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Ascent of Sap-Related to Movement of Water in Plants

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ABSTRACT: The **ascent of sap** in the xylem tissue of plants is the upward movement of water and minerals from the root to the aerial parts of the plant. The conducting cells in xylem are typically non-living and include, in various groups of plants, vessel members and tracheids. Both of these cell types have thick, lignified secondary cell walls and are dead at maturity. Although several mechanisms have been proposed to explain how sap moves through the xylem, the cohesion-tension mechanism^[1] has the most support. Although cohesion-tension has received criticism due to the apparent existence of large negative pressures in some living plants, experimental and observational data favor this mechanism.^{[2] [3]}

KEYWORDS: ascent, sap, xylem, conduction, cohesion-tension, plants, mechanism, roots, aerial parts, leaves, cell wall

I.INTRODUCTION

One early theory that has recently been revisited is the one presented by Jagadish Chandra Bose in 1923. In his experiment, he used his invention called a galvanometer (made of an electric probe and copper wire) and inserted it into the cortex of the Desmodium plant. After analyzing the findings his experiment, he saw that there were rhythmic electric oscillations. He concluded that plants move sap through pulses or a heartbeat. Many scientists discredited his work and claimed that his findings were not creditable. These scientists believed that the oscillations he recorded was an action potential across the cell wall. Modern-day scientists hypothesized that the oscillations that were measured in Bose's initial experiment was a stress response due to presence of sodium in the water. The results of this modern-day experiment showed that there were no rhythmic electric oscillations present in the plant. Despite not being able to replicate the oscillations that Bose recorded, this study believes that the presence of sodium played a role in his findings. Furthermore, plants do not have a pulse or heartbeat.^[4]

An alternative theory based on the behavior of thin films has been developed by Henri Gouin, a French professor of fluid dynamics.^[5] The theory is intended to explain how water can reach the uppermost parts of the tallest trees, where the applicability of the cohesion-tension theory is debatable.^[6]

The theory assumes that in the uppermost parts of the tallest trees, the vessels of the xylem are coated with thin films of sap. The sap interacts physically with the walls of the vessels: as a result of van der Waals forces, the density of the film varies with distance from the wall of a vessel. This variation in density, in turn, produces a "disjoining pressure", whose value varies with distance from the wall. (Disjoining pressure is a difference in pressure from that which prevails in the bulk of a liquid; it is due to the liquid's interaction with a surface. The interaction may result in a pressure at the surface that is greater or less than that which prevails in the rest of the liquid.) As a tree's leaves transpire, water is drawn from the xylem's vessels; hence, the thickness of the film of sap varies with height within a vessel. Since the disjoining pressure varies with the thickness of the film, a gradient in the disjoining pressure arises during transpiration: the disjoining pressure is greater at the bottom of the vessel (where the film is thickest) and less at the top of the vessel (where the film is thinner). This spatial difference in pressure within the film results in a net force that pushes the sap upwards towards the leaves.

Xylem tissue is one of two types of vascular tissue found in plants, and is composed of dead cells. It is used mainly for the transport of water, along with some small nutrients. The meristem of the stem creates cells which make up the cambium and pro-cambium. These cells then produce a highly branched poly-phenolic protein, called lignin, in a very high concentration. The cells then perform apoptosis, and the actual xylem tube begins to form. Being made of dead cells allows the xylem tube to function more efficiently by reducing friction, and by eliminating interactions xylem sap may have with living cells. It allows for a smooth and fast suction of water, and provides just enough friction



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to keep the column form rupturing. The rigid structure of the lignin protein gives a sturdy structure to the tube, and even provides some structure and support for the plant. Xylem mainly functions to transport water from the roots to the rest of the plant, however it also transports some nutrients, such as amino acids, small proteins, ions, and some other vital nutrients.^[7]

The phloem is the living portion of the vascular system of a plant, and serves to move sugars and photosynthate from source cells to sink cells. Phloem tissue is made of sieve elements and companion cells, and is surrounded by parenchyma cells. The sieve element cells work as the main player in transport of phloem sap. When fully matured, they have no nucleus, and only a handful of organelles. This allows them to be highly specified, and very efficient at transport, since they are not taking any of the solutes they are transporting. These cells are connected to form the full tube by their plasmodesmata. From here, the solutes traveling through the phloem can move either as a symplast, or apoplast. The loading and unloading of phloem sap is done mainly by pressure flow, and relies on loading of the cells and unloading of the same time to maintain the turgor pressure of the system.^[8]

