath Mountains.

Looking specifically at the conifers, one finds that *Chamaecyparis* and *Taxus* diminish in importance while *Libocedrus* and *Tsuga mertensiana* become more important as one progresses inland. *Pinus ponderosa* is rarely associated with Brewer spruce, although it becomes more common than *Pinus lambertiana* in other forest types near the eastern end of the transect. *Pinus jeffreyi* occurs with *Picea breweriana* only on infertile, unbalanced soils derived from ultrabasic material (serpentine and peridotite), which are extensive throughout the Klamath Mountains. *Pinus attenuata* is a fire type that is absent further inland, at least in Oregon.

Pseudotsuga menziesii is the conifer most commonly associated with Brewer spruce. It has an extremely broad environmental range, from warm and dry sites, where it is a climax, to moist and cool environments, where it is strictly a pioneer species in forest succession. It is of the latter status when associated with Brewer spruce. The spruce itself is shade tolerant and can become established under almost a closed canopy. Toward the eastern limit of its range, *Abies magnifica* var. *shastensis*[4] shares the spruces' successional position following the dominance of *Pinus monticola* and *Pseudotsuga menziesii*.

Significant in their rarity in the area encompassed by the survey were *Tsuga heterophylla* (Raf.) Sarg., *Thuja plicata* Donn, and *Abies amabilis* (Dougl.) Forbes. The reasons for their general absence and the marked distributional characteristics of other conifers are related to

[3]Personal communication from Oliver V. Matthews, dendrologist, Salem, Oregon. Also see Reports in Medford Mail Tribune, Sunday, October 7, 1962, and Grants Pass Daily Courier, Feb. 16, 1944.

[4]A controversy exists on nomenclature. Some think the taxon is closer to *Abies procera* Rehd. (Parker 1963; Griffin and Critchfield 1972), but others believe it is closer to *Abies magnifica* Murr. var. *shastensis* Lemm. (Waring 1969; Franklin and Greathouse 1968).

TABLE 1

Vegetation transect of Brewer spruce stands from 123°55′ W to 123°05′ W long.

Species	Plot No. (arranged from west to east)																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Conifers																					
Abies concolor (Gord. & Glend.) Lindl.	—	—	×	—	×	—	×	×	×	×	×	×	—	—	×	×	×	×	×	—	×
Abies magnifica Murr. v. *shastensis* Lemm.	—	—	—	×	—	×	—	×	—	—	×	—	×	×	—	×	×	×	×	×	×
Chamaecyparis lawsoniana Parl.	×	—	×	—	×	—	—	—	×	×	—	×	—	—	—	×	×	—	—	—	—
Juniperis sibirica Burgsd.	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Libocedrus decurrens Torr.	—	—	—	—	—	—	—	—	—	—	—	—	×	×	—	—	—	—	—	—	×
Picea breweriana S. Wats.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Pinus attenuata Lem.	—	—	—	—	—	—	—	×	—	—	—	—	—	×	—	×	—	—	—	—	×
Pinus contorta Dougl. ssp. *murrayana* Grev. & Balf.	—	—	—	—	—	×	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
Pinus jeffreyi Murr.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×
Pinus lambertiana Dougl.	×	×	×	×	×	—	—	—	×	×	×	×	×	—	×	—	—	×	—	—	×
Pinus monticola Dougl. ex D. Don	—	—	—	—	—	×	×	×	—	—	—	—	—	×	×	×	×	×	×	—	×
Pinus ponderosa Dougl.	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pseudotsuga menziesii (Mirb.) Franco	×	×	×	—	×	—	×	×	×	×	×	×	×	×	×	—	×	×	—	—	×
Taxus brevifolia Nutt.	×	—	—	—	—	—	—	—	×	—	—	—	×	—	—	—	—	—	—	—	—
Tsuga mertensiana (Bong.) Sarg.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	×	×	—
Broadleaf deciduous trees																					
Acer macrophyllum Pursh	×	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—
Alnus spp.	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cornus nuttallii Aud.	×	×	—	—	—	—	—	—	—	×	—	×	—	—	—	—	—	—	×	—	—
Broadleaf evergreen trees																					
Arbutus menziesii Pursh	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	—
Castanopsis chrysophylla (Dougl.) A. DC.	×	×	×	—	×	—	×	×	×	—	—	×	—	—	×	—	—	—	—	—	—
Lithocarpus densiflora (H. & A.) Rehd.	×	×	—	—	—	—	×	×	×	—	×	×	×	—	—	—	—	×	—	—	—
Quercus chrysolepis Liebm.	×	—	—	—	—	—	—	—	×	—	—	×	×	—	—	—	—	×	—	—	—

TABLE 1 (*Continued*)

Vegetation transect of Brewer spruce stands from 123°55′ W to 123°05′ W long.

