

HEAT AS A FACTOR IN GERMINATION OF SEEDS
OF CEANOETHUS VELUTINUS VAR. LAEVIGATUS T. & G.

by

HENRY JOHN GRATKOWSKI

A THESIS

submitted to


OREGON STATE UNIVERSITY

in partial fulfillment of
the requirements for the
degree of


DOCTOR OF PHILOSOPHY


June 1962

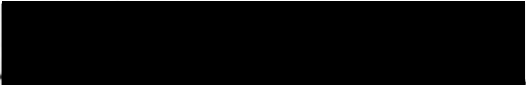
APPROVED:


Associate Professor of Botany

In Charge of Major


Chairman of Department of Botany


Chairman of School Graduate Committee


Dean of Graduate School

Date thesis is presented May 4, 1962

Typed by Florence Gratkowski

ACKNOWLEDGMENT

Research of the scope involved in this investigation cannot be carried out without the assistance of many others, and I am deeply indebted to those who have helped make this possible. First, the Pacific Northwest Forest and Range Experiment Station of the U. S. Forest Service, U. S. Department of Agriculture, financed all phases of the project. Mr. W. E. Hallin of the Roseburg Research Center and Dr. W. W. Chilcote, Associate Professor of Botany, Oregon State University, encouraged and facilitated the work in many ways. Doctors R. O. Belkengren, Te May Ching, J. C. R. Li, A. O. Mackey, H. K. Phinney, and R. R. Silen kindly provided many items of equipment or allowed consultation on technical details. Dr. W. B. Raymer, Chairman of the Greenhouse Committee, somehow managed to find suitable work space in already crowded greenhouses precisely when needed for the extensive germination tests. His quiet and unassuming aid is sincerely appreciated. I also wish to express appreciation to Mr. Vern E. McDaniel, Superintendent of the Oregon State Board of Forestry Nursery and Mr. D. Maus of the Board of Forestry who made a special effort in allowing me to stratify soil and duff samples in the cold rooms at the nursery. Finally, the field end of this project would not have been possible without the cooperation of the Umpqua National Forest, especially Supervisor V. Miller and Ranger J. Price.

Last, but far from least, I wish to gratefully acknowledge the cheerful and willing assistance of my wife, who undertook the tedious

task of extracting almost all of the seeds used in the experiments, assisted in examination of soil and duff samples, and ended by typing this thesis (twice) without complaint.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
REVIEW OF LITERATURE	4
SEEDS, SEED SOURCES, AND METHODS	19
LABORATORY EXPERIMENTS	22
HEAT TREATMENT OF SEEDS	22
Stratification	22
Steeping in Hot Water.	23
Heating Seeds in Wet and in Dry Soils.	27
Time-Temperature Interaction in Inducing Germination	34
Fire-induced Germination of Seeds in Soil.	37
Solar Radiation as a Factor in Germination	40
Summary: Use of Heat to Induce Germination	45
EFFECT OF HEAT ON SEED COAT IMPERMEABILITY.	47
Seed Anatomy	47
Sorpton Response of Treated Seeds	56
Heat Effect on Hilar Fissure	62
FIELD STUDIES	65
CONDITIONS BEFORE LOGGING	67
Tree Layer	69
Shrub Layer.	72
Herbaceous Species	77
CEANOTHUS SEEDS FROM DUFF AND SURFACE SOIL.	79
Collection and Preparation of Samples.	79
Seeds in Duff and Soil Samples	80
Germination Before Heat Treatment.	81
Germination After Heat Treatment	83
LOGGING AND SLASH DISPOSAL	86
Logging	86
Slash Disposal	86
Soil Temperatures During Slash Burning	90
VARNISHLEAF CEANOTHUS SEEDLINGS IN BURNED AND UNBURNED SLASH AREAS	95
Seedlings on Burned vs. Unburned Plots	95
Influence of Slash Disposal Methods on Germination	97

	Page
DISCUSSION	102
SILVICULTURAL APPLICATION.	109
BIBLIOGRAPHY	115

LIST OF FIGURES

Figure		Page
1	Varnishleaf ceanothus seeds	20
2	Trends of germination of heat-treated varnishleaf ceanothus seeds after stratification at $3\frac{1}{2}$ degrees Centigrade for various lengths of time.	24
3	Trends of soil temperature $\frac{1}{8}$ inch below the surface of a dry brown silty clay loam exposed to different oven temperatures	32
4	Emergence of varnishleaf ceanothus seedlings in relation to maximum soil temperature attained at seed depth	33
5	Emergence of varnishleaf ceanothus seeds heated in dry sand at soil temperatures ranging from 30° to 120° Centigrade for various lengths of time	36
6	Germination of varnishleaf ceanothus seeds was much greater in burned halves than in unburned sections of the flats	39
7	Flats of soil containing dormant varnishleaf ceanothus seeds were heat treated in the laboratory to induce germination of the seeds.	43
8	Longitudinal section of a mature varnishleaf ceanothus seed. X27.	48
9	Young fruit showing vascular tissue extending from placenta through the funiculus into the ovule. X24	50
10	Funiculus adhering to edges of the hilar fissure on an almost mature varnishleaf ceanothus seed. X24	51
11	Longitudinal section of hilum. X109.	53
12	Longitudinal section of a nearly mature seed showing deposits in parenchyma beneath the palisade layer. X60	54
13	Cross-section through seed coat to endosperm of a mature varnishleaf ceanothus seed	55

Figure		Page
14	Changes in moisture content of varnishleaf ceanothus seeds exposed successively in dessicators at different relative humidities	59
15	Changes in moisture content of varnishleaf ceanothus seeds exposed successively in dessicators at different relative humidities	61
16	Hilar fissure of a mature varnishleaf ceanothus seed in its normal, closed condition. X138	63
17	Hilar fissure opened after heat treatment of the seed in a dry loam soil. X138.	64
18	Slash disposal subdivisions in White Creek cuttings 1 and 3.	68
19	Dense forest of old-growth Douglas-fir and associated species on Cutting 1 before logging.	70
20	Road right-of-way through old-growth Douglas-fir forest on Cutting 3 before logging.	71
21	Phytographs showing the relative importance of tree species in the stands on White Creek cuttings 1 and 3 before logging	73
22	The shrub layer in both stands commonly consisted of a low cover of salal and Cascades mahonia, golden chinkapin, and various <u>Rubus</u> spp. under a taller, lacy canopy of vine maple	76
23	Undisturbed logging slash before burning in a broadcast burn subdivision of Cutting 3	88
24	Mechanically-piled logging slash before burning in cutting 3.	89
25	Soil temperatures attained at depths up to 3 inches below the surface during slash burning	93

LIST OF TABLES

Table		Page
1	Germination of varnishleaf ceanothus seeds after steeping in hot water at temperatures of 70° to 100° Centigrade	26
2	Emergence of varnishleaf ceanothus seedlings after heat treatment of seeds in wet and in dry soils	29
3	Emergence of varnishleaf ceanothus seedlings after heat treatment of seeds in a reddish brown clay loam	44
4	Frequency and cover of shrub species on sample plots in the stands of old-growth Douglas-fir on cuttings 1 and 3 before logging.	75
5	List of herbaceous species found in the understory of the stands of old-growth Douglas-fir on cuttings 1 and 3 before logging.	78
6	Comparison of numbers of varnishleaf ceanothus seedlings on burned and unburned parts of White Creek cuttings 1 and 3	96
7	Relative numbers of varnishleaf ceanothus seedlings in White Creek cuttings 1 and 3 after three different methods of slash disposal	98
8	Estimated numbers of varnishleaf ceanothus seedlings per acre after three different methods of slash disposal.	99

HEAT AS A FACTOR IN GERMINATION OF SEEDS
OF CEANOOTHUS VELUTINUS var. LAEVIGATUS T. & G.

INTRODUCTION

The genus Ceanothus of the family Rhamnaceae (Buckthorn Family), consisting of about 60 species of deciduous and evergreen shrubs and small trees whose natural range is restricted to North America, has attained its greatest differentiation in Mexico and in the southwestern part of the United States. However, eight species and at least two varieties occur naturally on forest lands in southwestern Oregon, where they are important components of the Broad-Sclerophyll Forest and Chaparral Associations of the Broad-Sclerophyll Formation in the Siskiyou Mountains and southern end of the Coast Range. Many of these also occur in coniferous forests of the Transition, Canadian, and lower Hudsonian Life Zones on the western slope of the Cascade Range. Varnishleaf ceanothus (Ceanothus velutinus var. laevigatus T. & G.)^{1/}, with a natural range extending throughout the Coast Ranges from Marin County, California, northward to British Columbia (55, p. 291), is one of the most abundant evergreen woody shrubs on old burns and cutovers in the Coast Range and foothills of the Cascade Range in Oregon.

^{1/} Common and scientific names of species that attain tree size are in accordance with Checklist of Native and Naturalized Trees of the United States (51); names of most shrubs and herbs are those listed in Standardized Plant Names (47). A few species not listed in the latter are named according to A Manual of the Higher Plants of Oregon (64).

Extensive dense stands of varnishleaf ceanothus that have occupied thousands of acres of old burns and cutover forest land in western Oregon are a matter of serious concern to foresters (34, p. 27, p. 32), for the tall ceanothus cover competes with conifers for light, soil moisture, and nutrients. In areas with critically low amounts of precipitation and on sites with low soil moisture storage capacity, the competition of this shrub cover for soil moisture during the dry summer season hinders regeneration of conifers. On all sites, varnishleaf ceanothus retards growth of established conifer seedlings and saplings by its effect on light and soil moisture.

Foresters and botanists have long speculated on the origin of the dense stands of ceanothus that appear on burns after wildfires or logging throughout the western United States. Ceanothus shrubs on burned areas have been regarded by different investigators as invaders (98, p. 9) or as sprouts from roots and crowns that survived the fire (40, p. 251; 91, p. 601). Others, finding new seedlings in burns, have attributed these to wind-borne seed blown in after the fire (91, p. 601) or to residual seed that survived the fire in the duff (21) or in the soil (35; 69; 57, p. 28).

Exposure to dry heat and steeping in hot water have long been known to stimulate germination of ceanothus seeds (97, 67). This knowledge naturally leads one to the hypothesis that heat from wildfires and slash fires may be the factor responsible for stimulating germination of dormant varnishleaf ceanothus seeds in duff or surface soil in cases such as described above. The autecological

investigation described in this report was designed to determine the effect of heat on germination of varnishleaf ceanothus seeds and to relate the information developed to forest management practices in the Douglas-fir Region of the Pacific Northwest.

REVIEW OF LITERATURE

The great economic importance of seeds as food and in agriculture, horticulture, and forestry has resulted in an overwhelming volume of literature dealing with seed anatomy, seed dormancy, germination, and storage. For obvious reasons, most of this work has been done on agricultural seeds and on weed seeds of special importance in agriculture. Much less is known about forest tree seeds, and very little is known about seeds of the shrubby brush species that are being accorded more and more attention in silviculture and forest land management.

The literature dealing with ceanothus seeds consists of only about a dozen articles, and none of these provide any specific information concerning varnishleaf ceanothus seeds.

Fruits of the ceanothuses are 3-lobed capsules, each carpel elastically dehiscent along the inner edge at maturity, releasing a small, somewhat flattened, albuminous seed. Most ceanothus seeds have extremely hard seed coats that are impermeable to water and thereby prevent rehydration and germination of the seeds under conditions favorable for germination. Seeds such as these, with coats impermeable to water at temperatures favorable for germination, are known as "hard seeds" by agronomists (13; 37, p. 761). In addition to impermeable seed coats, many ceanothus seeds also have dormant embryos (88, p. 117-121); and investigators in several fields have found that ceanothus seeds require special treatments to render the seed coats permeable to moisture and to overcome embryo dormancy

before germination can occur (65, 67, 90).

Physical characteristics of the seed and observations in the literature indicate that dissemination of *ceanothus* seeds is probably limited to a short distance around the parent plants; for *ceanothus* seeds, in general, are small and smooth-surfaced with no appendages suitable for wind-distribution or attachment to animals. In general, deciduous *ceanothus*es are considered palatable to browsing animals and evergreen forms are usually worthless (89, p. 86). But distribution of seeds by browsing animals is probably limited in nature, for the capsules are rejected in many areas by grazing animals (27, p. 105). Cronmiller (21) stated that seeds of *Ceanothus integrerrimus* are only infrequently used by birds, rodents, and other animals--a statement in agreement with observations of Jameson (46), who found that few fruits of this species were eaten by deer mice (*Peromyscus* spp.) in the northern Sierra Nevada. In contrast, Tevis (82, 83) reported that the long-eared chipmunk (*Eutamias quadrimaniculatus*) in the same area collects seeds of *Ceanothus integrerrimus* and *Ceanothus cordulatus* and that mantled squirrels (*Citellus lateralis*) ate seeds of *Ceanothus prostratus*. He reported that *ceanothus* seeds were masticated by the chipmunks.

Many investigators have observed seedlings and shrubs of a large variety of *Ceanothus* species on burns, and have speculated on origin of the seeds that produced the seedlings (21; 35; 45; 50; 55; 10, p. 176; 15, p. 86; 33, p. 218; 57, p. 28; 73, p. 64-67). Generally, those who speculated on origin of the seeds concluded that the seeds

were present in the soil when the fires occurred. Viable seeds of several chaparral species have been found in duff and surface soil (80, 81); but only Quick (68) provided quantitative proof of the presence of viable *Ceanothus* seeds in forest soils, when he found 1,865,000 seeds of *C. cordulatus* and *C. parvifolius* per acre under virgin mature stands of mixed conifers in the central Sierra Nevada.

Many different methods including scarification of seed coats, immersion in concentrated sulfuric acid, impacting, and heat treatments have been used to render hard seed coats permeable to moisture (19, p. 28-138); but the prolific germination of *Ceanothus* seeds and those of other chaparral species in burns has led several investigators to study the effect of heat on *Ceanothus* seeds to the almost total exclusion of other methods. Wright (97) found that a five-minute exposure to hot air at temperatures of 180° to 260° C. was effective in stimulating germination of seeds of *Ceanothus divaricatus* and *Ceanothus crassifolius* as well as seeds of some associated shrubby plants from the Upper Sonoran and Transition life zones in California. And Sampson (73) later learned that a similar treatment also increases germination of *Ceanothus leucodermis* and other chaparral species. From a limited experiment, Curtis (22) concluded that fire can increase the germinative capacity of *Ceanothus velutinus* seeds in damp soils. He also attempted a scarification treatment, but his germination data for seeds abraded by 5 minutes shaking in a container with three-quarter-inch stones seems no different from those of untreated seeds. Later, Peterson (65) learned that scarification by puncturing

the seed coats of Ceanothus sanguineus and Ceanothus velutinus with a dissecting needle was at least as effective as a hot water treatment in which 90 c.c. of boiling water was poured over seeds in a beaker and allowed to cool at room temperature for 30 minutes.

The most extensive series of experiments on heat treatment of ceanothus seeds are those of Quick (67, 69, 70). From an unreplicated experiment with seeds of 19 species of Ceanothus, he concluded that suspending seeds in hot water at 70° to 80° C. and allowing the water to cool to room temperature was more successful than boiling seeds for 5 minutes as a method for overcoming delay in germination due to seed coat hindrance. A hot water treatment was deemed desirable for seeds of most of the 19 species tested. Another trial demonstrated the astonishing ability of some ceanothus seeds to endure high temperatures. Twenty-five percent of a sample of Ceanothus cordulatus seeds germinated after being boiled in water for 25 minutes, but none germinated after being boiled thirty minutes (69). Later trials, however, showed the extent of natural variation among different lots of seed of the same species; for germination percentages of three different lots of Ceanothus cordulatus seeds boiled for 90 seconds ranged from about 27 to 98 percent--germination of one lot increasing and germination of the other two decreasing with increasing duration of boiling (70). Ceanothus integerrimus seeds displayed a low percentage of germination after being boiled for 20 minutes, but were not able to endure boiling as long as Ceanothus cordulatus seeds.

The generally accepted hot water treatment to overcome

impermeability of ceanothus seed coats consists of pouring water at a temperature of 170° to 180° F. over the seeds in a container and allowing the seeds to soak in the gradually cooling water for several hours or until it cools to room temperature (67; 90; 88, p. 117-121). An interesting side-light is the statement by one of these authorities that rain water should be used in hot-water treatment of ceanothus seeds--a recommendation that reflects the limited status of our knowledge about ceanothus seeds.

Average thickness of seed coats of five species (one a Ceanothus) showed a degree of correlation with heat endurance in one study--thicker seed coats being correlated with ability to endure higher temperatures (97). Unfortunately, this information is open to question; for the five species were also of five different genera.

A significant void in the limited literature on ceanothus seeds is the lack of any information on how heat treatments increase permeability of ceanothus seed coats. Nor was any information found on seed anatomy or cellular structure of ceanothus seed coats.

Most ceanothus seeds require after-ripening by stratification in a cold, moist medium at temperatures in the range of 1° to 5° C. for two to three months to overcome embryo dormancy after hot water treatment to render seed coats permeable to moisture. Data reported by Quick (67) indicates that stratification at 2.2° C. for 3 months is effective for seeds of many species of Ceanothus. But later work indicates that optimum stratification temperature may vary with species, for although stratification temperatures of 0°, 2.2°, and

5° C. all proved equally satisfactory for deerbrush ceanothus seeds, Ceanothus cordulatus seeds were best stratified at 2.2° or 0° rather than at 5° C. (70). Quick also learned that minimum duration of stratification appears to vary with altitude of the seed source--Ceanothus integerrimus seeds from low altitudes appeared to respond to shorter periods of stratification than those from high altitudes. In an experiment with seeds of Ceanothus cuneatus, soaking the seeds in a 3 percent solution of thiourea after hot water treatment seems to have substituted for overwintering (41).

Repeated observation of ceanothus species as pioneer plants on burns has led many to suspect that the seeds may be durable and long-lived in the soil, but experimental data on longevity of ceanothus seeds in soil is not available. Ewart (30) listed an attempt by A. de Candolle to germinate 15-year-old seeds of Ceanothus americanus. None of the seeds germinated, but Ewart believed that proper pre-germination treatments may not have been used on the seeds. Quick and Quick (70) germinated seeds of 12 different Ceanothus species that had been kept in dry storage for periods ranging from 9.4 to 24.3 years. Some seeds of all lots germinated, and more than 80 percent of the seeds germinated in 18 of the 22 lots tested--percentages comparing very favorably with those of fresh seed of the same species. Quick concluded that these data confirm the fact that seeds of many Ceanothus species are long-lived.

Not only is the literature on ceanothus seeds limited, but much of the information is based only on observation, on unreplicated

trials, and on studies limited in scope. Many questions concerning this vital aspect of the ecology of Ceanothus species must yet be answered before the information can be confidently applied in forestry, range management, and horticulture. Although generalized prescriptions have been laid down for pre-germination treatment of ceanothus seeds, nothing is known about: (1) seed anatomy and seed coat structure, (2) the hard seed mechanism, and (3) the way that heat treatment overcomes seed coat impermeability in ceanothus seeds.

Fortunately, much can be learned from the extensive work that has been done on hard seed problems in agricultural crop and weed species. Excellent reviews of this work have appeared periodically in the literature (18; 30; 66; 19, p. 28-138; 20, p. 87-151; 42, p. 5-24). Although it almost seems presumptuous to do so, a quick review will serve to single out some of the studies and findings that may be especially helpful in understanding the hard seed mechanism in ceanothus seeds and the effect of heat treatment upon these seeds.

Hard seeds are of much more common occurrence in nature than might generally be supposed. Although such seeds are especially common among the Leguminosae, the Malvaceae, Convolvulaceae, Myrtaceae, Chenopodiaceae, Convallariaceae, Cannaceae, Solanaceae, Geraniaceae, Nymphaeaceae, Solanaceae and other families also have species that bear hard seeds (19, p. 28-138; 30). The prevalence of hard seeds among the legumes and their importance in agriculture has stimulated more extensive research on hard seed problems of leguminous seeds than on those of other families.

Although many species produce seeds that lie dormant in soil, all such seeds are not "hard seeds" as defined by Harrington (37). Many of these take up water quite readily, but remain dormant due to other conditions such as: (1) immaturity, (2) hard seed coats, (3) germination inhibitors in the seeds or fruits, or (4) lack of light or deficiencies in other physical conditions required for germination.

Germination inhibitors have been found within seeds and in seed coats of a great number of species, including seeds of many woody plants. Evenari (29) listed about 100 species of plants that have been found to contain germination inhibitors. In more than 60 species, the inhibitor was found in seeds or fruits; and in 24 species, seeds were specifically mentioned as the source. Evenari's findings are substantiated by the work of many other investigators in Israel and other areas. Nord and Van Atta (58), for example, found that a water-soluble saponin from bracts and seed coats of Atriplex canescens inhibits germination of A. canescens and Purshia tridentata. Saponin has also been found in capsules of Ceanothus integrifolius (27, p. 107). And Ferenczy (32) determined that juice of fruits from Berberis vulgaris, Sorbus dacica, and Symphoricarpos racemosus contained germination inhibitors. Koller and Negbi (49) proved the presence of an inhibitor in the external layer of the caryopsis of Oryzopsis miliacea, and Knowles and Zalik (48) found a water-soluble inhibitor in seeds of Viburnum trilobum. Others have shown the presence of germination inhibitors in the cone oil of Abies alba and in volatile turpentine oil of Pinus sylvestris (23, 24). And Ooyama

(62), in Japan, illustrated the presence of water-soluble inhibitors in extracts of leaves of Chamaecyparis, Cryptomeria, and Pinus.

Germination inhibiting substances need not, however, be contained within the fruit or seed of the parent plant nor even in plants of the same species. Leaves of Encelia farinosa, a desert shrub, were found to contain a substance which inhibited germination and growth of seeds and seedlings of normally associated species (9, p. 60-62). Bonner also found that Artemisia absinthium produces an inhibitor to growth of other species. The substance tentatively identified as a glucoside (absinthin), is secreted by glandular hairs on the leaves. When this material is washed off by rain onto the ground, it severely stunts the growth of other species to a distance of one meter around the plant. Inhibitory substances may also be produced by mycorrhizal fungi in the soil (8).

