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Factors Affecting the Distribution of the Monterey Pine Cone Beetle (*Conophthorus radiatae* Hopkins) in Central California

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This paper reports a series of laboratory and field studies of the Monterey pine cone beetle. The author devoted much time and effort, on both the west and east slopes of the Berkeley Hills, in determining the effects of humidity and temperature on the insect's survival. His principal concern was to determine its ability to inhabit areas outside the coastal fog belt. • It was definitely established that the beetle's life cycle is favored by moderate temperatures and a plentiful supply of moisture. This was evident by its prevalence on the seaward side of the range, where fogs are frequent and summer heat is not excessive. On the other hand, when the insects were "planted" on the east side, near San Pablo Dam, the mortality rate was very high, thus showing the adverse effects of heat and low humidity. • The present study represents the second portion of the author's Ph.D. thesis; the first portion is cited herein under "Schaefer (1962)."

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Factors Affecting the Distribution of the Monterey Pine Cone Beetle (*Conophthorus radiatae* Hopkins) in Central California[1]

INTRODUCTION

THIS STUDY records the results of a series of experiments with *Conophthorus radiatae* Hopkins (Scolytidae), which attacks and aborts the second-year cones of *Pinus radiata* D. Don. in California. However, the distribution of *C. radiatae* is more limited than that of its host. The cone beetle is apparently restricted to stands of Monterey pine within a few miles of the Pacific Coast—areas which receive frequent fog during the summer months.

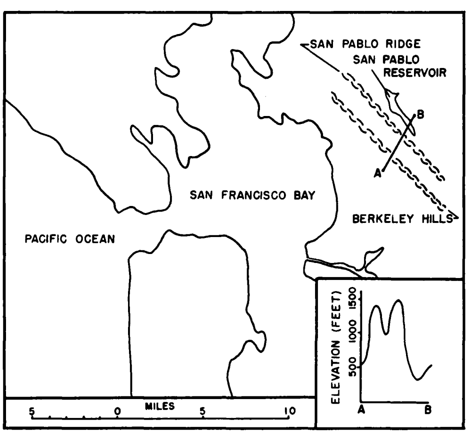

Fig. 1. Geographic location of study areas in relation to San Francisco Bay and the Pacific Ocean.

The limits of distribution were particularly noticeable in the San Francisco Bay area of central California. Monterey pine stands on the coastal hills above Berkeley were infested with the beetle, but plantations three miles east of Berkeley on the lee side of the same hills were almost free of attack (fig. 1).

The occurrence of summer fogs appeared to be associated with cone beetle distribution. It was postulated that amelioration of summer temperatures and increased available moisture owing to fog favored the occurrence of *C. radiatae* in the coastal stands, whereas inland, where summer fog was less frequent, temperature and moisture conditions became too extreme for its survival.

This study was undertaken to determine those factors affecting the distribution of the cone beetle, particularly the influence of temperature and moisture under summer fog conditions. Laboratory investigations included studies of techniques for determining cone temperatures and the effects of temperature and moisture on cone beetle survival. Field studies included measurement of cone temperature and mois-

[1] Submitted for publication September, 1962.

ture *in situ;* effects of direct radiation, cone orientation, reflection and reradiation, wind and fog on cone temperature; and a limited comparison of the effects of coastal and interior climatic conditions on cone beetle survival.

LIFE HISTORY OF THE CONE BEETLE

A detailed account of the life history of *Conophthorus radiatae* has been published recently (Schaefer, 1962).[2] A summary of it is given here as a general background to this study. Adult beetles overwinter in cones killed during the previous season. The beetles emerge in late February and March and attack cones which are beginning their second year of development. The female constructs a gallery which severs the vascular tissues, causing the death of the cone. Eggs are deposited in small niches along the gallery. The larvae feed on the cone tissues and pass through two instars before pupating within the same cone in June. The pupae transform into adults during late June and July.

Fig. 2. (*Above*) An aborted cone between two unattacked cones. (*Below*) Cone at left was aborted early in the season, while the one at right was attacked later; only the tip portion has undergone shrinkage.

Newly attacked cones show no symptoms for several weeks. Then, the underside and distal one-half gradually turn brown, while the base remains green. By summer, the entire attacked cone has turned reddish brown, and considerable shrinkage has occurred over the entire surface. Such cones are referred to as *aborted* cones (fig. 2). In contrast, the unattacked cones remain green and by late spring are much larger than the aborted cones. All cones remain attached to the tree for several years. The reddish cast of the currently infested aborted cones distinguishes them from cones aborted in previous years, which have a grayish cast.

LABORATORY INVESTIGATIONS

Measurement of Cone Temperatures

Methods. The proper placement and depth of thermocouples in both green (unattacked) and aborted cones was studied. Twenty-four-gauge, copper-constantan thermocouples were inserted into green cones (average diameter, 2 inches) at depths of one-quarter and one-half inch on the exposed surface and one-half inch on the shaded side. As aborted cones are smaller (average diameter 1.5 inches), depths of one-quarter, three-eighths, or one-half inch on the exposed side and one-half inch on the shaded side were used. Thermocouples were forced straight in toward the central cone axis in a path perpendicular to the place of insertion. Before insertion into aborted cones was possible, it was necessary to punch an opening slightly smaller than the diameter of the thermocouple. Radiation was provided by an ordinary heat lamp. Intensity of radiation was varied by changing the distance between lamp and cone. By this means, temperatures of 68 to 122° F. were obtained at a depth of one-half inch within the exposed sides of the cones. The temperatures at all other depths were com-

[2] See "Literature Cited" for citations, referred to in the text by author and date.

pared with those at one-half inch on the exposed side, the depth at which most beetles are found in green cones. Beetles are often nearer the surface in aborted cones.

Results. Heat conduction was greater in the green cones, perhaps as a result of their greater moisture content compared with aborted cones. Below 77° F., cone temperatures at varying depths were approximately equal, but as temperatures increased, the differences with depth increased markedly (fig. 3).

The size of cones did not significantly affect temperature. Temperatures measured at the same depth in cones of varying size were almost equal. Because there was considerable variation in temperature when radiation was changing, it was established that at least two thermocouples were necessary to estimate maximum and minimum cone temperatures at a given depth. These were inserted through the surfaces of greatest and least exposure to direct solar radiation.

Mortality at High Temperatures

Methods. Aborted cones containing adults were placed in temperature cabinets at 95, 104, 113, and 122° F. Since naturally infested cones were used, uneven sample sizes resulted. Eggs on moist filter paper and larvae and pupae in cone sections were subjected to temperatures above their favorable range (above 86° F.; see Schaefer, 1962), but similar to those they might encounter in the field during their respective spring developmental periods. Exposures varied from 4 to 8 hours. Two exposures (24 hours apart) were made at some temperatures. Mortality records were taken 48 hours after treatment.

Results. No mortality of any stage resulted from one 8-hour exposure at 95° F. Larval mortality of 8 per cent occurred after 3 days' continuous exposure, 53 per cent after 8 days, and 100 per cent after 12 days at this temperature.

Little mortality of any stage resulted from short exposures at 104° F. Exposures at 113° for more than a few hours caused significant mortality, and exposures at 122° were harmful, even for short periods (table 1).

(The seven tables in this issue are grouped on pages 99–102.)

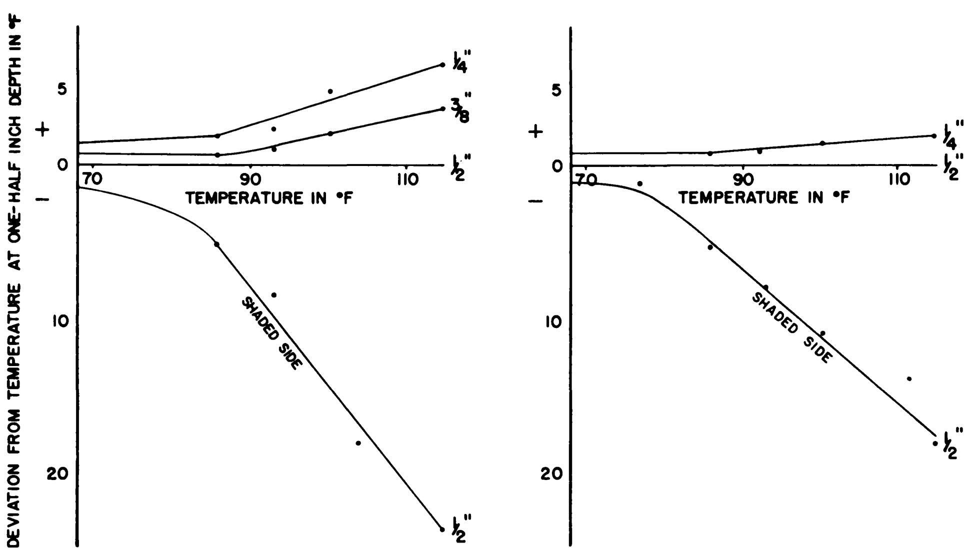

Fig. 3. Variation of temperature with depth in green, unattacked cones (*right*) and in aborted cones (*left*), exposed to artificial heat in the laboratory. The graphs show deviation from temperature readings taken at the half-inch depth.

Moisture Content of Aborted Cones in Subsaturated Atmospheres

Methods. Excised, aborted cones were placed in small chambers consisting of two pint Mason jars with their lids cut through and soldered together. Screening inserted between the lids kept the cones (in the upper jar) above the solutions (in the lower jar) used to control humidity. Relative humidities of 22, 55, 76, and 95 per cent were obtained, using KAc (potassium acetate), $Mg(NO_3)_2$, NaCl, and K_2SO_4, respectively. Temperature was maintained at 68° F. Relative humidities were determined with cobalt thiocyanate paper.

