BOSE INSTITUTE TRANSACTIONS VOL. V

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LONGMANS, GREEN AND CO.
LONDON NEW YORK TORONTO BOMBAY
CALCUTTA AND MADRAS

THE PHYSIOLOGY OF THE ASCENT OF SAP

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COSSIMBAZAR ENDOWMENT
PUBLICATION

WITH NINETY-FIVE ILLUSTRATIONS

LONGMANS, GREEN AND CO.
39 PATERNOSTER ROW, LONDON, E.C. 4
NEW YORK, TORONTO
BOMBAY, CALCUTTA AND MADRAS
1923

Made in Great Britain

Department of Botany

PREFACE

THE ascent of sap has been the most elusive problem in Plant-physiology. The obscurity which has surrounded the subject has been in a great measure due to the lack of adequate means of detection and accurate measurement of the rate of ascent, of transpiration, of exudation, and their induced variations. Various types of automatic recorders of great sensitiveness and precision have been devised and are described in the present work, which have been of signal service in the investigations of which an account is here given.

The result of these researches is to prove the existence of active pulsating cells throughout the length of the plant, in and from the absorbing root to the transpiring leaf. It is the pumping action of these cells that gives rise to the physiological conduction of sap, even in the absence of root-pressure and transpiration; it also injects liquid into the xylem, setting up an intra-vascular pressure with the consequent mechanical transport of fluid.

The situation of the active cells has been localised by means of the Electric Probe; the cellular pulsations concerned in the ascent of sap have been recorded by an automatic method. The invisible changes in the interior of the plant have thus been revealed, and the effect of the changes of the environment determined from the responsive variations in the pulse-record.

Other investigations are described which show that there are two distinct modes of inter-communication and inter-action between distant organs in plants: (1) the transfer of matter, and (2) the transmission of motion. The first of these is brought about by the movement of sap, and the second by the excitatory nervous impulse. They give rise to two reflexes at a distance, the hydraulic reflex being antagonistic to the nervous reflex. There are, no doubt, many such reflexes corresponding to the various modes of stimulation. The complexity of the life-movements is, in fact, the expression of the combined effects of concordant and antagonistic reflexes.

The ascertained facts justify the important generalisation of the unity of the physiological mechanism in plants and animals. Further investigation of the simpler life of plants may therefore be expected to lead to the solution of many intricate problems in animal life.

It affords me much gratification to associate this work with the 'Cossimbazar Endowment,' founded for my Institute by the enlightened interest taken by the Maharajah Sir Manindra Chandra Nandy, K.C.S.I., of Cossimbazar, in the advancement of research.

I also take this opportunity of acknowledging the very efficient help which has been rendered to me by my research-assistants and scholars.

J. C. BOSE.

Bose Institute, Calcutta,
January, 1922.

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THE ASCENT OF SAP

CHAPTER I

THE PROBLEM OF THE ASCENT OF SAP

Physical and Physiological theories—Inconclusive character of Strasburger's poisoning and scalding experiments—Root-pressure.

AMONG the fundamental activities in the life of the plant are the absorption of water from the soil and the conduction of the sap to all parts of the body. By them the plant obtains its inorganic food-material from the dissolved constituents of the soil, and is supplied with the water necessary to maintain its cells in that state of turgor without which its growth and various life-movements would become arrested. Every portion of a tall tree has to be supplied with water, which is absorbed by the root, conducted along the stem, and finally excreted by the leaves. Calculations have been made which show that the amount of water transpired by the leaves of a large Birch-tree may be as much as 38 kg. per day. The energy required for lifting such large quantities of water to the top of the tree must be very great, especially when, as in the giant *Eucalyptus amygdalina*, it attains a height approaching 450 feet (150 metres).

The problem of the ascent of sap has, from the earliest days of plant-physiology, enlisted the keenest attention of numerous investigators; but the results obtained have not yet been found to offer any wholly satisfactory solution of it. The obscurity of the subject is, in large measure, due to the presence of numerous co-operating agencies of but secondary importance; the inquirer is very apt to be led into the error of confining his attention to one or other of these, thus missing the essential factor in the problem.

There is a voluminous literature on the different theories proposed in explanation of the ascent of sap, the enumeration of which here is out of the question: I must content myself with mentioning only some of the more important of them. They may be roughly classified as physical or physiological. According to the first, living cells take no part in the process. The second or physiological theory assumes, on the other hand, that the transport of water is fundamentally due to the activity of living cells, the movement being promoted secondarily by physical agencies.

Of the physical forces that have been invoked, obviously neither capillarity nor atmospheric pressure can offer any explanation of the phenomenon. There is a mainly physical theory, due to Dixon and Joly, and to Askenasy (1895), that has received more support than any other, according to which the ascent is brought about by the transpiration from the leaves. The fluid in the mesophyll-cells of the leaves becomes concentrated by evaporation. An osmotic attraction is thus set up in the leaves, and the suction thereby exerted is supposed to be transmitted back to the roots through cohering columns of water in the wood-vascular tissue. This theory labours under various difficulties. To begin with, it is inconceivable that slow osmotic action could produce a sufficiently rapid current of water. For I show, in the chapters on the subject, that the velocity of ascent may become more than 20 metres an hour, *even in the complete absence of transpiration*. There is, moreover, no conclusive proof that, under actual conditions, the water-columns within the plant could possess the necessary tensile strength: for the cavities of the wood-vessels and tracheides contain air-bubbles which must impair their cohesion. Ewart (1905) has shown that, in order to maintain the transport of water, a pressure-column five or seven times as great as the height of the tree would be necessary. He insists that the osmotic attraction developed in the parenchymatous cells of the leaf could not possibly exert so great a force.

Turning next to the supposition that living cells may be instrumental in producing water-movement, Schwendener assumes 'that the requisite energy is furnished in some as yet unexplained fashion by the living elements of the wood, thereby confessing his adherence to the views previously formulated by Westermaier, Godlewski, and Janse, who all maintain that the ascent of sap is a vital and not a purely physical process.' Godlewski postulated a periodic variation in osmotic pressure, during which the osmotically active substance is alternately broken down and built up afresh; he was, however, 'unable to prove this hypothesis. Hence no discussion of his theoretical conclusions is necessary, nor of those of Janse and Westermaier as to the way in which living cells may act in raising water.'[1]

Strasburger (1891–1893), on the other hand, endeavoured to disprove the physiological theory by his experiments in poisoning and scalding trees. He showed that solutions of copper sulphate and of picric acid, in spite of their poisonous character, ascended to the top of the tree. He also killed portions of the stem by heat, and yet the upper living and leafy portions were found to remain turgid for a few days. My experiments on the subject will be found in Chapter V; they lead to a conclusion diametrically opposite to that of Strasburger.

Strasburger's views have met with strong criticism from Pfeffer (1892) and from Ursprung (1904–5). Ursprung thinks that the living cells of the stem may, in some way, maintain the vessels in a favourable condition for conduction of water, or be instrumental in the ascent

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[1] *Physiological Plant Anatomy*, Haberlandt, English translation, 1914, p. 321.

of sap. In support of this he carried out a series of experiments in which lengths of petioles and stems of plants were killed by the action of high or low temperatures, or by poisonous solutions. He found that by killing portions of the stem, the wilting of the leaves above the dead area took place in the course of two to nineteen days, and that the greater the length of the stem that was killed, the earlier was the resulting wilting of the leaves.

It has been objected that the wilting of the leaves may not be due to the death of the intervening tissue, but to secondary reactions. Boehm believed that the wilting was brought about by the plugging of the vessels with mucilage. Dixon regards it as being caused by the introduction of poisonous or plasmolysing substances from the dead tissue.

None of these various theories has been found to be completely satisfactory, as Pfeffer,[1] in summarising them, points out :

'How and by what means the water is so rapidly transferred even to the summits of the tallest trees has not yet been satisfactorily explained. It has unfortunately not even been determined whether the aid of living cells is quite unnecessary.' [2]

The experimental methods generally employed by observers labour under the disadvantage that long periods of time are required, which must necessarily introduce many complications. The wilting of the leaves, moreover, is a very crude index for the detection of induced physiological change. The ideal method would lie, not in the employment of average statistics, but in the quick measurement of the change in the rate of ascent of sap caused by some physiological variation. Such a method for the record of the ascent of sap would make it possible to subject the process to various crucial tests, which would decide once for all whether it is physical or

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[1] Pfeffer, *Physiology of Plants*, vol. i. p. 226.

[2] Pfeffer, *ibid.*, p. 220.

physiological. I describe in the succeeding chapters several appliances of great sensitiveness which I have been able to devise for the purpose.

Returning to the physiological theory, it should be borne in mind that a vague assumption of protoplasmic activity is not a sufficient explanation of the phenomenon of the propulsion of sap in plants. *It is necessary further to determine the character of the cellular activity underlying the ascent, how that activity is initiated, and by what means a definitely directed transport of sap is maintained.*

As regards the last point, no satisfactory explanation has been offered. Still greater difficulties and complications are introduced when we take into account other phenomena connected with the ascent of sap, such as the root-pressure, the occurrence of positive and of negative pressure, and the relation between the root-pressure and 'bleeding' of injured plants. The root-pressure is supposed to force the water up and thus to help in the ascent of sap. But when this pressure is most needed, as during the rapid ascent of water to meet active transpiration by the leaves, it disappears or becomes negative. The internal pressure of the tree is also subject to changes which appear to be erratic. Finally, the phenomenon of 'bleeding' is supposed to be due to root-pressure. No definite relation is however found to exist between the pressure and the exudation at the cut surface; the Palms, in fact, exhibit vigorous exudation in the complete absence of any root-pressure.

It is thus seen how necessary it is to arrive at a comprehensive theory which will explain not only the ascent of sap but also other phenomena associated with it, which are quite inexplicable in the existing state of our knowledge. My object in the present work is to attempt to formulate such a comprehensive theory, based upon experimental evidence.

Reference may be made to a long course of investigation which I undertook (1904–1906) on the subject of the ascent of sap.[1] It was shown that *the transport of water is maintained by physiological action, and that it is not the mere presence of living cells, but their rhythmic or pulsating activity, which maintains the ascent of sap.*

Very little definite information has hitherto been available as regards the characteristics of the rhythmic vegetable tissues. A detailed account of investigations on the subject will be found in the works just referred to: but I give in the next chapter a brief statement of the characteristics which distinguish the pulsating from the ordinary tissue, for these criteria will afterwards be employed in proof of the pulsatory character of the tissue concerned in the ascent of sap.

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[1] *Plant Response* (1906) and *Comparative Electro-physiology*, (1907): Longmans and Green.

CHAPTER II

AUTONOMOUS PULSATION

Rhythmic vegetable tissue — Autonomous pulsation in *Desmodium gyrans*—Multiple response under strong stimulus—Pulsations in growth—Characteristics of pulsatory activity—Effect of variation of internal hydrostatic pressure—Effect of maximal stimulus—Effect of sub-minimal stimulus—Modification of response in sub-tonic specimens—Effect of variation of temperature on rhythmic activity—Arrest of pulsation at the critical thermometric minimum—Effect of anæsthetics—Effect of dose—Action of poison—Tests for pulsatory activity—Summary.

BEFORE describing the characteristics of pulsating tissues in plants, it will be of interest to form a mental picture of the physiological mechanism in the propulsion of sap. I have, in my previous works,[1] shown the fundamental similarity of response in plant and in animal tissues. There is in fact no physiological action in the animal which is not to be found also in the plant. This being so, it may be instructive to refer to the means by which one-directioned propulsion of fluids is maintained by animal tissues. Let us take the instance of a multiciliated tissue; here the cilium at one end gives, as it were, a signal which is followed serially by the rest, the multiple activity being continued for a long time. It is clear that if such a multiciliated tissue took the form of a hollow tube, the ciliated surface inwards, and if the tube were filled with water, then, owing to this peculiarity of the multiple-responding cilia, water would be driven in one direction. In the circulation of blood in animals, it is the sinus which gives

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[1] *Plant Response* (1906); *Comparative Electro-physiology* (1907); *Irritability of Plants* (1912); *Life-Movements of Plants* (1919–20): Longmans and Green.

the signal, and the rhythmic contraction of the heart proceeds towards the ventricle; the pumping action thus initiated determines the uni-directional flow of blood.

Have we any proof that plant-cells are possessed of a similar rhythmic activity? The detection of this in a single cell is surrounded with many difficulties. Microscopical examination, even if practicable, would show little or no effect: for, assuming the diameter of a cell to be of the order of 0·05 mm., its contraction or expansion would not cause any change of more than ten per cent.; the variation of length would, therefore, be something like 0·005 mm. The period of a single pulsation of a plant is comparatively slow, being of the order of a minute or so. The problem then is the detection of a rate of change in length of the order of 0·00002 mm. per second, which is beyond the power of a microscope.[1]

Rhythmic Tissues

Fortunately we have other means for the detection of rhythmic activity in plants, specially in pulvinated organs. The most striking example of this is found in the lateral leaflets of the Telegraph Plant, *Desmodium gyrans.* The cells of the lower and upper halves of the pulvinule execute alternate contractions: the result of the contraction of the more excitable lower half is a quick down-movement of the leaflet; while the lower half is in the phase of recovery, the less excitable upper half undergoes contraction with a resulting slow up-movement. The period of a complete pulsation varies according to circumstances from a minute to four minutes or so. These pulsatory movements take place without any immediate external stimulus and are therefore described as 'spontaneous' or self-originated; such spontaneous pulsation of the vegetable tissue exhibits

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[1] It is, however, possible to detect ultra-microscopic movements by a special electric method which will be described in a subsequent chapter.

all the characteristics of the spontaneous movement of the animal heart.[1]

There are other plants which exhibit multiple pulsation under special conditions. An example of this is furnished by the leaflets of *Biophytum sensitivum,* which are normally in a state of quiescence. Multiple responses of the leaflets are, however, evoked by the application of a strong stimulus, the persistence of the pulsatory activity being dependent on the intensity and duration of the stimulus.

It is thus seen that under normal conditions certain tissues, like those of Desmodium, exhibit very pronounced pulsatory activity. In other words, rhythmic activity is strongly developed in certain tissues, while it is but feebly developed in others. The former maintain their rhythmic activity under normal conditions ; whereas intense stimulation is required to arouse the latter.

Further, there is no strict line of demarcation between the phenomena of multiple and of autonomous response. In very favourable circumstances for absorption of excess energy from without, *Biophytum* becomes an automatically responding plant like *Desmodium.* Conversely, under unfavourable conditions, that is to say, when the sum-total of its energy is below par, an automatically responding plant like *Desmodium* ceases to exhibit any pulsations : but the leaflets, now at standstill, will, like those of *Biophytum,* give multiple response under strong stimulus.

With regard to the uni-directioned propulsion of fluid in the plant, it has been pointed out that in the animal it is determined by the propagation of excitatory waves. Such a propagation of excitatory waves in vegetable tissues is exhibited in a very striking manner by *Biophytum.* If we apply a drop of strong salt solution at the inner end of the petiole, repeated excitations will be found to be

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[1] The pulsatory activity of tissues has been variously described as spontaneous, rhythmic or autonomous, and I use these terms in that sense.

propagated from the point of irritation, in strict sequence, from each pair of leaflets outwards to the next (fig. 1).

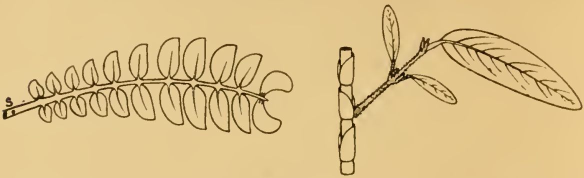

FIG. 1. Leaves of *Biophytum* (left) and of *Desmodium gyrans*
Application of salt at s gives rise to multiple excitation in the leaflet of *Biophytum*. The lateral leaflets of *Desmodium gyrans* (right) execute autonomous pulsations.

Autonomous activity of a pulsatory nature is also well marked in growing organs,[1] as is demonstrated in the records obtained by means of the High Magnification Crescograph. The growth-pulsations consist of a series of alternate expansions and contractions, the latter being the smaller of the two ; the resultant growth in length is the difference between the elongations and the contractions (fig. 2). Sometimes the growth-activity alternates on

FIG. 2. Record of Pulsation of Growth taken with the High Magnification Crescograph

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[1] *Irritability of Plants*, p. 288.

two sides of the organ as the result of lateral pulsations, just as the up-and-down oscillation of the leaflet of *Desmodium* is produced by the alternate activity of the upper and lower sides of its motile organ.

In previous investigations of these two typical instances of pulsatory activity it has been ascertained that it can be modified in very definite directions by variations of the physiological conditions: a brief summary of these investigations is given in the following pages. If now the ascent of sap be found to be similarly affected by the same physiological variations, it may reasonably be concluded that it too is essentially a phenomenon of pulsatory activity. The following table summarises what has been determined for the movements of *Desmodium* and for the rate of growth, as well as what may be anticipated for the ascent of sap.

TABLE I.—DIFFERENT MODES OF RESPONSE TO INDUCED VARIATION OF AUTONOMOUS ACTIVITY

Pulsatory activity	Induced enhancement of activity	Induced depression of activity
Pulsation of *Desmodium*	Enhanced frequency and amplitude, or both	Diminished rate or arrest
Movement of growth	Increased rate of growth	Ditto
Ascent of sap	Enhanced rate of movement of sap	Ditto

The Characteristic Modifications of Pulsatory Activity under Physiological Variations

The effects of physiological variation will be considered in the following order: (1) the effect of variation of internal hydrostatic pressure; (2) the effect of external stimulus of sub-minimal and of maximal intensity; (3) the modifying influence of the tonic condition; (4) the effect of variation of temperature; (5) the determination of the critical point of thermometric minimum for the arrest of response; (6) the effect of anæsthetics, and (7) the effect of poison.

(1) The Effect of Variation of Internal Hydrostatic Pressure

A certain amount of internal pressure is necessary for the initiation and maintenance of rhythmic activity. This is seen in the renewal of the pulsation in the quiescent heart of the snail when the intracardiac pressure is increased.

When a plant is subjected to drought, the turgor and the internal hydrostatic pressure become diminished. A diminution may also be produced artificially by the plasmolytic withdrawal of water. Conversely, an increase of internal hydrostatic pressure may be produced by fixing the cut end of the stem or of the petiole in the short arm of an U tube, and applying hydrostatic pressure by a water column in the longer arm of the tube.

Desmodium Pulsation.—When water is withheld from *Desmodium*, the leaflet ceases to pulsate, the activity being renewed on irrigation. The arrested pulsation of a detached leaflet may also be revived by the application of hydrostatic pressure. The pulsatory activity is thus dependent on the internal pressure. The converse is demonstrated by the plasmolytic withdrawal of water inducing an arrest of the normal pulsation. A solution of KNO_3 applied at the cut end of the petiole bearing the pulsating leaflet, induces a continuous diminution of the amplitude of pulsation culminating in an arrest. Restoration of the normal pressure by substitution of water renews the pulsation (fig. 3).

Growth.—Parallel effects are seen in the phenomenon of growth. Growth becomes arrested under drought and is renewed after irrigation. Partial drought diminishes the rate of growth; application of warm water at the root increases the turgor of the plant and enhances the rate of growth. A plasmolytic solution, on the other hand, diminishes the rate. Thus in a series of experiments with a growing specimen of the flower-stalk of *Zephyranthes*, the normal growth-rate under partial drought was 0·04 μ

per second. On irrigation with warm water the rate was enhanced to 0·20 μ; after this temporary increase the steady growth settled down to 0·08 μ. On application of KNO_3 solution to the root, the rate of growth was found to be diminished to 0·03 μ per second, or to a third of the previous rate.

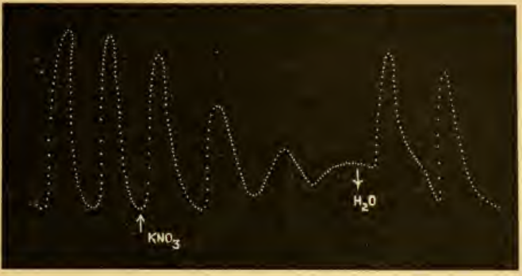

FIG. 3. Arrest of Pulsation of *Desmodium* Leaflet due to Diminished Internal Hydrostatic Pressure induced by KNO_3 Solution applied at Arrow; Subsequent Revival on Substitution of Water at Inverted Arrow

TABLE II.—EFFECT OF VARIATION OF INTERNAL HYDROSTATIC PRESSURE ON GROWTH (*Zephyranthes*)

Condition of experiment	Rate of Growth
Dry soil	0·04 μ per second
After application of warm water . .	0·20 ,,
Steady growth after one hour . .	0·08 ,,
After application of KNO_3 solution .	0·03 ,,

(2) The Effect of External Stimulus

In vigorous specimens, all modes of maximal stimulation induce a diminution of turgor, a contraction, and a decrease of pulsating activity. These may be regarded as the normal responses of the plant to stimulus.

Desmodium Pulsation.—The inhibiting action of stimulus on the pulsation is seen in the record (fig. 4) of the effect of electric stimulus of moderate intensity. The pulsation is seen to become arrested. On the stoppage of stimulus, the after-effect is often found to be an enhancement above the normal.

Growth.—Various stimuli, mechanical, electric, or photic, retard the normal rate of growth. This retardation increases with the intensity and duration of the stimulus, and culminates in an arrest of growth. Thus under electric stimulation, the normal rate of growth in a specimen was found depressed from 0·30 μ to 0·09 μ per second. Stronger stimulus induced an arrest. Under the action of light, the rate of growth in a second specimen was found to be diminished from 0·47 μ to 0·10 μ per second. Stronger intensity of light induced an arrest of growth.

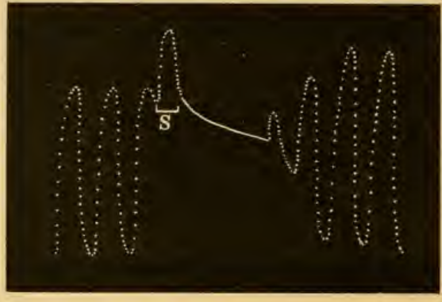

FIG. 4. Effect of Electric Stimulus on Pulsation of *Desmodium gyrans*

Note inhibition as the direct and enhancement as the after-effect of stimulus applied at S.

The above results are obtained with maximum stimulus ; sub-minimal stimulus, however, is often found to induce an effect which is opposite to that of the maximal, that is to say, an enhancement of activity.

(3) Modifying Effect of Tonic Condition

I will now refer briefly to certain very unexpected results obtained in the course of my investigations on the response of vegetable tissues to external stimulus. It was found that the normal sign of response is liable to modification, the variation being definitely related to the physiological condition of the tissue, which may be *at* or *below par.* These two conditions will be designated as the *normal* and the *sub-tonic.* This difference in the initial condition of the tissue, though outwardly indistinguishable, is revealed through characteristic changes in the response to a testing stimulus.

The generalisation arrived at in regard to the characteristics of response in the two conditions is that, *the response of a sub-tonic tissue is of opposite sign to that of the normal.* This applies to all tissues, ordinary or rhythmic. As an illustration, the pulvinus of *Mimosa* normally responds to stimulus by contraction and the resulting fall of the leaf. But if the plant be kept in darkness or in other unfavourable conditions, its physiological tone falls *below par,* and the sign of response undergoes a reversal ; the pulvinus now responds to the same stimulus by *expansion,* and consequent *erection* of the leaf. Successive stimulations, however, improve the tonic condition, with the result that the abnormal response is gradually converted to the normal.[1]

As regards the autonomous rhythmic tissues, their activity declines or becomes finally arrested with increasing sub-tonicity. This condition may be artificially induced by keeping the whole plant or a cut specimen under unfavourable conditions. The rhythmic activity manifested in pulsation or in growth may thus be made to undergo a continuous decline culminating in arrest.

Just as the response of *Mimosa* in a sub-tonic condition exhibits a response of opposite sign to the normal, so a

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[1] Cf. *Life-Movements of Plants,* vol. i. p. 221.

rhythmic tissue also exhibits this reversal in sign of response when it is in a sub-tonic condition; that is to say, that a stimulus which inhibits the activity in a normal specimen, renews or enhances the activity in a specimen which is in a condition of sub-tonicity.

Desmodium Pulsation.—If a cut specimen of *Desmodium* be kept in the dark, the amplitude of pulsation of the leaflets is greatly reduced in the course of about eight hours, and comes to a total stop in the course of eighteen hours. If we now apply the stimulus of an electric shock, the pulsatory activity is found to be revived, the persistence depending on the intensity and duration of stimulation. Similar effects are produced by the application of the stimulus of light. Thus the application of strong light for five minutes gave rise to a single pulsation in a leaflet previously at a standstill. The next application of light of the same intensity was for ten minutes, and this gave rise to four pulsations—two during and two after application (fig. 5). Light was next applied for forty-five minutes, and the pulsatory activity persisted for nearly an hour after the cessation of exposure. These results show that the spontaneous pulsation, so called, is not self-originated, but is really due to an antecedent external stimulus. The persistence of autonomous activity is thus dependent on the amount of stimulation to which the plant had previously

FIG. 5. Effect of Stimulus in renewing Pulsation of *Desmodium gyrans*, originally at standstill

Successive exposures to light for five, ten and forty-five minutes. A portion of record is omitted.

been subjected: the energy supplied by the environment becomes, as it were, latent in the plant, increasing its power of work.

Growth.—Diametrically opposite effects of stimulus on normal and on subtonic specimens are also met with in the phenomenon of growth. Thus while the effect of stimulus on a normal specimen is a retardation, its effect on a sub-tonic specimen is an enhancement of the rate of growth. The following table gives the quantitative results of the effect of stimulus on the growth of sub-tonic specimens.

TABLE III.—ACCELERATION OF GROWTH UNDER STIMULUS IN SUB-TONIC SPECIMENS

Specimens	Stimulus	Rate of Growth
Wheat-seedling	Previous . . .	0·05 μ per second
	After electric stimulation	0·12 ,,
Scirpus Kysoor	Previous . . .	0·30 μ per second
	After 5 minutes exposure to light . . .	0·40 ,,

In the sub-tonic Wheat-seedling, stimulus enhanced the rate two and a half times. In *S. Kysoor* also stimulus enhanced the rate of growth by more than thirty per cent. It is thus seen that the effect of stimulus is modified by the physiological condition of the tissue.

(4) The Effect of Variation of Temperature

If we take the cardiac muscle of the animal as an example of rhythmic tissue, it is found that a rise of temperature quickens the pulsation; lowering of temperature, on the other hand, slows it down.

Desmodium Pulsation.—A rise of temperature induces an enhanced frequency of pulsation. Thus in a particular series of experiments it was found that, during a period of twelve minutes, there were four pulsations at 28° C., which increased to six at 31° C., and to ten pulsations at 34° C.

Growth.—The effect of variation of temperature on growth is similar to the above. It is found that a rise of temperature enhances the rate of growth up to an optimum point which varies in different species of plants. The following table shows that the rate was continuously increased from 0·03 μ to 0·92 μ as the temperature was raised from 26° C. to the optimum temperature of 34° C. When the temperature was raised one degree above this optimum point, the rate of growth underwent a decline to 0·84 μ.

TABLE IV.—THE RATE OF GROWTH AT VARIOUS TEMPERATURES

Temperature	Rate of Growth	Temperature	Rate of Growth
26° C.	0·03 μ per second	31° C.	0·45 μ per second
27° ,,	0·12 ,,	32° ,,	0·60 ,,
28° ,,	0·16 ,,	33° ,,	0·80 ,,
29° ,,	0·22 ,,	34° ,,	0·92 ,,
30° ,,	0·32 ,,	35° ,,	0·84 ,,

(5) The Critical Point of Thermometric Minimum

Lowering of temperature slows down the pulsation of *Desmodium* leaflet till at a critical point it becomes arrested. This arrest is however not permanent, since a revival takes place as soon as the temperature is raised above the critical point. As I give in a subsequent chapter records of the arrest and revival of the pulsatory activity below and above the critical point, I need only state here that in *Desmodium* the pulsation generally becomes arrested at or about 17° C.

Lowering of temperature likewise induces a diminution of the rate of growth till, at a critical temperature, growth becomes arrested. This critical point varies in different species of plants; but in several tropical plants examined, it was found to be about 22° C.

(6) The Effect of Anæsthetics

Anæsthetics when given in large doses act as poisons, causing the death of the plant. With regard to the action of poisonous agents in general, the amount of the dose is of importance; the striking general result which I have obtained in this connection is, that while a poisonous solution of moderate strength arrests or abolishes all life-activity, a small dose enhances it. Opposite effects are thus produced below and above the critical dose. With strong poisons the range of safety is very narrow; with less toxic agents, however, the range is wider, and by regulating the dose it is not difficult to produce either a stimulating or a toxic effect.

Ether is less toxic than chloroform, and it is easy to obtain with it the stimulating effect of a small dose. Though the application of chloroform is apt to prove fatal to the plant, yet even here we can obtain the opposite effects of small and large doses without great difficulty. For when a large quantity of chloroform is applied, the plant absorbs it slowly; the preliminary effect is therefore the same as that of a small dose in the enhancement of activity. Long-continued application, however, brings about the toxic effect. While all modes of rhythmic activity are enhanced by the application of small doses of anæsthetics, continued application produces arrest of activity and ultimate death, as is illustrated in the following records of *Desmodium* pulsations and of growth.

Desmodium Pulsation.—Beginning with the effect of ether, the leaflet used was in a slightly depressed state, so the introduction of dilute ether-vapour into the plant-chamber induced an enhancement of activity (fig. 6, *a*). Continued application arrested the pulsation; but the arrested activity could be revived by substituting fresh air for the ether-vapour.

The effect of chloroform is shown in the record (fig. 6, *b*). The leaflet in this case was in a state of standstill; the preliminary stimulating effect is seen in the renewal of the arrested pulsation. The continued action of chloroform caused arrest, and the death of the plant as seen in the spasmodic contraction and the resulting down-movement.

Growth.—I have carried out numerous experiments on the effect of anæsthetics on the growth of various organs. The results obtained are similar in all cases. The specimens were placed in a closed chamber with an opening for the passage of the connecting link by which the plant was attached to the High Magnification Crescograph. The

FIG. 6

(*a*) Effect of small dose of ether in enhancing the pulsation of *Desmodium gyrans*

(*b*) Effect of chloroform; note the preliminary enhancement, followed by depression, arrest, and death as indicated by the spasmodic contractile movement downwards.

FIG. 7. Effect of Anæsthetics on Growth

(*a*) Enhancement under small dose of ether; (*b*) preliminary enhancement followed by spasmodic death-contraction, under the action of chloroform.

magnification employed was about 1000 times, the successive dots in the records being at intervals of fifteen seconds. The anæsthetic vapour was introduced into the chamber by means of an inlet pipe. The record was taken on a moving plate, and the first part of the curve indicates by its slope the normal rate of growth. Application of chloroform produced a preliminary enhancement of growth, seen in the sudden erection of the curve. Continued application induced an arrest, as seen at the turning point of the curve. This is the critical point, for further application of the anæsthetic produced a sudden spasmodic contraction giving rise to the reversal of the curve (fig. 7, *b*). The apex of the curve demarcates life from death. After this reversal, spots of discoloration appeared in the plant; these spread very rapidly and the specimen became wilted as a consequence of death.

(7) The Effect of Poison

In regard to the action of different poisons, it must be remembered that a certain substance may prove very toxic to one plant and not so much so to another. Plants may also become accommodated to the action of a poison.

Growth.—Poisons retard or abolish growth. Thus in a particular experiment, the application of one per cent. solution of copper sulphate depressed the rate of growth from the normal 0·45 μ to 0·13 μ per second. Prolonged application of the poison killed the plant.

Desmodium Pulsation.—A poisonous solution of potassium cyanide was applied directly to the pulvinule of the leaflet; this caused a complete arrest of pulsation in the course of seven minutes (fig. 8, upper record).

In another experiment the poison was applied at a distance, namely at the cut end of the petiole which carried the pulsating leaflet. In this case the arrest of pulsation took place much later, *i.e.* after thirty-eight minutes, the delay being due to the time taken by the poison to ascend through the intervening distance (fig. 8, lower record).

This experiment also demonstrates that a poisonous solution can pass through a killed tissue, owing to the suctional activity of the cells higher up, a fact that bears upon Strasburger's experiments already mentioned. The matter is discussed in Chapter V.

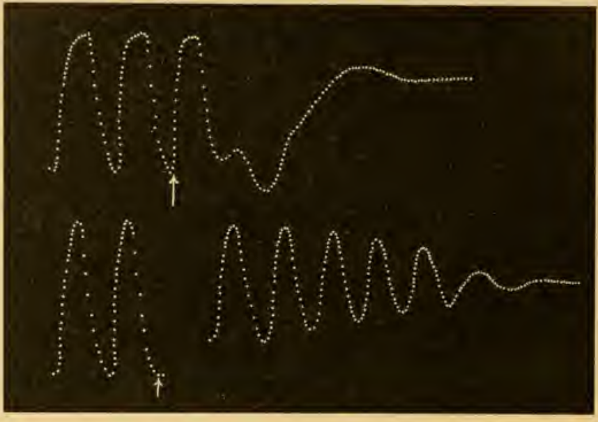

FIG. 8. Effect of Poison on the Pulsation of Leaflet of *Desmodium*

In the upper record the poison was applied directly on the pulvinule. The lower record exhibits the effect of application of poison at the cut end of the petiole, the arrest taking place much later. The gap in the lower record represents an interval of twenty-four minutes.

