ECOLOGICAL RELATIONSHIPS OF QUERCUS DOUGLASII (FAGACEAE) IN THE FOOTHILL ZONE OF SEQUOIA NATIONAL PARK, CALIFORNIA

GAIL A. BAKER, PHILIP W. RUNDEL
Department of Ecology and Evolutionary Biology,
University of California, Irvine 92717

DAVID J. PARSONS
Sequoia National Park,
Three Rivers, California 93271

ABSTRACT

Quercus douglasii (blue oak) forms the dominant element of foothill woodland communities in the lower foothill zone of Sequoia National Park below 500 m on north-facing slopes and 600–800 m on south-facing slopes. Small stands of this species occur up to 1500 m on dry slopes with relatively deep soils. Densities of *Q. douglasii* range from 111–321 trees per hectare. Soils beneath stands of *Q. douglasii* are significantly lower in total nitrogen, total phosphorus, and organic matter content than adjacent sites with mixed-evergreen woodland. Maximum water stress during the end of a two-year drought in 1977 reached −50 bars with little overnight recovery. Moderately low summer water potentials were also present in 1978, a wet year, but with overnight recovery to relatively low dawn stress. Mean levels of precipitation in 1979 produced intermediate values of water potential. Phenological patterns of *Q. douglasii* are variable among sites studied. Stem elongation begins in February or March and continues for 2–3 months. Leaf production began as stem elongation slowed in two sites but occurred contemporaneously with stem elongation at a third. Leaf fall occurs within a month after maximum water stress is reached. Catkins are developed from preformed buds from the previous growing season. No flowering was observed during the spring of 1978, despite abundant precipitation, because of the preceding two-year drought. Establishment of seedlings is an irregular event related to environmental stress, predation, and land-use history including fire frequency. The greatest proportion of trees at Sequoia National Park are estimated to be 60–100 years in age, with few young trees present.

The foothills of the Sierra Nevada contain a mosaic of plant communities, including the distinctive blue-oak woodland dominated by *Quercus douglasii.* While few studies to date have focused specifically on the ecological relationships of *Q. douglasii,* some data are available on this species in the Coast Ranges of California. Ecological studies of *Q. douglasii* have treated seedling survival and establishment (Griffin, 1971), community structure (Leonard, 1956; Johnson et al., 1959; White, 1966; Brooks, 1969; Vankat and Major, 1978; Pillsbury, 1978) rooting characteristics (Lewis and Burgy, 1964) and water potential relationships (Griffin, 1973). While a comprehensive description of blue-oak woodland vegetation in California can be found in Griffin

MADROÑO, Vol. 28, No. 1, pp. 1–12, 12 February 1981

(1977), no study in the past has integrated data on community structure, water relations, and phenology into a clear treatment of the ecology of *Q. douglasii.* In this paper we discuss the interaction of seasonal drought stress and qualitative and quantitative aspects of phenology of *Q. douglasii* in the foothill zone of Sequoia National Park. Quantitative stand structure is also treated as reflected by soil and environmental patterns and the dynamics of seedling establishment.

Quercus douglasii, distributed throughout the foothills of the Coast Ranges and Sierra Nevada of California, often occurs with other oak species but is usually restricted to relatively dry sites (Griffin, 1973). Its ability to survive in such areas has been attributed to a deep root system and to its deciduous nature (Griffin, 1973). These facts suggest an interaction between environmental conditions and plant responses to water stress and seasonal patterns.

Physiologically, *Q. douglasii* must be able to withstand or avoid drought characteristic of the hot and dry summers of California's Mediterranean climate. The responses of plant characteristics to limited moisture availability and the consequent physiological stresses are an important aspect of successful ecological adaptation in Mediterranean-climate species. For example, timing and duration of phenological events (specifically leaf longevity, amount of new growth, and reproductive effort) are all related to climatic patterns (Leith, 1974). In addition to these physiological and phenological factors, the distribution and structure of *Q. douglasii* communities are affected by conditions of seedling establishment and the historical background of land use, including fire history and grazing practices. Our goal in this paper is to integrate all of these factors in discussing the ecological relationships of *Q. douglasii* in Sequoia National Park.

METHODS

A vegetation inventory of the foothill zone of Sequoia National Park was carried out in spring 1977, including 20 stands of foothill woodland and nine additional stands of mixed evergreen woodland with *Q. douglasii.* These stands were sampled by means of two 25-m line-intercept transects. Data recorded for each stand included cover and height of woody species and the physical characteristics of the stands, including aspect, slope angle, elevation and soil type. Stands with *Quercus douglasii* were found between 338 and 1173 m elevation.

Soil samples were collected from each stand by pooling 30 subsamples from the top 10 cm of mineral soil. Analyses of N, P, K, Ca, Mg, $N\text{-}NH_4$, $N\text{-}NO_3$, soluble P, loss on ignition, and pH were carried out at the Soil Testing Laboratory of the University of Alaska, Palmer, following standard methods (Allen et al., 1974). Textural analysis and determinations of soil water-holding capacity were made at U.C. Irvine using standard hydrometer and soil pressure-plate techniques.