Each cone was weighed daily to the nearest centigram. Equilibrium moisture content was reached at the three lower humidities in 15 days, at which time cones were weighed, dried at 225° F. for 48 hours, and dry weights were determined. Cones in the 95 per cent chamber continued to gain weight until their tissues were saturated and the adults began to emerge (20 days). Dry weights could not be calculated, because of large quantities of boring dust ejected by the beetles before emergence. The dry weights given for these cones show the average dry weight of all cones used and should be approximately correct, as all were taken from the same source at the same time.

Results. The moisture content of apparently dry aborted cones varies directly with the relative humidity of the surrounding air (table 2). Cones in the 95 per cent range absorbed moisture until their tissues were saturated, but the moisture content of cones in lower humidities was in equilibrium at levels increasing with the atmospheric relative humidity.

Effect of Relative Humidity on Adult Cone Beetle Survival

Methods. Aborted cones collected in the field were placed in the controlled humidity chambers previously described and held at 68° F. Five cones in each humidity chamber were dissected after 64 and 85 days, and the adults were examined.

Results. The attempt to approximate natural conditions by exposing intact cones resulted in unequal sample size and no beetles in one sample of the 55 and 95 per cent humidities. The results (table 3) indicate that survival increases with increasing relative humidity; also, that some adults are capable of withstanding extremely dry conditions. The number of adults in the samples was not large enough to compare survival with time at any given humidity; however, at both 64 and 85 days, the survival increased with increasing relative humidity.

FIELD INVESTIGATIONS

Measurement of Temperatures within Cones *in Situ*

Methods. Monterey pine is an intolerant species; crown development is greatly affected by light. In pure, dense stands, the crown is well developed only in the upper part except for edge trees, which also have well-developed crowns on the exposed side. Cones are produced only in those portions of the crown that receive direct sunlight. There is great diversity in exposure of cones to solar radiation. Cones in the top of the crown are usually fully exposed on all four of their sides, with their proximal portions shaded, while cones on the periphery may have only one surface exposed, with the others shaded by adjacent foliage. Due to differences in cone position with regard to adjacent foliage and branches, cardinal directions could not be used alone for determining thermocouple sites. Thermocouples were inserted through the center of the surface of the longest exposure to sunlight (SLE) and the surface of shortest exposure (SSE). Thermocouples were inserted to a depth of one-half inch in green cones and three-eighths inch in aborted cones. The shallower depth in aborted cones was selected on the basis of greater temperature variation with depth found in the laboratory in aborted cones (fig. 3), and because beetles occur closer to the surface than in green cones.

The aborted cones were the main concern in this study, as this is the condition of all cones containing cone beetles in the summer and fall periods. Temperatures of green cones are of biological importance only during the spring period, as newly attacked cones remain green for some time before aborting. There are no green cones containing beetles in the summer, but the temperatures of unattacked green cones were measured for comparison with those of aborted cones.

A 69-foot "edge" tree with cones in its upper stratum (63 to 68 feet above the ground) and lower stratum (35 to 38 feet above the ground) was selected for initial field experiments on cone temperatures. Variables compared in relation to cone temperature follow.

1. *Cone Condition — Green Unattacked, or Attacked and Aborted.* Two thermocouples were placed in green and aborted cones at each crown level.

2. *Cone Orientation.* Two thermocouples were placed in two surfaces (SLE and SSE) of an aborted cone having its longitudinal axis approximately parallel to the solar rays at midafternoon and in another with its longitudinal axis approximately perpendicular to the radiation at the same time. Both cones were situated in the upper crown, and their positions were similar except for orientation to the sun at midafternoon (1500 hours P.S.T.)[3]

3. *Reflection and Reradiation of Foliage.* Foliage was removed from the vicinity of aborted cones so that reflection, reradiation, and other influences of nearby foliage were reduced. Extra foliage was placed around other aborted cones in order to maximize the influence of nearby foliage, and still other cones were left in their natural location with respect to adjacent foliage. Temperatures were recorded beneath the two surfaces (SLE and SSE) for cones in each category.

4. *Wind.* A metal, cup-type anemometer was placed in each crown stratum. Wind velocities were recorded throughout each experiment.

5. *Fog or Stratus.* The occurrence and persistence of fog or stratus in the experimental area were recorded throughout each experiment.

6. *Radiation.* Observations on sunlight striking the crown were recorded periodically. A black copper globe, 6 inches in diameter, was placed in each crown stratum to obtain an index of the mean effectual radiation intensity of the environment. The globe temperatures referred to in the text and figures were based on these black globes and were, of course, influenced by ambient air temperature and air currents as well as the radiation load. One thermocouple was placed in the center of each globe, and a second was placed in a shaded position 2 inches from the outer surface. The latter served to measure ambient air temperature. The measurement and use of black-globe temperatures have been described by Bond and Kelly (1955) and by Leigh and Smith (1959).

Temperature measurements from all thermocouples were recorded for periods of 12 to 48 hours on an automatic-recording, 16-point potentiometer. This was located in a trailer 50 feet from the test tree. Temperatures were recorded to the nearest tenth Fahrenheit degree every 4 minutes. Anemometer leads were connected to Foxboro recorders, also located in the trailer.

Results and Discussion. The effects of solar radiation on insect habitats have been widely studied. Wellington (1950) pointed out that there are often large differences between temperatures

[3] In this paper, the time of day is given by the "nautical" system: midnight to midnight, 24 hours.

of the insectan habitat and ambient air, mainly caused by radiant heating and cooling. Henson and Shepherd (1952) found that the heating effect in mines of the lodgepole needle miner is directly proportional to the radiation level, and is modified by degree of exposure, needle orientation, size of mine, and wind. Henson (1958) showed that aspect, exposure, orientation, ventilation, absorptivity, density, and size all affect the temperatures of an insect habitat exposed to radiation. At this writing, however, no published works are known which state the degree to which cone temperatures are affected by direct solar radiation or are modified by other factors.

Cone temperatures begin to increase at sunrise at a rate proportional to the degree of exposure to direct solar radiation. Aborted cone temperatures increase at a faster rate and to a higher degree than do those of unattacked green cones. During sunlight hours, temperatures of fully shaded, aborted cones are 3 to 5° F. above the ambient air temperature, but temperatures beneath aborted cone surfaces that are fully exposed have been observed to be 25 to 29° above this value. The temperatures in aborted cones beneath the SLE may be as much as 10 to 15° higher than those beneath the SSE at midafternoon on warm, clear days. These values vary, of course, depending on the radiation intensity and other variables which are discussed in this paper. Aborted cone temperatures fluctuate much as do black-globe temperatures (fig. 4), al-

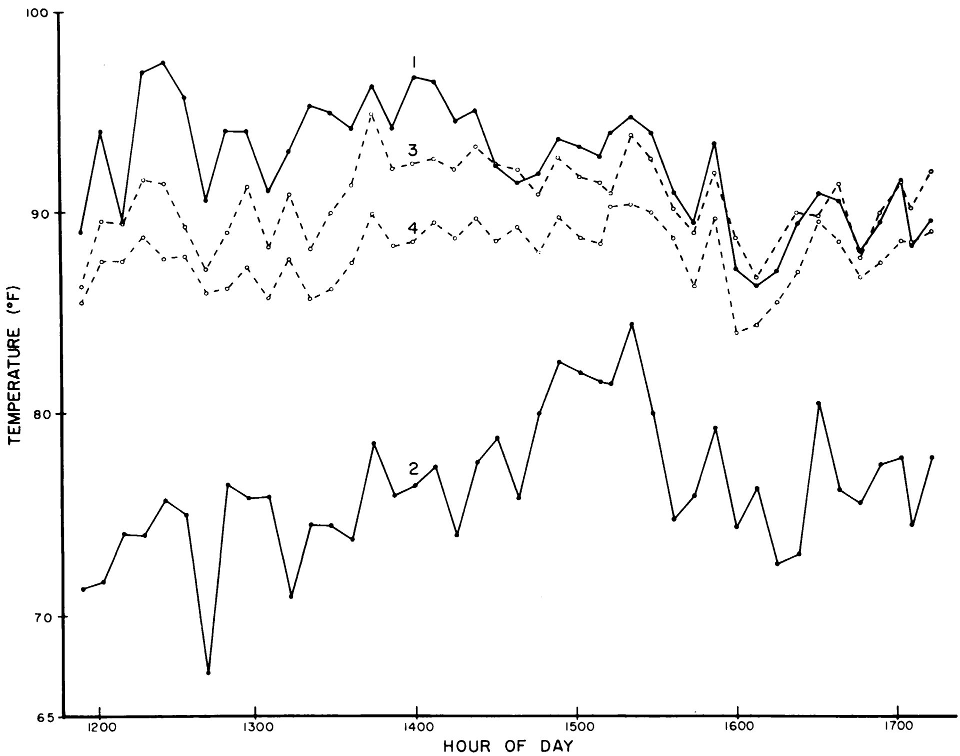

Fig. 4. Relationship between aborted cone and black-globe temperature. (*1*) Temperature in center of black globe. (*2*) Ambient air temperature two inches from black globe. (*3*) Temperature beneath surface of longest exposure (SLE) of aborted cone. (*4*) Temperature beneath surface of shortest exposure (SSE) of aborted cone. (Data were collected at Berkeley, California, July 13, 1960.)

though their respective temperatures vary because of differences in location and color.

The temperatures of green, unattacked cones increase more slowly in the morning than those of aborted cones and reach a more or less constant level during the afternoon hours. During the morning period of temperature increase, the temperatures beneath the SLE are about 3° F. greater than those beneath the SSE. The greatest differences seldom exceed 6°, even during maximum exposure. Decrease of temperature with shade is at a constant rate in contrast with the rapid, sharp decline in shaded, aborted cones.

Temperatures beneath the SLE were observed to be as much as 5° F. higher in the cones oriented perpendicular to the sun than in those oriented parallel to the radiation. This orientation was only at 1300 to 1600 hours, and the relative temperature levels varied during the morning and afternoon (fig. 5). The temperatures beneath the SLE and SSE of cones oriented perpendicular to the sun differed by 10° F., while they differed by only 5° in the cones with parallel orientation.

