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AD836239

TRANSLATION NO. 1634

[REDACTED]

DATE: 23 MARCH 1966

JUL 20 1966

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DEPARTMENT OF THE ARMY
Fort Detrick
Frederick, Maryland

CONCERNING LEAF DROP DUE TO BUDDING
AND CONCERNING THE OMBROPHILY OF EVERGREENS

[Following is a translation of an article by Julius Wiesner in the German-language periodical Berichte der Deutschen Botanischen Gesellschaft (Reports of the German Botanical Society), Vol 22, 1904, pages 316-323.]

In a note on "summer defoliation" that I published in these Reports (Vol 22, 1904, pages 64-72) I called attention to the extremely varied causation of leaf drop and showed that in this country even in the summer besides the specific "summer defoliation" conditioned by decreasing light intensity other forms of leaf drop also occur, e.g. heat defoliation, and also in the case of laurel and myrtle a partial defoliation of those plants connected with the leaf-bud development [see Note].

[Note] And there are still other types. I should like to observe here that in many deciduous woody plants summer defoliation is prepared for in spring, in that the little foliage leaves at the base of lateral shoots, which assimilate only relatively weakly, turn yellow and drop off with greatly increasing foliation. In the lilac this is extremely noticeable; often in May the ground on which the lilac stands is strewn with little yellowed leaves. The shedding of these oldest little leaves takes place within a brief span of time, after a long-lasting rain often all at once, while "summer defoliation" runs a continuous course. The plant thus sheds early the foliage leaves least suited to assimilation. The same behavior as the lilac's is observed in numerous other plants, e.g. Philadelphus coronarius, Acer negundo, Aesculus hippocastanum, Tilia. On the other hand others, such as elms, seem not to shed these leaves until the "summer defoliation," at least according to my observations up to now. Long-lasting spring rains or long overcast skies are also capable of eliminating a small part of the normally developed foliage even before the onset of "summer defoliation." But this too occurs within a brief period of time or all at once, and not continuously as in "summer defoliation."

Concerning this last form of leaf drop, which for the sake of brevity I should like to designate here as "budding defoliation," I shall present certain tentative summary data. I shall restrict myself here to the presentation of a few typical cases, and reserve a more detailed exposition of this subject until a later time, when I shall discuss my studies of leaf drop carried on over many years as a connected whole.

It is essentially obvious that this "budding defoliation" is limited to evergreen woody plants; for deciduous woody plants are after all characterized by the fact that long before the budding of the (hibernating) leaf buds they shed their whole mass of foliage. But I shall show further on that just as there exist transitional forms between deciduous and evergreen woody plants, with regard to the forms of defoliation, too, transitional forms between the two may be found, so that even among deciduous plants budding defoliation may show up to a certain extent.

"Budding defoliation" is an important device for bringing about defoliation in those plants in which the usual external influences do not suffice for the purpose. While deciduous plants, as I showed long ago [see Note 1], quickly shed their leaves in a humid space or do not endure long sprinkling with water or darkness, or, as I demonstrated for Azalea indica [see Note 2], almost immediately lose a large part of their leaves after extreme dryness of the ground, the plants subject to "budding defoliation" retain their foliage extraordinarily long under these conditions, the laurel affording an excellent example of this. Sprigs of laurel remain alive for months in a humid space, often without shedding a leaf, and the same is true in darkness or under constant sprinkling. A potted laurel 0.3 m tall which was protected against stagnant ground wetness by a rubber covering over the pot, was subjected for months in the cold greenhouse to a constant artificial rain day and night. It stayed quite fresh and did not shed a leaf the whole time (from January to the middle of April). When it was then taken into the hothouse the leaf-buds opened, quite normal shoots developed, and the little tree shed a part of the old foliage. A potted myrtle behaved in a similar way, though its vitality was not the equal of the unexampled toughness of the laurel. Still it endured almost two months of continuous artificial rain, losing a small part of its foliage. It too developed well again when returned to normal conditions.

[Note 1] "Studies of the Autumnal Defoliation of Woody Plants," Sitzungsberichte der Wiener Akademie, Mathematisch-Naturwissenschaftliche Klasse (Minutes of the Vienna Academy, Division of Mathematics and Natural Sciences), 1871.

[Note 2] Reported by Molisch in his studies of defoliation, Sitzungsberichte der Wiener Akademie, Mathematisch-Naturwissenschaftliche Klasse, 1887, which see for demonstration of numerous other causes of leaf drop.

These very marked cases of ombrophily [see Note] of evergreen woody plants are by no means exceptions. After undertaking numerous experiments on the behavior of evergreen woody plants I have arrived at the opinion that for these plants the ombrophilous character is the rule, and that the resistance of their foliage to long continuous exposure to rain is among the devices that result in the formation of evergreen foliage. To be sure, not all evergreen woody plants behave like the laurel in this respect. Even the myrtle, as already observed, shows a lesser resistance to continuous rain in comparison with the laurel. Evonymus japonicus is still less resistant. A potted specimen with 225 leaves shed about 30% of its leaves within two months (March, April) in the cold greenhouse under continuous dripping water. Nearly the whole loss of foliage was made up by fresh foliage within that time. The developing leaf shoots did not suffer under the continuous exposure to rain, for all the leaves were normally developed. A somewhat different behavior was exhibited under two months' dripping water by Aucuba japonica, which did not shed a single leaf during that whole time, while the newly developing shoots were stunted. The young shoots of these plants approach the ombrophobous type.