Species	Plot No. (arranged from west to east)																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Deciduous shrubs																					
Acer glabrum Torr.	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—	×	×	×	—	—	—
Amelanchier florida Lindl.	—	—	—	—	—	—	×	—	—	—	—	—	—	×	—	×	—	×	×	—	×
Prunus emarginata (Dougl.) Walp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
Rhododendron occidentale (T. & G.) Gray	—	—	—	—	—	—	—	—	—	×	—	×	—	—	—	×	—	—	—	—	—
Rosa gymnocarpa Nutt. ex T. & G.	—	×	×	—	×	—	—	—	—	—	—	—	—	—	—	×	×	×	—	—	—
Rubus lasiococcus Gray	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
Rubus parviflorus Nutt.	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rubus vitifolius C. & S.	—	×	×	—	×	—	—	—	—	—	—	—	—	—	—	×	×	×	—	—	—
Symphoricarpos albus (L.) Blake	—	×	—	—	—	—	—	—	—	—	—	×	—	×	—	—	—	—	—	—	—
Vaccinium membranaceum Dougl.	—	—	×	—	×	—	—	×	—	—	—	—	—	—	—	—	×	—	×	—	—
Vaccinium parvifolium J. E. Sm.	—	×	—	×	×	—	×	—	×	×	×	×	×	—	—	×	—	×	—	—	×
Vaccinium scoparium Leib.	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—
Vaccinium uliginosum L.	—	—	×	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
Evergreen shrubs																					
Arctostaphylos nevadensis Gray	—	—	×	×	—	—	×	×	—	—	×	—	×	×	×	×	—	—	—	—	×
Arctostaphylos patula Greene	—	—	—	×	—	—	×	—	—	—	—	—	—	—	—	×	—	×	—	—	—
Berberis nervosa Pursh	—	×	×	—	×	—	—	—	×	—	×	×	—	—	—	×	×	×	—	—	—
Cercocarpus ledifolius Nutt.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	—
Garrya buxifolia Gray	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—	—
Garrya fremontii Torr.	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—	×	—	—	×
Gaultheria ovatifolia Gray	—	×	×	—	×	—	—	×	—	×	×	×	—	—	—	×	—	×	—	—	—
Gaultheria shallon Pursh	—	×	×	—	—	—	—	—	×	×	—	×	—	—	—	—	—	—	—	—	—
Kalmiopsis leachiana (Hend.) Rehder.	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ledum columbianum Piper.	—	—	×	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leucothoe davisiae Torr.	—	—	×	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pachystima myrsinites (Pursh) Raf.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×
Quercus sadleriana R. Br.	×	×	×	×	×	—	—	—	×	—	×	—	—	—	×	×	×	×	×	×	—
Quercus vaccinifolia Kell.	—	—	—	×	—	—	×	×	—	×	×	—	—	×	—	×	—	×	—	—	×
Rhamnus californica Esch.	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhododendron macrophyllum G. Don.	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vaccinium ovatum Pursh	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 1 (*Concluded*)

Vegetation transect of Brewer spruce stands from 123°55′ W to 123°05′ W long.

Species	Plot No. (arranged from west to east)																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Herbs																					
Achlys triphylla (J. E. Sm.) D. C.	—	×	×	—	×	—	—	—	×	×	—	—	—	—	—	—	×	×	—	—	×
Apocynum spp.	—	—	×	—	×	—	—	—	×	×	—	—	—	—	—	—	—	—	—	—	—
Asarum hartwegii Wats.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	×	—	—	—
Campanula scouleri Hook.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	×	—	—	—
Chimaphila menziesii (R. Br.) Spreng.	—	—	—	—	—	—	—	×	—	×	×	×	—	—	×	—	—	—	—	—	—
Chimaphila umbellata (L.) Nutt.	—	—	—	—	—	—	—	×	—	×	×	×	×	—	×	×	×	×	×	—	×
Disporum hookeri (Torr.) Britt.	—	—	×	—	×	—	—	—	×	—	—	—	×	—	—	—	×	×	—	—	—
Goodyera oblongifolia Raf.	—	×	—	—	—	—	—	—	×	×	×	—	—	—	—	×	—	—	×	—	—
Lewisia cotelydon (Wats.) Robins.	—	—	—	—	—	—	—	—	×	×	—	—	—	—	—	—	—	—	—	—	—
Linnaea borealis L.	—	×	×	—	×	—	—	—	×	×	—	×	—	—	—	—	—	—	—	—	—
Pteridium aquilinum (L.) Kuhn	—	×	×	×	×	—	—	—	×	—	—	—	—	—	—	×	—	—	—	—	—
Pyrola picta J. E. Sm.	—	—	—	×	—	—	—	—	—	—	×	—	—	—	—	×	—	×	—	—	—
Pyrola dentata J. E. Sm.	—	×	—	—	—	—	—	—	—	×	—	×	—	—	—	—	—	—	—	—	—
Pyrola secunda L.	—	—	×	—	×	—	—	—	×	×	—	×	—	—	×	—	×	—	—	—	—
Sarcodes sanguinea Torr.	—	—	—	—	—	—	—	—	—	—	×	—	—	—	×	—	—	—	—	—	—
Smilacina racemosa (L.) Desf.	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—	×
Trientalis latifolia Hook.	—	—	×	—	×	—	—	—	×	—	—	—	—	—	—	×	—	—	—	—	×
Trillium ovatum Pursh	—	—	—	—	—	—	—	—	—	×	—	—	×	×	—	×	×	×	—	—	×
Veratrum californicum Durand	—	—	×	×	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Whipplea modesta Torr.	—	—	—	—	—	—	—	—	×	—	—	—	×	—	—	—	—	×	—	—	—
Xerophyllum tenax (Pursh) Nutt.	—	—	×	×	×	—	—	—	×	×	—	×	—	×	—	—	—	—	×	—	—