The inhibitory effect of hard seed coats on germination is most often due to their impermeability to water or to gases, especially oxygen and CO₂. In some cases, however, their effect is a simple mechanical restriction that prevents enlargement of the embryo (86, p. 302). Impermeability of seed coats to gases has been illustrated by the work of Crocker (17), who attributed dormancy of the upper seed of cocklebur (Xanthium sp.) to impermeability of the seed coat to oxygen. Later, however, Wareing and Foda (92) found water-soluble growth inhibitors in cocklebur seeds and learned that the testas were impermeable to these inhibitors, preventing them from leaching out. Exposing dormant seeds of Xanthium and other plants to high oxygen

concentrations has since been shown to result in a reduction in amount of inhibitors within the seeds (6, 7, 92). These results seem to indicate that hard seed coats may inhibit germination not only by mechanical restriction and by their impermeability to water, but by impermeability to oxygen resulting in maintenance of high levels of inhibitors within the seed. In general, however, the most common effect of hard or impermeable seed coats is to maintain contents of the seed at a very low moisture content; preventing rehydration and germination of the seed even under optimum conditions.

A thick layer of close-packed, columnar cells, palisade-like in appearance, and with no intercellular spaces, is a characteristic feature of seed coats of many hard seeds. The thick-walled cells, often referred to as "Malpighian" cells, are radially oriented, with a lumen wider on the interior than on the exterior end. The thick walls may be of cellulose, or be heavily cutinized or lignified (28, p. 374). Generally, the palisade layer also contains a "light line" extending transversely across the long axis of the cells and tangential to the interior of seed. Structural factors responsible for appearance of the light line have not yet been positively determined, but it has been attributed to deposition of wax globules in the cells (28, p. 374), to abutment of suberized cell caps on non-suberized cell walls of the lower ends of the Malpighian cells (36), or simply to a difference in refraction of light from the thicker and denser walls of the cells at this level (14, p. 32). In the literature, this sclerenchymatous layer is frequently called the "palisade" layer; and

is commonly believed to be an important factor in impermeability of seed coats in which it is found.

Although it is now generally agreed that the palisade cells are responsible for impermeability of the testa to water, there is little agreement as to the particular layers involved. Initially, impermeability was thought to be due to a cuticular layer on the external surfaces of seeds (63, p. 95; 71; 96); although White thought that the impermeable layer in larger seeds might be in the palisade layer. In recent years, other investigators have also concluded that the palisade layer is responsible for impermeability of many hard seed coats but disagreement still exists on the structural features involved. Most agree that the impermeable portion of the testa is located at the light line (14, p. 31-35; 43, p. 254; 54; 60) or in that portion of the palisade layer exterior to the light line (36, 53), but Shaw (74, p. 273) maintained that the palisade cells of Nelumbo lutea were impervious throughout their length.

Many different methods have been used on hard seeds in order to make the seed coats permeable to moisture and gases. Among these are mechanical scarification, scarification with sulfuric acid or strong bases, impaction, soaking in alcohol and solvents, cold treatments, alternate freezing and thawing, and exposing seeds to wet or dry heat or to a radio-frequency electric field. Effects of such treatments vary to some extent depending upon the type of seed treated. Barton (2), for example, used shaking (impaction) and alcohol soaking on seeds of 3 subfamilies of Leguminosae--Mimosaceae, Caesalpinaceae,

and Papilionaceae. Seeds of the Papilionaceae became permeable after shaking in a glass bottle, but were unaffected by soaking in alcohol. Seed coats of Caesalpinaceae were rendered permeable by alcohol, but almost without exception were unaffected by shaking. Seeds of Mimosaceae seemed intermediate between the other two subfamilies; some responded to shaking and others to alcohol soaking.

Heat treatments have been found to increase germination of a variety of hard seeds, including seeds of a number of shrubs; but few investigators have been able to determine the actual effect of heat on such seeds. In addition to the Ceanothus species enumerated earlier, high temperatures have been shown to increase germination of a number of other chaparral shrubs including Rhus laurina and Rhus ovata (80, 97). Hard seeds of many other woody and herbaceous species have also shown increased germination after heat treatment including those of Acacia spp., cotton, white clover, bur clover, alfalfa, rose clover, and Geranium sp. (4; 13; 52; 54; 56; 72; 77; 78; 84; 93; 36, p. 364; 87, p. 14; 95, p. 739-740).

Excellent research by a few investigators has provided some of the necessary--but difficult to determine--information required for an understanding of the roles of heat and fire in the ecology of hard-seeded species by disclosing the mode of action by which heat induces permeability in some hard seeds. Such information has been developed for Melilotus alba by Hamly (36), for Amorpha fruticosa by Hutton and Porter (42), for Rhus ovata by Stone and Juhren (80), and for Gossypium hirsutum by Christiansen and Moore (13). The way that heat

acts to induce permeability in hard seeds seems to differ considerably in each instance, depending upon anatomical structure of the seed.

Hamly (36) determined that heating hard seeds of sweet white clover at temperatures below 100° C. caused the seeds to become permeable at the strophiole, and that both dry heat and hot water treatments had the same effect. Soft seeds produced by heating were indistinguishable from naturally soft seeds. Hamly hypothesized that the Malpighian cells in the vicinity of the strophiole of hard seeds of Melilotus alba are in a state of metastable equilibrium due either to swelling or to compression as a result of seed coat tension; and that when this equilibrium is upset, softening results through a split that develops lengthwise along the middle lamellae of the Malpighian cells. Permeability of the softened seed centers on this split in the palisade layer.

Hutton and Porter (42) found different heat effects when they used shaking (impaction) and wet and dry heat to overcome seed coat impermeability of Amorpha fruticosa. The hilum of seeds of A. fruticosa is located in a rather deep, U-shaped depression near the narrow end of the incurved surface of the seed, and an opening in the Malpighian layer at the base of this depression is occupied by vascular tissue. Either impaction or dry heat (85° C. for 5 to 7 hours) causes a cleft to appear in the vascular tissue, which then becomes permeable to moisture. No other breaks occur in the seed coat. In contrast to Hamly's results with hard seeds of Melilotus alba, Hutton and Porter found that permeability caused by wet heat was of a

different type than that effected by dry heat in seeds of A. fruticosa. While dry heat produced an extremely localized permeability, wet heat caused the whole seed to become permeable, although in many cases no definite breaks occurred.

Dormancy in hard seeds of Rhus ovata results from impermeability of the second of three seed coat layers. Heat induces germination of the seeds by rupturing the second seed coat layer along the edge of the seed immediately above the micropyle, allowing entry of water through the underlying third seed-coat layer (80).

Still another mechanism was affected by heat treatments that rendered hard cotton seeds (Gossypium hirsutum) permeable to moisture. When Christiansen and Moore (13) studied hard seeds of cotton in an effort to detect the mechanism responsible for impermeability of these seeds to moisture, they learned that water enters the seed through an opening in the palisade layer at the chalazal end of the seed. In hard seeds, water is prevented from penetrating this opening by the chalazal cap and by a heavy deposit of lignin that forms a seal between the cap and the palisade layer. Immersing the seed in hot water (80° C.) renders the seal permeable, allows water to enter, and causes the palisade layer to buckle upward on each side of the cap. Dormancy does not recur when the seed is dried.

Although data on longevity of ceanothus seeds is extremely limited, much information has been accumulated on agricultural crop and weed seeds during the past century. Many seeds are now known to remain dormant but viable for a century or more in dry storage

and in the soil. Although some permeable seeds that readily absorb soil moisture have been found to retain their viability for periods as long as 80 years in the soil (26, 85), seeds with impermeable seed coats are considered especially well adapted for long life. Seeds of the Leguminosae are outstanding in this respect. Becquerel (5) determined that seeds of seven leguminous species were viable after periods of 81 to 158 years in dry storage in the National Museum of Paris, and estimated that some seeds of three of these species would remain viable for 155, 199, and 221 years. An outstanding example of long-lived seeds are those of Indian lotus (Nelumbo nucifera) taken from a dried lake bed in Manchuria. The seeds were found about 1.5 meters below the surface buried in peat under a layer of loess. Although the seeds were believed to be at least 120 years old and more likely 200 to 400 years old, they germinated "without exception" when the impermeable seed coats were filed through. Longevity of the seeds was attributed to their having been buried in the soil and their impermeability to water (59, 60, 61). Although Ewart (30) scoffed at the idea that seeds may remain dormant but viable for long periods in the soil, experimental evidence accumulated during the intervening period has shown that seeds of a large number of species may remain viable for much longer periods in the soil than in dry storage (19, p. 28-138; 25; 26). Deep burial in soil evidently tends to increase seed dormancy (12); an effect that has been attributed in at least one case to reduced availability of oxygen (85).

SEEDS, SEED SOURCES, AND METHODS

All except one small lot of the varnishleaf ceanothus seeds used in laboratory experiments during this investigation were collected at elevations of 2000 to 3000 feet above sea level in the Cascade Range 21 miles east of Roseburg, Oregon, during late summer in 1957 and 1958. The remaining lot of seed, gathered in 1957 at an elevation of 3500 feet in the Siskiyou Mountains west of Grants Pass, Oregon, was used in only one experiment in which seeds were heated in wet and in dry soils. When collected, the exterior pulp of fruits was dried and black; and the seeds within the capsules were full-sized, mature, and dark brown in color. Capsules were stripped from the plants just before natural dissemination of the fruits and seeds.

Due to the nature of the experiments in which the seeds were to be used, heat could not be employed to extract seeds from the capsules. Instead, seeds were extracted when needed for experiments by rubbing the capsules between soft cedar boards. No special provisions were made for storage of seeds or capsules; prior to extraction, the capsules were stored intact in open boxes in an unheated garage during the winter of 1957-58 and in an unheated basement thereafter. In the laboratory, extracted seeds were simply stored in dry glass jars at room temperature.

Mature varnishleaf ceanothus seeds are a glossy dark brown in color, and are about 2.8 mm. long, 2.3 mm. wide, and 2.0 mm. deep at the thickest part of the seed (Figure 1). Samples of seeds extracted

Figure 1. Varnishleaf ceanothus seeds.



from the capsules ranged from 61,400 to 67,700 seeds per pound. Most of these were hard seeds; impermeable seed coats prevented imbibition of moisture in a high percentage of the seeds even when immersed in water. A small percentage of soft seeds were found in each lot extracted from the capsules. However, it was not determined whether the permeable condition was a natural occurrence; for a small number of seeds with damaged seed coats were invariably present as a result of the method of extraction. Efforts were made to select only plump, undamaged seeds with good color for the experiments.

Both laboratory experiments and field studies were employed in this evaluation of heat as a factor in germination of varnishleaf ceanothus seeds. Objectives of the laboratory experiments were to determine whether heat stimulates germination of varnishleaf ceanothus seeds, the types of heat (dry, wet, fire, solar) that are effective, and to learn how heat renders the hard seeds permeable to moisture. Field investigations were designed to determine whether seeds are present in duff and surface soil under stands of old-growth Douglas-fir, to learn whether such seeds (if present) are viable, and to study the effect of logging and slash disposal practices on germination of the seeds. Where appropriate, data were analyzed statistically.

LABORATORY EXPERIMENTS

HEAT TREATMENT OF SEEDS

Stratification

Pre-germination treatments prescribed for seeds of most ceanothusus include after-ripening in a cold, moist medium for 60 to 90 days after a suitable treatment to render the seed coats permeable to moisture. However, seeds of some species such as C. arboreus and C. rigidus evidently do not require stratification, and the need is variable among seed lots of C. cuneatus (88, p. 117-121). Three months stratification has been prescribed for seeds of C. velutinus (88, p. 117-121), but no information seems to be available concerning stratification requirements for seeds of C. velutinus var. laevigatus, which grows under different climatic conditions. For proper performance of germination tests to evaluate heat treatments, it was necessary to determine: (1) whether varnishleaf ceanothus seeds require stratification, and (2) the minimum duration of stratification required for germination of a high percentage of the seeds.

Four replications of 50 seeds each were immersed in separate 1-liter flasks of hot water (80° C.) and allowed to remain until the water had cooled to room temperature. The heat-treated seeds were then placed on moist blotters in petri dishes, kept one day at room temperature, and then stratified between moist blotters at 3½° C. for 14 weeks. At appropriate times, additional replications were treated in the same way to provide stratification periods of 14, 12,

10, 8, 6, 4, 3, 2, and 0 weeks. Finally, all seeds were germinated on fresh, autoclaved moist blotters in petri dishes at a constant temperature of 75° C.

Varnishleaf ceanothus seeds require a period of stratification after heat treatment; and duration of the cold, moist period has a pronounced effect on percentage of seeds that germinate (Fig. 2). No seeds germinated without stratification (0 weeks) or after stratification periods of less than 4 weeks duration.

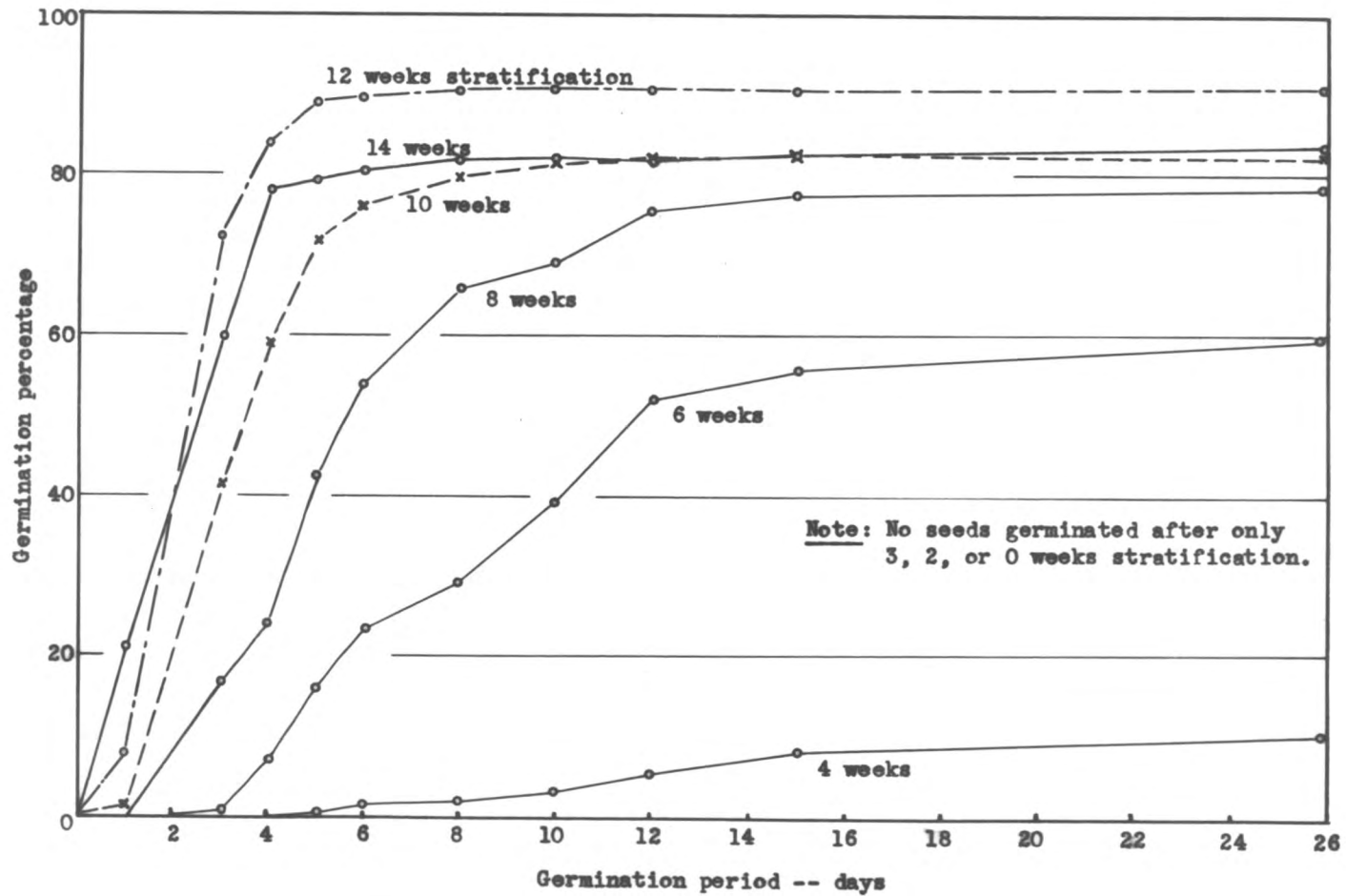
Although a few seeds germinated after only 4 weeks stratification, 8 weeks seems to be the minimum duration required for after-ripening a high percentage of varnishleaf ceanothus seeds under the stated conditions. Eight weeks stratification was used to save time in some of the other experiments. Twelve weeks stratification resulted in maximum germination; the longest period of fourteen weeks proved less effective than 12 weeks stratification. Observation indicated that incidence of molds and infections increased directly with length of stratification, and this may have been a factor in the lower percentage of germination after 14 weeks than after 12 weeks.

Duration of cold, moist storage also had a pronounced effect upon speed of germination. Seeds stratified for the longest periods began germinating more quickly and completed germination sooner than those stratified for shorter periods (Fig. 2).

Steeping in Hot Water

The generally prescribed heat treatment to stimulate germination

Figure 2. Trends of germination of heat-treated varnishleaf ceanothus seeds after stratification at $3\frac{1}{2}$ degrees Centigrade for various lengths of time.



of ceanothus seeds involves immersing the seeds in a fixed volume of hot water and allowing it to cool to room temperature (67; 90; 88, p. 117-121). Prescribed initial water temperatures range from 70° C. to 100° C. However, no information concerning the effect of such treatments on varnishleaf ceanothus seeds was found in the literature. An experiment was therefore designed to determine the effect of steeping in hot water on germination of varnishleaf ceanothus seeds and to determine the optimum initial water temperature to induce maximum germination.

Fourteen hundred varnishleaf ceanothus seeds were divided into 28 lots of 50 seeds each, and a table of random numbers was used to assign 4 lots to each of 7 treatments (initial water temperatures). Initial water temperatures were: 70°, 75°, 80°, 85°, 90°, 95°, and 100° Centigrade. Each lot of 50 seeds was encased in an open-mesh cotton sack and immersed in a 1-liter flask of water at the desired initial temperature. After heat treatment, the seeds were stratified for 9 weeks between moist blotters at 3½° Centigrade, then germinated on blotters in autoclaved petri dishes at a constant temperature of 75° Centigrade.

No obvious optimum initial water temperature is indicated in the data (Table 1). Instead, initial water temperatures in the range from 80° C. to 95° C. were equally effective in stimulating germination of varnishleaf ceanothus seeds. Temperatures above and below this range were less effective.

Table 1.--Germination of varnishleaf ceanothus seeds
after steeping in hot water at temperatures
of 70° to 100° Centigrade

Replication	Initial water temperatures in degrees centigrade						
	70	75	80	85	90	95	100
	- - - - - Number of seeds germinated - - - - -						
1	27	28	35	41	44	41	26
2	34	34	39	41	41	36	17
3	29	39	44	45	43	37	37
4	32	36	38	36	37	38	22
Totals	122	137	156	163	165	152	102

Heating Seeds in Wet and in Dry Soils

Although direct exposure to dry heat and steeping in hot water have long been known to stimulate germination of ceanothus seeds, little is known about the effect of heat on germination of ceanothus seeds buried in the soil. Despite this apparent lack of information, observation of ceanothus seedlings on burns has repeatedly led investigators to speculate that fire (in some unexplained way) stimulates germination of ceanothus seeds in the soil (35; 69; 57, p. 28).

Ewart (30) believed that coats of hard seeds in the soil were chemically softened when rain combined with an alkaline ash left on the soil after bush fires. He also thought that slight charring of the surface of the seed could make it permeable to water without necessarily destroying vitality of the contents. However, after consideration of evidence accumulated during the intervening period, it seems more logical that fire-stimulated germination of ceanothus seeds in the soil is probably due to a direct effect of heat on the seed rather than to a chemical action on the seed coat or slight charring of the seed.

Replicates of 300 one-year-old seeds each were planted $1/8$ inch below the soil surface in cans of wet and dry soil and heated in an electric oven at temperatures ranging from 100° to 420° Fahrenheit (approximately 38° to 216° C.). For dry soil treatments, cans 12.5 cm. in diameter and 8 cm. deep with pierced bottoms were filled with a < 16 -mesh fraction sieved from a brown silty clay loam soil; then 300 seeds were planted at the desired depth and at least one inch

away from the sides of the container. For wet soil treatments, a similar procedure was followed; but the soil was first watered to excess and allowed to drain for 24 hours before the seeds were planted. Replicates were heated separately for 5 minutes or 20 minutes at each of five treatment temperatures (Table 2). After heating, each can of soil and seeds was removed from the oven and allowed to cool to room temperature. The heat-treated seeds were then sieved out, stratified in moist vermiculite for 4 months at 5° C., planted in vermiculite, and germinated in a greenhouse. Temperatures in the greenhouse were maintained at 25° C. during the day and 18° C. during the night. Germination of varnishleaf ceanothus seeds is epigeous, and evaluation of treatments was based on periodic counts of seedlings whose cotyledons emerged above the surface of the vermiculite.

It must be recognized that the effective temperature influencing germination is that within the soil at the depth of the seeds and not the indicated air temperature in the oven. But in this experiment, the different temperatures and periods of exposure represent amounts of heat that might be delivered to the surface soil by various amounts of forest fuels burning with sustained intensity for 5-minute and 20-minute periods. Results of the experiment, therefore, show the effect of heat per se on germination of seeds in wet and in dry soil without the confounding effects of ashes and charring that Ewart considered responsible for germination of hard seeds after bush fires.

Each replicate evidently contained a small percentage of naturally soft seeds or seeds with damaged testas, for a small number of

Table 2.--Emergence of varnishleaf ceanothus seedlings after heat treatment of seeds in wet and in dry soils

Treatment				Treatment			
Oven temperature	Soil moisture condition	Duration of heating	Total seedling emergence	Oven temperature	Soil moisture condition	Duration of heating	Total seedling emergence
--of--		--min.--	--number--	--of--		--min.--	--number--
100	Dry	5	11	100	Wet	5	10
100	Dry	20	7	100	Wet	20	9
180	Dry	5	10	180	Wet	5	7
180	Dry	20	13	180	Wet	20	13
260	Dry	5	3	260	Wet	5	13
260	Dry	20	108	260	Wet	20	27
340	Dry	5	78	340	Wet	5	5
340	Dry	20	134	340	Wet	20	174
420	Dry	5	149	420	Wet	5	25
420	Dry	20	58	420	Wet	20	117

seeds germinated even at the lowest temperatures in both soil conditions (Table 2). With increasing temperatures, a significant increase in germination of seeds in dry soil was obtained in the replications heated for 20 minutes at 260° F. This duration and temperature was evidently necessary to raise soil temperatures above the critical minimum temperature for inducing germination of varnishleaf ceanothus seeds in the dry soil. Germination of seeds from dry soil was also high in both of the 340° treatments and in the 420° treatment for 5 minutes. Germination decreased somewhat, but not significantly, when seeds in dry soil were subjected to a 420° oven temperature for 20 minutes.

