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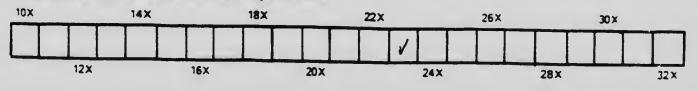
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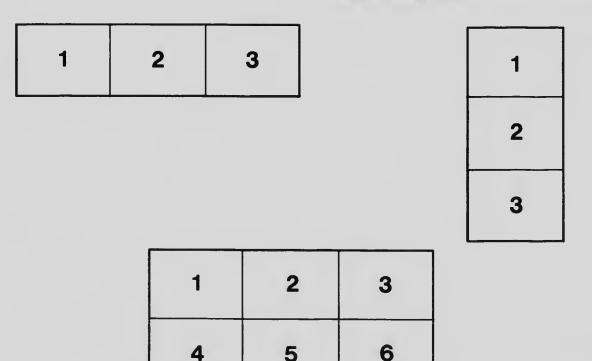
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An Undescribed Thermometric Movement of the Branches in Shrubs and Trees'.

BY

W. F. G. NONG, PH.D.

Professor of Botany in Smith College.

With six Figures in the Text.

S OME years ago I noticed an apparent radial movement of the ascending branches in certain shrubs and small trees, whereby the branches were brought closer to the main stem in the winter, quite independently of the leaf-fall, and were separated from it on the approach of spring. After trying in vain to find some account of this movement, and its causes, in the literature accessible to me², and from various persons informed on such matters, I undertook a study of it, with results which follow.

In the autumn of 1898 I chose six shrubs and small trees, in the Botanic Garden of Smith College, which showed the movement and which were isolated from other woody plants. Selecting long slender branches on the north, south, east, and west sides of rach plant, I made near the top of each, and on the side radial to the plant, small dots with water-proof India ink, the approximate positions of which were marked for convenience by coloured threads. It was then possible, with the aid of an assistant, to

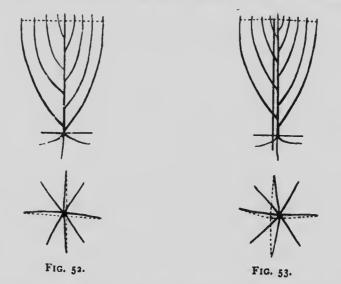
¹ Read before the Society for Plant Morphology and Physiology, at its Philadelphia Meeting, Dec. 29, 1903.

² I have found no direct references to this movement, although it seems unlikely that it could have escaped notice and description; and the only other monitor of it that I have heen able to secure by inquiry is a statement in a letter that a resident of Washington, D.C., has noticed it in the lowor branches of the *Ginkgo*. The inward movement of the branches after removal of the weight of the leaves in autumn is said to be known to nurserymen; and some measurements of this movement in a shrub arc given in a note by Agnes Frye in *Nature*, vol. lv, 1896, p. 198, and in a hranch of horse chestnu, by Miller Christy in *Journal of the Linnean Society*, xxxiii, 1898, pp. 501-506. The works of Wiesner, Baranetsky, and others on the determinants of hranch position appear not to touch this subject. Recently Mr. E. F. Bigelow, of Stamford, Conn., has written me that two correspondents of his have asked him the causes of branch movements noticed by them; in one case it was a spruce, whose branches rise in warm, and fall in cold weather. Apparently there is more in this subject than has hitherto been supposed.

[Annals of Botany, Vol. XVIII. No. LXXII. October, 1904.]