The physiological characteristics of pulsatory activity have now been described, as ascertained in fully investigated instances of plant-movement. It now remains to determine, by the application of similar methods, whether or not the ascent of sap responds in an essentially similar manner.

SUMMARY

The following have been shown to be the physiological characteristics of pulsating tissues.

i. Pulsatory activity is depressed or arrested under diminished internal pressure ;

ii. Normal pulsation is inhibited by the action of strong stimulus, the after-effect of which may be an enhancement of activity ;

iii. Sub-minimal stimulus enhances autonomous pulsation ;

iv. The response of a sub-tonic tissue is opposite to that of the normal ; that is to say, stimulus revives the arrested, and enhances the enfeebled, activity ;

v. Rise of temperature up to an optimum enhances and fall of temperature depresses, rhythmic activity ;

vi. Pulsation is arrested at a critical point which is the temperature minimum ; arrested pulsation is revived when the temperature is raised above this critical point ;

vii. A small dose of an anæsthetic induces an enhancement of activity ;

viii. Pulsation is arrested under the continued action of a large dose of the anæsthetic ;

ix. Rhythmic activity is permanently abolished by the action of poisons.

CHAPTER III

DETECTION AND RECORD OF THE ASCENT OF SAP

Detection and record of ascent of sap—Mechanical Method of Erectile Response—The Automatic Recorder—Erectile response of *Mimosa*, *Chrysanthemum* and *Impatiens*—The Osmotic Theory—Theory of suction and root-pressure—Ascent of sap in absence of root-pressure and transpiration—Depressed rate of ascent under increasing drought—Ascent of sap in cut stems previously exposed to air—Function of the xylem—Summary.

In the study of the ascent of sap great difficulty is encountered in the measurement of the rate of flow and its induced variations. The withering of leaves, as stated before, is a very crude and unreliable test ; some more exact method is essential.

Though the direct observation of the movement of sap inside the plant is practically impossible, yet we may detect and measure some of the effects induced by it. In electric measurements we are unable to see the passage of electricity, but are nevertheless able to detect and measure the current by its various effects, such as the production of heat, the directive action on the magnetic needle, the movement of a string across the magnetic field, the chemical effect, and so on. It is thus possible to construct different types of galvanoscopes or galvanometers possessing various degrees of sensibility. Similarly, by taking advantage of the effects produced by the conduction of flow of sap in a plant, we should be able to construct various instruments for the detection or measurement of its ascent. I have, in fact, devised two different methods for this purpose, namely, those of mechanical and of electrical response. In the present chapter I describe in detail the principle and construction of the automatic Mechanical Recorder, reserving the description of the Electrical Recorder for a subsequent chapter.

The Method of Mechanical Response

The principle of the method will be understood from the following experiments. A cut specimen of *Chrysanthemum coronarium* is subjected to drought, when the plant doubles over, the leaves shrink and appear crumpled up and dried ; in fact the plant seems to be dead. But irrigation brings about a marvellous transformation through the ascent of sap ; the original turgor is restored, the bent stem straightens up and the withered leaves spread out in their original vigour. This is shown in the photograph reproduced (fig. 9), in which complete recovery took place in a time as short as fifteen minutes. I also reproduce

FIG. 9. Full Erection of the cut Shoot with Drooping Leaves on Application of Water at the Cut End. (*Chrysanthemum*)
Photographs showing the difference before (right) and after irrigation (left).

photographs of a potted *Impatiens* subjected to drought. The rate of ascent of sap here is much slower than in *Chrysanthemum*; a partial recovery occurred in the course of two hours, complete recovery being attained after four hours (fig. 10). In nature the plant experiences great fluctuations in its state of turgor. Thus in Bengal there was no rain for six months from October last. The temperature in April had risen to 40° C. or 104° F., so that the plants were suffering from excessive drought when the rains came down in the middle of April. There was thus great variation as regards the available source of supply of water; and we shall presently have occasion to discuss the manner in which variable conditions of drought affect the ascent of sap. Potted plants are similarly subjected to periodic variation: on watering the plant, the stem and the

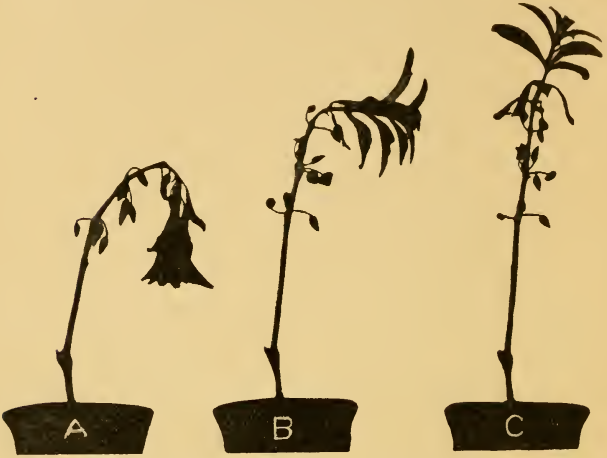

FIG. 10. Photographs of a Potted Specimen of *Impatiens*

The first shows the effect of drought, the second exhibits partial recovery two hours after irrigation, and the third shows full recovery after four hours.

leaves become turgid; after one or two days the loss by transpiration from the leaves will reach a point when it will be greater than the supply of water through the ascent of sap, the result being a slight drooping of the leaves. Confining our attention to a particular leaf, we find that fresh irrigation causes an erection of the leaf to the horizontal outspread position. This erectile movement does not take place immediately after irrigation; a certain time is required for the ascending sap to reach the leaf-joint so as to increase its turgor and thus cause the responsive erectile movement of the leaf. I designate this time-interval as the *latent period.*

In the case just mentioned, the leaf is the responding organ: but the bent portion of the drooping stem itself may be employed as the responder; for after irrigation, the ascending sap, reaching the bend in the stem, will cause it to straighten.

We have thus two means of detecting the ascent of sap, namely, the erectile response of the drooping leaf, and the erectile movement of the drooping stem. These are so slight that the course of erection from its initiation to uniform movement cannot be made out by mere eye-observation. Moreover, there remains the important element of the time-relations of the response. For the fulfilment of our requirements, it is therefore necessary to devise special apparatus giving automatic records.

The Automatic Recorder for Erectile Response

The responsive movement induced by the ascent of sap is recorded by the apparatus (fig. 11). The indicating leaf is attached by a thread to a magnifying lever made of fine glass fibre; the lever itself is mounted on jewel bearings. The magnification may thus be raised from five to a hundred times. The bent tip of the long arm of the lever inscribes the erectile response on a smoked glass plate, kept oscillating to and fro by means of clock-work.

This oscillating device offers the double advantage of eliminating any friction of the recording lever against the glass plate, and of securing the accurate time-relations of the curve of response. Adjustment is made so that the oscillation of the plate takes place once in fifteen seconds; the distance between successive dots therefore represents a definite interval of time.

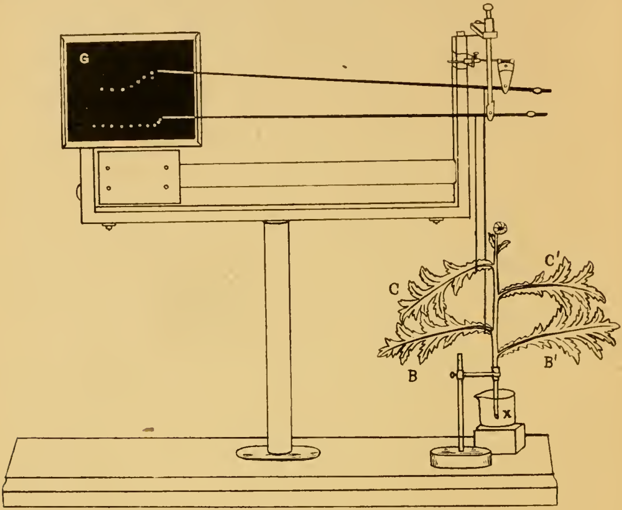

FIG. 11. Automatic Recorder for the Erectile Response of Drooping Leaf

Leaves B and C are attached to two recording levers, B to the upper and C to the lower. The sap reaches B before reaching C; hence the earlier response recorded by the upper lever. The clock-work for the oscillation and lateral movement of the plate is not shown in the figure.

The plant with the slightly drooping leaf is suitably clamped and mounted on a stand, the clamping being just sufficient to prevent slipping; too great a compression would, obviously, retard the ascent. The lower end of the plant is cut and water applied to it. We shall presently find how the curve of response enables us to determine the characteristics of the ascent of sap and its induced variations.

For the accurate determination of the velocity of ascent, two different levers are employed, as seen in the illustration; the first being attached to the lower, and the second to the upper leaf, one being vertically over the other. The advantage of this Duplex Method will be described later.

The record of the drooping stem is obtained by supporting it by means of a clamp a little below the point where it begins to bend, this bent portion being the responder. Water is supplied at the cut end of the stem, and the erectile response recorded in the usual manner. The arrangement for taking record of the response of an intact plant with root is shown in fig. 12; the pot containing the plant is placed inside a larger vessel, V, into which water is poured for irrigating the plant. The Oscillating Recorder illustrated here is of a more compact type than the one previously described.

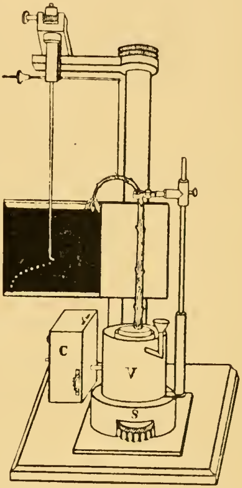

FIG. 12. Automatic Recorder for Erectile Response of Drooping Stem

C, clockwork; V, outer vessel; S, screw adjustment for raising or lowering the plant.

In illustration of the method described above, I will first describe an experiment with a potted specimen of *Mimosa pudica.* The plant was in a condition of a slight drought, and the responding leaf was exhibiting a slow and a continuous fall, due to diminishing turgor of the pulvinus. We know that a sudden diminution of turgor takes place under the action of stimulus which causes a quick fall of the leaf; in the present case the gradual diminution of turgor due to increasing drought caused a slow movement of fall. This is seen in the first part of the curve (fig. 13). On irrigation at the vertical line, the fall of the leaf became arrested and then reversed to an erectile movement. This took place in the course of thirty seconds, which is the time taken by the ascending sap to reach the pulvinus from the absorbing root. On the attainment of a uniform rate of erectile movement, cold water was applied to the root, at the point in the record marked with an arrow. This brought about an arrest of the erectile movement in the course of about fifteen minutes. We have already seen that the application of cold induces a diminution of pulsatory activity; the arrest of the erectile response in this experiment is thus attributable to a retardation

FIG. 13. Erectile Response of Leaf of *Mimosa* on Irrigation

Down-curve shows gradual fall of leaf under drought. Irrigation at the vertical line induced erectile movement. Application of ice-cold water at arrow arrested the movement in the course of fifteen minutes. The gap in the record represents an interval of ten minutes. (Successive dots at intervals of fifteen seconds.)

of the ascent of sap induced by physiological depression of rhythmic cells.

The method of experiment with *Mimosa* described above, though of much theoretical interest, labours under certain disadvantages. First, it may be supposed that the results are peculiar to 'sensitive' plants; secondly, the very great sensitiveness of the pulvinus demands special precaution against accidental disturbance. I therefore prefer to employ the leaves of ordinary plants as indicators of the ascent of sap. Most of the investigations described below have been carried out with *Chrysanthemum* and *Impatiens*. *Chrysanthemum* may be grown in Calcutta from December to March, *Impatiens* is available during the rest of the year. In the records of different cut specimens given in fig. 14, the distance intervening between the cut end of the stem and the responding organ is the same in all, namely 15 cm.

The response of the leaf of *Chrysanthemum* in the following experiments is shown in fig. 14, *a*, that of the drooping stem in 14, *b*. They are seen to be very similar, the cause of this resemblance being that in the two experiments the leaf and the stem function merely as indicators of the ascent of sap. In the record of the erectile response of the stem (fig. 14, *b*), it is seen to take place after the third dot, that is to say, forty-five seconds after the application of water to the cut end of the stem; as the intervening distance for the transport of sap was 15 cm., the velocity of ascent was 200 mm. per minute. The record (fig. 14, *c*) was obtained with a drooping stem of *Impatiens*; the erectile response occurred 2·5 minutes after irrigation, the velocity of ascent being 66 mm. per minute, or less than a third of the velocity in *Chrysanthemum*. The curve attained an uniform slope in the course of six minutes after the application of water, and this uniformity was maintained for a considerable length of time, in fact so long as the bent portion of the stem did not become too erect. For securing an uniform curve, the drooping stem should make an angle of about 5° below the horizon. Uniform slope of curve indicates uniform rate of the ascent of sap ; enhancement of the rate under stimulating agents is demonstrated by a sudden erection of the curve, also by wider spacings between the successive dots. Induced depression, on the other hand, is indicated by the flattening of the curve, and by the closeness of the successive dots.

FIG. 14. Records of Erectile Response of Drooping Leaf and Stem after Irrigation

(*a*) Erectile response of ' varnished ' specimen of *Chrysanthemum* with leaf as an indicator (see p. 36).
(*b*) Erectile response of drooping stem of *Chrysanthemum*.
(*c*) Erectile response of drooping stem of *Impatiens*.
(*d*) Erectile response of *Chrysanthemum* stem the cut end of which had been exposed to air (see p. 37).

Having secured accurate methods for the determination of the rate of ascent of the sap, I defer to a subsequent chapter the study in detail of the effect of physiological agents upon it. For the present I will describe certain important experiments which will show definitely that the generally accepted theory of the ascent of sap is quite untenable in its essential details.

The Osmotic Theory

The first stage in the process, the passage of water from the soil into the plant, is described as follows by a well-known author[1]: 'The cells of the root-epidermis absorb water osmotically from the soil. The water absorbed by the epidermis is transferred to the centre of the root since the cell-sap is in a state of greater concentration there than it is in the epidermis, and it will continue to be so transferred until a similar osmotic pressure prevails throughout all the cells of the transverse section. Water in the same way will pass osmotically into segments of young vessels while these are still in an embryonic state and possessed of normal cell-contents. When, however, a segment fuses with the next older segment, an immediate dilution of its osmotically active cell-sap must take place since it is essentially water that is found in adult vessels. The question then comes to be, how can water be abstracted from the cell-sap of a parenchymatous cell and transferred to the lumen of a vessel; one would expect the precisely converse process to take place.'

There is thus a barrier between the parenchymatous cell and the xylem which cannot be crossed by osmotic action. A different explanation has to be found for the transfer of water to and from the xylem according to different circumstances. This is afforded by the theory of cellular pulsation according to which the liquid is injected by the living cells into the wood-vascular tissue. Pulsatory activity is dependent, as we have seen, on the internal hydrostatic pressure and the resulting state of turgor. The difference of hydrostatic pressure between two points will be one of the factors in determining the direction of the propulsion of sap from a place of higher to a place of lower potential, from the more to the less active region. The sap-movement

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[1] Jost, *Plant Physiology*, English translation, p. 49.

will thus follow the 'turgor-gradient,' tending to equalise the difference of turgor in different parts of the plant.

Theory of Suction and Root-Pressure

Passing now to the consideration of the further movement of water in the stem, some idea of the prevalent view will be obtained from the following quotation: 'It is certain that the water is not merely driven upwards from the root, or base of the stem by the root-pressure acting like a force-pump, but that the removal of water from the conducting channels exerts a force transmitted backwards as far as the absorbing organs, causing in these a corresponding entry of water.'[1]

The motive power is thus assumed to be the root-pressure, supplemented by the backwardly transmitted negative pressure caused by transpiration from the leaves. Confining our attention to the latter, it would follow that the greater the partial vacuum produced by transpiration the greater would be the backwardly transmitted suctional force and the corresponding enhancement of the rate of ascent.

As regards the channel of conduction of water, it is considered as certain that the xylem alone subserves this function; the well-known 'ringing experiment' is supposed to offer conclusive proof: 'In order to break the continuity (of the cortex) two circular incisions are made round the stem right into the wood and the intervening ring of tissue removed. If this "ringing" be not done too extensively, and if due care be taken that the stem does not become dried up or rotten at the region of ringing, the leafy crown will remain fresh for a long time, and the transport of water will not be interrupted to any appreciable extent by the ringing. We may conclude therefore that the conduction of water is effected by the wood.'[2] This

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[1] Pfeffer, *Plant Physiology*, English translation, p. 208.

[2] Jost, *Plant Physiology*, English translation, p. 48.

experiment is by no means conclusive, since the injection of water into the xylem (see Chapter XII) by the active cortex below would carry the water through the short stretch of the woody tissue from which the cortex had been removed.

Another argument adduced in support of this view is the supposed abolition of ascent of sap in a stem when its cut end has been exposed for a short time to the air: 'When a stem has been cut across, air is drawn into the opened tracheæ and the tracheids, owing to the internal negative pressure, and hence the absorption of water is rendered more difficult. In herbaceous plants the lessened rate at which the water is then absorbed is sufficient to cause a pronounced flaccidity even when the cut stem is immediately placed in water.'[1]

Thus, according to the generally accepted theory, the ascent is mainly due (1) to the root-pressure together with the internal negative pressure and backward suction due to transpiration; it follows from that theory (2) that the greater the condition of drought caused by transpiration, the quicker should be the rate of ascent; and (3) that the ascent should be stopped by previous exposure of the cut end of the stem, the vessels being choked with injected air.

The theory of cellular pulsation asserts, on the other hand, that (1) the ascent is due to the independent activity of living cells which extend throughout the length of the plant, hence neither root-pressure nor transpiration is essential to the process; (2) the propulsion being due to cellular activity, which is enhanced under increased internal pressure, the rate of ascent should be *diminished* under condition of drought; and that (3) it is not the dead vessels, but the living tissue which takes an active part in the conduction; hence the previous exposure of the cut end of a stem to air should not cause a stoppage of the ascent. I proceed to describe experiments which prove (1) *that the ascent may take place at a vigorous rate in the complete*

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[1] Pfeffer, *Plant Physiology*, English translation, p. 231.

absence of root-pressure and transpiration, (2) *that the rate of ascent is diminished under increasing drought, and* (3) *that the exposure of the cut end of the stem to air does not abolish the conduction of water in the stem.*

Ascent of Sap in the Complete Absence of Root-Pressure and of Transpiration

I took a specimen of *Chrysanthemum* which had been subjected to incipient drought: its root and all but a single indicating leaf were removed. The stem and this single leaf were coated with vaseline for the complete elimination of transpiration. The specimen was duly mounted, and a fresh cut made at the lower end of the stem, to which water was applied by raising a beaker of water from below. It will be seen (Fig. 14, *a*) that the erectile response of the indicating leaf took place two dots, that is 30 seconds, after the application of water at the cut end; the intervening length was 15 cm., and the velocity of ascent was thus 300 mm. a minute, or 18 metres per hour. In certain other instances the velocity was found to be as high as 70 metres per hour.

It is obvious that this high rate of conduction could not possibly be due to slow osmotic action. Moreover, in the experiment just described, there was no root-pressure to propel the water, nor any transpiration to suck it. Hence it follows that *it is the cellular activity throughout the length of the stem which causes the propulsion of sap.*

Depressed Rate of Ascent under Increasing Drought

Experiments on the effect of increasing drought in depressing the rate of ascent will be given in full detail in the next chapter: I here give a summary of some of the results. In the stem of *Chrysanthemum,* the average rate of ascent under moderate drought was found to be

230 mm. per minute. This was depressed under excessive drought to 18 mm. per minute, or to about one thirteenth. In *Impatiens*, the average rate in cut stems was 70 mm.; under excessive drought this was depressed to 7·5 mm. per minute, or to about a tenth.

Ascent of Sap in Cut Stems previously exposed to Air

For this experiment, a shoot of *Chrysanthemum* subjected to drought was taken and its cut end was exposed to air for more than half an hour. The xylem-vessels would then be filled with air under atmospheric pressure which would block the channels. I also removed all the leaves except the solitary indicator, and smeared the stem and the leaf with vaseline, thus producing a complete abolition of transpiration. There could now be no backwardly transmitted suctional force, nor was there any channel for conduction through the xylem, now choked with air. According to the current theory, there should be a complete abolition of the ascent of sap under the particular circumstances described above. According to the pulsatory theory, however, there should be no such abolition; the pulsations of the semi-dried cells at the cut end would, it is true, be arrested; but this arrest would not be permanent. For after the absorption of water there would be a slow revival of activity; the record would thus show a prolonged latent period followed by an ascending curve less erect than that of plants in which drought was not so pronounced.

The record given in fig. 14, *d* shows that an ascent of sap did take place along the stem in which the cut end had been previously exposed to air, and from which the transpiring leaves had been removed. The response-record, moreover, shows the characteristics which were expected. The latent period is prolonged to eight minutes, and the relatively slow rate of ascent is found in the gentle slope of the curve of the erectile movement.

Thus by two independent tests we arrive at an identical conclusion that the ascent of sap takes place not by physical transference along the dead xylem, but along the living cells by means of their pulsating activity. Other experiments will be described in a subsequent chapter which will offer independent proof of the underlying physiological action in the transport of sap.

Function of the Xylem

The experiments described above prove that the xylem is not essential for the ascent of the sap. I have been able by an electric method to localise the tissue which by its pulsatory activity maintains the ascent of sap (see Chapters XIV, XV). This is the cortex which abuts on the fibro-vascular tissue. In dicotyledonous stems there is thus a cylindrical sheath, which subserves the purpose of rapid conduction of sap. The inactive xylem-vessels are situated very near the active cortex, within a fraction of a millimetre or so ; hence it is easy for the active cortex to force the sap laterally into the xylem during the phase of contraction. The xylem may, therefore, be regarded as a reservoir, water being pumped into or withdrawn from it according to the different circumstances.

It will also be shown in the chapters referred to above that the fundamental mechanism in the ascent of sap is the same in herbaceous plants and in tall trees. Additional means, however, become increasingly necessary to meet the excessive demand for water in trees during active transpiration. In herbaceous plants the distance of the soil-water is not too great : but in tall trees it is necessary to have a near source of supply of water, a ‘ soil-extension,’ as it were, in the shape of conduit-pipes filled with water. These conduit-pipes are the young xylem-vessels (alburnum) for mechanical transference of water during the emergency of active transpiration from the leaves. Physical forces alone, such as capillarity or the cohesive power of water-columns, cannot raise water to any great height. There is, however, no such limit in the case of propulsion of sap by the physiological action of living cells.

When transpiration is feeble, the normal ascent along the cortex supplies every portion of the tree with water. The leaves become turgid, and the xylem filled with sap. During active transpiration, however, the physiological conduction is not sufficient to meet the demand, and water is withdrawn from the xylem-reservoir. Two factors are thus brought into operation: the *physiological conduction* by and along the active cortex, and *physical transference* along the xylem.

SUMMARY

Drooping leaf and drooping stem become erected in consequence of restoration of normal turgor by the ascent of sap after irrigation. The automatic record of the erectile response gives an indication of the rate of ascent of sap.

According to the generally accepted theory, the ascent of sap is due to root-pressure and suction exerted by transpiring leaves, the rate of ascent increasing with increased drought and transpiration. Conduction is supposed to take place exclusively through the xylem; if this were so, the ascent would be stopped by exposure of the cut end of the stem, since the vessels would then be choked by the injected air. In disproof of these views the following facts have been experimentally demonstrated.

The ascent of sap takes place with great rapidity in complete absence of root-pressure and transpiration from leaves.

The rate of ascent is *decreased* under increasing drought.

The ascent of sap persists in stems whose cut ends have been previously exposed to air.

The above experiments prove (1) that the xylem is not essential for conduction, (2) that neither transpiration nor root-pressure is essential, and (3) that there are channels other than the xylem for the ascent of sap.

CHAPTER IV

DETERMINATION OF VELOCITY OF ASCENT BY MECHANICAL RESPONSE

Difference of velocity of ascent in cut and rooted specimens—Influence of the previous history of the plant—The Duplex Method—The effect of drought—The effect of physiological anisotropy induced by stimulus—Determination of velocity in the reverse direction—Summary.

In the last chapter two methods for obtaining records of the rate of ascent of sap were described. The results obtained by the application of these methods with the highest degree of accuracy will now be given, dealing with such questions as whether the velocity is the same in intact plants with roots and in cut stems ; the effect of increasing drought on velocity ; the effect of stimulus on the rate of ascent ; the effect of physiological anisotropy in inducing differences of velocity of ascent on the two sides of an organ ; and, finally, the velocity of movement of sap in a direction opposite to the normal.

In the determination of the velocity in different specimens, I was at first greatly puzzled by the widely divergent values obtained, which ranged from 0·3 mm. to about 700 mm. per minute. A long course of investigation enabled me, however, to detect the causes of this divergence : I found (1) that the velocity was not the same in different species of plants, the velocity in *Chrysanthemum*, for example, being higher than in *Impatiens* ; (2) that the velocity was higher in thick than in thin specimens ; (3) that it depended on the temperature, a rise of temperature up to an optimum enhancing the rate of ascent ; (4) that the velocity was higher in a cut stem than in a specimen with roots ; (5) that the rate of ascent is modified by the previous history of the plant; (6) that it is affected by the condition of drought to which it had been subjected; (7) and that it is modified by the action of stimulus, the after-effect of which may be persistent.

With regard to the velocity of ascent in specimens with roots, the following table gives results which I obtained with potted specimens of *Impatiens* in a condition of moderate drought:

TABLE V.—VELOCITY OF ASCENT OF SAP IN SPECIMENS OF *Impatiens* WITH ROOTS, 30° C.

Specimen	Length	Time	Velocity per minute
1	82 mm.	9 minutes	9 mm.
2	90 ,,	10 ,,	9 ,,
3	90 ,,	9 ,,	10 ,,
4	100 ,,	10 ,,	10 ,,
5	100 ,,	10 ,,	10 ,,

The velocity in *Impatiens* in a 'moderate' condition and at a temperature of 30° C. is thus found to be of the order of 10 mm. per minute. This velocity is lower than in cut specimens of *Impatiens*, which was found to be about 60 mm. per minute. The reason of this difference is found in the fact, already stated, that in specimens with roots, the fine root-hairs offer great resistance to the entrance of water.

The Influence of the Previous History of the Plant

In normal specimens of *Impatiens*, *i.e.*, those subjected to moderate drought, the velocity of the water-transport has been shown to be of the order of 10 mm. per minute. In a particular specimen, however, the result was found to deviate greatly from the normal. The latent period was very short, which meant a great enhancement of the rate of transport of water, which was independently exhibited by the marked steepness of the curve of erectile response. In attempting to discover the cause of the anomaly, I found that the specimen had been warmed artificially to hasten the drooping of the stem, and this must have necessarily raised the temperature of the soil. The specimen, however, had been kept in the experimental room for several hours before the commencement of the experiment, by which time the temperature had returned to the normal. It thus appeared that the warming of the soil had stimulated the roots, the after-effect of which persisted even after return to the normal temperature.

In order to put this surmise to experimental test, I took three batches of similar plants which drooped to the same extent from drought. The first batch was kept as the control, the temperature of the soil of the second batch was raised, while that of the third was lowered. For producing variation of temperature of the soil, two boxes were made with circular openings, through which the conical pots were let down, so as to close the opening, the pots being exposed to the air of the chamber. The temperature inside one of the boxes was raised by an electric heating coil, and that of the other lowered by fragments of ice placed at the bottom. The soil in the two sets was thus brought to about 10° C. above and below the normal. It should be noticed that it was not the plant as a whole, but the roots embedded in the soil, that were subjected to the action of variation of temperature. After this the pots were kept in the experimental room for several hours till they attained the normal temperature, as indicated by a thermometer imbedded in the soil. Records were next taken after irrigation with water at the ordinary temperature, which revealed in a striking manner the difference in their past history. The control batch gave the characteristic records which have been previously described, the average velocity of the transport of water being about 10 mm. per minute. The batch whose roots had been stimulated several hours before by warmth, now gave records which exhibited a very short latent period and a velocity which was more than ten times the normal. The batch whose roots had previously been cooled exhibited no response for a considerable length of time, sometimes not even for hours. The velocity in such cases was about 0·3 mm. per minute, or one-thirtieth the normal. It is thus seen how profoundly the activity of the ascent of sap is modified by the previous history of the plant. We shall see later how the depression of irritability of the root affects other activities of the plant.

The Duplex Method

It is necessary here to explain certain difficulties which are encountered in the accurate determination of the velocity of ascent. These arise (1) from the loss of time due to the physiological inertia of the responding leaf or cut portion of the stem, (2) from the loss of time required for absorption of water by the root, (3) from the difficulty of measuring the intervening distance from the root, since its exact position with its numerous side-branches is very indefinite. These difficulties are, however, eliminated by the Duplex Method of record, where two indicating leaves, situated vertically one over the other, give successive responses to the arrival of water at the two points (see fig. 11). The response of the lower leaf indicates the moment of the arrival of the ascending sap at that leaf ; the delay in the response of the second gives the time-interval for the ascent of sap from one leaf to the other. The physiological inertia of the two leaves being about the same, this source of error is eliminated by taking the difference of the two latent periods. The question of the distance of the root does not arise at all in this method of determination.

We have, however, to bear in mind the characteristics of the leaf-arrangement on the stem. The leaves in *Chrysanthemum* are arranged in a spiral, so that the fifth leaf is situated vertically above the first. A particular ascending fibro-vascular bundle, moreover, gives off lateral branches to the first, the fifth, and the ninth leaf counted in order from below; the vertically situated leaves are thus connected with each other. Another important fact is, as stated previously, that it is the cortex abutting on the fibro-vascular strand which is mainly concerned in the ascent of sap. It thus follows that a particular cortical strand of tissue goes straight up, supplying the sap to the first, the fifth, and the ninth leaf. If the root of an intact plant or the cut end of the stem be irrigated, we can observe the successive erection of the vertical row of the leaves, A, B, C, or F, E, D, on the two opposite sides, and thus determine the velocity

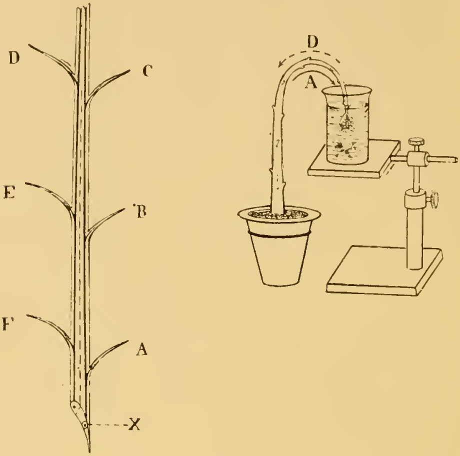

FIG. 15. Diagram for Determination of Rate of Flow of Sap in Up and in Reversed Direction

In the left diagram there is a vertical slit in the stem shown by dotted line; a piece of mica is inserted in this slit. Water applied at the slanting cut surface X travels upward from A to B to C, after which it crosses over to D, and follows the reverse course D, E, F. Diagram to the right shows reverse direction of flow by irrigation of the leaves. A is the normal direction of the ascent, and D the reversed direction of flow.

of ascent between A and B or between B and C and so on (fig. 15). I find that the velocity is approximately constant in the middle portion of the stem, which is neither too old nor too young. This will be seen in the results of the following experiment on the determination of the velocity in a specimen of *Chrysanthemum* which had been subjected to drought. The distance between A and B was 97 mm. and the time-interval between the successive responses was forty-five seconds. The velocity was therefore 130 mm. per minute. The distance between the leaves B and C was 62 mm., the time-interval thirty seconds, and the velocity 124 mm. per minute. The above results show that this differential method enables us to determine the velocity with great accuracy.

The Effect of Drought

The following experiments demonstrate that the velocity is decreased under increasing drought. The results given in the accompanying tables may be regarded as typical of the effect of slight and of excessive drought on velocity. The specimens employed were cut stems of *Chrysanthemum* and of *Impatiens*.

TABLE VI.—SHOWING THE EFFECT OF SLIGHT AND EXCESSIVE DROUGHT ON THE VELOCITY OF ASCENT

Chrysanthemum

Moderate drought				Excessive drought			
No.	Distance in mm.	Time in seconds	Velocity per minute	No.	Distance in mm.	Time in seconds	Velocity per minute
1	110	30	220 mm.	1	110	330	20 mm.
2	100	30	200 ,,	2	120	420	17 ,,
3	100	22	270 ,,	3	105	360	18 ,,
Mean velocity = 230 mm. per min.				Mean velocity = 18 mm. per min.			

Impatiens

Moderate drought				Excessive drought			
No.	Distance in mm.	Time in seconds	Velocity per minute	No.	Distance in mm.	Time in seconds	Velocity per minute
1	110	90	73 mm.	1	120	900	8 mm.
2	100	90	67 ,,	2	110	930	7 ,,
Mean velocity = 70 mm. per min.				Mean velocity = 7·5 mm. per min.			

From the above tables we find that in the case of *Chrysanthemum* the velocity was decreased under excessive drought from the average value of 230 mm. to 18 mm. per minute, and in *Impatiens* from 70 mm. to 7·5 mm. per minute. These results prove conclusively that the velocity of ascent becomes decreased under increasing drought.

The Effect of Physiological Anisotropy induced by Stimulus

I will next describe certain unexpected results which I obtained in the determination of the velocity. It is natural to expect that the velocity of ascent along the different flanks of the same stem would be the same. But in the determination of the velocity on the opposite sides of the stem of *Chrysanthemum* I found that though it was the same in a certain number of cases, it was widely different in others. Further investigation showed that the velocity was more or less uniform on all sides of specimens which had been grown in situations where the sunlight did not fall directly on the plant. In other specimens, of which the side facing south had been exposed to the action of sunlight, the north side being protected from it, though there was no visible difference in the two sides of the plant, yet an impressed physiological difference became revealed by the different speeds with which the sap ascended the two sides. I give in the following tables certain typical cases out of a large number.

