

FACTORS INFLUENCING SURVIVAL AND GROWTH OF A SEEDLING POPULATION OF ARBUTUS MENZIESII IN CALIFORNIA

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Differential survival in the seedling stage of potentially competing species is widely recognized to be of major significance in determining vegetational patterns and succession. Furthermore, an understanding of seedling ecology is essential to evaluate relative adaptation of different life cycle stages of a species, and to understand the mechanics of natural selection in plants. A brief review of these problems has been previously published by the writer (Pelton, 1953).

Arbutus menziesii Pursh, Pacific Madrone, is an ericaceous tree ranging from southern California to southern British Columbia. Tarrant (1958) has summarized much of what is known of the autecology of this species. The present study of a naturally-occurring seedling population of *Arbutus* was done from February to August of 1958 in the Santa Cruz mountains of central coastal California.

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GENERAL METHODS

The individual fates of several hundred emerging *Arbutus* seedlings were followed over a six month period, and mortality was correlated with observed or measured microenvironmental factors. Smaller numbers of seedlings of a few other species, especially *Sequoia sempervirens* (Lamb.) Endl. and *Heteromeles arbutifolia* (Ait.) M. Roem., also occurred in the plots and were included in the study.

The study area consisted of several hectares of second-growth *Arbutus-Quercus-Sequoia* forest on the northeast-facing slope of the Santa Cruz mountains, at about the 184 meter contour on Martin Creek. The plots were situated on both sides of the Old La Honda Road which bisects the area, 0.8 km. beyond the intersection with Portola Road, in San Mateo County.

Fifteen plots 30 cm. on an edge were established arbitrarily where seedlings were emerging in large numbers and representing the range of micro-

habitats in the study area. All seedlings were individually staked and charted to insure re-identification. Twice a week for most of the study period each seedling was examined and probable causes of mortality evaluated. Measurements of selected seedlings were made once a week, and the root systems of representative individuals adjacent to the plots excavated monthly.

Environmental measurements were made within the seedling stratum of air and soil temperatures, precipitation, vapor pressure deficit, evaporation, light intensity, soil moisture, pH, wilting percentage, and other conditions. In addition, rodent and bird exclosures were utilized for certain plots, and the vegetational structure and composition analyzed. Details of all these procedures are described below.

RESULTS

VEGETATIONAL ANALYSIS. The results of the vegetational analysis are summarized in Tables 1 and 2. The study area was not homogeneous, but ranged from a closed dense *Arbutus-Sequoia* forest above the road ("shade plots," fig. 1) to a semi-open and lower *Arbutus-Quercus* forest below the road ("sun plots"). Plots which were intermediate in environment were grouped in a third category ("all other plots"). Both evergreen (*Q. agrifolia* Nee) and deciduous (*Q. kelloggii* Newb.) *Quercus* species were of significance in the latter two forest types. These forests were on a northeast-facing slope of a narrow ravine, and graded into chaparral on adjacent ridges and south-facing slopes.

The entire area had been both lumbered and burned, the latter having been indicated by fire scars and multiple trunks. The closed forest in which the shade plots were located had almost no saplings of any species. The semi-open sun plot forest showed considerable numbers of *Arbutus* and *Quercus* seedlings and saplings. Less common trees not listed in Table 1 included *Aesculus californica* (Spach) Nutt., *Umbellularia californica* (Hook. and Arn.) Nutt., and *Pseudotsuga menziesii* Franco. The rarity of the latter tree and the almost complete absence of *Sequoia* seedlings suggest that a conifer overstory will not dominate the study area in the foreseeable future.

Tall shrubs (averaging over 1.5 m. at maturity) were locally abundant on the sun and miscellaneous plots, but rare on the shade plots. *Heteromeles arbutifolia* and *Corylus californica* (A. DC.) Rose were most frequent, with occasional individuals or clumps of *Ceanothus sorediatus* Hook. and Arn., *Rhamnus californica* Esch., *Holodiscus discolor* v. *franciscana* (Rydb.) Jepson, and *Sambucus mexicana* Presl ex DC. Low shrubs included mostly *Symphoricarpos mollis* Nutt., *Lonicera hispidula* v. *vacillans* A. Gray, and *Rhus diversiloba* T. & G., with occasional *Rosa gymnocarpa* Nutt. and *Rubus vitifolius* subsp. *ursinus* (Cham. & Sch.) Abrams, all least abundant again in the shade plots. Herbaceous species included *Trientalis latifolia* Hook., responsible for most of the density figures for "herbs" in Table 2, *Dryopteris arguta* (Kaulf.) Watt., which



FIG. 1. View of forest in an area where *Arbutus* dominates over one of the shade plots (not visible).

TABLE 1. SUMMARY OF THE TREE STRATUM WITHIN THE STUDY AREA

PLOT LOCATION	TREE SPECIES	Density per hectare						Average % cover
		Saplings less than 2.5 cm. DBH ¹		Trees ² over 2.5 cm. DBH		Basal area of trees over 10 cm. DBH (sq. m. per ha.)	Fre- quency ³ of trees over 10 cm. DBH	
		Over 1 year & under 30 cm. tall	Over 30 cm. tall	2.5-10 cm. DBH	Over 10 c.m. DBH			
SHADE	A. menziesii	0	0	0	561	49.0	60	49
	Q. agrifolia	0	239	0	0	0	0	0
	S. sempervirens	0	0	79 ⁴	478	90.7	60	42
	Totals	0	239	79	1039	139.7		94 ⁵
SUN	A. menziesii	1580	400	99	200	34.2	25	38
	Q. kelloggii	99	498	197	200	6.9	50	15
	Q. agrifolia	988	597	99	200	6.2	50	21
	Totals	2667	1495	395	600	47.3		75 ⁵
ALL	A. menziesii	0	67	0	1065	53.9	83	59
OTHER	Q. kelloggii	67	200	0	133	3.0	17	2
PLOTS	Q. agrifolia	534	400	0	67	1.1	17	12
	Totals	601	667	0	1265	58.0		85 ⁵

¹ Diameter at breast height.
² Or multiple trunks.
³ Percentage of 5 × 5 meter plots occupied.
⁴ Of sprout, not seedling, origin.
⁵ Includes minor species not listed.

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was absent from the sun plots, and *Bromus laevipes* Shear., *Satureja douglasii* (Benth.) Briq., and *Pityrogramma triangularis* (Kaulf.) Maxon, all three absent from the shade plots. The moss stratum, composed of several mosses and an *Anthoceros* sp., was present only on the sun plots where litter was scant. Mineral soil exposure averaged 8% on the sun plots and 0% on the shade plots. Nearly 30 additional vascular plants not listed above also occurred in the study area. Voucher specimens for most of these, including several seedling stages of *Arbutus* and certain other species, are in the herbaria of the writer or Butler University.