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measure with a tape the distance between the diametrically opposite marks (i. c. from the north to the south branch, and from the east to the west), and thus to determine any movement the branches might make. The method is illustrated by the accompanying diagram (Fig. 52). The resultant measurements for the four shrubs which showed the most marked move-



ment are plotted upon Fig. 54, and the more important figures are contained in the following table:--

The Plant.	Date.	Condition of Plant.	N. and S.	E. and W.
Salix laurifolia (about 3 meters high)	Oct. 10 Nov. 12 Jan. 20	In full winter condition	261.2 cm. 257 248.5	247 cm. 241.7 234
Cercidițhyllum japonicum (about 2 meters high)	Apr. 22 May 25 June 24 Oct. 1c Oct. 28 Jan. 20 Apr. 22	Buds beginning to swell Leaves all out In full summer condition Leaves all on (nearly) Leaves all gone In full where condition Buds beginning to swell	245 290.5 293 114.5 110.5 105 107	232 267 274 128 125-3 121-5 122
Cornus florida (under 2 nicters high)	May 25 June 24 Oct. 10 Nov. 12 Jan. 20 Apr. 6	Leaves nearly all out In full summer condition Leaves all on Leaves all gone In full winter condition Buds swelling	112 118 133-3 114-7 109-5	128 130 236.7 207.3 204
Broussonetia paperifera (about 1.5 meter bigh)	May 25 June :4 Oct. 10 Nov. 12 Jan. 20 Apr. 22 May 25	Leaves well out In full summer condition Leaves all on	113 121 136 168.2 152.4 142.5 136.5 129	204 217 235 206.8 187.8 174.5 164 156

These measurements showed :--

T. A large inward movement accompanying the fall of the leaves, and an outward movement accompanying the formation of new leaves.

2. A real seasonal movement independent of leaf-fall and leaf-formation, consisting in an inward movement during the advancing winter, and an outward movement on the approach of spring.

3. Certain fluctuations in the movements, the reasons for which were not evident.

The causes of the movement accompanying leaf-fall and leaf-formation are so evident as hardly to call for comment; the movement is simply due to the removal of the weight of the leaves and their contained water from the elastic, obliquely-ascending branches in the one case, and the addition of weight in the other. But the cause of the further seasonal movement of the leafless branches is not at once evident.

The measurements showed not only that there is a real movement of the leafless branches, but that it is of considerable amount, reaching between leaf-fall and leaf-formation —

12 cm., or 5% of the total diameter of the plant in Salix laurifolia;

3.5 cm., or over 3% of the diameter of the plant in Cercidiphyllum japonicum;

5.3 cm., or over 5 % of the diameter of the plant in Cornus florida;

And a larger though uncertain amount in Broussouetia papyrifera.

The results were of such interest that a more careful study of the subject was undertaken the following winter (1899-1900). An improvement was made in the method in two respects. First, the movement of each branch was measured separately in order to determine whether there was any difference in the movement of the different branches. This was effected by placing, in all measurements, the loop of the tape (a Chesterman steel tape as used the preceding year) over a brass screw held by a cork set in the top of a piece of stout gas-pipe, which was driven firmly into the ground as nearly as possible in the centre of the shrub (as represented by Fig. 53). It is important to note that this, like any other method of measuring such movements from a fixed point, does not give strictly accurate results, because the marks on the branches do not move in and out along the same radial line, but in different lines. In general, however, the errors from this source are very slight, they tend to neutralize one another, and as r whole they affect the results in the direction of a lesser rather than a greater amount. Secondly, some suggestion having arisen that temperature might have an effect upon the process, the air temperature was recorded at each measurement. The measurements were made by one of my senior students, Miss Phæbe Persons, as often as the weather would permit, throughout the autumn, winter, and spring. One of the greatest difficulties in this study consists in the fact that the measure-

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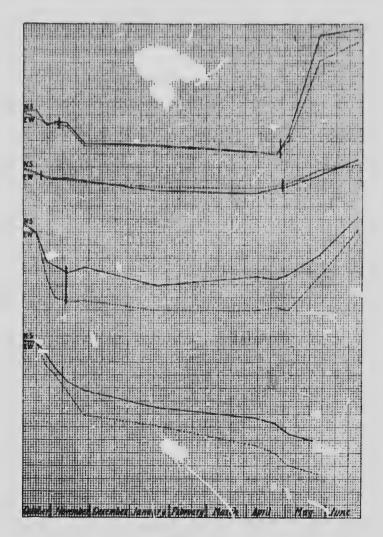


FIG. 54.

Abscissa spaces, each two days.

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Ordinate spaces, each 2.5 mm. of movement.

