the other types are to some extent involved,⁶ but for them the disentanglement of local system and galactic field is more difficult.

Quite analogous to the phenomenon of the Milky Way, the projection on the sky of the faint stars along the central plane of this local cloud gives rise to a sort of secondary Galaxy,⁷ the brighter stars of which coincide roughly with the Herschel-Gould belt. The distribution of the B stars indicates that the dimensions of the local system are large compared with those of a globular cluster; the local system is also more oblate. I believe it can be better compared in dimensions, and possibly in form, with the Magellanic Clouds or with the distinctly delimited small star clouds of the Milky

Way. The various phenomena of star streaming are undoubtedly connected with the motions of and within the local system. Probably a number of our brighter "moving" clusters should be considered sub-systems in the local cloud, rather than independent systems which for the time being are near at hand.

(To be continued.)

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Transport of Organic Substances in Plants.¹

By Prof. H. H. DIXON, Sc.D., F.R.S.

AMONG physiologists the usually accepted view is that organic substances are distributed throughout the plant by means of the bast. The wood also acts as a channel of distribution for these substances to opening buds and developing leaves, especially in spring when root-pressure is active. The sap of bleeding contains appreciable quantities of these substances, and their distribution to the developing buds in spring by means of the wood was recognised by Hartig and Sachs.

This upward transport of carbohydrates in the tracheæ seems to be accompanied with smaller amounts of proteins. Thus Schroeder showed that the quantity of proteins in the bleeding sap rises and falls with the quantity of sugar.

This view that the rising current in the tracheæ carries organic substances in it and distributes them to the growing regions has lately been impugned. It was pointed out that in many cases, ringing close below the terminal bud prevents the development of that bud because the wood is unable to transmit sufficient supplies of organic substance. As Strasburger has already shown, this interpretation rests upon the fallacy of supposing that the removal of the bark as far as the cambium leaves the wood uninjured. As a matter of fact, microscopic examination of the wood, from which the outer tissues have been stripped, shows that its tracheæ soon become blocked with air-bubbles and with substances probably exuded into them and their walls during morbid changes in the cells of the cambium, in the cells of the medullary rays, and in those of the wood-parenchyma. The blocking is accompanied with discoloration, and is most apparent in the outer layers of the wood. It is only reasonable to suppose that the efficiency of the tracheæ as channels of transmission is seriously impaired even before there is visible evidence of plugging.

It is evident that this clogging may act differentially on the water and the substances carried in it. In the first place, the whole cross-section of the wood is available for the transport of water, while probably the outer layers are mainly utilised by the organic substances. Further, colloidal deposits in the walls, and especially in the pit-membranes, would obstruct the passage

of organic substances much more than they would the water which carries them. These considerations readily explain how it is that, while the water-supply to the buds of ringed branches is adequate, the supply of organic substance may be deficient.

Apart, then, from the very slow movement of organic substances from cell to cell, there is very cogent evidence that their upward motion is effected in the tracheæ of the wood. There is no reason to believe that during this transport the walls or pit-membranes of these tracheæ oppose the passage of the dissolved carbohydrates or of the simpler proteins any more than the water which conveys them. Hence the velocity of transport of these organic substances is that of the transpiration current, and the amount conveyed in a given time depends on the velocity and concentration of the stream.

The transport of organic substances in an upward direction in plants is secondary, for, as is well known, carbohydrates certainly, and proteins most probably, are manufactured only in the upper green parts of plants—principally in the leaves, and must be transported in the first instance back from these to the stems to be distributed to the growing regions and to the storage organs.

This view that the channel for the backward and downward movement of organic substances is afforded by the bast received great support from Czapek's work published in 1897. By section of the conducting tracts in one half of the petiole he showed that depletion of the corresponding half of the blade was delayed. He also showed that only where vertical bridges connected the upper and lower portions of bark in ringed stems were the effects of ringing nullified. Oblique and zigzag bridges are ineffective. Thus transverse conveyance in the stem is negligible. The parallel and longitudinal arrangement of the elongated elements in the bast seemed to him to provide adequately for the observed longitudinal passage. Their narrowness and large colloid content did not present themselves as difficulties. Czapek also recorded the observation that the blades of leaves, the petioles of which had been killed by jacketing them with steam, did not become emptied of starch. Similarly, when the petioles were killed with chloroform-vapour, depletion was arrested. Again, anæsthetisation of the petiole, by surrounding

¹ From the presidential address delivered to Section K (Botany) of the British Association at Hull on Sept. 7.

it with a watery solution of chloroform, greatly delayed the disappearance of starch.

