be developed by genetic recombination aided perhaps by outside pollen sources. It may be that the balds have tended to develop, or at least grow larger, with cooling climate rather than warming, as the deciduous forest retreated faster than spruce has invaded downward.

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THE LIMITATION OF TWO LEAFY MISTLETOES OF THE GENUS *PHORADENDRON* BY LOW TEMPERATURES

Phoradendron, new world counterpart of the European *Viscum* or Christmas mistletoe, is mainly tropical or subtropical in occurrence. Only the group Boreales, found primarily in southern and western United States and in the highland plateau of northern Mexico, grows in temperate regions (Trelease 1916). In the Atlantic States, one species of this group extends as far north as New Jersey. In the milder Pacific States, several species are found in Oregon, one of them, *Phoradendron villosum* Nutt, up to approximately latitude 45° N. These limits are much more restricted than those of the host trees and shrubs, suggesting a differential response to some climatic factor, most probably temperature. The role of low temperatures in limiting the incidence and range of two species of *Phoradendron* occurring on conifers on the Pacific Coast is indicated by the following observations in California.

REDUCTION OF *Phoradendron densum* BY COLD

A period of unseasonable cold was experienced over most of the Pacific Coast in the first half of December, 1932. In northern California, record minimum temperatures were registered at many stations (U. S. Weather Bureau 1932). Early the following summer A. K. Crebbin of the U. S. Forest Service informed W. C. Bramble and the writer that much of the mistletoe, *Phoradendron densum* Torr., on western juniper, *Juniperus occidentalis* Hook., in Little Shasta Valley, northwest of Mount Shasta in California, appeared to have died from the effects of the unusual cold of the preceding December.

A preliminary examination at several locations on the Valley floor confirmed that practically all mistletoe plants were dead, including both external parts and the endophytic system within the bark and wood of the host junipers (Fig. 1). The only exceptions found were young plants which, at the time of the freeze, possessed only one or two small aerial shoots, with limited foliar development. The shoots of such plants had been killed back to the bases in the bark, but by the time of our examination in July new buds had developed on these bases. The host trees showed no primary damage.

A more extensive survey of the killing was made by the writer a year later, by which time the living and dead plants could be distinguished with certainty without recourse to sectioning of the host tissues to determine whether or not any portion of the endophytic system remained alive. Not only Little Shasta Valley but also portions of the main Shasta Valley, of which Little Shasta Valley forms a branch, were included in the survey. Shasta Valley, which extends in a northwesterly direction from the northwestern base of Mount Shasta, lies at an elevation of a little more than 2,600 feet in the

FIG. 1. Remains of mistletoe plants killed on western juniper by low temperatures, Little Shasta Valley, California. Photographed approximately 18 months after death.

lowest portion and rises gradually toward the southeast to about 3,300 feet. Parts of the valley floor are dotted with low volcanic hills rising 100 to 200 feet above the surrounding level. These hills and uncultivated portions of the Valley floor carry an open stand of western junipers, formerly heavily infected with mistletoe. The parasite was particularly heavy above the 3,000-foot level in the southeastern portion of the Valley at the time of the freeze in 1932 (Fig. 2).

FIG. 2. Mistletoe on western juniper at above 3,000 feet elevation in the southeast portion of Shasta Valley; photographed in 1934.

Living and dead mistletoe infections were tallied at 6 locations in the lower part of the Valley, the plants being divided in the tally according to their apparent size at the time of the cold wave into small, medium, and large sizes. The results are shown in TABLE I.

TABLE I.—Mortality of *Phoradendron densum* plants from low temperature at 6 sample areas in lower Shasta Valley, California, 1932

Area	Number of Plants by Size Classes								
	Small			Medium			Large		
	Living	Dead	Total	Living	Dead	Total	Living	Dead	Total
I	2	17	19	3	61	64	2	38	40
II	2	3	5	5	23	28	6[1]	20	26
III	11	17	28	6	78	84	4	48	52
IV	15	56	71	4	73	77	1	78	79
V	8	8	16	8	39	47	0[2]	34	34
VI	1	19	20	2	52	54	15	53	68
Totals....	29	120	159	28	326	354	28	271	299
Percent dead....	75			92			90		

[1] All but 1 of the 4 had only a small amount of foliage at the time of the freeze.
[2] All located in the tops of tall trees.