Downward direction means inward of the shrub, and upward means outward.

Showing the seasonal movement of four shrubs :--

The upper is Salix laurifolia,

the second is Cercidiphyllum japonicum,

the third is Cornus florida,

the lower is Broussonetia papyrifera.

The entire lines are the north and south measurement,

the dotted lines are the east and west measurement,

the vertical lines across the polygons represent the time first appearance of the leaves from the bad (the latt. The disagreement of Broussonetia was connected with the death (winter-killing) of the plant.

^c complete leaf-fall and of the or Cornus was not recorded).

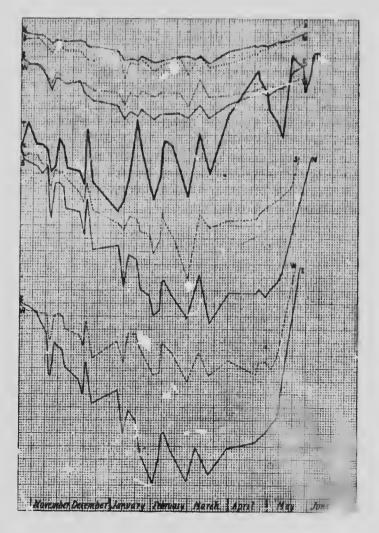


FIG. 55.

Abscissa spaces, each two days.

Ordinate spaces, each 2-5 mm. of movement, and 1 degree of temperature.

Downward direction means inward of the shrub, and upward means outward.

The plate shows the movement of the branches in two shrubs :--The upper ls Lindera Benzoin, the north, south, east, and west branches being secreted by the initials N.S.E.W.

The lower is Salix laurifolia, the respective branches being indicated as for the tora. The double line between the two shrubs represents temperature.

The records begin after the leaves were mostly fallen, and continue until the new leave largely formed.

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ments can be made, especially when any of the leaves are on, only in perfectly still weather; and hence a continuous study of the movement in exact correlation with external physical conditions is well-nigh impossible. Doubtless shelters could be devised to permit measurements in any weather, but with large plants this would be a matter of much d'"culty, and it was not attempted by us.

The shrubs studied during the winter were the seven listed in the table below. The results of the measurements of all seven were, except for minor differences, very similar, and they are fully illustrated by the two examples plotted on Fig. 55, which represents the movement for *Lindera Benzoin*, an average representative of the series, and *Salix lawrifolia*, which was one of the two which showed the greatest movement of them all. The total amplitude of the movement between leaf-fail and leaf-formation for all the branches, and the percentage which this movement is of the shrub radius, are shown by the following table :---

Plant.	Size in metres,	Movement in centimetres.				Percentage movement.					
Pyrus americana Salix laurifolia Ornus sericea Cercidiphyllum japonicum Cornus florida Lindera Benzoin Carpinus carolinianus	ht. diam. 1-90 x 1-20 4-50 x 3-10 2-20 x 1-90 2-80 x 1-40 2-30 x 1-90 1-60 x 1-20 2-30 x 2-00	N. 3.3 11.2 5.0 5.3 5.5 3.1 8.4 40.7 5.8	S. 1.4 6.0 5.6 2.8 2.5 5.4 9.5 33.2 4.7	E. 3.7 9.4 4.9 3.9 7.9 8.1 8.7 46.6 6.6	W. 1.4 8.0 4.7 3.1 5.9 4.5 9.5 37.1 5.3	Av. 2·20 8.65 5·05 3·75 5·45 5·27 9·02	N. 03 12 07 13 05 09 11 60 3.5	S. 03 09 05 03 06 07 34 4.8	E. 07 10 04 07 07 12 07 54 7.7	W. 02 09 05 03 06 07 34 4.8	Av 3.4 10 4.5 8.2 8.0

Further, in order to determine the effect of fluctuations of temperature through a single day, and the effect of the fall of temperature at night, Miss Persons made, after several unsuccessful attempts, a series of measurements through one still day and part of the next, and found that within the limits of a single day and night the movement was considerable, and that it was correlated with the temperature changes, though lagging somewhat behind the latter. Another series of measurements made by her was directed to determine whether the movement was most pronounced in the younger or older parts of the branches, and she found, as was to be expected, that it was much more marked in the young parts. In general the movement is greatest in the longest, most slender, and youngest branches, and it becomes less with the reverse of those features. Miss Persons also made a detailed study of the anatomy of the stems she measured, but she was unable, as I have been since, to connect the movement with any peculiarities of anatomical structure.