TABLE 2

Linkage of environment to specific plant responses following the concept of the operational environment (Mason and Langenheim 1957)

Environment	Plant responses
Temperature	Growth and photosynthetic response
Soil moisture	Equilibrium plant water potential
Evaporative demand	Leaf resistance
Light	Light saturation curve
Soil fertility	Uptake and plant nutrition
Mechanical	Breakage tolerance to wind and snow

the summer climate, with sparse rainfall and high temperatures, as will be discussed later.

Environmental Interpretation

To determine the environmental requirements of Brewer spruce, we shall first partition the host of possible variables into "operational" categories (Mason and Langenheim 1957). Following the general classification of Ellenberg (1950) and Bakuzis (1961), we can identify six major environmental factors controlling plant distribution (Table 2). These factors can be assessed operationally by observing certain plant responses. For example, soil moisture influences plant water status, which at night, when the plant is not transpiring, approaches an equilibrium with water available to the roots. Similarly, the importance of evaporative demand can be interpreted from a knowledge of leaf resistance (Waggoner and Turner 1971; Slatyer 1967). A summary of this general approach has been published by Waring *et al.* (1972). In this paper, we will focus on the interpretation and provide only sufficient details in methodology for reference and basic understanding.

Although more than a dozen conifers may be found with Brewer spruce, only five are associated consistently with it on typical forest soils. These include sugar pine (*Pinus lambertiana*), Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), Shasta red fir (*A. magnifica* var. *shastensis*), and western white pine (*Pinus monticola*). With rare exception, either Douglas fir or Shasta red fir shares the environmental range encompassed by Brewer spruce. By making environmental assessments through these two species, one may compare situations where Brewer spruce is competitively excluded.

As an outgrowth of more general studies, we have accumulated some field and laboratory data on the environmental restriction of Brewer spruce. The design and results of these studies will be presented following the organizational format given in Table 2.

Intensive monitoring of climatic conditions was centered to the east of the spruce's distribution. Only three climatic stations were established within the present geographic range of the species. Of these, one represented a typical habitat for Brewer spruce. Periodic climatic and physiologic measurements were taken in three other habitats selected from 21 survey plots (numbers 10, 15, and 18 in Table 1).

Temperature

Field Studies

Throughout two growing seasons, air and soil temperatures at 20 cm above and below ground level were recorded continuously under a well-established Brewer spruce stand near the eastern limits of the species in Oregon (Fig. 1). Comparative measurements were made at 24 other environments located nearby and in most instances somewhat to the east of the species' range (Fig. 2). The study encompassed extremes in forest environments well beyond the spruces' competitive limits. Parent materials ranged from acid igneous to ultrabasic, elevations ranged from 550 to 2135 m, and vegetation included communities dominated by black oak (*Quercus kelloggii* Newb.) at the warm extreme of the temperature gradient and mountain hemlock (*Tsuga mertensiana*) at the other. A detailed description of the vegetation and physiography is published elsewhere (Waring *et al.* 1972; Waring 1969).

Under the monitored Brewer spruce stand, air temperatures averaged 18°C during the day and 13°C at night throughout July and August. Soil temperature ranged from 7° to 11°C during the same period. For the entire growing season, from July to the middle of September, air temperatures ranged from 1°C to 32°C.

When daily extremes in temperature were compared throughout the growing season, a significant difference was found between three stands located in the Brewer spruce zone and those situated farther inland to the east (Fig. 2). Near the boundary, the three stands monitored in the western Siskiyou Mountains had more than one third of the days with temperature