Aborted cones with no adjacent foliage were much cooler than those with adjacent foliage, indicating a marked effect of reflection and reradiation (fig. 6). Cones with foliage matted beneath them had SLE temperatures 10 to 12° F. higher than those with no adjacent foliage. There was also a significant difference in SSE temperatures, even though shaded, probably as a result of greater cooling by wind on the cones with no adjacent foliage. Temperatures in cones with mats of foliage placed beneath them were significantly higher than those of cones in natural situations, i.e., with the foliage in the position it normally occupies.

Cone temperatures in the upper crown (63 to 68 feet) were consistently lower than those in the lower crown (35 to 38 feet). As those cones in which temperatures were compared were sim-

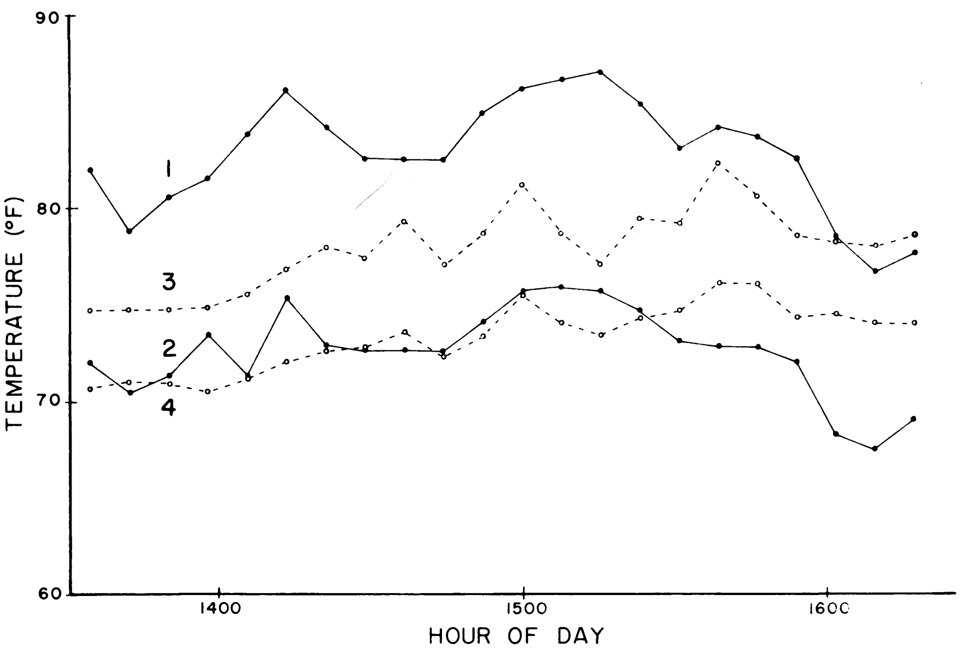

Fig. 5. Effect of cone orientation on temperature in aborted cones. The experimental cones were perpendicular or parallel to the sun at 1400 hours. (*1*) Temperature beneath SLE perpendicular to solar radiation. (*2*) Temperature beneath SSE perpendicular to radiation. (*3*) Temperature beneath SLE parallel to radiation. (*4*) Temperature beneath SSE parallel to radiation.

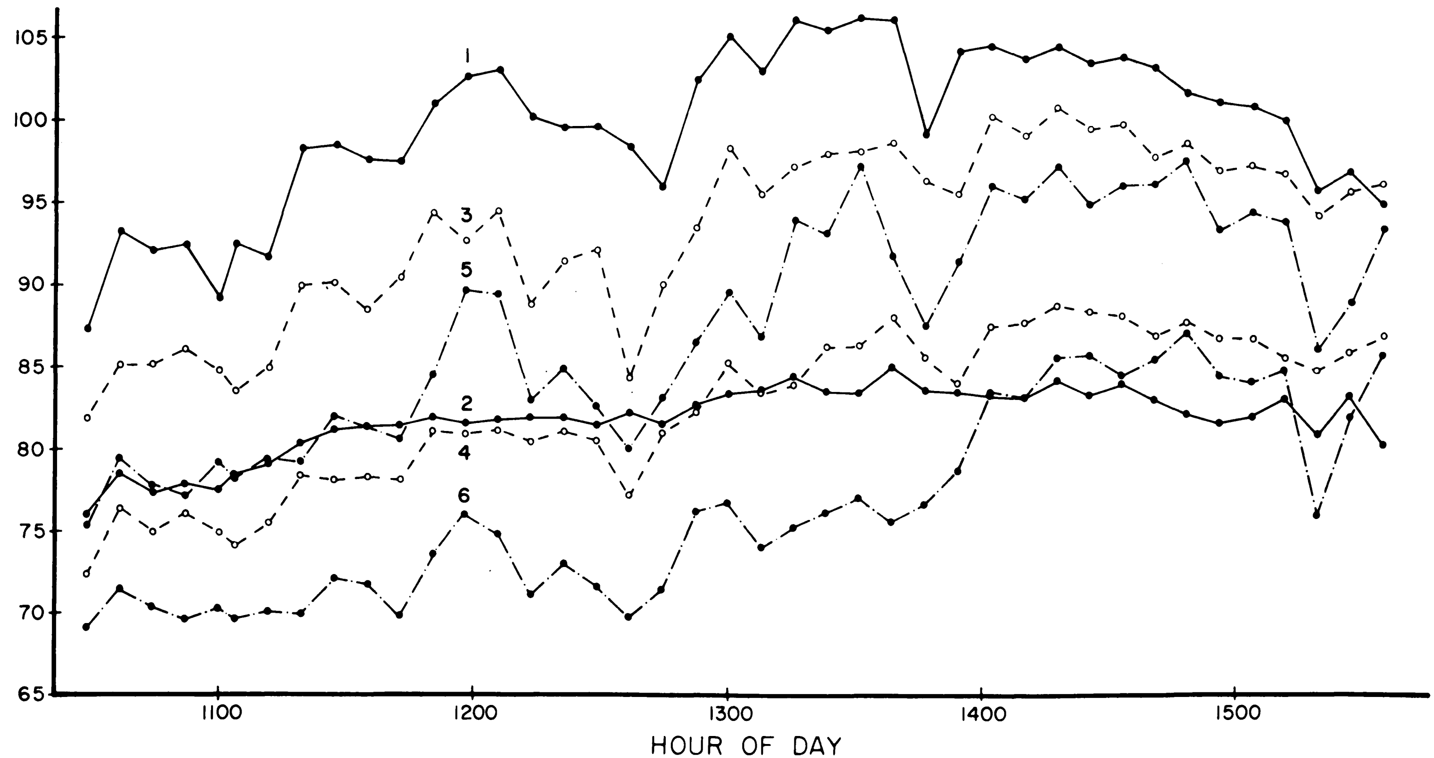

Fig. 6. Effect of adjacent foliage on cone temperature. (*1, 2*) Temperature beneath the SLE and SSE, respectively, in an aborted cone placed on a mat of foliage. (*3, 4*) Temperature beneath the SLE and SSE, respectively, in a cone in its natural location on a branch. (*5, 6*) Temperature beneath the SLE and SSE, respectively, in a cone with all adjacent foliage stripped away. (Data were collected on a clear, sunny day in July, 1960.) Figures at left indicate degrees F.

ilar with respect to other variables discussed, it was concluded that the temperature differences were caused by differences in wind velocity. The black-globe and ambient air temperatures substantiated this observation (fig. 7). Black-globe temperatures are affected by radiation, ambient air temperature, and air movement. Their positions in the two strata were selected to minimize variation in radiation, but there may have been some variation in concentration of nearby foliage.

It is well known that wind velocity increases with height in the crown (Geiger, 1950). Anemometer readings showed considerably greater air movement in the upper crown, and although low wind velocities (1 to 3 mph) were not recorded by the anemometer, they were frequently observed. Temperature fluctuations within individual cones during short periods when radiation intensity was apparently constant could not be directly correlated with wind records.

Cone temperatures were close to ambient air temperatures in the absence of solar radiation. Aborted cone temperatures decreased to air temperature within an hour after sunset, while green, unattacked cones did not decrease to this value for about two hours. Cone and black-globe temperatures remained within 1° F. of the ambient air temperature throughout foggy summer nights. Temperatures of both strata were within 1° during such nights. On clear evenings, cone and black-globe temperatures fell about 1° beneath ambient air temperatures until fog or stratus moved in from the ocean. After the latter event, all temperatures remained within 0.5° of ambient air. During one clear spring night, black-globe temperatures and those of attacked green cones remained 3 to 4° below the ambient air temperature throughout the night.

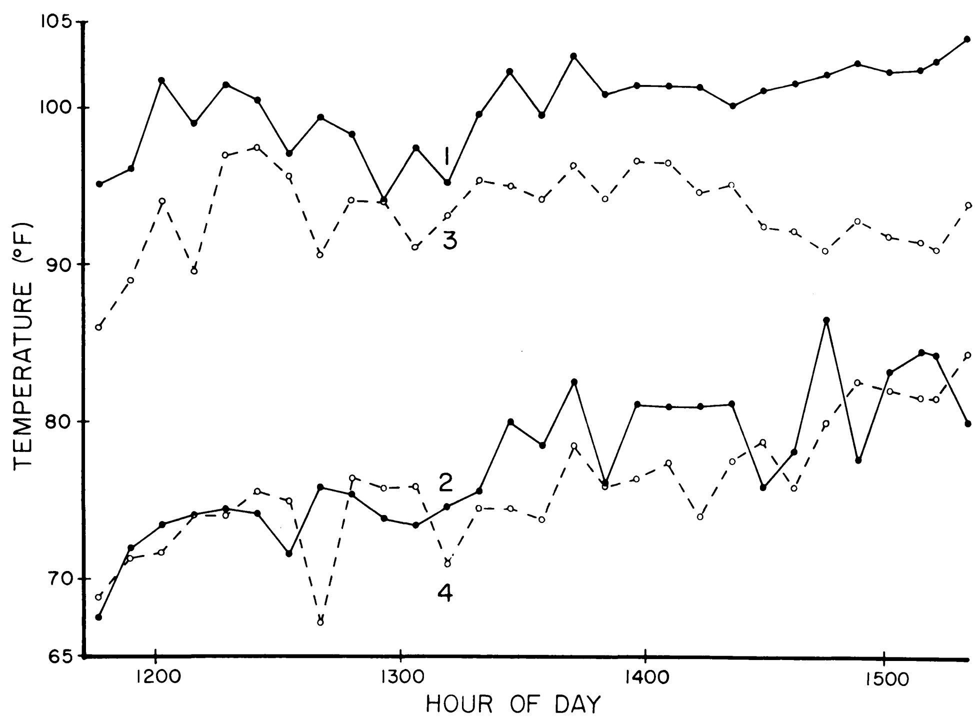

Fig. 7. Effect of height on black-globe temperature. (*1*) Black-globe temperature at 37 feet. (*2*) Ambient air temperature at 37 feet. (*3*) Black-globe temperature at 68 feet. (*4*) Ambient air temperature at 68 feet. (Data were collected on a clear, sunny day in July, 1960.)

