INVERTED POLARITY IN SALIX BABYLONICA L.

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With plates V and VI.

In a recent article, entitled: Eine botanische Polaritätstheorie, Went (1932) discusses the place of origin of the growth substance and the direction of its transport. He states that such transport can be due to:

a. a pressure drop inside the plant
b. a concentration drop of the growth substance
c. a potential drop, in case the transported substance is ionised.

He considers that the conditions which cause the polarity phenomenon are not likely to be influenced by external conditions and that polarity cannot be inverted and gives indeed the impression of having relied to a large extent on this assumption.

Whereas it is not improbable that the assumption that a potential drop in the plant causes a polarised transport of growth substance is correct, the argument on which the statement is based is open to criticism. Several cases of inverted polarity have gradually come to light.

Czaja's (1931) statement may therefore be quoted once more: „das nicht mehr ganz zeitgemäsze Polaritätsproblem (enthält) doch noch eine recht moderne Seite".

The Distribution of the Material.

As mentioned in a preliminary report (private, not published) the first time that I heard about the phenomenon was towards the end of 1929. This was the case noticed at Harrismith O.F.S. It was not, however, until October 1932 that opportunity occured for me to investigate the problem, but meanwhile, Dr. J. H. F. Wagener, Medical Inspector of Schools in the O. F. S., who had noticed the first case, was able to search constantly for more and his trouble was well rewarded by the extensive and magnificent collection of specimens he discovered. Material was discovered and photographed at Harrismith and Frankfort in the Wilge River, near Bethlehem in the Jordaan river, near Kroonstad in the Valsch River, between Heilbron and Lindley in Rhenoster River, on the farm Molendraai, and near Commando Nek (Ficksburg) in a dam. According to dr. Geo. Potts, Professor of Botany at the Grey University College at Bloemfontein, such cases may be observed near Bloemfontein in the Modder-river as well.

It should be mentioned that the term „river" in these instances does not indicate a flowing stream but a course for flood water, so that from time to time the rivers may be quite dry. During the last decennia efforts have been made to conserve some of the rain water by building dams across the riverbeds. Near all the towns named the rivers have been dammed and the water in the river is thus standing water.

The trees on the other hand, according to information that was carefully collected, are generally much older than the stretch of water alongside which they are found at present. They are all well developed, or have been so and their finer branches sweep the surface of the water or hang into it.

This is a rather remarkable feature. I have seen weeping willows at various places but rarely did the branches reach as low down as to sweep the ground. Before touching the surface of the water additional growth is essential.

In how far the change in the water level round or near the base of the tree is of importance in the coming developments is difficult to determine. At least in one locality, viz. the Jordaan dam North of Bethlehem, sometimes called Loch Lomond, it may be noticed that the trees have not altogether gained from the change in the water supply.

They are here growing very close to the water side. Formerly the water did not rise to the same level as now. Since the dam wall has been raised a few feet only, but sufficiently to inundate formerly dry soil. Some double rows of trees are growing on stretches of semi-dry soil extending for some distance into the dam. When the foliage of these trees is compared with that of trees growing at a distance of a few hundred feet from the dam, then the light-green colour and the smaller size of the leaves form points of striking contrast. Several specimens appear to be the remainders of previously existing, much larger trees and it is not impossible that these gradually died down in the same manner as their successors give the impression of doing.

This does not apply to all cases. The results of the change of conditions, however, may not become evident to the same extent. The branches with inverted polarity again produce larger leaves of a darker green colour and by this can be distinguished.

It is rather probable that the vitality of the trees has suffered to a greater or lesser extent from the flooding of the soil which must have affected at least part of their root system. It is a well known fact that soil saturated with water contains very little oxygen and standing water that is exposed to atmospheric conditions likewise contains oxygen to a far lesser degree than rain water.

The possibility has to be considered that the inversion of the polarity is partly influenced by changed external conditions. [1])

The Inversion.

Although there has been no opportunity of observing one case developing from beginning to end, still sufficient stages of development exist and are reproduced in the photographs, to enable one to reconstruct the process.

Salix is known for the readiness with which adventitious roots can be formed. The large number of S. babylonica in South Africa is a clear indication of this, since the tree is propagated from cuttings only.