In summary the results showed :---

1. The seasonal movement observed the year before is confirmed, and is shown to consist in a grainal inward movement from leaf-fall until March, when an outward movement begi.

2. There exists in addition to this seasonal movement a secondary movement, which is closely dependent upon temperature (as shown by the typical examples on Fig. 55), a higher temperature resulting in an outward, and a lower in an inward movement, and this movement is appreciable within a single day and night.

3. There are sundry irregularities in the movements, and apparently a greater movement in . or 1 and ease than in south and west branches.

The close correlation i etween the secondary movement and changes of temperature thus demonstrated is interesting and important, and it is close enough to warrant the application to the movement of the term thermometric. Since the minor movement is of this character, the question at once naturally arises whether the seasonal movement may not be of the same character, that is, whether the seasonal movement may not be simply a thermometric movement of huge amplitude. This point will be discussed below.

The results in relation to the respective amounts of movement in the different branches were not satisfactory. In general they showed more movement in the north and cast branches, but with so many exceptions and irregularities that no conclusions can be drawn from them, the more especially as no precautions were taken to select branches of the same lengt nd distance from the central post. Furthermore, both Miss Persons and . self were influenced by a belief that the north and east branches did move the most, and hence doubtless something of a personal equation, or rather an equation of prejudice, in this direction became incorporated

The reality of the seasonal movement, and the correlation of the secondary movement with temperature changes, being thus made apparent, it remained to ascertain their precise physical basis, a subject both of much interest in itself and also important for the light it might throw upon the significance of the movement to the plant. Reviewing the facts so far observed, it seemed plain that the relation of the two movements may be either one of these two:—(a) they may be due to the same causes, the secondary inward-and-outward fluctuations being the result of temporary intensifications and weakenings of the factors (connected with temperature) producing the seasonal movement; or (\dot{o}) they may be due to different causes (or at least to a difference in the mode of operation of the same causes), the secondary fluctuations being temporary movements due to special causes, either out from, or in from, the line of general seasonal movement. The facts at our command seemed at first to point to the las er

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probability, and in order to obtain a definite basis for experiment we assumed that the secondary fluctuations were simply outward movements from the seasonal position. As a physical (or mechanical) cause of this outward movement under higher temperature, it seemed to us likely that the warming up, and consequent swelling, of the inner faces of the long slender branches under the influence of the sunlight on the warmer days was sufficient. Evidently this hypothesis could be submitted to experiment, for not only ought the outward movement to be greater on a sunny than upon a cloudy day of approximately the same temperature, but the movement in branches illuminated at the time of measurement on their inner faces should show more movement than those at that time shaded, or, still better, than those illuminated upon their outer faces. Simple as such a test appears the weather never allowed us to put it to satisfactory use, and the season closed without its accomplishment.

The following winter, 1900-1, I was occupied with other matters and did nothing with this subject; but the next year, 1901-2, I resumed the



ү Fig. 56. study. Influenced by the theory above mentioned, I prepared to make more exact measurements than before of the respective movements of the four branches, for it was evident the theory could be tested by observing whether, as it requires, the greatest amplitude of movement occurs in the north branches, the next greatest in that east or west branch which happened to be illuminated on its inner face, and the least in the south branches. I made an improvement in Miss Persons's method by replacing the single gas pipe, which would yield a little under tension when the tape was drawn tight, by a perfectly firm tripod, formed of three gas pipes driven deeply into the ground, and bound immovably at their tops by twisted copper wire into which the brass screw was set, an arrangement illustrated diagrammatically in Fig. 56. Throughout the winter

very careful measurements were made of six shrubs, including the *Lindera* and *Cercidiplyllum* used the previous winter, together with two species of *Salix* and two species of *Populus* (young trees). The results need not here be given in detail, since in general they are simply confirmatory of those earlier obtained. As to the two main points at issue they were as follows :—

1. There was no such regularity or order in the amplitudes of movement of the respective branches as the theory required.