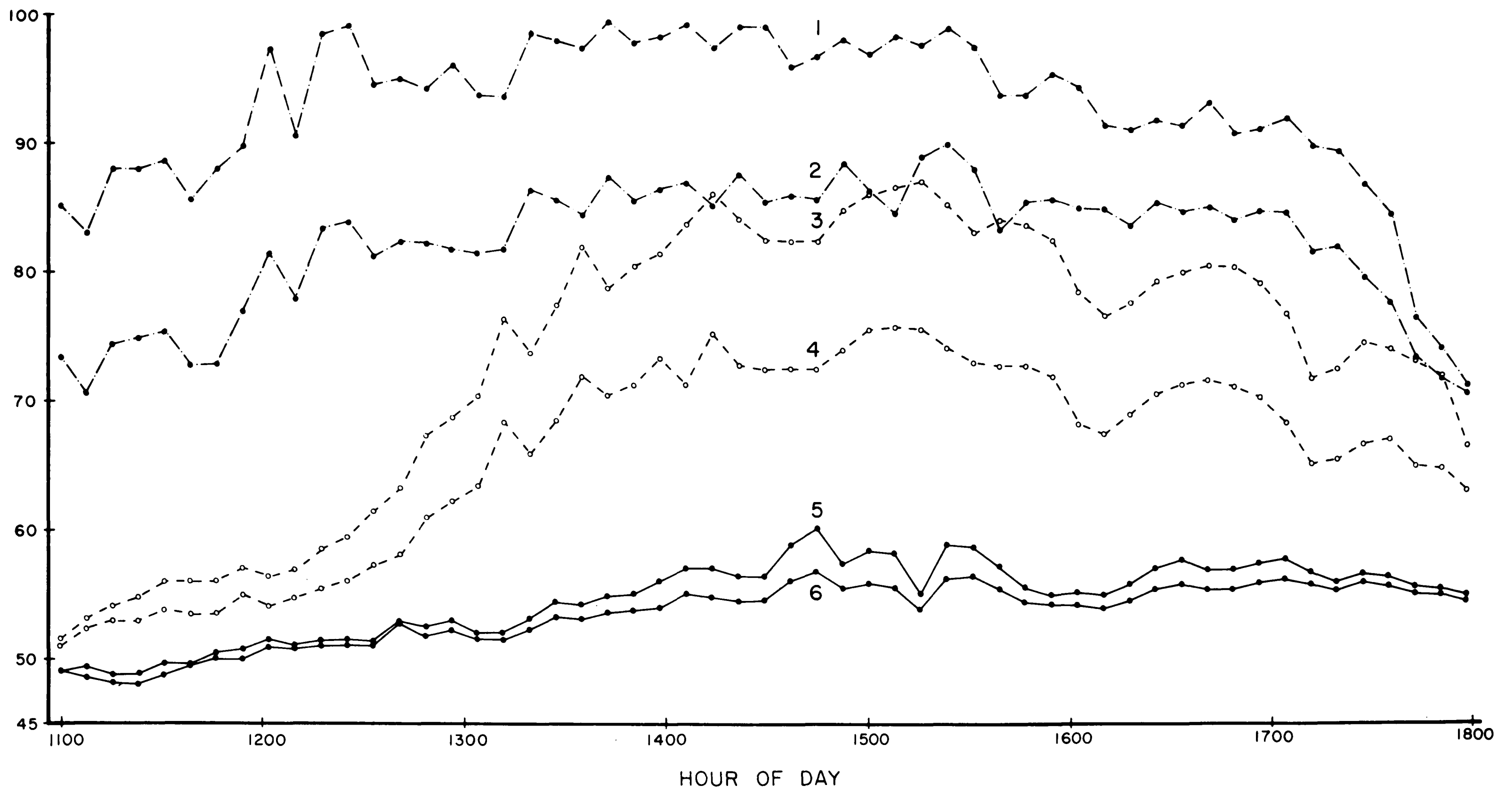

Fig. 8. Effect of fog on temperature of aborted cones. (*1, 2*) Temperature beneath the SLE and SSE, respectively, during a clear summer day (July 13, 1960). (*3, 4*) Temperature beneath same respective surfaces of same cone during a day with morning fog (June 29, 1960). (*5, 6*) Same information used on a day with persistent fog (June 28, 1960). Figures at left indicate degrees F.

Fog or stratus was present every summer night in which temperatures were recorded, which circumstance probably accounts for night temperatures remaining close to the temperature of the ambient air by the reduction of loss of radiant heat.

When fog or stratus is present, cone temperatures are drastically reduced (fig. 8). As long as fog or stratus persists during the day, cone temperatures remain only a few degrees above the ambient air temperature. The cooling effect is brought about in two ways: by reduction of solar radiation and by advective cooling.

Measurement of Cone Moisture Content

Methods. No instrumentation was available to determine directly the moisture content of aborted cones *in situ*. Aborted cones were suspended in trees in positions simulating natural locations. Three excised cones were placed 7 feet aboveground in trees at elevations of 500, 775, 960, and 1,200 feet on the same west-facing slope in Berkeley. Daily weighings (to the nearest centigram) were made with a portable torsion balance, and changes in weight were assumed to be caused by moisture gain or loss. Weighings were made at sunset, so that the net daily change (total moisture gain during night and early morning minus evaporation loss during day) was determined. After 19 days of measurements, the cones were collected and dried and the dry weights were determined. Temperatures and humidities were recorded with a hygrothermograph at the 960-foot elevation throughout the experiment. The hygrothermograph was placed 4.5 feet aboveground in a standard weather shelter, which was located in an open, grass-covered area.

Results. Four weather periods occurred during the 1961 experiment: July 6–11 was fogless, July 12–14 was foggy, July 15–19 was fogless, and July 20–25 was foggy. The moisture content of each cone at each elevation is shown for selected dates during each of the above periods (table 4). Temperature and relative humidity data, measured at the 960-foot elevation, are shown in table 5. The lower elevation (500 feet) did not receive the condensation at ground level during the foggy periods that the other elevations did, but the atmospheric humidity was high. Cones at the 500-foot elevation had the highest moisture content at the end of dry periods and about the same moisture content as cones at other elevations after foggy periods, indicating smaller gain and loss of moisture. The cones at the 1,200-foot elevation lost the greatest amount of moisture during the dry or fogless periods but gained the most during foggy periods. The 1,200-foot station was along a ridgetop, and the higher wind velocity probably accounted for the larger moisture loss during dry periods. The relationship of atmospheric temperature and humidity to aborted cone moisture gain and loss is shown for the three cones tested at 960 feet (fig. 9).

VARIATION OF SUMMER WEATHER IN THE SAN FRANCISCO BAY AREA

The strength and position of the North Pacific anticyclone control the circulation of air over the San Francisco Bay area. When the anticyclone is in its normal position (the center of this high-pressure system is in the Pacific Ocean and varies from 34 to 37° N. Lat. and 144 to 149° W. Long. during June through August), polar maritime air moves into the Bay area from the northwest (Patton, 1956). This results in marked differences in temperature and humidity between the coastal region and areas east of the Berkeley Hills. Rarely, however, the North Pacific anticyclone moves inland during