Three permanent study sites representing blue-oak woodland communities were selected in 1977 for detailed studies of water relations, phenological patterns, and growth rates of *Q. douglasii.* The Ash Mountain site at 520 m has a southerly exposure with only a gradual slope. This site receives a greater amount of solar radiation than the other two. Surface soil moisture was lower and ambient temperatures were higher here than at the other two sites during our study. The community composition is that of a typical blue-oak woodland, with widely spaced trees forming a savanna with a grass and herb understory. The Flume site, at 634 m, has a northwestern exposure and a 30° slope. The community is a buckeye-woodland phase of a blue-oak woodland with a more closed canopy than the Ash Mountain site. Buckeye Campground, at 830 m, has a westerly exposure and a 30° slope. Temperatures are coolest at this site due to its location in a canyon that channels cold air drainage. This stand is also a buckeye-woodland phase of blue-oak woodland. The canopy is closed with an herbaceous understory.

Water-stress measurements were made using a Scholander-type pressure chamber (Scholander et al., 1965; Ritchie and Hinckley, 1975). Predawn and midday readings were carried out over a 12-month period. During the growing season, March to May, measurements were made at 2-week intervals, otherwise at 4-week intervals. The sampling regime included measurements for 3–5 branches from each of two different trees. Water-potential values were calculated as the average of mean readings from each plant and the standard errors of these means were usually less than 1 bar. Midday samples were collected from branches in full sun to represent maximum diurnal stress conditions. The bomb chamber was pressurized during measurement at 0.5 bars/sec with "balancing pressure" recorded with the first appearance of xylem sap on the cut surface of the sample twig. Weather data, including temperature, relative humidity, and rainfall were monitored at permanent weather stations established at each site.

Qualitative observations of phenological stage (i.e., presence of leaf buds, new leaves, flowers, fruit, mature and senescent leaves) were recorded at the same intervals as the water stress measurements. Measurements of branch elongation were made at each site on five permanently tagged branches of each of five individuals (N = 25).

Results and Discussion

Blue-oak woodlands in the southern Sierra Nevada, the dominant phase of the foothill woodland community (Griffin, 1977), extend upward from approximately 200 m (possibly lower before the influence

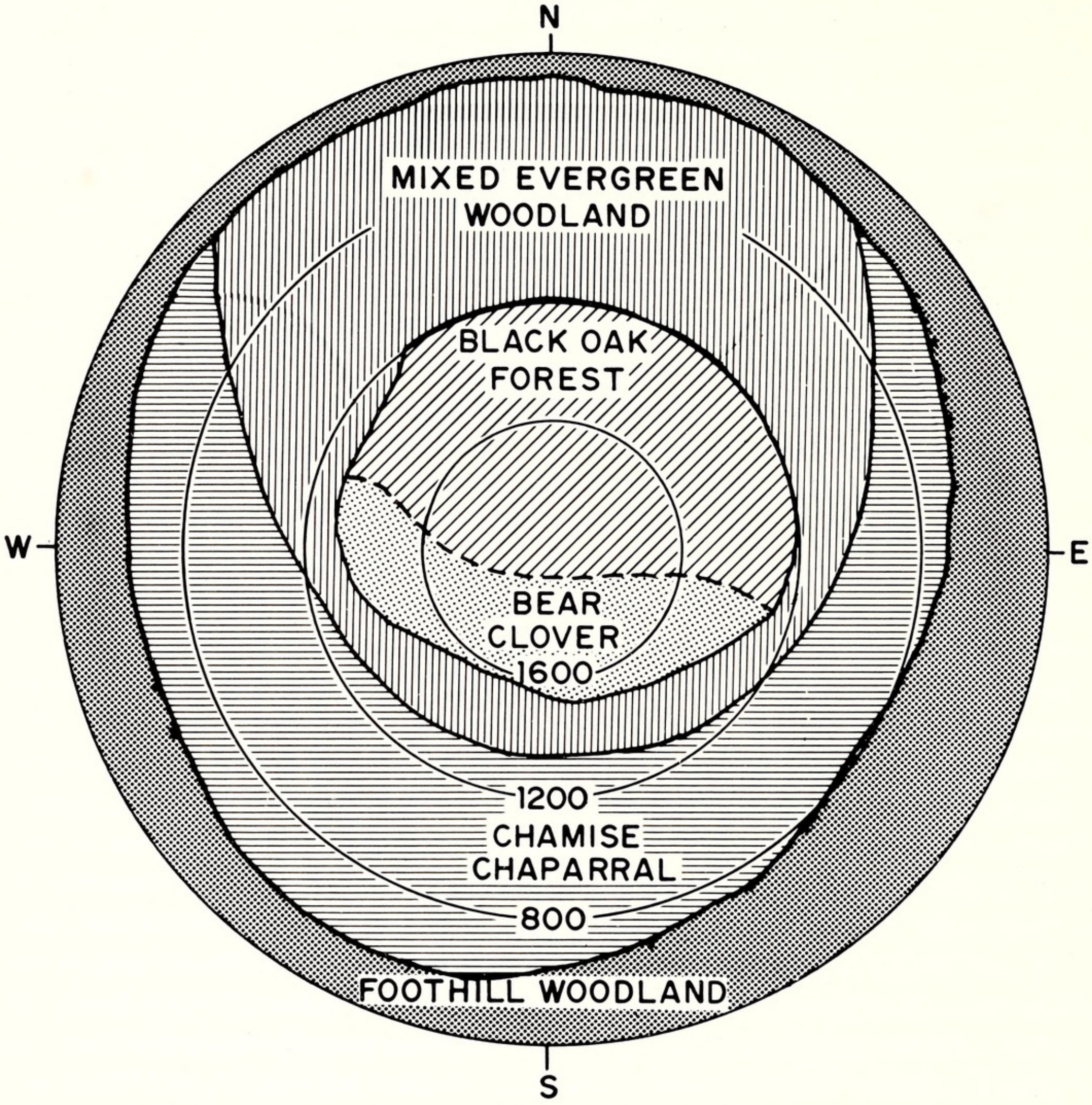


FIG. 1. Polar diagram of the distribution of foothill woodland and other major community types in the foothill zone of Sequoia National Park. Elevations are shown in meters.