A branch that dips into the water is likely to form adventitious roots from the buds. (Cf. Sachs: Stoff und Form der Pflanzenorgane. Gesammelte Abhandl. Vorlesungen über Pflanzenphysiologie. 2 Aufl. p. 253, p. 1159, and Vöchting, as stated in Goebel, Organographie der Pflanzen III (1922) 1, p. 1268). In a newly formed shoot it takes about three to four months before the root premordials are formed. These roots may or may not become of value and importance in subsequent stages.

While roots are developed in water, the shoot apex, leaves and stem premordials under water are in an environment unfavourable to their function and development. These parts of the branches frequently form a support for various kinds of algae and smaller water animals. The leaves are frequently covered with a dense, black layer of organic material together with a deposit of fine silt. That the normal leaf functions have become reduced, if not totally suppressed, is certain.

Relatively few data are available for comparison to

[1]) This reminds one of the results obtained by Noll and Winkler on Siphoneae. (Cf. Goebel, Organographie der Pflanzen. I (1913) p. 456—457).

note if the conditions would allow root development while suppressing that of the shoot. The material shows this, however.

In Kostytchew-Went (1931) it is stated: „Die Wurzelbildung wird offenbar von sehr verschiedenen Faktoren beeinfluszt; dabei spielt der Wassergehalt eine sehr grosze Rolle, auch andere äuszere Umstände, und daneben die Polarität". Thus, the development of the roots need not be caused by the polarity, and in the presented cases the rootformation can hardly have been influenced by it. On the other hand the polarity has clearly been influenced by the absence or presence of active roots.

The development of new roots at or near the tip of a branch may be the initial stage in the inversion of the polarity. If this is to take place then the roots must be sufficiently well developed to cause their functioning to be of influence on the near environment inside the plant, and this functioning should take place continuously over some length of time. The regularly recurring drought conditions, or periods with little or no rainfall even during the rainy period tend to reduce the number of successful inversions.

If an efficient root system can develop a few results may be considered. *a*. The water — generally the sapstream in its wider sense — absorbed by the adventitious roots supports the existing sapstream. *b*. The adventitious roots by their action give rise to a sapstream that opposes the existing stream.

a. offers only one possible theoretical solution, i. e. the tip of the branch that dips under water, or a side branch that develops at or near the surface of the water continues growth and in a few years' time the whole presents a picture of a branch that is rooted at some particular point. That the roots should be somewhere in the water, at least at first, is immaterial. Such cases have been observed.

b. can only arise when the tip of the shoot or the whole portion of the shoot under water shows a greatly diminished activity. This would be the case where the branch tip has been under water for at least one season. During the course of Summer the leaves that are present are more and more covered with an opaque layer of silt and organic material while respiration and transpiration are largely suppressed. Changes in the water level should have been absent or not pronounced.

In next Spring the two sapstreams must be found in opposition, that of the new roots tending to rise upwards, that from the main roots descending in the branch. Depending on the presence of a suitable bud or buds near the new roots, these can be supplied by the new roots, because there are no structural obstructions to such an eventuality.

When not interfered with a number of buds usually develop on the branch, the lower ones giving longer shoots in the first year than the higher ones so that in even one season the branch at its lower end resembles a small tree in that it shows a bluntly conical outline when the tips of the branches are connected by imaginary lines. Such cases have been observed and photographed.

Or a single bud may develop and give rise to an imitation young tree. In every case the buds, before the inversion of the polarity, point clearly downward and the first development resembles that of normal buds of the weeping willow. Soon, however, in the case I observed in my garden after 2—3 days, the leaves and the tips of the branches stand away from the shoot. In about 1—2 weeks time the young branches have, through curvature, assumed a position that is nearly horizontal or slightly ascending. Because of this feature they can be distinguished clearly from the normal pendant young branches of the parts of the tree that have retained their normal polarity.