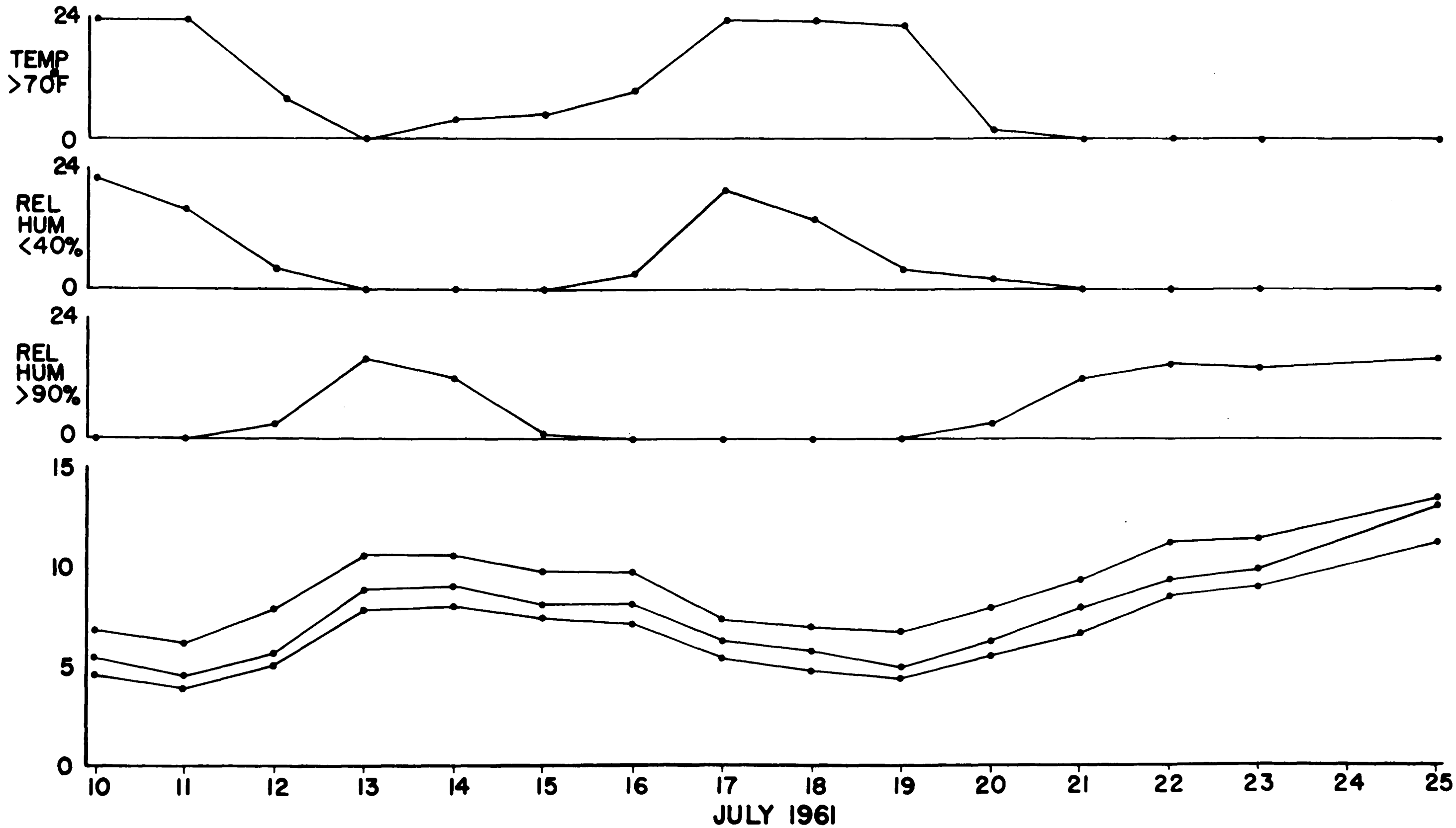

Fig. 9. Comparison of changes in moisture content of aborted cones with atmospheric temperature and humidity. (*Upper section*) Number of hours in preceding 24 hours. (*Lower section*) Per cent moisture of aborted cones. (Elevation, 960 feet, Berkeley, California.)

the summer and continental air moves into the Bay area. This air-mass type results in clear, extremely hot days, modified somewhat on the coast by the Pacific Ocean and San Francisco Bay.

Under the more common polar maritime air masses, summer temperatures along the coast are among the coldest within the continental limits of the United States. Mountain barriers, up to 1,500 feet, parallel the coast and separate the central valley of California from the Pacific Ocean. Berkeley is on the eastern shore of the large San Francisco Bay, directly east of the Golden Gate, through which extensive, fog-laden air masses pass inland.

East of the Berkeley Hills, the summer climate is hot and dry in contrast to the generally cool, humid coastal conditions. Humidity in the Bay area is highest in the summer when there is little or no precipitation, so that the annual variation in precipitation is opposite in phase to relative humidity (Patton, 1956).

Patton distinguishes between fog and stratus. Fog refers to low layers of condensation reaching to the ground level. Stratus refers to condensation that is well above ground level. Byers (1930) gives one explanation for the formation of fog: "The fog on the ocean is formed by the passage of saturated air over a cold surface caused by the upwelling of waters from the ocean depths. It is an advection fog. As the fog-bearing air moves over the cold water coastward, the surface of discontinuity in the vertical temperature gradient is elevated and the fog 'lifts' off the surface of the ocean." Fog is rare for most low elevations in the summer, but stratus is common. The daily pattern of stratus occurrence over Berkeley is illustrated for the summer of 1952 (fig. 10). Un-

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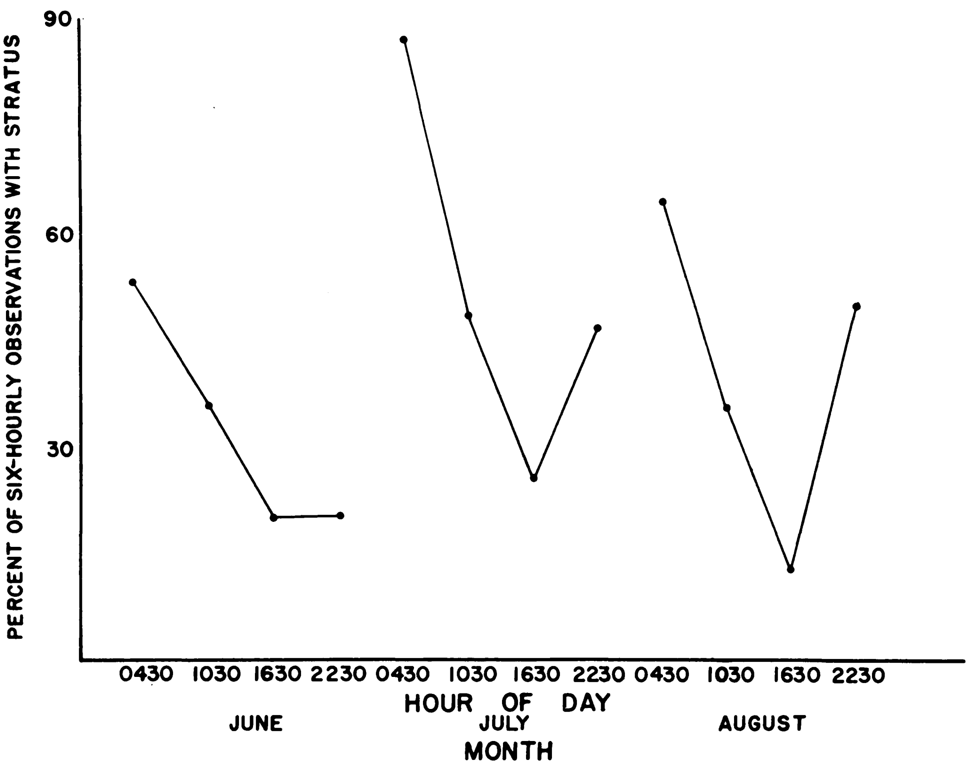

Fig. 10. Daily pattern of stratus occurrence over Berkeley, California, in the summer of 1952. Based on the data of Patton (1956), shown in his table 19.

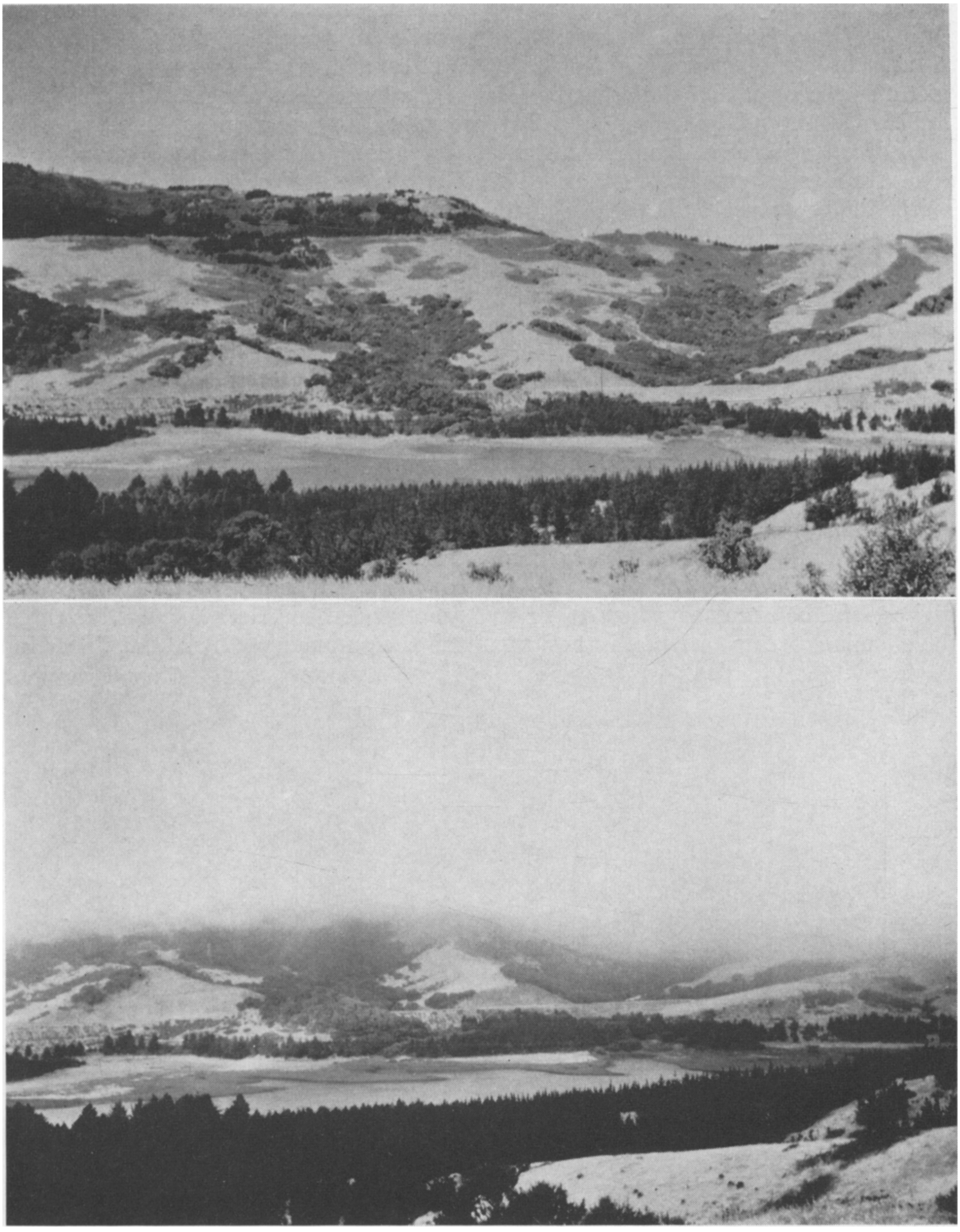

Fig. 11. (*Above*) San Pablo Dam plantation in foreground, San Pablo Ridge in background, on a clear, fogless day. (*Below*) Same area on a foggy morning. (Photos were taken toward the west.)