The average maximum height of the *Arbutus* canopy was 15 m. in the dense *Arbutus-Sequoia* phase, with occasional *Sequoia* emerging to a maximum of 32 m. The maximum height of the *Arbutus-Quercus* canopy averaged only 10 m. The 75% cover provided by the latter forest was at its maximum during the major part of this study; the deciduous *Q. kelloggii* had fully leafed out by the end of March, and the forest canopy did not begin to open significantly until *Arbutus* began abscising part of its foliage in August.

In general terms, that portion of the study area referred to as *Arbutus-Quercus* is comparable to the "Broad Sclerophyll Forest" of Cooper (1922), the "Black Oak-Madrone Forest" of Mason (1947), the "Mixed Evergreen Forest" of Munz and Keck (1959), Whittaker (1960), and Thomas (1961a), and the "Woodland" of Jensen (1939). The "shade" plots, on the other hand, are transitional with the "Redwood" (*Sequoia*)

TABLE 2. SUMMARY OF SHRUB AND HERB STRATA WITHIN THE STUDY AREA

PLOT LOCATION	SHRUB AND HERB STRATA	AVERAGE DENSITY PER SQ. METER	AVERAGE PER CENT COVER
SHADE	Tall shrubs	.02	27
	Low shrubs	14	
	Herbs	6	
	Moss	0
SUN	Tall shrubs	.1	36
	Low shrubs	45	
	Herbs	6	
	Moss	16
ALL OTHER PLOTS	Tall shrubs	.1	64
	Low shrubs	27	
	Herbs	34	
	Moss	0

forest of most of these authors. The entire study area is mapped as potential conifer cropland by the Forest Service (1950).

A number of vegetational and environmental studies have been made in the Santa Cruz mountains near the study area, including the classic researches of Cooper (1917, 1922) as well as the more recent ones of Springer (1935), Moeur (1948), and Oberlander (1953). Floristic work in the area has been recently reviewed by Thomas (1961b).

PHYSICAL FACTORS. Measurements of certain environmental conditions near the sun and shade plots are in figures 2 and 3. Where practicable, measurements were made within the air or soil strata in which the seedlings actually grew. Air and soil temperatures were recorded with Six's type maximum-minimum thermometers, the former at 2 cm. above the soil or litter surface and the latter at 3 cm. below this surface. A small ventilated reflective metal shelter was employed for the air thermometers. Maximum air temperatures on sun plots (Station 1, lower graph of fig. 2) reached 42°C. on July 15, but although actual surface soil temperatures were much higher, no stem girdle of seedlings resulted owing to hypocotyls having long since passed the "succulent stage" (Baker 1950:255).

Minimum air temperatures were likewise reached in the semi-open Station 1, but at no time did they fall below 2°C. Frost was therefore not a factor in mortality even though seedlings were emerging during the normally coldest part of the year. The nearest official weather station having long term temperature records (Redwood City) suggests that January and February of 1958 were appreciably warmer than normal although there was only slight deviation during the remainder of the study (United States Department of Commerce 1959). Under dense *Sequoia* canopy (Station 2) the maximum temperatures were greatly depressed but the minimum temperatures were only slightly raised, resulting in a much smaller diurnal variation. Soil temperatures at 3 cm. (upper graph

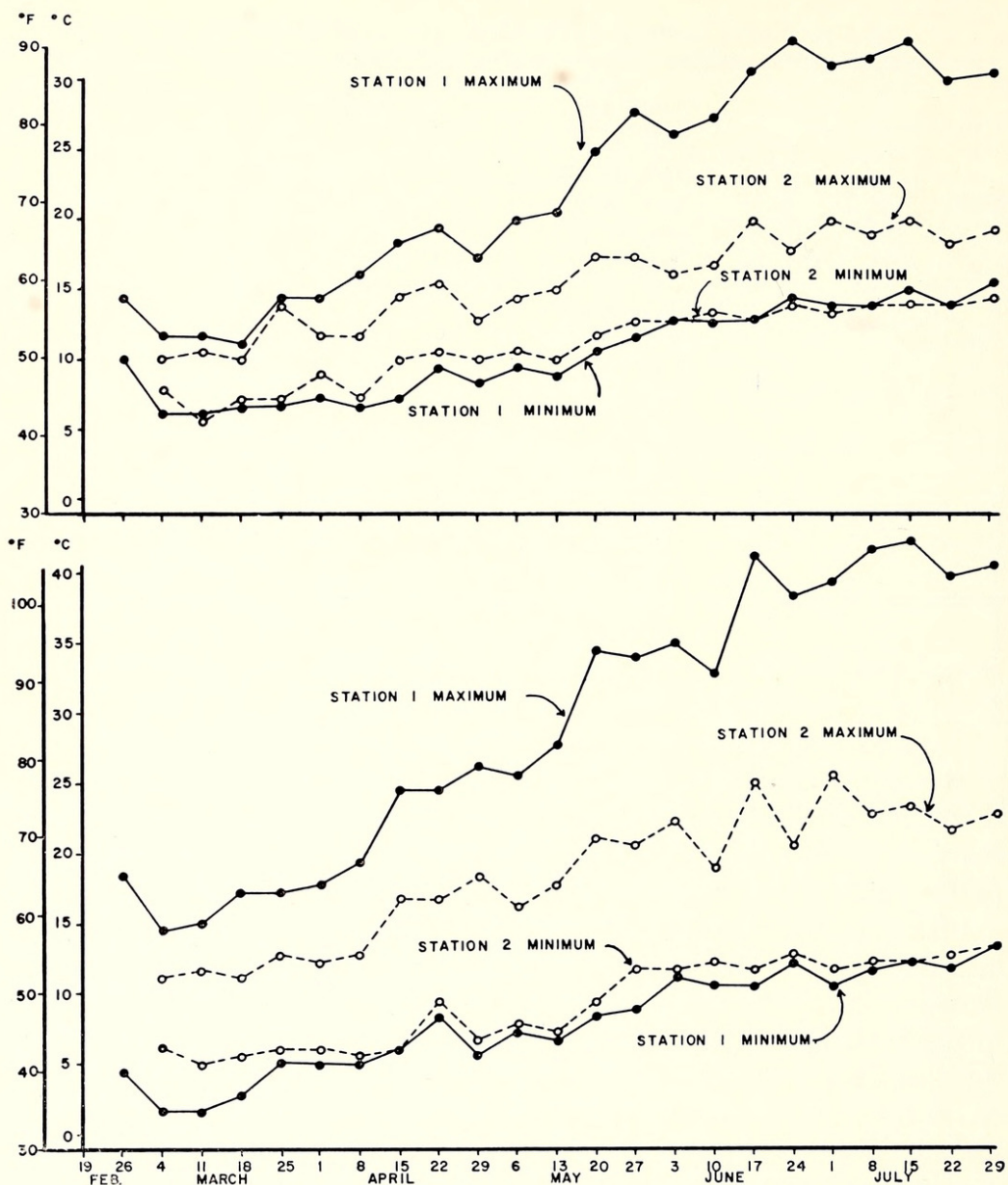


FIG. 2. Soil temperatures (above) at 3 cm., and air temperatures (below) at 2 cm. Station 1 semi-open, Station 2 in deep shade.

fig. 2) showed a pattern similar to that of air temperatures except for a tempering of the extremes. It is significant, however, that temperatures of 33°C . were reached at this level twice at Station 1. Such high temperatures at this depth help explain the soil drought which rapidly obtains in the upper soil level of semi-open areas following rains (fig. 3).