With the development of the buds the polarity has already become inverted. In some cases, of which seven have been noticed N. of Bethlehem in Loch Lomond and one near Frankfort, a remarkable phenomenon is or appears to be the result of the foregoing. Here the main branch, above the portion where the polarity has become inverted, has died. This can be explained only by assuming that in this portion the food and water supply has become insufficient to maintain this portion alive. Most likely this is due to stagnation of the sapstream. In the example from Frankfort a piece of dead side branch is visible on this dead portion, near Bethlehem they appeared to be bare and showed no branches at all. The absence of branches in itself cannot be considered the cause of death since other cases at Bethlehem and the one at Harrismith show no signs of dying.

It is due to the extremely difficult positions in which most of these branches were found that they had to be considered inaccessible for the time being. Access by water was impossible because of the absence of boats while the mud and relatively deep water excluded the possibility of wading up to them. On the other hand they were — by comparison — found to be too thin to support a normal human weight and approach from above was thus excluded as well. In one case only was it possible to make a kind of path with boulders to make experimental work relatively safe.

Before presenting the various cases for observation it may be useful to consider what changes did take place.

Comparing the results obtained with Went's theory of polarity it is noteworthy that the pendulous branches of Salix babylonica — according to his theory — must show a reduced polarity potential because of their position. The negative potential of the tip is already reduced by gravity. It will be further reduced by the absence of oxygen once it enters the water (cf. Lund 1931) and as Went states that in the inverted hypocotyls of Impatiens the polarity was not perceptible this may hold to the same extent for the presented cases.

From this it need not follow that reduced or stopped respiration will transform the negative branch apex immediately into a positive pole, or that the reduced negative potential induces a weakened positive one; but a strong positive pole developing close to it may suppress it to such an extent that this new positive pole creates a new negative pole. This new negative pole will then be situated between the new and the existing positive poles. Its exact locality will be determined by the opposing influences of these poles.

Once this has occurred the change in polarity appears to have become irreversible.

The conclusion may be made that the transpiration stream induces the polarity.

Czaja considers that the flow of growth substance, moving downwards from the apical meristem induces polarity, Went on the other hand that the pre-existent polarity induces this directed flow of growth substance. While the data presented here do not clearly support Went they are opposed to Czaja's theory. It might seem as if the transpiration current — at least in the cases under discussion — is of primary influence on the determination of the polarity while the direction of the transport of growth substance may be influenced by this.

The Determination of the Polarity.

Went uses in his polarity experiments the hypocotyls of etiolated seedlings of Impatiens Balsamina. His method is largely based on the work of the Prager biologisch-physikalische Arbeitsgemeinschaft. He uses basic and acid dyes in dilute solution and generally finds that the basic dyes move towards the top, the acid dyes downwards

(The exact concentrations and conditions are stated in his paper). He concludes from this that the base of the plant is a positive electrical pole, the apex a negative one.

This method unfortunately could not be applied. Owing to the thickness of the material a clean razor cut could not easily be obtained, only in the very young shoots and these did not come into consideration for experimental work. Pruning shears always gave a fairly rough surface which obscured the intensity of the staining.

In some cases where the coloured liquid clearly could be distinguished after its entrance into the pieces of shoot the results obtained are comparable with his. Even in the best of cases, however, my results could have been influenced by the required lengthwise cutting of the pieces, whereby some colouring substance may have adhered to the knife surface.

Another method had to be developed. Considering the general use made of methylenblue in vital staining a 0.1 % solution was used. The method as finally used is as follows:

With a cork borer, diameter 6 mm, a disc of the bark down to the cambium is cut out and in this opening a glass tube with an external diameter of slightly more than 6 mm fixed and supported by means of a piece of wire.

With collodion, already thickened by exposure to the air, an initial cover is made round the base of the tube. The collodion must be sufficiently thick not to enter between the tube and the bark and to cover part of the wood surface.

When the collodion layer is dry two or three successive layers of fast drying paint are applied. The cellulose lacquer paints proved to be eminently suitable for the purpose and the complete connection could finally be made within a few minutes.

Into the tube the methylenblue solution can now be poured. A drop bottle proved to be very useful.

During the preliminary experiments it was found that 2—4 hours sufficed to give clear results. The methylenblue was found to be absorbed mostly in the superficial wood vessels and it remained localised in a narrow band never wider than the opening of the tube. At the base of the tube it did spread sometimes radially but never far enough to cause more than a very much localised broadening of the blue band.