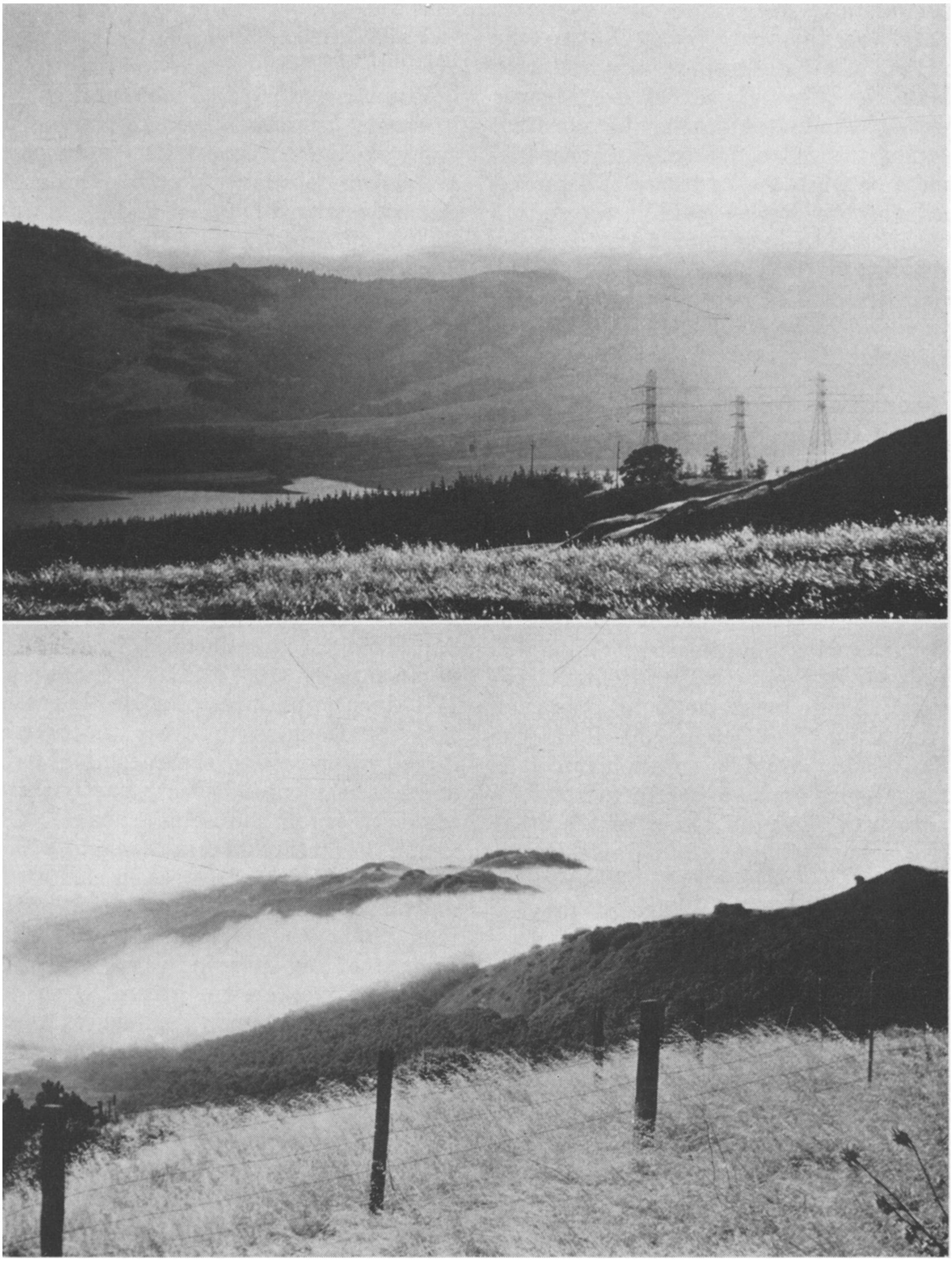

Fig. 12. (*Above*) Same area shown in figure 11, but slightly to the north, showing the evening fog which occurs from the coast east to San Pablo Ridge. (*Below*) A ridge in the Berkeley Hills on the edge of the fog belt. A morning fog is moving through a saddle in the ridge.

fortunately, such data are available only for this one year. During the night, stratus comes in contact with land elevations above 600 feet, but is usually dissipated during the morning.

The marked differences in macroclimate between the Bay area and the lee side of the Berkeley Hills seemed to constitute the most logical reason for the distribution of the cone beetle. Comparative studies were made of temperature and moisture on both sides of the Berkeley Hills.

Comparison of Coastal and Inland Temperatures

Hygrothermographs were placed in standard weather shelters in Monterey pine stands in three locations (fig. 1): Strawberry Canyon, Berkeley (960-foot elevation); San Pablo Ridge on the eastern edge of the fog belt (1,250-foot elevation); and east of San Pablo Dam out of the fog belt (500-foot elevation). These were kept in operation from June 7 to October 30, 1961. The San Pablo Dam plantation received many more hours of warm to hot temperatures than did either of the other two areas (table 6). San Pablo Ridge, immediately west of the reservoir, is characteristically the edge of the fog belt (figs. 11 and 12).

Most of the temperature differences (table 6) are characteristic of the weather which occurs when the North Pacific anticyclone is located northwest of the coast. However, about June 13 the anticyclone moved inland, causing high temperatures in the Bay region, as discussed earlier. The air temperature on June 14 reached 114° F. at San Pablo Dam plantation but only 99° in Berkeley. Similar conditions occurred again July 10 and 11, as indicated by the large number of hours above 90 and 100° at San Pablo Dam, but the maximum temperature was only 106° at San Pablo Dam and 98° in Berkeley. Under either weather system, temperatures are consistently higher inland during the summer months.

Comparison of Coastal and Inland Moisture

The effect of fog as a moisture source in coastal areas has been discussed by many workers. Almost every summer afternoon, fog collects on the hills at elevations above 800 feet and stays until it is dissipated the following morning. Occasionally, the fog remains the entire day. Means (1927) studied precipitation resulting from "fog drip" in the Berkeley Hills. Under 15–20-foot stands, he determined that equivalent precipitation from fog drip during June and July, 1927, was 2.87 inches under Monterey pines at 1,500 feet, 3.60 inches at 1,600 feet, and 2.33 inches under eucalyptus trees at 1,650 feet.

Oberlander (1956) measured the precipitation resulting from fog drip beneath trees on an exposed ridge of the San Francisco peninsula. From July 20 to August 18, 1951, fog provided 17.1 inches of precipitation beneath 125-foot Douglas fir trees that were directly exposed to the incoming fog, and lesser amounts beneath partly sheltered trees of the same species; 1.8 inches beneath 200-foot *Sequoia sempervirens* (redwood) trees in sheltered locations; and 58.8 inches beneath 20-foot *Lithocarpus densiflora* trees. The amount of fog drip increases with the height of tree crown, greater area of foliage surface, and greater ratio of foliage surface to ground area (Kittredge, 1948). Byers (1953) has pointed out that fog not only supplies moisture, but also reduces evapotranspiration. The latter effect results from reduction in the number of daylight hours and reduction of daytime temperatures.

The extent of fog in the Berkeley area is shown by the large number of hours when the relative humidity was above 90 per cent (table 7). The relative humidity reached 100 per cent on 21 mornings in June, 17 in July, and 25 in August. The atmosphere was saturated for over 10 consecutive hours on many such mornings; in fact, 5 days was the longest interval between mornings having 100 per cent relative humidity. Stratus replaced fog in September, and although saturation did not occur, relative humidities were over 90 per cent on 22 mornings during the month. The San Pablo Ridge study area was located on one of the channels through which fog moves to the east and northeast. Although the relative humidity seldom reached 100 per cent, the effect of fog was greatest here because it was blown against the foliage and cones, and condensed. Condensation onto foliage and cones was much greater when the fog was moving than when it was more dense but stationary. The plantation area east of San Pablo Dam receives no dense fog, but is often exposed to moist air when the coast fog dissipates inland.

The data clearly show marked differences in relative humidity among the three areas (table 7), largely as a result of differences in fog and stratus occurrence. Adults of *Conophthorus radiatae* remain within the aborted cones throughout the summer, fall, and winter, and there is almost no rain from May until late October. During this period, the atmospheric humidity is the only source of cone moisture. For these reasons, it was postulated that the large differences in temperature and moisture were responsible for the restriction of *C. radiatae* to those areas receiving summer fogs.

Effects of Temperature on Cones in the Study Area

Temperatures of attacked cones were measured during the spring of 1961 when eggs were present, and later during the larval development period. Cone temperatures were compared only in Berkeley and the San Pablo Dam plantation.