TABLE VII.—SHOWING THE DIFFERENCE IN THE VELOCITY OF ASCENT ON THE SUNNY AND THE SHADED SIDES OF *Chrysanthemum*

Under slight drought

Sunny side				Shaded side			
No.	Distance in mm.	Time in seconds	Velocity per minute	No.	Distance in mm.	Time in seconds	Velocity per minute
1	155	90	103 mm.	1	270	40	325 mm.
2	196	95	157 ,,	2	280	25	672 ,,
3	125	40	187 ,,	3	335	50	474 ,,
4	224	80	168 ,,	4	140	20	420 ,,

Under excessive drought

Sunny side				Shaded side			
No.	Distance in mm.	Time in seconds	Velocity per minute	No.	Distance in mm.	Time in seconds	Velocity per minute
1	100	340	18 mm.	1	125	130	58 mm.
2	150	480	19 ,,	2	130	150	52 ,,
3	160	660	14 ,,	3	156	180	44 ,,
4	60	250	14 ,,	4	170	170	60 ,,

It has thus been shown that, everything else being the same, (1) the velocity in a fully drooping specimen is, as previously shown, lower than in a semi-drooping specimen, and (2) the velocity of ascent in the shaded side is markedly higher than in the sunny side. This refers to the middle portion of the stem where the velocity is uniform.

This latter result also proves that osmotic action could not be the determining factor in the ascent of sap. For Arrhenius has shown that the osmotic pressure in a plant is lower when growing in shade than in the open.[1] The explanation of the lower velocity in the side stimulated by light has been arrived at by the experiments which will be described in detail in the next chapter ; it is that stimulus

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[1] Arrhenius, N. K. vet Akad, *Nobel Inst.*, 5, No. 15, 1–20.

in general induces a diminution of velocity of ascent, and that this diminished velocity persists as an after-effect of strong and long-continued stimulation.

Determination of Velocity in the Reverse Direction

In a plant subjected to drought, the root-cells cease to function from the absence of water-supply. The resultant diminution of turgor and hydrostatic pressure thus arrests the rhythmic activity underlying the ascent. If now, in a plant subjected to drought, water be applied to the top of the stem, it will be found that the direction of the flow of sap will be reversed, *i.e.* from above downwards. The following experiment demonstrates this in a striking manner. A drooping stem had all the leaves cut off except the terminal one. A beaker of water was raised so that the leaf was immersed in it (fig. 15). The result was that in a very short time the bent stem became erected, so that the leaf was lifted out of the water, the leaf having acted as an absorbent organ.

There next arises the question as to the relative rates of the flow of sap in the normal up direction and in the reversed down direction. This determination I have been able to carry out with great accuracy by the following arrangement (fig. 15). We make a vertical slit dividing the stem to a certain height into two halves, and place a piece of mica between the two; the slit is carried above the right leaf C, and 1 cm. below the left leaf D. A specimen was chosen which had been uniformly exposed to the light from the sky and not to one-sided sunlight. The normal conducting power was thus the same on all sides. The lower end of the stem has a slanting cut, so that, by partly immersing the end, only the right half of the stem was supplied with water. Owing to the physiological interruption by interposition of the piece of mica, the movement of sap on irrigation was from A to B, and then to C, causing successive erection of the drooping leaves. After this the sap had to ascend 1 cm. and cross over to the left through a distance of about 4 mm., which was the diameter of the stem; it then caused erection of the leaf D. After this the flow of sap was reversed in a downward direction, and the successive erections of the leaves took place in a reverse order, D, E, F. The respective time intervals enable us to determine the velocity of movement in an upward, in a transverse, and in a downward direction. The specimen, it should be remembered, was under considerable drought and the general rate of the flow of the sap was therefore slow.

TABLE VIII.—GIVING THE RATE OF ASCENT AND THE RATE OF REVERSED FLOW DOWNWARDS

	Distance	Time interval	Velocity per minute
Ascent . . .	AB 80 mm. BC 80 ,,	245 sec. 240 ,,	18 mm. 20 ,,
Reversed flow . .	DE 75 mm. EF 75 ,,	1620 sec. 1500 ,,	2·8 mm. 3·0 ,,

The average rate of ascent was thus found to be 19 mm. per minute, and the rate of flow in a downward direction to be 2·9 mm. The period required for the transverse conduction through 4 mm. was five and a half minutes, or at a rate of 0·7 mm. per minute. Thus, representing the slowest rate of transverse conduction by 1, the rate of reverse flow downwards would be 4, and the normal ascent rate 27.

SUMMARY

The velocity of ascent may be determined with the highest degree of accuracy by the Duplex Method, in which the latent periods of the absorbing and responding organs are eliminated.

The velocity in a cut stem is higher than in an intact plant with roots ; the difference is due to great resistance offered by the fine root-hairs to the entrance of water.

The velocity of ascent is modified by the plant's previous history as regards the favourable or unfavourable conditions to which it had been subjected.

The effect of excessive drought is to lower the rate of ascent of sap.

Sunlight, acting as a stimulus, retards the rate of ascent : the after-effect of this stimulus is persistent ; anisotropy is thus induced between the sun-exposed and the shaded side of the same stem. The velocity in the shaded side is higher than that in the sun-exposed side.

The velocity of flow of sap in the downward direction is about eight times slower than in the normal upward direction. The rate of transverse conduction is about 27 times slower than that of normal ascent.

CHAPTER V

THE EFFECT OF PHYSIOLOGICAL VARIATIONS ON THE ASCENT OF SAP

The Potograph—Effect of physiological agents in modification of ascent—Effect of diminished internal pressure—Effect of stimulus—Modifying influence of tonic condition—Effect of variation of temperature on ascent and on growth—The critical thermometric minimum—Drooping of leaves during frost—Phenomenon of accommodation—Effect of anæsthetics—Effect of poison—Method of exudation—Strasburger's experiments—Summary.

THE various crucial tests discriminating the pulsatory activity of living tissues have been given in Chapter II. These are, the effects of diminished pressure, of the action of stimulus, of the modifying influence of tonic condition on response, of variation of temperature, of the critical thermometric minimum, of small and large doses of anæsthetics and of poisons. In the present chapter will be considered the application of these physiological tests to the ascent of sap, not only in intact specimens with roots, but also in cut stems.

In addition to the two reliable and sensitive methods for the investigation of the velocity of the ascent of sap and its induced variations, namely, those of the response of drooping leaf and of drooping stem, a third method, the method of the Potograph, is now introduced as an independent and confirmatory test. The experiments were carried out, unless stated to the contrary, with cut stems.

The Potograph

The rate of water-movement may be indirectly deduced from the successive readings of the index of a potometer.

The results obtained with the apparatus in general use are not, however, free from error. The readings again are necessarily discontinuous, and important phases of the induced changes are thereby missed. In order to determine any variation of water-movement, a laborious process of construction of curves from the given data is necessary. It is therefore impossible to obtain any immediate indication of the normal rate of suction and its induced variations.

For overcoming these drawbacks I devised the Potograph, by which the curve is directly obtained; the inspection of the curve is sufficient to afford all the information as to the normal rate of water-movement and the direct and the after-effects of external agents on that movement. The apparatus consists of (1) an arrangement by which the immersed part of the specimen may be readily subjected to the action of different excitatory or depressing agents; (2) a potometric tube by which the normal rate of suction and its variation is observed; and (3) a contrivance by means of which the excursion of the water-index and its time-relation become recorded. For this last, I employ two different methods: the first is automatic, in which the image of the opaque index is thrown upon a photographic plate allowed to fall at an uniform rate by means of a clockwork. The second is a much simpler device, that of following the movement of the index with a recording pen resting on a drum, round which is wound the paper for record; the drum is kept revolving by a clockwork at a known and adjustable speed. When the excursion of water is followed in the way described, a curve is obtained the ordinate of which represents the quantity of water sucked up, and the abscissa the time. The slope of the curve gives the rate of water-movement; so long as this is uniform the slope remains constant. If any stimulating agent increases the rate, there is an immediate flexure in the curve, which becomes steeper. A depressing agent lessens the slope of the curve; the arrest of water-movement is indicated by a horizontal record.[1]

The new type of the Potograph is shown in fig. 16; it possesses several advantages over its predecessor, one of which is facility of regulating the temperature of water. The stopcock S allows the introduction of water or other solutions into the vessel. For this purpose the stopcock S_1, for exit of water, is opened and S_2, in connection with the capillary tube, closed. After the introduction of water or a solution, S and S_1 are closed and S_2 opened. A thermometer inserted into the water-vessel indicates the temperature. The spiral of platinum wire for electric heating is placed at the bottom of the vessel, care being taken that the rootlets do not come in contact with the heating coil. Electric connections are made

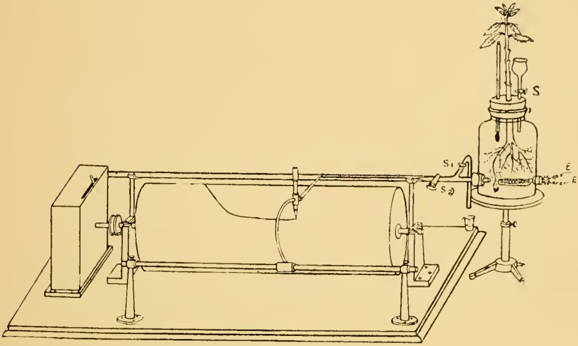

FIG. 16. The Potograph

The suction of water by the plant is recorded by following the excursion of the water-index in the capillary tube with the recording pen, which traces the curve on the drum D, kept revolving by the clock C. S, stopcock for the introduction of water; S_1 for exit; S_2 connects the capillary tube with the plant-vessel.

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[1] For greater detail, as also for the more sensitive Method of Balance, cf. *Plant-Response* and *Electro-Physiology*.

with the coil by means of the electrodes E and E′. The current from a battery of cells is regulated by a rheostat, and the rise of temperature in the water-vessel may thus be adjusted without any difficulty.

In order to secure accurate results it is necessary that the temperature of water in the vessel should remain constant. For ordinary experiments in which the effect of variation of temperature is not required, the temperature of the vessel does not in practice vary from the temperature of the room. But when we wish to study the physiological effect of variations of temperature, complications arise from the gain or loss of heat by the water in the vessel. This is reduced to a minimum by enclosing the plant-vessel in an insulating cover of thick felt, or by placing it inside a box filled with mica-dust. It is also easy to construct a correction-curve for the particular apparatus. The error introduced in neglecting this correction is, however, less than 2 per cent.

Having described the different methods for obtaining the record, we may now enter upon the detailed study of the effects of physiological changes in inducing variation of the normal rate of the ascent of sap.

Effect of Diminished Internal Pressure

Diminished internal pressure may be produced by the action of drought or by plasmolysis. These were shown to induce a depression or arrest of the pulsation of *Desmodium gyrans* and of growth (p. 12).

A condition of drought diminishes or arrests the ascent of sap. This is not solely due to the absence of water for transmission, but also to the depression of the pulsatory activity of the cells. Thus in a series of experiments carried out with the cut stem of *Chrysanthemum*, the conducting power of the specimens subjected to excessive drought was found to be depressed to as much as one-thirteenth the normal rate (p. 45).

The application of a plasmolytic solution of KNO_3 diminishes or arrests the ascent; thus a dilute solution of KNO_3 applied at the cut end of the stem of *Impatiens* arrested its erectile response; a stronger solution applied to a different specimen induced not only an arrest but an actual reversal, that is to say, a drooping movement (Fig. 17, *a*, *b*). The effect of plasmolytic solution in diminishing the rate of suction was also determined by the independent method of the Potograph. The normal rate of suction of a cut stem of *Croton* was 36 c.mm. per minute; application of dilute KNO_3 solution reduced it to 17 c.mm. per minute.

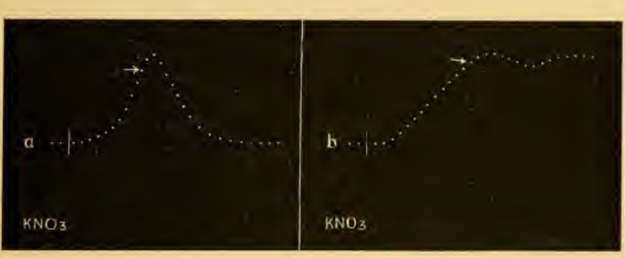

FIG. 17. The Effect of Plasmolytic KNO_3 Solution in Arrest of Ascent of Sap

Irrigation at vertical line induced normal erectile movement. Application of KNO_3 solution at arrow arrested the response. The left figure shows the effect of strong, the right figure the effect of dilute, solution of KNO_3.

The Effect of Stimulus

It has been shown that in normal specimens the effect of stimulus is to depress or inhibit pulsatory activity, whether in *Desmodium* or in growing organs. In experimenting on the effect of stimulus on the ascent of sap, a cut stem of *Impatiens* was taken, into which two pins had been thrust at a distance of two centimetres from each other, these serving as electrodes for the passage of induction-shocks. After attainment of an uniform erectile response, strong electric shock was applied (at arrow, fig. 18, *a*). This is seen to have induced an arrest of ascent in the course of fifteen seconds; the arrest persisted for a considerable length of time.

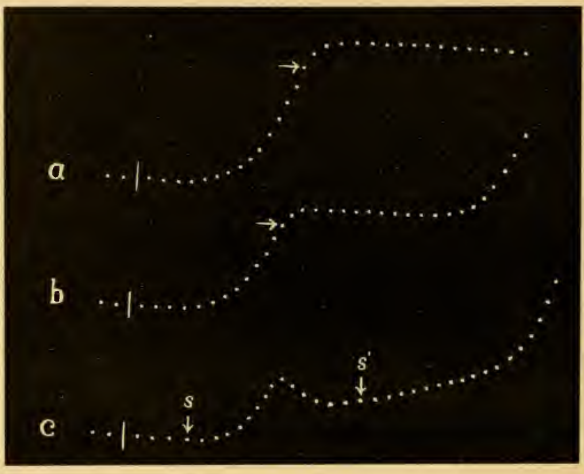

FIG. 18. Effect of Stimulus on the Ascent of Sap in Normal and Sub-tonic Specimens

(*a*) Effect of strong stimulus applied at arrow in arresting ascent.
(*b*) Effect of stimulus of moderate intensity inducing arrest with subsequent recovery.
(*c*) Effect of stimulus on sub-tonic specimen in which ascent was at a standstill. Stimulus of moderate intensity initiated ascent for a short time; stronger stimulus at s' produced persistent ascent.

In another experiment, the induction-shock applied was only moderate. This gave rise to a temporary arrest, followed by recovery after three minutes.

Results similar to those obtained with electric stimulus were also obtained with other modes of stimulation, such as that of light. The stimulus of sunlight has already been shown to induce a persistent diminution of the rate of ascent (p. 47).

Modifying Influence of Tonic Condition

The effect of stimulus on a sub-tonic specimen has been shown to induce renewal or enhancement of pulsation in *Desmodium,* or an enhanced rate of growth in growing organs (p. 15). The effect of stimulus on a sub-tonic tissue is thus diametrically opposite to that on the normal.

Similarly, the ascent of sap in sub-tonic specimens is enhanced under the action of stimulus. This is seen in the record of a sub-tonic specimen of *Impatiens.* The sub-tonicity of the specimen is evidenced by its inability to suck up water even after irrigation, the record remaining horizontal. Application of electric stimulus of moderate intensity at S induced a transient renewal of the ascent; stimulus of stronger intensity applied at S′ induced a renewal which persisted for a considerable length of time (fig. 18, *c*).

I also studied the effect of stimulus on sub-tonic specimens of plants with roots by the potographic method. The plants were mounted on the recording Potograph and afterwards placed in a dark room, till the normal suction was nearly abolished. This occurred in *Zea Mays* after twenty-four hours; but in *Impatiens* the arrest did not take place till after several days. In *Zea Mays* the rate of suction declined to 0·24 c.cm. per minute. Electric stimulation of a definite intensity and duration was now applied to the lower end of the plant, one electrode of the induction-coil being dipped in the water-vessel, and the other applied to the stem 2 cm. above the root. The effect of the first stimulation was to enhance the rate from 0·24 to 0·60 c.cm. per minute, that is to say, it more than doubled the rate. The second increased it to 0·85, and the third raised it still higher to 1·0 c.cm. per minute, which was the climax, for the fourth stimulation induced a decline, as in normal specimens. Effects similar to the above were also obtained with *Impatiens*.

TABLE IX.—THE EFFECT OF ELECTRIC STIMULUS ON THE ASCENT OF SAP IN SUB-TONIC SPECIMENS

Specimens	Stimulation	Rate of ascent of sap
Zea Mays	Normal	0·24 cubic cm. per minute
	First stimulation	0·60 ,, ,,
	Second ,,	0·85 ,, ,,
	Third ,,	1·00 ,, ,,
	Fourth ,,	0·40 ,, ,,
Impatiens	Normal	0·30 cubic cm. per minute
	First stimulation	0·78 ,, ,,
	Second ,,	0·26 ,, ,,

Effect of Variation of Temperature

Rise of temperature has been shown to enhance the autonomous activities of *Desmodium* pulsation and of growth; fall of temperature, on the other hand, causes a depression (p. 17). Variation of temperature also induces similar effects in the ascent of sap.

The investigation was carried out by two different methods, first by the Erectile Response of drooping stems and second by the method of the Potograph. The specimens were *Impatiens* with and without roots.

I will first describe the results obtained by the Erectile Method with a rooted specimen. Record was first taken of the actual rate, showing that the plant was exhibiting a continuous drooping, as seen in the down curve (fig. 19, *a*); watering the plant, at the vertical line, with water at normal temperature, arrested the drooping and brought on the erectile response. Cold water was next applied at C; this caused a flattening of the curve indicating the relative depression of the rate. Warm water was next applied at II, with the result of a great enhancement of the rate of erection, and therefore of ascent, as shown by the erect curve and the increased distance between the successive dots.

The record given by a magnifying lever labours under the defect that an arc is described, on account of which the flexure caused by the variation of the rate of ascent is not so pronounced towards the end as in the middle of the curve. The defect arising from the curvature in the record may, however, be eliminated; it is least pronounced in the middle part of the record through a length of about 5 cm. We take the record on a stationary plate, after adjusting the lever slightly below the middle; the plate is next moved sideways through about 1 cm., and the next record is commenced at the same level as the first. This is accomplished by lowering the plant, the stand on which it is placed being provided with a rack and pinion. Successive records of the effect of different temperatures are thus obtained in the middle part of the plate.

In fig. 19, *b*, are given successive records showing the effect of variation of temperature on the ascent of sap, the temperature rising from 30° to 35° C. and falling once more to normal 30° C. It will be seen that it took fifteen minutes to cover a distance of 40 mm. at the beginning of the experiment, and sixteen minutes for covering the same distance, at 30° C., after completing the cycle of temperature-variation; the two determinations for 30° C. are practically the same, the average period for the same length of the record being 15·5 minutes. At 35° C. the same distance was described in eight minutes. Hence the rate of ascent of sap at 35° is about 1·9 times that at 30° C.

I also reproduce, for comparison, a record of growth taken on a stationary plate at normal temperature, under cold, and under warmth (fig. 19, *c*).

METHOD OF THE POTOGRAPH.—We determine first the normal rate of suction of a cut stem of *Impatiens* at

30° C., which is the temperature of the room in summer. Warm or cold water is then introduced into the plant-vessel, and the record obtained shows the effect of rise or fall of temperature on the rate of suction. In studying the effect of rise of temperature we introduce warm water, say, at 35° C., or the rise is effected by means of the electric heating coil. After the attainment of the steady condition, record is taken of the resulting rate of suction.

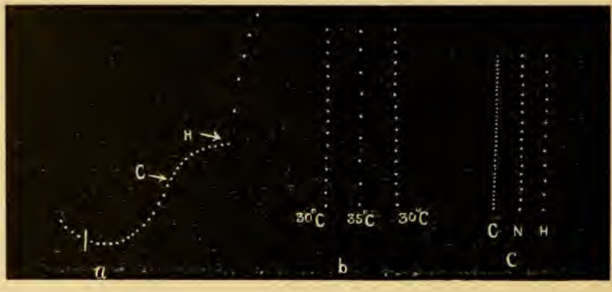

FIG. 19. Effect of Variation of Temperature on the Ascent of Sap and on Growth

(*a*) Record of erectile response on a moving plate. Cold water applied at C arrested the ascent, while application of warm water at H enhanced it.

(*b*) Effect of cyclic variation of temperature of 30°, 35°, and 30° C. on the ascent of sap; record taken on a stationary plate. Depressed rate is indicated by the closeness of successive dots; enhanced rate indicated by wider spacings of the dots.

(*c*) Effect of variation of temperature on the rate of growth taken on a stationary plate by the Crescograph. N, normal rate, C the depressed rate under cold, and H the enhanced rate under warmth.

Correction for thermometric effect.—In carrying out experiments on variation of temperature we have to apply a correction for the thermometric effect. It is to be remembered that the vessel of the potometer acts as the bulb of a thermometer. When the water in the vessel is at a higher temperature than that of the room, there is a loss of heat through conduction and radiation. The loss can be greatly reduced by a non-conducting cover. Again, other things being equal, the rate of loss of heat and of fall of temperature will be greater the greater the difference between the temperature of water in the vessel and that of the surrounding temperature. With a difference of one or two degrees, the rate of loss will be very slight. During the fall of temperature the water in the vessel will contract, and the index will show this by a movement which is in the same direction as that of the suction by the plant. For obtaining the absolute rate of suction we have, therefore, to apply a correction, which is to be *subtracted* from the observed rate. When the water in the vessel is at a lower temperature than that of the room there is a gain of heat and a consequent expulsive movement of the water-index, which is in a direction opposite to that of suction. The actual suction will be greater than what is observed, and we have to *add* a correction for the true rate. It is therefore necessary to obtain a correction-curve for different temperatures applicable for the particular apparatus.

Experimental method of obtaining the correction-curve.—For determining this correction, a glass stopper closes the aperture through which the lower part of the plant is inserted into the vessel. The water of the vessel is raised 5 degrees above the temperature of the room, this being the maximum rise generally employed in the experiments. Observations are commenced after the attainment of a steady condition. The thermometer inside the vessel shows the rate of fall of temperature ; and the movement of the water-index the rate of contraction of the water due to the fall of temperature. It was found that, under the conditions of the experiment, the temperature fell from 35·5° C. to 34·5° C. in the course of forty minutes, and the total contraction of the index was 98 mm. ; the average rate of contraction is therefore 2·4 mm. per minute for the mean temperature of 35° C. The average rate of suction of *Impatiens* at 35° is, on the other hand, about 135 mm. per minute. The correction for the apparatus at a temperature 5° C. above that of the room is thus 1·8 per cent. For temperature five degrees below that of the room the correction is of the same order but of positive sign. For smaller differences of temperature the correction is negligible.

In studying the effects of change of temperature on the ascent of sap, a rising temperature can be kept under better control by the electric heating of the platinum coil immersed in the vessel than by pouring in hot water. Lowering of temperature is effected by the introduction of cold water. The surrounding temperature in Calcutta varies from about 22° C. in winter to nearly 40° C. in summer.

Effect of variation of temperature.—The experimental plant employed was *Impatiens*; the temperature of the water at the cut end of the stem was first lowered and the record taken at 25° C.; it was next raised to 30° C., and afterwards to 35° C. The record obtained gives the movement of the index in mm. per minute. The absolute quantity of water in cubic mm. sucked up by the plant is found by multiplying the rate of movement of the index by a constant, which for the capillary tube used was 0·24. The following table gives the rate of suction at different temperatures.

TABLE X.—THE RATE OF SUCTION AT DIFFERENT TEMPERATURES

Temperature	Rate of movement of index per minute	Absolute rate of suction per minute
25° C.	38 mm.	8·7 cubic mm.
30° C.	81 mm.	19·4 ,, ,,
35° C.	150 mm.	36·0 ,, ,,

Effect of cyclic variation of temperature.—An investigation was next carried out on the effect of cyclic variation of temperature, that is to say, of the determination of the rate of suction at different temperatures for both thermal ascent and descent. Observations were made as the temperature rose successively from 25° to 30° and then to 35° C.; the temperature was next varied in a reverse direction from 35° to 30° and afterwards to 25° C. The two sets of results did not at first exhibit any close agreement. Further investigation showed that this was due to the fact that sufficient time had not been allowed for physiological adjustment to the changed conditions. In studying the effect of a given temperature, the specimen should be subjected to it for at least twenty minutes before taking the record. With this precaution the record of a cyclic change is extraordinarily consistent. The following table gives the results of the observations.

TABLE XI.—THE EFFECT OF CYCLIC VARIATION OF TEMPERATURE. (CAPILLARY CONSTANT 0·24)

Temperature rising	Rate of suction per minute	Temperature falling	Rate of suction per minute
25° C.	36 mm.	35° C.	120 mm.
30° C.	71 mm.	30° C.	69 mm.
35° C.	120 mm.	25° C.	36 mm.

It will be seen that the suctional activity is enhanced during rise and depressed during fall of temperature, and that the rate of suction for a given temperature during the ascent and descent is practically identical.

Comparison of the rate of Ascent and of Growth at different temperatures.—It will be instructive to compare the effect of variation of temperature on the two autonomous activities of the ascent of sap and of growth, at about the medium temperature between 30° and 35° C. By the Potograph we found the rates of ascent at the two temperatures to be in the ratio of 81 : 150 or as 1 : 1·85. By the method of Erectile Response also the ratio of the rates of ascent for the same difference of temperature was seen to be 1 : 1·9. The rates of growth (Table IV, p. 18) at the two temperatures were found to be 0·32 μ and 0·84 μ, the ratio being as 1 : 2·6. The induced variations in the activity of ascent and of growth may, therefore, be taken to be of the same order.

The Critical Temperature Minimum

I have explained (p. 18) that the autonomous pulsation of *Desmodium* leaflet becomes arrested at a temperature below the critical. This is shown in the record (fig. 20), in which the arrest in a summer specimen took place at 17° C., the pulsation being revived at 18° C. The plant becomes accustomed to a lower temperature in winter, when the critical temperature is 11° C. The mean critical point for the leaflet of *Desmodium* may therefore be taken as 14° C.

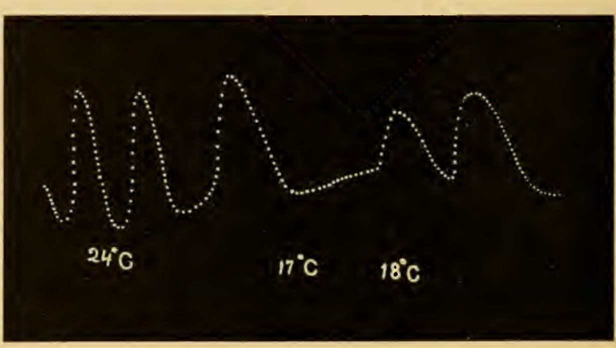

FIG. 20. Record showing the Critical Temperature for the Arrest of Pulsation of *Desmodium* Leaflet

The arrest took place at 17°C. and revival at 18°C.

When the temperature is lowered, the arrest of pulsation persists so long as the temperature remains at or below the critical point; rise of temperature above this point revives the pulsation. The same living tissue may thus exist in two different conditions, namely, an inactive and an active state, which can be made to alternate by merely lowering or raising the temperature below or above the critical point. No proof of physiological activity could be more direct or convincing than the alternate arrest and revival induced by this definite physiological variation.

As regards growth, the minimum temperature for arrest in *Scirpus Kysoor* I find to be 22° C.; the arrested growth becomes feebly revived when the temperature is raised by 1° C., the rate of growth being now $0 \cdot 02\ \mu$ per second. The critical temperature for arrest of growth in *S. Kysoor* is thus found to be about 8 degrees higher than the mean critical point for the *Desmodium* leaflet. This shows that the growing cells are more sensitive to the adverse influence of low temperature than the fully grown cells in the pulvinule of *Desmodium.*

It is thus seen that lowering of temperature below the critical point arrests the rhythmic activity of the *Desmodium* leaflet and of growth, a rise of temperature above that point causing a revival. Hence, *a crucial proof in demonstration that the maintenance of the ascent of sap is effected by the rhythmic activity of living cells would be afforded by the alternate arrest and renewal of the ascent by temperature-variations below and above the critical point.*

In endeavouring to ascertain whether or not the ascent of sap is arrested at a critical temperature, I used the method of Erectile Response for the determination in specimens with roots. The Potographic method was employed, more especially for ascertaining whether or not the critical temperature was the same or different for the stem and the root of the same plant.

Method of Erectile Response.—I obtained the erectile response of *Impatiens* after irrigation with water at the normal temperature of 30° C.; on the attainment of the steady rate, water at 10° C. was applied to the root; this was found to cause an arrest of the ascent, as indicated by the stoppage of the erectile movement. The temperature was next allowed to rise slowly, and when the thermometer buried in the soil indicated 23° C., there was a slow up-movement indicating resumption of the ascent of sap (fig. 21, *a*). The critical temperature for arrest was therefore below 23° C., or at 22° C.

Watering the soil does not produce a quick variation of temperature. It would be better, were it possible, to place the root in water and adjust the temperature. But a difficulty would arise in the washing of the soil from the roots, and the fixing of the plant in a vessel of water. By the time this had been accomplished the root would have

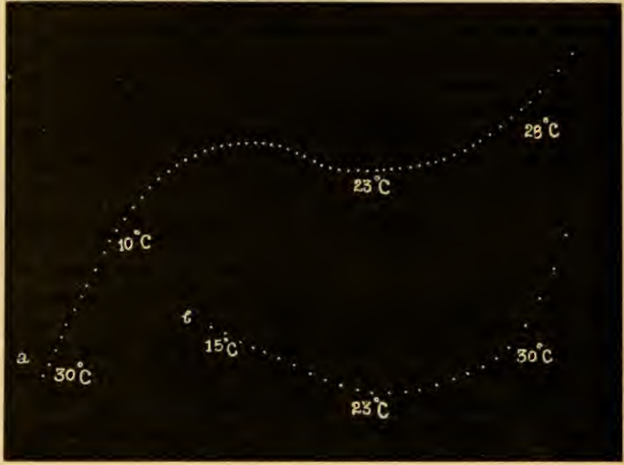

FIG. 21. Record of Erectile Response showing Critical Temperature for Arrest of Ascent of Sap

(*a*) First portion of the curve shows normal rate of erection under irrigation with water at 30° C. Application of water at 10° C. caused arrest in the course of fourteen minutes, after which the plant exhibited drooping. As the temperature rose to 23° C. there was a resumption of ascent, as seen in the erectile movement.

(*b*) The plant was placed with roots in cold water, which caused an arrest of suction and consequent drooping. When the temperature of water rose to 23° C. the ascent of sap and the erectile movement were resumed. (*Impatiens.*)

absorbed enough water to cause a more or less complete erection of the stem, after which it would be impossible to obtain any further record of any erectile movement. It now occurred to me that the difficulty could be overcome by washing the roots with water at a low temperature, say, at 10° C., and placing them in a vessel of water at 15° C. As this temperature is below the critical point, the rhythmic activity would be arrested, with the resulting arrest of absorption. This surmise proved to be amply justified, and nothing could be more surprising than the fact that the plant previously under drought, with its roots greedy for absorption of water, was unable to absorb even when immersed in water. In fact the record (fig. 21, *b*) shows that the plant continued to exhibit a drooping movement, as if the roots were buried in a very dry soil. The temperature of the water in the vessel was now allowed to rise; the drooping movement was arrested, and the reverse erectile movement commenced at 23° C. The critical point for arrest is again found to be at or about 22° C.

Drooping of leaves during frost.—The experiments described above offer a very satisfactory explanation of the drooping of the leaves which is observed during frost, and the recovery when the plant is brought into a warmer atmosphere. The ascent of sap, as we found, becomes arrested below the critical temperature, which is lower in cold climates than in the tropics. The temperature during frost would, in most cases, prove to be below the critical point; hence the drooping of the leaves is due to the arrest of the ascent of sap. The suctional activity is restored by the higher temperature, and by the renewal of the ascent of sap and the restoration of turgor, the leaves regain their normal condition.

The Potographic method.—I first tried to find out if suction by a cut stem of *Impatiens* was arrested at a sufficiently low temperature. The stem was mounted in the apparatus, the vessel being filled with water at 12° C.; after this the temperature was allowed to rise gradually.

It was found that no suction was recorded at the low temperature ; but as the temperature of water in the vessel rose to 16° C. there was an initiation of suction. The critical point of suction is thus about 15° C. Suction could be renewed or arrested repeatedly by variation of temperature above and below the critical point.

Phenomenon of accommodation.—While repeating the above experiment, I became aware of the very interesting phenomenon of accommodation by which the plant adjusts itself to changing external conditions. The critical point for the arrest of suction obtained from the first experiment was 15° C. ; repeating it a second time gave 14° C. for the arrest. A third repetition gave 13° C. as the critical point ; this was found to be the lowest obtained with this specimen, as further repetition did not exhibit any variation. The average critical point for the cut stem of *Impatiens* is thus 14° C., which is also the average critical point for the *Desmodium* leaflet. This coincidence is certainly very remarkable.

