Evidence has been submitted in this paper that *Pinus ponderosa* from cismontane California is more susceptible to cold than is *P. jeffreyi*, that *P. ponderosa* from northeastern California is at least as tolerant of cold as is *P. jeffreyi* and that the spread of *P. ponderosa* to higher elevations is checked in Arizona by low summer temperatures rather than by extremes of cold in winter. Most of this evidence is indirect, and a more precise determination as to the factor or factors which limit *P. ponderosa* in its many different habitats will have to await the outcome of future experiments. For the present, it appears reasonable to postulate that low temperatures, whether in the form of low winter minima or low summer maxima, play an important role in limiting the distribution of *P. ponderosa*.

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INFLUENCE OF TEMPERATURE AND OTHER FACTORS ON CEANOTHUS MEGACARPUS SEED GERMINATION

ELMER BURTON HADLEY[1]

One of the striking characteristics of chaparral is the absence of any kind of seedlings beneath mature, undisturbed stands. After such disturbances as bulldozing or fire, however, an abundance of seedlings appears, suggesting that scarification or heat make the germination possible (Cooper 1922, Went *et al.* 1952, Horton & Kraebel 1955, Quick 1959).

The density and dryness of this chaparral brush cover in California, the accumulation of large quantities of dry litter beneath the brush, and the Mediterranean type climate, all combine to create an extreme fire

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hazard during the long summer droughts. Many chaparral species are so specifically adapted to the resulting periodic fires as to indicate a long history of subjection to recurrent fires in the geologic past (Jepson 1925). Horton (1945) found that *Ceanothus* species in general have a life span of about forty years. In areas unburned for a period of at least forty years, however, other species have, to a large extent, replaced *Ceanothus* because there has been no regeneration by *Ceanothus*.

Two fire responses are very common among chaparral species: resprouting from burls (underground root crowns) that are not killed by fire, and heat induced seed germination due to cracking of impervious seed coats. *Arctostaphylos glandulosa*[2] is an example of a species that shows the first type of fire response. Almost no seedlings of this "stump sprouting" species are found following fires. *Ceanothus megacarpus,* wherein the entire shrub is usually killed outright by fires, represents the second type of response—regeneration by seed following fire. Other shrubs, such as *Adenostoma fasciculatum,* exhibit both types of fire responses.

In addition to the resprouting shrubs and seedlings of chaparral species, a recently burned-over area contains many annuals and short-lived perennial herbs and subshrubs as well as weeds. Eventually the chaparral vegetation dominates and the under vegetation perishes.

Fire or heat induced increases in germination were first investigated by Wright (1931), who found that oven heating greatly increased the germination of a number of chaparral species, including *Ceanothus megacarpus*. Sampson (1944), and Went *et al.* (1952) have also investigated increased germination of chaparral species due to fire. Stone & Juhren (1951), investigating germination of seeds of *Rhus ovata,* found that temperatures of 80°C induced the rupturing of impervious seed coats and thus permitted water to reach the embryos. Quick (1935), using seeds of several species of *Ceanothus,* also found that heat cracked the impervious seed coats. Stratification, following the heat treatment, resulted in further germination increases in these species.

In none of these investigations, however, were the possible modifying effects of natural field conditions on heat induced germination considered. In the present investigation an attempt was made to determine the effect of temperature, of mechanical injury, and of accumulated litter on the germination of seed of *Ceanothus megacarpus*.

Methods

Except for field observations and collecting the seeds, all other phases of this investigation were carried out in the greenhouse of the University of California at Santa Barbara. All results obtained must, therefore, be considered no more than suggestive of what might occur under field conditions.

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[2] Nomenclature is that of Munz (1959).

Large quantities of *Ceanothus megacarpus* seeds were gathered from the Santa Ynez Mountains above Santa Barbara, California, in June, 1959, and air dried for two months in the laboratory. Voucher specimens are on deposit at the herbarium of the University of California at Santa Barbara.

All experiments were conducted in controlled temperature boxes, using sterilized petri dishes with moistened filter paper. All seeds were treated with the fungicide, Semesan. Seeds were germinated at a temperature regime of 26°C and 17°C (alternating 12-hour periods at each temperature). Each experiment was conducted for a thirty-day period, and germination in all cases was defined as emergence of the radicle.

In order to determine the effect of heating or cutting of the seed coat on *Ceanothus megacarpus* seed germination, a first experiment was run using three lots of seeds. The first lot was subjected to a temperature of 100°C for 5 minutes in an electric oven, the second to mechanical rupturing of the seed coat at the micropilar end with a razor blade, and the third lot served as controls (no heating or cutting). Each of the above three treatments consisted of three replicates using 25 seeds per dish. These seeds were moistened with distilled water and germinated as described in the previous paragraph.