Czapek formed no definite theory as to how organic substances were moved in the bast. He was sure that the transport depends on living protoplasm. He did not consider that the streaming of protoplasm contributed materially to the motion, seeing that streaming does not occur in mature sieve-tubes. He regarded the sieve-tubes as the most important elements in the transmission of these substances, because the deposition of callus in the sieve-plates synchronises with the stoppage of transport. The transport, according to him, is not simply due to diffusion. He supposed the protoplasm to take up the organic substances and pass them on. If diffusion does not account for the passage from one particle of protoplasm to the next, it would seem that we must suppose the organic substance to be projected from one to the other.

These observations and their interpretation by Czapek have strengthened the opinion that the bast is the channel for the downward transport of organic substances. It is remarkable how little weight has been attached to the damaging criticism of Czapek's views by Deleano, especially as those views are so unsatisfactory from a physical point of view.

The latter author showed that it is inadmissible to compare externally similar leaves, which often behave, so far as depletion is concerned, very dissimilarly. He also pointed out that without any export a leaf may be depleted of all its starch within thirty-five hours, and partially anticipated an extremely interesting recent observation of Molisch—namely, that transpiring leaves lose their carbohydrates much more rapidly than those the transpiration from which is checked by being surrounded with a saturated atmosphere. Neglect of these facts led Czapek into error. Deleano also showed that organic substances continue to leave the blades even after the petioles have been killed by heat or by chloroform-vapour. The rate of depletion is reduced by the former agent to about one-third, and by the latter to one-half. If this observation is substantiated it would show that the intervention of living elements is not essential for the transport. He further found that the blades attached to petioles which were surrounded by chloroform-water lost their starch more quickly than those immersed in water.

The contradictory conclusions of Czapek and Deleano urgently call for a reinvestigation of the points at issue. If Czapek's work holds good, we shall have to regard the bast, and especially the sieve-tubes, as the channels for the transport of organic substances back from the leaf-blades where they are manufactured, and we must look for some hitherto un dreamed-of method of transmission through these most unlikely-looking conduits. On the other hand, if Deleano's conclusions are borne out, we should admit that protoplasm is not necessary for the transport, and we would turn to a dead tissue as furnishing this channel.

So far as I am aware none of the earlier investigators made any estimate either of the actual quantities of organic material which are transported or of the velocities of flow in the channels which are necessary to effect this transport.

We may approach this problem from two opposite directions—(1) by dealing with the amount of organic

substance accumulated in a given time in a storage organ, or (2) by using the amount exported from an assimilating organ. The cross-section of the supposed channels of transport and the volume of the solution containing the substances in each case will give us the other necessary data.

For the first method a potato-tuber will furnish an example. One weighing 210 g. was found attached to the base of a plant by a slender branch about 0.16 cm. in diameter. In this branch the bast had a total cross-section of 0.0042 cm.². This figure is a maximum; no allowance was made for the cross-section of the cell-walls, or for any non-functional elements in the bast. The cell-walls would occupy probably one-fifth of the cross-section of the bast. Now if the bast exclusively furnished the channel of downward transport, all the organic substance in the potato must have passed this cross-section during the time occupied in the growth of the potato. One hundred days would be a liberal allowance. According to analyses more than 24 per cent. by weight of the potato is combustible. Therefore we must assume that during this time more than 50 g. of carbohydrate has passed down a conduit having a cross-section of no more than 0.0042 cm.². The average concentration of the solution carrying this substance could scarcely have been as much as 10 per cent. (2.5-5 per cent. would be more probable; the concentration of sugar in bleeding sap is much below this figure, and seems never to reach 4 per cent.). Assuming, however, this concentration, the volume of liquid conveying 50 g. must have been 500 cm.³, and this quantity must have passed in 100 days. Therefore the average velocity of flow through this conduit, having a cross-section of 0.0042 cm.², must have been

$$\frac{500}{0.0042 \times 100 \times 24}, \text{ i.e. nearly } 50 \text{ cm. per hour.}$$

