

Freezing Spring Temperatures

Damage Knobcone Pine

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An anatomical study of ovule and conelet development was made on about 200 developing conelets in a plantation in the central Sierra Nevada of California, after an unseasonal April frost. Night temperatures as low as -6° C. were recorded. Conelets in pollination bags were most susceptible to cold damage; emerging conelets were the most badly damaged; conelets at maximum were only slightly damaged. Low temperatures did not affect final seed set of the surviving cones.

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(Key words: *Knobcone pine, conelets, freezing temperature*)

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Contents

	<i>Page</i>
Introduction -----	1
Methods -----	1
Results -----	3
Discussion -----	4
Literature Cited -----	5

The Author

STANLEY L. KRUGMAN is conducting studies of forest tree physiology as part of the Station's research on the genetics of western conifers at Berkeley and Placerville, California. A native of St. Louis, Mo., he completed his undergraduate work (1955) in forestry at the University of Missouri. He earned a master's degree (1956) in forestry and a doctorate (1961) in plant physiology at the University of California, Berkeley, where he did research on seed physiology in conifers before joining the Forest Service in 1962.

Freezing temperatures during spring have been reported to be a principal cause of mortality of first-year pine conelets. Schubert (1955) observed that a minimum temperature of -7°C . in June killed 93 percent of the conelets on an individual sugar pine tree (*Pinus lambertiana* Dougl.) growing on the Stanislaus-Tuolumne Experimental Forest in central California. Similarly, Barras and Norris (1964) attributed conelet mortality in red pine (*Pinus resinosa* Ait.) throughout Wisconsin to freezing spring temperatures. Hard (1963) noted that in a red pine plantation, spring frost-killing of conelets was associated with topography and elevation.

Unusually low spring temperatures rarely kill the entire crop of first year conelets. Certain conelet developmental stages are, however, more susceptible than others to low temperatures. Foresters generally believe that conelets at the stage of maximum pollen receptivity are most vulnerable (Campbell 1955; Hutchingson and Bramlett 1964). The variability in temperatures within a tree crown or within a stand also accounts for

partial conelet kill (Hard 1963; Peace 1962; Schubert 1955).

Besides killing first-year conelets, freezing spring temperatures may also reduce the number of sound seed in the cones that survive. Either certain ovules are killed without the cone being destroyed, or the pollen is made sterile, which causes ovule abortion at a later stage of development (Andersson 1965).

The opportunity to investigate the effects of freezing temperatures on conelet and seed development arose in late April 1964, when an unseasonal cold front caused extensive damage to conelets of knobcone pine (*Pinus attenuata* Lemm.) in the central Sierra Nevada of California. At the time of the frost, investigations of conelet development following controlled and wind pollination had just been started. These circumstances made it possible to determine those conelet developmental stages most susceptible to low temperature damage. The effects of the frost on final seed set were also investigated. This paper reports the results of that study.

Methods

Study area.--The Badger Hill plantation lies 12 miles east of Placerville, Calif., at an elevation of 3,300 ft. It includes 27 different geographic sources of knobcone pines. The plantation was established as a breeding orchard for the mass production of knobcone X Monterey hybrids.

Sampling procedure.--Two weeks before the frost, about 200 developing conelets had been enclosed in plastic pollination bags for the purpose of making controlled pollinations. As the bagged conelets reached maximum pollination stage, they were hand pollinated with either a mixture of 1-year old Monterey pollen or a mixture of 1-year old knobcone pollen. Bagged unpollinated conelets served as controls.

Two days before the frost, the developmental stages of 200 bagged and unbagged conelets were recorded. Care was taken to include a range of stages--from conelets still covered by bud scales

(conelet-bud large [stage 1]) to conelets whose scales had closed completely after pollination (conelet scales closed [stage 5]) (table 1). To obtain the complete range of developmental stages, four geographic seed sources of knobcone pine were included. On April 22, the morning of the frost, four unbagged and four bagged conelets of each developmental class were chemically fixed for an anatomical study. On April 24, about 41 hours after the frost, four conelets of each class were collected, two conelets of each class were examined immediately, and two were placed in a chemical fixative. Subsequent sampling was done 3 days later (April 27) and thereafter at about 2-week intervals for a period of 4 months. Damage to all classified cones that remained on the trees was visually estimated at about 2-week intervals for the first year. Additional cones were collected in 1965 and their contents were examined.