A similar pattern is evident in the wet soils, except that the major initial increase in germination did not occur until the wet soils were subjected to an oven temperature of 340° for 20 minutes. The additional increment of heat required to stimulate germination of seeds in wet soil can probably be attributed directly to the soil moisture condition and the high specific heat of water. Wet soil would naturally require a higher oven temperature or longer duration of heating to deliver the additional increment of heat required to raise soil temperatures to the critical level for stimulating germination of ceanothus seeds.

The germination data show quite conclusively that heat per se can stimulate germination of varnishleaf ceanothus seeds in both wet and dry soils without the associated ash and charring effects of fire.

Duration of heating had a significant influence on the

effectiveness of oven temperatures in stimulating germination of seeds in both wet and dry soils. This interaction affected germination only at the 260° F. oven temperature with dry soil, but was evident at both the 340° and 420° temperatures with wet soil. Twenty-minute exposures resulted in germination of a much larger number of seeds than were produced by 5-minute exposures at these temperatures (Table 2). This indicates that germination of the ceanothus seeds was stimulated only after soil temperatures were raised above a critical level. Furthermore, the continued increase in germination of seeds in dry soil with increasing oven temperature shows that the stimulating effect continues to increase through a range of soil temperature above the critical temperature. In wet soil, the critical soil temperature was evidently reached only during the longest heating periods at the two highest oven temperatures.

Next, thermocouples attached to a Model 153 Brown Electronik recording potentiometer were used to determine trends of soil temperature 1/8 inch below the surface of the dry soil in the course of each treatment (Fig. 3). Numbers of seeds germinated were then correlated with the highest soil temperatures attained at this depth during the appropriate heat treatments.

At soil temperatures up to about 45° C., there was no stimulation of germination (Fig. 4). Apparently the minimum soil temperature necessary for inducing germination of this lot of seed was in the vicinity of 45° Centigrade. As soil temperatures increased beyond this point, germination increased rapidly and reached a maximum at

Figure 3. Trends of soil temperature 1/8 inch below the surface of a dry brown silty clay loam exposed to different oven temperatures.

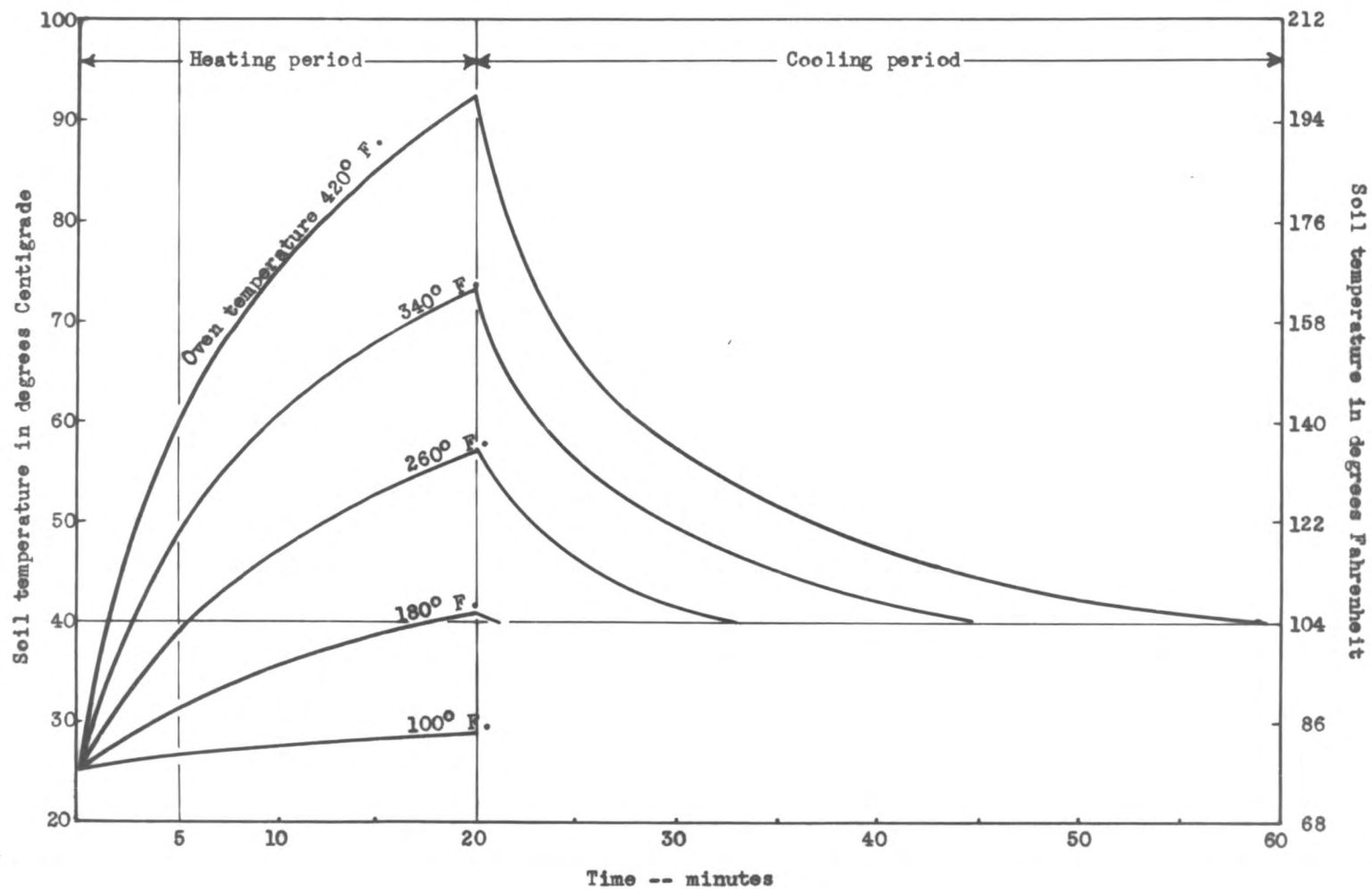
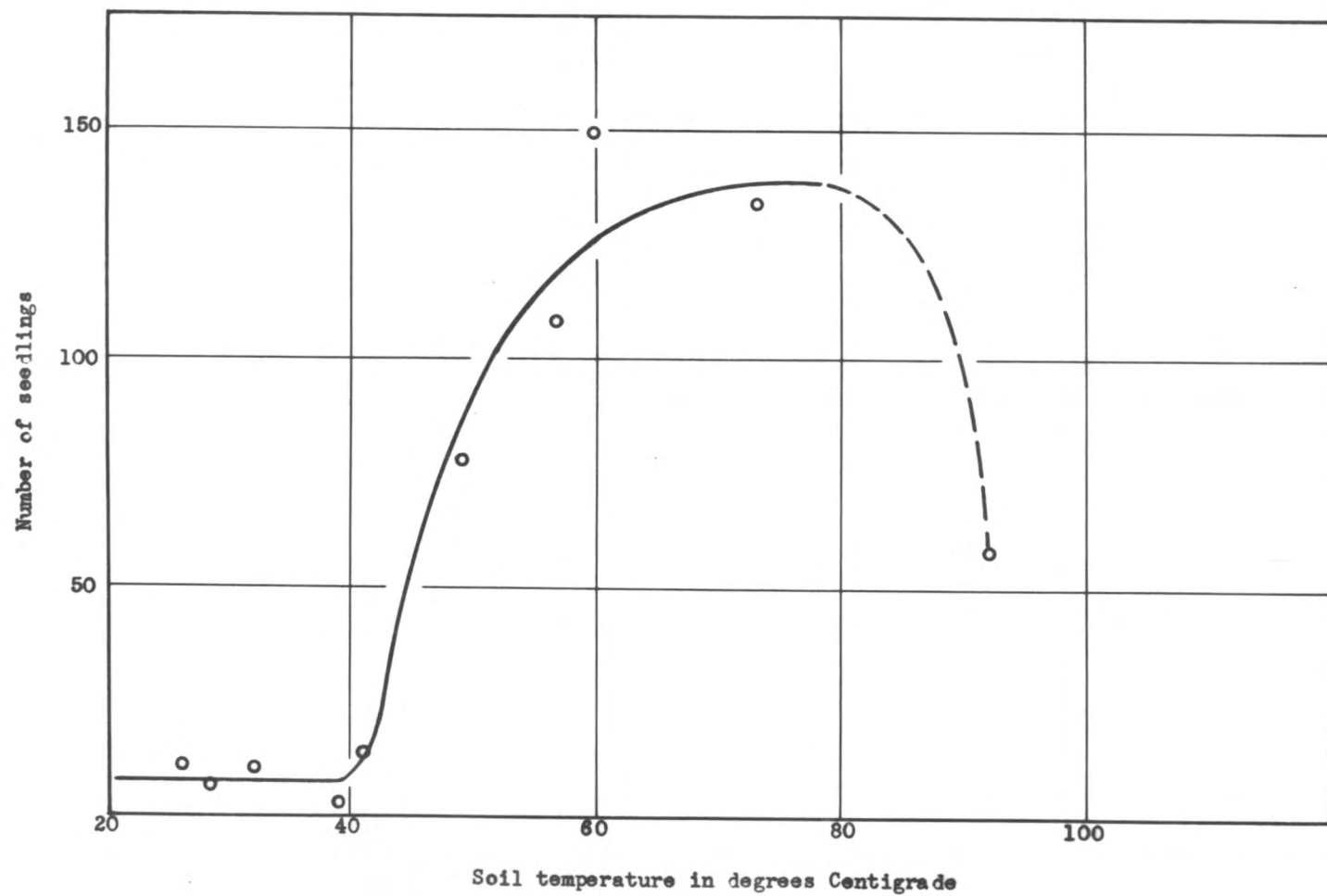


Figure 4. Emergence of varnishleaf ceanothus seedlings in relation to maximum soil temperature attained at seed depth 1/8 inch below the surface of a dry brown silty clay loam during heat treatment in an electric oven.



soil temperatures of approximately 80° C. Although germination appears to drop off at soil temperatures higher than 80° C. (as shown by the dashed line), statistical analysis indicated that the decrease may not actually occur.

Time-Temperature Interaction in Inducing Germination

The interrelated effects of time and temperature on germination of ceanothus seeds in the preceding experiment seemed worthy of further study. Several questions arose. Above the critical temperature, would a long exposure at a given soil temperature result in increased germination equivalent to that obtained by exposure to a higher temperature for a shorter time? Also, if a short exposure stimulated germination, would a longer exposure at the same temperature damage or kill the seeds? In an effort to answer these questions, varnish-leaf ceanothus seeds were exposed to soil temperatures of 30°, 45°, 60°, 75°, 90°, 105° and 120° C. for 8, 16, 24, 32, and 40 minutes.

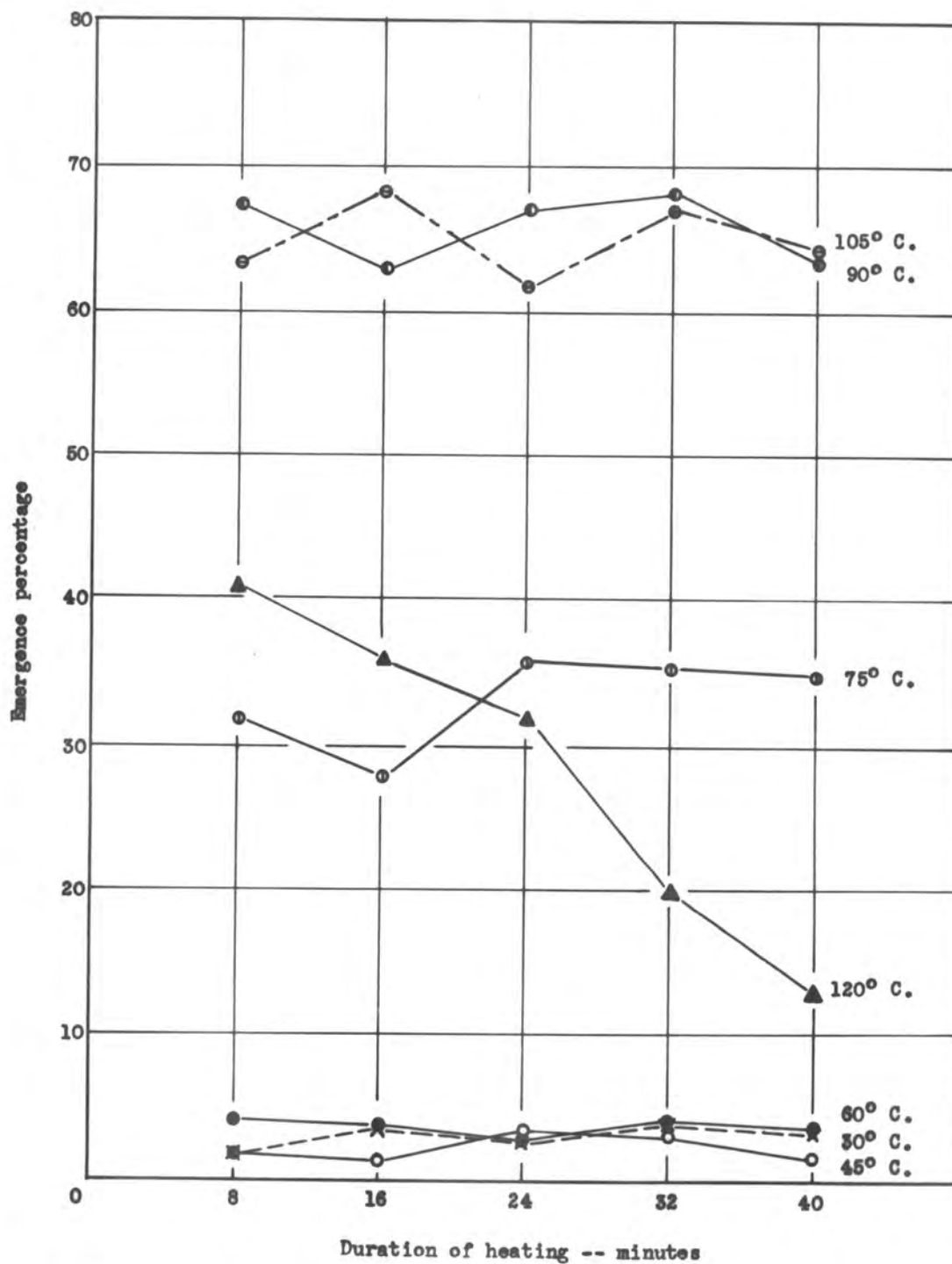
Seeds were heated in a fine-grained sand from which they could be extracted very rapidly at the end of each heating period. The sand was pre-heated in an electric oven until temperatures stabilized at the desired level before the seeds were inserted. This meant that once the seeds were inserted, they were instantly exposed to the desired soil temperature and that this temperature was maintained throughout the treatment period. Coiled thermocouples buried in the sand and attached to a multi-point recording potentiometer provided a constant measure of soil temperature at seed depth, and a thermostatic heat control on the oven was supplemented by manual adjustment

whenever necessary to maintain soil temperatures at the desired level. After heat treatment, the seeds were stratified in moist vermiculite for $2\frac{1}{2}$ months at $3\frac{1}{2}^{\circ}$ C., and then planted in flats of autoclaved sandy loam soil. The flats of treated seeds were germinated in a greenhouse, and periodic counts were made of seedling emergence.

In contrast to results of the earlier experiment, the critical soil temperature for inducing germination of varnishleaf ceanothus seeds was above 60° C. but below 75° C. in this experiment (Fig. 5). Maximum germination was obtained by exposure to soil temperatures in the 90° to 105° C. range. Age and sources of the seeds may have been factors responsible for the difference in critical temperatures in the two experiments. In the earlier experiment, seeds were 10 months old and contained seeds gathered during 1957 in the Siskiyou Mountains as well as in the Cascade Range; while the seeds used in this experiment were gathered a year later only in the Cascade Range. Quick and Quick (70) noted a variation in response to heat treatment in three lots of C. cordulatus seeds of different ages from different seed sources.

Duration of exposure proved less important than soil temperature in the 8-minute to 40-minute range, except at soil temperatures of 120° C. Germination was not induced by soil temperatures of 60° C. or less, regardless of duration of exposure. Within the range of induced germination (75° to 105° C.), the heat effect acted on the seeds within 8 minutes and continued exposure had no further effect

Figure 5. Emergence of varnishleaf ceanothus seeds heated in dry sand at soil temperatures ranging from 30° to 120° Centigrade for various lengths of time.



on either germination or vitality. Evidently the heat action that induced germination reached its maximum effect within 8 minutes in the dry sand. However, duration of exposure was important at the 120° C. soil temperature, which is evidently in the lethal range for varnishleaf ceanothus seeds. In sand heated to 120° C., mortality increased directly with duration of exposure. A similar effect at lower temperature was reported by Hopkins (39) for seeds of Brassica juncea.

Interestingly, ceanothus seeds--even within the same lot--seem to vary with respect to soil temperatures that will induce germination. Some seeds respond at lower temperatures than others. A certain percentage of the seeds responded to 8 minutes exposure to soil temperatures between 60 and 75° C., but continued exposure at 75° for up to 40 minutes did not affect any of the remaining hard seeds. When soil temperatures were increased to 90° C., germination was induced in another increment of the hard seeds that did not respond to the lower soil temperature.

Fire-induced Germination of Seeds in Soil

In nature, two common sources of heat that can raise soil temperatures high enough to stimulate germination of ceanothus seeds are solar radiation and fire (38; 73; 76, p. 35-40). The last two experiments described above demonstrated that hot soil can stimulate germination of ceanothus seeds and that heat applied to wet or dry soil can produce the same result. A small and simple experiment was set up to show that fire can serve as a heat source to stimulate

germination of seeds in the soil.

Six flats, 16 x 30 inches, were filled with a sandy loam. Each flat was then divided into two parts of equal area, and 300 varnish-leaf ceanothus seeds were planted in each half at a depth of $1/8$ to $1/4$ inch below the surface. One half of each flat was chosen to be burned; while the other half remained unburned. The two halves were separated by wooden dividers and sheet-metal flame shields to minimize heat transmission from the burned to the unburned sections. To remove the possibility of heat radiating from the flame shields to the soil in the unburned sections, the unburned halves of the flats were covered with a reflecting cover of aluminum foil. Finally, excelsior was piled to a depth of 6 inches on the surfaces of the sections to be burned, and ignited. After cooling, the flats were watered, stratified for 2 months at 2°C ., and then germinated in a greenhouse.

Three hundred and five seedlings emerged in the burned halves of the flats; only 32 in the unburned halves (Fig. 6). In making periodic counts of seedling emergence, many carbonized seeds were found in the burned sections of several of the flats, showing that some seeds were not planted deep enough to be thoroughly protected from the fire. If planted at a somewhat greater depth, it is possible that differences would have been even more pronounced. However, the greater germination in the burned sections shows that fire on wildlands can be expected to induce germination of varnishleaf ceanothus seeds buried in the soil.

Figure 6. Germination of varnishleaf ceanothus seeds
was much greater in the burned halves than
in unburned sections of the flats.



Solar Radiation as a Factor in Germination

Under natural conditions, surface soil temperatures exceeding 60° C. (140° F.) are frequently attained on hot summer days as a result of insolation. Results of the preceding experiments indicate that dormant varnishleaf ceanothus seeds in forest soils might be induced to germinate when turned up by logging disturbance and exposed to such temperatures on the surface or in the surface soil. Such solar-induced germination would explain the anomalous condition often observed in the field, where ceanothus seeds germinate in mineral soil that shows no evidence of exposure to fire.

An experiment was set up to test the hypothesis that surface soil heated by solar radiation will stimulate germination of ceanothus seeds exposed on the surface. Twenty 1-foot-square flats were filled with a reddish brown clay loam, and 200 seeds were embedded in the surface of each flat by scattering the seeds over the surface and pressing them into the soil with a flat board. This procedure placed most of the seed within the surface soil, but left the upper face of each seed exposed to sun and air. The flats were then exposed in groups of 5 with soil surfaces sloped at angles of 0, 10, 20, and 30 degrees from the horizontal toward a bearing of S. 30° W. This direction was selected as one of the hottest exposures in nature.

One flat in each treatment (angle of exposure) was fitted with a thermocouple inserted in the surface soil with the lead just below the surface and the thermocouple bent upward so that only the tip end of the bead was visible from above. This placed the thermocouple

in a position like that of the seeds, with almost all of the surface of the bead encased in the soil. In addition, tempils (75) covering a melting range of 113° F. to 175° F. were placed just below the soil surface to provide a rough check on accuracy of temperatures recorded by the thermocouples.

The flats were exposed for only one day in early August from 8:00 A.M. to 6:05 P.M. Five additional flats were prepared in the same way; but were kept in an open shed, where they were not exposed to the sun. At the end of the day, all flats were placed flat on the soil surface and allowed to cool overnight. Then they were watered, stratified at 5° C. for 3 months, and germinated in a greenhouse.

Although air temperatures reached a maximum of 96° F. in the shade, germination was not induced in the ceanothus seeds embedded in the soil surfaces exposed to solar radiation. The highest surface soil temperatures were produced in flats sloped at an angle of 20 degrees, where the thermocouple recorded a maximum temperature of 139° F. (59.4° C.) at the surface and tempils indicated a soil temperature in excess of 150° F. (> 66° C.) just below the soil surface. This difference in temperature is probably due to a greater loss of heat by convection and radiation at the surface. The temperature of the thermocouple is considered most indicative of the actual temperatures to which the seeds were exposed.

Soil temperatures resulting from insolation in this experiment failed to induce germination of the varnishleaf ceanothus seeds

exposed at the soil surface. However, the results are in agreement with results of the Time-Temperature Interaction experiment. Germination in the latter experiment was not induced until soil temperatures exceeded 60° C. Seeds of the same lot were used in both experiments.

To ascertain that lack of germination was due to low soil temperatures and not to poor seed or inadequate stratification, the flats were moved to the laboratory for heat treatment (Fig. 7) followed by an additional period of stratification. Six flats, selected by random methods, were given no additional heat treatment; but were stratified for two more months. Batteries of reflector spot lamps were used to heat similarly selected groups of six flats to 50°, 65°, and 80° C. at seed depth. Thermocouples were inserted at the depth of the seed layer and temperatures controlled by use of a recording potentiometer. As soon as soil temperatures rose to the desired level at seed depth, the lamps were cut off; and the flats of soil were allowed to cool. The clay loam soil still contained sufficient moisture to be plastic, and duration of heating averaged about 9 minutes in the 50° treatment, and about 21 minutes and 44 minutes in the 65° and 80° treatments, respectively.