Areas II and III were located on a rise of ground and the percentage of killed plants on them was somewhat lower than on Areas I and IV, the nearest areas on low ground. This difference indicated a rather pronounced temperature inversion at the lower levels in the Valley, an indication supported by the fact that all of the large-size infections that had survived on Area VI were located in the tops of tall trees. Area V was on low ground adjoining a meadow. No reason was apparent for the somewhat higher proportion of survivals of small and medium sized plants on it as compared with Areas I and IV. Most infections were alive on trees located on the upper slopes of hills projecting from the Valley floor. In the southeastern portion of the Valley, at elevations above about 2,900 feet, little or no killing of mistletoe had occurred.

In Shasta Valley, most plants of *Phoradendron densum* were found to occur at the end of short club-shaped branches of the host juniper, bearing no host foliage. Apparently such infections had become established on side twigs of the host and had eventually suppressed the foliage present, after which the branch was kept alive by the presence of the parasite. The ability of the leafy mistletoes to support woody branches or stems of the host without the aid of host foliage has been well established experimentally (Tubeuf 1923). Counts of annual rings in these stub branches indicated ages between 20 and 40 years in most instances. The absence of any stubs much older than 40 years although many supporting junipers were more than 150 years old and had numerous large branches, suggests that similar killing of mistletoe by cold may have taken place some 40 years earlier. Temperature records for the area are not available for that period, but it is known that January, 1888, was very cold in northern California, and heavy mortality in mistletoe plants may have occurred at that time.

Hourly records of temperature for the 1932 cold wave were recorded at the Montague Airways Weather Station, then located just outside of the town of Montague in Shasta Valley at an elevation of 2,630 feet. Minimum temperatures recorded at the Station between December 9 and 15 were:

December 9	— 6°F.	December 13	—10°F.
December 10	—14°F.	December 14	—11°F.
December 11	—14°F.	December 15	— 2°F.
December 12	—12°F.		

Between the evening of December 9 and the morning of December 14 there were 72 hours below 0°F. During the periods of lowest temperatures, the air was calm or nearly so and the sky was clear—conditions favoring the development of a temperature inversion over the valley floor.

This period of low temperature was noteworthy not only for its duration and for the low minimums reached at the lower elevations in Shasta Valley but also because it occurred relatively early in the season, following a November which was warmer and drier than usual. Accordingly, plants had not been conditioned to attain maximum dormancy and the effect was undoubtedly more pronounced than would have been the case had the cold period come later in the winter.

In January, 1937, another series of low temperatures occurred in the Valley but not as marked as in 1932 and with somewhat different effects. The lowest temperature registered at the Montague Airways Station was —9°F. on January 21, maintained for 4 hours. On January 7, temperatures had dropped to —5°F. and continued low for several days, but at no time during the month did they reach the minimum levels registered in 1932.

Where mistletoe killing was pronounced in 1932, there was practically no killing in 1937 of the plants that had survived the earlier freeze or had become established during the intervening period. Higher in the Valley, at around the 3,000-foot level, most of the external shoots of large mistletoe plants were killed, but many smaller plants escaped; the haustoria of more than half of the infections on which external shoots had been killed back appeared to be alive late the following July. No follow-up examination was made in succeeding years to determine ultimate mortality. Near Dwinnell Reservoir, in the southern portion of the Valley, at an elevation of about 2,800 feet, heavy mortality in mistletoe plants was noted, but the effects of cold were somewhat confused by dieback of the host trees from fall drought and by branch killing from the effects of cold convectional winds evidently induced during one or more of the periods of low temperature.

An interesting after-effect of the cold damage to mistletoe in 1937 was noted in the middle part of the Valley. Mistletoe was so dense in the tops of many trees here that it had almost totally suppressed the normal juniper foliage. When this mass of functioning leaf surface was suddenly killed by the low temperatures, the very small remaining amount of host foliage was apparently unable to support the tops and many of them died back as a result. Drought-caused dieback of the tops was not a complication here as around the Dwinnell Reservoir, probably because of better soil moisture conditions, and no dieback resulted in tops or branches that had not been heavily defoliated by the loss of mistletoe shoots.