[Note] Wiesner, "Concerning Ombrophilous and Ombrophobous Plants," Berichte der Wiener Akademie (Reports of the Vienna Academy), Vol 102, 1893, and 104, 1894.

Budding defoliation and ombrophily always appear to go hand in hand. At any rate I have found no exception, although the degrees of ombrophily are varied. It is self-evident that all the external influences that bring about the dying of leaves result in defoliation even in the case of evergreen plants, but even then the shedding of leaves is slow as compared to the analogous process in deciduous plants, as the experiments in the dark show.

The life-span of the leaves is limited even in evergreen plants, and these organs die so to speak from internal causes. Leaves that have died in this way separate themselves from the tree, and leaf drop, especially in the case of evergreens with very long-lived leaves, is partially attributable to a spontaneous mortality of the foliage.

But in this case, too, the shedding is very slow.

Thus the evergreen plants have few and usually inadequate external means at their disposal for ridding themselves

of their excess foliage, i.e. of those leaves which as a result of progressive development of foliage receive too little light for assimilation, and they are primarily thrown back on inherited devices for this purpose, namely on budding defoliation and on the separation of leaves dying from old age.

In order to find out exactly the influence of budding on leaf drop, I worked with healthy potted plants. Plants in open soil would perhaps be still better suited for these experiments, but in the open as a rule the danger of foliage being carried away by the wind, etc., is so great that no very exact results can be obtained.

However, I have observed plants cultivated outdoors as well as I could with respect to defoliation, and have reached the conclusion that their behavior is essentially the same as that found in pot cultivation. There did prove to be a difference, however, in that the leaf drop was heavier in the latter than in the former, or in other words the leaves of potted plants appear shorter-lived. In the open, too, the defoliation of one and the same variety does not always take place in the same way in different individuals. Thus I have observed that in the open very vigorously growing Buxus shrubs have a slighter leaf drop than those thriving less well. Related to this there is the phenomenon that the leaves of perennial plants of a particular species live longer the better the plant thrives. [See Note.]

[Note] G. Kraus has demonstrated, in an article cited below, that the leaves of Buxus attain an age of two to five years. Although he does not expressly say so, it appears to be implied in his observations that the leaves of Buxus and other woody plants last longer the more vigorously the branches that bear them or the whole plant thrives. According to his observations the leaves of Buxus grown in hedges get to be only two years old, while bushes standing alone, which under otherwise similar conditions thrive better, keep their leaves two to three years, and large-leaved forms bear four to five-year-old leaves. Kraus expressly mentions that Portiera hyemetrica, which ordinarily possesses two-year leaves, when it forms especially strong, vigorous bushes produce leaves that last three to four years.

I cite here only a few typical examples of "budding defoliation."

1. Spruce (Picea excelsa). -- On the basis of numerous observations made in the open I have formed the opinion that the spruce sheds needles throughout the entire year, for at whatever time of the year I shook branches of spruces, needles always fell off. At the time when the young shoots were undergoing their most rapid development or had just completed their development, the shedding of needles was always most abundant.

A few years ago I made precise observations on a little spruce grown in a pot, which was so placed in the cold greenhouse that the shedding of needles could be accurately checked.

Before the buds began to grow, this tree 0.8 meters tall bore an estimated 21,000 needles on 166 branches. The annual fall of needles amounted to about 9-10%. A definite swelling of the buds was observed on 4 April. From the middle of March on 2 to 13 needles a day, or an average of 5-6 needles a day were shed. When shoots began to develop the fall of needles only increased to a slight degree, but during the rapid development of the young shoots (11 to 20 May) 18 to 40 needles a day, or an average of 25.7 needles a day fell. After completion of the growth in length of the young shoots the fall declined again sharply (to an average of 10 needles), to reach the normal value again a few weeks later.

Whether the defoliation taking place in the open, i.e. under natural climatic conditions, occurs with the same regularity could not be determined, but it could be estimated that outdoors, too, the greatest fall of needles takes place at the time of the greatest budding or shortly afterwards.

On very vigorous trees with very long-lived needles the budding defoliation does not seem to be as heavy as on weaker specimens with a shorter life-span of the needles, and in the former case it appears that shedding as a result of the natural dying of the leaves plays a greater part.

I rely here on observations that I made in the open on spruce and fir (Abies pectinata). The latter in particular, in vigorous specimens, appears to be especially subject to dropping of foliage as a result of the dying of aged leaves. But, as has already been remarked, because of technical difficulties I was unable to make any adequate observations in the open.

