NOTES ON THE MONTEREY PINE.

GEORGE J. PEIRCE.

(WITH FIVE FIGURES)

IN the spring of 1898 the entomologists of Stanford University discovered a fly, *Diplosis pini-radiatæ* Snow,[1] which produced a leaf-gall or at least a basal hypertrophy of the leaves (needles) of the Monterey pine (*Pinus radiata* D. Don.) Some of the botanical features of this insect attack were described in 1900 by Cannon.[2] Certain other features, as well as notes on other matters connected with this tree, I wish to add to what Cannon said.

As its name implies, the Monterey pine is a coast tree, "very restricted in its distribution: Pescadero, southwest of Monterey and Pacific Grove."[3] It is commonly planted, however, over a rather extended territory, though with a success which is evidently proportioned to two things: the rainfall and the humidity of the air in summer. It seems to thrive about San Francisco and on the ocean side of the peninsula which separates the southern half of San Francisco Bay from the sea, but it needs moister, cooler air in summer than it gets in this part of the Santa Clara Valley, although careful watering will keep it in fair condition even here. Along with the coast redwood (*Sequoia sempervirens* Endl.) this tree is subject to a great variety of enemies, in addition to being exposed in cultivation to unfavorable climatic conditions. In the arboretum of the university the unfavorable factors in the environment are most evident. To mention only conspicuous enemies of the pine, one finds *Arceuthobium occidentale*,[4] a *Peridermium*, certain fungi causing spots on the leaves, scale-insects, bark-borers, and the gall-

[1] SNOW, W. A., and MILLS, MISS H., in Entomological News 11 :—. 1900.

[2] CANNON, W. A., The gall of the Monterey pine. Amer. Nat. 34 : 801–810. 1900.

[3] JEPSON, W. L., Flora of western middle California. 1901.

[4] I purpose publishing later a study of this phanerogamic parasite.

fly. In addition to these, field mice and other animals, whose depredations were concealed and facilitated by the long grass which was allowed to grow among the trees for a few years, made the already unfavorable environment almost unbearable. In various respects, however, conditions in the arboretum have improved.

Even at Pacific Grove, in a natural forest, this pine is just now having a hard struggle for existence. Conditions in this bit of forest have been considerably changed of late years, paths and roads having been cut through it, and a few years ago a serious fire swept over part of it. This forest is extremely important, for it is the main protection of the town of Pacific Grove against the sand which, now piled up in magnificent dunes, would otherwise be blown inland and over the town. It is still too early to determine whether the effort now being made to save this forest will be altogether successful.

The evident sensitiveness of these two trees, the redwood and the Monterey pine, is interesting in connection with their limited distribution. The redwood seems to be confined to the fog belt, the Monterey pine to only a small part of this. Moisture in the air is apparently the principal limiting factor, but the still further limiting one in the case of the Monterey pine is not evident. Seeds of this pine are now being extensively distributed for purposes of experiment. Whether it will prove under these new conditions to be more widely successful than it has hitherto been is a question of great theoretical as well as practical interest.

Turning now to the leaves of Monterey pines which have been attacked by the gall-fly, Diplosis, we shall see, in addition to the characters described by Cannon, certain other significant differences from normal leaves. At the same time that there is a very considerable thickening of the leaf throughout its length, but especially at the base, the leaf-surface is greatly decreased. The average diameter of 20 normal leaves one year old is 0.735^{mm}, as measured by micrometer caliper, and the length 94.8^{mm}. The average diameter of 20 galled leaves one year old ranges from 1.72^{mm} at the base to 0.62^{mm} at the middle, and the average length is 19.5^{mm}. The shape of all these leaves is far from mathematically regular, hence any attempt at measuring the surface area will necessarily give only approximate results; but let us assume for comparison that the difference between a galled and a healthy leaf on the one hand and a regular cone on the other is approximately equal. If we multiply the diameter at the base by $\pi = 3.14$, thus getting the circumference of a regular cone at the base, and this figure by one half the length of the needle (one half the height of a regular cone), we shall get the area of a regular cone. The calculated circumference is too large, for two of the lines bounding the base of a pine needle are straight; but, on the other hand, the diameter of a pine needle is less at the base than a short distance above. The cone, therefore, is not regular; the needle is larger above than at the base, tapering toward both base and tip. Nevertheless, using this faulty method of estimating surface areas, we have comparable figures —$109.35^{sq\,mm}$ as the area of an average normal needle, and $52.65^{sq\,mm}$ as the area of an average galled needle. The surface of average normal leaves, therefore, is approximately twice that of galled cones.