The critical point for *Impatiens* with roots was next determined. The experiment was commenced with the temperature of water at 14° C., when suction was found to be completely arrested ; it was found to be feebly renewed at 23° C. ; the critical point is therefore below this, *i.e.*, 22° C. A second experiment gave an identical result. This is a remarkable confirmation of the result obtained by the method of Erectile Response which has already been described.

Thus by the independent methods of the Erectile and of the Potographic Response, we arrive at the same value for the critical point for the activity of the root, which is 22° C. The critical point for the cut stem is 14° C., or 8 degrees lower. The root is therefore more sensitive than the stem to the adverse effect of lowering of temperature.

It is very remarkable that in certain tropical plants the critical point, 22° C., for the suctional activity of the root should be the same as the critical point for growth. This may be due to the fact that it is the growing portions of the root which are more actively concerned in the absorption of water; or it may be that the irritability of the root is, in general, greater than that of the stem, on which account its activity is arrested at a relatively higher temperature.

A rhythmic tissue may thus be alternately rendered active and inactive, above and below a critical temperature. Above the critical point, rhythmic activity is exhibited by the pulsation of the *Desmodium* leaflet and in the movement of growth: below the critical point, in the inactive state, these manifestations become arrested. Since variations of temperature above and below the critical point induce a similar alternation of states of activity and inactivity in the movement of the sap, the conclusion is inevitable that the movement is effected by a rhythmic tissue.

The Effect of Anæsthetics

We found that a small dose of ether induced an enhancement of pulsation in the *Desmodium* leaflet, and an enhancement of the rate of growth. Chloroform gave a preliminary enhancement followed by a decline and arrest (p. 19).

The effect of anæsthetics on the ascent of sap is precisely similar, as will be seen in the following experiments. After the attainment of the uniform erectile response, dilute ether was applied at the cut end of a stem of *Chrysanthemum*; this is seen to induce a great enhancement of response, which continued for a considerable length of time (fig. 22, *a*). A similar effect was induced when the anæsthetic was applied to the root (fig. 22, *b*).

Application of a dilute solution of chloroform causes an extraordinary increase of the rate of ascent as the immediate effect. The record (fig. 23, *b*) gives us a striking example of the immediate stimulation caused by the application of chloroform, the activity being enhanced more than fifteen-fold, as seen in the 'jumps' of successive dots inscribed by the lever on the oscillating plate. Continued action of chloroform causes depression and arrest.

The experiments described above prove that the action of anæsthetics on the various rhythmic activities is in every way uniform. A small dose of the anæsthetic enhances the pulsation of *Desmodium* leaflet, the rate of growth, and the rate of the ascent of sap. A strong dose, on the other hand, stops pulsation, growth, and the ascent of sap.

FIG. 22

FIG. 23

FIG. 22. Effect of Ether in Enhancement of the Erectile Response

(*a*) Effect of application at the cut end of the stem.
(*b*) Effect of application at the root. (*Chrysanthemum*.)

FIG. 23. Effect of Chloroform on Erectile Response

(*a*) Cut stem of *Chrysanthemum*.
(*b*) Drooping stem of *Impatiens*. Note sudden enhancement as the immediate effect.

The Effect of Poison

It has been pointed out (p. 21) that rhythmic activity is abolished, in the leaflet of *Desmodium* and in growing organs, by the action of poisons. I now give the results of experiments made in order to ascertain whether or not the ascent of sap is similarly affected.

I employed two different methods for the demonstration of the arrest of the ascent of sap by poison, the method of Erectile Response and the method of Exudation. It should, however, be borne in mind that certain poisons are more toxic for a given plant than for others. Moreover, plants often exhibit a certain amount of accommodation to poisonous agents.

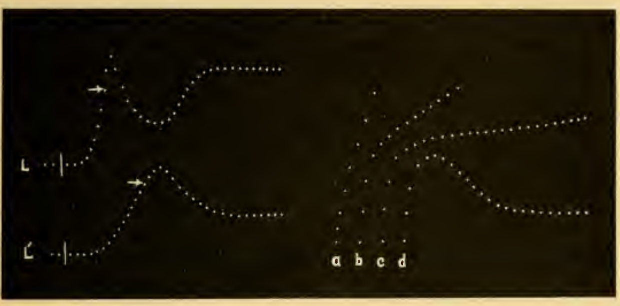

FIG. 24. Effect of Poison on the Ascent

L, Effect of dilute solution of formaldehyde on the response of a drooping leaf of *Chrysanthemum*. L′, the effect of stronger solution in inducing quick arrest.

a, The normal erectile response of drooping stem of *Impatiens*; *b*, *c*, and *d*, the effects of increasing strengths of solutions in retardation and ultimate arrest of ascent. (See text.)

The Method of Erectile Response.—After the attainment of an uniform rate of erectile response in water with a drooping leaf of *Chrysanthemum*, a dilute solution of formaldehyde was applied at the cut end of the stem. This induced at first an arrest of ascent, followed by a feeble attempt at recovery; but the arrest soon became permanent. In a second experiment a stronger solution was applied. This caused a quick arrest (fig. 24, L, L′).

Another series of experiments was carried out with cut shoots of *Impatiens*. In fig. 24, *a*, is given the erectile record of a drooping stem, when the cut end was placed in a vessel of water. The erectile movement is seen to take place with great rapidity. After the commencement of the normal erectile response, 1 per cent., 1·5 per cent., and 2 per cent. solutions of formaldehyde were applied to different specimens. The records *b*, *c*, and *d* exhibit the effects of increasing strengths of solution in inducing increasing retardation of ascent, culminating in an arrest.

The Method of Exudation.—In the following experiments I employed specimens of seedlings of Wheat with roots. The exudation of water at the tips of the seedlings of various *Gramineæ* is a visible indication of the activity of the ascent of sap. The experiments to be presently described were carried out with more than 100 different seedlings, and the results obtained were, without a single exception, in perfect agreement with each other. The mode of procedure was as follows : the apparatus has two trenches ; one of these was filled with water and the second with 1 per cent. solution of poisonous agents like potassium cyanide or sodium arsenite. A dilute solution of poison was used, as the object was to paralyse the plant and thus arrest its activity : too strong a dose would have caused immediate death and wilting of the plant. Each row of seedlings was placed with their roots in water and in the solution of the poison respectively. The specimens were placed under a glass cover, and in the course of a few hours it was found that while drops were being exuded vigorously by the seedlings with their roots in water, not a single drop was found at the tips of the poisoned plants (fig. 25). These experiments were repeated many times with the same result.

The exudation of drops of water is not the only mode of expression of spontaneous activity. This is also exhibited in active growth, and nothing could be more striking than the simultaneous arrest of exudation and of growth under the action of poison in the same seedlings. The experiments described below were carried out on three groups, each group consisting of six seedlings, so selected that for every specimen of a given length in one group there were two of the same length in the other two groups. The first group had their roots placed in water; the second, in dilute solution of potassium cyanide; the third, in dilute solution of arsenious acid. The following tabular statement gives the results in the three groups, the observations being continued for forty-eight hours.

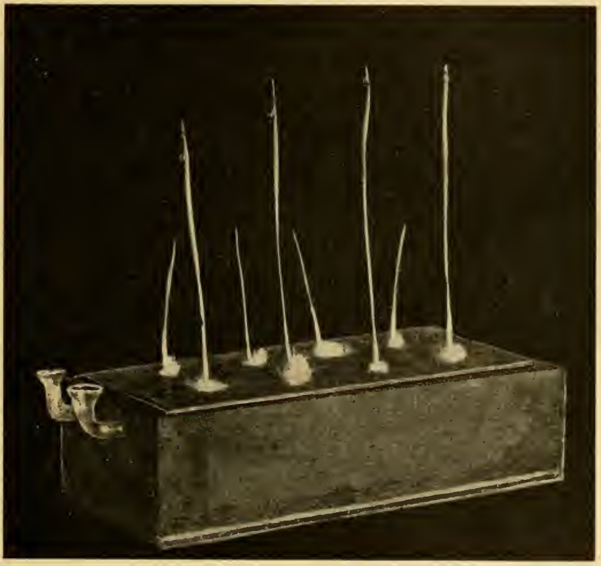

FIG. 25. Photographs of Normal and Poisoned Wheat Seedlings
Note exudation of water-drops and active growth in the former (front row), and the absence of exudation and growth in the latter.

TABLE XII.—THE EFFECT OF IRRIGATION WITH WATER AND POISONOUS SOLUTIONS ON GROWTH AND ON EXUDATION

No.	Original length	Length after forty-eight hours		
		Group I (water)	Group II (KCN)	Group III (arsenious acid)
1	40 mm.	100 mm.	43 mm.	44 mm.
2	42 mm.	100 mm.	43 mm.	45 mm.
3	43 mm.	102 mm.	44 mm.	46 mm.
4	45 mm.	107 mm.	47 mm.	48 mm.
5	45 mm.	108 mm.	46 mm.	47 mm.
6	46 mm.	109 mm.	47 mm.	50 mm.

Exudation of water was copious and growth active in Group I, but completely arrested in Groups II and III.

It will be noted that while the normal specimens became more than doubled in length by growth, the poisoned specimens showed practically no growth. These latter drooped and died in the course of a few days. The difference between the normal and poisoned specimens will be seen in the photograph of the apparatus containing two rows of four seedlings each, originally all of the same length. The seedlings with roots in water are seen exhibiting vigorous growth, and with exuded water trickling down the side. The seedlings in the second row are seen to be in a state of arrested growth and with no exudation (fig. 25).

As regards the effect of poison on erectile response of drooping stems, nothing could be more striking than the photographs reproduced below of the effect of formaldehyde solution in the arrest of ascent of sap in drooping shoots of *Chrysanthemum* (fig. 26). In a previous illustration (fig. 9) it is shown how the stem with its cut end in water becomes fully erected, with its leaves outspread in a turgid condition, in so short a time as fifteen minutes. In the present case, however, the cut stem in formaldehyde solution persisted in the drooping condition ; so presumably the ascent of sap was completely abolished. The specimen never recovered, but exhibited even greater drooping after eight hours; subsequently it died from the effect of the poison and became decomposed.

These results give conclusive evidence that poisons affect the ascent of sap just as they do the movements of the *Desmodium* leaflet and the process of growth; it may therefore be inferred that, like them, the ascent of sap is dependent upon the activity of living cells.

The experiments described above on the effect of poison in the arrest of ascent of sap have an important bearing upon Strasburger's results, already referred to (p. 22). The erroneous inferences drawn from them have had the most disastrous effect on the advance of investigation of this subject, as will be seen from the following extract: 'Owing to the researches of Strasburger, all vital theories have received a severe blow, if indeed they have not been directly disproved. Further, no positive evidence has been advanced in support of these theories, and one accepted them because purely physical explanation appeared to be inadequate.'[1] Now, no evidence could be more direct and convincing in support of the physiological theory than the continued arrest of ascent in a drooping stem with its cut end in a poisonous solution, and the renewal of ascent in a similar

FIG. 26. Photographs of Drooping cut shoot of *Chrysanthemum* placed in solution of Formaldehyde, which caused increased drooping, instead of full erection by ascent of water as in fig. 9

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[1] Jost, *Plant Physiology*, English translation, p. 75.

specimen with its cut end in water. The results of a complementary experiment described below will be found to be even more convincing. In this, we take two vigorous specimens, A and B, with their cut ends in water. They are in every respect similar to each other, the rate of suction in A being 1·1 c.c., that in B, 1·0 c.c. per hour. A and B were then placed in two similar test-tubes, one filled with water and the other with a 10 per cent. solution of formaldehyde ; a layer of oil was spread over the surface of the two liquids to prevent evaporation. The two test-tubes being previously calibrated (making allowance for the volume of the immersed stem), the rates of subsidence of the liquids will show the rate of suction and the ascent of sap in the two cases. The experiments were carried out inside the laboratory before a window. It was a rainy day, and the variation of temperature during the five hours of the experiment was slight. The specimen B, which was as erect and outspread as A, being placed in the poisonous solution, exhibited a collapse of the first pair of leaves in the course of five minutes, similar effects being produced in others in sequence from below upwards. The rise of poison could be followed by the discoloration ; the stem also collapsed, and the plant became a huddled mass of dying tissue (fig. 26A).

The difference in the rate of suction observed in the two cases offers the most striking and conclusive proof of the activity of living cells in the ascent of sap. In specimen A the rates of suction and ascent were practically uniform throughout the five hours of the experiment. The suction continued unabated for several days in succession. In contrast with this is the rapid fall of the rate in B due to gradual rise of poison, which put the successive zones of the living stem out of operation. The normal rate of 1·0 c.c. fell to 0·6 c.c. one hour after the action of the poison ; after two hours it was reduced to 0·35 c.c., after three hours to 0·2 c.c., and after four hours to 0·1 c.c. Suction was completely abolished after five hours. The difference in the two cases is exhibited in a striking manner by the two curves given in fig. 26B.

It may be thought that the effect of poison in woody trees might be different from that in the herbaceous stem of *Chrysanthemum*. The next experiment was, therefore, undertaken with two similar shoots of a Mango-tree, each bearing a rosette of eleven leaves. The average rate of suction of the specimen maintained with its cut end in water was 0·9 c.c. per hour ; the normal rate of the other specimen was 1·1 c.c. After treatment with the poisonous solution, the rates at successive hours were 0·7 c.c., 0·4 c.c., 0·21 c.c., and 0·12 c.c. The suction was practically abolished after five hours.

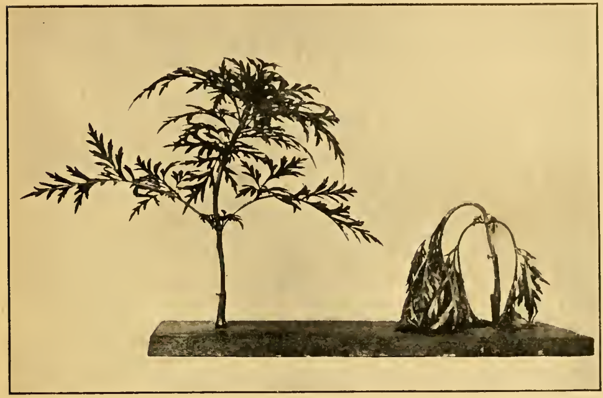

FIG. 26A. Photographs of two Shoots of *Chrysanthemum*, originally erect: the one to the left with cut end in Water, and the other in Formaldehyde Solution

But to return to the consideration of Strasburger's experiments on the ascent of poisonous solutions in the trunks of trees. They do not afford conclusive evidence that the ascent of sap is independent of living cells : for it is only reasonable to attribute the ascent, in his experiments, to the suctional activity of the living tissues beyond and above the poisoned region. That liquid, even poisonous liquid, can travel through dead tissue is proved by the experiment with *Desmodium*, described on p. 22, as also by others. The killed tissue of the poisoned stem becomes passive; but so long as the parts above remain alive, it continues to exhibit suction, which is completely abolished only when the stem is killed throughout its entire length. It would take a long time to kill a large tree by applying poison to the root or to the cut surface of the trunk.

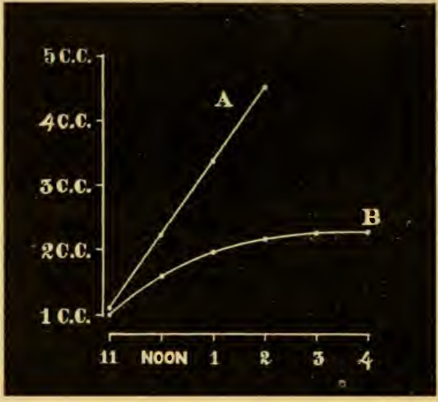

FIG. 26B. Curves of Suction of A in Water, and B in Poisonous Solution. Ordinate represents Quantity of Water sucked, and the Abscissa, the Time

Note that the slope of the curve A remains unchanged for days, indicating continuous suction (the portion of the curve after 2 P.M. has been omitted), while the curve B shows continuous diminution and final abolition of suction.

Incidental reference may be made to Strasburger's scalding experiments. The account of the following experiment will be of interest. The root of a plant was killed by boiling water. On return to the normal temperature, the suction of water, instead of being arrested, was found to be enhanced even above the normal. This result does not in any way invalidate the physiological theory; for it was only the portion of the plant killed by boiling water which lost its activity, whereas that of the unkilled portion above remained unaffected. The greater rate of suction after killing of the root is due to the fact that instead of the extremely attenuated channels of the root-hairs through which water was previously absorbed, there was now substituted the broad-sectioned stem, the dead mass of the roots acting as a piece of moist cloth for supplying water to the living tissue.

The experimental evidence condensed in the following table proves that, under certain physiological changes, the ascent of sap undergoes variations which are identical with those of other forms of rhythmic activity, and justifies the conclusion that it is, like them, a rhythmic phenomenon carried on by essentially the same mechanism—that of living pulsating cells.

TABLE XIII. SHOWING THE EFFECT OF PHYSIOLOGICAL CHANGES ON ALL FORMS OF RHYTHMIC ACTIVITY

Physiological variation	Induced effect of rhythmic activity		
	Pulsation of *Desmodium*	Activity of growth	Ascent of sap
Diminished pressure	Arrest	Arrest	Arrest
Effect of sub-tonicity	,,	,,	,,
Effect of stimulus on			
Normal specimens .	Inhibition	Inhibition	Inhibition
Subtonic ,, .	Renewal	Renewal	Renewal
Effect of poison .	Arrest	Arrest	Arrest
Effect of anæsthetics			
Small dose . .	Enhancement	Enhancement	Enhancement
Large dose . .	Arrest	Arrest	Arrest
Rise of temperature .	Enhanced frequency	Enhanced growth	Enhanced ascent
Fall ,, ,, .	Diminished frequency	Diminished growth	Diminished ascent
Critical temperature			
Mature organs .	About 14° C.	..	About 14° C.
Growing organs .	..	About 22° C.	About 22° C.

SUMMARY

Diminished internal hydrostatic pressure induces a depression of the ascent of sap.

In sub-tonic specimens stimulus causes an enhancement of the rate of ascent; in normal specimens it induces a retardation or arrest of ascent.

Rise of temperature enhances the rate of ascent, while fall of temperature depresses it.

The ascent is arrested at a temperature below the critical point; an identical tissue can thus be made a conductor or non-conductor of the sap by raising or lowering the temperature above or below the critical point.

In the tropics the critical temperature-minimum is higher than in colder climates. The following relates to the critical point in several tropical plants:—

The critical point of the fully grown pulvinule of *Desmodium* is about 14° C., which is the same as the critical point of ascent of sap in the cut stem of many plants: in growing organs, growth-activity is arrested even at the relatively high temperature of 22° C.: absorption and the ascent of sap in rooted plants are also arrested at about 22° C.

The effect of small doses of anæsthetics is to enhance the rhythmic activity of *Desmodium* leaflet, of growth, and of the ascent of sap. Large doses induce an arrest.

Poisons arrest the ascent of sap in specimens with roots and also in cut shoots.

These experimental results prove conclusively that it is the pulsatory activity of living cells which maintains the ascent of sap in the plant.

CHAPTER VI

TRANSPIRATION

Physical evaporation and physiological excretion—Isolation of absorbing, conducting, and excreting organs—The Bubbling Method for measurement of transpiration—Comparison of transpiring activity of different species of plants—Ratio of transpiration from upper and lower surfaces of leaves—Determination of transpiration from a single stoma—Transpiration in the absence of evaporation—The *rôle* of evaporation—Physiological continuity in stem and leaf—Crucial tests of physiological activity underlying transpiration—Effect of variation of temperature—Effects of sub-minimal and maximal stimulus—Summary.

The study of the ascent of the sap in the stem has shown that it is effected by an independent activity of its own: that it takes place in the absence of a root to propel the sap or of leaves to suck it (p. 36). The direction of propagation is determined, as we have seen (p. 34), by the turgor-gradient, from the more turgid to the less turgid region of the plant.

We have found that the activity of the root is not specifically different from that of the shoot, for the modification of the ascent of sap under physiological variation is essentially similar in cut stems and in intact plants with roots. We have arrived at the conclusion that the various manifestations of the ascent are brought about by the co-operative activity of living cells throughout the length of the plant, the absorbing root and the conducting stem. It now remains to study in detail the excretion of water at the upper end of the plant by the transpiring leaves. This is important, inasmuch as the state of turgor, internal pressure, exudation, and various other phenomena connected with the ascent of sap, are determined by the relative gain and loss of water by absorption and by transpiration.

The problem is highly complex, since the different organs of absorption, of conduction, and of excretion are subjected to different conditions and to diverse modes of stimulation. The root buried in the soil is to a great extent protected from the fluctuating changes in the environment. It may nevertheless exhibit a diurnal periodicity; though whether or not such periodicity exists is not definitely known, and it would be necessary to undertake an investigation on the subject. I have observed that exposure of the stem to the action of light has the remarkable effect of checking the rate of conduction (p. 47). Sunlight, which by its heating effect enhances the transpiration from the leaves, may thus exert an inhibitory action on the conduction of water in the stem. Finally, the transpiring leaves are subjected to the numerous fluctuating changes of the environment, to variations of humidity, to mechanical disturbances caused by the wind, to variation of temperature, and to the alternating action of light and darkness.

The combined effects of these varying influences, which act unequally upon the three regions of the plant, are thus seen to be very numerous, and the complications which thus arise may well appear baffling. But the difficulty in the solution of such intricate problems will by no means be lessened by the employment of mere verbal phrases, nor by any argument of a teleological character which offers no real explanation of the underlying physiological mechanism. Nor can any scientific advance be made by the unjustifiable employment of physico-chemical processes in explanation of phenomena which are beyond their scope. There has hardly been any recent contribution to plant-physiology so important as that of the investigation of osmotic action. But it would be a distortion of truth if it were to be assumed that the extremely slow osmotic action could give rise to a velocity of ascent of sap which may be as high as 70 metres per hour; or that the quick pulsatory movements of certain plant-organs is brought about by the alternate and spontaneous manufacture and destruction of osmotically active substances.

The problem of the ascent of sap and its diverse manifestations, though highly complex, is not insoluble. By isolation and separate investigation of the individual factors it will be possible to remove the obscurity which surrounds it. It is obvious how necessary it is to isolate an individual organ for the study of its characteristics. Neglect of this has often led to conclusions which are quite unjustifiable; thus from the observation that the application of dilute acids at the root induces a reduction in transpiration, it has been concluded that this agent has a retarding effect on transpiration itself. This inference is not logical, since the effect might as well have been due to an induced variation in the absorptive power of the root, or in the conducting power of the stem. It is more likely that the chemical agent affected all the different activities of absorption, conduction, and transpiration alike.

The difficulty attending the separate investigation of the activities of the three regions of the plant arises principally from the absence of exact methods and suitable apparatus for investigation: but I have endeavoured to overcome it by the invention of various instruments of precision which will be presently described. Complete isolation of the different regions from each other is impossible, since, as will be shown, a physiological continuity exists throughout the plant. Approximate isolation may, however, be secured. Experiments have already been described on the ascent of sap in isolated stems from which the root and transpiring leaves had been removed. The root may be isolated by cutting the root-stock close to the ground and studying its activity by observing the rate of exudation from the cut end of the stock. Finally, the transpiring activity may be studied by taking a single leaf with the cut end of its short petiole immersed in water.

The current view of transpiration is that it is mainly a phenomenon of physical evaporation. Thus, to quote Pfeffer:

'Transpiration is influenced by the same external conditions as the evaporation of water in general. . . . Transient and rapid changes, such as the movements of the stomata, serve to modify the transpiration according to the conditions existing at the moment, and thus exercise a certain regulatory control. . . . The actual evaporation of water is a purely physical phenomenon, dependent in a plant, as in a dead body, upon the physical properties of the body in question.'[1]

The object of the following experiments is to ascertain whether the giving up of water by the transpiring leaf is essentially a physical process, as Pfeffer suggests in the above quotation, or a physiological process of excretion effected by the pulsatory activity of living cells.

In carrying out this investigation on transpiration it was necessary to devise a sensitive apparatus by which the rate of normal excretion and its induced variations could be rapidly determined with a high degree of accuracy, which will now be described.

The Bubbling Method

A moderate-sized transpiring leaf is mounted water-tight in a graduated vessel with a side-tube containing a drop of non-adhesive oil to act as a valve. This prevents evaporation from the side-branch, and also serves as a means of counting the air-bubbles that enter the vessel from the outside (fig. 27). Transpiration, by removing a certain quantity of water from the vessel, causes a slight vacuum; the normal pressure is, however, immediately restored by a bubble of air, which enters the vessel by lifting up the oil-valve. The drop of oil falls back and the valve is closed once more, and the process is repeated time after time.

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[1] Pfeffer, *Plant Physiology*, English translation, pp. 236, 240.

Each bubble thus indicates the removal of a definite quantity of water by transpiration. This Bubbling Method has proved to be a very accurate and valuable means of investigation. Under constant external conditions the interval between successive bubbles is extremely regular. Thus transpiration from a full-grown leaf of *Nauclea*, kept in a room temperature of 30° C., caused the appearance of successive bubbles at exact intervals of ten seconds, without any variation. The specimen was next removed to a cooler room with a temperature of 28° C. The bubbling period now became slowed down to twelve seconds, and this remained constant for the next hour. It will presently be shown that this depression in the rate of excretion is due not to physical but to physiological variation. Other experiments will be described which will show that definite physiological changes are attended by induced variation in the excretion, as detected in the change in the bubbling period; that is to say, a stimulatory agent quickens the rate of bubbling; depressors, on the other hand, cause a slowing down of the rate. The rate of bubbling observed in a given specimen depends (1) on the sensibility of the apparatus, (2) on the transpiring activity of the species of

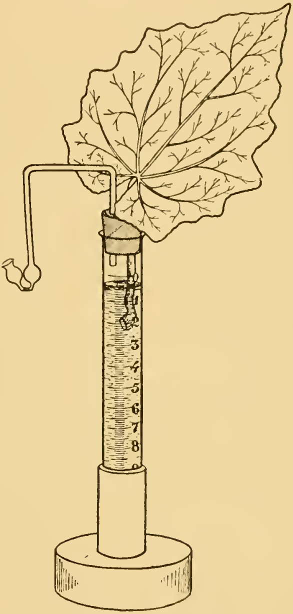

FIG. 27. The Bubbler

Note the drop of oil at the bend which acts as a valve.

the plant, (3) on the size of the leaf and (4) on its physiological condition. The rate of bubbling, on account of the above circumstances, exhibits a wide variation in different specimens. But in one and the same specimen a great uniformity of excretion is observed under constant external conditions.

The absolute rate of transpiration may easily be determined by finding the constant of the apparatus. For this purpose we ascertain, by a sensitive balance, the difference of the weight of the Bubbler containing the leaf at the beginning and at the end of an hour. This difference represents the loss of weight by transpiration. A count having already been taken of the number of bubbles in the course of the hour, each bubble represents the loss of a definite quantity of water by transpiration. Thus, in a particular experiment, the leaf of *Thunbergia grandiflora* lost 0·168 gram of water in the course of an hour, during which 60 bubbles were counted. The loss per bubble was thus 0·0028 grm. With a still more sensitive apparatus it is possible to detect a loss of one mgrm. Determination of the loss of water by weighing requires a long time, whereas the Bubbling Method enables us to obtain an immediate indication of the absolute rate of transpiration and its induced variations.

In less vigorous specimens of leaves the average rate is found to be constant, though the intervals between successive bubbles vary slightly above and below the mean interval. Thus in a particular leaf of *Thunbergia* the successive bubbles occurred at intervals of 29, 31, 30, 30, and 29 seconds.

In order to find the relative transpiring activity of different species of plants, I took leaves the area of which was nearly the same. I thus found that the rate of transpiration of *Thunbergia* was half that of *Nauclea*. In Crassulaceæ the transpiration is very feeble; in *Bryophyllum calycinum* the activity of excretion was found to be one-fifth that of *Nauclea*. I also determined the evaporation of water from a free surface, and the transpiration from an approximately equal area of leaf. Representing the evaporation as 100, transpiration from *Nauclea* was 45, from *Thunbergia* 20, and from *Bryophyllum calycinum* it was 9.

Ratio of Transpiration from the Upper and Lower Surfaces of Leaves

Many leaves bear stomata only on the lower surface, on account of which transpiration at that surface is relatively greater. This may be qualitatively found by the use of cobalt paper, which becomes reddened earlier at the lower surface. To obtain quantitative results, Garreau employed the laborious method of cementing the leaf in two bell-jars containing vessels of calcium chloride. The relative increase in weight of the two vessels of calcium chloride gives the amount of water transpired respectively by the upper and the lower surfaces of the leaf. The following method is more direct and simple ; the results moreover are very accurate. The cut end of the petiole of the leaf is fixed air-tight in the apparatus (fig. 27), which is then placed on a sensitive balance, and the loss of weight determined for, say, fifteen minutes ; this is the total transpiration, T, for both the upper and the lower surfaces. The upper surface of the leaf is then smeared with freshly boiled vaseline, which prevents transpiration from the upper surface : the loss of weight in fifteen minutes now indicates the transpiration, L, of the lower surface only. The leaf is now smeared on the lower surface as well ; the loss of weight should now be zero ; if any loss occurs in this condition, it must be due to some unavoidable leakage ; in practice this is found to be negligible. Having found the total transpiration T, and L, the transpiration from the lower surface, T—L gives the transpiration from the upper surface. Representing the total transpiration, T, by 100, we thus obtain the percentage of transpiration at the upper and lower surfaces respectively. The experiment is next repeated with a fresh specimen, but this time the lower surface is smeared with vaseline, which gives U, the transpiration from the upper surface: T−U is then the transpiration from the lower surface.

The results of the first experiments were not found to be very consistent; this was traced to impurities in the vaseline, which contained traces of moisture. The difficulty was overcome by boiling the vaseline before applying it to the leaf. With this precaution the results were found to be highly satisfactory The following is a summary of the results.

1. Leaf of *Nauclea* (small size):

Rate of total transpiration per minute	0·000382 grm.
Upper surface	23 per cent.
Lower surface	76 ,, ,,
Leakage	1 ,, ,,
Total	100

2. Leaf of *Nauclea* (large size):

Rate of total transpiration per minute	0·000681 grm.
Upper surface	21·5 per cent.
Lower surface	77·0 ,, ,,
Leakage	1·5 ,, ,,
Total	100

The leakage is thus seen to be negligible; the average ratio of transpiration from lower and upper surfaces of the leaf of *Nauclea* is thus 76·6 : 22, or about 3·5 : 1. In *Thunbergia* the ratio is about 4 : 1.

Determination of Transpiration from a Single Stoma

It may be of interest to obtain an approximate idea of the transpiration from an individual stoma at a temperature of 30° C. By means of a standardised Bubbler, the loss of transpiration from both the surfaces of a particular leaf of *Nauclea* was found to be 600 mgrm. per hour. The transpiration from the lower surface of the *Nauclea* leaf is, as we have seen, $\frac{3\cdot5}{4\cdot5}$ part of the total, and was therefore 467 mgrm. per hour. Portions of the epidermis taken from different parts of the lower surface of the leaf gave the average number of stomata to be 820 per sq. mm. The area of the leaf was 20,800 sq. mm.; hence the total number of the transpiring stomata was approximately 17 millions. Transpiration from an individual stoma was thus about 0·000028 mgr. per hour.

In investigating the induced changes of transpiration, it is not necessary to determine the absolute rate, but only the relative variation. Thus in an experiment on the effect of change of temperature, the normal rate of transpiration was one bubble per ten seconds, or one-tenth of a bubble per second. In order to avoid fractions, it is better to take an hour for the unit of time. The hourly rate of transpiration at 30° C. was thus 360 bubbles, and it was depressed to 300 bubbles per hour at 28° C. The relative change in the transpiring activity induced by slight cooling is thus in the proportion of 360 : 300. As the investigation on the induced variations of activity of transpiration is carried out with an identical specimen and with the same bubbler, it is sufficient to determine the ratio of the normal rate to that of the changed rate. *The transpiratory activity will therefore be relatively measured by the number of bubbles per hour.*

Transpiration in the Absence of Evaporation

It has already been mentioned that the generally accepted view of transpiration is that it is essentially a phenomenon of physical evaporation. I am, however, able to describe several decisive experiments which prove that excretion from leaves takes place even in the absence of evaporation, thus affording a conclusive proof that transpiration is an active physiological process.

The first experiment of the series was carried out in the Mayapuri laboratory in the hill-station of Darjeeling during continuous downpour of rain on the break of the monsoon. The air was surcharged with moisture. The temperature indoors was 16° C., and the transpiring activity of a single leaf of *Hydrangea* was found to be 40 bubbles. Water was sprayed on both the upper and lower surfaces of the leaf ; this did not arrest the transpiration ; the bubbling persisted at the rate of 24 per hour.

In a second experiment the transpiring activity during a heavy downpour was 38, the leaf being placed outside, but protected from the rain. The transpiration persisted, after exposure to the rain, at the same rate for half an hour, after which it was lowered to 20.

The next experiment is still more decisive ; evaporation from the leaf was prevented by thickly coating both the upper and the lower surfaces of the leaf with freshly boiled vaseline. It is true that the leaf under this abnormal condition is deprived of the supply of oxygen on which the various activities of its life depend. If it be a case of active secretion, this will induce only a depression of the rate, but not arrest. If, on the other hand, transpiration is dependent on evaporation, the fact will be demonstrated by the immediate arrest of transpiration. Experiments on these lines were carried out with various leaves. Thus in a vigorous leaf of *Nauclea* the normal rate of transpiration was 180 bubbles per hour ; *after smearing both the surfaces with vaseline the bubbling was found to persist ;* after an hour the rate was 139 ; at the eighth hour the excretion was still persistent, the rate being 30 bubbles per hour. The results of other experiments were similar, the only difference being that in less vigorous specimens the decline of the rate of bubbling was more rapid than in the above case.