Vapor pressure deficit measurements were taken on each visit to the area among the sun plots between 12 noon and 1 p.m., as close to the ground as a small sling psychrometer could be used (about 30 cm.). There was a detectable upward trend as the season progressed (fig. 3), but the summer advection fogs from the ocean characteristic of the *Sequoia* belt (Cooper 1917) raised the humidity significantly above that which would

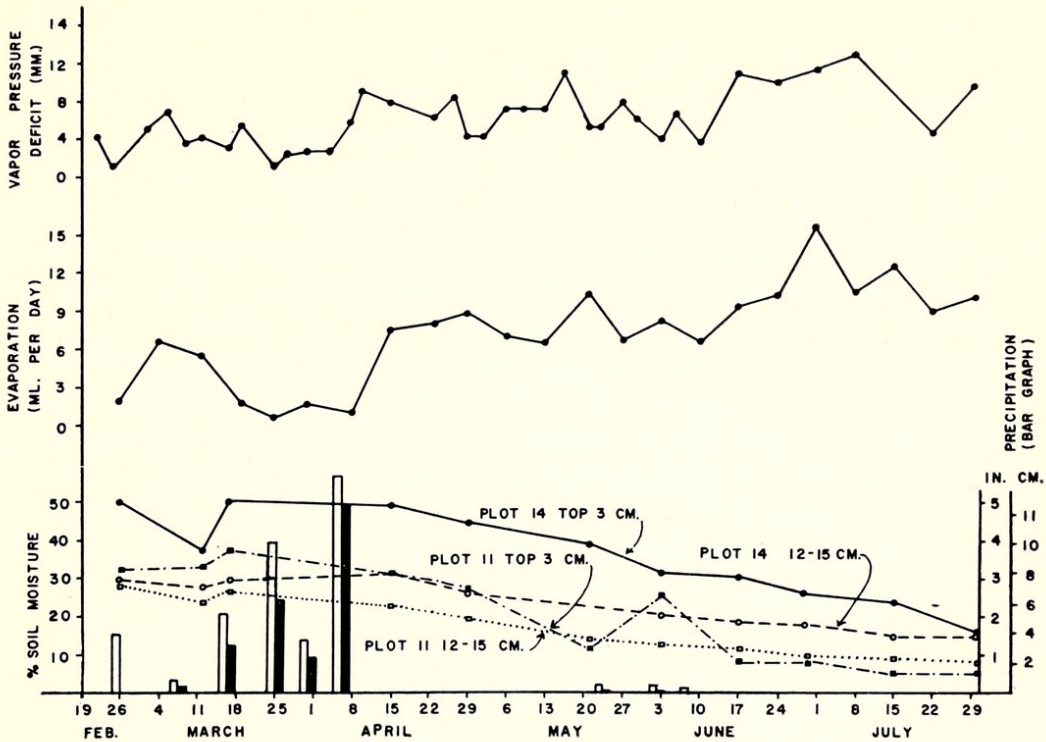


FIG. 3. Vapor pressure deficit, evaporation, precipitation, and soil moisture. Plot 11 in semi-open, plot 14 in shade. Shaded bars represent precipitation under dense canopy, unshaded bars under an opening, only the latter record being available on February 26.

otherwise prevail. Although the study area was near the inland edge of the fog belt, this factor is doubtless significant in prolonging survival in the face of intensifying summer drought. In addition, several light showers in May and June had a detectable effect on depressing the vapor pressure deficit.

Evaporation data as shown in figure 3 represent the average of corrected readings of two standardized and periodically checked spherical porcelain atmometers placed with the base of the spheres 10 cm. above the soil surface among the sun plots. The figures represent the maximum evaporation stress to which the seedlings were subjected. Again, an upward trend is apparent in spite of depression during rainy and foggy periods.

Precipitation data were obtained from two 7.5 cm. diameter rain gauges, one under an opening in the canopy among the sun plots, and the second under complete cover adjacent to the shade plots. Precipitation was concentrated in winter and early spring, as is normal for Mediterranean-type climates. Excluding the February rain, at which time only one gauge was operating, an average of 30% more precipitation was received under the light than under the dense canopy. Since the gauges were but 50 m. apart and in similar positions with regard to topography, rainfall interception by the vegetational canopy was probably responsible for this difference. Official precipitation records from nearby weather stations indicate that the rainfall during the study period was 2.7 times normal, reflecting the unusually wet year for the region.

Light intensity was measured photoelectrically by reflection for each seedling plot. This was done five times between 9 a.m. and 3 p.m. on a clear day in early May. The resulting foot candle figures were arbitrarily corrected for estimates of the cover of low vegetation below the level at which readings could be made. The final results facilitated the distinction of "sun" from "shade" plots, although not permitting expression in absolute terms. In the former plots, sun reached the seedlings a small to moderate part of each day, but only an occasional sun fleck penetrated to the shade plots.

Soil moisture determinations were made adjacent to six sun and shade plots at two-week intervals. Two depths were sampled in duplicate with a soil tube, the top 3 cm. of mineral soil, and the depth range of 12 to 15 cm. Data for one representative shade plot (Plot 14) and one sun plot (Plot 11) are given in figure 3. Greenhouse determinations of permanent wilting percentages (method of Daubenmire, 1959) for these soils gave the following results:

PLOT	DEPTH (CM.)	WILTING (PER CENT)	DATE WILTING FIRST REACHED IN FIELD (PER CENT)
14	1-3	19.8	July 29
14	12-15	13.9
11	1-3	18.5	May 21
11	12-15	11.8	June 17

In marked contrast to Plot 11, Plot 14 reached the wilting percentage only by July 29 at the surface and at no time deeper than this. Soil drought arrived much earlier and reached a greater intensity on sun than shade plots.

The contrast of mineral soil drought does not take into account the litter through which seedling roots often did not penetrate. The sun plots were all similar in having usually less than 1 cm. of litter, often exposing mineral soil or moss on small hummocks. Litter on shade plots averaged 5 cm., but reached 8 cm. on Plot 14. Although the but slightly decomposed (mor-type) litter was thicker under *Sequoia*, the large coriaceous leaves of *Arbutus* often forced roots to grow horizontally for long periods. Litter of sun plots was dry to the touch within a day following rains, but the lower layers of shade plot litter were moist in July on some plots. It is clear that the "sun" and "shade" plots differed in other important conditions than light alone. The shade plots can best be viewed as densely shaded sites with heavy litter and moist mineral soil, while sun plots are those of moderately open sites with thin litter, if any, and dry soil. Past and present soil disturbance by rodents was also much more important in the semi-open than in the shade, and the incidence of injurious invertebrates and fungi also differed.