of agricultural activities). They are replaced at 500–800 m by evergreen-dominated communities (Fig. 1). On north-facing slopes this community is replaced at about 500 m by mixed evergreen woodland dominated by *Aesculus californica, Quercus wislizenii,* and evergreen shrub species. On south-facing slopes it may extend up to 600–800 m where it is replaced by chamise chaparral. In many areas complex mosaics of communities occur, with blue-oak woodland on drier sites and mixed-evergreen woodland on more mesic sites, or blue-oak woodland on deeper soils and chaparral on shallower soils. Small stands of foothill woodland can be found at higher elevations up to 1500 m on relatively dry ridge lines, where soils are moderately deep or bedrock fractured. In these higher sites *Q. douglasii* is replaced by *Q. kelloggii* (black oak), but the open, savanna-like structure of stands

TABLE 1. CANOPY COVER (PERCENT), TOTAL WOODY PLANT COVER (PERCENT) AND MEAN HEIGHT (M) OF *Quercus douglasii* IN WOODLAND COMMUNITIES OF SEQUOIA NATIONAL PARK. Cover ranges are given in parentheses.

Community type	No. of stands sampled	Mean cover of *Q. douglasii*	Woody plant cover	Mean height of *Q. douglasii*
Foothill woodland				
Blue-oak woodland	10	42 (23–74)	70	7.7
Buckeye woodland	7	22 (26–40)	75	5.1
Black-oak woodland	3	6 (0–19)	74	6.0
Mixed-evergreen woodland				
Oak-buckeye woodland	9	3 (0–20)	94	6.0

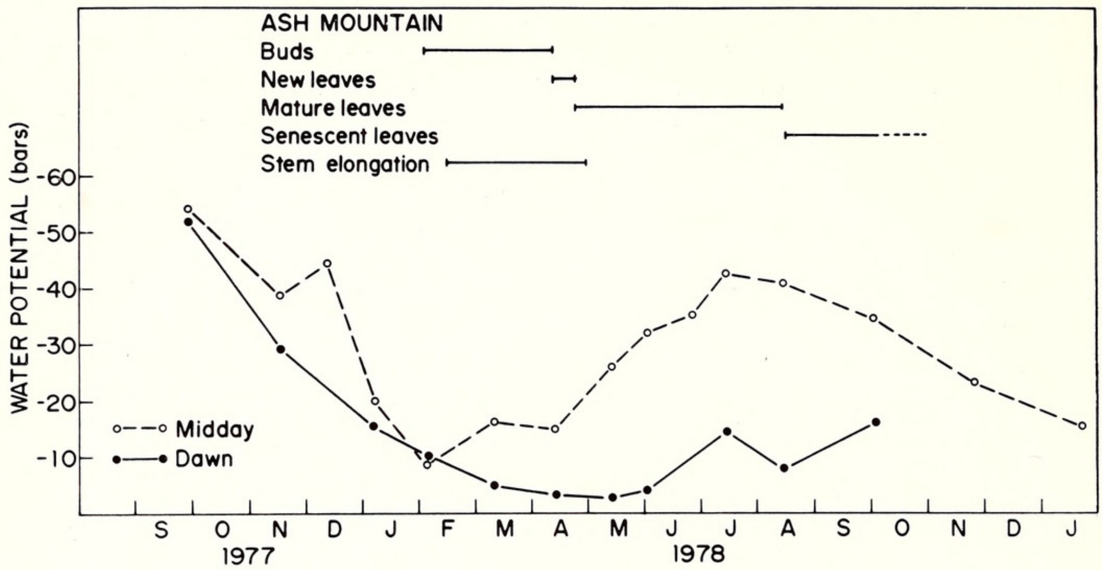
remains much the same. These stands are quite distinct from typical black-oak forest.