Table 1. --Percent mortality in bagged and unbagged conelets of different developmental stages, after a spring frost

Developmental stage number	Developmental stage at time of frost	Unbagged	Bagged
		<i>Percent</i>	<i>Percent</i>
1	Conelet-bud large: conelet not visible	0	0
2	Conelet bud opening: conelet visible	20	45
3	Conelet scales partly opened	18	30
4	Conelet scales open to maximum	2	8
5	Conelet scales closed	0	0

Temperature conditions.--Temperature data for this study were provided by two recording thermographs--one in a standard weather shelter at the north end of the plantation, and the second in the middle of the crown on an experimental tree at the south end of the orchard. Five maximum-minimum thermometers near the unbagged conelets provided additional information on temperature extremes in the tree crowns. Temperature extremes inside two pollination bags were recorded by individual maximum-minimum thermometers.

The mean air temperatures during the week before the frost was 18°C. during the day and 7°C. during the night. On the evening of April 22--the first night of the frost--the temperature dropped to a low of -3°C. at the weather shelter and a low of -2°C. in the tree crowns; it remained below the freezing point for 4 hours (table 2). During the next 3 days, freezing temperatures prevailed for periods up to 16 hours in the tree crowns. A temperature low of -6°C. was reached in the early morning hours of April

24. The cold period was immediately followed by 4 days of warming temperatures. A high of 20°C. was recorded in the afternoon of April 28. Temperatures remained well above freezing during the week that followed the frost.

The maximum and minimum temperatures in pollination bags differed from the temperatures outside the pollination bags. The maximum temperature in the pollination bag recorded the afternoon of April 24 was 10°C., with a minimum of -4°C. On April 27, a maximum temperature of 16°C. was recorded in the pollination bag, with a minimum of 4°C. But the duration of these extreme temperatures was not recorded.

Temperatures were within 3°C. at both the south and north ends of the breeding orchard. This condition was somewhat surprising because the orchard slopes from south to north, varying from 9 to 16 percent in steepness. From the limited temperature instrumentation there was no suggestion of frost pockets.

Table 2.--Thermograph temperatures as recorded in the tree crown during freeze period

Date	Maximum temperature	Minimum temperature	Duration of freezing temperatures
	<i>C. °</i>	<i>C. °</i>	<i>Hours</i>
April 22	13	-2	4
April 23	3	-4	16
April 24	6	-6	13
April 25	12	-2	6

Results

Conelet mortality.--Both the presence of pollination bags and the conelet developmental stage at the time of the frost were factors in conelet damage by low temperatures. Conelets in pollination bags were most susceptible to cold damage--sustaining on a percentage basis twice as much mortality as unbagged conelets (table 1). Forty-five percent of bagged conelets emerging from the bud scales (stage 2) were killed, compared to 20 percent mortality for unbagged conelets at the same stage of development. Conelets whose scales were partly open (stage 3) were almost as vulnerable to low temperatures. Thirty percent of the bagged stage 3 conelets were killed, compared to 18 percent for unbagged conelets. Similarly, bagged conelets whose scales were opened to their maximum, suffered higher mortality (8 percent) than unbagged conelets (2 percent).

Unexpectedly, conelets in two of the stages--(a) still completely covered by bud scales (stage 1), and (b) those whose scales were completely closed (stage 5)--had no mortality whether they were bagged or unbagged.

The higher mortality among bagged conelets probably resulted from the more rapid thawing rather than exposure to lower temperatures because both bagged and unbagged cones were exposed to essentially the same minimum temperatures. But the maximum temperatures in the two pollination bags were consistently higher than the free air temperatures, suggesting a more rapid warming cycle. Usually, greater frost injury can be expected if thawing is rapid (Levitt 1956). But since the cycles of the temperatures were not recorded for the bagged conelets, I can only speculate on this point.

The length of time from exposure to low temperature to visual appearance of conelet damage depended on the developmental stage at the time of the frost. Cold damage to elongating conelets (stage 2) could be seen within 2 weeks of the cold period; damage to conelets in developmental stages 3 and 4 was apparent only after 3 or more weeks. The injured conelets first lost their luster and then began browning and shriveling.