There are two different types of sap that are in a plant.^[9] These types are xylem and phloem sap, both differing in their compositions. Sap that is transported in the phloem is mainly made of water. The second most abundant substance is sucrose.^[10] One study found that the rice plant Oryza sativa had a sucrose concentration of 570 nm,^[11] but the sucrose concentration is unique to each organism. Another important component of phloem sap is nitrogen. Nitrogen is usually not being transported in its ionic form.^[10] Instead it is incorporated in amino acids such as glutamate and aspartate.^[10] Hormones, inorganic ions, RNA, and proteins are found in the phloem sap as well.^[10]

Xylem sap is mostly made of water. This is because one of the main roles of xylem is to transport water and inorganic nutrients throughout the plant.^[12] Water is not the only thing that makes up xylem sap though. Xylem sap contains long-distance signaling hormones, proteins, enzymes, and transcription factors. One study found that proteins transported in this sap can be as large as 31 kDa.^[12]

II.DISCUSSION

The upward movement of water from the root to the top of the plant is called as ascent of sap. Plants absorb water through the roots and transpire through leaves. The water moves from the root to the tip portion of the plant body against the force of gravity.

The mechanisms involved in the transport of water from the roots to the leaves of plants, some of them being more than 200 metres tall (e.g. Sequoia gigantea, Eucalyptus), is still un-resolved. We are, however, certain about the pathway of the water current which is through the lumen of the xylem . The main pathway of water transport is through the xylem vessels and tracheids and their walls play a minor role. Second, the phloem does not participate in the ascent of sap. Such traced the ascent of lithium salts in different plants by a spectroscope. He observed that the rate of upward ascent of sap varies from 25-1230 cm per hour.¹

Huper devised a method which did not involve cutting of the tissues, but involved sudden local warming of a part of the stem by an electrical heating element, and testing by a sensitive thermoelectric method the appearance and passage of warmed column of water at measured distances above the point of heating.

By such a method, a maximum rate of water transport of 75 cm per minute was observed in trees with ring-porous wood.²

Relatively slow rates, usually under 500 cm/hr, were observed in the diffuse-porous wood, and less than 600 cm/hr in gymnospherms.

In general, the daily variations in the rate of ascent of water parallel daily variations in the transpiration rate.

Theories of Ascent of Sap:

The ascent of sap takes place in the lumen of vessels and tracheids situated between the parenchyma root hair and cortex of the root below, and the mesophyll tissue of the leaf above. A number of theories have been put forward from time to time to account for the ascent of sap.

These theories can be discussed under the following headings:

- 1. Vital Force Theories, and
- 2. Physical Force Theories.³

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A. Vital Force Theories:

The intimate association of the vessels and tracheids with living cells (xylem parenchyma and xylem ray cells) has tempted many workers to suggest that upward translocation of water is brought about in some manner by the living cells of the stem, although there is no direct evidence in favour of such a view.

A brief account of various vital force theories is given below:

(i) Westermaier:

(1883-84) suggested that tracheary elements hold water by capillarity and as a reservoir.

(ii) Godlewski's Theory:

Godlewski (1884) put forward his relay pump theory to explain the ascent of sap. He thought that the upward movement of water was due to the pumping activity of the cells of wood parenchyma and medullary rays brought about by the periodic changes in their osmotic pressure.

With an increase in the osmotic potential Ψ_{π} of these cells, water is withdrawn from the tracheids.

This is followed by a decrease in osmotic potential, and water is pumped into the tracheids above. In this way a sort of staircase movement of water takes place in the xylem.

However, the structure of wood does not support this view. If xylem parenchyma did perform some kind of pumping action, the cells should be arranged between the two xylem elements and not at the sides of the vessels as they actually do.

(iii) Strasburger:

(1839) showed that water continued to rise in plants even after their living cells were killed by exposure to high temperatures, or by their immersion in solutions of poisonous substances such as picric acid.⁴

In one experiment he cut off an old oak tree nearly 22 metres tall and the cut end of the trunk was immersed in a solution of picric acid. The picric acid solution moved up the stem. Fuchsin was added to the liquid three days after the picric acid and it also ascended to the top of the tree through the tissues in which the living cells had been killed by the picric acid.

(iv) Bose's Pulsation Theory:

Sir J.C. Bose (1927) experimented to show that water continued to rise in the absence of root pressure and transpiration.

According to him, the ascent of sap is due to the pulsatory activity of the inner-most layer of the cortex, just outside the endodermis. Bose attached one terminal of a galvanometer to some point on a potted plant and the other to a probe of an electric cell. A thin copper wire was used for making connections.

As he inserted fine needle of the electric probe into the stem the needle of galvanometer showed some momentary oscillations but when the needle tip reached the innermost layer of the cortex, oscillations became fast and sustained. This led Bose to believe that the cells of this layer were pulsating i.e. expanding and contracting alternatively.