During warm spring days, cone tem-

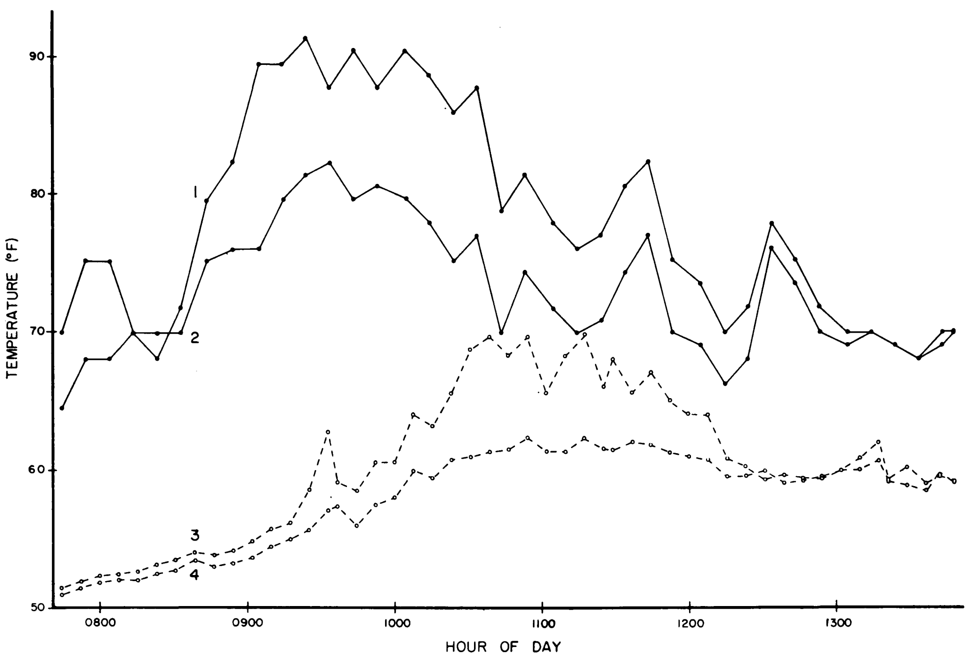

Fig. 13. Temperature beneath SLE (*1*) and SSE (*2*) of an aborted cone near San Pablo Dam; temperature beneath SLE (*3*) and SSE (*4*) of an aborted cone in Berkeley. Both were on the east side of the crown, and were consequently exposed in the morning and shaded during the afternoon. The Berkeley area was covered by stratus in the morning, and during the afternoon the ambient air temperature was much lower than at San Pablo Dam because of the effect of advective cooling.

peratures, coastal and inland, occasionally exceeded 95° F. but never reached 104°. Results of laboratory experiments indicated that little, if any, mortality could be expected at these temperatures unless they persisted. Summer cone temperatures in the San Pablo Dam plantation area are consistently higher than those of the Berkeley area, but seldom reach the tolerance limits of the beetle. Figure 13 shows the temperatures recorded from similar cones in Berkeley and the San Pablo Dam plantation on a typical summer day.

During the infrequent hot periods described earlier, when ambient air temperatures rose to over 100° F., it is certain that cone temperatures rose to levels causing mortality. On clear, warm days, the temperature beneath the SLE was observed to be 25 to 29° greater than that of the ambient air, which at this time was below 65°. It is possible that even greater differences occur when the ambient air temperature becomes high. Unfortunately, temperature-recording equipment was not in place during one of the infrequent hot periods. Many of the exposed surfaces of cones were scalded on June 14, 1961, and dissection of cones showed a high mortality of pupae and second-instar larvae. This mortality was greater in the San Pablo Dam plantation area than in Berkeley.

Effects of Moisture on Cones in the Study Area

Four aborted cones were suspended in trees on San Pablo Ridge, in Strawberry Canyon (Berkeley), and at the San Pablo Dam plantation, each group near the site of the hygrothermograph in its area. The cones were periodically weighed from July 28 through October 27, 1961, when the first rain occurred. The average moisture content and standard deviation for each weighing and each location are shown in figure 14. The standard deviations are small following dry periods and high after foggy periods. The high standard deviations result from differences between exposure of cones to fog, amounts of foliage adjacent to cones (on which fog condenses and drips or runs off), and permeability differences.

The cones in Berkeley received the greatest number of hours of fog and maintained a consistently higher moisture content than did the cones placed in the San Pablo Dam plantation. Aborted cones on San Pablo Ridge had high moisture contents throughout most of the study period, even though they did not receive as many hours of fog and were exposed to longer periods of low humidity than the cones in Berkeley. The San Pablo Ridge area, being located on one of the few channels through which fog moves inland, is restricted to a relatively small area but does demonstrate the great effect that fog can have.

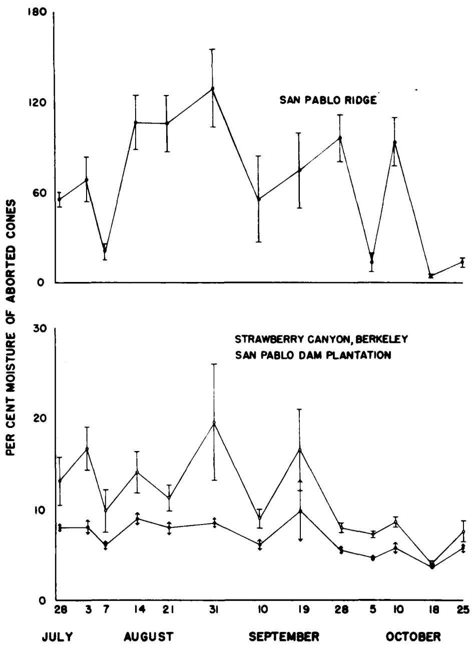

Fig. 14. Average moisture content (dry-weight basis) and standard deviation for three groups of four aborted cones, suspended in trees on San Pablo Ridge, in Strawberry Canyon (Berkeley), and at the San Pablo Dam plantation, respectively. Graphs appear in that order, reading from top to bottom. Weights were recorded periodically from July 28, 1961, until the first rain late in October.

Comparative Field Studies of Cone Beetle Mortality

To evaluate the effects of temperature and moisture in the San Pablo Dam plantation area, ovipositing females were collected in Berkeley in March, 1961, and transferred into cones of the San Pablo Dam plantation. In June, aborted cones from Berkeley were fastened to trees at the San Pablo Dam plantation in similar locations to those originally occupied, and were compared with similarly treated cones placed on San Pablo Ridge and in Berkeley. Since the cone beetle was already present on San Pablo Ridge and no geographic barrier occurred from this location to the San Pablo Dam plantation a mile below, there was no real threat in artificially transporting living beetles into the plantation. Collections were made from the above cones on September 29 after the end of the summer fog period and on October 27 after the first fall rain.

The first collection of aborted cones from the San Pablo Dam plantation contained 62 adults, of which 12 (19 per cent) were alive. Cone samples from San Pablo Ridge contained 20 adults, and 5 (25 per cent) were alive. No sample was taken in Berkeley at this date. The second collection of cones from the San Pablo Dam plantation contained 68 adults, and only 1 (1.4 per cent) was alive; 39 adults were collected from cones on San Pablo Ridge, and 24 (63 per cent) were alive; and 32 out of 96 adults from test cones in Berkeley were alive (33 per cent). Unfortunately, the number of adults present in the aborted cones used in this study was much less than anticipated, so that the sample size was much smaller than planned. This, of course, reduced the certainty of results; nevertheless, a general pattern was evident. The highest adult survival occurred on San Pablo Ridge, where the cone moisture content was high and temperatures lower than for the plantation to the east. The lowest survival occurred at the San Pablo Dam plantation, where the cone moisture content was consistently lower than in the other areas throughout the summer.

Progeny were present in only 5 out of 30 cones on the San Pablo Dam plantation, into which ovipositing females were placed in March. Only 14 of the total of 51 progeny developed into adults. Most, if not all, of the remainder were killed by high temperatures during the period June 13 to 15. The stages killed (pupae and large second-instar larvae) indicate that this was the approximate period of death.

This study was concerned with the ability of *Conophthorus radiatae* to inhabit areas outside the fog belt. The cone beetle is not present throughout all coastal areas inhabited by Monterey pine (Schaefer, 1962). No information was found that might explain the absence of the beetle from Monterey pine stands at Cambria and Swanton, California, coastal areas to the south which receive frequent summer fogs and to which Monterey pine is native. However, it has been found at Pacific Grove and on nearby Point Lobos, where the tree is very common (Schaefer, 1962). A heavily forested area near Monterey gave rise to the tree's common name.

SUMMARY

The survival of *Conophthorus radiatae* Hopkins is greatly reduced in areas east of the coastal fog belt. The spring climatic conditions are similar in coastal and inland areas, but there are great differences in summer conditions, resulting mainly from the effects of fog in coastal areas. It appears that infrequent high summer temperatures are primarily responsible for the reduction of immature survival, while the combination of low humidity, warm to high temperatures, and no precipitation reduces adult survival in inland areas.

Fog accompanying a cold air mass markedly reduces the temperatures in coastal areas and provides precipitation equivalent to many inches of rainfall; these effects appear to reduce mortality to a large degree.

Although a small per cent of the beetles implanted into the inland area survived throughout the study period, it is possible that further mortality would occur during the late fall and winter and also that underpopulation phenomena might operate to prevent successive generations from becoming established. During two years of study and collection at the San Pablo Dam plantation, no living beetles were seen. Since beetles were found just above this region on San Pablo Ridge and no geographic barriers are present, it appears that the species is unable to establish itself in the San Pablo Dam plantation.

It may be possible that a small per cent of incoming beetles could survive in such an inland area; however, it is very unlikely that high populations, like those occurring in Berkeley, could become established in such localities as the San Pablo Dam plantation because of the reduced survival described above. A few living beetles have been found on the east slope of San Pablo Ridge, a few hundred feet below the crest. The fog often "slops over" into this area, thus producing more favorable conditions.