The weight of the 20 normal leaves which I measured is 0.8595^{gm} and of the 20 galled ones 0.395. So far as expenditure of leaf-building material is concerned, there is a difference of about 50 per cent. between normal and galled leaves. But besides weight and surface area the number, size, etc., of stomata should also be considered. The stomata appear alike on normal and on galled leaves, but there are four times as many on the former as on the latter.

Between normal and galled leaves the physiological differences will at least equal the anatomical ones. Thus there will be considerable differences in the amount of water lost through the stomata, in the amount of food made in the chlorophyll-containing tissues, and in the amount of food consumed in healthy and in diseased leaves. The larvae in the galls may consume more food than is made in the leaves at the bases of which they develop from the eggs, as they may be sufficiently nourished from the leaves alone. On this point there is at present no light. If the larvae consume more food than the immediately adjacent leaves make, this food will certainly consist mainly of organic compounds drawn through, if not exclusively from, the branch on which the leaves stand. It is therefore the phloem elements upon which the demand for food will be made directly. If bundles coming into fallen leaves be cross-sectioned, for example at such a point that the bundles lie in the cortex of the branch about midway between the epidermis and inner bark, and these cross-sections be compared with corresponding ones of the bundles of healthy leaves, the differences between the bundles will be clear. The simplest way to compare is to cut out and weigh the pieces of bristol-board on which camera drawings of the sections have been made. Thus the cross-section of the normal "leaf-trace" (phloem, xylem, and enclosed pith) weighs 0.429^{gm}, that of the "leaf-trace" of a group of the galled leaves weighs 0.210^{gm}; the xylem of the former 0.082^{gm}, the phloem 0.335^{gm}; the xylem of the latter 0.052^{gm}, the phloem 0.155^{gm}. That is, the normal "leaf-trace" is more than twice as large as that of the galled cluster, the xylem of the normal one and a half times the galled, while the phloem of the normal is also more than twice that of the galled. If one judge the efficiency of tissues by the extent to which they are developed—a criterion by no means above criticism—the conclusion is forced upon one that, so far as one year old leaves show, healthy leaves have more work done in them than do galled leaves. This work is of various kinds. *First*, more water and mineral solutes pass through the bundles into normal than into galled leaves, and more water is transpired from healthy than from diseased leaves. *Second*, more food is made in normal than in galled leaves, assuming that the greater amount and more favorable exposure of chlorophyll-containing tissues in normal leaves is a safe index. *Third*, more food is removed through the phloem to other parts of the plant from healthy than from galled leaves. Although the galled leaves nourish larval insects, the development of their conducting tissues is less than that of normal leaves. The processes especially characteristic of leaves—food-manufacture and the attendant movements of solutions up and down the leaf—are less active in galled than in healthy leaves, and the conducting and other tissues especially concerned with these processes are developed correspondingly.

Passing from the leaves to the branches, comparison of cross-sections of branches bearing galled leaves with cross-sections of other branches bearing only normal leaves, reveals certain differences. If one makes a series of cross-sections through successive segments of one branch, the leaves of which have been attacked in successive years by the gall-fly, and a similar series of cross-sections through a branch which has borne only healthy leaves, we shall see that the growth of the branch in thickness each year is proportioned to the amount of galling which has taken place. The accompanying figures show this. In *fig. 1* we