Induced germination occurred only in the soils heated to 65° and 80° C. (Table 3). This is in agreement with results of the Time-Temperature experiment, and shows that failure of the seeds to germinate after exposure to solar radiation was due to the fact that soil temperatures remained below the critical level. Furthermore,

Figure 7. Flats of soil containing dormant varnishleaf
ceanothus seeds were heat treated in the
laboratory to induce germination of the seeds.



Table 3.--Emergence of varnishleaf ceanothus seedlings
after heat treatment of seeds in a reddish
brown clay loam

Replication number	Heat treatment			
	No heat	50° C.	65° C.	80° C.
1	1	0	10	29
2	1	1	57	44
3	0	1	8	6
4	2	2	13	17
5	0	40	8	105
6	0	0	13	22
Totals	4	44	109	223

the critical temperature appears to have been in approximately the same range ($> 60^{\circ}\text{C.}$) in both the dry sand and the slightly damp clay loam.

Summary: Use of Heat to Induce Germination

The experiments described so far show quite conclusively that heat per se does stimulate germination of varnishleaf ceanothus seeds. They have shown further that heat may be applied to the seeds through a variety of media (dry sand, water, and wet or dry loam soils) and that fire can serve as the heat source in nature. Critical soil temperatures inducing germination in these experiments was in the range of 45° to 65°C. , and seemed to vary somewhat depending upon time of collection and location of seed source. Critical temperature seems to vary among seeds within a given seed lot; some seeds respond at lower temperatures than others in the same seed lot. Beyond the minimum period required for heat to act on varnishleaf ceanothus seeds, duration of exposure at a given temperature has no further influence on germination during periods of exposure up to 40 minutes in length. The minimum required exposure to heat within the range of temperatures where germination is induced is less than 8 minutes with dry heat. However, within the lethal range with dry heat (about 120°C.), mortality increases directly with increasing length of exposure.

None of these experiments, however, revealed the mechanism of heat action on varnishleaf ceanothus seeds or the part of the seed affected. Therefore, additional work on seed anatomy and seed physiology was carried out to determine the way that heat affects varnishleaf

ceanothus seeds and renders the seed coats permeable to moisture.

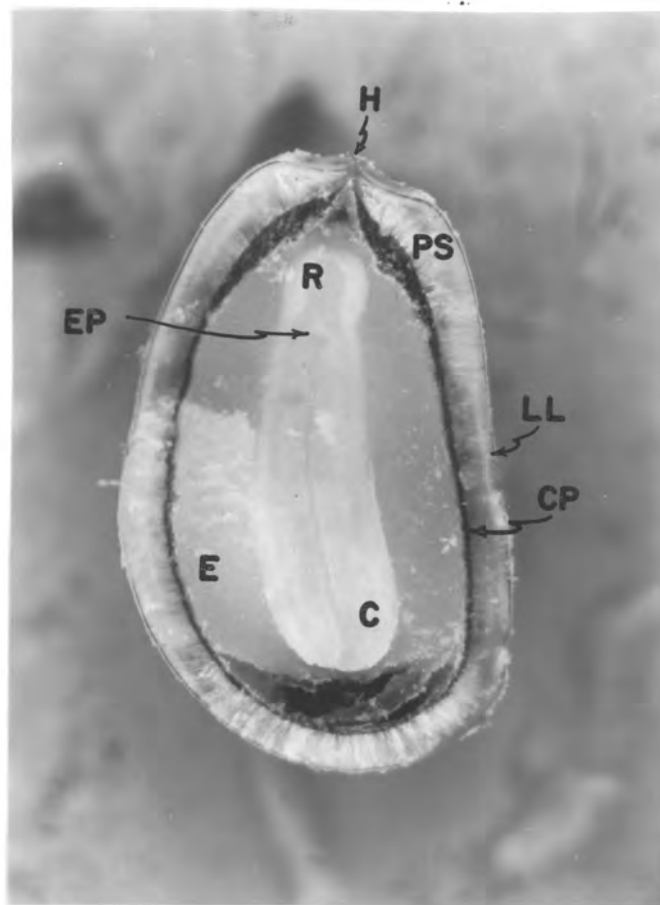
EFFECT OF HEAT ON SEED COAT IMPERMEABILITY

Seed Anatomy

Mature varnishleaf ceanothus seeds are a glossy brown in color, somewhat egg-shaped, and slightly flattened in cross section (Fig. 1). The hilum, a flattened oval area on the small end of the seed, is covered by a hilar cap of funicular tissue that remains attached to the hilum of the mature seed. Beneath the hilar cap, a hilar fissure or hilar groove similar to those found in some leguminous seeds (16, 43) extends about two-thirds of the distance lengthwise through the center of the hilum.

The anatomy of varnishleaf ceanothus seeds is similar in some respects to that of hard seeds of legumes. A thin layer of cuticle covers the exterior surface of a thick, palisade-like layer of Malpighian cells that form the main structure of the seed coat (Fig. 8). The palisade cells display a light line located approximately one fifth of their length inward from the exterior surface. This closely packed, sclerenchymatous layer is evidently responsible for impermeability of the seed coats of varnishleaf ceanothus seeds as it is for impermeability of seed coats of leguminous seeds. Beneath the palisade layer is a thin layer of collapsed parenchyma, remnants of tissues that seem analogous to what is sometimes termed the nutrient layer in legume seeds (94, p. 386-394). The collapsed cells of this layer contain the pigments that are responsible for the characteristic brown color of mature seeds. Inside the collapsed tissues, a generous amount of endosperm encloses a well-developed, dicotyledonous

Figure 8. Longitudinal section of a mature varnishleaf
ceanothus seed. X27. (C.--cotyledon; CP.--
collapsed parenchyma; E.--endosperm; EP.--
epicotyl; H.--hilum; LL.--light line; PS.--
palisade layer; R.--radicle).



embryo with thick, broadly flattened cotyledons.

Fully mature seeds could not be sectioned either when embedded in paraffin or in a water or gelatin matrix on the freezing microtome, but suitable sections were obtained of young fruits and seeds that were approaching maturity. Fruits and seeds were killed and fixed in a modified Navashin-type fluid of formalin, glacial acetic acid, chromic acid, and distilled water. They were then dehydrated in a tertiary butyl alcohol-paraffin oil series, infiltrated with paraffin, and embedded in Tissuemat. The embedded seeds and fruits were sectioned at 8 to 20 microns on a rotary microtome.

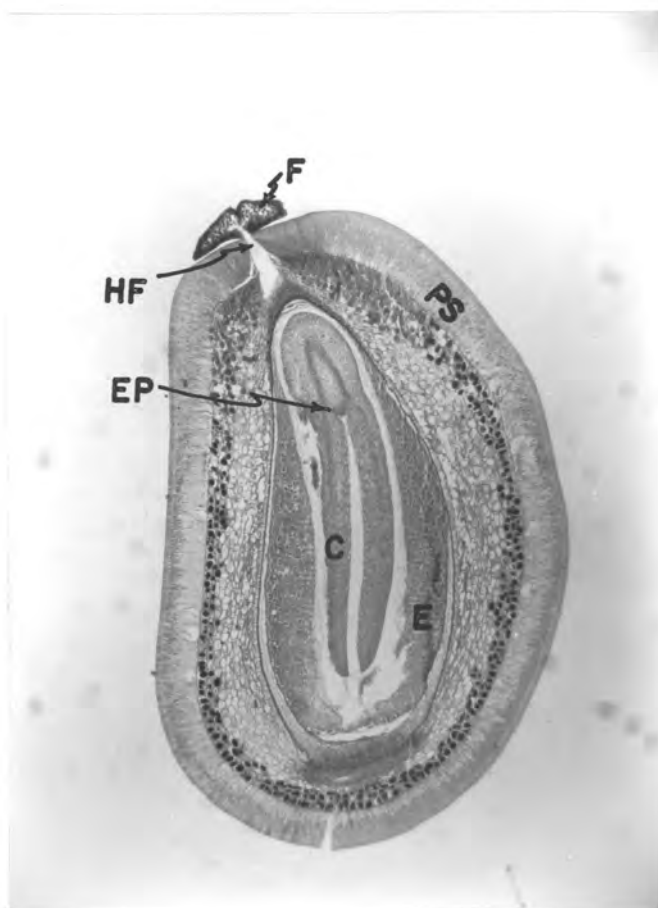
In young fruits of varnishleaf ceanothus, vascular tissues extend from the placenta through the central section of a short funiculus into the ovule through the undeveloped hilum (Fig. 9). As the seed matures and the hilar region of the palisade layer develops, the vascular tissues are broken where they pass through the palisade layer. The funiculus, however, remains on the hilum of the mature seed as a hilar cap over the hilar fissure (Fig. 10), but is only lightly attached along a short section of the edges of the fissure near the center of the hilum.

The hilum of mature varnishleaf ceanothus seeds is similar in some respects to that of legumes as described by Hyde (43) and Corner (16). Like seeds of Papilionaceae, varnishleaf ceanothus seeds possess a hilum with median groove and a short funiculus, but they do not have a counter-palisade layer at the hilum or a tracheid bar below the hilar fissure. Instead the hilum is sealed by a single

Figure 9. Young fruit showing vascular tissue extending from placenta through the funiculus into the ovule. X24.
(F.--funiculus; OW.--ovary wall; PS.--palisade layer; V.--vascular tissue).



Figure 10. Funiculus adhering to edges of the hilar fissure on
an almost mature varnishleaf ceanothus seed. X24.
(C.--cotyledon; E.--endosperm; EP.--epicotyl; F.--
funiculus; HF.--hilar fissure; PS.--palisade layer).



layer of palisade cells as in the Mimosaceae and Caesalpiniaceae. At the hilum, the light line lies deeper below the surface of the seed than in any other part of the seed coat. The palisade cells adjacent to the hilar fissure are gradually reduced in length, resulting in a lip-like arrangement with the edges of the fissure being closest to each other at the exterior surface of the seed (Fig. 11). In mature seeds, the hilar fissure apparently is sealed by opposing pressure of the two edges of fissure against each other. This seal is evidently sufficient to prevent penetration of moisture into the seed at the hilum--an important factor in maintaining impermeability of the seed coat. Beneath the sealed hilar fissure, the position occupied by a tracheid bar in the Papilionaceae is empty in varnishleaf ceanothus seeds; rupture of the vascular tissue as the seed matures leaves a space that extends from the closed fissure at the surface inward to the endosperm.

Approaching maturity, varnishleaf ceanothus seeds display two or three layers of regular, parenchymatous cells containing dark-colored deposits of undetermined materials beneath the palisade layer (Fig. 12). Beneath this layer and extending inward to the incompletely developed endosperm is a deep layer of large, clear, parenchyma. In the fully mature seed, endosperm almost completely fills the interior of the seed about the well-developed embryo, and the parenchymatous cells and disorganized remnants of the nutrient layer are collapsed between the endosperm and the base of the palisade layer (Fig. 13). At least some of deposited material in the

Figure 11. Longitudinal section of hilum. X109.
(HC.--hilar cap (funiculus); HF.--hilar
fissure).

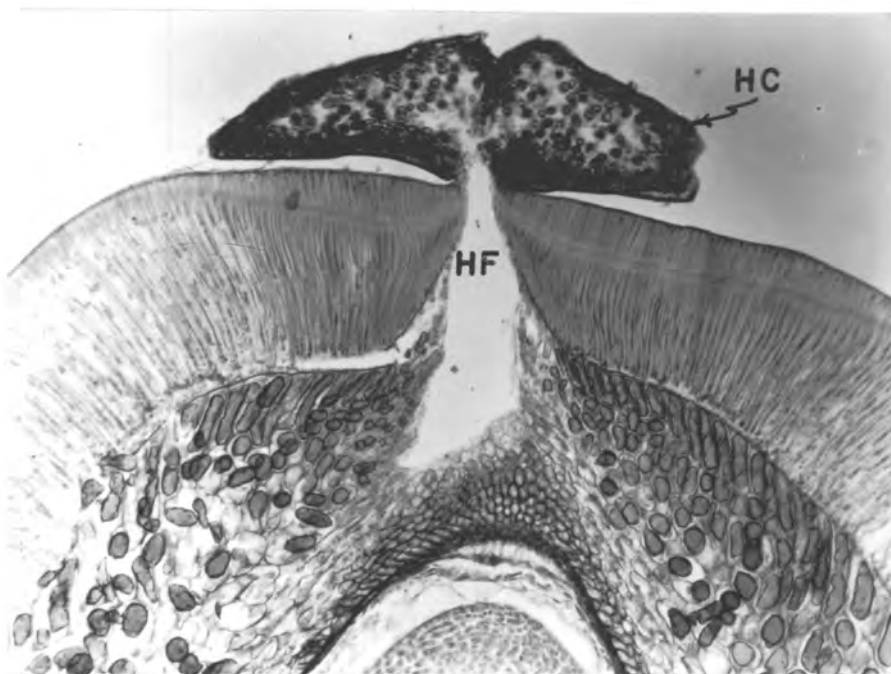


Figure 12. Longitudinal section of a nearly mature seed showing deposits in parenchyma beneath the palisade layer. X60. (D.--deposits; E.--endosperm; PS.--palisade layer).

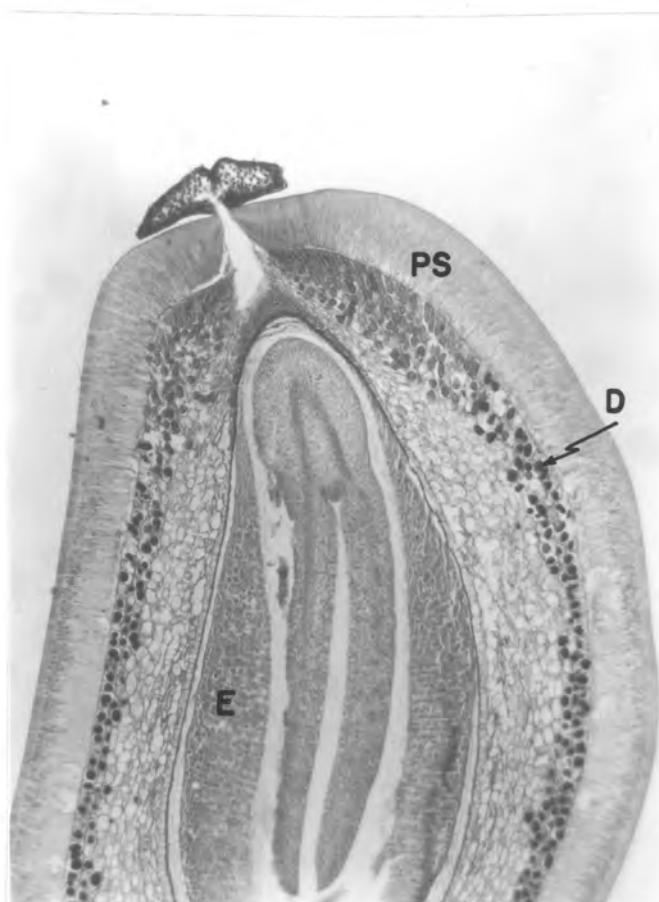
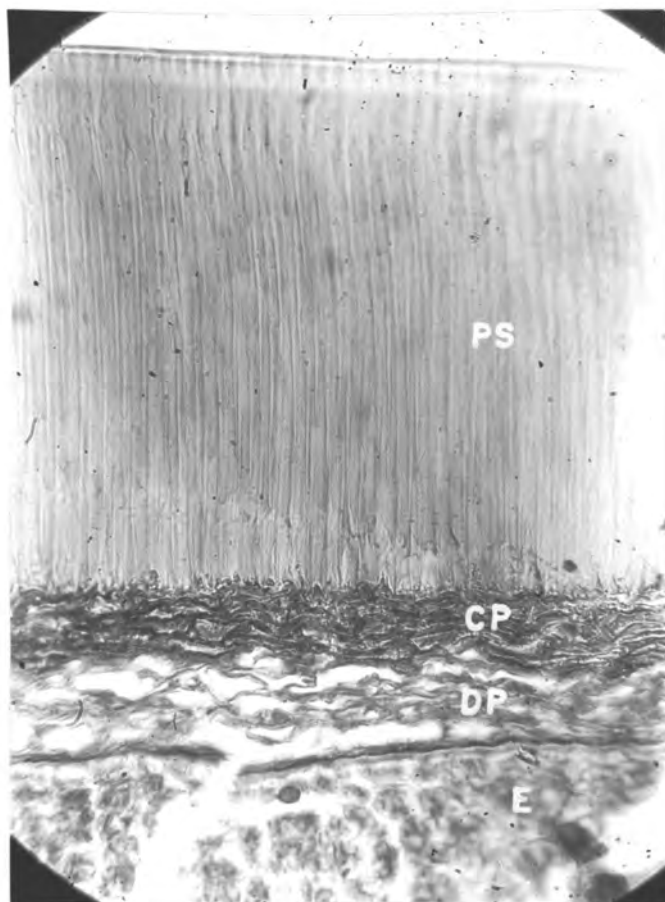


Figure 13. Cross-section through seed coat to endosperm
of a mature varnishleaf ceanothus seed. X265.
(CP.--collapsed parenchyma; DP.--disorganized,
collapsed parenchyma of nutrient layer; E.--
endosperm).



collapsed parenchyma directly beneath the palisade layer is pigmented, for when this is scratched away, that part of the seed coat becomes translucent.

Sorption Response of Treated Seeds

When heat-treated varnishleaf ceanothus seeds were examined with a microscope, it was found that the hilar fissure was open on seeds that had been subjected to temperatures known to stimulate germination; and the openings in the hilum appeared large enough to allow ready absorption of moisture from a humid atmosphere or from moist soil. An experiment was set up to determine whether this was the only portion of the seed rendered permeable by heat and to determine whether the heat effect on hard seeds is irreversible. Other treatments were also included to gain additional information on the response of mature seeds to changes in relative humidity of the ambient atmosphere.

Five samples of 31-month-old varnishleaf ceanothus seeds, each consisting of 200 seeds weighing about 1.4 g. wet weight, were pretreated as described below, placed in vials, and then subjected to controlled relative humidities. One sample was left untreated. The second sample was scarified by puncturing the chalazal end of the seed coat with a sharp dissecting needle. An effort was made to puncture the seed coat to the endosperm, but to leave the embryo undisturbed. The third sample was given a 10-minute heat treatment at 93° C. in air in an electric oven. Preliminary trials had shown that this treatment produced the heat effect without the secondary effects

of imbibition of moisture, swelling of seed contents, and splitting of some seed coats that occur when seeds are heated in water. The fourth sample was heat-treated in the same manner (dry air), but the hilum of each seed was immediately coated with a thin layer of vaseline using a small camel's hair brush and a binocular microscope. When placed in vials, each vaselined seed was carefully placed with forceps and small copper screens were inserted between successive layers of seeds to minimize spreading of vaseline from the coated hilums to uncoated portions of adjacent seeds. The screens prevented "nesting" of the seeds. The fifth sample was heat-treated in the same manner, but hilums were left uncoated until the end of the fourth week of the experiment. Each treatment was replicated four times.

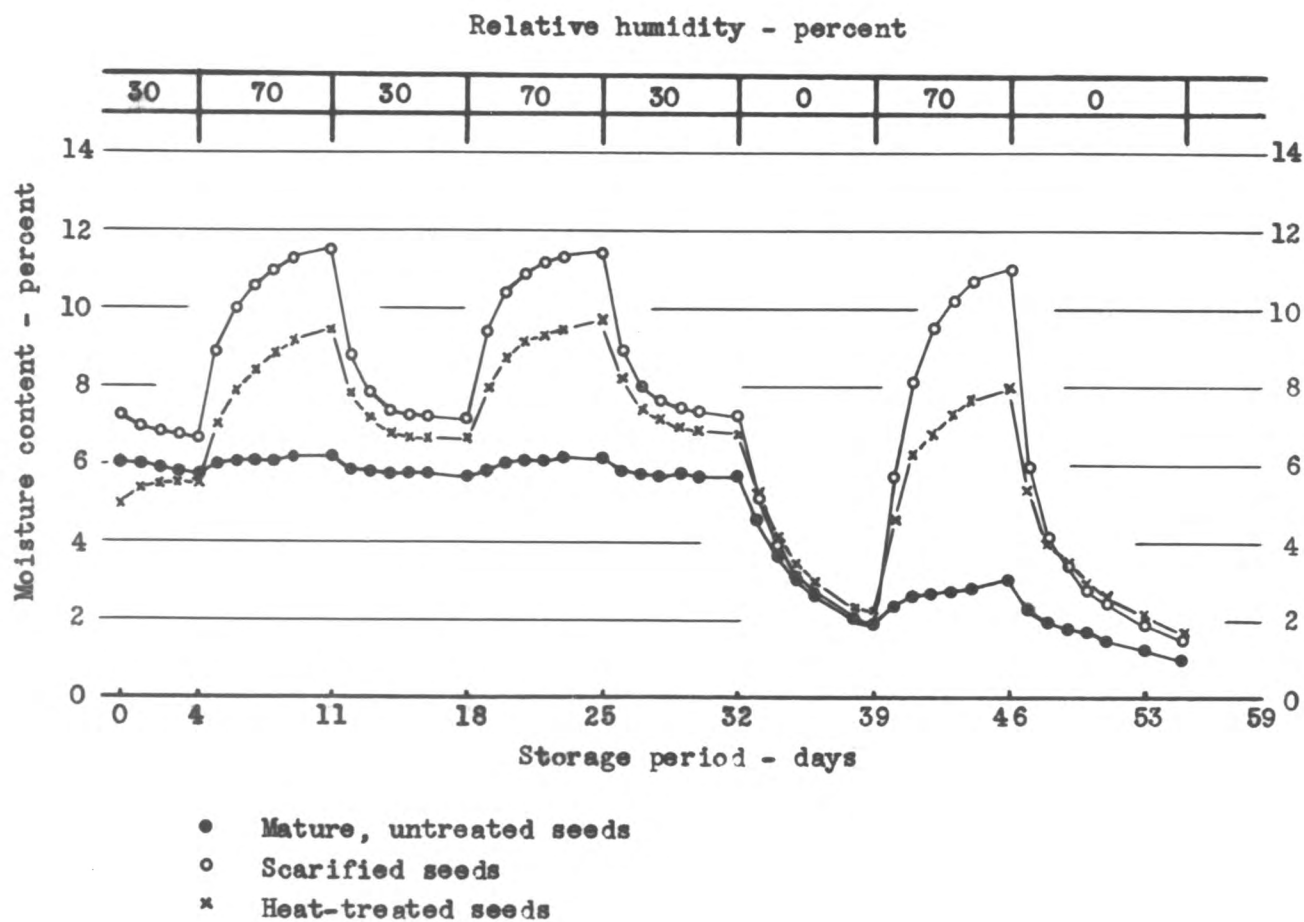
After the preparatory treatments, the open vials of seeds were exposed to controlled relative humidities in closed vessels in which sulfuric acid solutions were used to maintain atmospheric humidity at levels of 70 percent, 30 percent, and approximately 0 percent relative humidity. All samples were first allowed to come to equilibrium at 30 percent relative humidity, and then transferred successively to dessicators at 70, 30, 70, 30, 0, 70, and 0 percent relative humidity. They were allowed to remain one week in each dessicator; each vial being weighed daily and before each transfer. At the end of the seventh week, the seeds were dried for 8 hours in a vacuum oven at 85° C. and a vacuum of 29 inches of mercury. The vials were then removed, capped, cooled for 15 minutes in the 0 percent relative

humidity dessicator, and weighed to determine dry weight of the seeds. Seeds treated with vaseline were washed in petrol ether before drying in the vacuum oven.