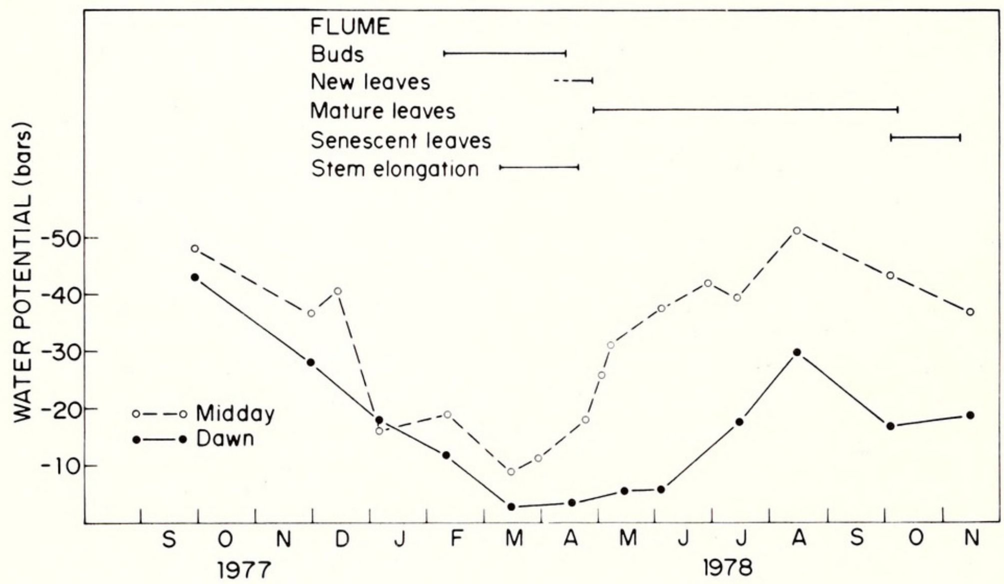
Cover of *Q. douglasii* ranged from 23–79 percent in the 10 stands of blue-oak woodland we sampled (Table 1). Densities of blue oaks in these stands range from 111 to 321 trees per hectare (Brooks, 1969). The mean height of *Q. douglasii* is greater in this community than in woodland communities and decreases as cover of *Q. douglasii* decreases (Table 1). Herbaceous understories in blue-oak woodlands are invariably dense and dominated by introduced annual grasses. Woody shrubs and trees including *Aesculus californica, Arctostaphylos viscida, Quercus wislizenii, Rhamnus ilicifolia, Toxicodendron diversilobum, Quercus chrysolepis, Quercus dumosa,* and *Ceanothus cuneatus* are frequently present but never dominant.

In the buckeye-woodland phase of the foothill woodland, *Aesculus californica* and evergreen shrubby species combined have greater coverage than *Q. douglasii* (Table 1). *Aesculus* generally has 20 percent or more coverage in these stands. Herbaceous species also provide a continuous ground cover in this phase of foothill woodland, but the denser canopy structure in comparison to the blue-oak phase (Table 1) leads to a dominance of broad-leaved, herbaceous species over grasses.

Quercus douglasii occurs infrequently as a minor element in mixed-evergreen woodland. Its cover may reach 20 percent in such stands, but evergreen oaks are more dominant. We have termed these communities, with or without blue oak, as the oak-buckeye phase of mixed-evergreen woodland.

Soil characteristics of foothill-woodland communities differ from those of the oak-buckeye phase of mixed-evergreen woodland in many respects despite the common parent materials. Values for mean total nitrogen, total phosphorus, and loss on ignition are all much lower in


ASH MOUNTAIN
Buds
New leaves
Mature leaves
Senescent leaves
Stem elongation
WATER POTENTIAL (bars)
-60
-50
-40
-30
-20
-10
Midday
Dawn
S O N D J F M A M J J A S O N D J
1977
1978


FLUME
Buds
New leaves
Mature leaves
Senescent leaves
Stem elongation
WATER POTENTIAL (bars)
-50
-40
-30
-20
-10
Midday
Dawn
S O N D J F M A M J J A S O N
1977
1978

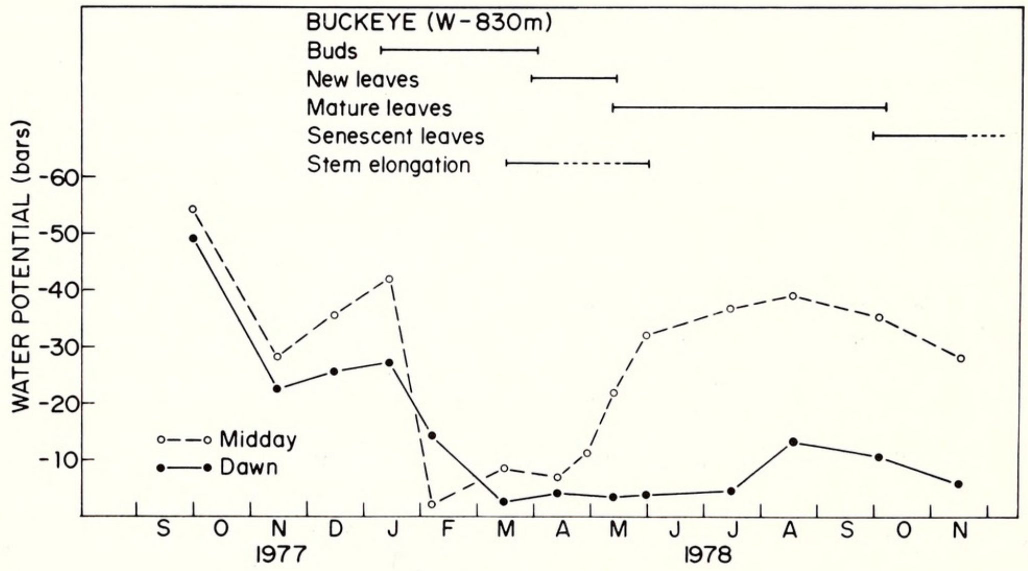

BUCKEYE (W-830m)
Buds
New leaves
Mature leaves
Senescent leaves
Stem elongation
WATER POTENTIAL (bars)
-60
-50
-40
-30
-20
-10
Midday
Dawn
S O N D J F M A M J J A S O N
1977
1978

TABLE 2. SOIL CHARACTERISTICS OF COMMUNITIES WITH *Quercus douglasii* IN SEQUOIA NATIONAL PARK. Nutrients are reported as ppm (±s.d.). Soil particle-size classes, loss on ignition and moisture content are reported as percents (±s.d.).