It may now be asked : what happened to the excreted water ? Examination of the smeared leaves showed that the excreted water became collected in small patches under the film of vaseline, which prevented its escape into the atmosphere. This was specially marked on the lower surface of the leaf which bore the greater number of stomata.

The experiments described above prove conclusively that *the excretion from leaves is an active process independent of evaporation.*

I shall, in order to avoid ambiguity, use the term transpiration only in the sense of active excretion in the further discussion of the subject.

The Rôle of Evaporation

Though evaporation is not essential for excretion, it is important in the removal of the excreted water, and thus in maintaining a state of diminished turgor in the transpiring region. We have seen that the flow of sap is determined by the turgor-gradient, and this difference could not be permanently maintained unless evaporation quickly removed the excreted water, and caused a partial drought at the upper end of the plant. The reason for the gradual diminution of excretion in the vaselined leaf is the accumulation of water which could find no vent for escape, and which tended to produce a flow of sap in the reverse direction.

Physiological Continuity in Stem and Leaf

The ascent of sap involves physiological continuity throughout the plant. The existence of this continuity is demonstrated in the fact, already described (p. 48), that, in a plant subjected to drought, the leaf on being supplied with water exhibits absorption, thereby producing a reversal in the direction of the flow of sap. The terminal leaf in the above case functions as a root, that is to say, the organ which excretes is also capable of absorption.

Further experiments are given below which prove the existence of this continuity in the leaf. Just as it has already been shown that the root and the shoot are affected alike by definite physiological changes, so now it will be shown that the petiole, the midrib, and the lamina respond in an identical manner.

The Effect of Variations of Temperature

The effect of raising the temperature of the water at the cut end of the stem, in enhancing the rate of ascent, has already been described, as also the converse effect of a fall of temperature (p. 58). I have now to describe experiments on the effect of thermal variation on transpiration, (1) when the lamina is subjected to a change of temperature, and (2) when the distant petiole is subjected to thermal variation, the lamina itself being kept at a constant temperature. As regards the effect of change of temperature on the lamina, it may be remembered that the transference of a leaf from a warm to a cold room was found to be attended by depression of the rate of transpiration (p. 85).

The experiment on the effect of variation of the temperature of the petiole was carried out as follows. The cut end of the petiole of a leaf of *Nauclea* was mounted, with a thermometer, in a metallic tube. This tube was placed inside a larger vessel, which could be filled with water at different temperatures. I first produced a gradual lowering of temperature from 29° C., which was the temperature of the room, to 10° C. It is to be understood that the petiole alone was subjected to the lowering of the temperature, the lamina being maintained at the temperature of 29° C. After completion of the series of observations, the temperature inside the tube was allowed to return to the room-temperature, and afterwards raised from 29° C. to 32° C. The following table shows the effect on transpiration of cyclic variation of temperature of the petiole.

TABLE XIV.—EFFECT OF VARIATION OF TEMPERATURE OF THE PETIOLE ON TRANSPIRATION

Temperature falling	Transpiring activity	Temperature rising	Transpiring activity
29° C.	219	29·5° C.	275
23° C.	124	30·5° C.	300
18° C.	82	32° C.	360

It will be seen that during the fall of temperature of the petiole the transpiration underwent a decrease, while during the rise the activity was enhanced, in spite of the fact that the transpiring lamina itself was maintained at an uniform temperature.

Effect of Electrical Stimulation

One of the crucial tests of the rhythmic nature of a tissue is its reaction to stimulus: sub-minimal stimulus inducing an acceleration of activity, maximal stimulus retarding or inhibiting it (p. 14). This test was applied to the various parts of the leaf in the following experiments.

Stimulation of lamina.—The electrical stimulus has the special advantage that it can be easily graduated from sub-minimal or from maximal intensity. Electrical connections were made at two diagonal points on the lamina of *Nauclea*, which was stimulated by feeble induction shocks lasting for a minute. The normal transpiring activity was 116; but after feeble stimulation it was increased to 150, the enhancement being 29 per cent. The normal activity was restored in the course of twenty minutes. The electrical stimulus was now gradually increased. This induced a diminution of activity from the normal 116 to 87, or by 25 per cent. Further increase of intensity of stimulus induced a continuous diminution of activity, culminating in an arrest. Similar effects were also obtained with the leaves of *Thunbergia*.

Stimulation of the midrib.—I next applied stimulus to the midrib of the leaf; this induced results similar to those of the stimulation of the lamina. Under feeble stimulation the transpiring activity was enhanced from the normal 150 to 190, *i.e.*, an enhancement of 27 per cent. Recovery took place after fifteen minutes ; strong stimulation now depressed the activity by 67 per cent.

Stimulation of the petiole.—Electrical stimulus was applied to the petiole of another leaf of *Nauclea.* Feeble stimulus was found to enhance transpiration by 34 per cent. ; stimulus of stronger intensity induced a depression by 44 per cent.

The foregoing experiments show that the tissues of the transpiring leaf, both petiole and lamina, give the reactions characteristic of rhythmic tissue to electrical stimuli, subminimal or maximal.

We are now in a position to trace a complete picture of the physiological mechanism of the ascent of sap throughout the length of the plant. The pulsatory activity is initiated in the root, effecting the absorption of water from the soil. Similar activity in the cortex pumps the water up through the stem from cell to cell, and also injects water into the vascular tissue of the xylem (p. 175), along which it is physically transferred. The water conveyed by physiological conduction and physical convection reaches the leaf, where it is distributed along the veins and their numerous ramifications, and is eventually excreted or transpired into the intercellular spaces, whence it finds exit to the atmosphere outside by evaporation.

Physiological continuity as regards the ascent of sap thus exists in the plant, and any distinction of a specific activity of the root, of the shoot, or of the leaf is not merely arbitrary but highly misleading. For the excretion at the upper end results from the additive activities in all the regions of the plant.

Brief reference may here be made to other modes of excretion, by glands, by water-pores, and from wounded surfaces. No hard and fast line can, however, be drawn in these different manifestations. Excretions in general result from the additive action of cells throughout the length of the plant. The possession of a specially active terminal layer may, however, render the excretion by an organ more or less independent of the rest. Such a specially active layer is found in the glands of the pitcher of *Nepenthes* (fig. 28). The pronounced rhythmic activity of the layer is shown by the multiple electric responses exhibited by it (fig. 29). Excretion can therefore take place in the pitcher even in a condition of partial drought.

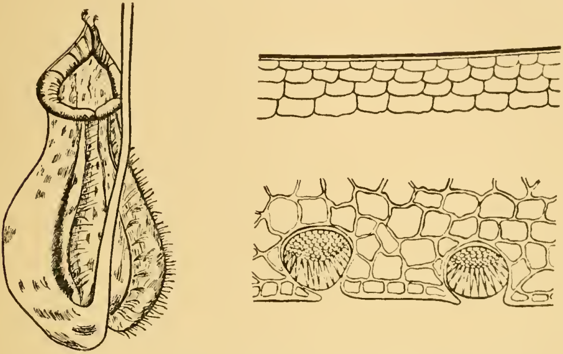

Fig. 28. The Pitcher of *Nepenthes*, and Transverse Section showing the Glandular Structure

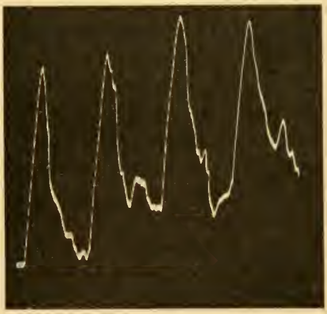

Fig. 29. Multiple Response given by the Glandular Tissue of the *Nepenthes*

Further, active excretion may take place even in the absence of glandular organs, for we shall find that Palms, which possess no glandular organs, exhibit active excretion even in the absence of root-pressure. Excretion by the nectaries is no doubt helped by the osmotic withdrawal of liquid by the concentrated sugar-solution outside; but the first excretion must have occurred without this adventitious aid. Similarly, evaporation from the leaves promotes the maintenance of the turgor-gradient in the plant, by which the uniformity of transpiration is secured.

SUMMARY

The activity of transpiration can be accurately determined by the Bubbling Method.

Taking the evaporation from a given surface of water as 100, the transpiration from an equal leaf-surface of *Nauclea* is 45, of *Thunbergia* 20, and of *Bryophyllum calycinum* 9.

Accurate determination can be made of the relative transpiration from the upper and the lower surfaces of the leaf by the Bubbling Method. In *Nauclea* the ratio is 1 : 3·5; in *Thunbergia* it is 1 : 4.

On the lower surface of an average-sized leaf of *Nauclea* there are 17 millions of stomata; at a temperature of 30° C. the rate of transpiration from an individual stoma is 0·000028 mgrm. per hour.

Transpiration persists for a length of time even after the smearing of both the surfaces of the leaf with vaseline. It is thus an active process not essentially dependent on evaporation.

Transpiration is appropriately modified under physiological variations. Application of feeble electrical stimulus to the lamina enhances transpiration, while strong stimulus retards or arrests it. The effects described are also produced when the midrib, or the petiole, is stimulated instead of the lamina. When the lamina is subjected to a rise of temperature, its transpiring activity is enhanced: the same result is obtained on raising the temperature of the distant petiole, and lowering of the temperature of the petiole induces a depression in the rate of transpiration.

These experiments prove that transpiration is a physiological process carried on by rhythmic tissue forming part of a rhythmic system continuous throughout the plant for the absorption and distribution of water.

CHAPTER VII

VARIATION OF TRANSPIRATION UNDER PHYSIOLOGICAL CHANGE

The Micro-Transpirograph—Effect of diminution of turgor on transpiration—Effect of stimulus—Opposite effects of stimulation of upper and lower surfaces of leaf—Effect of high frequency Tesla-current—Effect of electric waves—Effect of statical electric induction—Effect of thermal rays—Effect of light—Effect of red and of blue light—Effect of carbonic acid—Effect of ether and of chloroform—Summary.

IN the previous chapter we found that transpiration is a phenomenon of active excretion; it was also shown that it undergoes responsive variations under changes of temperature and under the action of electric stimulus. We shall in the present chapter consider the response of the excreting leaf to various further tests of its pulsatory activity. These are: (1) the effect of diminished internal pressure; (2) the effect of diverse modes of stimulation; (3) the effect of light; and (4) the action of anæsthetics. In addition an account of the action of thermal rays, of electric waves, of high frequency Tesla-current, and of statical electrical induction will also be given.

Detailed explanation has already been given of the very reliable and sensitive Method of Bubbling for the determination of induced variations of transpiration. As it cannot, however, be made to *record* the induced variation, it was necessary to devise a second method, which would be automatic and would inscribe a record of the effects induced. This has been secured by the Micro-Transpirograph, whose automatic records afford all the necessary information as regards the normal rate of transpiration and its induced variations.

The Micro-Transpirograph

In fig. 30 a reproduction is given of the photograph of a moderately sensitive apparatus. An U-tube filled with water has a float, F, on one side and the transpiring leaf on the other. The free water surface bears a certain thickness of oil to prevent evaporation, the cut end of the short stem bearing the leaves (or the petiole of a single leaf) being immersed in the water below the oil. The float is attached to a recording lever which inscribes the record on a smoked glass plate kept oscillating by a clock-work. For continuous record to exhibit diurnal periodicity, the sensitiveness may be considerably reduced by making the diameter of the U-tube large and reducing the magnification of the recording lever. For researches on the effect of various external agents on the rate of transpiration, the sensitiveness may be exalted to any extent desired (1) by selecting an U-tube with a narrow diameter, and (2) by increasing

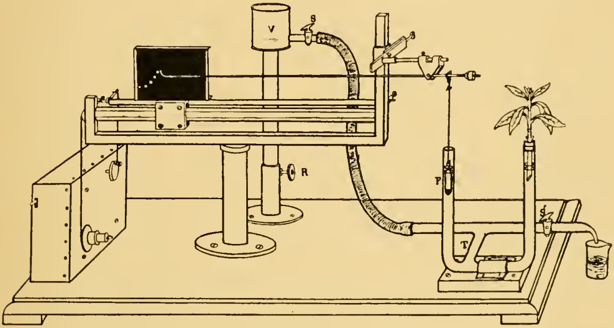

FIG. 30. The Micro-Transpirograph

The transpiring leaf on one side of an U-tube, and a float, F, on the other. The descent of the float caused by transpiration from the leaves is recorded by a writing-lever on a smoked oscillating plate of glass. For obtaining balance, the vessel V is raised or lowered by rack and pinion R. S^1, stop-cock by the manipulation of which the writer may be adjusted at any position on the recording plate.

the magnification produced by the recording lever. For ordinary purposes a magnification of 50 times by a single lever is quite sufficient. But this magnification can be greatly increased, and it is thus possible to record the loss of a milligram of water from the transpiring leaf.

The greatest difficulty encountered in practice is that of the sticking of the float against the side of the U-tube, arising from unequal capillary action at the opposite sides. This may be obviated by making the tube in which the float moves perfectly vertical and preventing rotation of the float. The first is secured by a levelling arrangement of the tube, not shown in the figure. The float is attached to one arm of the lever which moves in a vertical plane ; jewel-bearings reduce its friction to a minimum. The float itself is made of a hollow aluminium tube which is very accurately turned. These precautions remove all difficulties in the perfect working of the apparatus. Subsidence of the float, caused by loss of water by transpiration, gives a record on the smoked glass plate, kept oscillating at intervals of twenty or thirty seconds according to different requirements. The record is taken on a moving plate, and the slope of the curve gives an indication of the rate of transpiration. The effect of any physiological variation is seen in the change of the slope of the curve, or in the widening or shortening of the intervals between the successive dots, the former indicating the enhancement, and the latter the depression of the rate.

There is, however, a far more sensitive method available which enables us to detect not only the immediate but also the after-effect of the external agent. This is the Method of Balance, in which the level of the float at the beginning is maintained constant, the rate of loss by transpiration being exactly compensated by an equal rate of supply. Under these circumstances the record becomes horizontal. The balance is easily secured by the supply of water from the vessel V, the rate of which is roughly adjusted by the stop-cock, the finer adjustment being produced by a slight raising or lowering of the vessel by means of a rack and pinion. The normal rate is shown in the up-curve in the first part of the record of transpiration given in fig. 31; after the establishment of the balance, the record is seen to become horizontal. The leaves were next subjected to a saturated atmosphere by holding a hollow vessel coated with moist blotting-paper over them. The effect of the reduced transpiration is seen in the immediate upsetting of the balance downwards. After the removal of the cylinder the balance became re-established as seen in the record, which again became horizontal. Had the after-effect been one of enhancement, the balance would have been upset in the opposite direction with an upward movement. The horizontality of the record thus denotes recovery to the normal rate.

FIG. 31. The Record of Transpiration, N without, and M with Balance, which is upset downwards by subjecting Leaf for a Short Time to Saturated Atmosphere

Note re-establishment of balance, shown by record becoming horizontal, on restoration to original atmospheric condition.

We have now two independent means, namely, the methods of Bubbling and of the Micro-Transpirograph, for investigating the effect of external agents on transpiration. In some of the following cases both these methods were employed, the results of which will be found to be in perfect agreement with each other. Most of the experiments described below were carried out with a single leaf, with the cut end of the petiole in water.

Effect of Diminution of Turgor

This condition may be artificially induced by a plasmolytic agent. The Bubbling Method was employed. The experiment was made with a leaf of *Nauclea*; the cut end of the petiole was placed in water, and the normal rate of transpiration was determined. On substituting a 2 per cent. solution of glycerin for the water, the effect was found to be a depression of transpiration. The normal activity, 120, of the leaf was reduced to 85 in the course of fifteen minutes. Transpiration persisted at the lower rate during the whole time of the experiment, which lasted for two hours.

The Effect of Stimulus

We shall next study the effect of various modes of stimulation on transpiration. These are, the action of electric stimulus, which could be easily varied from sub-minimal to maximal; the effect of mechanical friction; and the action of light.

Electrical Stimulus.—The effect of this, as determined by the Bubbling Method, has already been described in the last chapter; it was shown that while feeble stimulus induced an enhancement, strong stimulus gave rise to the opposite effect of retardation and arrest. These results are confirmed by the Method of the Balanced Transpirograph. In this a record was first taken after securing exact balance, as shown in the horizontal record. An electric shock of feeble intensity was next applied to the lamina, which is seen to upset the balance in an upward direction, indicating an enhancement of activity (fig. 32, *e*). The restoration of normal activity is seen to have taken place after a certain interval of time, as indicated by the record becoming horizontal.

The effect of a strong stimulus applied at E is seen in the next record (fig. 32, F); the balance is upset downwards, which indicates a depression of transpiration. After a certain interval of time the record is seen to have become horizontal, indicating the restoration of normal rate, and then there was an up-movement of the curve followed by a permanent horizontal record. The result is significant, showing that while stimulus depresses activity, its after-effect may be an enhancement of activity. This was also found to be the case in the record of *Desmodium* pulsation (see fig. 4). The opposite effects of small and of large doses of chemical agents may be regarded as a phenomenon analogous to the above ; a small dose being equivalent to a feeble, and a large dose to an intense, stimulus.

FIG. 32. Effect of Electric Stimulus on Transpiration

(*e*) Enhancement of transpiration under feeble stimulus.
(E) Depression induced by strong stimulus. Note the enhancement as the after-effect, indicated by the subsequent up-curve.

Mechanical Stimulus.—Electric stimulation acts diffusely on the lamina, and it is therefore impossible to apply it locally on the upper or on the under side of the leaf. Mechanical stimulation, however, labours under no such difficulty, and the upper or the lower side may thus be stimulated, one surface at a time. This brought out a very interesting difference in the two responses, as will be seen in the following experiments.

Responses to stimulation of the upper and the lower surfaces.—For this purpose different leaves of *Thunbergia* were taken and the surfaces stimulated by rubbing them with a brush. The experiments were carried out in the following order. The normal activity of transpiration was first determined, after which the upper surface was stimulated, causing an increase in the rate of transpiration. The rate was once more determined after an interval of fifteen minutes, by which time it had returned almost to the original value; this I will designate as the second normal. The lower side was next stimulated, and a diminution was the effect. It was invariably found that while the stimulation of the upper surface induced an enhancement of transpiration, that of the lower surface caused a diminution of the rate. The following are typical results obtained with three different specimens :

TABLE XV.—VARIATION OF TRANSPIRATION BY MECHANICAL STIMULATION OF UPPER AND LOWER SURFACES OF THE LEAF (*Thunbergia*)

Number	Condition of experiment	Transpiring activity	Percentage of variation
I.	Normal	35	
	Stimulation of upper surface .	50	+ 43
	Second normal	38	
	Stimulation of lower surface .	20	− 47
II.	Normal	36	
	Stimulation of upper surface .	48	+ 34
	Second normal	40	
	Stimulation of lower surface .	22	− 45
III.	Normal	88	
	Stimulation of upper surface .	128	+ 45
	Second normal	91	
	Stimulation of lower surface .	35	− 61

Effect of stimulation of upper surface enhanced transpiration by 40 per cent.

Effect of stimulation of lower surface depressed transpiration by 51 per cent.

The important result obtained from the above experiments is that, *under moderate stimulation, the upper and the lower sides of the leaf exhibit responses of opposite sign.* The following considerations may possibly offer an explanation of this difference :

1. The transpiration of the lower surface is the more effective, the excretion from this surface being about four times greater than that from the upper. Now friction of the lower causes a *direct*, and of the upper, an *indirect*, stimulation of the more irritable and effective lower surface. It will be shown (Chapter XVIII) that direct and indirect stimulation often give rise to responses of opposite sign.

2. In a dorsi-ventral organ, the lower side is, generally speaking, more irritable than the upper. Thus in the pulvinus of *Mimosa* the lower side I find to be eighty times the more excitable. There is reason to believe that in the lamina also the excitability is greater on the lower side. Moreover, it has already been demonstrated (p. 93) that while a sub-minimal stimulus induces an enhancement of transpiration, a maximal stimulus retards it. Now an identical stimulus which is sub-minimal for the less excitable upper side of the leaf may prove to be maximal for the more excitable lower side. Hence it is probable that the friction of the upper surface acted as a sub-minimal stimulus, enhancing transpiration, whilst the friction of the under surface acted as a maximal stimulus, retarding it.

Effect of High Frequency Tesla-Current

If one terminal of a Tesla-coil be connected with a plate of metal, the latter becomes charged with oscillatory current several hundred thousand times per second. The space round the plate now becomes the field of alternating lines of electric force. When a leaf is placed in this field, its transpiring activity undergoes a definite variation, as will be seen in the following experiment. A leaf of *Thunbergia* was placed at a distance of 15 cm. from the plate of metal in connection with the Tesla-coil. The normal activity was 29; this was depressed to 22 after exposure to the field of alternating current, the variation being – 24 per cent. On the stoppage of the action of the coil, the leaf recovered its normal rate after an interval of twenty minutes.

Effect of Electric Induction

A plate of metal was held at a distance of 15 cm. above the leaf and parallel to it. The plate was charged by a Wimshurst-machine, alternately with positive and negative electrification. In both these instances the rate of transpiration was found to be increased. Thus in a leaf of *Thunbergia* the normal rate of 38 was enhanced to 54 under electric induction, the increase being 30 per cent. This effect takes place when the plate is held parallel to the leaf so that the lines of induction are perpendicular to the leaf. There is, however, no change in transpiration when the surfaces of the plate and the leaf are perpendicular to each other, that is to say, when the lines of induction are parallel to the surface of the leaf.

In electric culture, the high tension net-work no doubt exerts a statical induction and thus enhances the normal transpiration on which the supply of inorganic food-material to the plant depends. But if the high-tension current were alternating, then the transpiration would undergo a diminution; and the result would be the differential effect of statical induction and of alternating field of electric force. This latter effect may be eliminated by the use of a valve by which an uni-directional current can be maintained.

Effect of Electric Waves

I have shown elsewhere that Hertzian Waves of sufficient intensity diminish the rate of growth.[1] They have a parallel effect in the depression of the rate of transpiration.

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[1] *Life-Movements in Plants*, vol. i.

Thus the normal rate of transpiration in a leaf of *Thunbergia* was 76 ; the effect of Hertzian Waves of short length acting for a minute was to induce an immediate diminution to 68 ; this continued for the next five minutes, by which time it reached the value of 62, the diminution being 18 per cent. After this the leaf exhibited a gradual recovery, and in the course of twenty minutes it attained the normal rate of 76.

Effect of Thermal Radiation

Thermal radiation was produced by means of an electric heating-iron, the heat-rays being allowed to impinge on the leaf. The normal activity of the experimental leaf of *Nauclea* was 63, and the immediate effect was an enhancement of the rate of transpiration to 80 ; this increase continued for ten minutes after the cessation of radiation, the activity being enhanced to 109, or an increase of 73 per cent. The increase is due to the rise of temperature, which has a very pronounced effect in enhancing transpiration. The increase of transpiration under ordinary light is to some extent due to the presence of heat-rays.

Effect of Light

It is supposed that light enhances transpiration, either directly by widening the opening of the stomata or in some other way at present little understood. That the widening of the opening of the stomata under light plays but a subordinate part in enhancing transpiration is made probable by the following considerations :

(1) Bonnier and Mangin found that exposure to light enhanced transpiration in Fungi ; the effect of light is thus independent of the presence of stomata.

(2) In ordinary leaves the transpiration is modified by the action of light on the upper surface which bears no stomata.

(3) The enhancement of transpiration by slight rise of

temperature is more pronounced than that induced by exposure to light. The increase may therefore be more or less due to the heat-rays present in the light

(4) Light does not always induce an enhancement of transpiration ; under definite conditions it causes a diminution.

Action of Light on the Widening of the Stomata and on Transpiration

The following experiments were undertaken to find the relative variation of transpiration due to the widening of the stomata under light. A leaf of *Thunbergia* placed in a dark corner of the room at constant temperature at 30° C. exhibited a transpiring activity of 38. It was next brought near the window and subjected to the action of the stronger diffused light of the sky. This should, according to the generally accepted view, enhance the transpiration by the widening of the stomata under light. The temperature might have been slightly higher near the window, though a sensitive thermometer did not indicate any difference. But in spite of the greater illumination and the possible rise of temperature, the leaf exhibited a *diminished* rate of transpiration which was lowered from the normal 38 to 29, a diminution, that is to say, of 23 per cent. The theory that the widening of the stomata enhances transpiration is thus seen to fail in this particular case, which shows that transpiration is actually diminished under light.

In a second experiment I made continuous observation of the transpiring activity of two different leaves of *Nauclea*, A and B, from 6 P.M. to 6 A.M. next morning. The results obtained were very similar (fig. 33) ; it will therefore be sufficient to give a detailed account of the variation of transpiration in B. The fall of temperature from 6 P.M. to midnight was fairly uniform, from 32·8° C. to 29·8° C., or a fall of half a degree per hour. The transpiring activity declined from 116 to 71·5. It will be noted that the transpiration was still considerable, though the leaf had been subjected to continuous darkness for several hours. The subsequent changes were practically determined by variation of temperature; there was a sudden fall of temperature of half a degree after midnight to which the leaf responded by a diminution of transpiration from 71·5 to 55, *i.e.*, a depression of 23 per cent. At 2.30 A.M. there was a rise of temperature of one-third of a degree, and the trans-

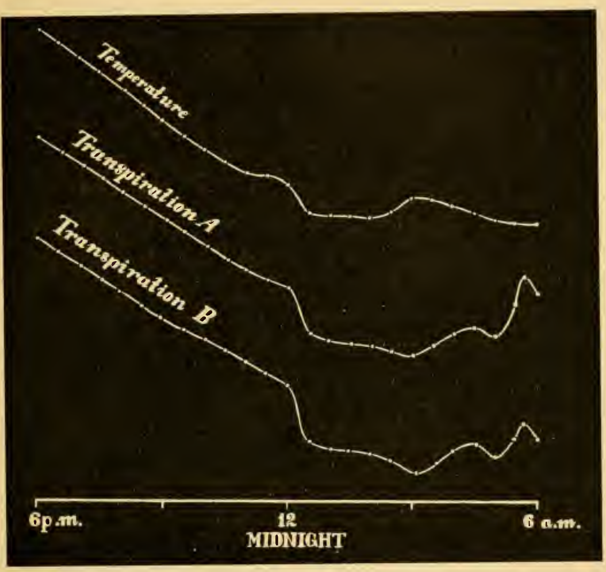

FIG. 33. Curves exhibiting Variation of Transpiration at Night in two Leaves, A and B

Note sudden depression of transpiration by a fall of half a degree in temperature at midnight, and an enhancement of transpiration by a rise of one-third of a degree after 2.30 A.M. Light early in the morning caused a *transient* enhancement of transpiration.

piration exhibited an enhancement of 10 per cent. Light began to appear at 5 A.M.; this induced a transient rise, which subsided after a time, and the curves of temperature and of transpiration subsequently followed a parallel course.

The experiments described above show (1) that the effect of rise of temperature on transpiration is far more pronounced than that of light; (2) that the heating effect of light may often account for increased transpiration; and (3) that *light sometimes induces a diminution of transpiration instead of an enhancement.*

Light as Stimulus

The pulsation of *Desmodium* is arrested by exposure to strong light, which also retards or arrests growth. We have seen, moreover, that while moderate stimulus retards growth, a feeble stimulus enhances it. The growth of a less excitable sub-tonic tissue exhibits acceleration under an intensity of light which in a more excitable tissue would induce retardation (p. 17).

As regards the relative effectiveness of various rays in retarding growth, it is known that while the more refrangible rays of the spectrum, blue and violet, are highly effective, the red rays at the opposite end of the spectrum are less effective or ineffective.

Bearing these facts in mind, I undertook the following experiments with the object of ascertaining whether or not the process of transpiration responds to the action of light of different wave-length in the same manner as the process of growth.

Light-filter for Red and Blue-violet Light

In order to determine the relative effect of the less refrangible red at one end of the spectrum, and of the more refrangible blue-violet rays at the other, I at first employed a bichromate of potash solution as a light-filter to separate the former, and an ammoniated solution of copper sulphate for the latter. The results I obtained with these filtered lights were often found to be anomalous: in consequence, as I discovered later, of the impure character of the light, due to the overlapping of the spectra. The light transmitted through the bichromate solution contains red, orange, yellow and green, while that transmitted through copper sulphate includes green, blue and violet rays. I therefore made special light-filters with coloured glasses which gave red in the region of Fraunhofer's lines B and C, the wave-lengths being from 680 to 600 $\mu\mu$; and blue-violet light in the region of Fraunhofer's line G, the wave-lengths being from 460 to 380 $\mu\mu$. I thus obtained two spectral lights widely separated from each other.

The source of light was an incandescent electric lamp of 200 candle-power. This was used in preference to the arc-lamp, the light from which cannot be maintained constant, which radiates a very large amount of heat-rays. The incandescent lamp was placed inside the lantern and a slightly divergent beam was allowed to fall on the leaf for a definite length of time by manipulating a shutter. The interposition of the colour-screen and a parallel-sided glass trough filled with alum-solution eliminated the heat-rays. The room was kept in perfect darkness.

The Effect of Red and Blue-violet Rays on Transpiration

The mode of procedure in the following experiments was: (1) the observation of the normal rate in darkness; (2) observation of the effect of exposure to blue-violet light for five minutes; (3) observation of recovery which was practically complete in the course of twenty minutes; (4) the effect of exposure to red light for five minutes; (5) the observation of recovery to normal after twenty minutes ; (6) the effect of exposure to blue-violet light for the second time.

A complete cycle of operations was thus carried out with a particular leaf. In other cases the order of procedure was reversed, that is to say, the observation was taken first with red, and afterwards with blue-violet light.

The following is the detailed account of a typical experiment. The normal transpiring activity of a leaf of *Thunbergia* in the dark was found to be 45. On exposure of the more sensitive lower surface for five minutes to blue-violet light, *the rate of transpiration underwent a diminution to* 36, *or a variation of* – 20 *per cent.* On the cessation of exposure, the normal rate of 45 was restored in the course of twenty minutes. *Red light was next applied for five minutes, and this caused an enhancement of rate to* 59, *or a variation of* 31 *per cent.* After an interval of twenty minutes, recovery was nearly complete, the rate being 42. Exposure to blue-violet light was resumed for five minutes ; this caused a depression to 33, *i.e.*, a variation of – 21 per cent. ; this is practically the same as the variation of – 20 per cent. obtained at the beginning of the series.

The table on p. 113 gives the results obtained with three other specimens of *Thunbergia* and one specimen of *Nauclea*.

In all the cases given above, it was invariably found that the blue-violet light, which is effective in inducing a retardation of growth, also caused depression in transpiration ; red light, which is ineffective in retarding growth, acted like a sub-minimal stimulus, inducing an enhancement of the rate of transpiration. These results show that the average depression under blue-violet light was about – 36 per cent., the mean acceleration under red light being about + 68 per cent.

I also experimented on the effect of stimulation of the less excitable upper surface of the leaf : curiously enough, this gave responses similar to those obtained by mechanical stimulation of the two sides, but reversed. In this experiment, the blue-violet light acting on the upper side caused an acceleration of transpiration, while the red induced a depression. The effects produced were, however, feeble compared to those induced by the stimulation of the more excitable lower side: the increase of transpiration caused by blue-violet light was + 4·5 per cent. of the normal, the depression by red being 9 per cent.

Table XVI.—Showing the Variation of Transpiration under Red and Blue-violet Light for Exposures of Five Minutes

Specimen	Light	Transpiring activity	Percentage of variation
1. *Thunbergia*	Normal	24	..
	Red light	42	+ 75 per cent.
	Blue-violet	17	− 29 ,,
2. *Thunbergia*	Normal	34	..
	Red light	51	+ 50 per cent.
	Blue-violet	25	— 27 ,,
3. *Thunbergia*	Normal	82	..
	Red light	116	+ 41 per cent.
	Blue-violet	50	— 33 ,,
4. *Nauclea*	Normal	124	..
	Red light	300	+ 142 per cent.
	Blue-violet	40	— 68 ,,

We study next the effect of various anæsthetics on transpiration; of these carbonic acid gas may be taken as the mildest; chloroform, on the other hand, as the most intense and toxic after long application.

The Effect of Carbonic Acid

A broad inverted funnel was made to enclose the transpiring leaf. After measuring the normal rate of transpiration of a leaf of *Nauclea*, a glass jar containing carbonic acid was emptied over the funnel. This increased the transpiration almost three-fold, from the normal 28 to 70, after the application of the gas. Continued application of the gas, however, caused a slight depression compared with the normal. In another specimen of the *Nauclea* leaf, the first effect was an enhancement from the normal 106 to 133 ; continued action of the gas induced a depressed activity of 100. I may here describe the remarkable effect of moderately high temperature in modification of the above effect. The result described above was in winter, in January of the present year. The experiment was repeated in May, when the room temperature was 32° C. The preliminary effect of enhancement was now practically absent, and the rate of transpiration became depressed from the beginning under the action of the gas. Thus in a given experiment with *Nauclea* the normal rate of 200 was depressed to 163 in the course of a few minutes.

Fig. 34

Fig. 35

Fig. 34. Effect of Carbonic Acid Gas in Enhancing the Rate of Transpiration

Fig. 35. Effect of Ether ; Preliminary Enhancement followed by Depression

The enhanced transpiration under carbonic acid is shown in a record (fig. 34) of the balanced Transpirograph, in which the balance is upset in an upward direction.