The soils in the study area are classifiable as the "rough broken phase" of the Altamont clay loam, a residual group largely derived from interbedded sandstones and shales, and retentive of moisture but well drained. Rocks are uncommon, and a B horizon is not distinguishable. Electro-

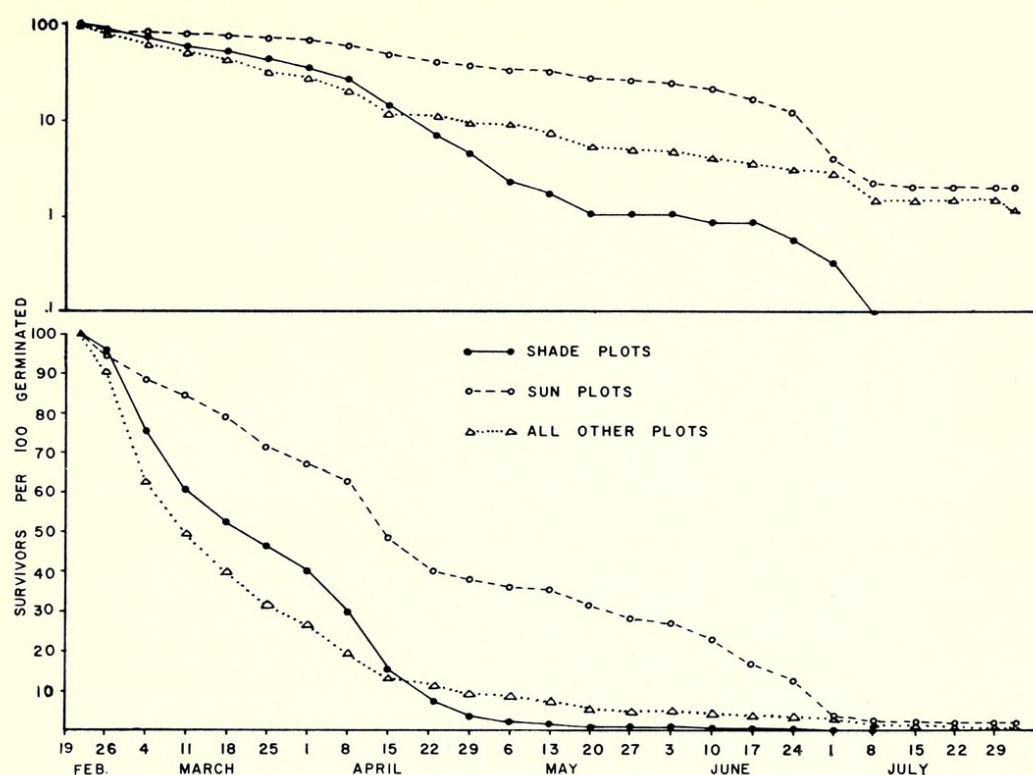


FIG. 4. Survivorship curves of *Arbutus* on log scale (top) and arithmetic scale (below).

metric pH determinations of the top 3 cm. of mineral soil ranged from 5.7 to 6.6, averaging 5.96. At 15 cm. the range was 4.7 to 6.5 with a mean of 5.65. The surface soil pH of the thin-littered sun plots averaged slightly lower (5.9) than that of the thickly covered shade plots (6.2); this anomaly probably resulted from rodents mixing acid subsoil with topsoil on only the sun plots.

MORTALITY. *Arbutus* seedling mortality results are presented graphically in figures 4, 5, and 6. The survivorship curves in figure 4 compare the seasonal advance in mortality on shade, sun, and all other plots. Since a straight line on a log scale indicates a constant mortality rate, the top curves show that such a condition prevailed only during certain periods in each habitat. The greater mortality in the shade at almost all times is evident in comparison with the sun plots.

Most *Arbutus* seedlings had already germinated by the time the study was initiated on February 19, but all were in the early cotyledon stage. Of the ultimate total number, 92% had germinated on the sun plots, 77% on the shade plots, and 86% on all others. The remaining seedlings appeared sporadically up to April 8 on the sun plots and April 15 in the shade. Consequently, the curves of figure 4 are expressed as survivors per 100 germinated rather than as survivors of an initial maximum population. A total of 829 *Arbutus* seedlings approximately equally divided between the sun, shade, and other plots varied from 20 to 108 per plot 30 cm. on a side, or 222 to 1200 per square meter.

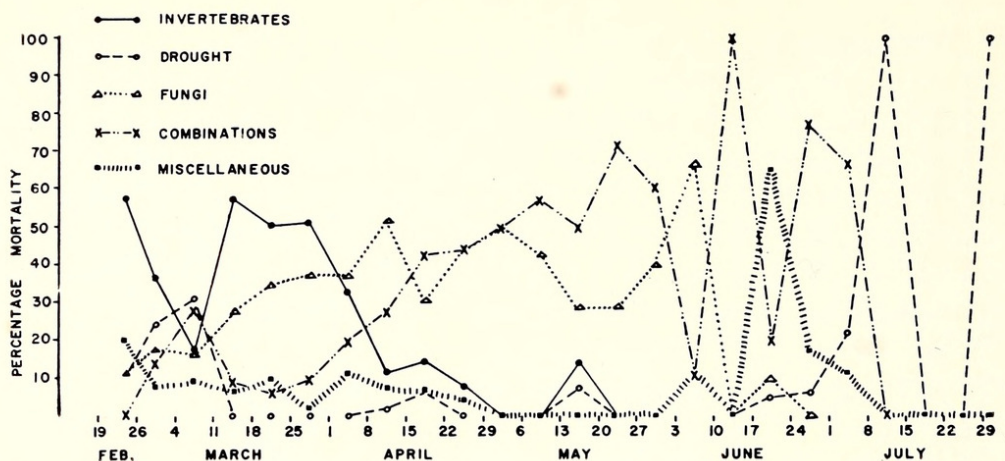


FIG. 5. Seasonal variations in causes of mortality of *Arbutus* seedlings on all plots combined, expressed as a percentage of total mortality for a given week.

At the termination of the study on August 2 no *Arbutus* seedlings were present on the shade plots, 2% had survived in the sun, and 1% on all other plots. Seedlings of other species which happened to occur on the plots, totalling 75, were also included in the study. Of these, *Sequoia* was represented by 32 individuals, all on the shade plots, of which none survived beyond April 23. Twenty-one seedlings of *Heteromeles* were present on sun and other plots (none in the shade), one of which was living at the end of the study. There were no survivors from three seedlings of *Sanicula crassicaulis* Poepp. ex DC., three of *Satureja douglasii*, or of eight unidentified plants of several other species. Four seedlings of *Pyracantha* sp. and one of an *Acacia* sp., probably carried in by birds from nearby gardens, also failed to survive. On the other hand all three seedlings present of *Lonicera hispidula* survived the entire period. Other species having occasional seedlings in the locality but not on the plots included what were probably *Rhus diversiloba*, *Osmorrhiza chilensis* H. & A., *Rosa gymnocarpa*, *Rhamnus californica*, *Dentaria californica* Nutt., *Bromus laevipes*, *Symphoricarpos mollis*, and *Hedera helix* L. (probably bird-disseminated from nearby gardens).