In contrast, a conelet's ability to continue elongation after frost damage did not depend solely on its developmental stage at the time of the frost. Of 50 conelets that were measured and eventually died, 40 continued to elongate during the 2 weeks after the frost. Of the conelets

that were killed, those just emerging from the bud scales (stage 2) had the least elongation. Only 18 percent of the stage 2 conelets that eventually died elongated after the frost, compared with 40 percent for stage 3 and 43 percent for stage 4 conelets.

No obvious signs of cold damage were observed in sectioned material collected 2 days after the first cold exposure. But 5 days after the first frost, definite indication of damage was observed in both fresh and fixed sectioned conelets. Longitudinal sections revealed collapsed cells in the vascular region of the middle and lower cone axis, in which the cytoplasm had coagulated into a dense mass. In contrast, the vascular system of the conelet scales appeared undamaged. Other cells in the cone axis had lost their turgidity. This type of cold damage is apparently the result of the dehydrating effect of extracellular ice formation (Siminovitch and Scarth 1938; Levitt 1956). Severe cold damage was characterized by brownish-black necrotic areas scattered throughout the middle and lower regions of the conelet axis in fresh hand-sectioned conelets. This condition was the result of a complete breakdown of the injured cells.

In most of the sectioned ovular material the ovular region appeared undamaged and the megaspore mother cell had not been formed. Even in those ovules (conelet stages 4 and 5) where an occasional megaspore mother cell had developed, however, the megaspore mother cell appeared not to have been damaged by the frost.

Two weeks after the frost--concurrent with the rapid visual deterioration of the conelet--the whole cone axis was necrotic. The vascular system of the developing conelet was badly destroyed, and obvious degeneration of the ovule was now apparent.

Typically for this species, the dead conelets did not immediately absciss. Some remained on the trees as long as 15 months after the frost. But most of the dead conelets fell during the winter months after the spring kill.

Contrary to my expectation, the amount of sound seed produced in the surviving cones was comparable to seed production for frost free seasons. The amount of seed produced per cone under both bagged and unbagged conditions showed no apparent reduction (table 3). The results might be explained if the cold period reduced seed number equally in all conelet classes. This possibility,

Table 3.--*Number of knobcone seeds per cone the second year after a spring frost*

Conelet stage at time of frost	Unbagged				Bagged ¹			
	Sound	Hollow	Total	Number of cones	Sound	Hollow	Total	Number of cones
	Number of seeds per cone ²							
Conelet-bud large	36	75	111	4	42	76	118	5
Conelet-bud opening	40	81	121	4	41	58	99	6
Conelet scales partly opened	35	72	107	6	38	71	109	6
Conelet scales open to maxi- mum	37	79	116	8	39	70	109	8
Conelet scales closed	39	69	108	10	42	74	116	7

¹Knobcone pollen mixture was used in the control pollination.

²Seeds by from were extracted removing the cone scales the cone.

however, is unlikely for two reasons: (a) conelet mortality was so closely related to developmental stage of the conelet at the time of the freeze, and

(b) seed set was comparable to that of the 2 previous years which did not have unseasonal spring freezes.

Discussion

This study showed that newly developing conelets of knobcone pine are not equally susceptible to freezing damage. Conelets are most susceptible to frost damage before pollination, when they are rapidly elongating and not protected by bud scales. In contrast, the post-pollination stages are resistant to cold temperatures.

In addition, only certain parts of the conelet are initially damaged by the frost. The ovules showed damage only after the deterioration of the vascular system of the cone axis. Although the freezing temperatures were severe enough to kill some conelets, the seed set of the surviving cones was not affected. Both of these observations

showed that the ovules are more resistant to cold damage than is the cone axis.

The high mortality of conelets at certain developmental stages is an example of the impact a late spring freeze can have on a cone crop. In some years, low spring temperatures can be an important factor in reducing the annual cone crop. And an unseasonal spring freeze could be an important contributing factor to periodicity in mature cone production. The higher mortality of conelets in the pollination bags strongly suggests that to avoid conelet mortality due to freezing temperatures, care must be taken in the location of breeding orchards.

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