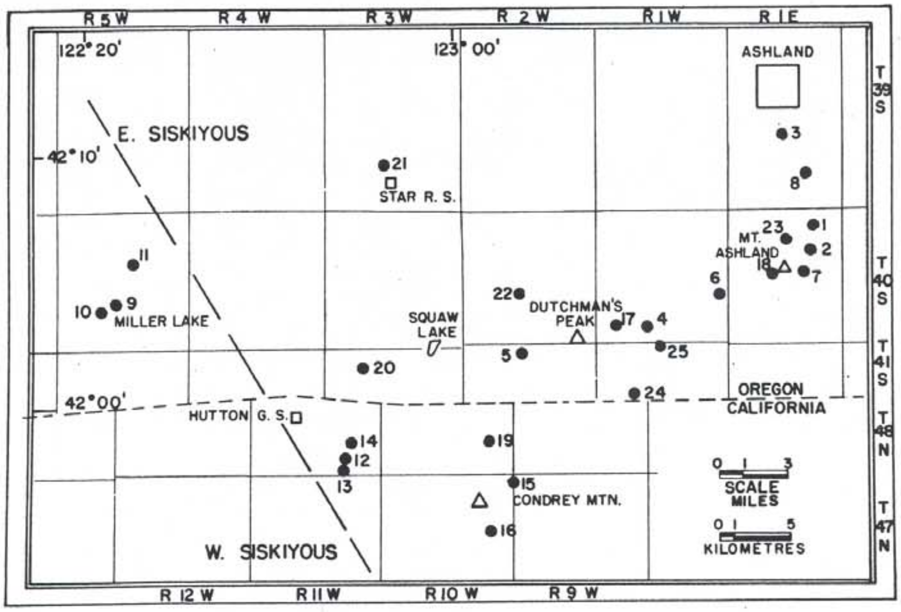

FIG. 2. The monitored Brewer spruce stand, No. 10, was near the species' eastern distributional limit, designated by the broken diagonal line. Other climatically monitored stands represented the range of environment and forest vegetation encountered in the eastern Siskiyou region (Waring 1969). Stand 23, located 35 km from the nearest Brewer spruce, contains a relict population of *Picea engelmanii* Parry. The grid is based on the U.S. Geological Survey, where a complete township and range unit represents 36 mi^2.

extremes differing by less than 5°C. Immediately to the east of the boundary, only 5% of the days during the growing season exhibited such variations. Closer inspection indicated that afternoon temperatures normally were lower in the region where Brewer spruce occurs, as a result of increased cloud cover and cool air masses derived from the not-too-distant Pacific Ocean. These findings are important with respect to evaporative demand, as demonstrated by Reed and Waring (1974).

We believe that soil temperature is a major factor in controlling initiation of cambial shoot growth. By inserting insect mounting pins into the cambium, as described by Wolter (1968), we found no cambial or bud growth in Douglas fir on 25 forest sites as long as soil temperatures at 20 cm depth remained below 4°C. Havranek (1972) recently demonstrated that cold soils can even reduce photosynthesis and transpiration for subalpine species such as *Larix decidua* Mill. and *Picea excelsa* Link. These observations support our attempt to interpret the effect of air and soil temperatures together upon conifer distribution.

Our colleagues, Lavender and Overton (1972), conducted a series of controlled-temperature experiments with different populations of Douglas fir. They also found that soil temperature was important and that biomass accumulation was 40% less at 10°C than at 20°C. With response surfaces defined by their original data, Cleary and Waring (1969) developed a temperature–growth index by summing the potential growth of Douglas fir for each day during the growing season. The maximum potential growth occurred when day temperatures averaged 25°C and soil temperatures were at 20°C. Such days were assigned values of 1.0. Fractional reductions were assigned for less-favorable combinations of air and soil temperatures. When these indices were computed for the 25 monitored stands (Fig. 2), they ranged from 30 near timberline to nearly 100 at lower elevations, where pine and oak forests dominated. The monitored Brewer spruce stand had an index of 52. Douglas fir was absent from stands with temperature indices below 40, and Shasta red fir was restricted to a range from 30 to 55. Thus, by association, Brewer spruce seems to be well adapted to cool temperatures during the growing season.

Laboratory Studies

By conducting experiments in controlled

growth rooms, some additional insight into the comparative behavior of Brewer spruce, Douglas fir, and Shasta red fir was obtained.

One experiment consisted of growing pregerminated seeds of spruce and Douglas fir together in a variety of soils under a regime of 25°C and 0.15 cal cm^{-2} min^{-1} in the 400- to 700-nm range for an 18-h day with a night temperature of 13°C. Soil temperatures fluctuated between 18 and 22°C. After 6 months under this particular environment, the biomass of Douglas-fir seedlings was four times greater than that of Brewer spruce when the two were grown together on fertile soils. On all but the most infertile of soils, growth of Douglas fir was superior even under the low-light regime. On infertile ultrabasic soils, Brewer spruce was able to approach the growth rate of Douglas fir. This suggests that Brewer spruce should compete poorly with other conifers on the better sites. The nutritional significance of this comparative study will be discussed under the subject of soil fertility.

In another study, growth of Shasta red fir and of Douglas fir was compared under a cooler temperature regime more characteristic of subalpine environments. Unfortunately, because of lack of seed Brewer spruce was not included in this comparison. After 5 months, under a constant 21°C day of 15 h and a 10°C night with soil temperatures fluctuating between 14° and 17°C, Shasta red fir outgrew Douglas fir by one third on 25 replicated soils (Waring and Youngberg 1972). This experiment indicated that subalpine species may have a competitive advantage over Douglas fir if growing-season temperatures remain sufficiently cool.

Soil Moisture

Soil moisture, although measurable, is difficult to interpret ecologically, even when converted to soil water potential. Difficulty of interpretation results from spatial variability and from the fact that roots absorb water where it is most available and where other conditions favor root activity. Thus, attempts at assessing plant moisture status from soil moisture profiles are frustrating. Fortunately, the plant itself can serve as an index of available soil moisture.

Plant water stress, defined as the absolute value of xylem sap potential, usually increases from a predawn minimum to some maximum level in the afternoon. Predawn plant water stress represents an equilibrium with available water in the root zone (Hinckley and Ritchie 1973; Sucoff 1972). By monitoring predawn stress with a pressure chamber (Scholander *et al.* 1965; Waring and Cleary 1967), a seasonal comparison of the 25 stands was possible. Douglas fir or Shasta red fir saplings 1–2 m tall were chosen as reference trees in each stand.