Figure 6 is a summary of *Arbutus* mortality under different conditions. The damage by invertebrates was probably mostly by slugs (Order Pulmonata). A small species of this group was found feeding upon seedlings on several occasions in early morning, although most damage was nocturnal. Frequently the cotyledons were completely eaten, leaving the decapitated hypocotyl, and sometimes the entire shoot disappeared. Two plots were temporarily covered on sides and top with 3 mm. mesh hardware cloth enclosures to test for bird or rodent feeding, but without effect on injury by this cause. By comparing the data in figure 5 with that in figure 3, it can be seen that mortality of this type correlated positively with precipitation. It was also of greater relative importance on the shade plots than the sun plots (fig. 6). In addition, covering of seedlings by falling leaves increased their chances of being eaten. All these observations would tend to implicate slugs or other soil-dwelling invertebrates. A mite (Order

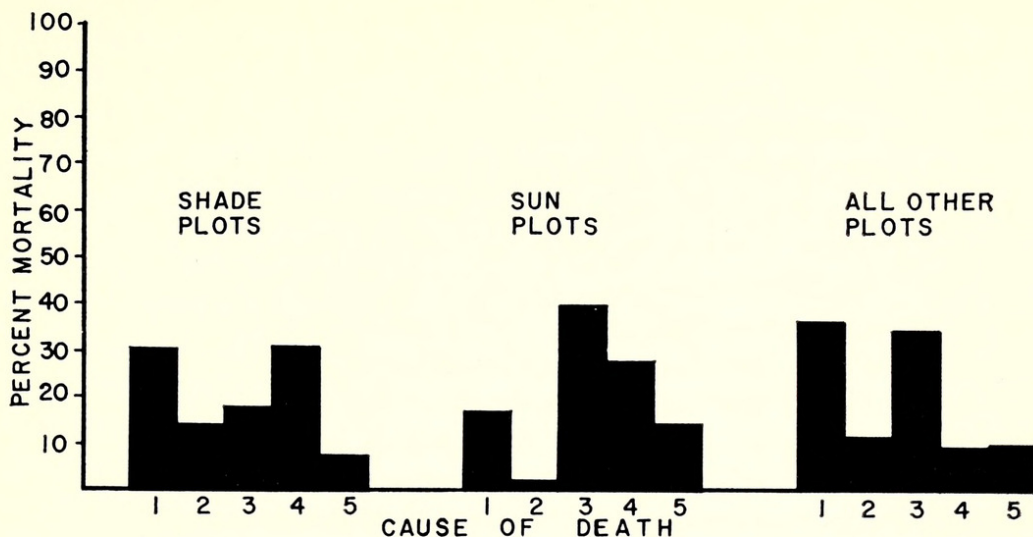


FIG. 6. Causes of mortality of *Arbutus* seedlings in different habitats. Numerals on horizontal line refer to: 1 = invertebrates, 2 = drought, 3 = fungi, 4 = combinations, 5 = miscellaneous.

Acarina) was found in abundance on hypocotyls of several seedlings early in the season, but damage seemed slight. Mites have been reported to be vectors of damping-off fungi, however, and may have contributed to mortality from this cause (Wilde, 1958). Insects were only rarely found feeding on seedlings. A total of 29.2% of the total mortality on all plots was classified under the heading of invertebrates, slugs probably accounting for nearly the whole amount.

Drought, when acting alone, is operative very soon after germination, and again, towards the end of the study, in July, when only a handful of seedlings remained (fig. 5). The early mortality, which included the great majority of the drought-killed plants, was due to recently emerged seedlings being rooted only in rapidly drying surface litter, even though this mortality occurred at the height of the wet season. The presence of a thick litter on the shade plots and its absence on the sun plots explains the anomalously larger mortality from drought in the shade (fig. 6). Actually, there was no mineral soil drought even in the surface soil on the shade plots until July (fig. 3). The more extreme sun plots, on the other hand, lacked growth water (moisture above the wilting percentage) at the surface by late May and at 15 cm. by late June. So few seedlings had survived by this time, however, that the toll from drought alone was very small (6%) on the sun plots in terms of the initial number of seedlings. Total mortality on all plots from drought acting alone was only 10.4%.

Death of *Arbutus* seedlings from fungus attack was more important quantitatively, comprising 28.1% of total mortality on all plots. This factor was positively correlated with precipitation, by June becoming of little importance as a factor in seedling mortality (figs. 3 and 5). Surprisingly, fungi were of much greater relative importance on sun than on shade plots. In part, this is a natural consequence of the lesser mortality from invertebrates on the sun plots, thereby leaving a larger proportion

to be killed by other agents. Also, several etiological agents were involved in the fungus attacks, one of which occurred only in the sun. Fungus damage was classified in the field into three categories: (1) Typical post-emergence damping-off, with collapse of the hypocotyl (and usually root decay also); (2) Root decay alone; (3) Leaf spot, usually with root decay as well. On the sun plots these conditions were in the proportion of 39%, 25%, and 36%, respectively. Leaf spot was absent from shade plots, giving a ratio of 59%, 26%, and 0%. The other plots were intermediate.

From external appearances it is probable that most of the damping-off and root decay of the *Arbutus* seedlings was produced by water molds (*Pythium*, *Phytophthora*, etc.). The unusually heavy rains in March and April (fig. 3) correlated well with maximum seedling damage, as is normal for these fungi. In addition, *Rhizoctonia* seemed also to be present on a number of seedlings, and semi-parasitic mycorrhizal fungi may have played a role as well. The leaf spot of *Arbutus*, which was present only on the seedlings growing on the sun plots, developed at the height of the March rainy period, but owing to its crippling effect, mortality was mostly delayed until April. The spots generally started as small necrotic areas which gradually enlarged until coalescence of several spots killed most of the cotyledon, although epicotyledonary leaves, the epicotyl, or the hypocotyl were often also affected. The disease was mainly concentrated on plants of a single sun plot with much exposed mineral soil. If the etiological agent were a bacterium which required splashing from mineral soil to the cotyledons by raindrops, the absence of the disease from the thick-littered shade plots might be understood.

A total of 22.7% of all mortality was attributed to "combinations" of factors. Of this amount 67% was a consequence of rather mild drought preceded by crippling from root decay fungi. If fungi had not limited the depth and volume of root penetration, the seedlings presumably could have survived at least until the summer drought intensified. This category predominated after the rainy season when the weakened root systems resulted in drought-death (fig. 5). The effect of the light showers in May and June in temporarily reducing mortality from this cause is clearly shown.