2. There was no regular influence produced upon the movements by the presence or absence of direct sunlight upon the faces of the branches, though in some individual cases this did appear to have some slight effect.

It occurred to me during the winter, especially when it became plain that the direct sunlight played little part, that perhaps the movement might be due to a warming, and hence swelling, of the inner faces of all the branches through a general warming up of the air among the branches of the shrub due to the reflection of the sun's heat from one branch to another. To test this I placed very accurate thermometers, reading precisely alike and graduated to tenths of a degree, both near the centre of the shrub (but in the sun), and outside the shrub a few feet away. They showed that the temperature among the branches and that outside the shrub were not appreciably different, thus eliminating another possible cause of the movement.

The idea that a direct action of the sun upon the plant produced the movement had therefore to be abandoned.

The following winter, 1902-3, I continued the study, concentrating attention upon two plants, Lindera Benzoin and a species of Salix, which had shown themselves particularly sensitive to temperature changes. Incidentally I re-measured these two shrubs very carefully through the winter, and the results for Lindera are given on Fig. 57, not because they bring out anything new, but because they show with particular clearness the correlation of movement with temperature. But the principal work during the winter was experimental, and directed to discover the precise physical basis of the movement. Its results were as follows. Certain observations made while measuring the shrubs seemed to render it probable that the outward movement was caused by the straightening of the curved branches due to the swelling of the air, and perhaps also the water, in the stems under the influence of the higher temperature. A marked swelling of this kind should produce a straightening of the branch upon precisely the same principle as it straightens the bulb of a Richard thermograph. This could be tested by bringing typical curved branches from the shrubs on very cold days directly into a warm greenhouse, and comparing the distance between the base and tip before and after the branch had time to warm up. I tried this in a variety of ways, even bringing them abruptly from a temperature much below o° (C.) directly into a large case kept at a temperature above 30°. To make the conditions as to water supply as uniform as possible, I plunged the branches at once into water in some cases (cutting them under water higher up the stem in some instances), and immediately sealed the cut ends with shellac in others. The results in all cases were the same. A slight straightening could often be observed within a few minutes under the higher temperature, but this was always lost within an hour or thereabouts, and was then replaced by a gradually increasing curvature. It became plain, therefore, that while a rise in temperature might cause

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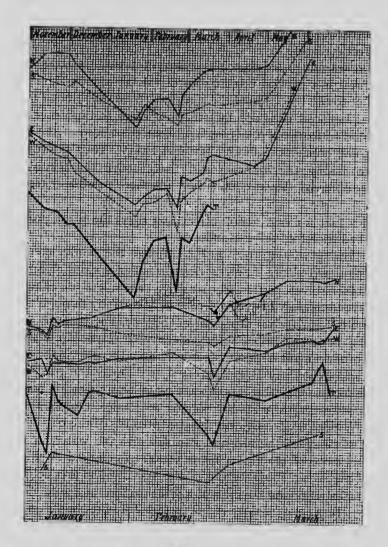


FIG. 57.

Abscissa spaces of upper five polygons, each two days; of lower six polygons, one half-day. Ordinate spaces, each 2 mm of movement (thus differing slightly from two preceding plates) and I degree of temperature, and 1% of water (for lower polygon).

Downward direction means inward of the shrub, and upward means outward.

The plate shows the movement of the branches of Lindera Benzoin, the north, south, east, and west branches being indicated by the initials N. S. E. W.

The upper four polygons show the movement through the season, and the four below them show it upon a larger lateral scale through the period of greatest secondary movement. The double line represents temperature.

The lowermost line represents the percentage of water contained in Salix.

(On irregularities in this plate see note on page 644.)

a slight straightening and hence outward movement, which might in the uninjured plant remain constant, such a cause was wholly insufficient to account for the entire amount of movement. That the swelling of air in the stem did not produce the result was proven by forcing air powerfully into the stem with a foot pump, a process always without appreciable result.