By the second method we arrive at a different figure. Various investigators, from Sachs onwards, have measured the rate of photo-synthesis per square metre of leaf per hour. Under the most favourable conditions the amount may approach 2 g., and it has been estimated as low as 0.5 g. Taking Brown and Morris's determination for *Tropæolum majus*, namely, 1 g. per square metre per hour, and assuming one-third of the carbohydrate formed is used in respiration in the leaf, we find that a leaf of 46 cm.² may form during ten hours' sunshine 0.46 g.; during the twenty-four hours one-third of this will be respired, leaving 0.31 g. to be transported from the leaf. The volume of the solution (again assuming a concentration of 10 per cent.) will be 3.10 cm.³. The cross-section of the bast of the bundles in the petiole was 0.0009 cm.²; therefore the velocity of flow, if the bast was used as the channel of transport, must have been $\frac{3.10}{0.0009 \times 24}$ or 140 cm. per hour.

Similar figures to these were derived using measurements obtained from a number of potato-tubers and from various leaves. The velocities indicated, even assuming a concentration of 10 per cent., lay in all cases between 20 cm. and 140 cm. per hour. These figures are in agreement with those arrived at by Luise Birch-Hirschfeld, as to the weight of organic material transported from leaves.

A flow of this rate through the bast seems quite

impossible. The narrow transverse section of its elements, the frequent occurrence of transverse walls, and the lining of protoplasm and large protein contents practically preclude the mass movement of liquid through this tissue. If we imagine the flow restricted to the sieve-tubes the velocity must be correspondingly increased, and the excessively fine sieve-pores, more or less completely occupied by colloidal proteins, must be reckoned with. Simple diffusion, as Czapek recognised, cannot account for the transport, and there is no reason to suppose that adsorption on the surfaces of the colloid contents of the sieve-tubes can increase the velocity of diffusion, as Manghan suggests.

As soon as one realises the volume of the solution which has to be transported, and the velocity of the flow that this necessitates, one naturally turns to consider if the open capillary tubes of the wood may not be utilised as channels of transport. Deleano's results, indicating that the depletion of leaves continues even after the living elements of their petioles have been killed, support this conjecture.

The emphasis which has been laid on the function of the wood as providing a channel for the upward movement of water usually obscures its function as a downward and backward channel also. Early experimenters, however, fully recognised that, under certain conditions, the current in the wood may be reversed. There is, of course, recent work also showing this reversed current.

By means of an eosin solution this reversal of the transpiration current may be very easily demonstrated. If the tip of a leaf of a growing potato-plant is cut under eosin solution, the coloured solution is very quickly drawn back into the tracheæ of the conducting tracts of the leaf; from there it passes into those of the petiole, and makes its way not only into the upper branches and leaves, but also passing down the supporting stem may completely inject the tracheæ of the tuber, and from thence pass up into the wood of the remaining haulms of the plant. Its passage is entirely in the tracheæ of the wood of the conducting tracts.

Another very striking experiment may be carried out with the imparipinnate leaf of *Sambucus nigra*. Its petiole is split longitudinally for a few centimetres and half removed. The remaining half is set in a solution of eosin. The solution is rapidly drawn up the wood-capillaries of the intact half-petiole, and soon appears in the veins of the pinnæ on the same side of the leaf, beginning with the lowest, and gradually working up into the upper ones. Finally it appears in the terminal pinna. All this while the veins of the pinnæ on the other side remain uncoloured. Now, however, the eosin begins to debouch into the base of the uppermost of these pinnæ and spreads through its veins; finally it makes its way down the offside of the rachis to the bases of the lower pinnæ, and from thence spreads into their veins. In this case we see very clearly how transpiration actuates an upward current on one side and a downward current on the other. It is interesting to note that if the terminal pinna and its stalk is removed the eosin does not appear in the pinnæ of the second side, or only after a considerable time, when the small anastomosing conducting tracts are utilised.

Luise Birch-Hirschfeld also described recently many

experiments with herbaceous and woody plants, tracing the path of the reversed current by means of lithium nitrate and eosin.