Untreated hard seeds of varnishleaf ceanothus proved impermeable to moisture and did not imbibe moisture from or lose moisture to the atmosphere when transferred back and forth between the 30 and 70 percent relative humidity dessicators (Fig. 14). The slight increase in moisture content when in the 70 percent dessicator is attributed primarily to absorption by the hilar caps, for hilar caps separated from seeds proved hygroscopic when exposed to similar changes in a separate vial.

However, when the untreated mature seeds were exposed to 0 percent relative humidity--a lower relative humidity than any to which they had previously been exposed during treatment or in storage--the seeds responded by losing almost 4 percent moisture. This moisture was not regained when the dessicated seeds were transferred again to higher humidity (70%), but additional moisture was lost when they were again exposed to the extremely dry air. As in clover seeds (43), hilums of the untreated 31-month-old varnishleaf ceanothus seeds evidently possessed the ability to function as a hygroscopic valve--opening and allowing the seeds to lose moisture when exposed to low humidity, but closing and preventing reabsorption of moisture when again exposed to high humidity. This ability of 31-month-old seeds to lose more and more moisture when exposed to drier conditions than any previously experienced and to prevent reabsorption when

Figure 14. Changes in moisture content of varnishleaf ceanothus seeds exposed successively in dessicators at different relative humidities.



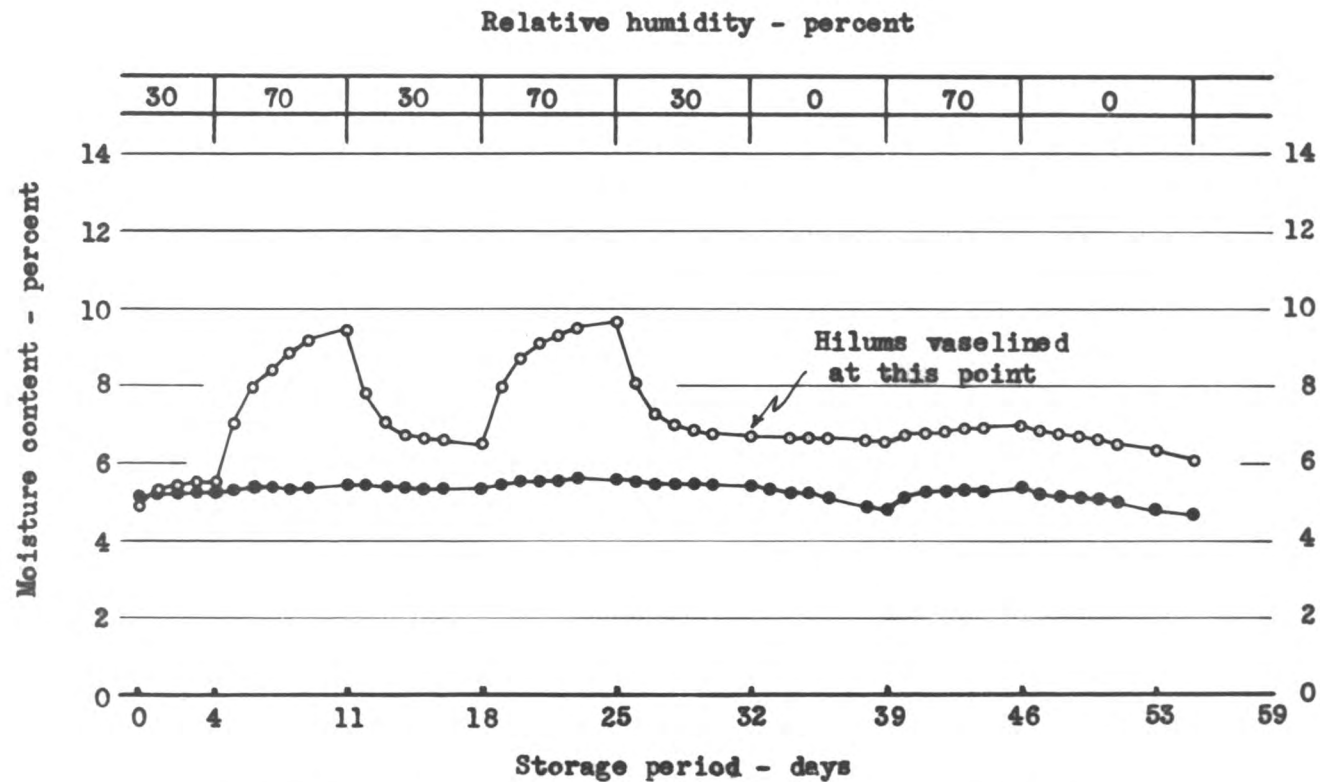
subsequently exposed to higher humidities can be of great survival value in nature. Since physiological processes take place in aqueous media, dessication may act to increase dormancy by reducing rates of respiration, conserving stored foods, and increasing longevity of the seeds after dissemination from the parent plant. Increased longevity, in turn, allows the seeds to survive longer periods of adverse conditions until more favorable conditions for germination and survival occur in nature.

Scarified seeds responded hygroscopically to changes in relative humidity, absorbing moisture in higher humidities and losing it in lower humidities (Fig. 14). Since absorption did not occur when unscarified hard seeds were exposed to higher relative humidities, it was concluded that the seed coats of varnishleaf ceanothus seeds are impermeable to moisture.

The heat-treated seeds also responded hygroscopically to all changes in relative humidity, following a pattern similar to that of scarified seeds (Fig. 14). Heat-treatment, therefore, was concluded to have rendered the seed coats permeable to moisture. Furthermore, the continued hygroscopic response of heat-treated seeds until the experiment was terminated after seven weeks, shows that the heat effect on varnishleaf ceanothus seeds is permanent and irreversible.

In contrast to the hygroscopic behavior of heat-treated seeds described above, heat-treated seeds on which the hilums were vaselined immediately after treatment did not gain or lose water with changes in humidity (Fig. 15). Heat, therefore, evidently affects only the

Figure 15. Changes in moisture content of varnishleaf ceanothus seeds
exposed successively in dessicators at different relative
humidities.



- Heated seeds; hilum vaserlined immediately after heating
- Heated seeds; hilum vaserlined on thirty-second day

hilum of hard seeds, rendering it permeable to moisture; while the rest of the seed coat is not affected and remains impermeable. The pattern of response of heat-treated seeds on which hilums were vaselined on the thirty-second day is further proof that this conclusion is correct, for these seeds responded hygroscopically to each change in relative humidity until the hilums were vaselined. After that, no further changes occurred in moisture content of the seeds.

Heat Effect on Hilar Fissure

Observation of open hilar fissures in heat-treated seeds in conjunction with the evidence above indicates that heat induces germination of varnishleaf ceanothus seeds by permanently opening the hilar fissures. Furthermore, this appears to be the only effect of heat on varnishleaf ceanothus seeds. Open fissures in a sample of heat-treated seeds averaged 0.02 mm. in width and 0.39 mm. in length (Figures 16 and 17). Size of the open fissures seems entirely adequate to permit passage of liquid water as well as humid air into the interior of the seed, where the moisture can be absorbed by the hygroscopic components of endosperm and embryo. After imbibition has taken place and the seeds have been suitably stratified, germination can occur.

Once the hilar fissure is opened by heat, the effect seems to be permanent and irreversible. Hilar fissures in one sample of varnishleaf ceanothus seeds were still open 45 months after heat treatment.

Figure 16. Hilar fissure of a mature varnishleaf ceanothus seed
in its normal, closed condition. The ragged edges
along the middle section of the fissure are remnants
of tissues by which the hilar cap (funiculus) was
attached to the hilum. X138.

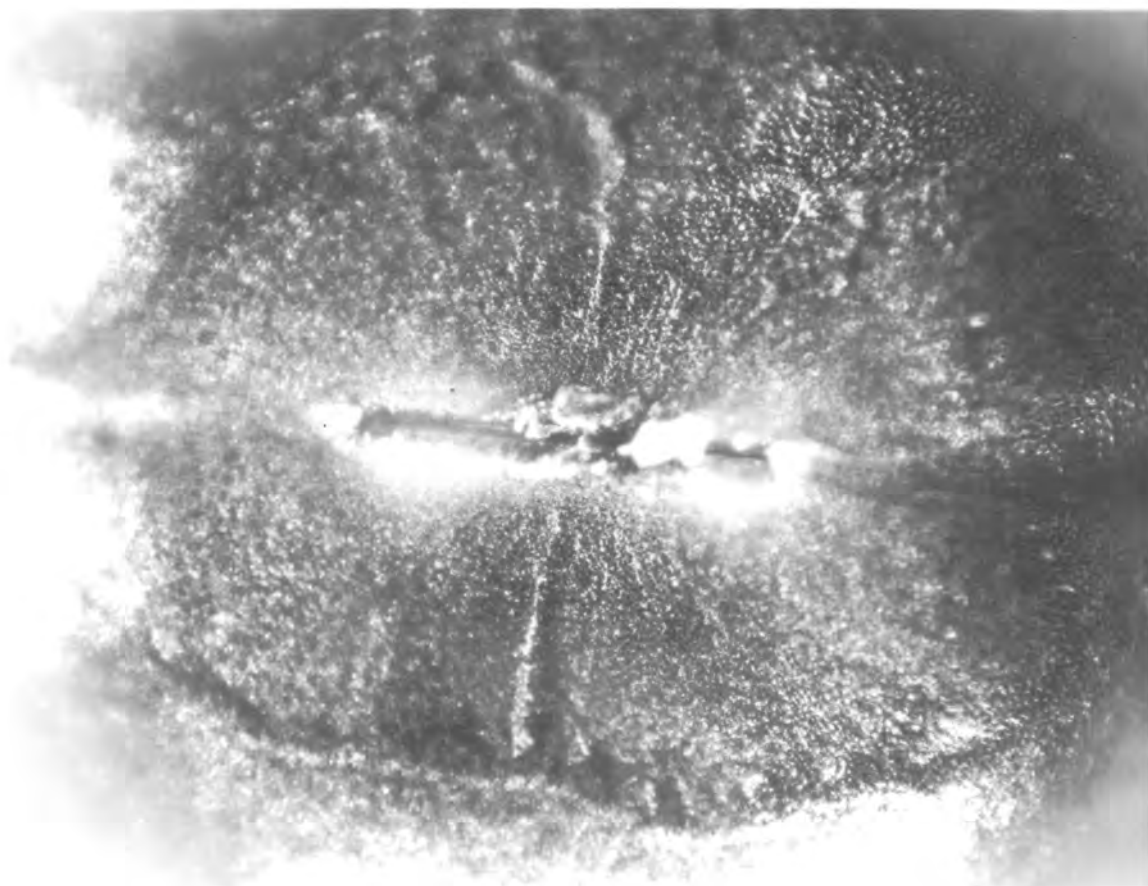
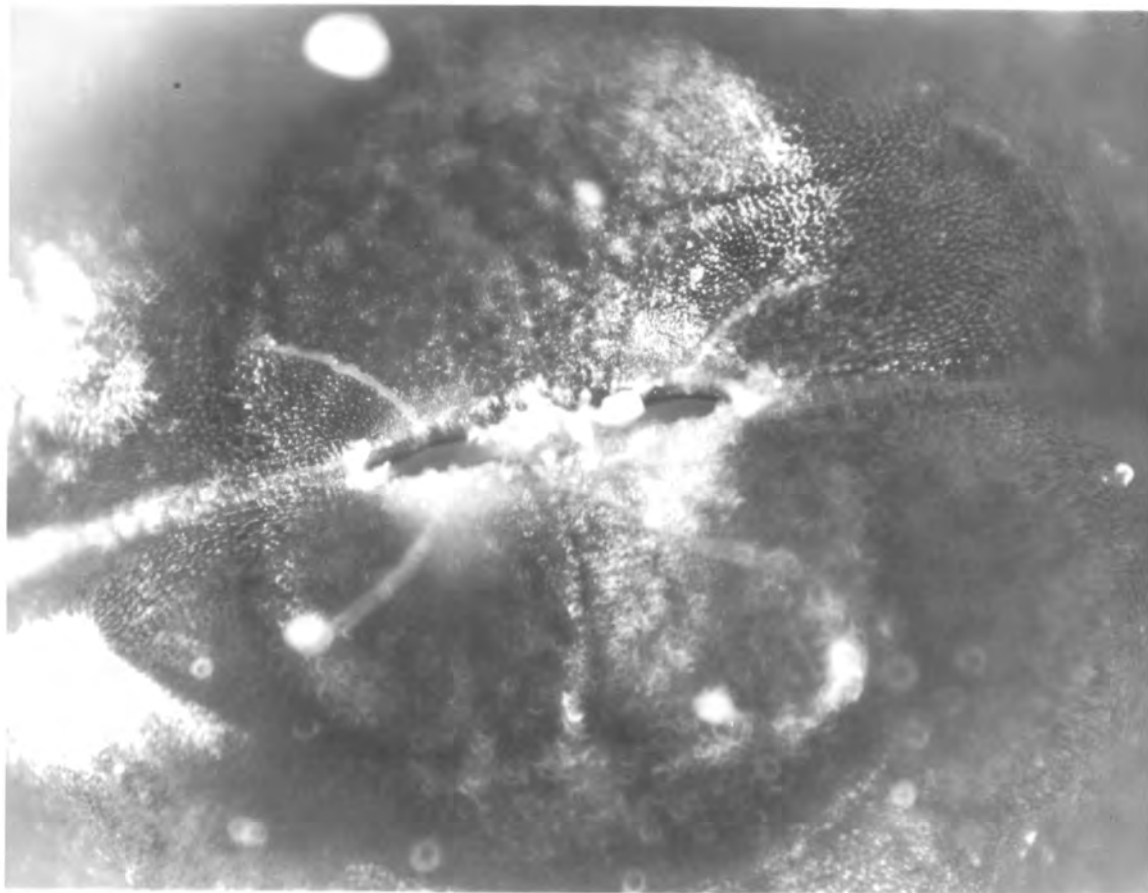


Figure 17. Hilar fissure opened after heat treatment of the seed
in a dry loam soil. X138.



FIELD STUDIES

Experimental results obtained in the laboratory often appear to be quite conclusive, but the significance seems to disappear when the investigator attempts to apply the information in the field. In the uncontrolled conditions of nature, the myriad combinations of climatic conditions, soils, vegetation, and wildlife, interacting and not interacting, supplementing and counteracting, can so confound results that interpretation becomes almost impossible. Yet field studies are a necessary step in biological research where results are to be applied in natural conditions. In this investigation, results of the initial laboratory experiments supported the original hypothesis that heat from prescribed burning of logging slash could stimulate germination of dormant varnishleaf ceanothus seeds in the soil. Therefore, a silvicultural investigation was designed to determine if this would actually occur under current forest practice on forest lands in southwestern Oregon.

Two stands of old-growth Douglas-fir (Pseudotsuga menziesii) in the Cascade Range were selected for intensive investigation of vegetation on the sites before logging and to determine the relationship between current slash disposal practices and germination of varnishleaf ceanothus seeds in the cuttings after logging and slash disposal. Both stands are located in the White Creek drainage on the Umpqua National Forest, 20 miles east of Roseburg, Oregon. White Creek is a tributary of Little River, which drains, in turn, into the North Umpqua river. Cutting No. 1, $12\frac{1}{2}$ acres in size, is located at

an elevation of 2800 feet above sea level on a gentle north slope; and Cutting No. 3, 36 acres, is at an elevation of 2000 feet on a moderate northeast slope. The former is located in the N.E. $\frac{1}{4}$, Sec. 29, T. 27 S., R. 1 W.; and the latter one mile distant in the S.E. $\frac{1}{4}$, Sec. 17, T. 27 S., R. 1 W., W.M.

Climatic conditions in the area are generally mild, with a short, dry summer and a long, wet winter season. Annual precipitation averages about 60 to 80 inches, most falling as rain.

Soils in the area are light brown to reddish brown clay loams with many shot-like concretions in the surface layer. Mottling indicative of poor drainage has been found in localized areas at depths of $1\frac{1}{2}$ - 2 feet, and a hardpan has been observed in some road cuts at a depth of 3 - 4 feet.

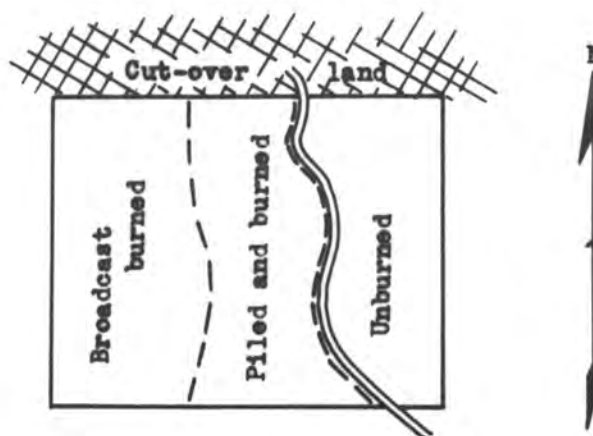
CONDITIONS BEFORE LOGGING

Both stands of old-growth Douglas-fir were very much alike, and the interiors of both stands were relatively undisturbed before this investigation began. The timber along the north edge and below Cutting 1 was logged during 1948 (Fig. 18); but there was no disturbance within the stand, and light and other physical conditions were relatively unaffected. The stand on Cutting 3, however, was disturbed to some extent when the timber on the east, west, and south sides was cut in 1948. This disturbance left the forest on Cutting 3 as a peninsula of timber extending southwestward into the cut-overs. In addition, a road right-of-way was cut through the southwest end of the stand, and two tractor skid trails were pushed into the timber below the road to remove a small number of dead trees scattered through the west end of the stand. Although light and other physical conditions were somewhat changed along the perimeter of these disturbed areas, conditions within the 38-acre peninsula of timber appeared to be largely those of a virgin stand of old-growth Douglas-fir timber except in the immediate vicinity of the disturbance.

The vegetation in both stands was stratified into three fairly distinct layers. The uppermost layer was composed of trees such as Douglas-fir, sugar pine, western hemlock, and western redcedar. Beneath this was an intermediate layer of shrubs and small trees including vine maple, golden chinkapin, Pacific dogwood, and grand fir. The lowest layer near the ground consisted of low shrubs and herbs typified by salal, Cascades mahonia, vanilla leaf, Oregon oxalis, and

Figure 18. Slash disposal subdivisions in White Creek cuttings 1 and 3.

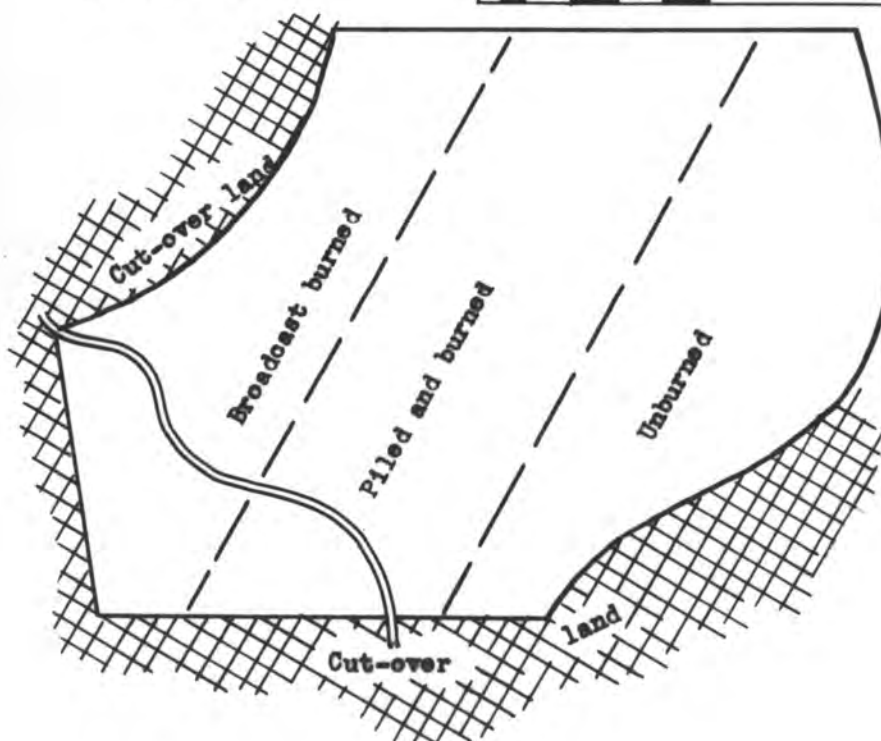
Cutting No. 1



Scale: Hundreds of feet

Cutting No. 3

0 1 2 3 4 5 10



other herbaceous species.

Tree Layer

Large old-growth Douglas-firs were by far the most abundant species in the stands on both areas (Figs. 19 and 20), but dominance was shared with western hemlock (Tsuga heterophylla) and a few scattered sugar pines (Pinus lambertiana). Understory trees included species commonly associated with Douglas-fir, such as: western redcedar (Thuja plicata), grand fir (Abies grandis), Pacific yew (Taxus brevifolia), Pacific dogwood (Cornus nuttallii), golden chinkapin (Castanopsis chrysophylla), and incense-cedar (Libocedrus decurrens).

Cruised timber volumes on Cutting 1 included 962,000 board feet of Douglas-fir and sugar pine and 22,000 bd. ft. of western hemlock and other merchantable species; a total of 984,000 bd. ft. or an average merchantable timber volume of approximately 78,700 bd. ft. per acre. The stand on Cutting 3 had a slightly lower merchantable volume per acre. Cruised volumes indicated the presence of 2,156,000 bd. ft. of Douglas-fir and sugar pine and 61,000 bd. ft. of western hemlock and other species; a total of 2,217,000 bd. ft. or an average merchantable volume of about 61,600 bd. ft. per acre.