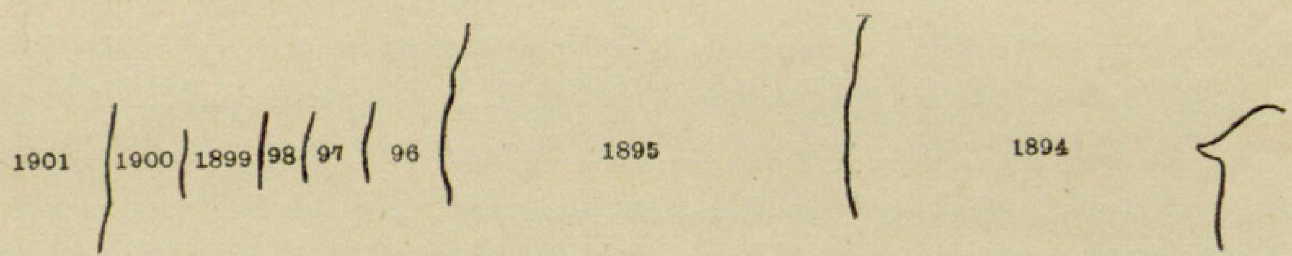

Fig. 1.

have part of a cross-section of a branch, the oldest wood in which was formed in 1894. The drawing is by Leitz drawing prism. I have known this tree and watched it constantly, beginning with the spring of 1898, the year when, according to entomologists, the attacks of the gall-fly were the worst. The fly first appeared in noticeable numbers in 1896, and since 1900 it has been far less numerous than in the preceding five years. The narrow annual rings indicated in the above drawing coincide exactly with the most serious attacks of the gall-fly.

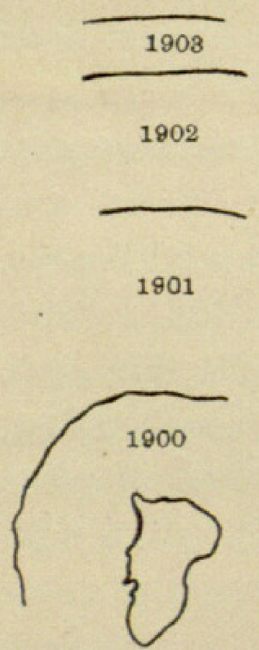

Fig. 2.

In *fig. 2* we have a branch the oldest wood in which was found in 1900. The terminal bud of this branch had been injured shortly before I cut it, which was in March 1903, when I collected all the material here figured. On this branch I counted all the leaves still present, and the numbers were as follows: 1 normal leaf still attached to the part of the branch begun in 1900, 40 galled and 26 normal leaves on the 1901 segment, 31 galled and 70 normal leaves on the 1902 segment, and no galled leaves at all on the new growth of 1903. It may be mere accident, of course, that the one leaf which held on from 1900 to 1903 should have been a normal one, but this is what one should expect from the nature of the case. A healthy leaf, contributing normally to the plant which bears it, should be retained longer than diseased leaves.

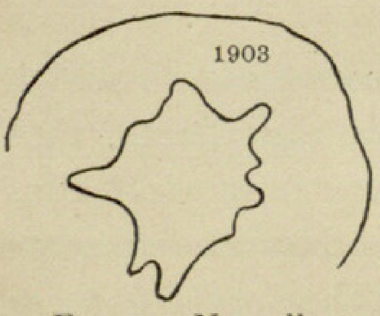

FIG. 3.—No galls.

In *fig. 3* is shown a cross-section of the youngest part of a branch on which there were no galled leaves. The growth at the time of collecting had already been considerable. This growth is greater than that on a branch which had borne galled leaves, for the diameter of this branch is greater than the diameter of the whole first season's growth of the branches shown in *figs. 2–5*, which were drawn on the same scale. I believe this to be a general difference, for all the sections I have made are consistent with those here figured. And we should expect on general principles that the growth of a tree or a branch which had been healthy in preceding seasons would be greater and better than that of diseased trees or branches.

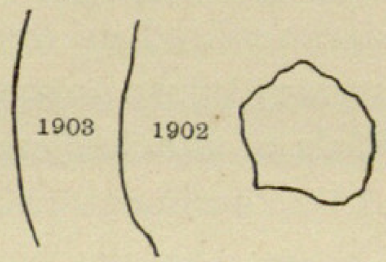

FIG. 4.—1902, 15 g. to 68 n. 1903, no galls.