Where Brewer spruce grows, summer precipitation is scanty, thus plant water stress generally increases as transpiration exhausts the available soil water. In such a climate, a simple index of water available during the growing season can be obtained by recording the maximum predawn plant stress near the end of the growing season (Waring and Cleary 1967). The ecological distribution of major tree species in relation to this moisture and the previously defined temperature index gives a fair picture of the environmental field within which Brewer spruce must compete (Fig. 3). The monitored spruce stand

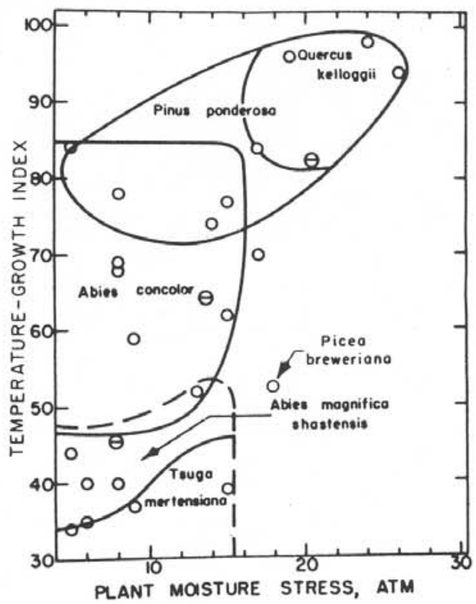

FIG. 3. Distribution of important tree species in the eastern Siskiyou Mountains of southwestern Oregon and northwestern California in relation to plant-response indices for temperature and moisture. In the western Siskiyou Mountains, Brewer spruce occurred with associated subalpine conifers on drier sites where the evaporative demand is less. Circles represent monitored stands where environmental and physiological assessments were made. The circles with diameter symbols indicate validation stands where environmental indices were predicted successfully from knowledge of the vegetation (Waring *et al.* 1972).

had a moisture stress index of 18. Stress greater than 18 atm was associated with a cessation of cambial activity of Douglas fir a month before the normal end of the growing season, which is in late September (Waring 1969).

Microsite variation also may be important, for Brewer spruce tended to occupy areas where rock outcrops were prominent. Within the monitored stand, four Brewer spruce averaged 28 atm predawn stress, while the same size Shasta red fir or white fir averaged 10 atm less stress. Temperature and available moisture indices, however, are still inadequate to define fully the environmental restriction of Brewer spruce. Another index reflecting evaporative demand is important in interpreting the spruce's limited distribution.

Evaporative Demand

Field Studies

The potential loss of water from a forest is controlled by the amount of energy available to change the state of water from a liquid to vapor. It can be expressed as a function of the water vapor concentration gradient between the evaporative surface and the atmosphere and the velocity of the wind. An estimate of evaporative demand can be made knowing the humidity and the temperature of the air. Reed (1971) estimated daily potential transpiration at sites where we had temperature recorders at a height of 20 cm above the ground. Humidity data were not directly available but were predicted from fire weather data (Reed and Waring 1974). For calculations, a constant foliage area with a leaf resistance of 4 s cm^{-1} was assumed so that evaporative demand could be estimated.

For the period from April 1 through September 30, Reed found that the Brewer spruce stand had less than half the evaporative demand of some oak and pine stands (Waring *et al.* 1972). Low evaporative demand, however, also characterized Shasta red fir and mountain hemlock stands. However, given the same elevation and physiographic situation, stands within the geographic range of Brewer spruce had lower evaporative stress than those located further inland. This trend, presumably, becomes more striking as one proceeds westward toward the Pacific Ocean. Why then does Brewer spruce not extend its range further toward the coast? We suspect that it is because of an absence of tall peaks, where snow can accumulate, and also because of increased competition from *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Sequoia sempervirens* (D. Don) Endl., and *Picea sitchensis*.

The evaporative demand does not determine actual water loss by the vegetation. If plants are subjected to drought, stomatal and mesophyll resistances may increase and reduce transpiration or the leaf area may be reduced. Reed (1971), using a pressure infiltration technique (Fry and Walker 1967), demonstrated in the Siskiyou Mountains that Douglas fir stomatal control was in part a function of hydration during the night. When predawn stress was less than 5 atm, stomata often remained open throughout the day, averaging leaf resistances of less than 10 s cm^{-1}. When predawn stress increased to 15 atm, leaf resistance increased to at least 50 s cm^{-1}, and at 30 atm, stomata were closed with leaf resistances more than 200 s cm^{-1} (Running 1973). Gindel (1967) reported similar control by Aleppo pine growing in an arid region.

Neither Douglas-fir nor Shasta red fir stomata appear particularly sensitive to moderate diurnal changes in the evaporative demand. Brewer spruce, on the other hand, responds not only to soil drought but also to increased evaporative demand. During days with high evaporative demand, we found Brewer spruce stomata significantly more closed than those of Douglas fir, both in July, when new foliage was expanding, and in the cooler month of September. On both occasions predawn stress was less than 8 atm. Stomatal response was evaluated on excised needles with an infiltrometer (Fry and Walker 1967).