Another period of below-normal temperatures occurred in Shasta Valley in January, 1949, but was not as severe as the two previously described. By this time, the Airways Weather Station had been moved to a new location several miles distant from the former one but at approximately the same elevation. The coldest temperature registered there during the cold spell was —3°F. on January 25.

An examination of mistletoe plants on junipers the following May disclosed that considerable killing back of shoots and foliage of the parasite had occurred in the lower parts of the Valley, but no case could be found in which the endophytic system had been killed. Growth of new shoots from this system was just beginning.

The observed effects of subnormal cold on the mistletoe plants in Shasta Valley for these three periods within the past 25 years supply strong evidence that minimum temperatures constitute a major control of the incidence of the parasite there. These observations also suggest that low temperatures account for the absence of the species in juniper stands to the eastward, where absolute minimum temperatures become lower with the transition to a continental type of climate.

Interesting physiological questions are raised by the partial damage of very young plants with limited shoot development as contrasted with the complete death of larger and older plants in comparable locations during the 1932 freeze. Evidently, more than the specific minimum temperatures reached by the tissues of the parasite was involved in determining whether or not the effect would be lethal.

Reduction of *Phoradendron pauciflorum* by Cold

Phoradendron pauciflorum Torr., a mistletoe that characteristically colonizes the tops of white fir, *Abies concolor* (Gord. & Glend.) Lindl. (Fig. 3) over part of the range of the latter host in California, is another species with a distribution much more restricted than its host. White fir is found without any extensive interruptions throughout the Sierra Nevada, and along the west slope of the southern part of this mountain range, *P. pauciflorum* is very common in white fir tops. However, there is no record of the occurrence of this mistletoe north of the Stanislaus River drainage. The viscid-coated seeds of the species, as in other species of *Phoradendron,* are disseminated primarily by birds. No observations appear to have been made as to the species of birds chiefly concerned in the dispersal of the seeds of *P. pauciflorum,* but no bird species likely to be concerned has a northerly range limit corresponding to the northern limit of the parasite. There seems to be no reason for believing that the restriction in range of the mistletoe can be attributed to the absence of bird carriers over the rest of the Sierra Nevada.

Fig. 3. *Phoradendron pauciflorum* in the tops of white firs, Stanislaus National Forest near Pinecrest, California.

In 1930, two permanent plots were established on conservatively logged forest land near Pinecrest, California, with the objective of recording changes in pathologic conditions on the plots at intervals over a long sequence of years. Detailed re-examinations of the plots have been made at approximately 10-year intervals. Considerable numbers of young sapling and pole-sized white firs remained on the plots after logging, and on one plot most of the large, overmature firs, many with heavy *P. pauciflorum* infections in the tops, had been left. When the original plot records were taken in 1930, young infections of the parasite were noted in crowns of approximately 60 pole-sized trees. Heavier infections were present in the tops of the larger trees, for which it was not possible to distinguish and record the individual mistletoe plants. Ten years later practically all of the individual infections were still present and a few additional ones had become established. In the 1951 re-examination, however, 42 infections, scattered over 26 trees, were noted as dead or disappeared. On many additional trees, reduction in mistletoe was observed where the parasite had been recorded on a quantitive basis rather than by individual plants. On other trees, especially those with top infections, the rating for the parasite had not changed.

No changes in shading or other stand conditions sufficient to account for this reduction in mistletoe incidence were found to have occurred. The most likely hypothesis concerning the cause appeared to be that the dead plants had been killed by low temperatures during the exceptionally cold winter of 1949. This conclusion was supported by their condition. In protected locations, many of the dead external shoots were still present and all were about the same in appearance and state of preservation, indicating that all had died at about the same time and within the preceding 2 or 3 years.