On the shade plots 25% of the "combination" category was considered to have been a consequence largely of deep shade, which predisposed the seedlings to death from another cause such as drying litter. Again, root fungi were usually involved here also, and occasionally mechanical injury from rains, falling leaves, leaf chewing, and other factors. Even on the most densely shaded plots, low light intensity was probably never by itself a cause of death during the period of study, the proximal or immediate cause of mortality always being some other factor. One completely albino seedling even survived for 25 days.

An average of 9.6% mortality was attributed to "miscellaneous" causes. Much of this category resulted from causes which were too uncertain to classify. On the sun plots, however, 67% was the result of mechanical

disturbance by rodent undermining. Also included were seedlings covered by fallen leaves or exfoliating bark of *Arbutus* for extended periods. The average angle of slope of the plots (18.4°), however, resulted in a gradual shifting of the litter downslope such that a seedling would usually be released within a few days and in such cases covering was considered a predisposing or contributing ("crippling") rather than a proximal (or immediate) environmental factor contributing to mortality. Temporary covering not only predisposes seedlings to injury from drought and fungi but during the moist season to attacks by slugs as well. Conversely, drought predisposes seedlings to covering by litter, since wilted seedlings are easily bent by falling leaves or even by heavy rains, and once bent horizontally are readily covered by downslope shifting of litter.

On October 7, 1961, the study area was again revisited. The winter and spring of this year received less than half normal precipitation, and yet the number and size of visible *Arbutus* seedlings of the 1961 season was comparable to that observed in 1958 on and near certain sun plots. All but two seedlings, adjacent to one sun plot, were dead but had probably survived to about mid-summer. The two living seedlings had 4 to 6 live but wilted and reddish leaves (the cotyledons had dried) and probably could have been expected to survive if the normal fall rains materialized. Neither living nor dead seedlings were visible on the shade plots nor on any sun plot where mineral soil was not exposed, emphasizing again the inhibiting influence of litter as well as of shade.

With regard to seedlings of other species than *Arbutus*, a similar complex pattern of mortality causes occurred. Of the *Sequoia* seedlings, 32% were eaten by invertebrates and 6% succumbed to drought in the rainy season as a result of rooting in thick litter which soon dried out in the upper layers. Damping-off and root decay fungi accounted for 13%, but at least 23% died from drying of the litter combined with attacks by root fungi. Other combinations (16%) or miscellaneous (10%) accounted for the remainder of the *Sequoia* seedlings by the early date of April 23.

Over half of the *Heteromeles* seedlings died primarily by direct fungus attack, either typical damping-off, or much more commonly (38% of total mortality from any cause) from a leaf spot apparently caused by *Fusicladium dendriticum* (Wallr.) Fckl. v. *eriobotryae* Scalia. Combinations of factors killed 14%, the remaining seedlings dying from miscellaneous causes excepting one survivor which was nearly dead from leaf spot and probably did not survive the year.

GROWTH. Weekly measurements of shoot length, cotyledon and leaf size, and hypocotyl diameter of several marked seedlings on each plot were made until death of the plants. Plants adjacent to and of size comparable to those being measured were excavated monthly (fig. 7). Several points are noteworthy. First, the very small amount of growth of all *Arbutus* seedlings over the span of half a year is evident. Even by August the cotyledons had not died, although by then they were wilted, and only three to five nodes were visible by this time. The greater root

system was present on plants in the sun, except where fungus attacks reversed this relation. Rotting of the root tip often stimulated branching. A slight bend in the hypocotyl usually resulted when a seedling was bent by rain or leaf litter for a few days, although one of the "E" seedlings probably grew between two impenetrable leaves before becoming vertical. Leaf injury by slugs (or insects) was evident on several plants. In the sun the hypocotyls changed from pale green or yellowish-white to pink or even red in about a month, but remained pale in the shade for much longer. By early May in the sun hypocotyls began shrinking with the collapse of the cortex following periderm production, as is normal in woody species, becoming brown or dark red and hard and wiry. On the other hand in the shade the hypocotyls were still quite succulent even by June, and none survived there long enough to appreciably harden.

Within a few months a number of the roots developed what appeared to be short, stubby mycorrhizal nodules (fig. 7), similar to the "root tubercles" in *Arbutus unedo* L. (Rivett, 1924). They occurred at the tips of certain main roots or on short branches, and developed into small and frequently branched pear-shaped tubercles enveloped in a dense mantle of hyphae from which minute root hair-like setae projected. Root hairs appeared to be absent from all naturally-occurring *Arbutus menziesii* seedlings, which agrees with observations by Rivett (1924) on other species of the genus.

Arbutus menziesii provides an interesting juvenile morphology which may not have been previously recorded. The epicotyledonary leaves of seedlings for several nodes are opposite, doubly serrate, glandular hairy, and thin (fig. 7), while mature foliage is alternate, essentially entire, glabrous, and coriaceous. Leaves of sprouts and saplings intergrade between these extremes.

DISCUSSION

In spite of good seed crops being produced regularly (Tarrant, 1958), *Arbutus* seedlings are reported to be uncommon in comparison with stump sprouts (Jepson, 1910). On nearby Jasper Ridge, Cooper (1922) recorded no *Arbutus* seedlings in a *Quercus-Arbutus-Aesculus* forest. *Arbutus* seedlings and saplings of a number of age classes were present on the study area (Table 1), however, but only in the semi-open forest, along road cuts, or at the bases of large fallen trees. Healthy two- to several-year old seedlings and saplings were also present under moderate *Arbutus-Quercus* canopy. Nevertheless, the classification of this species by a majority of silviculturists as "tolerant" of shade (Baker, 1949) is probably based entirely on the behavior of mature trees and stump sprouts rather than seedlings, and the writer agrees with the considerable segment of dissenting opinion reported by Baker to class the tree as "intermediate," based upon its local behavior. Even in the absence of general fire or other disturbance, *Arbutus* probably maintains its position in dense forests not only by stump sprouting but perhaps also by a process similar to "gap phase" reproduction described elsewhere by Bray (1956).