	Foothill woodland			Mixed-evergreen woodland
	Blue-oak woodland	Buckeye woodland	Black-oak woodland	Oak-buckeye woodland
Total N	1920 ± 830	1900 ± 310	2130 ± 570	2990 ± 1310
Total P	650 ± 300	620 ± 190	720 ± 520	1040 ± 650
K	455 ± 281	353 ± 395	353 ± 79	460 ± 195
Ca	1695 ± 734	1793 ± 504	1738 ± 422	2426 ± 998
Mg	134 ± 60	150 ± 59	150 ± 28	186 ± 89
N-NH_4	16.3 ± 8	20.1 ± 27	13.7 ± 1.9	12.8 ± 4.5
N-NO_3	11.4 ± 5.2	10.7 ± 7.6	6.8 ± 1.8	11.0 ± 3.9
Soluble P	52 ± 36	57 ± 15	64 ± 85	74 ± 60
pH	6.53 ± 0.39	675 ± 0.16	6.45 ± 0.10	6.59 ± 0.34
Loss on ignition	6.6 ± 3.2	6.8 ± 2	8.7 ± 2.2	11.0 ± 4.6
Sand	79.8 ± 6.5	82.2 ± 3.4	82.1 ± 1.6	80.2 ± 3.6
Clay	9.0 ± 5.4	6.8 ± 2.3	5.8 ± 1.3	7.1 ± 1.7
15-bar soil moisture content	7.5 ± 2.9	7.8 ± 2.3	9.9 ± 1.0	12.3 ± 6.1

the foothill woodland, indicating lower soil fertility (Table 2). Cation contents and available forms of nitrogen and phosphorous are not significantly different. Soils in all community types are sandy loams, with a mean sand content of about 80 percent. The higher organic matter content of the oak-buckeye communities, however, gives these soils a higher moisture content at −15 bars water potential.

Seasonal water-stress patterns in *Quercus douglasii* reflect patterns in precipitation. Although *Q. douglasii* is able to use water from relatively great depths (Lewis and Burghy, 1964), it must rely on a limited ground-water supply that apparently is depleted by autumn.

Quercus douglasii showed similar seasonal patterns in dawn and midday water potentials at all three study sites over 1977–1978 (Figs. 2–4). The highest stress at all sites occurred during the initial (September, 1977) measurement at the end of a severe two-year drought. With the onset of precipitation in November, water potentials began to increase, although that increase was much slower than in evergreen shrubs at the same sites. There was a secondary peak of stress at all

←

FIGS. 2–4. Seasonal water potentials at dawn and midday and qualitative phenology of *Quercus douglasii*. FIG. 2 (top). Ash Mountain site. FIG. 3 (middle). Flume site. FIG. 4 (bottom). Buckeye Campground site.