The dye is not absorbed and transported in one direction only. While it largely is carried upwards by the transpiration current some moves downwards, but the distances over which this happens are very unequal. They were measured after a 4-hour period, the rise amounting to 9 inches, the descent to 3. Repeats gave approximately the same values: about 3 times faster rise than descent. Eosine was found to rise and descent at about equal rates in these experiments.

These figures cannot be taken to indicate the rate at which the sapstream itself ascends. (Huber, 1932).

Repeating this on a branch with inverted polarity in Bethlehem, it was found that after 2 hours, at a height of 2 feet 3 inches above the roots, methylenblue passed upwards over a distance of 7½ inches, downwards over 4¾ inches. On the same branch at 4 feet high the ascent was visible over 6¾ inches, descent over 5 inches.

Thus, nearer the top where the branch was severed from the tree the rate of ascent decreased.

The only conclusion is that the sapstream in the branch actually moves in a direction opposite to the normal one and that the polarity in this case is inverted.

Illustrative Material.

The various cases that have been observed and photographed are too numerous to be presented here together.

A few have been selected for presentation and discussion.

No. 1, near Harrismith, shows the first case that was observed. (Oct. 1929). It is a clear and straightforward illustration of the phenomenon. The photograph does show the former tip, at present the base of the branch, as the thickest portion.

As mentioned above the greater number of cases were found near Bethlehem in the Jordaan valley.

The branch on which the experiments were performed is shown in No. 2, one of the tubes with methylenblue solution can be seen in the centre, just above the side branch which is growing upwards.

The most striking example is shown in No. 3. The tree of which a part only is visible consisted of three heavy trunks, 1½ feet in diameter and two thinner ones. It is but likely that they developed after the original tree died or was chopped down. One of these trunks bore the branch shown in the photograph.

The photo was taken from about 10 feet above the ground. In the right centre the trunk gives off the arched branch, while the portion that grows upwards is slightly thicker than the branch. As may be noticed the main branch grows downwards and is rooted there. It was not possible to see clearly if the stem that grows upwards from its base, slanting to the left, is the result of a bend. Judging by appearance it must be considered as a side branch that developed at about the average water level. In between these two an accumulation of silt, rotten leaves and live branches rendered closer investigation very difficult.

From the top of this live, arched branch a second arch descends. The place where it entered the water was inaccessible. At the place where the double bend occurs, (two near-right angles), a live branch grows upwards. From the point of origin of this branch to its other end, this second arch is dead. The bark is peeling off everywhere and near its origin nothing is left. It is noticeable that there is a sudden constriction as a demarcation line between dead and live parts.

In this locality several more of these arched branches have been observed.

Two types of arched branches can be distinguished here. On trees growing near the water side the arches frequently consist of two straight portions, the one slanting upwards, usually the shorter piece, and the second growing either straight down or with its base further away from the base of the tree. It is probable that this arch is the result of continued growth in the vertical portion. At the sharp bend, side branches are usually found. This might be taken to indicate a healed wound.

The second type of arch is more or less limited to a slightly elevated part of a land tongue in the water. This is illustrated by No. 4. The branches here appear to function as buttresses; they form acute angles with the main trunk and soil level and are usually without any leaves or side branches. The buttress function is presumed from the fact that the vertical diameter in some cases is nearly twice the horizontal diameter, though more frequently the difference is less pronounced while they are clearly oval in cross section.

Conclusions.

The polarity of Salix babylonica L. can be inverted. The circumstances under which this take place in nature in certain areas in the Orange Free State have been described.

The new plants that have been formed as a result of the inversion of polarity are perfectly independent of the original mother plant to which they can remain attached for some length of time.

After inversion of the polarity the branches in which the phenomenon has taken place can be severed from the parent tree and raised as independent trees in the same manner as normal cuttings.

The reported facts to a certain extent are in support of Went's theory of polarity.

Literature.