In all these cases the tension of the sap determines the flow from a source wherever situated, and transpiration from the leaves, or parts of leaves, which are not supplied with liquid water from without, draws the water through the plant along the channels of least resistance. Hence it is that if the cut vein of a lateral pinna provides the point of entry, the solution may pass backwards in some of the conducting tracheæ, leaving others quite uncoloured, so that some of the veins only of the pinna are injected. The injected tracts bring the solution down the rachis and petiole into the stem, while a few or many, as the case may be, remain filled with colourless liquid, presumably the sap drawn upward to supply the transpiring surfaces of the leaf. Generally the coloured liquid descends an appreciable distance in the tracheæ of the stem before it begins to rise in the ascending current, mounting to other transpiring leaves. As a rule after some time—depending on the rate of transpiration and the amount of water supplied by the roots—the presence of the coloured liquid may be demonstrated in certain continuous series, or filaments of tracheæ in several bundles of the lower parts of the stems. Similarly, if tubers or rhizomes are present, examination of these parts, after a suitable interval, will show that many of their filaments of tracheæ are injected. Meanwhile the parts above the supplying leaf become coloured, and it will be seen that the distribution of coloured tracheæ is decided by the anatomical connexions of those filaments of tracheæ which convey the coloured liquid directly from the point of supply through the petiole to the stem. In tracing the path of the solution one is impressed with the fact that the path of least resistance is by no means always the shortest path in the wood. Transverse motion across several tracheæ seldom occurs, and the separate linear series of conducting tracheæ are practically isolated from each other laterally. Here we may recall Strasburger's experiments showing the very great resistance offered to the flow of water in a transverse direction in the wood of trees. This isolation of the separate filaments of tracheæ in the leaf and in the stem enables the tension developed by the transpiring cells of the leaves, while it raises a column of water in one series of tracheæ, to draw down a solution in a neighbouring filament of tracheæ terminating above in some local supply. If the anatomical connexion of the two series is located in a subterranean organ the tracheæ of the subterranean organ may become filled from that supply.

So far the evidence of reversed flow in the water-conducting tracts which we have been considering has been derived from plants under artificial conditions—plants the conducting tracts of which have been cut into and otherwise interfered with. Is there any evidence that reversal of the transpiration-current normally occurs in uninjured plants?

Some recent work on the transmission of stimuli seems to me to indicate that these reversals are continually occurring in normally growing plants.

The first piece of work to which I would direct attention is that of Ricca on *Mimosa*. It has long been known that the stimulus which causes the folding of the

pinnules and the bending of the petioles of *Mimosa* could traverse portions of the petioles or stems which had been raised to such a temperature as would kill the living elements in these organs. Notwithstanding that observation, Haberlandt's view, that the stimulus is transmitted as a wave of pressure through certain tubular elements of the bast, was generally accepted as the least objectionable of any of the theories which had been put forward to explain this transmission. Ricca saw that, among other difficulties, the slowness of transmission—never more than 15 mm. per second—was a grave objection to this view. Accordingly, working with a woody species of *Mimosa*—*Mimosa Spegazzinii*—he removed the whole bast and outer tissues of the stem for as many as twenty-three centimetres and was able to show that the stimulus was still transmitted. Similarly he found that the stimulus was transmitted through narrow strips of the wood from which even the pith had been removed. These experiments and others in which the transmitting organ had been killed for a considerable length caused Ricca to recognise that the stimulus is transmitted in the wood and not in the bast, as had been previously held. Thus he was led to assign the transmission to the transpiration-current. He was able to confirm this conjecture by showing that the transmission to the various leaves of a plant is largely controlled by the rate of the transpiration from the individual leaves. Thus, other things being equal, a rapidly transpiring leaf receives the stimulus sooner than a sluggishly transpiring one equidistant from the point of stimulation. He was able to show further that the stimulus may be transmitted through a glass tube filled with water, just as it is transmitted through a dead portion of the stem. Evidently a hormone set free into the transpiration-stream is the long-sought-for mechanism by which the stimulus is transmitted throughout *Mimosa*.