Laboratory Studies

To test more rigorously these limited field observations, we potted some small Douglas fir and Brewer spruce from the Siskiyou Mountains and brought them to a nursery site in the Willamette valley of northwestern Oregon. After 6 months of preconditioning outdoors, five Brewer spruce and three Douglas-fir seedlings were brought inside for a series of CO_2 gas-exchange measurements.

An experiment was designed to compare the effect of high evaporative demand upon Douglas fir and Brewer spruce. With a closed cuvette system designed by Cleary (1970), we measured CO_2 exchange with an infrared gas analyzer while maintaining shortwave radiation at 1.0 cal cm^{-2} min^{-1}, air flow at 40 litres min^{-1}, and cuvette temperature at 23°–27°C. Seedlings first were monitored under a water vapor concentration gradient equivalent to 7 mbar. The next day, the evaporative demand was increased to 19 mbar.

With well-watered roots, Douglas fir showed no reduction in net photosynthesis when the evaporative demand was increased almost threefold, at least during the experiment. Brewer spruce, in contrast, reduced CO_2 uptake by 50% at the higher evaporative demand and, after a 2-h exposure, completely closed stomata, which halted all photosynthesis. Sitka spruce reportedly has similar sensitivity to high evaporative demand (Watts and Neilson 1975).

These studies, both in the field and laboratory, suggest that Brewer spruce is able to withstand considerable soil drought but is extremely sensitive to sustained high evaporative demand. Its general occurrence on rocky, north-facing slopes and in protected canyons lends further credence to this assumption. In such environments, Brewer spruce can conserve water daily by reducing transpiration by way of stomatal control before depletion of water triggers a response. However, only in areas where soil drought actually will develop is the spruce favored over *Abies magnifica* var. *shastensis* and *Tsuga mertensiana*. Within a stand, spruce may establish itself in shallow crevices where seedlings of other subalpine conifers would die. There, it can grow slowly with little competition for the meager supply of water available to its roots.

Light

Within the forest stand, Brewer spruce is able to survive in the dense understory as a suppressed seedling or sapling. Atzet and Waring (1970), using a spectroradiometer in the Siskiyou Mountains, reported that Douglas fir and true firs could survive at light levels less than 2% of full sunlight, in the 400- to 700-nm range, integrated over the entire day. Under drought stress, they reported that additional light was required for survival. They found that Brewer spruce also survived at less than 2% of full light. In contrast, no seedlings of ponderosa pine were found at levels below 10% of full sunlight and normally did not become established at less than 20%.

In a more comprehensive study of sapling growth in relation to light, Emmingham and Waring (1973) found Douglas fir usually was replaced by true firs at light intensities below 7% of full sunlight if soil moisture was not limiting. Brewer spruce appears to have a lower light compensation point than Douglas fir and to be favored in partial shade or sheltered physiographic situations where the evaporative demand is not extreme. Small Brewer spruce survive overstory removal but rarely are established in the open. Only on particularly infertile ultrabasic soils where competition is limited have we observed seedlings established in open situations.

Soil Fertility

Laboratory Assays

Brewer spruce is found on a wide range of soils with differing fertility. In our reconnaissance survey, we found it on granite, gabbro, metavolcanic, metasedimentary, and ultrabasic parent materials. A bioassay, reported in the discussion of temperature response, indicated that the spruce grew best on soils similar to those favored by Douglas fir and Shasta red fir. It did relatively better on the less-fertile soils and almost held its own with seedlings of Douglas fir when grown on ultrabasic soils, even at temperatures favoring the latter.

Chemical analyses of major soils and relative growth of Douglas fir and Brewer spruce are reported in Table 3. From the chemical analyses alone, an interpretation is most difficult. This reflects, in part, the inadequacies of present chemical methods to indicate nutrient availability for conifers. A more realistic assessment of soil fertility can be provided by not reducing the volume of rocks or mixing the horizons together. Waring and Youngberg (1972) followed this procedure with four replicated profiles collected from under the 25 instrumented stands mentioned previously. The results of the bioassay with Douglas fir and Shasta red fir gave essentially the same ranking of soils (rank correlation coefficient = 0.923), although Shasta red fir grew one third more than Douglas fir under the selected cool-temperature and low-light regime.

The Brewer spruce stand was growing upon soils derived from hard metavolcanic material. These soils were assayed at 20% of the fertility of the best soil. Only one of the ultrabasic soils ranked lower. The assay of soil fertility, however, represents only nutrient supply and not demand.

TABLE 3

Chemical analyses and bioassay of screened surface soils[a]

Parent material	pH[b]	%N[c]	Ca[d]	Mg[e]	K[f]	CEC[g]	DF[h]	Bsp[i]
Mica schist	4.6	0.25	0.9	0.3	0.21	9.5	100	24
Meta volcanic	5.2	0.22	1.9	0.6	0.65	8.1	36	14
Granitic	5.1	0.09	2.2	0.5	0.27	7.4	4	2
Ultrabasic	7.2	0.10	2.8	14.1	0.08	14.1	5	4

[a]Soils were collected at elevations from 1850–2000 m.
[b]pH from saturation paste.
[c]Total Kjeldahl nitrogen.
[d]Replaceable calcium in meq/100 g.
[e]Replaceable magnesium in meq/100 g.
[f]Replaceable potassium in meq/100 g.
[g]Cation exchange capacity in meq/100 g.
[h]Douglas-fir biomass (percentage of maximum) after 6 months growth in controlled environment, average of three seedlings per pot, three replications on each soil, maximum weight = 1.48 g/seedling = 100%.
[i]Brewer spruce biomass (percentage of Douglas-fir maximum) after 6 months growth in controlled environment, average of three seedlings per pot, three replications on each soil.