Having thus to abandon this hypothesis I turned to another, more than once taken up and dropped in the earlier part of the study, that the movement was in some way connected with the quantity of water present in the stem. This was, indeed, very strongly indicated by two facts: (a) the Broussonetia earlier referred to (p. 634) showed a continuous incurving of its branches after the plant was dead, which incurving was apparently correlated with the drying out of the branches; and (b) invariably during the experiments a drying out of any branch was accompanied by an incurving, that is, by an inward movement. The incurved, or extreme inward position, is evidently the natural position of the dry tissues, and it seemed probable, therefore, that the outward movement might be correlated with, and proportional to, the amount of water in the stem. This supposition could evidently be readily submitted to experiment. Accordingly on certain days showing extreme outward and inward movement, and therefore of extreme high and low temperature, during the winter, I cut from each of these shrubs ten healthy branches each 10 cm. long, tied them in bunches, and immediately weighed the latter. They were then dried for several months in a dry room, and subsequently for some days in a water bath. They were then again weighed, and the percentage of water in the original branches was thus readily determined. The results were as follows :---

Date.	Temp.	Plant.	Original Weight.	Dry Weight.	Amount of Water.	Percentage of Water.	
Jan. 19	-18	Lindera Salix	3.991 2.960	2.552	1.439 1.388	36.0 46.8	
Jan. 22	8	Lindera Salix	3.628 2.613	2-281 1-371	1.347 1.242	37-1	
Feb. 20	-11	Salix	4.027 2.785	2.465	1.562	38.7	
Feb. 21	-15	Lindera	4.032	1-490 3-494	1.295 1.538	46·4 38·1	
Feb. 24	5	Lindera Salix	3·572 2·884	2.220	1.352 1.361	35.0	
Mar. 13	15	Lindera Salix	3.820 2.870	2.072 1.483	1.748 1.387	45·7 48·3	

Comparison of these figures with the amount of movement at the corresponding dates (as shown on Fig. 57) will show at once that in *Salix* the agreement between amount of water and amplitude of movement is very close, a fact graphically illustrated by the polygon at the foot of

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Fig. 57. In Lindera, however, while there is agreement in some places, there is a wide deviation in others, so it becomes plain that either my figures are in error or else this method is worthless. There is, however, this difference between the two plants, that as the Lindera dries it loses some of its buds and bud-scales, while the Salix does not, and my method of drying the stems did not originally allow for this possible source of error. Despite the lack of agreement in the Lindera, however, I believe that the testimony of the Salix, and also that afforded by the gradually increasing curvature of all branches as they lose water, indicates a fundamental fact, namely, that the movement is connected with the amount of water in the stem, and that this amount of water is dependent upon temperature.

This conclusion involves two further questions: (1) by what mechanical method does the increased amount of water produce the movement; and (2) by what method does the variation in temperature produce a variation in the amount of water? We consider first the former, for which there are two possible explanations: (a) the weight of an added quantity of the water will tend to depress the obliquely-ascending branches and may thus produce the outward movement; (b) the added water may permit of the larger absorption by the various cells of the younger branches and their consequent swelling, whereby the straightening of the stem must result, precisely as any flaccid tissue straightens with more abundant water-content.

I have carefully tested both of these possibilities. As to the first I have repeatedly placed branches horizontal, and forced water into them both under an atmosphere of mercury, and also under the greater pressure of the water directly from a water tap. In such cases the water would be forced out in a few minutes from any injury incidentally or purposely made near the tip of the stem, showing that the water penetrated to the end. In such a case a distinct depression of the branch can usually be measured, but it is never of an amount as great as the natural amplitude of the movement in the branch attached to the plant. Furthermore, this small amount of movement occurs in the most favourable possible position (horizontal) of the branch, and would be much less when the branch is partially upright upon the tree. When the branches are placed upright, and the water is then forced into them, there is very little, if any, measurable movement. There is yet another consideration which shows that it cannot be the weight of the water which causes the outward movement, namely, that in many of the shrubs which showed marked movement of the branches the latter are nearly vertical as a whole, and hence the weight of the water cannot act to move them outward. The weight of the water, therefore, may aid the movement somewhat, but it cannot be the principal factor in causing it.