The cruise figures are not truly indicative of relative stand density in an ecological sense, but they are of interest to foresters and others who understand the considerations applicable to such data. Living decayed trees and portions of trees, trees below merchantable size, and non-merchantable species are not reflected in the stated volumes; although such trees do affect the amount of light reaching

Figure 19. Dense forest of old-growth Douglas-
fir and associated species on Cut-
ting 1 before logging.



Figure 20. Road right-of-way through old-
growth Douglas-fir forest on
Cutting 3 before logging.



understory shrubs and herbaceous vegetation and compete with these plants for soil moisture and nutrients.

Of more value are the comparisons presented in the phytographs (Fig. 21). Dominance of Douglas-fir is clearly shown by fact that almost 44 percent of the stems were Douglas-firs of large diameter represented on every one of the 72 one-fifth acre plots sampled in the two stands. Although western hemlock was also fairly well distributed throughout both stands, the median diameter of the hemlock stems was much smaller than that of Douglas-fir and represented only a small percentage of the basal area in these stands. Sugar pines were of large diameter, but were infrequent in occurrence in both stands. Western redcedar were more numerous than sugar pine, but were not as abundant or as well distributed through the stand as western hemlock. Pacific yew, Pacific dogwood, and golden chinkapin were sparsely distributed throughout the understory of both stands. Together, the trees produced almost a complete canopy that cast a moderately dense shade over the entire understory.

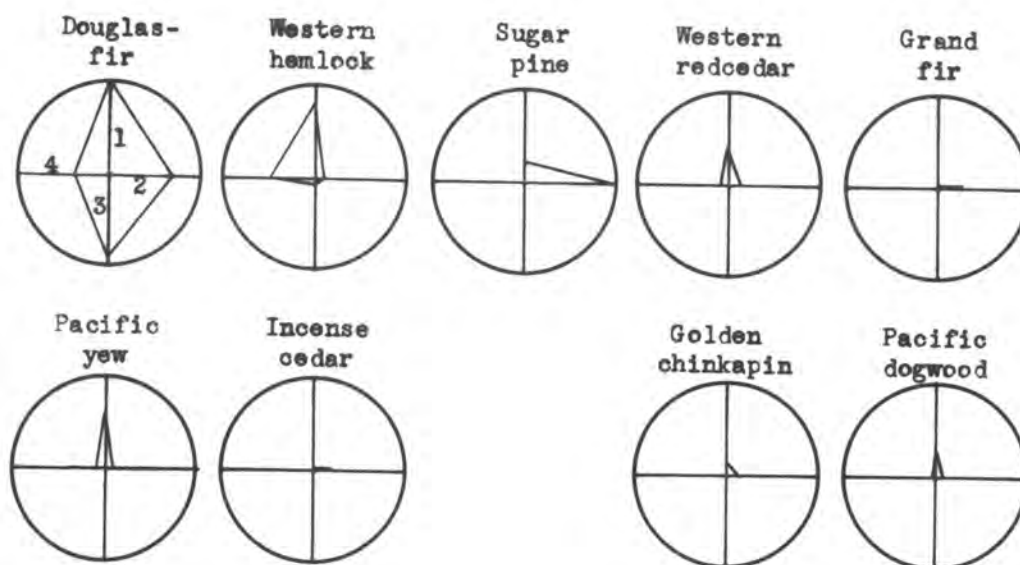
Ring counts on stumps later showed that most of the large old-growth Douglas-firs were between 250 and 325 years of age with only a few trees of greater age. Age class distribution was similar in both stands.

Shrub Layer

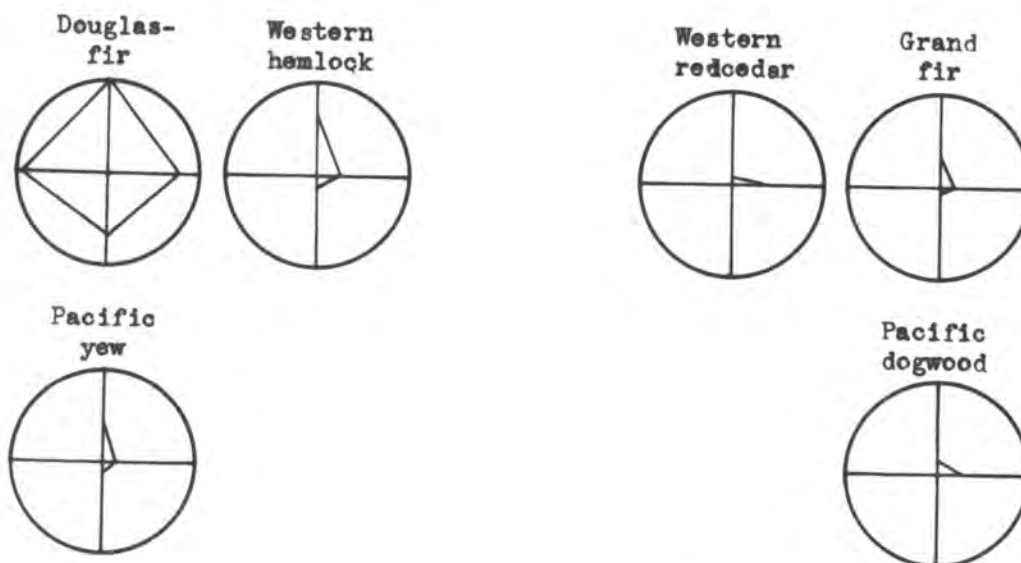
At least 16 different species were represented in the shrub layer of the two stands, although only 12 of these were present on the 120 one-milacre plots sampled. Cascades mahonia, salal, and

Figure 21. Phytographs showing the relative importance of tree species in the stands on White Creek cuttings 1 and 3 before logging.

Cutting No. 3



Cutting No. 1



Radius 1, percentage frequency; Radius 2, median diameter at breast height from 0 to 60 inches; Radius 3, percentage of total basal area; Radius 4, percentage of all tree stems in the stand. The inner end of each radius represents the absence of the assigned sociological value.

vine maple were by far the most abundant shrubs and were almost universally distributed throughout the two stands (Table 4). These species were supplemented in the shrub layer by golden chinkapin, snow dewberry, and grapeleaf California dewberry, which also were well-distributed throughout the stands but were less abundant than the three species mentioned above. Salal and Cascades mahonia in combination with golden chinkapin, various Rubus spp., and herbaceous species such as deerfoot vanilla-leaf formed a low ground cover under the taller, lacy canopy of vine maple (Fig. 22). In turn, all of these understory species were almost constantly in a fairly dark shade cast by the deep canopy of the tree layer.

Foliage and stems of vine maple provided a higher percentage of the ground cover than did salal and Cascades mahonia, although less widely distributed than the latter species. Together, vine maple and salal provided a far higher percentage of ground cover than all other shrub species combined. As a result of habit of growth and size and distribution of foliage on stems, such species as Cascades mahonia and grapeleaf California dewberry did not produce a ground cover in proportion to their abundance and widespread distribution in the shrub layer.

No mature varnishleaf ceanothus shrubs of seed-producing size were found in the understory of either stand. However, five small seedlings, ranging from 3 to 5 years in age and all less than 20 inches tall, were found in a skid trail in Cutting 3; and one somewhat older shrub, approximately 3 feet tall, was also found in the

Table 4.--Frequency and cover of shrub species on sample plots in the stands of old-growth Douglas-fir on cuttings 1 and 3 before logging^{1/}

Botanical name	Common name	Frequency ^{2/}	Ground cover ^{3/}
		Percent	Percent
<u>Acer circinatum</u>	Vine maple	79	29.7
<u>Gaultheria shallon</u>	Salal	90	19.7
<u>Mahonia nervosa</u>	Cascades mahonia	91	7.2
<u>Castanopsis chrysophylla</u>	Golden chinkapin	35	4.5
<u>Rubus nivalis</u>	Snow dewberry	18	0.3
<u>Rubus ursinus</u> var. <u>vitifolius</u>	Grapeleaf California dewberry	20	1.3
<u>Vaccinium parvifolium</u>	Red whortleberry	8	0.2
<u>Ceanothus velutinus</u> var. <u>laevigatus</u>	Varnishleaf ceanothus	1	T
<u>Garrya Fremontii</u>	Fremont silktassel	1	T
<u>Rubus leucodermis</u>	Whitebark raspberry	1	T
<u>Rhododendron macrophyllum</u>	Coast rhododendron	1	T
<u>Cornus nuttallii</u> ^{4/}	Pacific dogwood	7	1.0

^{1/} Common snowberry (Symphoricarpus albus), western thimbleberry (Rubus parviflorus), baldhip rose (Rosa gymnocarpa), and bitter cherry (Prunus emarginata) were also present in the understory, although none of these were found on the 120 one-mileacre plots upon which these figures are based.

^{2/} Percentage of plots containing the designated species.

^{3/} Weighted average of surface area covered by foliage of the designated species in the two cuttings.

^{4/} Seedlings and saplings of C. nuttallii were included in the shrub layer.

Figure 22. The shrub layer in both stands commonly consisted of a low cover of salal and Cascades mahonia, golden chinkapin, and various Rubus spp. under a taller, lacy canopy of vine maple.



road right-of-way. No other varnishleaf ceanothus seedlings or shrubs were observed anywhere else within the stands on Cutting 3 or Cutting 1. It is notable that both the seedlings and the small shrub in Cutting 3 were in locations directly exposed to solar radiation during the hottest part of the day, where insolation could have raised soil temperatures above the critical level for stimulating germination of ceanothus seeds in the surface soil. This lack of varnishleaf ceanothus under dense stands of old-growth Douglas-fir, except at the south edges of reserved stands between cuttings and on sites exposed by disturbance to direct solar radiation, is generally typical of conditions in southwestern Oregon.

Herbaceous Species

In the course of the mid-summer sampling of trees and shrubs, a list was compiled showing herbaceous species found on 1-square-foot plots in the center of each of the 120 milacre shrub plots (Table 5). Although undoubtedly incomplete, this list is included as additional descriptive evidence of the stands where the field experiments were conducted.

Table 5.--List of herbaceous species found in the under-
story of the stands of old-growth Douglas-fir
on cuttings 1 and 3 before logging

<u>Botanical</u>	<u>Common Name</u>
<u>Achlys triphylla</u>	Deerfoot vanillaleaf
<u>Adenocaulon bicolor</u>	American adenocaulon
<u>Anaphalis margaritacea</u>	Common pearleverlasting
<u>Anemone deltoidea</u>	Threeleaf anemone
<u>Campanula scouleri</u>	Scouler's campanula
<u>Chimaphila umbellata</u> var. <u>occidentalis</u>	Western pipsissewa
<u>Coptis laciniata</u>	Cutleaf goldthread
<u>Disporum smithi</u>	Smiths fairybells
<u>Epilobium angustifolium</u>	Fireweed
<u>Epilobium minutum</u>	Small-flowered willow-herb
<u>Equisetum</u> sp.	Horsetail
<u>Galium triflorum</u>	Sweetscented bedstraw
<u>Goodyera (Peranium) decipiens</u>	Western rattlesnakeplantain
<u>Hieracium albiflorum</u>	White hawkweed
<u>Linnaea borealis</u> var. <u>americana</u>	American twinflower
<u>Lotus americanus</u>	Spanishclover deervetch
<u>Monotropa uniflora</u>	Indianpipe
<u>Oxalis oregana</u>	Oregon oxalis
<u>Polystichum munitum</u>	Western swordfern
<u>Psoralea physodes</u>	Californiatea scurfpea
<u>Pteridium aquilinum</u> var. <u>pubescens</u>	Western bracken
<u>Pyrola bracteata</u>	Large pyrola
<u>Pyrola picta</u>	Whitevein pyrola
<u>Smilacina racemosa</u>	Feather solomonseal
<u>Thermopsis gracilis</u>	Slender thermopsis
<u>Tiarella unifoliata</u>	Coolwort foamflower
<u>Trientalis europaea</u> var. <u>latifolia</u>	Western starflower
<u>Trillium ovatum</u>	Pacific trillium
<u>Vancouveria hexandra</u>	Inside-out flower
<u>Viola glabella</u>	Pioneer violet

CEANOTHUS SEEDS FROM DUFF AND SURFACE SOIL

Although mature, seed-bearing shrubs of varnishleaf ceanothus were not present in the understory of either stand before logging the possibility existed that dormant but viable ceanothus seeds might be present in the duff or surface soil. Therefore, duff and surface soil were sampled throughout the two stands to determine whether varnishleaf ceanothus seeds were present, and--if present--to learn whether the seeds were viable.

Collection and Preparation of Samples

Sixty samples of duff and surface soil were collected during late June, 1959, from the forest floor of the two stands. The samples were taken at random intervals on three lines through each of the two areas--thirty from each stand. A specially-constructed sampling frame with hinged front (its 11.2-inch inside measurement representing 1/50,000th acre), was designed to insure accuracy and uniformity in sampling. In use, the rigid, square frame was centered on the point to be sampled and pinned in place with 3 heavy wire pins to prevent movement during removal of duff and surface soil. Next, the soil in front of the frame was excavated to a depth of at least 6 inches, and a large knife was used to cut through the litter and duff to the surface soil around the inside of the frame. Then the hinged front of the frame was unlatched and opened; and the duff, litter and soil formerly under the front section were removed, leaving a smooth, vertical soil face to a depth of 6 inches. Duff and

litter down to mineral soil were carefully removed from inside the frame and placed in labeled cotton bags for later processing. Loose material on the soil surface was also brushed off and included in the duff sample. Although this meant that some loose soil was invariably included, it insured that any ceanothus seeds shaken out during removal of duff and litter were recovered and included in the duff sample. Finally, the mineral soil to a depth of approximately 4 inches was removed and placed in a separate labeled cotton bag.

Both duff and surface soil samples were processed to reduce their size before germination in the greenhouse. Duff samples were reduced with a "Clipper Grain, Seed, and Bean Cleaner" using methods similar to those described by Stone and Holt (79) and Quick (68). All material discarded during processing was first carefully examined for varnishleaf ceanothus seeds. The reduced samples were then stored in labeled paper sacks at room temperature until germinated in the greenhouse.

The soil samples could not be satisfactorily reduced with the "Clipper" cleaner. Instead, a special set of screens was constructed; and the samples were reduced by a series of screenings, soakings, and washings to prepare concentrates that would contain any varnishleaf ceanothus seeds present in the original soil samples.

Seeds in Duff and Soil Samples

Total area of the forest floor represented in the sixty samples was only 52.27 square feet out of a total area of approximately 2,134,440 square feet in the two cuttings. In other words, this

represented a 0.00245 percent sample of the soil area in the two cuttings--an exceedingly small sample, but as large as could be practicably handled. Considering habit and size of the crowns of mature varnishleaf ceanothus shrubs, germination of only one seed per 100 square feet of surface area (436 per acre) would be sufficient to produce a complete ceanothus cover in the cutover areas. Since the entire sample was only 52.27 square feet, the presence of only 1 viable varnishleaf ceanothus seed in the samples would indicate the presence of sufficient residual seed in the duff or surface soil to produce a dense cover of ceanothus in the cuttings. It was considered possible that one or more seeds might be present in the sample and, although viable, fail to germinate later in greenhouse tests designed to detect viable seeds in the soil and duff concentrates. Therefore, it was deemed desirable to make an ocular examination of some of the concentrates to see if varnishleaf ceanothus seeds were present and, if present, to gain some idea of their number.

Twenty soil concentrates and 20 duff concentrates were examined piece by piece. Varnishleaf ceanothus seeds were found in 9 of the 20 soil samples (45%), but none were found in the duff samples (0%). Seeds were found in more soil samples from cutting 1 (50%) than from Cutting 3 (40%). The number of seeds found in the samples indicated the presence of approximately 102,500 seeds per acre in the forest floor of the two stands.

Germination Before Heat Treatment

Each duff and soil sample was planted in specially-prepared soil

in a separate one-foot-square flat and subjected to proper conditions for germination in a greenhouse. First, soil fractions that would pass through a 20-mesh screen were sieved from a silty sand alluvial soil and from Aiken silty clay loam, a forest soil with a high content of kaolinite clay. Prior experience had shown that varnishleaf ceanothus seeds are retained in a 14-mesh screen, and Quick (1956) stated that nearly all ceanothus seeds are retained in a 20-mesh screen. Therefore, the sieved material should have contained no ceanothus seeds and certainly no varnishleaf ceanothus seeds. Both sieved soil fractions were autoclaved for 5 hours at 9 pounds steam pressure (about 114° C.) to kill as many weed and brush seeds as possible and to further reduce any chance that these soil fractions might contribute viable ceanothus seeds in the germination tests. After sterilization, the soil fractions were mixed together--1 part silty clay loam and 2 parts silty sand. The clay was added to give the soil heat transmission and retention characteristics resembling those of most forest soils. One hundred and twenty flats were filled with this autoclaved soil mixture to within one inch of the top, and a table of random numbers was used to assign each soil and duff sample to a numbered flat. Each duff and soil sample was then spread evenly over the surface of the appropriate flat and covered with a 3/8-inch layer of the soil mixture. Finally, soil in the flats was soaked with a fog nozzle, allowed to drain, and watered as needed during the following 81-day germination period in the greenhouse. Temperatures in the greenhouse were maintained at 75° F. during the

day and 55° F. at night, and the flats were examined 4 or 5 times each week for seedlings.

Although varnishleaf ceanothus seeds were known to be present at least in the soil concentrates, none of the seeds germinated in either the soil samples or the duff samples during this initial 81-day germination period in the greenhouse.

At the end of the germination period, soil in the flats was allowed to dry out for 41 days in the greenhouse. During this time, one varnishleaf ceanothus seed germinated in one of the soil samples. After drying, the 120 flats were moved to the laboratory for heat treatment.

Germination After Heat Treatment

In the laboratory, a narrow trench was dug into the seed layer from a slit in the side of each flat to the center of the flat. A thermocouple was inserted in the trench with the thermocouple bead inside the upper part of the layer of duff or soil concentrate and the lead extending out through the slit. Soil from the trench was then used to cover the thermocouples and leads to the same depth as the rest of the flat, and the disturbed soil was firmed at the surface. A battery of four 150-watt Reflector Spot lamps were arranged over each flat so that the surface was relatively evenly illuminated, and these were then used to heat the soil and seed concentrates to a temperature of 80° C. in a 10 to 15 minute heating period. Temperatures of the thermocouples in the soil were automatically registered on a Brown Electronik recording potentiometer that provided a

periodic record of changing soil temperatures and showed when the desired temperature was reached at the depth of the soil or duff concentrate. The lamps were then shut off, the flats were allowed to cool to room temperature, again thoroughly watered with a fog nozzle, drained, and stratified for two months in a refrigerated room at the Oregon State Forest Nursery. After stratification, the flats were moved back into the greenhouse and again provided suitable conditions for germination. Periodic counts were made of seedling emergence during the next two months.

Emergence after heat treatment was equivalent to germination of 131,000 varnishleaf ceanothus seeds per acre. This seems conclusive evidence that dormant but viable varnishleaf ceanothus seeds were present in the surface soil of these stands, where no mature, seed-bearing shrubs of this species were present in the understory. In agreement with results of the ocular examination of soil samples, emergence of seedlings was also observed in a greater number of samples from Cutting 1 (43%) than from Cutting 3 (33%). And finally, the abundant germination after heat treatment in contrast to the almost complete lack of germination before heat treatment verifies results of the laboratory experiments in which heat treatments were shown to induce germination of varnishleaf ceanothus seeds.

Although the seed concentrates were not stratified before the initial germination period in the greenhouse, germination after heat treatment cannot be attributed to the period of stratification after heating. The soil samples were collected in the latter half of June,

1959--during the flowering period of varnishleaf ceanothus and long before maturation and dissemination of seeds would occur in nature. Therefore, seeds in the soil samples had to be at least one or more years old, and must have been present in or on the soil throughout the moist, cold weather of the preceding winter. The seeds in the soil samples, therefore, had been subjected to conditions suitable for stratification before the samples were collected; yet they did not germinate until after heat treatment.

LOGGING AND SLASH DISPOSAL

Logging

The stand on Cutting 1 was tractor-logged in September 1959; but logging on Cutting 3 was not finished until late March, 1960. The southwest corner above the road in Cutting 3 was logged with tractors, and the large area northeast of the road was yarded with a high-lead cable system. On the gentle slopes within these cuttings, there was no need to cut special tractor skid roads; so there was little difference in appearance between areas logged by tractors and that logged with the cable system.

Slash Disposal

Under current forest practice in the Douglas-fir Region of western Oregon and Washington, logging slash--branches and unmerchantable tops of trees, broken and cull logs, decayed trees, and unmerchantable small trees--is usually destroyed by burning. Disposal of slash has two prime objectives: (1) to reduce the fire hazard resulting from presence of the dry highly-inflammable logging debris, and (2) to expose the mineral soil seedbed most suitable for natural regeneration of Douglas-fir. Broadcast burning, the most common method of slash disposal, consists of burning the debris where it falls and is left during logging. Less frequently, slash is mechanically piled with tractors before burning--a method that is somewhat more expensive and practicable only on gentle slopes.

When the two stands were first selected for investigation of

the relationship between slash disposal and germination of varnish-leaf ceanothus seeds in the cuttings, each was subdivided into three parts of approximately equal area (Fig. 18). Logging slash in the two exterior subdivisions was allowed to remain where it fell during logging (Fig. 23). The slash on one of these exterior subdivisions in each cutting was broadcast burned; that on the other was left unburned. In the center subdivision of each cutting, a TD-24 tractor equipped with a 5-toothed Allied brush blade was used to pile the logging slash in windrows before burning (Fig. 24). Scarification of the soil was avoided in order to minimize movement of soil into the windrows where it would result in smoldering fires instead of quick, clean burning of the slash. This precaution also reduced the possibility that varnishleaf ceanothus seeds in the soil would be brought to the surface, and that seeds in the surface soil would be windrowed with the slash and destroyed in the fires.

Logging slash on the Broadcast Burn and Pile-and-Burn subdivisions of Cutting 3 was burned on Friday, October 14, 1960. One-third of an inch of rain fell on this cutting on Tuesday and Wednesday, but no precipitation was recorded on Thursday. Although this allowed almost two days of dry weather before burning, slash was still damp when burning began; and fires in the broadcast burned subdivision had to be forced in all but the heavier concentrations of slash. By mid-afternoon, heat from the fires had dried slash between the concentrations to the point where it would carry fire, and the fires burned through many of the areas of light and medium slash that were

Figure 23. Undisturbed logging slash before burning in a
broadcast burn subdivision of Cutting 3.