The demand for nutrients is a function of the plant's requirements under the actual environment in which it grows.

Field Studies

We found foliar analysis on understory Douglas fir and Shasta red fir a good indicator of the nutritional status when samples were taken on 1-year-old foliage at the time of maximum demand when new foliage is beginning to expand (Waring and Youngberg 1972). When 1-year-old foliage was sampled in the dormant season, the Shasta red fir in the Brewer spruce stand, as well as at other subalpine sites, showed high levels of nitrogen (1.33–1.49%). Spring sampling, however, indicated consistently low nitrogen levels commonly dropping below 1% on all the soils with low bioassays. Thus, Brewer spruce appears generally restricted from the more-fertile soils where competition from the true firs and other conifers is more intense. The species actually may be favored over other subalpine conifers on sites with low fertility.

Mechanical Factors

In the environment where Brewer spruce survives, snowfall not only is deep, usually more than 2 m, but is heavy. At timberline in the Siskiyou Mountains, the temperature rarely drops below −10°C. Thus, the branches as well as the stems must bear loads that injure many conifers. According to Shidei (1954), snow may create stress in three ways: through the weight on the crown; through the settling force on the entire tree; and through creeping pressure on the stem. The pointed top and drooping branch habit of Brewer spruce (Fig. 4) reduce the impact of heavy snow upon the crown. Damage from the settling of deformed and compressed layers of snow is a function of the perimeter of the crown and tree height. Thus, a broad crown and rapid height growth are traits unadapted to environments with heavy snowpack. The most damaging effect of snow, however, is that associated with creep, because the force exerted upon the stem is proportional to the square of the water content of the snow (Shidei 1954). Snow creep pulls small, poorly rooted trees from the ground and causes the crook observed at the base of most Brewer spruce, mountain hemlock, and Shasta red fir. Brewer spruce, like its subalpine associates, remains sufficiently limber at low temperatures to bend under this pressure, and produces compression wood to counterbalance the force. This certainly is not true with ponderosa pine, Douglas fir, or other species generally found at lower elevations (Williams 1966).

Discussion

To summarize the environmental limits of Brewer spruce, we have prepared a tolerance table contrasting the adaptive ability of the spruce with its major competitors (Table 4). One immediately notes that Brewer spruce ranks in the categories most tolerant to cold temperature, low light, infertile soils, and snow pressure. It also is tolerant of soil drought but sensitive to evaporative stress.

Some of the spruce's adaptive characteristics, such as tolerance for ultrabasic soils, may have been valuable during times of climatic change; since in the Siskiyou mountains, large masses