The Effect of Ether-Vapour

The vapour of ether was applied in a manner similar to the above. The immediate effect was an enhancement of transpiration as seen in the upset of the balance upwards, followed by depression under the continued action of the anæsthetic as seen in the down-curve (fig. 35).

The Effect of Chloroform

Finally, I studied the effect of chloroform-vapour on the transpiring lamina. This is seen to induce a great depression of the rate, as indicated by the upsetting of the balance downwards (fig. 36). In another experiment, dilute chloroform was applied to the cut end of the petiole by a side-tube. This internal application also caused a great depression of transpiration, as seen in the right-hand record. The results of applications of the anæsthetic to the lamina and to the petiole are thus identical.

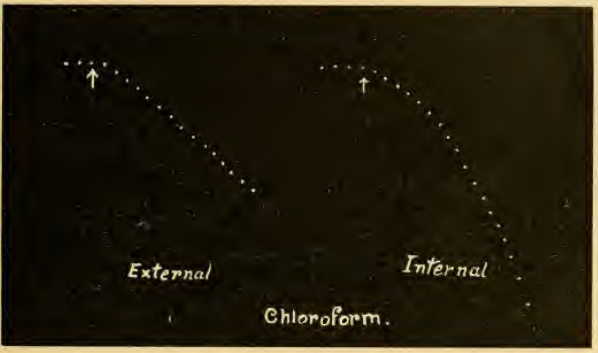

FIG. 36. Effect of External and Internal Application of Chloroform in depressing Transpiration

SUMMARY

Transpiration and its induced variations can be automatically recorded by the Micro-Transpirograph.

Plasmolytic agents applied at the cut end of the petiole induce a diminution of transpiration of the leaf.

Application of feeble electric stimulus to the lamina causes an enhancement, while stronger stimulus induces a depression or arrest of transpiration; the after-effect of a moderately strong stimulus is often an enhancement of transpiration above the normal.

Mechanical stimulus of moderate intensity applied to the upper surface of the leaf induces an enhancement of the rate of transpiration; the same stimulus applied to the more sensitive lower surface causes a depression of the rate.

The activity of transpiration is depressed when the leaf is placed in a field of rapidly alternating electric force. Electric waves also induce depression.

Statical electric induction, both positive and negative, enhances the rate of transpiration.

Rise of temperature of the leaf caused by thermal radiation enhances the rate.

The effect of light is complex on account of the presence of two antagonistic factors: of heat-rays which enhance transpiration, and of light-rays which, acting as a stimulus, retard it.

The rays at the two extreme ends of the spectrum affect transpiration in opposite ways. The action of blue-violet light on the under side of the leaf causes diminution; that of the red rays causes enhancement. The action of light on the upper surface of the leaf induces an effect opposite to that of its action on the lower surface.

Carbonic acid induces an enhancement of transpiration; long-continued action induces a depression.

Ether induces a preliminary enhancement followed by depression.

Chloroform depresses the transpiring activity of the lamina. The same effect is induced by application of dilute chloroform to the cut end of the petiole.

The above experiments offer independent proof that transpiration is, essentially, not a physical but an active physiological process.

CHAPTER VIII

THE DIURNAL VARIATION OF TRANSPIRATION

Diurnal variation of transpiration in plants with roots—Diurnal variation after removal of the root—The Radiograph—Diurnal variation of temperature and of light—Balancing evaporation against transpiration—The Differential Balance—The optimum-temperature for transpiration—Summary.

HAVING studied the effect of physiological variations on transpiration, we may attempt to ascertain if the rate of transpiration undergoes a daily variation. Should this prove to be the case, it will be necessary to determine the external changes to which this variation is due.

For the purposes of this investigation it is necessary to obtain a continuous record of the transpiration for twenty-four hours. The self-recording Transpirograph, already described, may be used for this purpose, taking the precaution of reducing its sensitiveness to a considerable extent, for the record would otherwise go off the plate. The sensitiveness may be diminished to any extent desired by increasing the diameter of the tube at the opposite ends of which the plant and the recording float are adjusted. The apparatus was fixed in a place free from vibration, the leaves being exposed to the light of the sky, but not to direct sunlight. Two separate records with two specimens of *Chrysanthemum* were taken simultaneously on the same plate, which was allowed to fall down vertically at an uniform rate by means of a clockwork. It was not necessary to move the plate laterally for obtaining the time-record, since this was secured by the dots in the record produced by the oscillation of the recording plate at definite intervals of half an hour. The distance between the successive dots then affords a striking indication of the relative rapidity of transpiration at different periods of the day. The general similarity of the two records affords strong evidence that the result is not accidental, but is due to similar physiological changes in both.

Diurnal Variation of Transpiration in Plants with Roots

The record for twenty-four hours obtained with *Chrysanthemum* with root is given in fig. 37. The vertical record is reproduced as horizontal for convenience of inspection. The successive dots, as already stated, are at intervals of half an hour, and the enhanced rate of transpiration is seen in the widening of the spacings. The upper record represents the transpiration from 10 A.M. to 4 P.M., *i.e.*, for six hours, and the lower record from 4 P.M. to 10 A.M. next morning, that is to say, for eighteen hours. The distance covered is the same in the two records, hence the average transpiration between 10 A.M. and 4 P.M. was three times quicker than that between 4 P.M. and 10 A.M. We also find that the maximum transpiration occurred at 2 P.M., which was also the thermal noon, or the period of temperature maximum; the minimum transpiration coincided with the temperature minimum between 4 and

FIG. 37. The Record of Diurnal Variation of Transpiration (*Chrysanthemum*)

5 A.M. The rate was 1·7 c.c. per hour at 6 A.M.; it increased with the rise of temperature; at midday it was 9·8 c.c.; the maximum temperature at or about 2 P.M. was also the period for maximum transpiration, which was 12·9 c.c. After this the temperature fell and the rate of transpiration also declined; at 4 P.M. it had fallen to 9·8 c.c.; the minimum transpiration of 1 c.c. was attained at or about 5 A.M. The maximum transpiration at thermal noon was thus about thirteen times that at thermal dawn.

Diurnal Variation after Removal of the Root

The record was continued for the next twenty-four hours, but now after the removal of the root. We observe a diurnal variation similar to that in the last experiment, but with a general enhancement of the rate. Thus the ratio of the maximum transpiration of the plant with the root and without it was 12·9 : 22·3. The ratio at the minimum temperature at 5 A.M. was 1 : 1·5. The transpiration of the shoot was thus increased to about 1·7 times after the removal of the root.

The table on p. 121 gives the rates of transpiration for twenty-four hours of the plant with and without root. The curves in fig. 38 also show the relative rise and fall of the rates in the two cases; the lower curve with the root, and the upper curve after the removal of it. The rate of transpiration at every hour of the day and night was relatively greater after the removal of the root.

What, now, is the cause of this difference in transpiratory activity? The answer to this question will also solve the difficulty concerning the disparity between the amount of water absorbed by the root and the power of the stem to conduct and the leaves to transpire it. That this is regarded as anomalous, is clear from the following quotation:

'We may imagine that the water was forced up by root-pressure. . . . But the question at once rises as to whether the amount of water supplied by the root is approximately enough to replace what is lost by transpiration. Some experiments carried out by Sachs (1873) are worthy of consideration on this latter point. He compared the amount of sap given off in a definite time from the root of a herbaceous plant, with the amount sucked up by the shoot, whose cut end had been submerged. A root-stock of *Nicotiana latissima* gave off about 16 c.cm. of sap in five days, but its shoot absorbed 200 c.cm. A similar disparity was exhibited in other cases also. Further, it is very improbable that the secretory capacity of the root is sufficient of itself to compensate for loss of water due to transpiration.' [1]

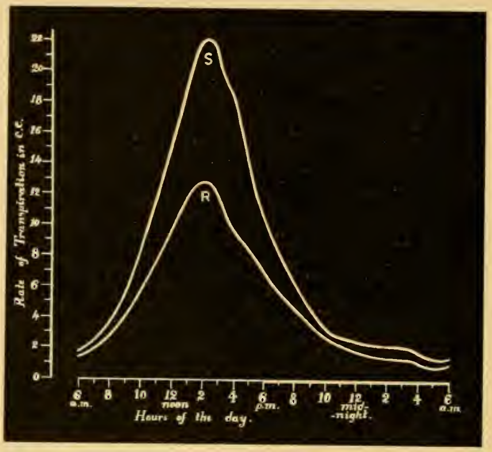

FIG. 38. The Diurnal Curve of Transpiration
The lower is the record of *Chrysanthemum* with root; the upper, of the shoot without root.

The apparent anomaly arises from the erroneous supposition that transpiration from leaves is merely a phenomenon of physical evaporation. It has been shown,

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[1] Jost, *Plant Physiology*, English translation, p. 63.

however, that it is effected by the activity of living cells, not only of the terminal layers from which excretion actually takes place, but also of a system of cells extending throughout the plant from the absorbing root to the excreting leaf. There is thus a co-ordinated physiological mechanism such that each region of the plant controls and is controlled by the rest. Examples of this have already been described, where drought, by depressing the cellular activity, affected not only the absorption by the root, but also the conduction of sap through the stem and the transpiration from the leaves.

Thus an increased absorption in one region affects the rate of ascent or of excretion in a different region. The root-hairs by their attenuated channels offer great resistance to the inflow of water into the plant. Consequently the removal of the root accounts for the enhancement of the quantity of water absorbed, as in Sachs's experiment, and of the transpiration from the leaves, as seen in Table XVII.; for the root (on which the supposed root-pressure depends), far from increasing the rate of ascent, actually impedes the flow of sap.

TABLE XVII.—SHOWING THE ABSOLUTE RATE OF TRANSPIRATION FOR 24 HOURS IN *Chrysanthemum*, WITH AND WITHOUT ROOT

Time	Rate of transpiration		Time	Rate of transpiration	
	With root	Without root		With root	Without root
6 A.M.	1·7 c.c.	1·9 c.c.	6 P.M.	7·1 c.c.	10·3 c.c.
7 ,,	2·3 ,,	2·7 ,,	7 ,,	5·9 ,,	8·5 ,,
8 ,,	3·4 ,,	4·2 ,,	8 ,,	4·8 ,,	6·4 ,,
9 ,,	4·6 ,,	5·8 ,,	9 ,,	3·8 ,,	4·9 ,,
10 ,,	6·0 ,,	8·6 ,,	10 ,,	3·0 ,,	3·6 ,,
11 ,,	7·7 ,,	12·2 ,,	11 ,,	2·4 ,,	2·8 ,,
Noon	9·8 ,,	15·6 ,,	Midnight	2·0 ,,	2·5 ,,
1 P.M.	11·8 ,,	20·2 ,,	1 A.M.	1·7 ,,	2·4 ,,
2 ,,	12·9 ,,	22·3 ,,	2 ,,	1·5 ,,	2·3 ,,
3 ,,	12·0 ,,	20·5 ,,	3 ,,	1·4 ,,	2·2 ,,
4 ,,	9·8 ,,	17·8 ,,	4 ,,	1·2 ,,	1·8 ,,
5 ,,	8·5 ,,	14·2 ,,	5 ,,	1·0 ,,	1·5 ,,
6 ,,	7·1 ,,	10·3 ,,	6 ,,	1·2 ,,	1·6 ,,

The Radiograph

We shall next attempt to determine the cause of the diurnal periodicity of transpiration. We have here two variables, namely, the daily variation of temperature and the recurrent change of light and darkness. The daily variation of temperature was recorded by a thermograph placed near the transpiring leaf: but there was, unfortunately, no apparatus available for the continuous record of the variation of light.

This difficulty was, however, overcome by an apparatus which I have devised for the automatic record of variations in the intensity of light.[1] Selenium exhibits a diminution of resistance under light, and the increasing deflection given by a galvanometer in circuit with a battery of voltaic cells gives an indication of the increasing intensity of light. But the continuous passage of a current gives rise to a counter electromotive force, and the selenium-cell then becomes unreliable. For overcoming this difficulty, the photo-electric cell was placed in the fourth arm of a Wheatstone-bridge, so that there was no deflection in the galvanometer under condition of balance in darkness. A vertical tube projects over the selenium-cell, which is closed with an electro-magnetic shutter. The battery of cells is normally cut off from the circuit, which is closed at definite intervals by a clockwork which actuates three keys in succession. By these means the battery is closed, the shutter of the selenium-cell is opened, and the deflected index of the galvanometer is recorded on a moving piece of paper. The keys are then automatically opened, and the process repeated at definite intervals of time, which may be varied from five minutes to an hour.

I reproduce curves of diurnal variation of temperature and of light taken in March (fig. 39), which will give a general idea of the hourly changes. In summer the light

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[1] The detailed account of the Radiograph will be given in vol. iii. of the *Transactions*, Bose Institute.

appears about an hour earlier, and disappears an hour later; in winter the day is shorter by about two hours. The temperature-curve shows a steep rise, attaining its maximum at the thermal noon, about 2 P.M.; the fall is more gradual, and the minimum temperature is attained between 5 and 6 A.M. The above is true in settled weather conditions; in unsettled weather there are fluctuations in the diurnal curve.

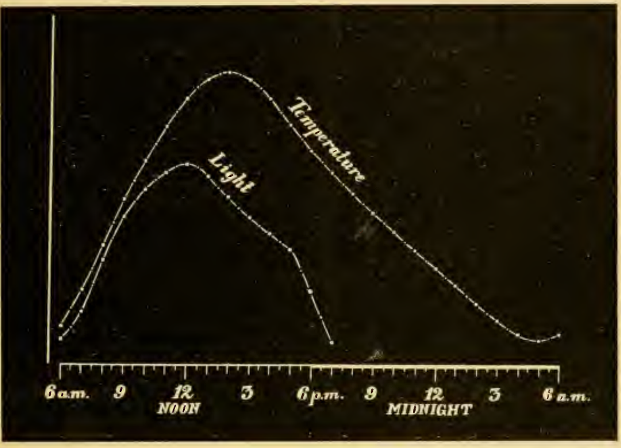

FIG. 39. The Curves of Diurnal Variation of Light and of Temperature

As regards light, there is a very steep rise in intensity during the forenoon, the maximum being attained at noon; the thermal noon, as already stated, is later by about two hours. There is a steady decline in intensity from noon to 4 P.M., after which the fall is abrupt till the total disappearance of light after 6 P.M.

Comparing the transpiration-curve with those of light and temperature, we find that the effect of light is practically negligible. The maximum light is at noon, but the maximum transpiration occurs two hours later, at the thermal noon. The similarity of the curves of transpiration and of temperature is, moreover, very striking. This proves that the diurnal variation of transpiration is mainly due to the periodic change of temperature.

The question next arises as to whether the increase of transpiration with the rise of temperature is simply due to increased evaporation, or whether a physiological element also enters into the problem : for rise of temperature enhances not only evaporation but physiological activity also. Hence it becomes necessary to distinguish the effect of one factor from that of the other by some discriminating test. Evaporation no doubt helps indirectly in the uni-directioned ascent of sap by maintaining the turgor-gradient. But the independent factor of physiological activity in transpiration may exhibit a course which is not exactly parallel to that of evaporation.

The Differential Balance

It is possible to discriminate between evaporation and transpiration by balancing one against the other. This is done by placing the transpiring leaf on one pan of a balance, say the right, an equivalent area of water-surface being placed on the left pan for evaporation. It has been shown (p. 87) that the equivalent area of water is about one-fifth that of the leaf-surface of *Thunbergia*. But for our present purpose it is necessary to obtain not an approximate but a very exact balance. This is secured by the Surface-Variator which will be presently described. By this adjustment the loss by evaporation from the water-surface in the one pan is made to balance exactly the loss by transpiration from the leaf placed in the other pan.

If transpiration be a simple phenomenon of evaporation, then the loss at the two pans of the balance will be equally affected by variations of temperature, and the index of the balance once adjusted to zero will always remain there. But the index is found to be upset in one direction or the opposite according to the variation of

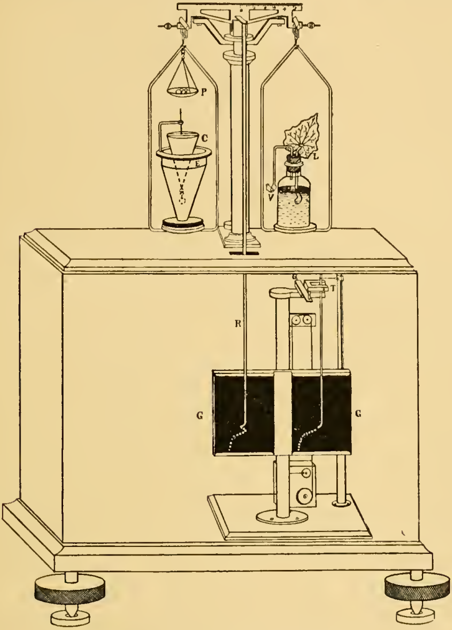

Fig. 40. The Differential Balance

The Surface Variator, C, seen on the left pan of the balance. A vertical wire from C passes through a guide-hole in the bent piece of metal. P, the upper pan containing shots for transference to C. The right pan contains the transpiring leaf L, mounted in a vessel with a side-tube with an oil-valve. G, plate for recording movement of index R of the Differential Balance. On the right-hand smoked glass is recorded the variation of temperature.

temperature. This proves that transpiration is not the same as evaporation, but that an additional physiological factor is involved in the process.

The Differential Balance is shown in fig. 40. On account of the various sizes of the leaves and their different physiological condition, it is not easy to obtain an exact balance between evaporation and transpiration. This difficulty has been overcome by the device of the Surface Variator, which consists of an inverted cone floating in a beaker of water : the area of the evaporating surface may be continuously varied by varying the depth of immersion of the inverted cone used as a sinker. The cone is sunk by the addition of small shots. After obtaining a balance of weights on the two sides of the balance, the shots, which are kept on the small upper pan, are transferred to the sinker. The balancing thus remains the same, the change produced being only in the area of the evaporative surface of water. The exact balancing of transpiration against evaporation at any definite temperature may be secured by this contrivance without any difficulty. The long index records any variation in the balance throughout twenty-four hours. The record is taken on a small glass plate which oscillates to and fro at intervals of half an hour. The record of diurnal variation of temperature is also taken on a second plate ; for this the usual metallic thermometer is employed. For prevention of disturbance of the index by air-currents, it is necessary to place a cover over the apparatus. For this a glass cover is not suitable, since it interferes with the free evaporation and transpiration ; fine netting was therefore substituted for glass in the cover. The whole apparatus was placed in a large greenhouse.

The record of the differential result of transpiration balancing evaporation is given in fig. 41. The transpiration from a leaf of *Thunbergia* was exactly balanced at 5 P.M. The index did not, however, remain in the zero position, but drifted to the left till next morning, indicating a depression of transpiration compared with evaporation. Comparison with the thermographic record brought out the interesting fact that this relative depression of transpiration occurred during the fall of temperature. When the temperature began to rise next morning, the index began to return to zero. As the temperature rose further, the balance became displaced once more, but this time to the right, showing that the transpiration was relatively increased with the rising temperature. This increase was, however, arrested as the temperature rose above 33° C.; at 34° C. the balance was upset to the left. The curve of relative enhancement of transpiration which had hitherto

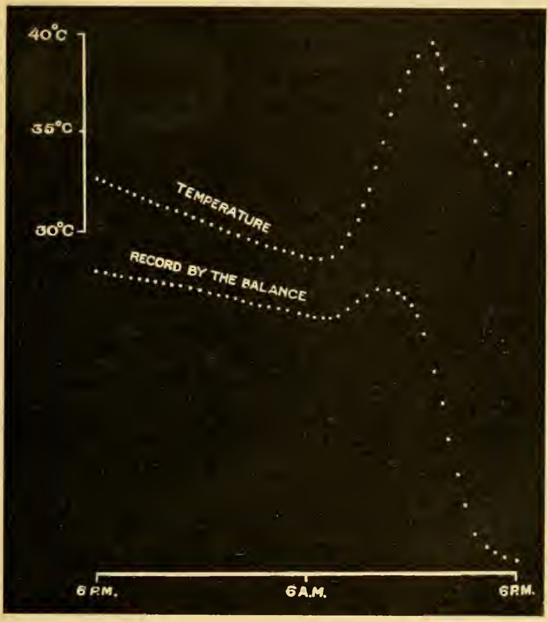

FIG. 41. Diurnal Record of Transpiration balancing Evaporation

Note the drift of the balance index to left (downwards in the Fig.) with falling temperature, indicating relative diminution of transpiration, rise of temperature inducing opposite effect. Reversal of curve above optimum-temperature of 33° C.

followed the rise of temperature became reversed above 33° C. This showed that the transpiration exhibited a relative increase up to that temperature, above which there was a decline.

The Optimum Temperature for Transpiration

This upsetting of the balance at about 34° C. at first appeared inexplicable; further experiments showed that transpiration reaches its maximum at an optimum temperature. For an independent demonstration of this I took a leaf of *Thunbergia*, mounted on the Bubbler, and placed it in the conservatory, where the previous record had been obtained with the Differential Balance. The light in the conservatory was practically uniform in the forenoon, but the temperature exhibited a gradual increase from 31·5° at 10 A.M. to 33·5° at 11.30 A.M. The transpiring activity of the leaf was taken for each half degree rise of temperature. The following table gives the result of the experiment.

TABLE XVIII. SHOWING THE OPTIMUM DEGREE OF TEMPERATURE FOR TRANSPIRATION (*Thunbergia*)

Temperature	Activity of transpiration
31·5° C.	45
32·0° ,,	50
32·5° ,,	62
33·0° ,,	71
33·5° ,,	52

It is thus seen that the transpiration of the leaf was increased continuously from 45 to 71, as the temperature rose from 31·5° to 33°. A sudden decline from 71 to 52 occurred as the temperature rose from 33° to 33·5°. The temperature of 33° may therefore be regarded as the optimum temperature for transpiration in the leaf of *Thunbergia*.

We thus demonstrate a phenomenon which discriminates transpiration from evaporation. Evaporation is continuously increased with rise of temperature, but transpiration is enhanced up to an optimum point beyond which there is a decline.

Since the autonomous activity of growth has a definite temperature-optimum beyond which it undergoes a decline, it is very interesting to find that transpiration also exhibits an optimum, the existence of which is a remarkable demonstration that pulsatory activity underlies transpiration.

In conclusion, we have now evidence of the existence of a physiological mechanism by which the absorption, the conduction, and the transpiration of water are automatically regulated, and the life of the plant maintained. During excessive drought caused by summer heat and intense sunlight, the following regulating devices are brought into play. The excessive loss of water is prevented, first, by the enfeebled rate of ascent of sap that is induced by drought (p. 45) ; secondly, by the stimulus of strong sunlight which retards conduction along the stem (p. 47) ; and finally, by the rise of temperature, which, though it continuously increases evaporation, interposes a physiological check on transpiration when it exceeds the optimum. It is indeed remarkable that the physiological activity which maintains the ascent of sap and the process of transpiration should possess automatic powers of regulation by which the plant is enabled to survive periods of severe drought.

SUMMARY

Transpiration exhibits a diurnal variation which is principally determined by the daily variation of temperature. Transpiration is at its maximum at thermal noon and at its minimum at thermal dawn. The effect of variation of light is comparatively slight.

There is a continuity of physiological action throughout the plant, in consequence of which each part of the plant controls and is controlled by the rest. Transpiration is thus increased with the enhancement of the ascent of sap resulting from the removal of the root.

The relative effect of physical evaporation and physiological transpiration is determined by balancing evaporation against transpiration by means of the Differential Balance. It is thus found that, with rising temperature, transpiration is relatively greater than evaporation.

Transpiration exhibits an optimum temperature which in *Thunbergia* is 33° C. Above the optimum degree the activity of transpiration, like that of growth, undergoes a rapid decline.

The foregoing characteristic discriminates transpiration from evaporation. Evaporation is continuously increased by rise of temperature, but transpiration is enhanced only up to an optimum, above which there is a depression.

CHAPTER IX

EXUDATION BY THE ROOT-STOCK

The Recorder of Exudation—The Tilter and the Electromagnetic writer—Composition of exuded sap—Continuous record of exudation—Effect of drought—Effect of mechanical and electrical stimulus—Effect of poison—Effect of anæsthetics—Continuity of action in root and in shoot—Activity of terminal layer at the cut end—Expulsion of sap by living cells—Summary.

HAVING studied the relation to the ascent of sap of the activity of the excretory organ, the leaf, at the upper end of the plant, we pass on to consider that of the absorbent organ, the root, at the opposite extremity.

It commonly happens, when a plant is cut across at the level of the ground, that liquid is exuded, sooner or later, at the cut surface of the root-stock. This exudation of sap is attributed to a force generally termed 'root-pressure'; it is this that has been investigated with results now to be given.

We approach the subject with the conviction that the conclusions already reached concerning the movement of the sap in the stem are equally applicable to the root. The absorbed water is pumped from cell to cell; and when the rate of absorption is too rapid for this physiological conduction, the excess water is pumped into the wood-vascular tissue in which it is driven upwards by an increasing 'intra-vascular' pressure, to escape when the root-stock is cut across. The value of the intra-vascular pressure depends upon the relation between absorption and transpiration: when the former is the more active, the pressure is positive; when the latter, it is negative.

The Recorder of Exudation

The varying activity of the root-cells may be gauged by the measurement either of the rate of exudation[1] from the root-stock, or of the pressure exerted by the ascending sap ; the latter method of measurement will be described in the next chapter. It is of essential importance to be able to obtain a continuous record of the rate of exudation, so that any induced charge in it can be referred to some definite variation in the environmental conditions.

I have been able to perfect an apparatus by which the normal exudation and its induced variations may be recorded. It consists of a Tilter, an Electromagnetic Writer, and a Revolving Drum round which is wrapped a sheet of smoked paper for the inscription of the record (fig. 42). The cut end of the root-stock is enclosed water-tight in an india-rubber cork, and a glass tube led from it allows the drops of exuded sap to fall on to a contrivance by which they are counted electrically.

The Tilter.—This consists of a delicately poised lever, one end of which is spoon-shaped for catching the exuded drops of water. The balanced lever, when upset by the falling drops, empties the liquid into the vessel V, and at the same time completes an electrical circuit, in consequence of which a dot is marked on the revolving drum by the Electromagnetic Writer. The tilting lever is balanced by a sliding weight, which allows adjustment to be made within wide limits. The sensitiveness can be so exalted that it is possible to obtain a record of the fall of a single grain of sand.

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[1] I have, in the absence of better phraseology, used the terms 'exudation,' 'exudation-pressure,' and 'root-pressure.' Root-pressure is, however, not due to any specific action of the root, but to the co-ordinated activity of pulsating cells common to both root and shoot ; 'cell-pressure' would be a better term. Again, 'exudation' rather suggests a passive process ; but the expulsion of liquid from the living cells of the plant is an active process. 'Excretion' is a better term ; but it has become associated with the expulsion of undesirable waste-products, a distinction that is purely gratuitous.

The Electromagnetic Writer.—This consists of a horseshoe electro-magnet with a polarised armature to which is attached the vertical marker. Only a feeble current is required for actuating the Writer; a couple of dry cells is found sufficient for the purpose. The duration of electric contact is short, hence the current drawn from the cells is very small.

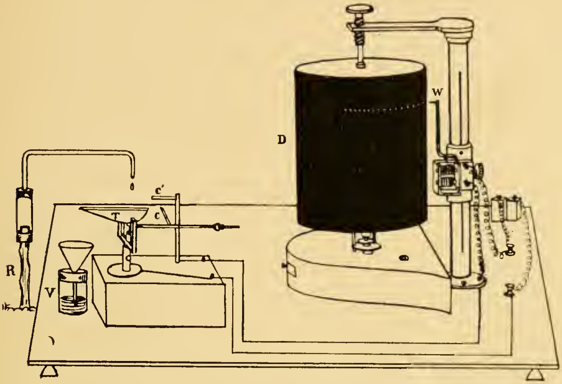

FIG. 42. The Tilter and Recorder

Exuded drops fall on the tilting lever T from the tube attached to the root-stock R by means of an india-rubber cork. The upsetting of the Tilter completes an electric circuit, causing the Electromagnetic Writer to inscribe a dot on the smoked paper wrapped round the revolving drum D. V, vessel for reception of the exuded sap from the tilter.

The Recording Drum.—The drum has three speeds of rotation: one revolution in an hour, or in twelve hours, or in twenty-four hours. A smoked paper is wrapped round the drum, and the strokes of the writing-point inscribe the successive dots. The Writer, if desired, may be made to carry a soft pencil for the inscription of marks on white paper. The Recording Drum may be placed inside the laboratory at a considerable distance from the plant grown under field-conditions: the electric connection with the Tilter is then made by means of sufficient lengths of line-wire. It is easy to obtain simultaneous records of four different root-stocks on the same drum : the necessary adjustment is the employment of four electro-magnetic writers placed one over the other

Portable Apparatus.—It was sometimes necessary to have a self-contained and complete set of apparatus for obtaining records of exudation of sap by Palms in a place out of the way. Such a compact apparatus is contained in a cubical box, each side of which is only 15 cm. The box can be locked, and strapped to the tree, out of reach. The apparatus requires little attention, and the automatic records are taken out at intervals of 24 hours.

Each dot in the record represents the exudation of a definite quantity of sap, and the distance between the successive dots represents the time required for the exudation of this quantity. Hence the rate of exudation at any moment can easily be determined. The record itself gives a vivid picture of the normal rate and its induced variations. Enhancement of the rate reduces the distance between successive dots, while depression induces the opposite change of widening the intervening distance.

For experiments lasting a few hours the rate of the complete revolution of the drum is adjusted to once in an hour, the length of the recording surface being 300 mm. Successive marks when recorded by drops falling at intervals of, say, six seconds, are a little over 1 mm. apart. It is more convenient to have the successive dots marked for every three drops, in which case the dots are 3 mm. apart ; the adjustment of the counterpoise on the Tilter allows this to be done with great precision. The weight of the three accumulated drops causes a sudden tilt of the lever by which the water is completely emptied into the vessel V, after which the Tilter assumes its normal horizontal position. The following precautions should be observed for accurate work : the plant should be so placed that the drops fall near the fulcrum of the lever, to avoid upset of the lever by the momentum of the falling drop. Another precaution is to prevent the adhesion of any remnant of the exuded drop to the spoon-shaped receptacle : the maintenance of a very clean and even surface removes this source of error.

In long-continued experiments, say, for the determination of the diurnal periodicity, the Electromagnetic Writer is arranged to subside vertically through 10 cm., which is the height of the drum, in the course of twenty-four hours. The record is in the form of a spiral, its total length being 720 cm., too long for reproduction in a book. To obviate this difficulty, the drum is adjusted to a speed of revolution of once in twenty-four hours. The period of successive tilting of the lever is also appropriately modified by moving the sliding counterpoise, so that successive electric contacts are made on the exudation of every 5 to 10 c.c. of sap. The Tilter empties the exuded liquid into the vessel placed underneath ; this serves as an independent check for the total quantity of exudation during twenty-four hours.

I have carried out experiments on exudation with numerous plants ; those with *Cucurbita* and *Zea Mays* may be regarded as typical. In *Cucurbita* the root-system is very extended and, generally speaking, buried deep in the soil : in *Zea Mays*, on the other hand, the root is nearer the surface and does not cover a large area.

The Composition of the Exuded Sap

The sap exuded contains inorganic and organic substances in solution. I shall give later the composition of the exuded sap of Palm trees, which contains a large quantity of sugar. The following is the result of the analysis of the exudate from *Cucurbita* and *Zea Mays*.

TABLE XIX.—ANALYSIS OF EXUDED SAP

Cucurbita	Quantity exuded in 24 hours	100–500 c.c.
	Total quantity of solid in 100 c.c. after evaporation	0·33 gram.
	Mineral solids in 100 c.c.	0·175 ,,
	Organic matter burnt off during ignition in 100 c.c.	0·155 ,,
	CaO (lime) in 100 c.c.	0·036 ,,
	Phosphoric anhydride in 100 c.c.	0·080 ,,
	Soluble alkali salts in 100 c.c.	0·014 ,,
Zea Mays	Quantity exuded in 24 hours	10–15 c.c.
	Sugar in 100 c.c.	0·5 gram.
	Total quantity of solid in 100 c.c. on ignition of residue after evaporation	0·15 ,,
	CaO (lime) in 100 c.c.	0·41 ,,
	Phosphoric anhydride in 100 c.c.	0·05 ,,

Continuous Record of Exudation

The normal rate of exudation was found to remain constant under uniform external conditions, for the record obtained with a root-stock cut close to the ground shows that the exudation continued practically uniform from hour to hour, and this for several days. Allowance must be made, however, for the general physiological depression caused by the decapitation of the plant. But this change is continuous and not marked by any diurnal variation. This will be seen from the reproductions of portions of a continuous record taken for thirty-six hours; the portions of the record are for four hours at intervals of twelve hours, *i.e.* from 9 A.M. to 1 P.M., from 9 P.M. to 1 A.M., and from 9 A.M. to 1 P.M. from February 11 to 13 (fig. 43). The intervals between successive dots in each row are practically the same; but the gradual slowing down of the rate is seen in counting the number of dots at the beginning, the middle and the end of the rows, in which each dot represents 1 c.c. of exuded sap. It will be noted that on the first day the exudation for four hours was 43 c.c.; after an interval of twelve hours it had fallen to 30 c.c.; and after a further period of twelve hours to 21 c.c.; the total for these twelve hours was thus 94 c.c. The sap collected for twenty-four hours was 180 c.c., which is practically double the quantity recorded for twelve hours. The notable fact is that the decline was continuous, there being no variation due to the alternation of day and night. The reason for this is to be found in the uniform conditions in which the deep-seated root-system was maintained. It was protected from light, and there was no great range in the variation of temperature of the subsoil in February. The external variations, moreover, did not affect the root in the soil.