Figure 24. Mechanically-piled logging slash before burning in Cutting 3. Note that a large percentage of the soil surface will not be exposed to fire when the windrows are burned.



difficult to ignite earlier. No such difficulty was encountered in the windrowed slash. The piled slash was readily ignited and burned well.

Slash on Cutting 1 was not burned until several weeks later, and a moderately heavy rain began to fall after ignition. The piled slash burned readily despite the rain, but lighter depositions of slash became damp and did not burn well in the broadcast-burned subdivision. As a result, destruction of logging slash in the broadcast burned subdivision of Cutting 1 was not as complete as in Cutting 3.

Soil Temperatures During Slash Burning

Before logging slash was burned on Cutting 3, thirty simple pyrometers were installed in the soil under light, moderate, and heavy concentrations of slash in the Broadcast Burn subdivision to measure maximum soil temperatures attained at depths up to 3 inches below the surface during burning. Eleven more were installed under windrowed slash in the Pile-and-Burn subdivision. The pyrometers consisted of Tempilaq strips painted on thin sheets of mica and covered with sheets of asbestos as described by Fenner and Bently (31). Melting points of the Tempilaq strips were 150, 200, 250, 350, 450, 550, 650, 750, 950, and 1150 degrees Fahrenheit. Each pyrometer was carefully inserted in the soil with the mica sheet pressed against a vertical soil face that was disturbed as little as possible during insertion.

Where light slash was burned in Cutting 3, a thin layer of

white ash was generally found over a small amount of charred but recognizable litter on the soil surface. Almost invariably, none of the organic matter was burned out of the soil, and the soil was still moist at the surface when the pyrometers were extracted.

Burning medium concentrations of logging slash usually consumed all duff and litter and left a $\frac{1}{2}$ - to 1-inch deep layer of white ash on the soil surface. In a few cases, organic matter at depths of $\frac{1}{4}$ to $\frac{1}{2}$ inch below the soil surface was charred or consumed in the fire; and some drying of the surface soil was observed.

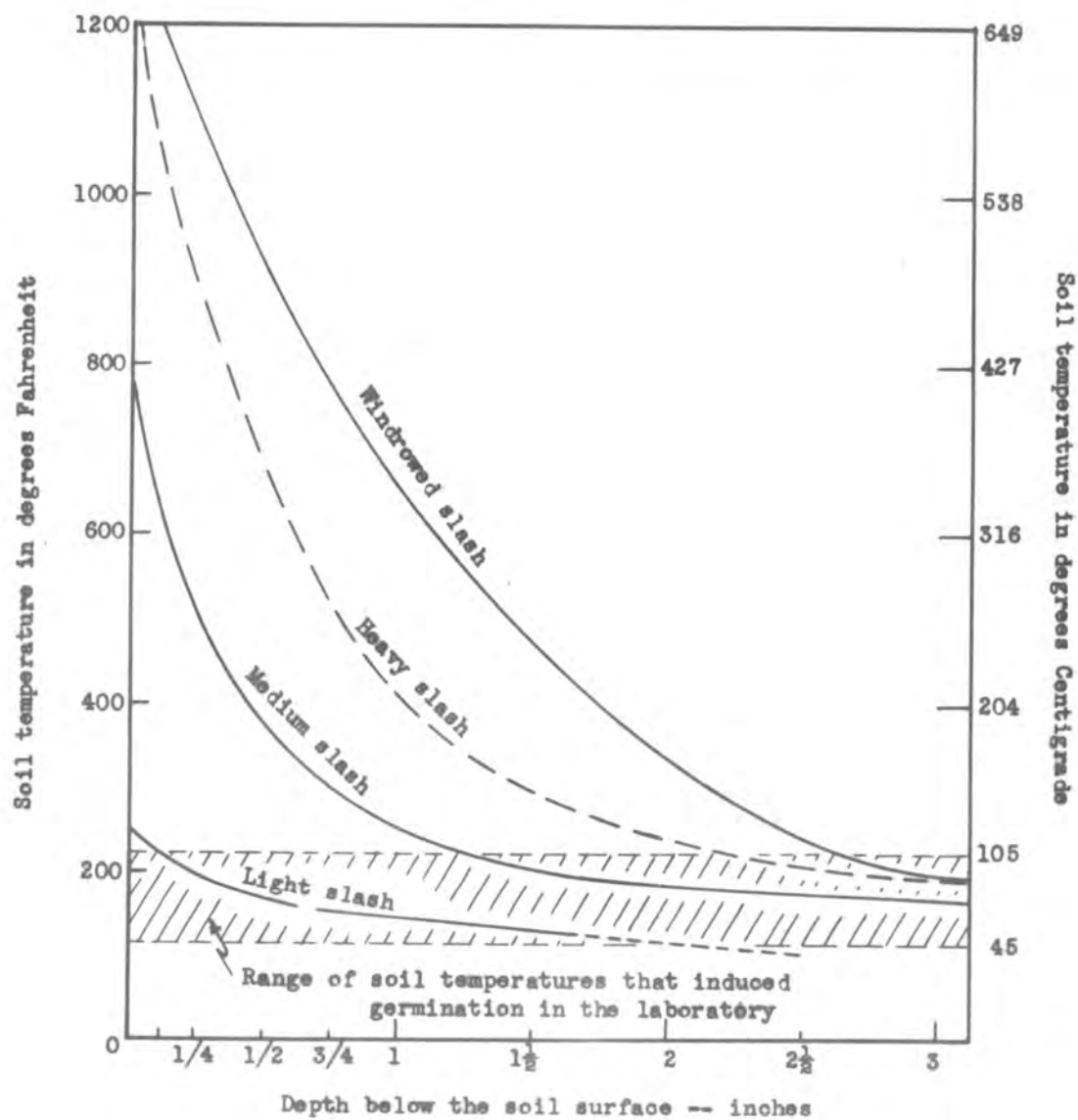
Where heavy concentrations of slash were burned, all organic matter above ground was consumed, leaving a $\frac{1}{2}$ - to 1-inch layer of ash on the soil surface. In addition, organic matter in the soil at depths up to 2 inches below the surface was often consumed or charred in the fires. In many cases, the soil was incinerated to a depth of $\frac{1}{4}$ to $\frac{1}{2}$ inch, leaving a loose mass of clinker-like fused particles of mineral soil on the surface.

Windrowed slash produced the highest soil temperatures, and resulted in the greatest destruction of organic matter within the soil. Generally all litter on the surface was consumed under the piled slash, and often only a light sprinkling of ash was left on incinerated soil. Loose, burned-out soil was more prevalent where windrowed slash was burned than where heavy concentrations of slash were burned in the broadcast-burned subdivision. In many places under the windrows, the loose, dry mass of brittle, burned out soil exceeded 6 inches in depth.

As expected, soil temperatures increased directly with amounts of logging slash consumed during burning (Fig. 25). Within the 3-inch depth sampled by the pyrometers in the broadcast-burned subdivision, soil temperatures low enough to induce germination of varnishleaf ceanothus seeds (45° to 105° C.) were registered only under light and medium concentrations of slash. Under light slash, soil temperatures that would induce germination were registered from just beneath the surface to depths of 3 inches below the surface, with optimum temperatures generally at depths of $1/8$ inch to about 1 inch below the surface. Under medium slash, soil temperatures that would induce germination were generally attained from about 1 to 3 inches below the surface, with optimum temperatures at 1 inch to 2 inches below the surface. Under heavy concentrations and windrowed slash, soil temperatures were generally in the lethal range at depths up to $2\frac{1}{2}$ or 3 inches below the surface.

Adams (1) recently determined that the most favorable planting depths for seeds of Ceanothus integerrimus, C. Lemmonii, and C. cuneatus in exposed sites are 1, $\frac{1}{2}$ to 1, and 1 to $1\frac{1}{2}$ inches below the surface, respectively. Although the best planting depth has not been determined for varnishleaf ceanothus seeds, it seems evident that burning of light slash should result in emergence of the greatest number of ceanothus seedlings. Under light slash, soil temperatures most effective in inducing germination of varnishleaf ceanothus seeds occurred at about $1/8$ to 1 inch below the surface--a depth that is probably also most favorable for emergence of the seedlings.

Figure 25. Soil temperatures attained at depths up to 3 inches below the surface during slash burning.^{1/}



^{1/} Curves based on median soil temperatures at indicated depths

Emergence might be reduced somewhat under medium slash, where soil temperatures within the range most effective for inducing germination were generally attained at depths in excess of 1 inch below the surface--a depth beyond the optimum determined for C. integerrimus and C. Lemmonii and perhaps beyond the optimum for varnishleaf ceanothus seedlings, as well. Emergence seems unlikely from depths in excess of 3 inches below the surface where soil temperatures could be low enough to induce germination under windrowed or heavy concentrations of slash. Results of the laboratory tests described earlier indicate that all seeds under windrowed slash at the shallower depths most favorable for emergence would either have been killed or consumed in the slash fires.

VARNISHLEAF CEANOTHUS SEEDLINGS IN BURNED AND UNBURNED SLASH AREAS

In June 1961, the year after slash burning, two hundred and forty 1/5000th-acre circular plots were examined to determine the number of newly-germinated varnishleaf ceanothus seedlings in the different slash treatment areas of each cutting. Forty plots were systematically spaced along two lines through each subdivision. In addition, supplementary plots were examined in the broadcast-burned subdivisions of each cutting to obtain an 80-plot sample of varnishleaf seedlings on burned plots for comparison with emergence on a similar series in unburned slash. Fire had covered at least 2/3 of the surface of each acceptable burned plot, but no effort was made to limit the sample to lightly, moderately, or severely burned areas.

Seedlings on Burned vs. Unburned Plots

Slash burning stimulated germination of large numbers of varnishleaf ceanothus seeds in the soil, for seedlings were far more numerous on burned than on unburned plots. Almost 39 percent of the burned plots were stocked with one or more newly-germinated seedlings, while only 7½ percent of the unburned plots contained seedlings (Table 6). In addition, burned plots stocked with ceanothus seedling contained more seedlings per plot (average, 4.3) than were found on stocked plots in the unburned areas (average, 1.3 per plot). The data showed an average emergence of 10,192 varnishleaf ceanothus seedlings per acre in the areas actually burned over in the broadcast-burned subdivisions, in contrast to only 439 seedlings per acre on unburned

Table 6.--Comparison of numbers of varnishleaf
ceanothus seedlings on burned and un-
burned parts of White Creek cuttings
1 and 3¹/₂

Item	Plot condition	
	Burned	Unburned
Percentage of plots stocked	38.75	7.50
Seedlings per stocked plot	4.323	1.333
Weighted average number of seedlings per acre ² / ₂	10,192.	439.

¹/₁ Based on one hundred and sixty 1/5000th-acre circular plots; 80 in burned and 80 in unburned portions of the two cuttings.

²/₂ Weighted by acreage in each cutting.

parts of the cuttings (Table 6).

Influence of Slash Disposal Methods on Germination

Method of slash disposal had a pronounced influence upon the number of varnishleaf ceanothus seedlings in the cuttings (Table 7). Broadcast-burning produced a greater number of seedlings (average, 8,305 per acre) than piling and burning (average, 1,568 per acre). Seedlings were least numerous in unburned slash (average, 439 per acre).

Although the percentage of plots stocked with varnishleaf ceanothus seedlings was the same in both broadcast-burned and windrowed and burned slash (18.75%), the average number of seedlings per plot was much greater after broadcast burning (average, 1.225) than after piling and burning (average, 0.350 per plot). In both areas, seedlings were observed to be most numerous on lightly burned sites; and such sites were far more abundant in areas where slash was broadcast-burned than where it was piled and burned. Examination of 23 transects through burned windrows showed that lightly burned sites were largely confined to edges of the windrows, and that ceanothus seedlings were far more abundant on such sites than on more severely burned or unburned areas within and around the windrows.

Although newly-germinated ceanothus seedlings were most abundant on the broadcast-burned subdivisions when both cuttings were considered together, the number of seedlings was slightly greater in the windrowed slash area than in the broadcast-burned area in Cutting 1 (Table 8). This can probably be attributed to the fact that slash

Table 7.--Relative numbers of varnishleaf ceanothus seedlings in White Creek cuttings 1 and 3 after three different methods of slash disposal^{1/}

Item	Slash disposal treatment		
	Broadcast-burn	Pile-burn	Unburned
Percentage of plots stocked	18.75	18.75	7.50
Seedlings per stocked plot	6.533	1.867	1.333
Weighted average number of seedlings per acre ^{2/}	8,305.	1,568.	439.

^{1/} Based on two hundred and forty 1/5000th-acre circular plots; 40 in each slash disposal subdivision of each of the two cuttings.

^{2/} Weighted by acreage in each cutting.

Table 8.--Estimated numbers of varnishleaf
ceanothus seedlings per acre after
three different methods of slash
disposal^{1/}

Cutting	Slash disposal method		
	Broadcast burned	Piled and burned	Unburned
- - average number of seedlings per acre - -			
1	1,625	2,125	625
3	10,625	1,375	375
Weighted average for both cuttings ^{2/}	8,305	1,568	439

^{1/} Based on forty 1/5000th-acre plots in each subdivision.

^{2/} Weighted by acreage in each cutting.

on Cutting 1 was burned during a heavy rainfall. Duff and litter and the lighter accumulations of slash most effective in stimulating germination became damp and did not burn well in the rain on the broadcast-burned subdivision, but burning of windrowed slash did not appear to be affected. Both ocular examination of soil samples and greenhouse germination of seeds in the samples showed that varnish-leaf ceanothus seeds were more abundant in the soil in Cutting 1 than in Cutting 3. Since burning of windrowed slash was not retarded by the rain, the influence of heat from the burning windrows on seeds in the soil also was probably not significantly affected. And germination in the unburned subdivisions of both cuttings was probably dependent upon insolation during the dry summer season rather than upon soil temperatures during the period of slash disposal. Therefore, since viable seeds were more abundant in the soil of Cutting 1, the greater number of ceanothus seedlings in the unburned and windrowed subdivisions of Cutting 1 in contrast to the number on comparable subdivisions of Cutting 3 is understandable. The low germination in the broadcast-burned portion of Cutting 1 evidently reflects the influence of rain on proportion of light slash burned and a reduction in intensity of burning with its concomitant effect on soil temperatures. Forty percent of the plots sampled in the broadcast-burned subdivision of Cutting 1 were not burned, in contrast to 32 percent unburned in Cutting 3. In addition, lightly burned plots--the degree of burn most effective in stimulating germination of seeds in the soil--were fewer in number on Cutting 1 (25.0 percent) than in

Cutting 3 (37.5 percent). Both the larger percentage of unburned area and the smaller percentage of lightly burned would tend to decrease germination of varnishleaf ceanothus seeds in the soil.

DISCUSSION

Hard seeds of Ceanothus velutinus var. laevigatus are characterized by several structural features and responses similar to those of hard seeds of leguminous plants. The thick, impermeable seed coats of both are characterized by a palisade-like layer of Malpighian cells that comprise the main structure of the seed coat. The hilar fissure of the ceanothus seed is similar in some respects to that of seeds of the sub-family Papilionaceae, and the seeds evidently respond in a similar manner to changes in relative humidity of the atmosphere. As in white clover seeds (43, p. 245-247), the hilum of a mature varnishleaf ceanothus seed acts as a hygroscopic valve--allowing the seed to lose moisture when exposed to a drier atmosphere than any to which it has previously been exposed, but preventing re-absorption of moisture when the seed is again exposed to a more humid atmosphere.

Varnishleaf ceanothus seeds seem to possess several ecologically important survival mechanisms. Impermeable seeds of several leguminous species have been found to remain dormant but viable for periods in excess of a century, and the remarkable similarity of varnishleaf seeds to those of legumes indicates that these seeds also may be extremely long-lived. Furthermore, the ability of mature varnishleaf ceanothus seeds to lose more and more moisture when exposed to successively drier conditions for years after maturation and dissemination also should be of great survival value in nature. Dessication would increase longevity of the seeds and allow them to survive long

periods of adverse conditions until environmental conditions are favorable for germination and growth. One such adverse condition for varnishleaf ceanothus would probably be a dense overstory of tree species, for observation indicates that the shrubs are intolerant and cannot survive in the understory. The ability of varnishleaf ceanothus seeds to respond to fire as demonstrated earlier in this paper is an important key in their ability to survive and persist under such conditions. When wildfire sweeps through a stand where dormant seeds are present in the soil, it not only removes the overstory vegetation and creates conditions favorable for growth of the shrubs; it also triggers germination of the seeds at the same time.

Age and origin of varnishleaf ceanothus seeds found in the soil under the two stands of timber were not determined in this investigation. Considering the abundance of such seeds in the soil (at least 131,000 viable seeds per acre) and their widespread distribution through both stands, as well as limited use of ceanothus seeds by wildlife reported in the literature, it seems unlikely that the large numbers of seeds found in the soil samples could all have come from mature plants on adjacent cuttings. Furthermore, structural characteristics of the stands of reserved timber in this area indicate that the original stand was similar to those studied and was a relatively uniform, dense stand of old-growth Douglas-fir over the entire area of many square miles. Therefore, even though the seeds found in the soil of Cuttings 1 and 3 might have come from ceanothus plants on earlier cuttings, there was no such source of seed for the

dense stands of varnishleaf ceanothus that have developed on the initial cuttings in this area. The seed must already have been present in the soil when the first stands of timber were logged. In addition, varnishleaf ceanothus seeds were found only in the soil under the stands investigated; no seeds were found in the duff and litter despite precautions to insure that they would be included in the duff sample if present. If the seeds found were of recent origin, it seems logical that at least a few seeds would have been found in duff and litter of the 60 samples processed in this investigation.

Finally, dense stands of varnishleaf ceanothus with clear-cut edges often develop in one part of a uniformly burned cutting, while adjacent areas are relatively free of the shrubs. The density of shrubs and the clearcut edges of the ceanothus cover appear to be more indicative of the abundant natural dissemination of seeds one might expect under a similar cover that once existed on the area rather than a distribution of seeds into the cut-over areas by birds or rodents. A scattered, more random distribution of shrubs would seem more probable, if the seeds had been carried in by birds and rodents. There seems, therefore, to be a distinct possibility that the seeds found in the soil samples may have come from shrubs present on the site during early development of the two stands. Unfortunately, this hypothesis cannot be verified at present. If true, the seeds would probably be between 200 and 300 years old. This is too old for historical records in this area and too young for satisfactory use of carbon dating procedures.

Variability of conditions in nature makes it obvious that the comparison of slash disposal methods in this investigation must be regarded simply as a case history rather than as representative of what will invariably occur on all sites under any conditions. Variation in amount and types of logging slash, slope and exposure of sites, methods of logging, and differences in climatic conditions before and during burning can drastically change the relative effect of methods of slash disposal on germination of ceanothus seeds in the soil. The effect of variation in climatic conditions is effectively illustrated by the reversal of effects of broadcast-burning vs. piling-and-burning on numbers of varnishleaf ceanothus seedlings in Cuttings 1 and 3. However, broadcast burning during a heavy rain as was done on Cutting 1 may not only minimize germination of ceanothus seeds in the soil; it may also reduce destruction of logging slash to a point where the prime objectives of burning--reduction of fire hazard and exposure of a mineral soil seedbed--also are not accomplished. Under conditions where the primary objectives of slash burning are accomplished, it seems reasonable to conclude that the general relationship between methods of slash disposal and germination of varnishleaf ceanothus seeds will follow the pattern revealed in this investigation--broadcast burning will stimulate germination of a greater number of dormant but viable ceanothus seeds in the soil than will burning of mechanically piled slash; and leaving slash unburned will result in the least germination of ceanothus seeds.

It must be stressed once again that our knowledge of the ecology

of brush species is extremely limited. Silvicultural practices that minimize germination of ceanothus seeds may produce conditions more favorable for survival and germination of seeds of other, perhaps even less desirable, shrub species.

Several investigators have found that lethal temperatures for seeds are somewhat lower under humid conditions than under dry conditions (11, 42)--an effect possibly associated with a greater heat capacity of humid air and more effective transmission of heat to the seed surface. Carried to the extreme, this relationship is illustrated by results of the laboratory experiments in which varnishleaf ceanothus seeds were steeped in hot water and heated in dry sand. In the steeping experiment, initial water temperatures of 100° C. were evidently near the lower limit of the lethal range; for germination was reduced from that achieved with lower water temperatures. In contrast, the lower limit of the lethal range for seeds of the same lot in dry sand was evidently near 120° C. Continuous exposure of the seeds for 40 minutes to a 105° soil temperature in dry sand had no adverse effect on germination.

The greater frequency and abundance of varnishleaf ceanothus seedlings on lightly burned sites than on more severely burned or unburned sites in the two cuttings is in agreement with results of the laboratory experiments and with pyrometer data on soil temperatures during burning. In the laboratory, germination of varnishleaf ceanothus seeds was induced by soil temperatures in the range from approximately 45° C. to 105° C., with optimum soil temperatures

ranging from about 80° to 105° C. in dry soil. Considering the relationship discussed above, optimum temperatures for germination in moist soil of the two cuttings may have been in the range of 75° to 100° C. Where light slash was burned, the pyrometers indicated that such temperatures were attained at depths of 1/8 inch to about 1 inch below the surface--depths that should be extremely favorable for emergence of the seedlings. Under medium slash, such temperatures were generally attained at depths in excess of 1 inch--depths that are probably less favorable for emergence of the resultant seedlings. Furthermore, it is also possible that abundance of ceanothus seeds in the soil may decrease with increasing depth below the surface. This would also favor production of greater numbers of seedlings in lightly burned areas than on more severely burned sites. Both laboratory and pyrometer data indicate that the more numerous seeds in the surface inch of soil would be induced to germinate on lightly burned sites; while many of those at similar depths on more severely burned sites would be killed by soil temperatures in the lethal range.

Since none of the ceanothus seeds in soil samples obtained before logging germinated without a heat treatment that rendered them permeable to moisture, germination of seeds in the unburned slash must be attributed to either: (1) scarification of seed coats during logging, or (2) heat effects on the hilums as a result of high soil temperatures due to insolation during the dry summer period. Observation indicated that ceanothus seeds germinating on unburned

sites were almost invariably in bare mineral soil directly exposed to solar radiation. Several investigators have shown that solar radiation during summer can raise surface soil temperatures on exposed sites to the range of 65° to 73° C. (3; 44, p. 5-21; 76, p. 35-40)--temperatures that the laboratory experiments proved sufficiently high to induce germination of varnishleaf ceanothus seeds in soil. In the laboratory, the thick, hard seed coats proved extremely resistant to scarification by abrasion. Therefore, although some seeds are undoubtedly abraded and scarified during logging, insolation is considered primarily responsible for germination of most of the seeds that germinated in unburned slash and in mineral soil not exposed to fire.