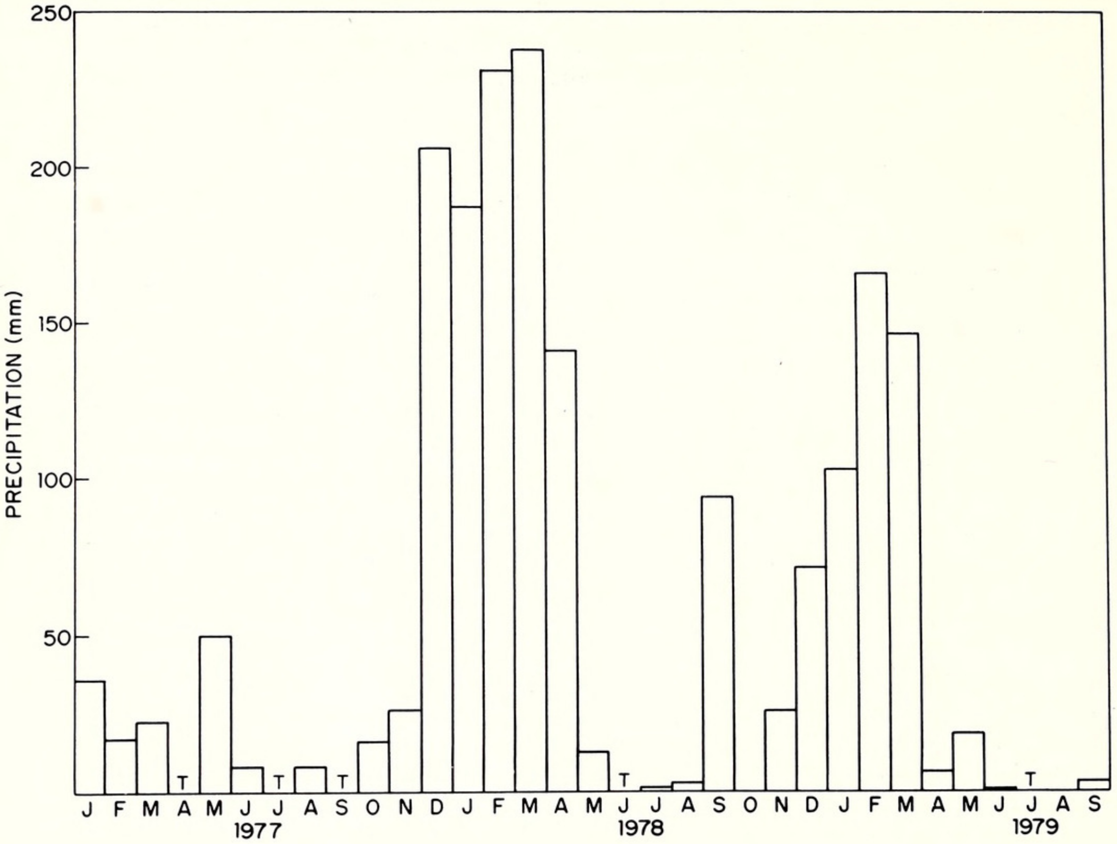


FIG. 5. Monthly precipitation for Ash Mountain over the 1977–1979 period of study. Trace precipitation is indicated by a "T".

sites; in December at the Flume and Ash Mountain and during December–January at Buckeye Campground, reflecting continued drought conditions following initial fall rains (Fig. 5). The highest water potentials occurred in February and March when the soil was recharged with water. Minimum water potentials occurred in July at Ash Mountain and in August at the other two sites.

Extreme summer water potentials are low for all three years from 1977–1979, but there is a large difference between the dawn water potentials of the drought (1977) and mesic (1978) years (Fig. 6). In 1977 the greatest difference between dawn and midday values was −6 bars. The following year the differences ranged from −21 to −30 bars, indicating considerable overnight recovery. Intermediate values of water potential and dawn-to-midday stress differentials were generally present in 1979 when precipitation was close to mean levels. Maximum 1979 water stress at the Flume site, however, exceeded that reached during the drought of 1977.

Intensive studies of the water relations of *Quercus douglasii* trees in the coast ranges of Monterey County over a three-year period found minimum dawn water potentials of −40 bars (Griffin, 1973). This is higher than our minimum dawn water potential (below −50 bars in

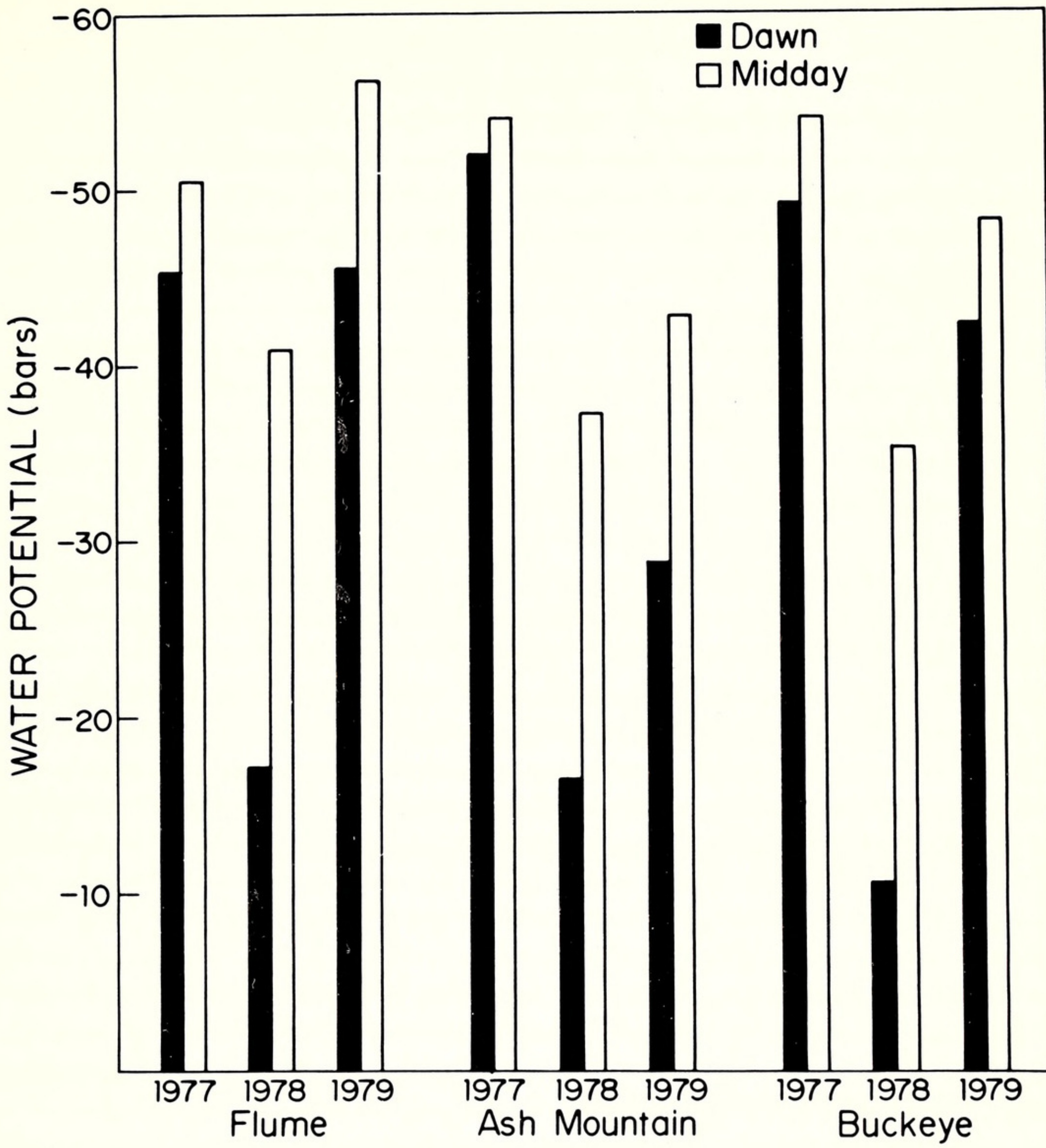


FIG. 6. Minimum water potentials for 1977–1979 in three populations of *Quercus douglasii*.