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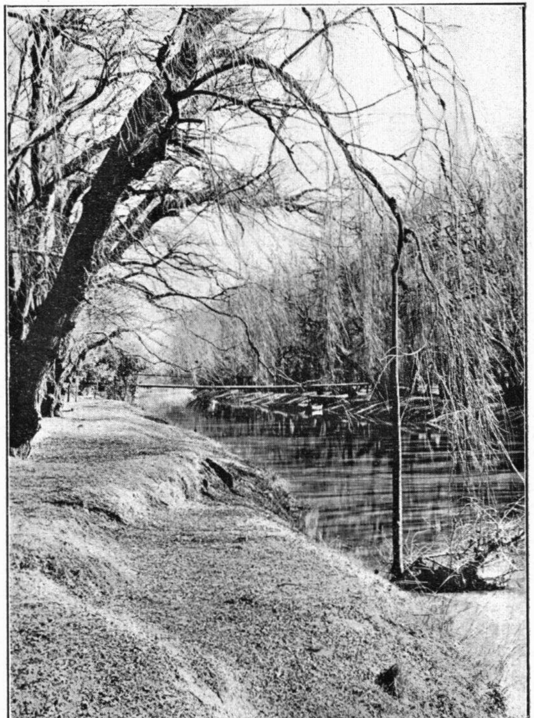
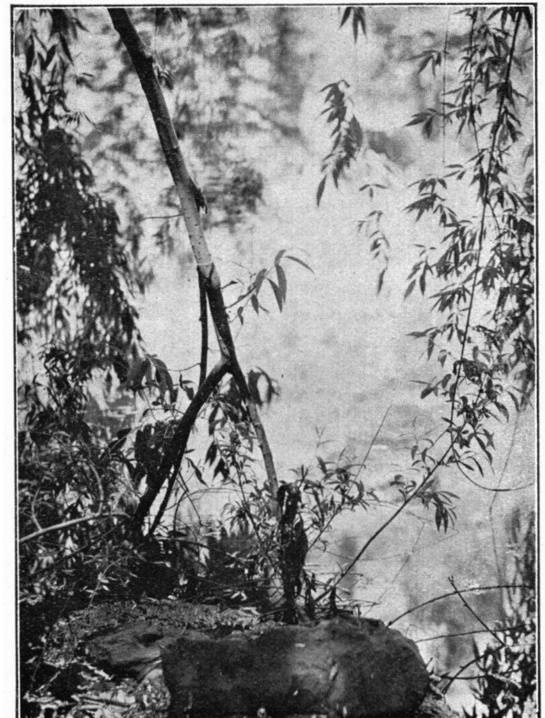
PLATE V.

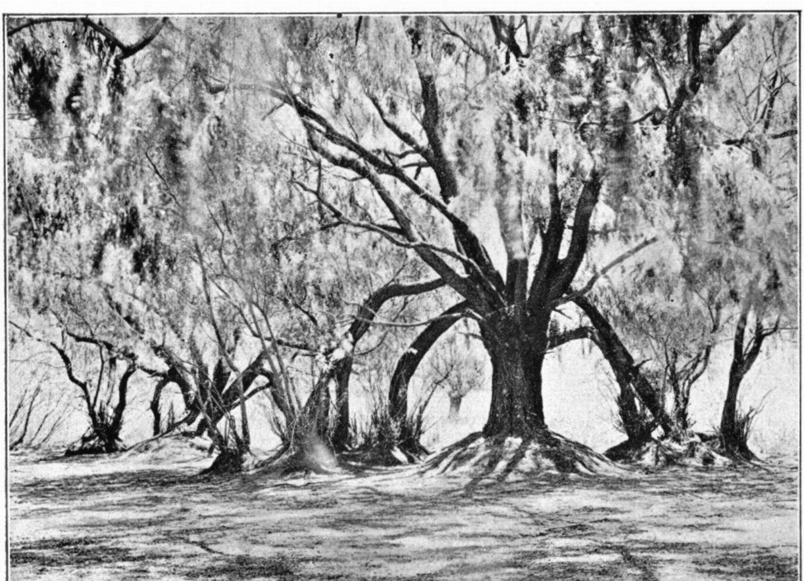


No. 1. Bethlehem. „Kloof".



No. 2. Harrismith.

No. 3. Bethlehem. „Loch Lomond".



No. 4. Bethlehem. „Loch Lomond".