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TABLE 1

MORTALITY OF *CONOPHTHORUS RADIATAE* EGGS, LARVAE, PUPAE, AND ADULTS AT HIGH TEMPERATURES

Stage	Temp. °F.	Number of exposures	Length of exposure (hours)	Number in sample	Number in check	Per cent mortality	Per cent check mortality	Adjusted mortality
Adults	122	1	4	33	55	76	5	71
	122	1	8	17	55	100	5	100
	113	1	6	14	20	50	25	25
	113	1	8	53	20	60	25	35
	113	2	8	29	55	100	25	100
	104	1	8	9	20	33	25	8
	104	2	8	14	20	36	25	11
Pupae	113	1	4	6	7	0	0	0
	113	1	8	10	7	10	0	10
Second-Instar	113	1	4	5	5	0	0	0
	113	1	8	5	10	100	0	100
	104	1	8	5	10	0	0	0
	104	2	8	4	5	0	0	0
First-Instar	104	1	6	3	4	0	0	0
	104	2	4	4	4	0	0	0
	104	2	6	4	4	0	0	0
Eggs	104	1	6	10	12	0	17	0
	104	2	6	12	12	42	17	25

TABLE 2

MOISTURE CONTENT OF ABORTED CONES OF *PINUS RADIATA* UNDER CONTROLLED RELATIVE HUMIDITIES AT 68° F.*

Replicate number	IMC†	EMC‡ at 22% R.H.	IMC	EMC at 55% R.H.	IMC	EMC at 76% R.H.	IMC	EMC at 95% R.H.
1	7.2	3.7	7.8	8.0	5.3	10.1	7.2§	>20
2	7.1	3.8	7.5	7.9	6.4	10.2	7.2	>24
3	7.1	3.8	7.0	7.2	9.3	10.7	7.2	>21

* All data are shown as per cent of dry weight.
† IMC = "initial moisture content."
‡ EMC = "equilibrium moisture content."
§ Dry weight, based on average dry weight of all cones placed in other humidities.

TABLE 3

SURVIVAL OF *CONOPHTHORUS RADIATAE* ADULTS IN ABORTED CONES AT CONTROLLED HUMIDITIES AND 68° F.

Exposure in days	22% R.H.		55% R.H.		76% R.H.		95% R.H.	
	No. in sample	Per cent living	No. in sample	Per cent living	No. in sample	Per cent living	No. in sample	Per cent living
64	22	27	16	56	22	95	0	..
85	32	22	0	..	13	38	23	48

TABLE 4

PER CENT MOISTURE OF ABORTED CONES (DRY-WEIGHT BASIS) DURING FOGGY AND FOGLESS PERIODS* IN BERKELEY, CALIFORNIA—JULY, 1961

Elevation (feet)	Replicate number	July 7	July 11	July 14	July 19	July 25
500	1	9.3	6.2	9.7	7.2	12.8
	2	13.3	6.2	8.8	6.7	10.7
	3	..	..	..	..	....
775	1	8.1	4.1	9.9	5.2	12.9
	2	9.5	4.1	7.8	5.0	10.7
	3	12.5	4.2	7.8	5.1	10.8
960	1	11.2	3.9	8.2	4.3	11.3
	2	11.3	6.2	10.7	6.7	13.5
	3	10.7	4.7	9.1	5.0	13.3
1,200	1	9.8	2.5	5.8	3.0	8.2
	2	7.8	2.7	6.4	3.3	10.9
	3	7.3	2.8	6.1	3.2	11.8

* July 12–14 and 20–25 were foggy; other days were fogless.

TABLE 5

HUMIDITY AND TEMPERATURE DATA FROM THE 960-FOOT ELEVATION, BERKELEY, CALIFORNIA, DURING JULY, 1961

Period	Relative humidity (hours)				Temperature °F. (hours)		
	Saturated	Greater than 90%	Less than 40%	Less than 30%	Greater than 90	Greater than 80	Less than 70
July 6–11	0	1	68	47	14	53	93
July 12–14	22	29	2	0	0	0	5
July 15–19	0	2	43	19	1	26	80
July 20–25	56	72	0	0	0	0	10

TABLE 6

NUMBER OF HOURS PER WEEK* ABOVE INDICATED FAHRENHEIT TEMPERATURE LEVELS FOR BERKELEY, SAN PABLO RIDGE, AND SAN PABLO DAM PLANTATION, JUNE 7–OCTOBER 30, 1961

Week	Berkeley				San Pablo Ridge				San Pablo Dam			
	70° +	80° +	90° +	100° +	70° +	80° +	90° +	100° +	70° +	80° +	90° +	100° +
June 7–12	4	0	0	0	0	0	0	0	16	0	0	0
12–19	79	43	6	0	59	40	15	2	67	46	28	8
19–26	30	2	0	0	22	2	0	0	60	38	6	0
June 26-July 3	38	8	0	0	19	4	0	0	45	20	7	0
July 3–10	45	20	4	0	25	12	0	0	47	27	15	5
10–17	73	27	10	0	40	18	0	0	79	42	24	11
17–24	61	22	1	0	51	20	0	0	71	36	24	3
24–31	6	0	0	0	14	3	0	0	20	7	0	0
August 1–7	35	1	0	0	36	12	0	0	48	16	5	0
7–14	19	0	0	0	38	5	0	0	48	19	1	0
14–21	36	5	0	0	58	10	0	0	47	17	5	0
21–28	4	0	0	0	8	0	0	0	39	4	0	0
August 28–September 4	23	4	0	0	34	10	0	0	58	19	9	0
September 4–11	10	2	0	0	55	23	4	0	38	24	11	0
11–18	6	2	0	0	17	5	0	0	19	7	1	0
18–25	6	0	0	0	18	2	0	0	27	11	1	0
September 25–October 2	46	5	0	0	61	22	0	0	54	37	6	0
October 2–9	16	0	0	0	38	14	0	0	35	15	0	0
9–16	64	21	2	0	58	19	4	0	42	24	15	0
16–23	34	5	0	0	48	15	3	0	24	15	7	0
23–30	0	0	0	0	0	0	0	0	5	0	0	0
Totals	635	167	23	0	699	236	26	2	889	424	165	27

* Each week includes from 0800 hours on the first day to the same time on the last indicated day.

TABLE 7

NUMBER OF HOURS PER WEEK* ABOVE INDICATED RELATIVE HUMIDITY LEVELS AT BERKELEY, SAN PABLO RIDGE, AND SAN PABLO DAM PLANTATION, JUNE 7–OCTOBER 30, 1961

Week	Berkeley				San Pablo Ridge				San Pablo Dam			
	20% and below	30% and below	90% and above	100%	20% and below	30% and below	90% and above	100%	20% and below	30% and below	90% and above	100%
June 7–12	0	0	35	14	0	0	30	8	0	0	20	1
12–19	0	13	26	19	2	45	32	4	2	17	18	1
19–26	0	0	44	36	2	12	36	1	0	5	30	1
June 26–July 3	0	4	36	22	0	8	36	0	0	18	29	1
July 3–10	0	19	36	17	12	38	30	1	3	20	12	0
10–17	1	19	32	24	16	66	22	1	2	26	16	0
17–24	0	4	44	35	4	58	40	0	2	19	27	0
24–31	0	0	94	75	0	4	84	0	0	8	68	0
August 1–7	0	0	68	54	1	6	38	0	0	5	31	0
7–14	0	0	72	52	0	2	62	0	0	2	31	0
14–21	1	13	59	41	12	33	42	0	8	13	40	0
21–28	0	0	102	66	0	0	66	0	0	3	45	0
August 28–September 4	11	16	66	55	27	38	61	0	23	37	44	0
September 4–11	0	1	44	0	20	54	36	0	5	26	27	1
11–18	0	0	84	0	0	5	81	0	0	5	43	0
18–25	0	0	64	0	4	8	46	0	6	14	24	2
September 25–October 2	0	14	22	0	19	72	21	0	7	38	18	0
October 2–9	0	14	30	1	5	40	14	0	6	20	24	0
9–16	0	19	29	0	0	36	36	0	0	32	24	0
16–23	0	0	17	0	0	22	21	0	0	7	8	0
23–30	0	15	37	0	0	20	34	0	2	20	21	0
Totals	13	151	1,041	511	124	567	868	15	66	335	600	7

* Each week includes from 0800 hours on the first day to the same time on the last indicated day.

LITERATURE CITED

BOND, T. E., and C. F. KELLY
1955. The globe thermometer in agricultural research. Agr. Eng. **36**:251–55.

BYERS, H. R.
1930. Summer sea fogs of the central California coast. Univ. Calif. Publ. Geog. **3**:291–338.
1953. Coast redwoods and fog drip. Ecology **34**:192–93.

GEIGER, RUDOLF
1950. The climate near the ground. (Translated by M. N. Stewart *et al.*) Harvard University Press, Cambridge, Mass. 482 pages, 181 figures.

HENSON, W. R.
1958. The effects of radiation on the habitat temperatures of some poplar-inhabiting insects. Can. Jour. Zool. **36**:463–78.

HENSON, W. R., and R. F. SHEPHERD
1952. The effects of radiation on the habitat temperatures of the lodgepole needle miner, *Recurvaria milleri* Busck (Gelechiidae: Lepidoptera). Can. Jour. Zool. **30**:144–53.

KITTREDGE, J.
1948. Forest influences. McGraw-Hill Book Co., New York. 394 pages.

LEIGH, T. F., and R. F. SMITH
1959. Flight activity of *Colias philodice eurytheme* Boisduval in response to its physical environment. Hilgardia **28**(19):569–624.

MEANS, T. H.
1927. Fog precipitated by trees. Science **66**:402–3.

OBERLANDER, G. T.
1956. Summer fog precipitation on the San Francisco peninsula. Ecology **37**:851–53.

PATTON, C. P.
1956. Climatology of summer fogs in the San Francisco Bay area. Univ. Calif. Publ. Geog. **10**(3):113–200.

SCHAEFER, C. H.
1962. Life history of *Conophthorus radiatae* (Coleoptera: Scolytidae) and its principal parasite, *Cephalonomia utahensis* (Hymenoptera: Bethylidae). Ent. Soc. Amer. Ann. **55**: 569–77.

WELLINGTON, W. G.
1950. Effects of radiation on the temperatures of insectan habitats. Sci. Agr. **30**:209–34.

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