both 1977 and 1979). The density of *Q. douglasii* on slopes with shallow soils has been shown to be directly related to water stress (Griffin, 1973).

Phenological patterns and periods of vegetative growth among sites showed variability. The greatest amount of growth and development occurred from March through May when surface soil moisture was highest, temperatures were increasing (Table 3) and water uptake by plants was highest (Figs. 2–4).

Stem elongation preceded the major phenological events (Figs. 2–4). Trees at Ash Mountain showed a pattern of gradual stem elonga-

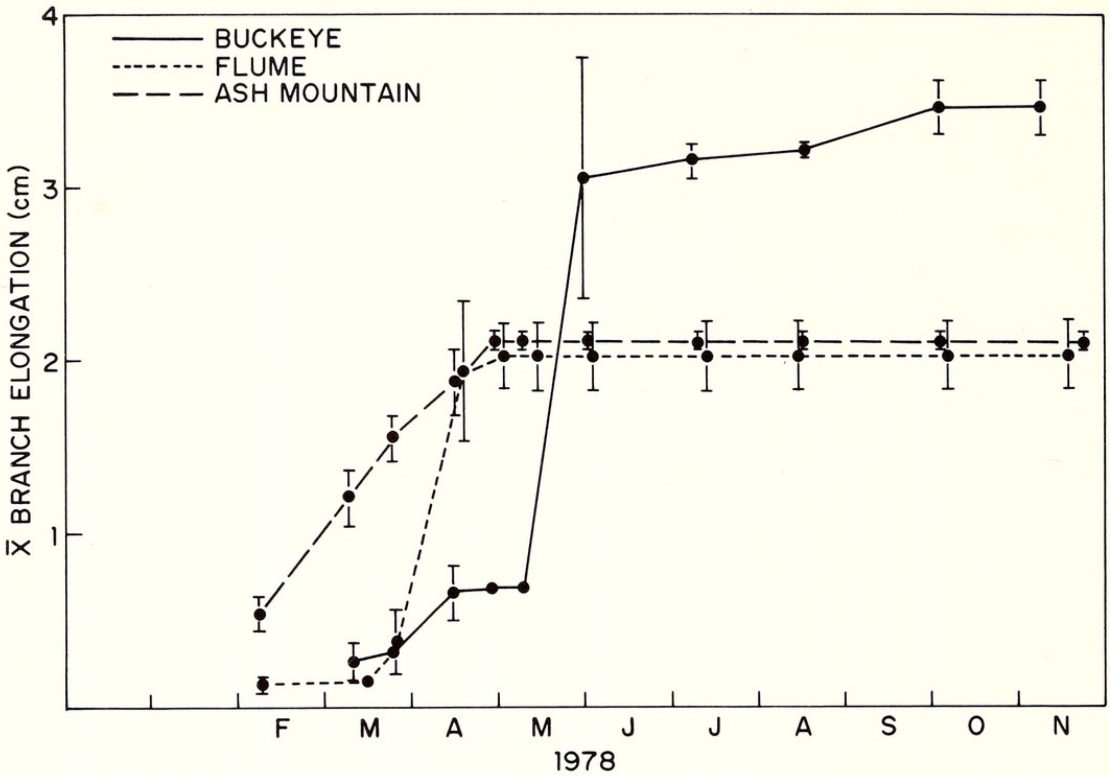


FIG. 7. Seasonal pattern of stem elongation in three populations of *Quercus douglasii*. Brackets enclose one standard error around the mean.

tion from February through April, while growth at the other two sites occurred rapidly over a shorter period of time (Fig. 7). This rapid growth occurred at the Flume site in March and at Buckeye Campground, the coolest of the sites, in May. Total mean stem elongation for the Flume, Ash Mountain, and Buckeye Campground sites was 2.0, 2.1, and 3.7 cm, respectively.

The first initiation of bud swelling occurred one to two months earlier at Buckeye Campground than at the other two sites despite the cooler temperatures (Figs. 2–4). New leaves formed after the main

TABLE 3. MEAN MONTHLY HIGH AND LOW TEMPERATURES (°C) DURING THE 1978 GROWING SEASON AT THE *Quercus douglasii* STUDY SITES. Data for March are means for a single week.

	Ash Mountain		Buckeye Campground		Flume	
	High	Low	High	Low	High	Low
February	15.2	4.2	11.6	3.6	10.5	4.2
March	19.3	7.7	13.5	5.7	12.2	7.2
April	17.9	7.0	—	—	13.5	6.3
May	23.6	11.0	21.6	9.1	21.5	10.7
June	27.5	14.0	26.8	13.9	27.9	15.9

branch elongation at Ash Mountain and Flume, but at Buckeye the appearance of new leaves and branch elongation continued simultaneously. New leaves appeared at all sites by the end of March and were mature by mid-April, with a blue-green caste and a thick cuticle. The leaves remained on the trees throughout the major portion of summer and began to fall at the end of August when trees were under maximum water stress. By October all trees had lost the majority of their leaves and remained leafless until the following March.