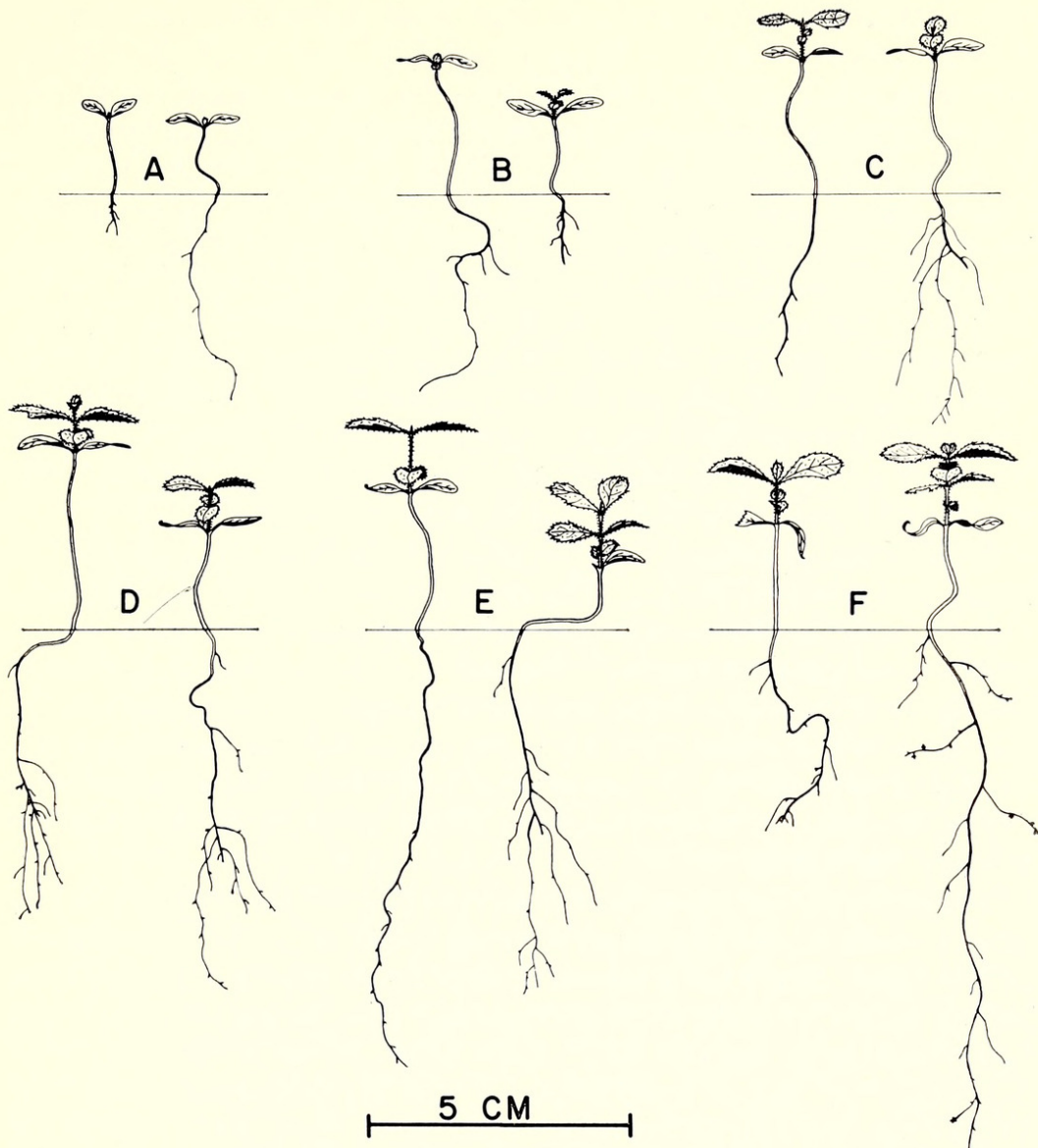


FIG. 7. Representative seedlings of *Arbutus* showing the usual range of behavior found in the field. A to F represent monthly intervals from March to August. The seedling on the left of the letter is in each case from near one of the shade plots while that on the right is from near a sun plot.

Shade can best be considered a predisposing factor increasing susceptibility of *Arbutus* seedlings to other more immediate causes of mortality, as has been found to be the case with other species (Baker, 1950: 266–267). In the present study, shade was always associated at least with a thick drying litter. Much earlier mortality occurred on the shade plots, in spite of the fact the mineral soil never reached the wilting percentage even at the surface at these sites (fig. 4). This is, however, partly due to the greater incidence of slugs on the shade than on the sun plots (fig. 6). The direct effects of shade were seen in the prolonging of the succulent hypocotyl stage and the usually smaller root-shoot ratio. Since one albino seedling survived for 25 days, we may assume that enough food reserves

were present in green seedlings so that shade alone could not eliminate them before this time.

Seedbed requirements of *Arbutus menziesii* elsewhere are not known. Sudworth (1908) states that germination is best in moist soil when seed is well covered, while lack of seed covering and drier soils inhibit seedlings. There is apparently nothing in the nature of *Sequoia* or *Arbutus* litter which prevents germination. Instead, the ease of drying of upper litter layers (associated with extremely high wilting percentages of litter), in conjunction with the dense shade usually provided in such habitats, renders them highly unfavorable. Normal germination varies from February to April, depending on climate (Tarrant, 1958). The early (mostly February) germination in the present study probably reflects the unusually warm January and February of 1958, and also the southerly location of the area in relation to the main range of the species.

Germination of *Arbutus* is epigeous, and the cotyledons remain photosynthetic for several months. The mesomorphic traits of the strikingly different juvenile foliage, although perhaps in part of a vestigial nature, probably are adaptive in certain respects. The dense glandular hairs may inhibit the occasional foliage-eating insects, but apparently have no inhibiting effect on slugs. The thin, non-coriaceous, serrate leaf of the juvenile plants may also be photosynthetically more efficient at low light intensities than xeromorphic mature foliage which is usually more exposed to desiccation.

The occurrence of drought-death as classified in figures 5 and 6 is misleading, since this mostly occurred at the height of the rainy season and on the shade plots, when a few sunny days would dry out the upper litter layers. Somewhat later, drought eliminated most of the seedlings which had been crippled by root fungi, often before even the upper layers of the mineral soil had dropped below the wilting percentage. But by June 17 the sun plot soils had dropped below the wilting percentage at the 12–15 cm. level. Although a healthy root system could probably penetrate below this depth within four months, the usually continued drought for four or five more months usually presents an insurmountable obstacle to seedlings of most perennials. That a few *Arbutus* seedlings actually do survive nearly every year is shown by the several seedlings and sapling age classes present on the area, usually in the same microsites in which the healthier current-year seedlings occurred (Table 1). Two or three exceptionally vigorous seedlings of the present season which occurred off the plots in favored sites appeared as if they might survive the summer, but all the *Arbutus* on the plots doubtless would not have survived many more weeks even had they not been excavated for root studies. The fact that two live 1961 seedlings were found near one plot near the end of the dry season in October, in spite of the unusual drought of this year, suggests that the abnormally heavy precipitation of 1958 did not significantly reduce death from drought over that of more normal years, perhaps because precipitation was concentrated in early spring.

Damping-off and root decay fungi have not been frequently incriminated in studies of tree establishment under natural conditions, although they are often destructive in coniferous tree nurseries. The prevalence of these agents in this study, both as predisposing and as proximal causes of mortality, was probably in part associated with the unusually wet spring of 1958. A problem arises, however, in interpreting the relation of root decay and mycorrhizal fungi. It is possible that some of the root decay of seedlings was caused by the same fungus producing the tubercles. The tubercles resemble those of *Arbutus unedo*, where they are considered to be ecto-endotrophic mycorrhiza in which the relationship is one of balanced parasitism rather than symbiosis (Rivett, 1924). If this is true also in *A. menziesii*, it would be understandable that the fungus might gain the upper hand during an unusually wet season and become a crippling parasite. It is probable, however, that the typical damping-off symptoms, and perhaps much of the root decay itself, were produced by other agents even if mycorrhizal fungi were also involved.