In order to determine the possible effects of leaf litter on germination, a second series of experiments was set up using actual leaf material on top of the seeds in the petri dishes. Sets of seeds were prepared, each with three replicates as in the previous experiment, i.e., heated seeds, cut seeds, and controls. Fresh leaves, duff (dead fallen leaves not yet decayed beyond recognition), and ashed duff (7 grams of duff ashed at 700°C in a muffle furnace for 45 minutes) of *Adenostoma fasciculatum* were used in equal quantities on each of the first three sets of seeds, while a fourth set of three petri dishes of seeds was left as a control. *Adenostoma fasciculatum* was chosen because it is one of the most abundant and cosmopolitan species comprising the chaparral community. Except for the presence of leaf material, the seeds were germinated with distilled water as in the previous experiment. To test the hypothesis that any stimulation of seed germination due to duff is really a mineral effect, another part of this second experiment was run using a modified Hoagland's solution containing trace elements (Hoagland and Arnon 1950) in place of the distilled water.

In the third experiment, the effect of using leached duff (partial removal of minerals) was investigated. The duff was leached in eight changes of distilled water for 96 hours before being placed over the seeds.

All data were subjected to an analysis of variance using the individual degrees of freedom technique (Snedecor 1956). Space does not permit its inclusion, but a complete analysis of variance for the data may be found in Hadley (1960).

TABLE 1. EFFECT OF TEMPERATURE, MECHANICAL RUPTURING OF SEED COAT, AND ADENOSTOMA FASCICULATUM LEAF LITTER ON CEANOTHUS MEGACARPUS SEED GERMINATION.

	Percentage Germination* Treatment	Cut seed	Heated seed (100°C for 5 min.)	Untreated seed
I.	Distilled water	86	23	0
II.	Distilled water +			
	Adenostoma duff	87	75	1
	Adenostoma duff ashed	41	24	0
	Adenostoma fresh leaves	24	13	0
	Control	83	25	0
	Hoaglands solution +			
	Adenostoma duff	95	57	0
	Adenostoma duff ashed	31	29	0
	Adenostoma fresh leaves	21	21	0
	Control	88	77	1
III.	Leached duff	85	41	1
	Unleached duff	87	80	4

* All experiments run in replicates of 3 with 25 seeds in each replicate.

Experiment I—Effect of heating and cutting of seed coat on *Ceanothus megacarpus* seed germination.

Experiment II—Influence of *Adenostoma fasciculatum* leaf litter and/or Hoagland's solution on the germination percentage of *Ceanothus megacarpus* seeds.

Experiment III—Effectiveness of leached *Adenostoma fasciculatum* duff vs. unleached duff in stimulating *C. megacarpus* seed germination.

RESULTS

Under the conditions of this investigation, germination of *Ceanothus megacarpus* seeds is facilitated by either heating or cutting the seed coats. As shown in Table 1, however, mechanical rupturing is the more effective treatment.

Presence of the various *Adenostoma* leaf material did not significantly affect the germination of the untreated controls, but did significantly affect the germination of the heated and cut seed (Table 1). Presence of duff over the heat treated seeds significantly stimulated the germination percentage of these seeds, resulting in a four-fold increase over the controls. This increase was shown by later experiments to be attributable to increased minerals made available by the decayed duff. Since cut seeds displayed maximum germination with or without duff being added, the effect of adding duff could not be measured accurately in the case of the cut seed.

Presence of fresh leaf material resulted in a significant reduction of cut seed germination, possibly due to the presence of an inhibitor in the fresh leaves (Naveh 1960). Application of ashed duff also caused a significant reduction in the germination of cut seed.

Substitution of Hoagland's solution in place of distilled water resulted in little change in the germination per cent of seed treated with either ashed duff or fresh leaves (Table 1). These results show that fresh leaf material or ashed duff have the same inhibiting effect, whether distilled water or Hoagland's solution is used. Germination per cent of heated seeds is very similar, whether treated with distilled water plus *Adenostoma* duff or only with Hoagland's solution. Leaching of this duff (partial removal of minerals) significantly reduced the effectiveness of duff in stimulating germination of the heat treated seeds (Table 1).

Discussion and Conclusions

Ceanothus megacarpus seed germination percentage was increased by heating these seeds for 5 minutes at 100°C. Mechanical rupturing of the seed coat was found to have an effect similar to heating, but to a greater degree. This would suggest that the stimulatory effect of heating involved in this species is primarily one of rupturing a previously impervious seed coat, thus allowing water to reach the embryo. The smaller increases in germination in the case of the heated seed may be due to injury to some of the embryos due to heat, to a random cracking of the seed coat away from the micropilar end which might hamper radicle emergence, or to the variability in seed coat thickness (some of the seed coats may not be cracked by this particular temperature).

Application of leaf material of another chaparral species, *Adenostoma fasciculatum*, has a definite effect on the germination percentage of *Ceanothus megacarpus*. *Adenostoma* duff enhances the germination of heat treated *C. megacarpus* seeds. Since a similar effect was obtained when Hoagland's solution was substituted in place of the distilled water and duff, this stimulation of germination can possibly be attributed to increasing mineral concentration provided by the decaying duff. The conclusion that germination was stimulated by available minerals in the duff is supported by the fact that there was marked reduction in percentage of seed germination when the seeds were topped by leached duff.