SILVICULTURAL APPLICATION

The autecological knowledge concerning varnishleaf ceanothus seeds gained from this investigation should not be--and cannot be--applied on all sites according to one generalized silvicultural formula. Instead, a forester must evaluate the environmental conditions of each site separately in relation to requirements of the tree species he desires to regenerate. Then he must weigh the influence a ceanothus cover would have on the environment and decide whether this would be beneficial or disadvantageous for germination, survival, and growth of the tree seedlings. Only then can he determine whether he should use a method of slash disposal that will favor or minimize germination of any varnishleaf ceanothus seeds in the soil.

Varnishleaf ceanothus seeds are not universally present in forest soils throughout the Douglas-fir Region. As stated earlier, presence of seed in the soil varies even within limited areas and distribution often seems to have been determined by the extent of a stand of parent shrubs of which the last vestiges have long since vanished from the site. At present, there seems to be no quick and easy way to determine whether seeds are present in the soil under extensive, virgin stands of old-growth Douglas-fir. Soil sampling and processing of samples is a long and laborious process. A somewhat easier method might be to obtain samples of the surface soil, spread it in a $\frac{1}{4}$ - to $\frac{1}{2}$ -inch layer on the ground in a safe place exposed to the elements, cover it with a thin layer of soil known to

be free of ceanothus seeds, and then burn a 4- or 5-inch layer of excelsior over this in the fall. Exposure to the elements during the following winter would serve to stratify any seeds, and if varnishleaf ceanothus seeds were present, seedlings would probably appear in the burned soil the following spring. The process might be speeded up by planting soil concentrates in flats, burning excelsior on the surface, providing artificial stratification for 2 or 3 months, and then germinating the samples in a greenhouse. However, even this procedure involves considerable work and would take 4 or 5 months before the results would be known.

Where the initial cuttings have already been made and slash has been burned, determination of the presence of viable varnishleaf ceanothus seeds in the soil is simplified. If no ceanothus seedlings appear in the burned areas, it is reasonably safe to assume no ceanothus seeds are present in the soil of adjacent reserved stands. If ceanothus seedlings are present in the burned areas, one may, of course, assume that seeds are also present in the intervening reserved stands and take this into consideration in planning slash disposal.

On many areas, young stands of varnishleaf ceanothus seem to act as an effective nurse crop providing a degree of shade suitable for establishment of Douglas-fir seedlings. But research has not yet provided reliable guides for determination of sites where a ceanothus cover will be beneficial and where it will be detrimental.

A light ceanothus cover may someday be proved beneficial for

regeneration of Douglas-fir on sites with a moderately heavy annual rainfall (perhaps 50 to 70 inches per year) and deep soils that can store sufficient moisture for use by both tree seedlings and ceanothus during the dry summer season. However, once the trees are established, a tall, dense cover of varnishleaf ceanothus can seriously retard growth and development of the saplings. To obtain the beneficial influence on establishment of seedlings and prevent the adverse effects on growth, the trees should be released from this brush competition as soon as they are well established on the site.

On dry sites (less than 30 inches of rainfall per year), any brush competition (including varnishleaf ceanothus) may be undesirable even on deep soils with good moisture storage capacity. Again, reliable guides must be developed by research; for the degree of competition between brush and trees will depend upon competitive characteristics of the tree and brush species involved, their rooting habits, and their density. However, if varnishleaf ceanothus seeds are known to be present in the soil on such sites, it would probably be wise to select a method of slash disposal that will minimize germination of the seeds. On such sites, mechanical piling and burning in windrows or--if slash is light enough--leaving the slash unburned would probably be preferable to broadcast burning.

Areas of relatively shallow soil underlain by rock or hardpan through which tree roots cannot penetrate should also be considered "dry sites" even though located in areas of heavy or moderately heavy rainfall. Available moisture during the extremely dry summer season

in the Douglas-fir region is largely limited to that amount that is available within the soil at depths that tree roots can occupy. Competition of shrubs for the limited moisture may hinder or prevent establishment of conifers or retard growth of established trees on such sites.

As is undoubtedly evident from the statements above, no clear-cut rules can be given at present for silvicultural application of the information gained from this investigation. Additional research is necessary to determine the degree of competition between varnishleaf ceanothus and our commercial tree species under different environmental conditions. Until such information is available, successful use of the knowledge gained from the research reported in this paper will depend largely upon the individual forester's knowledge of the silvicultural requirements of the tree species he desires to regenerate, his knowledge of local environmental conditions, and his skill in evaluating the probable influence of a ceanothus cover on germination, survival, and growth of the tree seedlings. However, once the forester decides whether he wishes to favor or prevent germination of varnishleaf ceanothus seeds in the soil, results of this investigation provide a sound basis upon which he may base his selection of a method of slash disposal that will accomplish his purpose.

The fact that seeds of many other Ceanothus species can also be induced to germinate by hot water treatments indicates that results of this research on varnishleaf ceanothus will also be applicable to other ceanothus seeds. However, the results should be applied with

caution in the field when extended to other Ceanothus species. The degree of competition afforded conifers by other species of Ceanothus can be quite different from that of varnishleaf ceanothus due to differences in rooting depth and types of root systems, size of shrubs, and degree of shade cast by the foliage, as well as other characteristics of the species. On cuttings where a moderate amount of varnishleaf ceanothus would not only be acceptable but favorable for regeneration of a given conifer, even a light cover of another Ceanothus species may be entirely unacceptable. Results of the present investigation can be applied in selecting a method of slash disposal that will minimize germination of other ceanothus seeds, and this can be supplemented by judicious use of herbicides to further reduce numbers of seedlings on the burned areas, if necessary.

Finally, the research described in this paper was conducted to obtain fundamental ecological information on one small but vital part of the life cycle of varnishleaf ceanothus--germination of the seeds--in the belief that this information would be useful in minimizing encroachment of brush species on cutover lands in the Douglas-fir Region. Each year, large areas of newly-logged forest land in the Pacific Northwest are occupied by brush species in a secondary succession that hinders regeneration of conifers, wastes the productive capacity of the land, and necessitates expenditure of large sums for brush control and brushfield reclamation. A thorough understanding of the ecology of even a few of our more important brush species would provide a sound basis for modification of present silvicultural

practices or for development of new practices to retard encroachment of brush on cut-over land and help insure the rapid regeneration of commercial tree species.

BIBLIOGRAPHY

1. Adams, Lowell. Planting depths for three species of Ceanothus. 1962. 3 p. (U. S. Dept. of Agriculture. Forest Service. Pacific Southwest Forest and Range Experiment Station. Berkeley, Calif. Research Note No. 194)
2. Barton, Lela V. Special studies on seed coat impermeability. Contributions Boyce Thompson Institute 14:355-362. 1947.
3. Bates, Carlos G. The transect of a mountain valley. Ecology 4:54-62. 1923.
4. Beadle, N. C. W. Soil temperatures during forest fires and their effect on the survival of vegetation. Journal of Ecology 28:180-192. 1940.
5. Becquerel, Paul. La longévité des graines macrobiotiques. Comptes Rendus des Séances de l'Académie des Sciences 199:1662-1664. 1934.
6. Black, M. Dormancy studies in seed of Avena fatua. I. The possible role of germination inhibitors. Canadian Journal of Botany 37:393-402. 1959.
7. Black, M. and P. F. Wareing. The role of germination inhibitors and oxygen in the dormancy of the light-sensitive seed of Betula spp. Journal of Experimental Botany 10:134-145. 1959.
8. Bokor, R. A mykorrhiza-gombak által termelt antibiotikumok hatása egyes fenyőfélék magjának csirázására. I. Közlemény. Erdészeti Kutatások 1:67-69. 1956. (Abstracted in Forestry Abstracts 18:3783. 1957.)
9. Bonner, James. The role of toxic substances in the interactions of higher plants. Botanical Review 16:51-65. 1950.
10. Brandegee, Katherine. Studies in Ceanothus. Proceedings California Academy of Sciences, Second Series, 4:173-222. 1894.
11. Carmichael, Alan J. Determination of the maximum air temperatures tolerated by red pine, jack pine, white spruce, and black spruce seeds at low relative humidities. Forestry Chronicle 34: 387-392. 1958.
12. Chepil, W. S. Germination of weed seeds: II. The influence of tillage treatments on germination. Scientific Agriculture 26: 347-357. 1946.

13. Christiansen, Meryl N. and R. P. Moore. Seed coat structural differences that influence water uptake and seed quality in hard seed cotton. *Agronomy Journal* 51:582-584. 1959.
14. Coe, H. S. and J. N. Martin. Sweet clover seed. 1920. 39 p. (U. S. Dept. of Agriculture, Bulletin 844)
15. Cooper, William S. The broad-sclerophyll vegetation of California. Washington, D. C., 1922. 124 p. (Carnegie Institution of Washington. Publication 319)
16. Corner, E. J. H. The leguminous seed. *Phytomorphology* 1:115-150. 1951.
17. Crocker, William. Role of seed coats in delayed germination. *Botanical Gazette* 42:265-291. 1906.
18. Crocker, William. Mechanics of dormancy in seeds. *American Journal of Botany* 3:99-120. 1916.
19. Crocker, William. Growth of plants. Twenty years' research at Boyce Thompson Institute. New York, Reinhold Publ. Corp., 1948. 459 p. ✓
28-128
20. Crocker, William and Lela V. Barton. Physiology of seeds. Waltham, Mass., Chronica Botanica Co., 1957. 267 p.
21. Cronemiller, Fred P. The life history of deerbrush--a fire type. *Journal of Range Management* 12:21-25. 1959.
22. Curtis, James D. Effect of pregermination treatments on the viability of Ceanothus seed. *Ecology* 33:577-578. 1952.
23. Daessler, H. G. and W. Zentsch. Keimungshemmende Wirkung von Bestandteilen des Kiefernterpentinoels. *Pharmazie* 14:46-48. 1959. (Abstracted in Biological Abstracts 33: no. 42986. 1959.)
24. Daessler, H. G. and W. Zentsch. Ueber die keimungshemmende Wirkung von Bestandteilen des Tannenzapfenoels. *Pharmazie* 14: 111-112. 1959. (Abstracted in Biological Abstracts 34: no. 5489. 1959.)
25. Darlington, H. T. The sixty-year period for Dr. Beal's seed viability experiment. *American Journal of Botany* 28:271-273. 1941.
26. Darlington, H. T. and G. P. Steinbauer. The eighty-year period for Dr. Beal's seed Viability experiment. *American Journal of Botany* 48:321-325. 1961. ✓

27. Dayton, William A. Important western browse plants. 1931. 214 p. (U. S. Dept. of Agriculture, Miscellaneous Publication 101)
28. Eames, Arthur J. and Laurence H. MacDaniels. An introduction to plant anatomy. New York, McGraw-Hill Book Co., 1947. 427 p.
29. Evenari, M. Germination inhibitors. Botanical Review 15:153-194. 1949.
30. Ewart, Alfred J. On the longevity of seeds. Proceedings Royal Society of Victoria, new ser., 21(1):1-203. 1908.
31. Fenner, R. L. and J. R. Bentley. A simple pyrometer for measuring soil temperatures during wildland fires. 1960. 9 p. (U. S. Dept. of Agriculture. Forest Service. Pacific Southwest Forest and Range Experiment Station, Berkeley, Calif. Miscellaneous Paper no. 45)
32. Ferenczy, L. Examinations of ether extractable germination inhibitors of fleshy fruits separated by paper chromatography. Acta Biologica Academiae Scientiarum Hungaricae 8:31-37. 1957. (Abstracted in Biological Abstracts 33: no. 42988. 1959.)
33. Foster, Harold D. Interrelation between brush and tree growth of the Crater National Forest, Oregon. Society of American Foresters. Proceedings 7:212-225. 1912.
34. Gratkowski, H. Brush problems in southwestern Oregon. Portland, Ore. U. S. Dept. of Agriculture. Forest Service. Pacific Northwest Forest and Range Experiment Station, 1961. 53 p.
35. Gratkowski, H. Brush seedlings after controlled burning of brushlands in southwestern Oregon. Journal of Forestry 59:885-888. 1961.
36. Hamly, Douglas H. Softening the seeds of Melilotus alba. Botanical Gazette 93:345-375. 1932.
37. Harrington, George T. Agricultural value of impermeable seeds. Journal of Agricultural Research 6:761-796. 1916.
38. Heyward, Frank. Soil temperatures during forest fires in the longleaf pine region. Journal of Forestry 36:478-491. 1938.
39. Hopkins, Clarence Yardley. Thermal death point of certain weed seeds. Canadian Journal of Research 14(C):178-183. 1936.

40. Horton, J. S. and C. J. Kraebel. Development of vegetation after fire in the chamise chaparral of southern California. *Ecology* 36:244-262. 1955.
41. Hubbard, Richard L. Hot water bath and thiourea break dormancy of wedgeleaf Ceanothus seed. 1958. 4 p. (U. S. Dept. of Agriculture. Forest Service. California Forest and Range Experiment Station. Berkeley, Calif. Research Note no. 143)
42. Hutton, Mary Erne-Jean and R. H. Porter. Seed impermeability and viability of native and introduced species of Leguminosae. *Iowa State College Journal of Science* 12:5-24. 1937.
43. Hyde, E. O. C. The function of the hilum in some Papilionaceae in relation to the ripening of the seed and the permeability of the testa. *Annals of Botany, new ser.*, 18:241-256. 1954.
44. Isaac, Leo A. Factors affecting establishment of Douglas fir seedlings. 1938. 45 p. (U. S. Department of Agriculture Circular no. 486)
45. Isaac, Leo A. Vegetative succession following logging in the Douglas fir region with special reference to fire. *Journal of Forestry* 38:716-721. 1940.
46. Jameson, E. W., Jr. Food of deer mice, Peromyscus maniculatus and P. boyleyi, in the northern Sierra Nevada, California. *Journal of Mammalogy* 33:50-60. 1952.
47. Kelsey, Harlan P. and William A. Dayton. Standardized plant names. Harrisburg, Pa., J. Horace McFarland Co., 1942. 675 p.
48. Knowles, Robert High, and Saul Zalisk. Effects of temperature treatment and of a native inhibitor on seed dormancy and cotyledon removal on epicotyl growth in Viburnum trilobum Marsh. *Canadian Journal of Botany* 36:561-566. 1958.
49. Koller, D. and M. Negbi. The regulation of germination in Oryzopsis miliacea. *Ecology* 40:20-36. 1959.
50. Leiberg, John B. Cascade Range and Ashland Forest Reserves and adjacent regions. U. S. Geological Survey. Annual Report 21(S): 211-498. 1900.
51. Little, Elbert L. Check list of native and naturalized trees of the United States (including Alaska). 1953. 472 p. (U. S. Dept. of Agriculture, Handbook no. 41)
52. Lute, Anna M. Alfalfa seed made permeable by heat. *Science* 65: 166. 1927.

53. Lute, Anna M. Impermeable seed of alfalfa. Fort Collins, 1928. 36 p. (Colorado. Agricultural Experiment Station. Bulletin 326)
54. Martin, J. N. The structure and development of the seed coat and cause of delayed germination in Mellilotus alba. Proceedings Iowa Academy of Science 29:345-346. 1922.
55. McMinn, Howard E. An illustrated manual of California shrubs. Berkeley, University of California Press, 1951. 663 p.
56. McNair, A. D. Boiling buffalo clover seed. Science, n. s., 45: 220-221. 1917.
57. Morris, William G. Influence of slash burning on regeneration, other plant cover, and fire hazard in the Douglas-fir Region. 1958. 49 p. (U. S. Dept. of Agriculture. Forest Service. Pacific Northwest Forest and Range Experiment Station. Portland, Ore. Research Paper 29)
58. Nord, Eamor C. and George R. Van Atta. Saponin--a seed germination inhibitor. Forest Science 6:350-353. 1960.
59. Ohga, Ichiro. On the longevity of seeds of Nelumbo nucifera. The Botanical Magazine, Tokyo Botanical Society 37:87-95. 1923.
60. Ohga, Ichiro. On the structure of some ancient, but still viable fruits of Indian lotus, with special reference to their prolonged dormancy. Japanese Journal of Botany 3:1-20. 1926.
61. Ohga, I. The germination of century-old and recently harvested Indian lotus fruits, with special reference to the effect of oxygen supply. American Journal of Botany 13:754-759. 1926.
62. Ooyama, Namio. The growth-inhibiting substances contained in the leaf-litter of the trees. (1) The inhibiting effect on germination of the coniferous seeds. Journal of the Japanese Forestry Society 36:38-41. 1954.
63. Pammel, L. F. The anatomical characters of the seeds of Leguminosae, chiefly genera of Gray's Manual. Transactions Academy of Science, Saint Louis 9:91-274. 1899.
64. Peck, Morton Eaton. A manual of the higher plants of Oregon. Portland, Oregon, Binforde and Mort, 1941. 866 p.
65. Peterson, Roald A. Comparative effects of seed treatments upon seedling emergence in seven browse species. Ecology 34:778-785. 1953.

66. Porter, R. H. Recent developments in seed technology. Botanical Review 15:221-344. 1949.
67. Quick, Clarence R. Notes on the germination of Ceanothus seeds. Madrono 3:135-140. 1935.
68. Quick, Clarence R. Viable seed from the duff and soil of sugar pine forests. Forest Science 2:36-42. 1956.
69. Quick, Clarence R. Ceanothus seeds and seedlings on burns. Madrono 15:79-81. 1959.
70. Quick, Clarence R. and Alice S. Quick. Germination of Ceanothus seeds. Madrono 16:23-30. 1961.
71. Rees, Bertha. Longevity of seeds and structure and nature of seed coat. Proceedings Royal Society of Victoria, new ser., 23(2):393-414. 1911.
72. Rincker, Clarence M. Effect of heat on impermeable seeds of alfalfa, sweet clover, and red clover. Agronomy Journal 46:247-250. 1954.
73. Sampson, Arthur W. Plant succession on burned chaparral lands in northern California. Berkeley, 1944. 144 p. (California. Agricultural Experiment Station. Bulletin 685)
74. Shaw, Margaret Fenton. 1929. A microchemical study of the fruit coat of Nelumbo lutes. American Journal of Botany 16:259-276. 1929.
75. Silen, Roy R. Use of temperature pellets in regeneration research. Journal of Forestry 54:311-312. 1956.
76. Silen, Roy Ragnar. Lethal surface temperatures and their interpretation for Douglas-fir. Ph.D. thesis. Corvallis, Oregon State College, 1960. 170 numb. leaves.
77. Staker, E. V. The effect of dry heat on alfalfa and its adulterants. Journal American Society of Agronomy 17:32-40. 1925.
78. Stewart, George. Effect of color of seed, of scarification, and of dry heat on the germination of alfalfa seed and of some of its impurities. Journal American Society of Agronomy 18:743-760. 1926.
79. Stone, E. C. and J. Holt. A rapid method of separating seed of chamise (Adenostoma fasciculatum) from the duff. Ecology 31:149. 1950.

80. Stone, E. C. and G. Juhren. The effect of fire on the germination of Rhus ovata Wats. American Journal of Botany 38:368-372. 1951.
81. Stone, E. C. and G. Juhren. Fire stimulated germination. California Agriculture 7:13-14. 1953.
82. Tevis, Lloyd, Jr. Autumn foods of chipmunks and golden-mantled ground squirrels in the northern Sierra Nevada. Journal of Mammalogy 33:198-205. 1952.
83. Tevis, Lloyd, Jr. Stomach contents of chipmunks and mantled squirrels in northeastern California. Journal of Mammalogy 34:316-324. 1953.
84. Thornber, J. J. Some practical suggestions concerning seed germination. In: Timely hints for farmers. Tucson, 1903. p. 536-541. (Arizona. Agricultural Experiment Station. Bulletin no. 51)
85. Toole, E. H. and E. Brown. Final results of the Duvel buried seed experiment. Journal of Agricultural Research 72:201-210. 1946.
86. Toole, E. H., S. B. Hendricks, H. A. Borthwick and Vivian K. Toole. Physiology of seed germination. Annual Review of Plant Physiology 7:299-324. 1956.
87. Uggla, Evald. Ecological effects of fire on north Swedish forests. Uppsala, Växbiologiska Institutionen, University of Uppsala. 1958. 18 p.
88. U. S. Forest Service. Woody plant seed manual. 1948. 416 p. (U. S. Dept. of Agriculture, Miscellaneous Publication no. 654)
89. Van Dersal, William R. Native woody plants of the United States, their erosion-control and wildlife values. 1939. 362 p. (U. S. Dept. of Agriculture. Miscellaneous Publication 303)
90. Van Renssalaer, Maunsell and Howard E. McMin. Ceanothus. Santa Barbara, California, Santa Barbara Botanical Gardens, 1942. 308 p.
91. Wahlenberg, W. G. Effect of Ceanothus brush on western yellow pine plantations in the northern Rocky Mountains. Journal of Agricultural Research 41:601-612. 1930.
92. Wareing, P. F. and H. A. Foda. Growth inhibitors and dormancy in Xanthium seed. Physiologia Plantarum 10:266-280. 1957.

93. Watanabe, Akira. Effects of drying of soil upon the germination of seeds and upon the water relation of seedlings of Acacia mollissima. Bulletin of the Tokyo University Forests 55:161-169. 1959.
94. Watson, Donald P. Structure of the testa and its relation to germination in the Papilionaceae tribes Trifoliae and Loteae. Annals of Botany, new ser., 12:385-409. 1948.
95. Williams, William A., and John R. Elliott. Ecological significance of seed coat impermeability to moisture in crimson, subterranean and rose clovers in a Mediterranean-type climate. Ecology 41:785-790. 1960.
96. White, Jean. The occurrence of an impermeable cuticle on the exterior of certain seeds. Proceedings Royal Society of Victoria, new ser., 21(1):203-210. 1908.
97. Wright, Ernest. The effect of high temperatures on seed germination. Journal of Forestry 29:679-687. 1931.
98. Yerkes, Vern P. Occurrence of shrubs and herbaceous vegetation after clear cutting old-growth Douglas-fir in the Oregon Cascades. 1960. 12 p. (U. S. Dept. of Agriculture. Forest Service. Pacific Northwest Forest and Range Experiment Station. Portland, Ore. Research Paper 34)