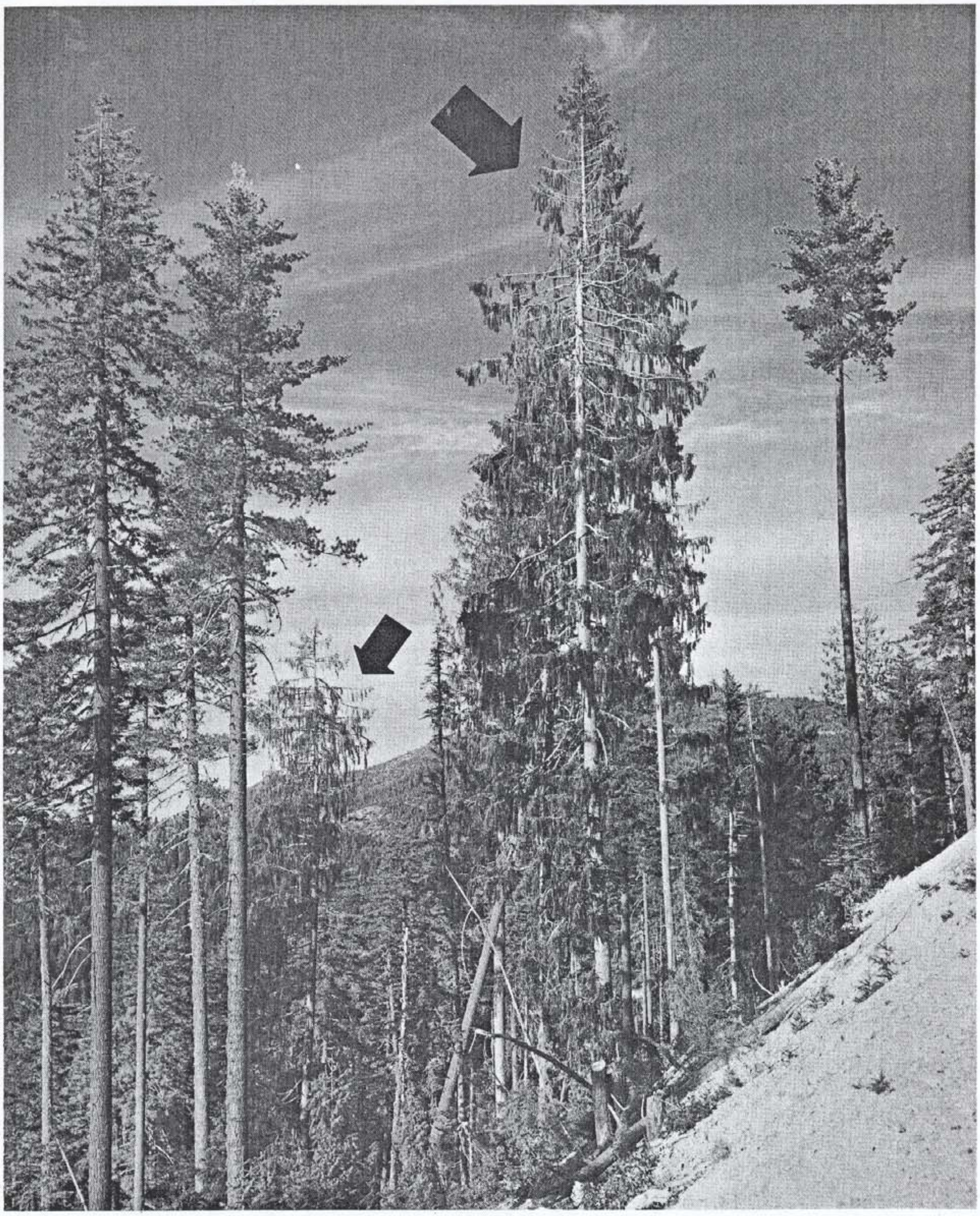

FIG. 4. Brewer spruce (marked with arrows) growing in a stand with *Pseudotsuga menziesii* and *Pinus monticola* as associate species. Note drooping form of spruce branchlets, which reduces snow accumulation.

TABLE 4

Environmental tolerances for Brewer spruce and associate conifers

Species	Environmental variable[a]					
	M[b]	E[c]	T[d]	L[e]	F[f]	P[g]
Abies concolor	2	2	2	3	2	2
Abies magnifica var. *shastensis*	1	2	3	2–3	2	3
Picea breweriana	2–3	1	2–3	3	3	3
Pinus jeffreyi	3	3	3	1	3	2
Pinus lambertiana	3	3	1	2	2	1
Pinus monticola	2	2	3	2	2	2–3
Pseudotsuga menziesii	3	3	1–2	2	2	1
Tsuga mertensiana	1	2	3	2–3	2	3

[a]Tolerance classes range from 1 to 3 with 3 signifying the highest tolerance to each environmental variable.
[b]Soil moisture stress.
[c]Evaporative demand.
[d]Cold temperature.
[e]Low light.
[f]Low fertility.
[g]Snow pressure.

of ultrabasic rocks occur at all elevations. The fact that plant competition on soils derived from such material is always sparse could mean these soils provided a temporary refuge along both vertical and lateral migration routes.

Where established, Brewer spruce grows slowly during an abbreviated growing season, which reflects the late melt of a heavy snowpack and early depletion of available water from poorly developed soils. Its slow rate of growth and drooping branches protect it from snowbreak.

On the better sites at lower elevations, the spruce can be outgrown easily by a host of other conifers. It can survive in deep shade and has, in fact, difficulty establishing in the open. It exhibits preference for sheltered and north-facing slopes, where evaporative demand is reduced and soil water conserved. There, an all-age stand may develop with little danger of fire.

Both in the open and in more-continental regions to the east, high evaporative demand causes stomatal closure and limits photosynthesis. The spruce apparently does not extend its range further toward the Pacific coast because of the absence of high peaks with heavy snowpack, cool summer temperatures, and low evaporative demand. Other temperate forest species such as Douglas fir, western hemlock, and coast redwood seem to compete better in the cool coastal areas.

Certainly, the types of environment that Brewer spruce now occupies were much more extensive during the Pleistocene, when the higher peaks in the Klamath range were glaciated. Brewer spruce may owe its existence to the past and present diversity of environments offered within the Siskiyou mountains.

Acknowledgments

Our initial interest in Brewer spruce can be traced to a conversation 10 years ago between the senior author and Mr. Oliver V. Matthews, dendrologist from Salem. Mr. Matthews enthusiastically shared his knowledge about locations of Brewer spruce, which he discovered during many years of travel about the state of Oregon. His careful records and maps indicate that his first finding of Brewer spruce was in 1928. His records formed the basis for many of the points on the range map.

Others have been most helpful in providing documentation of the range: Mr. J. T. Howell listed the collection in the California Academy of Science herbarium; Dr. J. McBride provided a check on the herbarium at the University of California, Berkeley; and Mr. Allen Wolfsan of the U.S. Forest Service kept careful records of his sightings on the Siskiyou National Forest. Dr. James G. Griffin of the University of California was particularly helpful in checking out the range map with his own field records. To all of these we extend sincere appreciation.

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