Temperature records were not available from the immediate vicinity of the plots, but at the Stanislaus Branch of the California Forest and Range Experiment Station, approximately one mile distant and at almost the same elevation, the following minima were recorded during January and February of 1949:

January 4	— 9°F.	February 8	— 6°F.
January 10	— 7°F.	February 13	—12°F.
January 25	—10°F.	February 14	—11°F.

During normal winters at this location, minimum temperatures do not ordinarily fall below 0°F., as indicated by the following tabulation:

Year	*Lowest minimum temp.—degrees F.*	*Date*
1945	4	Jan. 20; Dec. 13
1946	0	Feb. 12
1947	3	Jan. 15
1948	—3	Dec. 24
1950	—9	Jan. 3
1951	3	Dec. 20
1952	—1	Mar. 20
1953	0	Mar. 2
1954	3	Mar. 12
Average	0	

Comparisons of temperatures at the Stanislaus Branch Station with a station operated until 1942 in a situation comparable to that of the plots but on the slope of an intervening ridge, suggest that temperatures on the plots may not have been quite as low in 1949 as those registered at the Branch Station. Moreover, the plots vary in degree of slope from very gentle to moderately steep as well as over a range of approximately 160 feet in elevation. On this account, temperatures undoubtedly differed on different portions of the plots as well as in individual tree crowns at different heights from the ground. Such differences, plus those resulting from different degrees of shielding, might well account for the fact that mortality of the mistletoe was not uniform on the plots and that many infections showed little evidence of damage when examined 1½ years later.

It is unfortunate that at this location the observations on death of the mistletoe plants were not made closer to the time that the killing appears to have occurred, but the writer has been able to adduce no probable cause for the death of the plants other than cold. Moreover, this conclusion correlates well with the fact that the plots are located near the northern limit of this mistletoe species and that there appears to be no influence other than temperature that logically accounts for the location of the existing limit.

Conclusion

In the case of *Phoradendron densum* in Shasta Valley, the evidence seems strong, and for *P. pauciflorum* in the Stanislaus drainage the probability is favorable, that occasional very low temperatures restrict these parasites to their present limits and account for their absence over other parts of the ranges of the hosts.

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INDEX OF BIOTAL DISPERSITY

The spatial relationships of living organisms have been analyzed by biologists with emphasis upon either their geographical or their physiological aspects. The two fields of study are known as biogeography and ecology although differences of opinion exist as to their definition and scope. For the most part, biogeographical theory has originated from the analysis and interpretation of the geographical patterns of the distribution of taxa. Theory in ecology, on the other hand, has been derived largely from data from experimental techniques in the field concerned with relating the variance of the factors of the environment to the tolerance or adaptability of living organisms. Whereas biogeographers have tended to express their ideas in geographical terms and almost always were initiated into the fraternity of scientists as taxonomists, ecologists have tended to express their ideas in physiological terms, and often have classified organisms according to their tolerance of, and response to, the factors of the environmental complex.

Following the idea of Good (1947), who termed the combination of phytogegraphy and plant ecology as geobotany, a similar combination of biogeography and ecology can logically be known as "geobiology." For practical reasons, the definition of geobiology should be as simple and as inclusive as possible; embracing all aspects, now known or to be discovered, of the transactions of living organisms and their environments.

The physiological-ecological approach preoccupies twentieth century biologists almost as thoroughly as the taxonomic-geographical point of view dominated the thinking of biologists in the nineteenth century. As analytical tools, each of the two methods no doubt will continue to contribute to our understanding of geobiological transactions. As long as scientific inquiry prevails, the need for such, admittedly artificial, analytical intellections, will continue. Logical analysis is a prerequisite to synthesis; a holistic approach to knowledge, unsupported by analysis, may be philosophically more satisfying but is scientifically unsound. Our fragmentary knowledge of the spatial transactions of organisms still precludes the possibility of satisfactorily synthesizing the knowns of the biogeographical approach and the ecological one.

The history of Jaccard's *coefficient of community* demonstrates the existence of confusion of these two aspects of geobiology. As a result of his floristic study in the European Alps, Jaccard (1902) proposed the Coefficient of Community as:

$$\frac{\text{The number of species common to two districts}}{\text{The total number of species in the two districts}} \times 100$$

To my knowledge, this important contribution to biogeo-