When the cells expand, they absorb water from the lower cells and when they contract, water is pumped into the next higher cells. Molisch repeated some of the experiments of Bose and supported his theory.⁵

(v) Root Pressure Theory:

Under certain conditions, plants exhibit exudation of the xylem sap from the stump of a freshly cut stem Most of such exudations result from the development of a pressure in the dilute sap of the xylem ducts resulting from the operation of mechanism in the roots, termed the root pressure. It can also be shown experimentally that water is forced up the stem by root pressure.

This led to the view that root pressure is the mean by which water is raised in tall trees. The maximum of observed root pressure is 5 to 6 bars.

However, many trees have height much in excess of 10 m. Furthermore, many tall trees e.g., conifers have no demonstrable root pressure, neither is the rate of flow adequate to compensate for the known rates of transpiration. In addition to these objections, there is another difficulty that at times of rapid transpiration; plants actually show negative root pressure. The cut ends of stem, instead of exuding sap actually absorb water if it is supplied at the cut surface. All these objections support the argument that root pressure is not an important factor in water translocation.⁶

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B. Physical Force Theories:

(i) Atmospheric Pressure:

Evaporation from the leaves by reducing the pressure in the xylem ducts is adequate to bring about a flow of water through the xylem of short-stemmed plants.

The maximum height to which water could be raised by this differential pressure mechanism would be limited by the external atmospheric pressure which can raise water up to 5 m.

The rise of water in tress 10-100 metres high cannot be accounted for by atmospheric pressure alone.

(ii) Imbibition:

According to such, water rises by imbibition through the thick walls of the xylem cells, as well as those of the sclerenchyma of the phloem.

The forces of imbibition range from 100 to 1000 atm. and this would seem adequate for carrying water to any required distance.

However, the rate at which water moves through imbibing colloids of the cell walls is extremely low.⁷

The theory was given up as it was shown experimentally that water moves through the lumina of the xylem ducts and not through the walls.

(iii) Capillarity:

It has been suggested that water moves through the lumina of tracheids and vessels by capillarity.

The height to which water can rise in the smaller tracheids with diameter of 0.02 mm is only 150 cm, which in the large vessels with diameter up to 0.5 mm the height would be only 6 cm. If water were to rise to a height of 29.95 mm, the capillaries should have a diameter of 1 μ .

At this diameter the resistance to flow becomes too great to supply water at adequate rates.

Moreover, in plants the functional xylem elements are completely filled with water from top to bottom and they do not contain open menisci which are essential for capillary rise. Thus capillarity in the usual sense does not operate in plants.

(iv) Cohesion-tension or transpiration pull:

The salient points of cohesion theory are as under:

(i) Water forms a continuous column extending between the root and the leaf parenchyma cells through the xylem ducts. This is also called hydrostatic system.⁸

(ii) Evaporation from the surface of the parenchyma cells of the leaf (or other issues) increases the water potential (Ψ) and they withdraw water from the xylem elements. This puts the column of water under a strain or tension.

(iii) The column resists breaking because of the cohesion (mutual attraction) between the water molecules.

Furthermore, because of an attraction between water molecules and the molecules of the wall of the tube (adhesion), the water column is put under stress but does not result in putting the water away from the enclosing wall.

Water molecules have a strong cohesion force due to hydrogen bonding between water molecules.

The value of cohesion force for plant sap is calculated as 45-207 atm. Cohesion force is also called tensile strength.⁹

(iv) The water is pulled up from the root like a wire or a rope is pulled through the tube.

(v) Furthermore, since it is fluid, the tensile strength of water can be exhibited when it is confined to a tube, the walls of which are rigid enough to prevent collapse.

For this mechanism to be effective the following requirements must be met:

(i) The magnitude of the osmotic suction (water potential, Ψ) of the leaf parenchyma should be sufficient not only to draw water up the tallest tree at the rate at which it is transpired but also to overcome the frictional resistance between the water column and the inner surface of the xylem ducts.

(ii) The cohesive and adhesive strength of the water column must be sufficient to withstand the transpirational pull exerted upon it.¹⁰

(iii) The tubes must prevent the entrance of air bubbles, which if they expand would break the water columns.

(iv) The water conducting tubes must be rigid enough to prevent collapse when the contents are under tension.

III.RESULTS

Points Favouring the Dixon's Theory:

(i) The osmotic concentration or solute potential (Ψ_s) of the cells in the upper part of a plant are commonly in excess of the equivalent of 10 to 20 atm. They are more than adequate to raise the water to the top. For a tree 130 metres high, a



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tension of 13 atm is required to overcome the frictional resistance of the pathway. It means a tension of about 30 atm in the water column is required to maintain the transpirational flow.