The apparent inhibition of germination by fresh leaves of *Adenostoma* may be due to the presence of an inhibitor or inhibitor complex in these leaves (Naveh 1960). The reduced germination of cut seed in the presence of ashed duff may be due to increased pH. Sampson (1944), using several grass species, has noted this ash inhibition, which was attributed to increased pH. The germination percentage of heated seeds in the presence of ashed duff, remained similar to that of non-treated heated seeds. This would suggest that ashed duff did not have an inhibitory effect on heated seed.

What part heating, mechanical rupturing, and plant litter actually play in the field can only be suggested, for in the field the situation created in the laboratory does not exist. Obviously, rupturing of the seed coat due to mechanical injury can be of only minor ecological significance in the field except where bulldozing, sharp deer hoofs, or some other agent may crack the seed coats. Accidental rupturing may therefore account for at least a portion of the few young seedlings that are sometimes found in disturbed but unburned areas.

The extremely low percentage of germination noted for untreated seed may serve to explain the field observation that young seedlings of *Ceanothus megacarpus* are not found under undisturbed, mature chaparral in which this species is a constituent. Heat treatment of *Ceanothus megacarpus* seeds by fires should be of tremendous importance in the repopulation of burned areas. This increase in germination percentage due to cracking of the seed coat by heat could account for the abundance of *Ceanothus* seedlings found immediately following a fire.

It must be remembered that all chaparral fires are not alike; they differ in intensity, duration, and temperatures reached during the fire. Some fires consume both shrub crowns and litter; others are principally confined to the shrub crowns leaving pockets of litter unconsumed. Therefore a differential destruction of duff by fire is noted in the field. Some fires could easily provide the required temperatures for the duration of time necessary to crack the seed coats and yet not burn away all of the duff that would be present. Other fires, even though they might burn away most or all of the duff and seeds, would still provide temperatures necessary to crack the seed coats of those seeds which were buried in and therefore protected by the soil. Thus breaking of the seed coat by heat would account for the *Ceanothus* seedlings that Quick (1959) and others have encountered after fires in the chaparral.

Only *Adenostoma fasciculatum* leaf litter was used in these experiments. It is possible that the duff and fresh leaves of many of the other chaparral species might exhibit similar effects on *Ceanothus megacarpus* seeds and those of several other chaparral species. This is a subject that would indeed be worth further investigation.

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REVIEWS

Flora of the Santa Cruz Mountains of California. A manual of the vascular plants. By John Hunter Thomas. viii + 434 pages, 249 figs. and 16 photos, 1 map. Stanford University Press, Stanford, California. 1961. $8.50.

The first impression, upon taking up the "Flora of the Santa Cruz Mountains," is of an attractive, well-designed book with clear typography, generous spacing, indented keys, good illustrations, and with an adequate binding. The Stanford University Press is to be congratulated upon producing a volume of exceptionally fine appearance.

Although the book is entitled "Flora of the Santa Cruz Mountains," it encompasses the whole San Francisco peninsula, and thence southward to the Pajaro River and from the ocean east to the middle of the Santa Clara Valley. Coverage is comprehensive, including both native and introduced plants. The number of kinds of introduced plants occurring spontaneously is amazing; 31 per cent of the 1799 taxa listed fall into this category.

For each of the species listed, Thomas gives the scientific name, common name, habitat, localities in the area, time of blooming, and place of origin for introduced species. Sometimes elevation is given and, occasionally, associated species. Brief comments, often on taxonomic problems, are made for some species. Synonyms are included only for convenience in referring to the same taxon in other regional and sectional floras. Specimens are not cited except in a few instances. There are no new names or combinations.

The flora is written for the serious beginner as well as the trained botanist. The beginner, especially, will appreciate the 250 line drawings which are from the "Illustrated Flora of the Pacific States." As a result of better spacing and better paper they are clearer and more attractive than many of the original reproductions in the Illustrated Flora. The common names also appear to correspond to those used by Abrams. Possibly the influence of the latter flora may be responsible in part for the recognition of certain families, for example, Melanthaceae, Parnassiaceae, Hydrangeaceae, Grossulariaceae, Amygdalaceae, Malaceae, Mimosaceae, Caesalpinaceae, Monotropaceae, Pyrolaceae, Vacciniaceae, Convallariaceae, Amaryllidaceae, all of these segregated from the Liliaceae, Saxifragaceae, Rosaceae, Fabaceae, and Ericaceae. Nevertheless, Thomas' taxonomic concepts are, in general, conservative. For example, *Berberis* rather than *Mahonia* is recognized; *Montia exigua* is considered as synonymous with *M. spathulata*; ssp. *decurrens* of *Eriogonum nudum* is not recognized. However, *Dudleya* (not *Echeveria*) and *Horkelia* are used; *Allium breweri* is considered distinct from *A. falcifolium*; and all the forms of *Arctostaphylos* in the Santa Cruz Mountains are accorded specific status. The varietal designation is usually employed rather than the subspecific except when the latter designation has been used

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