2. Yew (Taxus baccata). -- A potted specimen, grown in the cold greenhouse, about 1 meter tall. Before budding set in, it bore 287 branches with an estimated 17,000 leaves. From 9 to 17 April, during which time the buds were still in a dormant state, 3 to 21 needles fell daily, with an average of 9.3 needles. On 18 April the swelling of the leaf-buds began. During the first period of budding (18-27 April) 4 to 22 needles fell daily, with an average of 21.1 needles [sic; arithmetically impossible]. During the most rapid budding (28 April to 7 May) 372-2640 needles fell daily, with an average of 510 needles. Then, with a still detectable further development of the young shoots (8 to 23 May), 72-243 needles, with an average of 131. After completion of the growth of the new

shoots the number of needles shed dropped back again to a much smaller figure.

Outdoors too I observed a relatively very abundant defoliation during the period of rapid budding, but also for a few weeks afterwards, i.e. even after the young shoots had completed their growth in length.

3. Box (Buxus sempervirens). -- A bush cultivated in a pot was observed in the cold greenhouse from 9 April until the end of May. Before budding, this bush bore 1580 branches with an estimated 14,300 leaves. Before the beginning of budding (19-27 April) 3-21 leaves fell daily, with an average of 9.2. In the beginning of budding 8-52 leaves fell daily, with an average of 26.3. Then during the rapid budding (28 April to 6 May) 325-2064 fell daily, with an average of 917 leaves. Until the end of the growth of the young sprouts 33-211 fell daily, with an average of 61 leaves still. Later the number of falling leaves dropped to a still smaller figure. During budding the bush lost about two thirds of its old leaves.

Outdoors, too, the defoliation of Buxus was noticeably greater during budding, but on the outdoor bushes a greater part of the old foliage was kept, evidently as a result of more favorable conditions of vegetation. Only specimens freshly set out outdoors behaved like my pot-cultivated experimental bushes.

4. Aucuba japonica. -- Potted specimens. Before budding the shedding of leaves was very slow, as it was at first even during budding. After development of the new shoots (beginning of May) about a third of the old foliage fell in a few days.

5. Laurus nobilis. -- I have already briefly set down the data concerning the course of defoliation in the laurel during the year and called attention to the increase during budding in my article on "summer defoliation."

In this preliminary report I must restrict myself to the presentation of these few results of observations and should like further merely to indicate those experimental findings which concern

6. Quercus cerris. -- As is well known, a more or less large part of the foliage of this tree falls off in the autumn, the rest not until spring. But both the leaves falling in the spring and those falling in the autumn are completely dead.

At the beginning of March two branches of this tree which were still provided with their full number of leaves were taken into the cold greenhouse. The buds were still in the winter dormant state. The leaves were still firmly attached. Even after the buds had entered the stage of swelling, the

leaves could be separated from the twigs only by the use of force. But when the buds began to sprout the leaves dropped off -- not in order of their age, but precisely in reverse order. Now the most vigorous buds are at the end of the shoot, and their size decreases toward the bottom, and the degree of development of the buds also progresses in the basipetal direction. It is thus unmistakable that the shedding of leaves runs parallel with the development of the buds.

The increased fall of leaves as a result of the growth of the leaf-buds is really a quite conspicuous phenomenon. I had not known of it, however, until my studies of "summer defoliation" led me to it, nor had I come across anything about the matter in the literature.

After the publication of my little article concerning "summer defoliation," my esteemed friend and colleague Prof. G. Kraus called my attention to the fact that he had published an article about the length of life of leaves in 1880 in the Sitzungsberichte der Naturforschende Gesellschaft zu Halle (Minutes of the Scientific Research Society at Halle), in which he made a relevant observation which had unfortunately remained unknown to me, as had the whole article. It is stated there that fine young specimens of Podocarpus macrophylla shed all the leaves of the preceding year at the beginning of April, just as they were forming new shoots (Pincio). The ground beneath them was covered with leaves, as under new trees in September and October. The same thing was observed for bushes of Cneorum tricoccum. Kraus believes that this phenomenon is quite general among evergreen woody plants with relatively short lifetime of the leaves.

In this brief notice I have not been able to go into either the physiological or the anatomical side, and must therefore content myself with stating the following results:

1. The evergreen woody plants thus far studied are characterized by a high degree of ombrophily, enduring (artificial) rain lasting continuously for months with little or no loss of leaves.

2. Evergreen woody plants show little reaction to external influences which lead to rapid defoliation in deciduous plants. Their loss of leaves is thus relatively little dependent on external influences, and they possess in an inherent mutual relationship between budding and the shedding of leaves

the principal means of getting rid of superfluous foliage and so adapting themselves to a stationary minimum photic ration.

3. The transition between deciduous and evergreen plants manifests itself also in the fact that among the former there are some which also make use of the development of leaf-buds to rid themselves entirely of their foliage, which is very slow to fall as a result of external influences, in the spring.