(ii) The estimated minimum cohesion required to lift water to the top of the tallest tree is, therefore, about 30 atm. The cohesive strength of water has been demonstrated to be more than adequate, being in excess of 300 atm. The result is that the water column does not break.

(iii) Although air bubbles are found to enter occasionally in tracheids and vessels, the wet walls are adequate in effectively preventing such bubbles for spreading into the other units.

(iv) The strongest evidence in favour of the cohesion hypothesis is demonstrated by a movement of water through the stem when it is actually under tension.¹¹

Using leafy twigs of different kinds of woody plants it has been demonstrated that there is a rise of 118 cm of mercury, 43.5 cm above the atmospheric pressure. The recent opinion regarding the path taken by water from the xylem to the transpiring surface has been reappraised. It is believed that the water intended for evaporation normally does not come from vacuole.

On the other hand, it comes from the xylem along the apparent free spaces (cells walls) of the cells in between. In such situations the driving force is the water potential of the vapours when in the air of the intercellular spaces. In any case the mesophyll cells show high water potential when transpiration enhances. This is due to the fact that there is partial loss of water from them. The rate of transpiration becomes more than the rate of movement of water. The increased water potential of mesophyll cells may be helpful to them to withdraw water from the wet walls.¹²

Downward Movement of Water:

Downward movement of water is also explained on the basis of the cohesion theory. The prerequisite is that local region of the plant must have negative water potential more than the apical region. It has been demonstrated that during heavy rain, especially after high transpiration, water may be absorbed by the leaves and moves downwards.

Lateral Movement of Water:

Here again water potential gradient is responsible for water movement. The lateral movement of water occurs through xylem especially ray cells. In a plant, if roots are removed from one side, the water content of leaves of both the sides remains the same. The experiment shows: that water conducting system of plants works as a unit, and second, lateral movement of water takes place.

Water Storage:

In same plants, water is stored in enormous quantities especially during the season when available in abundance. One group of plants is succulents having fleshy leaves and shoots. Some cacti can store up to 500 kg of water and have reduced transpiration. In such plants stomata open at night. These plants have CAM pathway of CO_2 fixation and physiologically work at high water potential.¹¹

IV.CONCLUSIONS

Weakness of the Cohesion-Tension Hypothesis:

(i) The cohesion theory requires the existence of continuous columns of water stretching tight through the plant. They must be free from air bubbles since the presence of the air bubbles would destroy cohesion in the water column and break its continuity as soon as columns are subjected to tension.

The fact is that the water columns within the vessels often include air bubble, but Dixon maintained that the contents are free from bubbles in a sufficient proportion of the vessels to provide the necessary degree of continuity. The sap stream passes around the air bubbles, like water of a rivet- passes around the islands.

It is also suggested that the walls of the xylem elements are irregular so that the air bubbles never completely fill the cell and water column remains continuous through films of water in the crevices of the walls.

In conifers tracheid walls are provided with bordered pits in which torus serves as a check valve to prevent entrance of air into the tracheids and thus isolate occasional bubbles from the water columns. It is also suggested that if gas bubbles are formed due to water being under tension or due to rise of temperature of twigs after exposure to sun, the wet walls



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of the vessels are highly permeable to these dissolved gases ; these may then pass out through the walls, preventing formation of the bubbles.⁸

(ii) Another point against the theory is that it assumes tracheids to be more efficient than vessels because the partition walls of the tracheids give stability to the tensile stressed transpiration stream. On the basis of this assumption, it is difficult to explain why in angiosperms; the channels of water transport are vessels and not the tracheids.⁹

Despite flaws in the cohesion theory, most plant physiologists agree that the theory provides the most plausible mechanism, sufficient to account for the observed upward water conduction in the tallest tress or through small herbs. Other factors, such as root pressure, play a minor role in the process.

There is no doubt that living cells are also involved in the phenomenon of root pressure. There is also a possibility that the living cells of the xylem parenchyma are essential for the functioning of the cohesion mechanism.¹⁰

Flow of Water:

The movement of water is regulated by the gradient of water potential (Ψ), and several resistances hinder its movement and flow.

These hindrances are viscosity of the solution, membrane permeability, and the resistance to flow of narrow passages. The flow rate (F) in any part of the system may be expressed as under:

 $F = \Delta \Psi / resistance^{11}$

and for the whole system it is as

F= overall $\Delta \Psi / \sum$ of resistance

In a hypothetical soil-point-air system (where plant is a small tree, soil is well-watered and the air is nearly 50% humid at $22^{\circ}C = -1000$ bars), it is possible to estimate values for water potential (Ψ) and water potential differences ($\Delta\Psi$).¹²

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