Flowering in *Q. douglasii* is determined by conditions of the previous growing season, because reproductive buds are formed at that time. No flowering was observed during the 1978 season at any site, reflecting conditions of drought in 1977. However, many catkins developed after the appearance of new leaves at the Ash Mountain site in 1979. There was also somewhat greater stem elongation during this season. Average elongation was 1.5 cm on 20 March 1978 and, for the same branches a year later (16 March 1979), elongation 2.2 cm.

Studies of oak community structure by Griffin (1971, 1976) and White (1966) have shown that a combination of favorable conditions must occur for successful reproduction and establishment. With their limited root systems, seedlings of *Q. douglasii* must endure much lower summer water potentials than mature trees (Griffin, 1973). Not only are temperature and rainfall important, but also such factors as acorn and seedling predation, grazing pressure, and fire history. Phenological variability from season to season has been shown by Griffin (1971) and in unpublished National Park Service data. Establishment every year is not necessary for populations of long-lived species, such as oaks, to maintain themselves. When the correct combination of favorable conditions occur, the result is the establishment of a cohort of oaks of similar ages (Griffin, 1977).

Quercus douglasii stands in Sequoia National Park have a high proportion of even-aged individuals of similar size (Brooks, 1969). The greatest proportion of trees are between 60 and 100 years old and 12 to 30 cm dbh. Stand density affects diameters to some degree, so that dense stands (163 trees/ha) have trees with an average dbh of 18 cm and open stands (25 trees/ha) show a greater average dbh of 36 cm in the Coast Range of Central California (White, 1966). The factors responsible for the increased density of *Q. douglasii* in Sequoia National Park and other areas in California are believed to be changes in land-use history and concurrent occurrence of favorable establishment conditions in the 1860's and 1870's (Vankat and Major, 1978). During this period grazing was increased and increased density of *Q. douglasii* was favored by removing herbaceous competition for oak seedlings and decreasing fuel levels so that fires were not as intense or frequent. In addition to direct effects on oak seedlings, fire has an indirect effect on young blue oaks by increasing vulnerability to insect damage (Lawrence, 1966).

The survival of *Q. douglasii* in drier habitats is the result of a coordination between physiological and phenological characteristics in response to environmental conditions. Initial distribution of blue oaks and subsequent stand structure are affected by patterns of climate and physical events.

Acknowledgments

We thank Mignonne Bivin, Mavis Hasey, Jason Greenlee, Celia Hemphill, Carolyn Wallace, and Steve DeBenedetti for help in the field work for this project. This research was supported by the National Park Service.

Literature Cited

Allen, S. E., H. M. Grimshaw, J. A. Parkinson, and C. Quarmby. 1974. Chemical analysis of ecological materials. John Wiley and Sons, New York.

Brooks, W. H. 1969. Some quantitative aspects of the grass-oak woodland in Sequoia National Park. Unpubl. report, Sequoia National Park, Three Rivers, Calif.

Griffin, J. R. 1971. Oak regeneration in the upper Carmel Valley, Calif. Ecology 52:862–868.

———. 1973. Xylem sap tension in three woodland oaks in central California. Ecology 54:152–159.

———. 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. Amer. Midl. Naturalist. 95:422–435.

———. 1977. Oak Woodland. *In*: Barbour, M. G. and J. Major, eds., Terrestrial vegetation of California, p. 383–415. Wiley-Interscience, New York.

Johnson, W., C. M. McKell, R. A. Evans, and L. J. Berry. 1959. Yield and quality of annual range forage following 2,4-D application on blue oak trees. J. Range Managem. 12:18–20.

Lawrence, G. E. 1966. Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. Ecology 47:278–291.

Leith, H. 1974. Phenology and seasonality modeling. Springer-Verlag, New York.

Leonard, O. A. 1956. Effect on blue oak (*Quercus douglasii*) of 2,4-D and 2,4,5-T concentrates applied to cuts in trunks. J. Range Managem. 9:15–19.

Lewis, D. C. and R. H. Burghy. 1964. The relationship between oak tree roots and ground water in fractured rock as determined by tritium tracing. J. Geophys. Res. 69:2579–2588.

Pillsbury, N. H. 1978. Hardwood stand density characteristics for central coast counties in California. Unpubl. report, Central Coast Resource Conservation and Development Area, Salinas.

Ritchie, G. A. and T. M. Hinckley. 1975. The pressure chamber as an instrument of ecological research. Ecological Research 9:166–254.

Scholander, P. F., H. T. Hammel, E. Bradstreet, and E. A. Hemmingsen. 1965. Sap pressure in vascular plants. Science 148:339–346.

Vankat, J. L. and J. Major. 1978. Vegetation changes in Sequoia National Park, California. J. Biogeography 5:377–402.

White, K. L. 1966. Structure and composition of foothill woodland in central coastal California. Ecology 47:229–237.

(Received 23 Jan 1980; accepted 7 Jun 1980; final revision received 14 Jul 1980.)