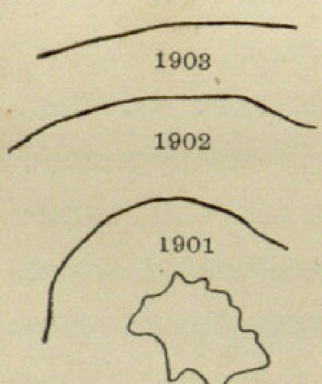

FIG. 5.—1901, 14 g. to 8 n. 1902, 15 g. to 68 n. 1903, no galls.

In *figs. 4* and *5* we have further evidence to confirm the opinion expressed above, that the width of the annual ring, or to put it more generally, the growth of the vascular bundle, is proportioned to the growth of the leaves borne on the branch. When one realizes that these sections are from different branches on the same sides of the same trees, that therefore the conditions other than those produced by the parasite were similar each season for healthy and for galled branches, one is compelled to attribute the difference to the effects of insects.

Taking into account what was said above about the differences in area between normal and galled leaves, and also the fact that there are no anatomical or microchemical differences in the surface cells of the two sorts of leaves, one is led to infer that the differences in the quantities of water (and solutes) drawn up through the xylem into galled and normal leaves furnish the reason for the differences in the amounts of conducting tissue as shown by the annual rings.

In 1893 Jost[5] concluded from a series of experiments which he made on seedlings and on certain older woody plants, that the development of the vascular bundles is very intimately connected with the development of the leaves. His experiments consisted in part in removing the leaves when the seedlings were very young or in forcing leaves to develop from the bud in darkness. Any experiment which involves amputation or other serious injury is obviously to be used only very guardedly as the basis of conclusions regarding the relations of parts to each other. An experiment involving the amputation of a leaf shows two things: the effect of the wound and the effects due to abuses of the leaf and of the processes normally going on in it. Which is the predominant influence no one knows, and whether the result is not a *resultant* rather than the *sum* of two different effects is also unknown. It is conceivable that a reduction of the leaf surface, or the suppression of the whole organ without wounding, might have a different effect from cutting off a leaf. This Jost tried by causing leaves to develop in darkness from the bud. But here again more than one thing is involved. The formative and directive influences of light as well as its influence on the photosynthetic and other processes connected with nutrition going on in the leaf, are all eliminated. Though no wound is made, the result may again be a *resultant* rather than the *sum* of the factors concerned. The results which Jost obtained agreed, however, in that, whether the leaves were removed or were reduced by being grown in darkness, the vascular bundles were much smaller. Jost used among other plants two species of Pinus.

If we now compare Jost's results with ours, we see that they

[5] JOST, K., Beziehungen zwischen Blattentwickelung und Gefässbildung in der Pflanze. Bot. Zeit. 51:89–138. 1893.

are similar. Normal seedlings and normal-leaved pine branches develop bundles of normal proportions, while amputated seedlings and branches bearing galled leaves develop bundles which vary from the normal according to the degree of injury which the leaves have undergone. In the case of Jost's seedlings the consequences of amputation are clear. That they are the results of any one set of factors is by no means clear. In the case of these Monterey pines we have plants which are also profoundly although gradually influenced by the treatment to which they have been subjected. No wounds are produced by the gall-fly depositing its eggs at the bases of the young pine needles, there is no sudden shock to the whole plant, and there is no sudden or great change in the weights, or the position of the weights of the leaves. The galled leaves have less area and less chlorophyll-containing tissue than normal leaves, they lose less water by evaporation and contribute less food to the plant as a whole than normal leaves do. They may consume more food than normal leaves, but this is by no means certain. The products of the gall-larvae—excreta of various sorts—certainly affect the leaves at the bases of which they live and it may be that these substances are carried to considerable distances and affect the growth of the tissues in the branches. But of this there is no evidence unless we assume that these excreta affect only the young cells of the xylem. It seems to me reasonable, therefore, to conclude that it is principally the reduced surface from which water is evaporated, and that the decreased food-manufacturing tissue is only a minor cause, to which the smaller amount of wood and the narrower annual rings can be attributed. We have then in this pine a confirmation of Jost's conclusions that leaves and vascular bundles are closely correlated in their development, a confirmation the more interesting because it is furnished by gradual change rather than by sudden and shocking influences, by influences which operate out of doors, under natural conditions, where there can be no suspicion that the results are due to more or less obscure laboratory causes.

STANFORD UNIVERSITY,
California.