FIG. 43. Record of Exudation from the Root-stock of *Cucurbita*

Having thus found that exudation remains constant under uniform external conditions, we can proceed to study the effects of physiological variations on the rate.

The Effect of Drought

Having seen how the cellular activity underlying the ascent of sap is depressed by drought, we may expect that exudation will be found to be similarly affected. Thus, in a particular experiment with *Cucurbita*, the root-stock under drought did not exhibit any exudation; but application of water near the root-stock induced it, though in a spasmodic manner. On digging up the plant it was found that the water had only reached a limited portion of the root, most of the root-system being still in dry soil; the spasmodic exudation was thus due to the irrigation of a restricted portion of the root. After extensive irrigation in a second experiment, the arrested exudation was found to be renewed, and this at a very uniform rate.

The Effect of Stimulus

The following experiments show the effect of mechanical and electric stimulation on the rate of exudation.

Mechanical Stimulus.—Experiments were carried out with a field-specimen of *Cucurbita* to ascertain the effect of increasing intensity of stimulus on the rate of exudation. In the first experiment a small lateral root was dug up, taking care that it remained coated with moist clay. A portion of this root was then cut off with a pair of scissors; the effect of the moderate stimulus of this cut was to reduce the rate from the normal 52 c.mm. to 42 c.mm. per minute. The normal rate was restored after seventeen minutes. A larger lateral root was next cut off, which caused a more intense stimulation, and induced a depression of the rate of exudation from 52 c.mm. to 7 c.mm. per minute, or about one-eighth the normal; the period of recovery was now found prolonged to 50 minutes. Pricks were then administered to the main root, inducing a diminution of the rate to 4 c.mm. per minute, or to one-thirteenth; the period of recovery from this intense stimulation was prolonged to three hours. Thus an increase in the intensity of the stimulus gave rise to an increased depression in the rate of exudation, and a corresponding prolongation of the period of recovery. In the first two experiments described above, the diminished rate of exudation could not have been due to the loss of a portion of the root, which was quite negligible compared to the very extensive root-system; the subsequent recovery to the normal rate shows, moreover, that the induced diminution was undoubtedly due to the retarding action of stimulus.

Electric Stimulus.—After the normal rate of exudation of another root-stock had been recorded, two metallic prongs were buried in the soil on opposite sides of the plant to act as electrodes, and the root was stimulated by the passage of an induction-shock of moderate intensity applied for a minute. The normal rate of exudation of this specimen was 80 c.mm. per minute. After the passage of the shock the rate of exudation was greatly depressed, the rate being now 6 c.mm. per minute; complete recovery was only attained after several hours. I give two records in fig. 44, in which M represents the effect of mechanical, and E that of electrical, stimulus on the rate of exudation.

FIG. 44. The Effect of Mechanical and Electrical Stimulus in Retardation of Exudation

M, the effect of mechanical, E, that of electrical, stimulus.

TABLE XX.—SHOWING THE IMMEDIATE EFFECT OF STIMULUS ON EXUDATION AND SUBSEQUENT RECOVERY

Time	Rate of exudation
Normal	52·0 c.mm. per minute
On stimulation	7·0 ,, ,,
After 8 mins. 30 secs.	18·0 ,, ,,
,, 15 ,, 50 ,,	23·0 ,, ,,
,, 20 ,,	27·0 ,, ,,
,, 25 ,,	32·0 ,, ,,

The successive dots are relatively close at the beginning; but after the application of the stimulus the intervals become widened, showing a depression of the rate of exudation. The slow recovery is seen in the gradual approximation of the successive dots to each other. The rest of the record is not long enough to exhibit the complete recovery. In Table XX. (p. 139) are given the quantitative results of a different experiment, showing the immediate effect of stimulus in retardation of exudation and the gradual recovery towards normal.

The Effect of Poison

The effect of a poisonous solution of formaldehyde was next observed. The normal rate of exudation of the particular specimen of *Cucurbita* was 28 c.mm. per minute. Application of the poisonous solution caused a marked depression, the rate of exudation being now reduced to 0·35 c.mm. per minute. Continued action of the poison produced complete arrest.

The Effect of Anæsthetics

Wieler found that exudation ceased when the roots of seedlings, or of older plants from water-culture, were placed in a dilute solution of chloroform. Pfeffer's criticism of these results is 'that the experiments are not always conclusive, since if the chloroform is too strong, the plant is readily injured, or may be killed.'

In order to meet this objection, a definite physiological test was employed which is free from the uncertainty arising from the possibility of a fatal effect caused by the anæsthetic. We found that, in the case of the stem, the preliminary action of chloroform was to induce an enhancement of the rate of ascent; this being followed, under continued action, by a depression or abolition of the ascent. In regard to exudation, results have been obtained in every way similar to the above. Thus, with a given root-stock of *Cucurbita*, the normal rate was 52 c.mm. per minute. The preliminary effect of the application of chloroform was to enhance it to 68 c.mm.; after this, the depressing effect set in, the maximum depression reducing the rate of exudation to 36 c.mm. per minute. Owing to the dissipation of the chloroform-vapour in the soil, the plant exhibited a recovery after two hours. I then applied chloroform for a second time, when the phenomenon of accommodation, or acquired immunity, was shown in a very interesting manner; for the dose had to be increased to obtain the previous effects.

Continuity of Action in the Root and in the Shoot

According to the generally accepted theory, the exudation from the cut end of the stock is due to filtration under pressure, the active force being the root-pressure set up by some specific activity of the cells in the root.

There is no ground for the assumption that the activity of the root-cells is in any way specifically different from that of the cells of the stem. We have found that the effects of variation of temperature, of anæsthetics, and of poisons are the same in the one case as in the other. The active pressure which causes the expulsion of sap from the cut surface of a stem is not generated by the root alone; the stem also contributes. Thus stems of Grasses, with their cut ends placed in moist sand, exhibit exudation under pressure, just as do specimens with roots. This propulsive force therefore exists not only in the root but also in every portion of the stem. It is moreover not strictly true that the sap is forced through a passive layer of tissue at the cut end by filtration under pressure exerted by the distant root. The root and every section of the stem exerts pressure; the total pressure is the sum of their additive effects.

Effect of Local Application of Chloroform.—The following experiment will show that the terminal layer also takes an active part in the outflow of sap from the cut end. We have seen that the application of dilute chloroform to the root caused a transient enhancement of exudation. Taking another root-stock of *Cucurbita*, I applied dilute chloroform to the cut end itself. The specimen was young and its rate of exudation was one drop in 220 seconds. On the application of chloroform, the rate of exudation was continuously increased till after twenty-five minutes the rate had become one drop in fifty seconds, that is to say, more than four times as rapid. The plant recovered its normal rate in the course of an hour.

Effect of Variation of Temperature.—It has been shown that the rate of ascent of sap is increased when the root or the cut end of the stem is raised in temperature (p. 58). Exudation is likewise enhanced by raising the temperature of the stem-portion of a root-stock. In the case of a root-stock of *Cucurbita* cut close to the ground, there was, we saw, no change in the rate of exudation though the external temperature underwent a diurnal variation. This was because the roots were buried in the soil, and moderate variation of the atmospheric temperature did not affect the temperature of the root. When, instead of cutting the stem close to the ground, a short length was allowed to remain above ground, the exudation was then found to undergo an increase with a rise of temperature of the outside air. The temperature outside was at its maximum at 2 P.M., and the exudation from the cut surface of the stock was also found to attain its maximum rate at that hour. This will be studied in greater detail in the next chapter, where it will be shown that, under conditions described above, the pressure exerted by the sap also undergoes a parallel increase. In other words, exudation and root-pressure are brought about not merely by the activity of the root, but also by that of the shoot.

In conclusion, the expulsion of sap by living cells may be generally considered. Electric stimulus has been shown to induce a diminution of the rate of ascent of sap in the stem, and a diminution of the rate of exudation from the root-stock. It is possible to arrive at a definite explanation of these effects by reference to the responsive action common to all living cells, rhythmic or ordinary. This identity is made evident by a comparison of the curves of mechanical response and recovery of *Mimosa* leaf, and of responsive diminution of exudation and subsequent recovery in the root-stock of *Cucurbita.* In the former, stimulus causes the physiological change in the cells which we call contraction, resulting in a diminution of turgor and the fall of the leaf; gradual recovery of the cells restores the normal turgor and the expanded position of the leaf. A similar physiological change, in response to stimulus, must undoubtedly occur in the active cells that propel the sap; which, affecting, as it does, the conducting channels, causes a concomitant diminution of the rate of flow. The identical character of the two responses will be seen in the records given (fig. 45) of the response of the leaf of *Mimosa* and that of the root-stock of *Cucurbita,* in which the ordinate represents the diminution (negative variation) of turgor and of exudation respectively. In both, the height of response is increased with the increasing intensity of stimulus, with corresponding prolongation of the period of recovery.

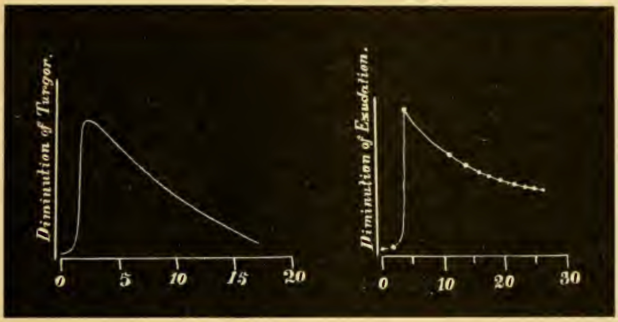

FIG. 45. Curves showing Similarity of Response to the Action of Stimulus and Recovery of *Mimosa* (left figure) to that of Exudation in *Cucurbita* (right-hand figure)

It is recognised that the expulsion of sap by the cells of the pulvinus of *Mimosa*, on stimulation, is an essential part of its motile mechanism, and this applies also to the pulvinule of the leaflet of *Desmodium* in its 'spontaneous' oscillation. In the preceding pages, evidence has been accumulated which demonstrates that the active expulsion of sap by living cells is an essential part not only of the mechanisms of movement, but also of the mechanisms for the distribution of liquid throughout the plant. Experiment has shown that the ascent of sap in the stem, and the excretion (transpiration) of water by the leaves, are manifestations of this cellular activity; and now exudation from the cut surface of the root-stock has been shown to be traceable to the same cause. In herbaceous plants, where the wood-vascular tissue is but slightly developed, exudation takes place mainly from the cortex of the cut surface; whereas in trees, 'bleeding' comes from the vascular tissue which has become charged with liquid by the pumping activity of the cortex.

What may be precisely the mechanism of the process of expulsion in the individual cell is not yet clear. It may be (1) an active contraction of the lining layer of protoplasm; or (2) an increased permeability of this layer, permitting the escape of cell-sap under the elastic pressure of the stretched cell-wall; or probably the co-operation of both these factors, and perhaps others. In any case it is a manifestation of that contractility which is one of the fundamental properties of living protoplasm.

SUMMARY

The exudation from the cut end of the root-stock is depressed or arrested by drought, and renewed after irrigation.

Mechanical or electric stimulus induces a retardation or arrest of exudation; this is followed, on the cessation of the stimulus, by recovery, which becomes protracted if the stimulus has been strong.

Dilute chloroform applied at the cut surface enhances the rate of exudation, showing that the terminal layer at the surface also takes an active part in the exudation.

The resultant exudation is thus due to the co-ordinated action of active cells throughout the whole length of the root-stock.

The responsive action of the cells concerned in exudation is fundamentally similar to the expulsion of water by the cells in the pulvinus of *Mimosa* when stimulated.

CHAPTER X

THE RELATION BETWEEN ROOT-PRESSURE AND EXUDATION

General considerations—Diurnal periodicity of root-pressure—The recording apparatus—Relation between temperature and pressure—Diurnal variation of pressure in deciduous trees—Diurnal variation of exudation—The effect of light—Summary.

The mechanism of the propulsion of sap in a plant has been compared with the action of a pump, and the analogy holds good even in many details. Let us imagine a tubular well supplied with water from the deep soil; the water is raised by a pump, the activity of which may be gauged in two different ways, dynamic and static. The activity of the pump may thus be found from the rate of the outflow, or from the height of the balancing column of water. In the corresponding phenomenon in plants, the activity of the root-stock may be measured, either by the rate of exudation, or by the root-pressure, *i.e.*, the column of liquid which that pressure can sustain. As the exudation and the root-pressure are different expressions of an identical cellular activity, a relation might be expected to exist between the two, under similar conditions, *i.e.*:

(1) Plants with high root-pressure should also exhibit a high rate of exudation, and *vice versâ*.

(2) External stimulus should induce similar variations in both.

(3) Other changes in the environment should cause similar responsive variations in root-pressure and in exudation.

The above conclusions would follow as necessary consequences of the theory of cellular activity in the ascent of sap. In practice, however, we are confronted with numerous anomalies, which are given below in order of increasing complexity and difficulty of explanation.

(*a*) *Apparent independence of exudation and pressure.*—It is often found that a plant with low root-pressure exudes a large quantity of sap; conversely, other plants with high root-pressure exhibit feeble exudation.

(*b*) *Irregular distribution of pressure.*—Manometers attached to the tree at different heights should exhibit a decrease of pressure from below upwards; but this is seldom the case.

(*c*) *Eccentricities in the diurnal variation of exudation.*—Exudation from plants often exhibits an erratic diurnal variation. Thus while some may exhibit a minimum exudation of sap in the forenoon and a maximum exudation in the afternoon, other plants exhibit precisely the converse results. These eccentricities are so inexplicable that, according to Jost, 'there can be no hesitation in concluding that we are still far from having reached a satisfactory explanation of the phenomenon.'[1]

(*d*) *Exudation in Palms.*—The widest divergence in the relation between pressure and exudation presents itself in certain Palms. In many deciduous trees, in the absence of transpiration from the leaves, there is a considerable intra-vascular pressure; so that when a hole is drilled in the trunk, a copious exudation of sap under pressure follows. In Palms, however, the phenomenon is very different. The Palmyra Palm (*Borassus flabellifer*), which attains a height of 100 feet (30 metres), grows very slowly and is said to live for a couple of centuries. Under appropriate conditions, as described in Chap. XIII., the exudation of sap from it is very copious. Disregarding the great resistance offered by the tissue to the ascent of sap, a pressure of three atmospheres would be necessary to raise water to this height. But Palms do not exhibit any root-pressure; this has been found to be the case by Molisch in *Arenga saccharifera*, and I find it to be equally

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[1] Jost, *Plant Physiology*, English translation, p. 51.

the fact in *Phœnix sylvestris.* The drilling of auger-holes in the trunk is not followed by any exudation, though the outflow of sap is copious after the surface of the trunk has been subjected to repeated injury. Here we have an apparently inexplicable phenomenon of exudation without any pressure to enforce it.

In approaching this complex problem, we must realise that the ascent of sap and its diverse manifestations are due to the activity not of any single part of the tree, but of all its parts. The different regions, the root, the shoot, and the transpiring leaves, are subjected, as already stated, to external variations which affect them unequally, and the resultant effect is, to a great extent, due to the algebraical summation of the partial effects. The physiological activity is modified by the state of turgor of the tree, and this is determined by the relative gain or loss of water. As regards the gain, the organ of absorption, the root, is completely shielded from light, and to a great extent from the diurnal variation of temperature. The conducting stem is, on the other hand, subjected to physiological changes in the diurnal variation of temperature, and the alternation of light and darkness. In the case of herbaceous plants, light acts as a stimulus on the cortical tissue concerned in the transport of sap, and lowers the power of conduction. But in the case of trees, the thick bark is impervious to light; hence the incidence of sunlight on the trunk would raise the temperature and enhance the velocity of the ascent.

Turning next to the negative factor—the loss of water by transpiration—we have diverse influences which, by their physical and physiological actions, enhance or depress the rate of loss. Among these may be mentioned the effects of diurnal variation of temperature and of light, the action of wind, the varying hygrometric condition of the air, and so on.

It will thus be seen that the internal pressure and the exudation, which depend on the relative gain or loss of water by the plant, are modified by numerous factors, some of which are concordant and others in conflict ; these vary in different degrees according to the changing external conditions. It is therefore not at all surprising that the observed results should have appeared to be so capricious.

It may, however, be possible to unravel the complexities by the process of isolation. We shall therefore take up in this chapter the question of the relation between pressure and exudation in a root-stock which bears no side-branch with transpiring leaves to complicate the phenomena.

In discussing the relation between root-pressure and exudation, especially the case of high root-pressure with minimum exudation and *vice versâ*, we have to take full account of two factors, namely, the resistance offered by the tissue and the area of supply of water. In the action of a pump in a tubular well, it is evident that the outflow will be diminished when the pipe is choked with sand ; again, too quick an outflow from the pump may dry up the well unless the subterraneous supply of water is adequate. Similarly, in the exudation of sap, tissues of different plants will offer unequal resistance to the flow of water. The modifying influence of the area of the absorbing root is shown in experiments with two specimens of *Cucurbita*, one grown in a pot, and the other under field-conditions. In the former, though the exudation was at first moderate, it slowed down on account of the limited area of its absorbing root-system. The *Cucurbita* grown under field-conditions gave, on the other hand, a copious exudation which remained practically constant day after day. From the facts described above it will be seen that a fair comparison between pressure and exudation can only be made when the two factors of resistance and source of supply remain constant, as in experiments carried out with one and the same plant. When this condition is fulfilled, the relation between exudation and pressure will be found to be very definite, as will be seen in the experiments detailed in the next chapter.

As a gauge of cellular activity, the statical method of balancing root-pressure by a column of water or mercury is perhaps more satisfactory than the rate of exudation; for in the former the variable factors of conductivity and the area of supply do not enter into the question. They may prolong the period for the attainment of balance, but do not modify the balancing pressure itself.

The explanation of the irregular variation of pressure will be dealt with in the next chapter.

Returning to the discussion of the relation between pressure and exudation, we may first enquire whether these exhibit any diurnal variation, and in the case of such periodicity relate it to some definite external change. No definite information is, at present, available. According to Baranetzky, Detmer, Brosig, and Wieler, 'a decided daily periodicity cannot be detected in all cases, and it is even doubtful whether the maximum for a given plant always occurs at the same time.' As regards the cause of this periodicity 'Baranetzky found that an alteration in the periods of illumination caused the daily periodicity to change; Brosig remarked that in a certain plant no such effect was produced; Baranetzky again has shown that in many cases no daily periodicity at all is exhibited.'[1]

I find, however, that both pressure and exudation show a definite periodicity related to the diurnal variation of temperature; that it is affected to a small extent by the recurrent action of light and darkness, and that the periods of maxima and minima are modified in a definite way, according to the presence or absence of transpiring leaves.

Diurnal Periodicity of Root-Pressure

We shall first study the diurnal variation of root-pressure in a root-stock cut about 10 cm. above ground. Though the root buried underground is but slightly influenced by external changes, the short piece of stem

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[1] Pfeffer, *Plant Physiology*, English translation, p 267.

above ground is affected by them. The root-stock bore no leaves.

The Recording Apparatus

Success in obtaining accurate results depends greatly on the sensitiveness and reliability of the self-recording apparatus. I have already described the special devices for recording the rate of exudation. For recording pressure and its variations, the movement of a float, making a tracing on a revolving drum, has been used. But this method is subject to numerous errors: the float is apt to turn round and get stuck to one side of the manometer tube; friction against the recording surface, moreover, restricts the free movement of the float, introducing considerable error into the record. These difficulties have been completely removed by attaching the float to one arm of a recording lever with jewel-bearings. The other arm of the lever records on an oscillating plate of smoked glass the movement of the column of liquid in the manometer; the error arising from friction is thus eliminated. By a system of double levers, magnification may be increased to any extent desirable. I have thus been able to devise an apparatus for certain special investigations, by which a variation of pressure as small as a millionth of an atmosphere may be recorded. For our present purpose, the record of pressure to 0·1 mm. of mercury is quite sufficient. A diagrammatic representation of the method employed is given in fig. 46. A manometer is connected with one arm of a three-way tube fixed to the cut end of the plant. In certain experiments the plant had a side-branch bearing leaves, shown in dotted outline; in others, the side-branch was cut off. The diagram explains how the closure of the stopcock S and the opening of S_1 enable us to record the root-pressure, by means of the recording lever attached to the float; opening of S and closure of S_1 allow the record of exudation by means of the tilting lever T.

The internal pressure of the plant is usually measured in relation to that of the atmosphere, but this may lead

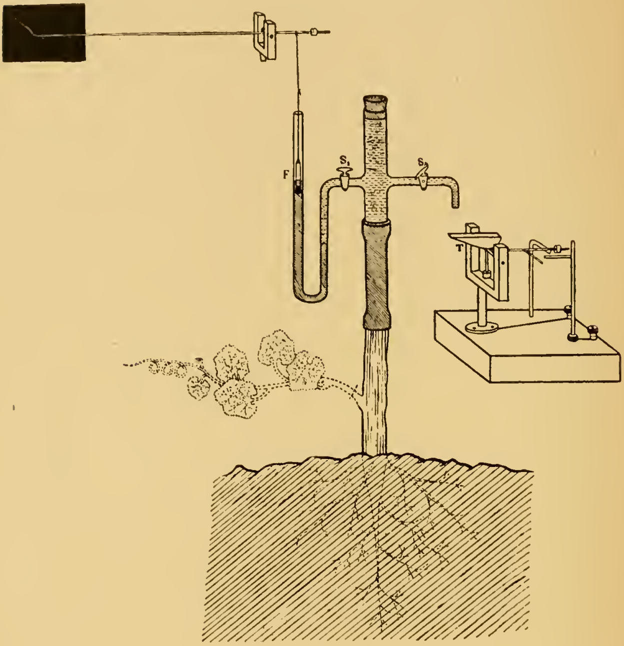

FIG. 46. Diagrammatic Representation of the Methods of obtaining Record of Exudation by the Tilter T, and of Pressure by the Recording Lever attached to a Float, F, in the Manometer

The attached branch and leaves are shown in dotted outline. In certain of the experiments this branch was removed.

to serious misunderstanding. Atmospheric pressure has little or nothing to do with the ascent of sap and its various manifestations. It would be desirable to record the absolute pressure, taking vacuum as zero. The results can easily be converted to the atmospheric scale by subtracting 760 mm. from the absolute value.

The plant *Zea Mays* is very suitable for this investigation, since its root-pressure is considerable. The following experiments with a large number of plants were commenced in February and continued for more than ten weeks. It was cold in February, but later it became excessively warm, on account of a heat-wave that passed over Bengal in April. There were periods of stormy weather, which settled down after a time. In spite of these fluctuations in the weather-conditions, the results were very definite, as will be seen from the following.

The first of the series of experiments with *Zea Mays* was undertaken in February; the automatic records obtained show that the pressure early in the morning was at its minimum, *i.e.*, 916 mm. of mercury, or 156·5 mm. above the atmospheric pressure. The internal pressure increased and attained a maximum value of 931 mm. shortly after 2 P.M., which is the moment for the attainment of the highest temperature. After this, the pressure declined with the fall of temperature, the minimum being reached once more early in the morning.

In demonstration of the close relation between the diurnal variation of temperature and of pressure, I reproduce the two curves taken on the same plate (fig. 47); the variation of temperature was here recorded by a differential metallic strip-thermometer. The close agreement between the two curves proves that the variation of pressure is practically determined by the variation of temperature.

The period for the attainment of the highest temperature I have designated as the *thermal noon*, that of the lowest temperature as the *thermal dawn*. The maximum temperature, under normal conditions, is attained at or about 2 P.M., and the lowest temperature about 6 A.M. These two periods, speaking generally, correspond to the periods of maximum and minimum pressure respectively. In exceptional cases, as during the stormy condition of the weather which occurred in March, there were numerous fluctuations in the temperature-curve, due to the intermittent passage of clouds and changes in the direction of the wind. *Under these conditions the pressure-curve was found to follow very closely the curve of temperature;* so close was the resemblance between the two, that one could use the physiological plant-manometer as a sensitive thermometer.

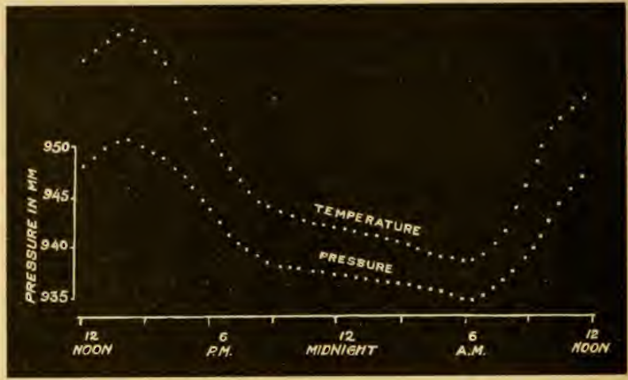

FIG. 47. Record of Diurnal Variation of Internal Pressure in *Zea Mays*

The upper record is of the diurnal variation of temperature.

The activity of living cells in the maintenance of pressure is proved by the fact that it declined and became finally abolished with the growing physiological depression in the decapitated plant.

After the subsidence of the stormy weather, the atmospheric conditions became more stable, though on account of the periodic change in the direction of the wind there were two thermal maxima instead of one in the course of twenty-four hours (April 13–14), a preliminary small maximum about 1.30 P.M. and a higher maximum at 4 P.M. The pressure-curve also exhibited a double maximum at the corresponding periods (fig. 48). This record was taken in the second week of April, when the plants were bearing ripened fruits. The records were taken after a brief period of rain. The maximum pressure was now 1175·8 mm., instead of 951·2 mm. before the rain.

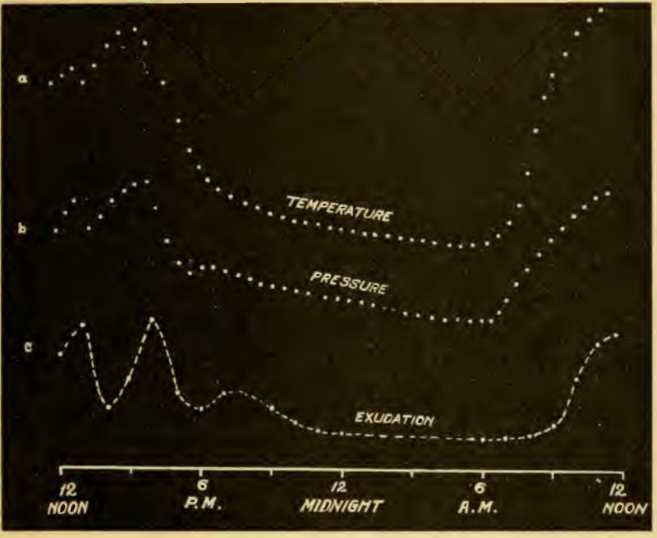

FIG. 48. The Diurnal Record of Pressure and of Exudation in Root-stock of *Zea Mays* exhibiting Double Maxima corresponding to the Two Thermal Maxima

b, record of plant A; *c*, record of plant B.

Diurnal Variation of Pressure in Deciduous Trees

At the period of the year when a deciduous tree is bearing no leaves, its diurnal record of pressure may be expected to exhibit a certain resemblance to that of a root-stock without leaves. The following is the record (fig. 49) obtained with a leafless tree (*Poinciana regia*). The pressure is seen to undergo a continuous increase with the rise of temperature, attaining a maximum at thermal noon at or about 2 P.M., and then to decline with the fall of temperature. The diurnal curve of the deciduous tree is thus similar to that of the root-stock without leaves.

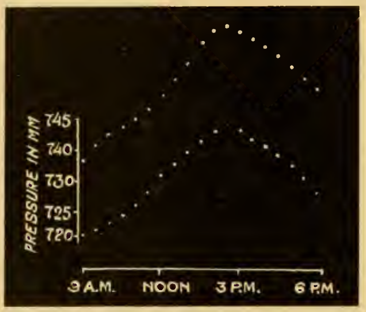

FIG. 49. The Record of Variation of Pressure in a leafless Tree, *Poinciana regia* (lower record)

The upper record is the diurnal variation of temperature.

The results given above lead to the following generalisation:

The diurnal variation of root-pressure in a root-stock without leaves, and in a leafless deciduous tree, is determined by the variation of temperature, the maximum being attained at thermal noon, and the minimum at thermal dawn.

Diurnal Variation of Exudation

In this investigation I sought to ascertain whether exudation exhibits any diurnal variation, and secondly, whether this variation of exudation bears any relation to the variation of pressure. In order to study the question of exudation and pressure under identical external variations, I prepared two root-stocks of *Zea Mays*, which were growing side by side; A was employed for the record of the variation of pressure, and B for the variation of exudation. As the temperature was high, a possible error in the determination of exudation might arise from rapid evaporation of the exuded sap. For the elimination of this error I employed the following device (fig. 50). From the india-rubber cork closing the glass tube attached to the root-stock, a narrow glass tube was led to a graduated burette, in the cork of which was fixed another glass tube communicating with the air, evaporation being prevented by a drop of oil which acted as valve. The exudation of each drop from the plant caused an expulsion of an equal volume of air, which bubbled through the oil ; the quantity of sap exuded at definite intervals was measured by the graduations on the burette.

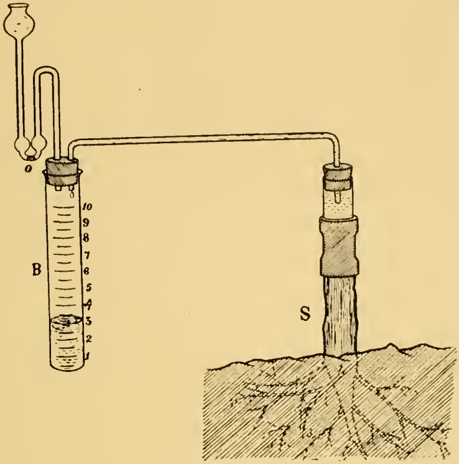

FIG. 50. Arrangement for Measurement of Exuded Sap
Loss by evaporation is prevented by the oil-trap o.

The determinations of the diurnal periodicity of exudation and of pressure were carried out for twenty-four hours from April 13 to 14, when, it should be remembered, two thermal maxima occurred, one at 1 P.M. and the other at 4 P.M. The record of plant B, fig. 48, shows that the rate of exudation increased with the rise of temperature, attaining its first maximum at 1 P.M. and the second maximum at 4 P.M. The record of the pressure of the adjoining plant A exhibits a corresponding change. It is thus seen that, under similar external changes, pressure and exudation exhibit parallel variations.

The Effect of Light

Light exerts two distinct effects, which may be distinguished as thermal and photic. Absorption of light raises the temperature and enhances the physiological activity; light also acts as a stimulus, inhibiting the rhythmic activity: the actual result represents the difference between these two effects. The retarding effect of light is, however, masked by the predominant thermal action. Certain characteristic features shown in the records given in fig. 48 indicate, however, the retarding action of light in a very interesting manner. In *Zea Mays* there is no thick bark to shield the active cells from the action of light, which was exceptionally strong in April. It will be noted that after five o'clock, when the light was rapidly fading, there occurred a transient enhancement of pressure and of exudation, though the temperature had been undergoing a slow decline. It would appear that this transient rise was due to the removal of the retarding action of light. The effect due to light is, however, negligible compared with the effect of the diurnal variation of temperature.

SUMMARY

A root-stock without a side-branch bearing leaves, and a leafless tree, exhibit a diurnal periodicity of pressure. This periodicity is determined by the variations of temperature, the maximum being attained at thermal noon, and the minimum at thermal dawn.

The diurnal variation of exudation also follows that of temperature, the maximum and the minimum exudation corresponding to the periods of the maximum and the minimum temperature.

A relation exists between pressure and exudation, such that an increase of pressure is attended with an increase of exudation and *vice versâ*.

CHAPTER XI

DIURNAL VARIATION OF PRESSURE AND EXUDATION IN PLANTS WITH LEAVES

Complexity arising from fluctuating factors of absorption and excretion —Hydraulic and electric model—Diurnal variation of pressure in root-stock—Effect of light—Explanation of irregular variation of pressure in trees—Diurnal variation of exudation in root-stock —Positive and negative exudation—Exudation from *Pithecolobium* —Summary.

In the last chapter we studied the changes in the pressure and in the exudation of root-stocks and deciduous trees, and found that the diurnal variation is determined principally by the variation of temperature, the maximum being attained at thermal noon, and the minimum at thermal dawn ; and it is concluded that the variations of pressure and exudation are to be attributed to responsive variations in the activity of the cells concerned in the propulsion of the sap.

We will now consider the case of the plant which bears transpiring leaves. Transpiration, as we have seen, attains a maximum at thermal noon, and a minimum at thermal dawn (p. 118). The state of turgor at any time of the day (and also the internal pressure and the power of exudation) will thus depend on the relative gain and loss of water at that particular time.

The problem is thus the investigation of the resultant effect brought about by the algebraical summation of the two fluctuating factors, one positive and the other negative. The positive is the absorption of water by the root ; and the negative, excretion by the leaves. Our experience of water and electric supply in the house will, however, give us a clearer conception of this resultant effect. In fig. 51, the diagram to the left represents the water-main with two side-pipes, of which the larger exit-pipe S may be taken to represent the outlet for transpiration, and the smaller, S_1, that for exudation, while M is the manometer for the measurement of pressure. The diagram on the right side represents the electric main, with an arc-lamp and an incandescent lamp, which consume the current. In the water-main, if the stop-cock S is opened widely (increased transpiration), the exudation through S_1 will be diminished. Similarly, the lighting of the arc-lamp, by withdrawing a large amount of current, will dim the incandescent lamp.