As the stimulus travels both in a basipetal and acropetal direction we may assume that movement of the transpiration-stream in a downward direction is of normal occurrence in plants.

Contemporaneous with, and subsequent to, Ricca's important work on *Mimosa*, experimental evidence has been accumulating to indicate that the transmission of other stimuli—phototropic, traumatotropic, thigmotropic, and geotropic—is effected by means of the passage of a dissolved substance. Boysen-Jensen appears to have been the first to announce that phototropic and geotropic stimuli may be transmitted across protoplasmic discontinuities. Paál emphasised this by showing that these stimuli are able to pass a disc of the tissue of *Arundo donax* impregnated with gelatine, which is interposed between the receptive and responding regions. These observations rendered the view that the stimulus is transmitted in the form of a hormone extremely probable; and later Stark showed that this hormone is thermostable, just as Ricca had done in the case of the hormone of *Mimosa*. Another very interesting point discovered by Stark—working with traumatic stimuli—is that the hormones are to a certain extent specific. Thus if the perceptive tip of a seedling is removed from one plant and affixed in position on another, the certainty of the response depends on the genetic affinity of the two plants.

In all these cases it seems certain that the perceptive tissues are the point of origin, when stimulated, of a dissolved substance, the hormone, which makes its way to the motile tissues and releases the response.

In the case of *Mimosa* just alluded to, and of the labellum of *Masdevallia* examined by Oliver, there is direct evidence that the transmission of the hormone is effected by the vascular bundles. In *Mimosa* the channels are more precisely localised as being the tracheæ of the wood. Furthermore, the rapidity of transmission renders it certain that simple diffusion through the tissues of the plant will not account for the process. Some recorded velocities of transmission are here enumerated for the sake of comparison:

Plant,	Nature of Stimulus,	Transmission Time in secs. per mm.
<i>Mimosa</i>	Heat	0.07
<i>Drosera</i>	Chemical	6.00
Seedling	Light	180-300
"	Gravity	300
Tendrils	Contact	17
Diffusion in tissue		2250-3600

There is thus every reason to believe that the transmission of stimuli generally through the tissues of the higher plants is effected by the conveyance of a hormone in the wood of the vascular bundles from the receptive to the motile regions, and whenever this transmission is in a downward direction evidence is afforded of the downward movement of water in the tracheæ. It is reasonable to suppose that this downward current is able to carry organic foodstuffs as well as hormones.

Thus the evidence for the existence of a backward flow of water in the tracheæ of wood, in addition to the more obvious upward stream, is convincing. With regard, however, to the mechanism by which the backward stream is supplied we have but scant information.

The volume-changes of leaves which Thoday has recorded are suggestive in this connexion. These changes he found of various magnitudes, occurring simultaneously in different or in the same leaves. They may cause a linear contraction amounting to 2.5 per cent. in ten minutes, and may produce a volume contraction of 7 per cent. in the same time. The water corresponding to this volume-change in the cells of the leaf if transmitted into the tracheæ would produce a considerable downward displacement, as may be seen from the following figures:

Name of Plant.	Volume of 1 per cent. Contraction in mm ³ .	Cross-section of Tracheæ in Petiole in mm ² .	Downward Movement in cm.
<i>Aucuba japonica</i> .	22.8	0.05	45.6
<i>Solanum tuberosum</i>	28.0	0.07	40.0
<i>Syringa vulgaris</i> .	42.15	0.013	16.5
<i>Acer macrophyllum</i>	42.2	0.22	19.2

If these changes in volume are caused by, or accompanied with, a development of permeability of the contracting cells, evidently a backward movement of organic substance having a velocity of about 120 cm. and more per hour would be produced.

It is possible that the tension which causes these contractions of the leaf-cells at the same time acts as a stimulus to increase the permeability of the plasmatic membranes of the cells; and so one might imagine that the development of a certain tension would automatically release organic substances from the cells and draw them through the tracheæ downwards. Direct experiment on this point presents difficulties, but it may be worth recording that when the internal osmotic pressure of the leaf-cells was overbalanced by an external gas-pressure, the water pressed from the cells and forced out of the tracheæ of the supporting stem was found to be practically pure, and if it contained carbohydrates they were in such small quantities that no reduction could be detected with Benedict's solution either before or after inversion. This experiment was repeated several times with branches of *Sambucus nigra* and *Tilia americana*. The cut branch, well supplied with water, was first exposed for several hours to conditions favourable to photosynthesis, and then either immediately or after a sojourn in darkness subjected to the gas-pressure. A pressure of thirteen atmospheres was found sufficient to drive water back from the leaves out of the stem.