Shade and summer drought are doubtless normally more significant in seedling establishment of *Arbutus* than is suggested by the histogram (fig. 6). Shade does not there appear among the causes of mortality because it was classified as a predisposing condition under the heading of "combinations" of factors. Furthermore, on the shade plots, the early and complete mortality resulting from other conditions than shade prevented shade alone from exerting its full potential influence. In a similar fashion, summer drought was a minor factor in this study, most of the drought-killed seedlings of figure 6 having perished at the height of the wet season owing to a thick drying litter. Summer drought would be expected to act as a final "coup-de-grace" for most of the few seedlings which have survived prior dangers and which are often crippled by fungi or shade-induced exhaustion of food reserves. The results of this study emphasize the importance of predisposing or contributing ("crippling") factors even though these may not be the proximal or immediate cause of death.

With regard to *Sequoia sempervirens*, the present limited results confirm the conclusion of Fritz (1950) that litter and shade do not prevent germination of this tree, but rather strongly inhibit survival. The present unusual results, however, which implicate fungi and invertebrates as being of greater importance than drought in causing mortality, may be due to the shady site and unusually wet spring. The *Fusicladium* leaf fungus of *Heteromeles* was also probably favored by this wet weather.

In evaluating survival in seedling populations the following important questions are asked. To what extent are adaptive genetic differences involved in differential survival within seedling populations ("natural selection" in the present sense)? Or, is seedling survival dependent primarily upon the chance vagaries of seed dispersal to physically favorable microsites (the "safe sites" of Harper *et al.*, 1961) combined with the subsequent chance absence of injurious biotic agents?

The difficulty of demonstrating a correlation between genotypes and survival in nature explains the paucity of field data supporting natural selection in plants (Stebbins, 1950: 106). No genetic races of *Arbutus menziesii* have been yet recognized within its range (Tarrant, 1958). Nevertheless, genetic differences were probably present among the *Arbutus* seedlings in the present study which were significant to survival. This was obvious in the case of the few albino seedlings. Date of germination ranged over almost a four month period in *Arbutus*, and probably involved both genetic and environmental factors. Late germination was conducive to drought injury and in fact no late germinating seedlings survived long. *Arbutus* cotyledons varied greatly in size and shape, probably again partly owing to genetic differences; cotyledon structure certainly is involved in shade tolerance.

Presumably, distasteful biochemical products such as may be present in the glandular hairs of *Arbutus* seedlings could influence destruction by slugs. Possibly this feature helps explain why some seedlings of *Arbutus* remained untouched adjacent to others which were thoroughly chewed. Also, adjacent seedlings of this species were not always affected similarly by fungus parasites. In view of the problem of root penetration of layers of rapidly drying litter as well as of their maintenance of contact with moist subsoil during the prolonged summer drought, any genetic variation promoting the development of a diffuse rather than a tap root system by *Arbutus* seedlings would be expected to be selected against. Injury of the tap root by fungi was one of the most frequent causes of mortality.

The fact remains that at least all the "shade" plots were located in "unsafe sites" where the lack of seedlings or saplings of any but the current year showed that survival depended on thinning of the canopy and litter by fire, lumbering, or the falling of one or more trees. Under such conditions, the genotypes within the population could influence only the duration of survival by a few weeks, and natural selection, in the sense of either differential survival to reproductive age or differential reproduction by the resulting survivors, has not occurred. Chance "catastrophic" events, such as covering of seedlings by falling leaves or exfoliating bark and perhaps much of the biotic injury, also were important "non-selective" factors, little influenced by seedling genotypes. On the sun plots, selective pressures would be expected to operate severely on the 2% survivors, although if all seedlings eventually succumbed before maturity the effects of natural selection would there also be nullified. Selection pressure, however, would be somewhat relaxed on these few survivors if the effects of the intensifying summer drought were more than compensated for by the reduced competition for light and moisture occasioned by the lower seedling density resulting from early high mortality. But in the present case this was probably not the situation, even if all survived, since seedling size was small and densities were only locally high enough to result in much mutual shading or root competition

during the first year. Consequently, in spite of much or most mortality resulting from "non-selective" factors, *all* survivors must be fit, even though the genetically "fittest" may have been eliminated by chance events. The rigors of the environment are such that although the "fittest" may not survive, the unfit never do.

SUMMARY

Emerging seedlings were marked and their fates followed in comparison with microenvironmental records from February to August in an *Arbutus-Quercus-Sequoia* forest in the Santa Cruz Mountains of central California. By August 2, 2% of the *Arbutus* seedlings had survived in a semi-open forest and 0% in deep shade. Invertebrates, primarily slugs, accounted for 29.2% of the mortality, and were of greatest importance in the shade and during the rainy season. Death from drought acting alone was minor (10.4%), and occurred mainly soon after germination during the wet season in deep shade where thick litter prevented seedling roots from reaching moist mineral soil. Attacks by fungi, especially post-emergence damping-off and root decay types, accounted for 28.1% of the mortality, and were more important for several reasons in the semi-open than in shade. Combinations of factors killed 22.7% of the seedlings, mostly from mild drought preceded by crippling root decay fungi, or weakening by shade. Unknown or miscellaneous causes, especially undermining by rodents or covering by leaves or bark, took the remainder (9.6%) of the *Arbutus* seedlings. A number of seedlings of several other species, especially *Sequoia sempervirens* and *Heteromeles arbutifolia*, were also included in the study and showed a similar high mortality resulting from complex causes. Although chance or non-selective factors were probably responsible for most mortality, natural selection still operates severely on the few survivors.

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A NEW SPECIES OF DOWNINGIA

JOHN H. WEILER

A systematic study of the genus *Downingia* now in progress has revealed a new entity heretofore included by all workers in *D. elegans* (Dougl. ex Lindl.) Torr. Investigation of plants in the field and in cultivation suggests that this new entity should be accorded specific recognition. The new species I have chosen to name for Dr. Rimo Bacigalupi, Curator of the Jepson Herbarium, who has stimulated my interest in *Downingia* and given me a great deal of time and valuable advice.

***Downingia Bacigalupii* sp. nov.** Planta annua caulibus simplicibus vel e basibus ramosis, 0.5-3.0 dm. altis; foliis bracteisque linearibus vel lanceolatis; lobis calycis adscendentibus vel rotatis, quam sinibus lateralibus tubi corollae longioribus; corollis caesiis lineis conspicuis azureis reticulato-venosis, labio inferiore concavo, labium superiore longitudine aequante vel quam id paulo longiore, centraliter albo haud venoso maculis



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