We turn now to the other explanation, that an added supply of water

permits a more active absorption by the cells (osmotic absorption by the living, and imbibition by the walls of the dead, cells) and their consequent swelling, thus producing a straightening and therefore an outward movement of the branch. The inward movement would be caused by a lesser absorption, which would permit the loss by transpiration to exceed absorption and hence render the cells flaccid, permitting the branch to assume its natural curve. That there is a steady loss of water from the twigs during the winter, including even the coldest weather is, I believe, well known. I have myself noted that, on the coldest days in the winter on which measurements were made, little ice crystals stood upon the lenticels of both Lindera and Salix. Now this steady loss of water implies a steady, even though small, absorption through the winter. It is well known, however, that with decreasing temperature the power of osmotic absorption falls much more rapidly than the rate of transpiration; hence with a falling temperature the loss of water from the parenchyma cells becomes increasingly great as compared with the possibility of renewing the supply osmotically; the turgidity of the cells must then decrease, and the same effect will follow as if the stem is dried out by any other method, namely, its curvature is increased and hence an inward movement results. The lagging of the movement behind the temperature-changes, earlier mentioned, is strongly in confirmation of this view. Unfortunately, my attempts to test this hypothesis experimentally have given very unsatisfactory results, so that I am unable to either confirm or disprove it, and as further experiment is not now possible until another winter, I must leave its completion to a future time or to others. But I regard this as by far the most probable explanation of the movement.

Turning to the question as to how a higher temperature increases the water-content of the stem, it is obvious that this is bound up with the still unsolved problem of the physics of sap-ascent. The roots of these shrubs extend down below the frost line in the soil, so there is no difficulty as to the root supply.

The explanation here attributed to the movement obviously applies to both seasonal and secondary unations, and would make them the result of the same causes.

As to the significance of the movement to the plant, I think the probabilities are that the movement is a purely physical phenomenon, merely an incidental result of the operation of a physical agency upon the mechanism the plant happens to present, and that it has no ecological advantage. It must be noted, however, that it still remains a possibility that the movement may be due to a differential absorption of water, this occurring more actively in the cells on the inner than on the outer faces of the branches, in which case it might not belong under incidental or physical, but under irritable movements, when it would be removed from the ther-

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mometric towards the thermotropic category. If this should prove to be true it will render it probable that the movement has some ecological value. The inward movement of the branches might be supposed to be protective, decreasing slightly the leverage of winter winds upon them, and as well the loss of heat and loss of water, but so slight is the amount of movement that the advantage can hardly be appreciable.

Since it is not the application of heat directly which determines the movement, but an indirect action through water absorption, it might be more exact to speak of the movement as an indirect thermometric movement.

In summary :---

(a) Some shrubs and small trees, and probably very many, exhibit a marked inward and outward movement of their naked winter branches.

(b) Two forms of the movement occur, a primary or seasonal movement, inward during the early part of the winter and outward in spring, and a secondary movement which is inward with a fall and outward with a rise of temperature. Probably these two are due to the same causes, the seasonal being simply a secondary movement of large *e.*nplitude.

(c) The movement is correlated with changes of temperature, though it is not caused by temperature directly, but by the larger or smaller quantities of water which the temperature determines in the plant. A smaller quantity of water, due to transpiration exceeding absorption, decre ses turgidity and permits the natural inward spring of the branches to manifest itself, while a larger quantity, due to absorption exceeding transpiration, permits an increase of turgidity and consequent swelling, straightening, and outward movement of the stem.

(d) The movement has probably no ecological significance, but is merely incidental to the construction of the stem, and is properly indirectly thermometric.

NOTE.—The irregular lines near the N line on the lower half of Fig. 57 were accidentally introduced into the copy, and they cannot be removed from the plate. They have of course no meaning for the subject under consideration.