Of course the conditions of this experiment are not those obtaining in the normal plant, where during transpiration the volume of a leaf, or part of a leaf, changes. In the transpiring plant we can also imagine the accumulation of a substance or an ion which would give rise to an alteration of the permeability of the plasmatic membranes of the leaves.

When, in order to imitate these conditions, the cells of the leaves in the foregoing experiment are rendered permeable by the introduction of a little toluene into the pressure-chamber, the application of a smaller pressure is sufficient to press the cell-contents into the water-channels and liquid emerges from the base of the stem which readily reduces Benedict's solution.

In the same way, if a pinna of *Sambucus nigra* is surrounded with toluene vapour, transpiration from the adjacent pinnae draws back the cell-contents of the toluened pinna, and afterwards their track in the wood of the vascular bundles of the rachis may be traced by the browning of this tissue.

Another possibility presented itself, namely, that the direction of the current might act as a stimulus regulating the permeability of the cells in contact with the tracheæ. To test this, short lengths of stem set in their normal position were supplied, first through their

lower and afterwards through their upper end, with distilled water. In neither case could carbohydrates be detected in the issuing stream.

The foregoing short consideration of some recent physiological work leads us, then, to the following conclusions:

The transport of the organic substances needed in the distal growing regions is effected through the tracheæ of the wood. The substances travel dissolved in the water filling these channels, which is moved by transpiration, expansion of the growing cells, or root pressure.

Physical considerations forbid us admitting that sufficiently rapid transport can be afforded by the bast either for the observed upward or downward distribution of organic substance.

The existence of downward as well as upward movement of water in the tracheæ of the wood may be demonstrated by suitable experimental means, and may be inferred by the transport of hormones in the wood.

The occurrence of local contractions in leaves suggests that local increases of permeability supply dissolved organic substances to the distal ends of certain of the filaments of tracheæ. The tension developed by the transpiration of other regions draws these along downward as well as upward channels in the wood.

In thus ruling out the participation of the bast in the longitudinal transport of organic substances in plants one naturally is forced to speculate on its probable function. Its distribution and conformation are such that, while it possesses a very small cross-section, it appears with the other living elements of the vascular bundles, medullary rays, wood-parenchyma, etc., to present a maximum surface to the tracheæ.

This large surface may find explanation in the necessity of interchange between the living cells and dead conduits. The colloidal contents of the former render this process slow, hence the necessity for the large surface of interchange to enable sufficient quantities of organic substances to be abstracted from and introduced into the tracheæ to meet the needs of the plant.

Before concluding I would like to add that the experimental work carried out on this matter would have been quite impossible for me were it not for the assistance and ingenuity of Mr. N. G. Ball. He also has contributed materially by his criticisms and suggestions.

Obituary.

COLONEL E. H. GROVE-HILLS, C.B.E., C.M.G., F.R.S.

COLONEL EDMOND HERBERT GROVE-HILLS, whose death occurred on October 2 at his residence at Campden Hill, W., was the son of Herbert A. Hills of High Head Castle, Cumberland. Born on August 1, 1864, he was educated at Winchester, whence in 1882 he passed into the Royal Military Academy, Woolwich. There his abilities were recognised as giving promise of a distinguished career, and he passed out as the senior cadet of his term, receiving a commission in the Royal Engineers in 1884.

Scientific subjects specially interested him, and in 1893 he was elected a fellow of the Royal Astronomical Society; in the following year a paper by him on the photographs of the spectrum of the eclipsed sun taken at the solar eclipse of April 1893 was communicated to the Royal Society. The study of solar physics strongly attracted him, and he also took part in the eclipse expeditions of 1896 to Japan, of 1898 to India, and in that of 1914 to Kieff, whence he was recalled on the outbreak of war to military service. In 1898 he took up the appointment of instructor in chemistry and photography at the School of Military