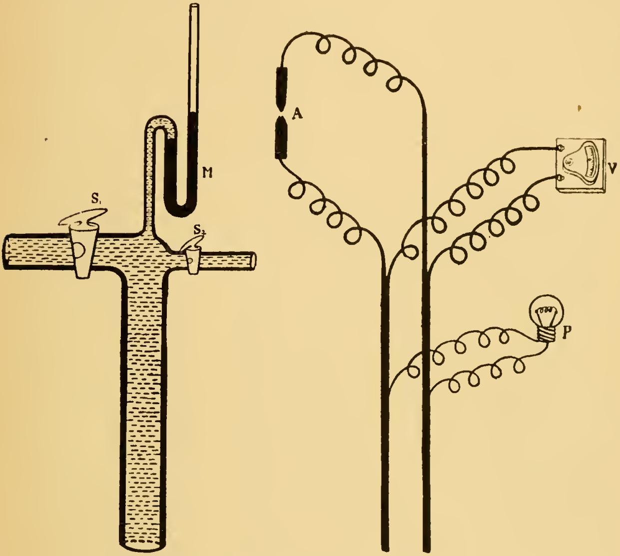

FIG. 51. Diagram of Water-supply, showing the Diminution of outflow of S_1 by opening the Stop-cock at S, which also causes a Diminution of Pressure indicated by the Manometer M

The diagram on the right shows the effect of lighting an arc-lamp in diminishing the current through the incandescent lamp P, and in diminishing voltage indicated by the voltameter V (see text).

The excessive loss will also diminish the pressure, as indicated by the manometer and the voltameter, respectively.

We may now take up the question of the effect of varying rates of transpiration on pressure and on exudation, beginning with pressure.

Diurnal Variation of Pressure in Root-Stock with Leaves

I prepared a root-stock of *Cucurbita*, with a side-branch bearing six leaves (see fig. 46) ; the plant was growing under field-conditions. The cut end of the root-stock was connected with the Recording Manometer. The specimen was exposed to diffuse light from the sky, and shaded from the rays of the sun. The internal pressure was 860 mm. at six in the morning, but it fell rapidly with the rise of temperature; at thermal noon, after 2 P.M., the pressure was at its minimum of 680 mm. The temperature began to fall after 3 P.M., and this was attended by a rise of pressure (fig. 52). The diurnal record of the variation of pressure in a root-stock with leaves is thus diametrically

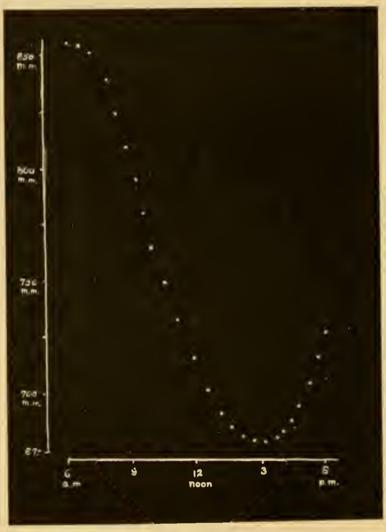

FIG. 52. The Diurnal Variation of Pressure in *Cucurbita* with Leaves ; the Minimum Pressure is at Thermal Noon

opposite to that in one without leaves: in the former, the pressure at thermal noon is at its minimum, whereas, in the latter, it is at its maximum. The reason for this difference is that transpiration increases with the temperature, attaining its maximum at thermal noon; though the ascent of sap is also enhanced by the rising temperature, yet the loss by transpiration is disproportionately greater. Fall of temperature produces a converse resultant effect.

The Effect of Light

When the diurnal curve of the above *Cucurbita* in the shade was exhibiting increasing pressure during the fall of temperature after 3 P.M., sunlight was thrown on the leaves by means of an inclined mirror, thus raising their temperature. Transpiration was suddenly increased: this was at once reflected in the pressure-curve by a responsive diminution of pressure (fig. 53). After cessation of the exposure to light, the pressure again increased with the falling temperature, attaining its maximum early next morning.

FIG. 53. Variation of Internal Pressure by the Action of Light on the Leaves

The pressure was rising on account of fall of temperature. Incidence of light, L, induced a diminution, followed by recovery on the cessation of light. Application of light a second time induced similar result.

The response by pressure-variation is extremely sensitive; I have been able to obtain response by merely striking one of the leaves. The internal pressure is caused to undergo variation by the action of light, by mechanical stimulus, by the action of the wind, in fact by the action of any agent which induces a variation of transpiration.

Explanation of Irregular Variation of Pressure

The pressure indicated by lateral manometers attached to a cylindrical vessel containing water, undergoes a regular diminution from the base upwards. If there is any leak in the vessel, all the manometers will immediately indicate a diminution of pressure, for there is no resistance to delay the readjustment of the pressure throughout the column. The case is, however, different in a tree, where the tissues offer great resistance to the flow of water. Hence a lateral leak, however produced, will take a considerable time to cause readjustment of pressure throughout the tree. In a tree-trunk, moreover, there is not a single leak, but many leaks through side-branches irregularly disposed at various heights; the leaves in their turn are subjected to diverse influences which modify transpiration. Under these circumstances the irregular variation of pressure at different heights of the tree is by no means anomalous; it would have been surprising had it proved to be regular.

Diurnal Variation of Pressure in Trees with Leaves

We now consider the case of the periodic variation of pressure in the intact tree with leaves. For this I experimented with a large Rain-tree (*Pithecolobium*) growing in the grounds of the Institute. It was about 8 metres in height, with numerous outspread branches. The tree was shaded by the neighbouring trees, except at midday, when the sunlight fell on it: otherwise it was subjected to the diurnal variation of temperature, which attained its maximum at about 2 P.M. A recording manometer was attached to the trunk at a height of a metre from the ground. I give the automatic records of the variations of pressure and of temperature (fig. 54), which show that with the rise of temperature the pressure underwent a decline, and that the minimum pressure was attained at thermal noon. In the case of plants without leaves we saw that the curves of temperature and pressure were parallel to each other (see fig. 47): in the present case, the one curve appears to be an inverted reflection of the other.

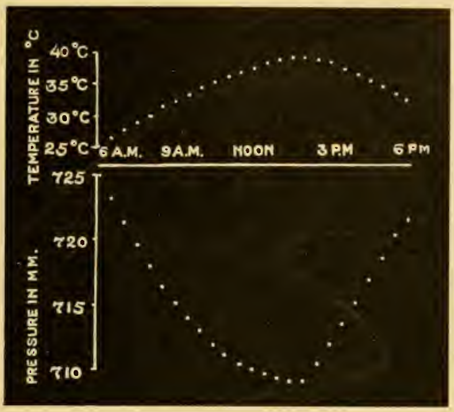

FIG. 54. Diurnal Curve of Variation of Pressure in the Rain-tree (*Pithecolobium*)

The upper curve shows the variation of temperature, and the lower curve the variation of pressure. Note that the pressure was at its minimum at the thermal noon, 2 P.M.

The diurnal variation of pressure in the root-stock with leaves, and in intact leafy trees, is the reverse of that in plants without leaves. The maximum pressure in plants with leaves is attained at thermal dawn and the minimum at thermal noon.

Diurnal Variation of Exudation in Root-stock with Leaves

Root-stock of Cucurbita with side-branch.—Observations were made on the change in the rate of exudation at different times of the day. The specimen was exceptionally vigorous, and in spite of the loss by transpiration from a side-branch, the exudation was considerable, specially at night-time. The rate of exudation attained its maximum early in the morning, after which it began to decline rapidly. After 10 A.M. there was a total arrest, which persisted till 5 P.M. The exudation recommenced after that hour, and increased continuously till it attained the maximum at thermal dawn.

Positive and Negative Exudation

The next problem was to find out what happened during the arrest. We have already found that the internal pressure of *Cucurbita* with a side-branch underwent a rapid diminution with the rise of temperature, the minimum pressure being at or about 2 P.M. (p. 162). For obtaining an automatic record of the change in exudation, I employed the following device.. The free end of a bent glass tube attached to the cut end of the root-stock was immersed in a cylinder partially filled with water in which was a float : a continuous record of the variations in the level of the liquid was obtained by connecting the float with the recording lever. Fig. 55 gives a record obtained from *Cucurbita* for a period of twenty-four hours, from 7 P.M. to 7 P.M. the next day, which shows that exudation continued till 10 A.M., when it stopped for an hour. After 11 A.M. the sign of exudation was reversed from positive to negative, that is to say, the cut end of the root-stock began to *suck in water* instead of exuding it. This negative exudation continued till about 5 P.M., after which the positive exudation was resumed.

There are thus two points of inversion in the curve, one after 10 A.M., and the other after 5 P.M. The explanation of the transition from the positive to negative and back once more to the positive is as follows : At night the loss by transpiration was slight, hence there was but little diversion of the sap from exudation. In the forenoon, the temperature was rising, and the loss by transpiration was increasing at a disproportionately higher rate ; between

10 and 11 A.M. there was a balance between the sap sent up by the root-stock and the loss arising from the excretion by the leaves: after 11 A.M. the loss was the greater, and the condition of turgor fell below the normal; hence the root-stock began to exhibit a *negative exudation* by sucking back the exuded sap. The activity of suction attained its maximum about 2 P.M., after which the temperature began to fall and the transpiration decreased, resulting in a transition from negative to positive exudation after 5 P.M. The two transitional points are thus at 11 A.M. and at 5 P.M.; at the former transpiration just exceeded exudation, and at the latter exudation began to exceed transpiration.

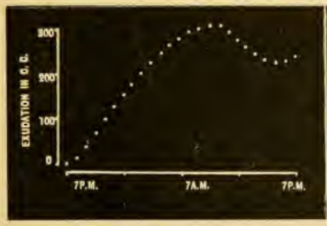

FIG. 55

FIG. 56

FIG. 55. Record showing the Positive and Negative Exudation in *Cucurbita* with a Side-branch

The up-curve represents positive exudation, and the down-curve negative exudation.

FIG. 56. Positive and Negative Exudation exhibited by a Tree with Leaves (*Pithecolobium*)

The record also gives a rough idea of the relative excretion from the leaves. The average rate of exudation in the plant at night, from 6 P.M. to 6 A.M. in the morning, was 23 c.c. per hour. The loss by transpiration at night is very much less; we found it to be about 10 per cent. of that in the day-time (p. 119). Hence the average rate of exudation from evening to morning may be taken to be about 25 c.c. per hour. At 10 A.M. exudation and transpiration were balanced. Hence the rate of transpiration at that hour may be regarded as 25 c.c. per hour. From 11 A.M. to 5 P.M. the plant should have exuded at a rate slightly greater than 25 c.c. per hour, since the rate of exudation would be at its maximum at the thermal noon at 2 P.M. Neglecting this correction, the total exudation for the six hours between 11 A.M. and 5 A.M. should have been at least six times twenty-five, or 150 c.c. Instead of this, the plant sucked in 80 c.c., on account of excessive transpiration during this period. The total loss by transpiration is thus 150 + 80 or 230 c.c., or an average loss of 38 c.c. per hour. The hourly loss by transpiration at midday is thus greater than the 25 c.c. which the plant is able to supply; hence a condition of drooping of the leaves becomes noticeable at that period.

Exudation from the Rain-tree

I obtained similar results with *Pithecolobium*. The leaves were very numerous, hence the normal exudation was relatively low: nevertheless, the diurnal curve of exudation shows a remarkable similarity to that of the *Cucurbita* with a side-branch. Here also the exudation continued throughout the night and early morning. It was arrested at about 9 A.M.; at 10 A.M. there was negative exudation which continued till 4 P.M., after which positive exudation was resumed (fig. 56).

We are now in a position to explain the quantitative relation between absorption and the sum total of excretion from the plant. In the case where the gain is greater than the loss, the turgor is increased, the xylem-reservoirs are filled up, and the internal pressure exhibits an increase. A cut made in the plant in this condition is followed by exudation of sap. Under the opposite condition of excessive loss by transpiration, the expenditure is greater than the income; the turgor falls below par, the xylem-reservoirs become emptied, the intra-vascular pressure changes from positive to negative, so that water, instead of being exuded, is sucked in at the cut surface.

The contrasted effects of pressure and exudation in trees with and without leaves are given in the following table :

TABLE XXA.—SHOWING THE VARIATION OF PRESSURE AND OF EXUDATION IN PLANTS WITH AND WITHOUT LEAVES

Environment	Root-stock and trees without leaves	Root-stock and trees with leaves
Effect at thermal noon	Maximum exudation and maximum pressure.	Minimum exudation and minimum pressure.
Effect at thermal dawn	Minimum exudation and minimum pressure.	Maximum exudation and maximum pressure.

SUMMARY

In plants bearing leaves, the diurnal variation of pressure and of exudation is such that the maximum is attained at thermal dawn, and the minimum at thermal noon.

In plants without leaves, the diurnal variation of both pressure and exudation is exactly the opposite : the maximum is attained at thermal noon, the minimum at thermal dawn.

When the internal pressure undergoes rapid diminution, positive exudation becomes converted into negative.

CHAPTER XII

THE 'WEEPING' MANGO-TREE

Exudation from the Mango-tree—Chemical analysis of the exuded sap—Period of maximum pressure—Absence of exudation from hole drilled into the tree—The existence of a cavity due to disintegration of alburnum—The lateral injection of sap by active cortex—Enhanced secretion due to local rise of temperature—Summary.

THE results of investigation given in the previous chapters show that the various phenomena of pressure and exudation, though apparently anomalous, are yet capable of satisfactory explanation by taking full account of the numerous factors which complicate them. A very curious phenomenon has, however, been recently brought to my notice, which could not be explained by the consideration of the different factors which have already been enumerated. This unexpected occurrence is that of the periodic 'weeping' of an intact Mango-tree in the suburbs of Calcutta. The mysterious event came to be regarded as of evil omen, and thus roused considerable alarm among the people in the neighbourhood.

The particular tree is full grown and about 39 feet high (13 metres). The circumference of the tree is 38 inches (1 metre), and the outspread branches with their numerous leaves cover an area of about 90 sq. metres. The exudation or weeping commences every day punctually at 1 P.M., from a point high up in the tree. This weeping, so-called, is very copious at the beginning, the rate of fall of successive drops being once in two seconds; it gradually slows down; the intervals between successive drops come to be five seconds at 2 P.M., eight seconds at 3 P.M., fifteen seconds at 4 P.M., and 150 seconds at 5 P.M., after which the exudation comes to a standstill. The performance is repeated every day punctually at 1 P.M., and with the same sequence.

FIG. 57. Photograph of the 'Weeping' Mango-tree
Exudation takes place through a small aperture marked with an arrow. The pressure-recorder is seen attached to the tree.

Examination of the tree brought out the fact that there was a small aperture in the bark, which will be designated as the *vent,* which has been enlarged in the photograph (fig. 57). Analysis of the exuded sap gave the following results :

Total solid after evaporation per 100 c.c.	1·56 grams.
Solids after ignition per 100 c.c.	0·99 ,,
K_2CO_3 in solids after ignition	0·90 ,,
Phosphates and other solids in 100 c.c.	0·09 ,,

The organic matter consisted mostly of gums and tannins.

The problem of the weeping of the Mango-tree is essentially the determination of the cause of the abrupt commencement of exudation at 1 P.M., approximately the hour of the thermal noon : this suggests an analogy with the maximum exudation of the deciduous tree without leaves which, as previously stated, occurs at the same time. But the Mango-tree bears innumerable transpiring leaves, on which account thermal noon should be the period of maximum transpiration and minimum exudation as we found to be the case with the Rain-tree with leaves (p. 168).

The Period of Maximum Pressure

As pressure and exudation have been shown to be closely related to each other, the maximum exudation at thermal noon might be attributed to the occurrence of maximum pressure at that hour brought about by some unknown cause. In order to test the correctness of this supposition, I attached a recording manometer to the tree, and found that the pressure underwent a continuous decrease with rising temperature, reaching its minimum at or about 2 P.M. Fig. 58 gives the record of the variation of pressure from 9 A.M. to 9 P.M. ; the lower record gives, by the spacings between successive dots, an indication of the different rates of exudation at 1, 2, 3 and 4 P.M. Thus the internal pressure of the Mango-tree exhibits no characteristic distinguishing it in any way from that of other trees with transpiring leaves.

The anomaly presented here is that the maximum exudation should occur simultaneously with the minimum internal pressure. It was thought that possibly, in the particular zone of the plant, tissues had been developed which were unusually active. Investigation was therefore undertaken to find out whether an auger-hole made at the diametrically opposite side of the trunk would give an exudation at thermal noon, as occurred at the natural vent. There was, however, not the slightest indication of any exudation from the drilled hole.

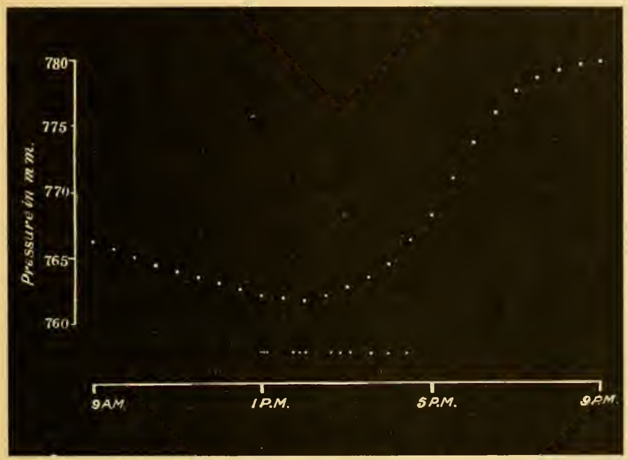

FIG. 58. Record of Exudation and of Pressure of the 'Weeping' Mango-tree

The lower record shows the rates of exudation at 1, 2, 3 and 4 P.M.; the upper record exhibits the variation of pressure from 9 A.M. to 9 P.M.

What then can be the difference, in the same zone of the trunk, which would account for the active exudation from the vent on one side, and the total absence of it from the auger-hole on the opposite side? In pursuing this enquiry I cautiously removed the bark and the underlying tissue round the vent. This led to the discovery of a large elongated cavity which was irregular in shape, the maximum length being one metre and the breadth 15 cm.

The cavity was formed by the decomposition of the alburnum, which had fallen to the bottom and become decomposed. Its outer boundary was the rind with its layer of phloem and cortex, which were all in a healthy condition ; the inner boundary was formed of duramen.

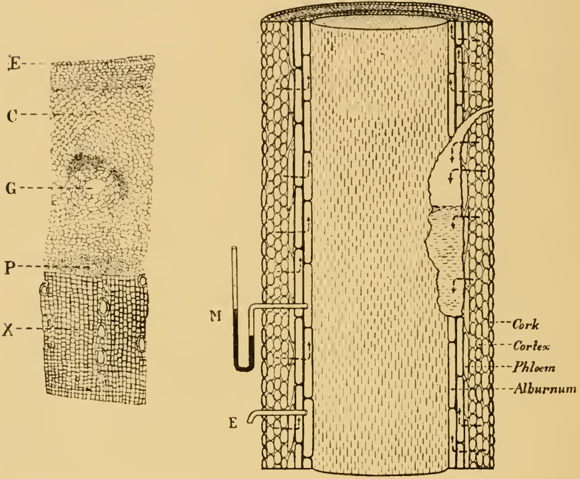

FIG. 59. Sections of the Mango Stem

Figure to the left is a magnified transverse section of a young stem. E, epidermis, C, extended cortex, G, gland, P, phloem, X, xylem. Figure to the right is a diagrammatic representation of the trunk with the cavity from which exudation takes place. The sap pumped laterally by the cortex is accumulated in the cavity. On the left side the laterally injected sap is rapidly removed by the alburnum which is under negative pressure on account of transpiration from leaves. The pressure is indicated by the manometer, M. No exudation took place through the drilled hole, E.

A transverse section of a young Mango-stem is shown in fig. 59 : to the right of the figure is seen a vertical diagrammatic longitudinal section of the trunk of the weeping Mango-tree. In the former E is the epidermis, under which a thick bark is formed in older trees ; C is the cortical tissue in which there are glands which secrete resin. The endodermis, forming the most internal layer of the cortex, abuts on the phloem, which is separated from the young xylem, the alburnum, by the cambium-layer : the rest of the xylem is the duramen.

We return to the question of the total absence of exudation from the drilled hole on the left side of the trunk and the copious outflow from the cavity on the right side ; this can only be due to the structural difference between the two sides, the presence of alburnum on the left and its absence on the right. The active cortex borders the cavity, and the excretion of the fluid that fills it can only be due to a lateral pumping action of the cortex. The cellular activity, as we shall presently find, is greatly enhanced by the local rise of temperature which takes place at 1 P.M. The cavity, which has been slowly filling up with the excreted sap, now becomes overcharged, and the plug of mucilage which closes the vent is suddenly forced out ; the removal of the obstacle is immediately followed by the rapid outflow which characterises the commencement of exudation.

On the left side of the trunk the alburnum is uninterrupted ; the active cortex injects water into the alburnum, in which it is rapidly conveyed to the transpiring leaves. There is therefore no exudation from the hole drilled on the left side.

The results given above furnish conclusive proof—(1) *that the pulsatory activity of the cortex propels the sap not only upwards but also in a lateral direction so as to inject it into the contiguous alburnum ; and* (2) *that the alburnum is a channel for the mechanical transport of water, the force of injection being supplied by the active cortex.*

We have still to explain the reason of the commencement of exudation punctually at 1 P.M. Further inspection of the tree showed that for the greater part of the day the leaves cast a shadow on the trunk. There was an opening, however, among the branches such that, during the course of the sun from east to west, sunlight fell directly upon the exuding portion of the trunk at 1 P.M., causing a local rise of temperature. Consequently, the cortex underneath had its activity greatly increased, and the resulting enhanced exudation caused a rapid rise of the level of the sap collected in the cavity. This expelled the closing plug, with a resulting sudden outflow of sap. Later in the day, the sun became hidden by the leaves, and the temperature underwent a rapid fall. The weeping of the tree consequently declined and became arrested in the evening.

SUMMARY

In the 'weeping' Mango-tree, exudation from a vent on the right side of the trunk took place daily, beginning at 1 P.M. and continuing till 5 P.M. The vent opened into a cavity formed by the decomposition of the alburnum, the outer wall of the cavity being formed by the uninjured cortex. The internal exudation, effected by active lateral pumping by the cortex, caused sap to accumulate in the cavity. The maximum internal exudation by lateral pumping took place at 1 P.M., when sunlight fell on the side of the trunk containing the cavity. The local rise of temperature caused a great enhancement of exudation by the cortex at 1 P.M., such as to set up a pressure sufficiently great to force out the plug of mucilage with which the vent was periodically closed.

There was no exudation from a hole drilled on the opposite side of the trunk. A manometer attached to that side exhibited a maximum negative pressure at 1 P.M., when the exudation from the vent was at its maximum; the negative pressure on the left side was due to maximum transpiration at 1 P.M., which caused rapid conduction of sap by the alburnum.

The difference of action on the two sides is thus due to the presence of the alburnum on the left side and its absence on the right side.

The above results afford conclusive proof that the alburnum is the channel for the mechanical transport of sap, and that the driving force for the lateral injection of sap into the alburnum is supplied by the activity of the cortex.

CHAPTER XIII

EXUDATION IN PALMS

The Indian Date Palm—The Palmyra Palm (*Borassus flabellifer*)—The maximum quantity of exudation in a season—The total yield of sugar —Diurnal variation of exudation in *Phœnix sylvestris*—Explanation of greater exudation at night—Diurnal variation of exudation in Palmyra Palm—The action of sunlight—Absence of root-pressure—Stimulus for initiation of exudation—The magnetic analogue of polar action of cells in absorption and excretion—Summary.

Many trees before the unfolding of leaves in early spring are filled with sap under considerable pressure, on account of which the sap exudes as soon as a hole is drilled into the tree. The exudation of sap by Palms appears to belong to a different class of phenomena, for which it has hitherto been impossible to offer any explanation. Molisch has shown that in the Palm *Arenga saccharifera* there is no root-pressure, yet the quantity of sap exuded from an incision may be as much as 4 litres a day. Exudation is even more copious in other Palms. In *Phœnix dactylifera* it is, according to Semler, as much as 10 litres a day, a value which has been regarded as exceptionally high, since Molisch did not obtain such large quantities.

The Indian Date Palm

My investigations have been carried out with two different species of Palm growing in Bengal, from which large quantities of sugar-containing sap are gathered every year, forming no inconsiderable portion of the sugar-supply in the province. The Indian Date Palm (*Phœnix sylvestris*) grows to a height of 30 to 40 feet. The sap is drawn from the upper end of the trunk. All the leaves situated below are cut off ; vertical thin slices are then cut at the top of the stem, and an inclined V-groove is made, in which is inserted a small drainage-pipe made of a piece of Palmyra Palm : this is led to an earthen pot suspended from above (fig. 60). According to the prevailing custom, the surface of the tree to be wounded is one which faces the sun, so that the exuding surface is stimulated by sunlight either in the forenoon or in the afternoon.

FIG. 60. *Phœnix sylvestris*
The stem is sliced for collection of sap in the pot.

The Date Palm is tapped for its sap during the months of November, December, January and February. The sap is drawn for four days at a time, with two following days for rest ; and it is collected on about sixty days in the season. The yield of sap is very considerable ; a tree growing in the dry lands of the Sijbaria Research Station gave an average of about 4 litres per day : another tree growing near a water-course gave as much as 19 litres per day ; and the yield of sap during the whole season is more than a thousand litres. The sugary sap is drunk fresh, or used for the manufacture of sugar ; it is also fermented for making intoxicating liquor.

The sap of the Indian Date Palm, as already stated, is drawn from November to February ; but it should not be inferred from this that the exudation takes place only in the winter months. I have been able to obtain it even in summer ; but it is not worth while doing so out of season. The reason for collecting the sap during the winter months is twofold : first, the amount of exudation is not so seriously affected by loss from transpiration as in summer ; and secondly, in hot weather the sap is spoilt by fermentation. Very special precautions are taken to prevent this even in winter by careful cleaning of the collecting pots ; in spite of this the sap is sometimes spoilt and becomes sour on particular days, when it becomes warm in consequence of change in the direction of the wind.

The Palmyra Palm

The Palmyra Palm (*Borassus flabellifer*) is a tree of very slow growth, and is said to live for more than a century. The tree attains a height of 100 feet (30 metres). The sap is drawn from the cut end of the spadix bearing the flowers ; about nine such spadices are borne at the top of the tree, some of which bear only male flowers, in March. In others the inflorescence bearing both male and female flowers appears about the middle of April.

Some of the leaves are removed before tapping the tree. An incision into the spadix is, by itself, ineffective in inducing exudation : a preliminary process is necessary, which consists in bruising the axis of the inflorescence and crushing the young flowers. The axis is also kneaded from above downwards. After going through this preliminary process for several days, a very thin slice is cut off from the tip of the inflorescence. The exudation then takes place with great rapidity. The wound, which becomes blocked by bacterial growth, has to be re-cut every day, the thinnest slice being sufficient for this purpose.

There is no choice of season for the collection of sap from the Palmyra Palm, since the inflorescence appears only in early summer. Fermentation is very pronounced at high temperatures, and very special precautions have to be taken to obtain the sap unfermented. Ordinary cleaning of the pot is found insufficient for the purpose ; the prevailing custom is to smear the vessel with quicklime and wash it afterwards. This antiseptic treatment is often successful in securing the fresh sap as a drink. But on hot days the sap ferments, when it is employed for the preparation of the intoxicating *toddy*.

The tree employed in my experiments was 30 feet in height. The exudation from a single spadix was 2100 c.c., and the total daily exudation from all the spadices was 11 litres. Trees may yield nearly twice this quantity. The sap is usually collected for four or five months in the year. The tree begins to yield sap at the age of fifteen years, and continues it for a further period of fifty years. The operation is discontinued one year in three. The total quantity of sap exuded by a single tree during its life may be as much as 120,000 litres.

The sugary sap contains about 0·25 gram of mineral solids per 100 c.c. It is very rich in sugar, the content being as high as 10 per cent. Since a Palmyra Palm gives out, as already stated, about 120,000 litres of sap, the yield of sugar from a single tree during its life may thus reach the enormous total of 12,000 kilograms.

Diurnal Variation of Exudation in Phœnix sylvestris

In order to determine the characteristics of exudation, a continuous record was taken from which the rate of exudation for every hour of the day and night was obtained.

FIG. 61. Record of Exudation from the Indian Date Palm for Twenty-four Hours

Each dot represents exudation of 50 c.c. of sap. Note separation of dots after 1 P.M. and closeness of dots about 3 A.M.

The Automatic Tilting Recorder, already described on page 134, was strapped high up in the tree. A short pipe allowed the sap to fall on to the tilting lever. This latter was adjusted so as to be upset after the collection of 50 c.c.

TABLE XXI.—SHOWING RATE OF EXUDATION FROM *Phœnix sylvestris* FOR EVERY HOUR OF THE DAY AND NIGHT

Time	Exudation per hour	Time	Exudation per hour
Noon	34 c.c.	Midnight	198 c.c.
1 P.M.	32 ,,	1 A.M.	204 ,,
2 ,,	40 ,,	2 ,,	212 ,,
3 ,,	50 ,,	3 ,,	210 ,,
4 ,,	62 ,,	4 ,,	206 ,,
5 ,,	80 ,,	5 ,,	186 ,,
6 ,,	112 ,,	6 ,,	142 ,,
7 ,,	136 ,,	7 ,,	94 ,,
8 ,,	164 ,,	8 ,,	56 ,,
9 ,,	190 ,,	9 ,,	43 ,,
10 ,,	196 ,,	10 ,,	38 ,,
11 ,,	194 ,,	11 ,,	36 ,,
Midnight	198 ,,	Noon	34 ,,

of sap. Each successive dot in the record thus represents the exudation of 50 c.c. of sap. Inspection of the record given in fig. 61 gives a vivid idea of the various rates at different times of the day and night. The dots are very wide apart from 11 A.M. to 2 P.M., the minimum rate being attained after 1 P.M. The dots, on the other hand, are closest about 2 A.M., when the rate of exudation is at its maximum.

Explanation of the Greater Exudation at Night

The total quantity of exudation from 6 A.M. to 6 P.M. was only 700 c.c., while that for the succeeding twelve hours of night was as much as 2,150 c.c., or three times as great. In seeking an explanation of this characteristic difference in the exudation during the day and the night, it is to be remembered that the total loss of fluid depends upon two factors: (1) the excretion by the leaves, and (2) the exudation from the wounded surface: consequently maximum transpiration should correspond with minimum exudation and *vice versâ*. The maximum transpiration would occur at the period at which the temperature of the leaves is at its highest. This is determined (1) by the highest temperature of the surrounding air which is attained at about 2 P.M., and (2) by the rise of temperature of the leaves by the direct action of sunlight, the intensity of which is at its maximum at noon. Hence the resulting temperature is at its highest between noon and 2 P.M., *i.e.*, at about 1 P.M. The maximum transpiration at 1 P.M. thus corresponds to the minimum exudation of 32 c.c. per hour. The temperature fell gradually after 2 P.M., with diminution of transpiration and corresponding increase of exudation, the latter attaining its maximum at night about 2 A.M. Sijbaria is situated in an open country and the minimum temperature there is attained earlier than in the town. The curve of exudation of this Palm (fig. 62) thus follows the general course of diurnal variation of temperature, but in an inverse manner, *i.e.*, maximum exudation at minimum temperature and *vice versâ*. I have been able to obtain independent confirmation that the exudation is actually diminished by transpiration from the leaves. After completing my observations with one particular Palm, I cut off the leaves which still remained at the top of the tree. This was found to enhance the normal exudation by 25 per cent.

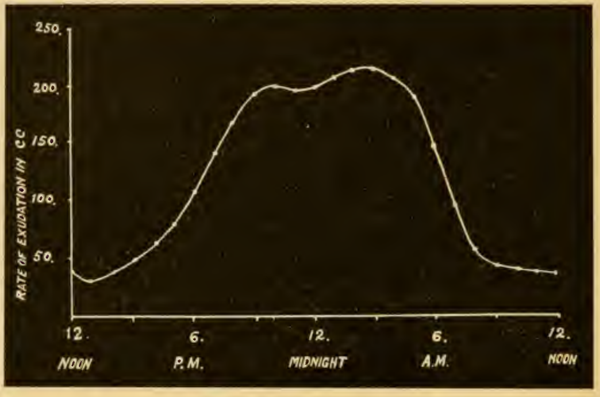

FIG. 62. The Curve of Diurnal Variation of Exudation in *Phœnix sylvestris*

There are additional causes which produce a slight modification of the loss by transpiration: among these may be mentioned the varying intensity of the wind, its changing direction, and the varying percentage of moisture which it contains. At Sijbaria the land and the sea breezes alternate, and after a lull in the evening the air-current increases in intensity; the wind also veers round. Neglecting these minor variations, the curve of exudation is seen to follow closely the diurnal variation of temperature. This is clear in the record of the Palmyra Palm, in which variation of temperature is also recorded (see p. 186, fig. 63).

Diurnal Variation of Exudation in the Palmyra Palm

I next describe the variation of the rate of exudation in the Palmyra Palm from hour to hour. An automatic record of the exudation was taken in the usual manner. The rate during successive hours of the day and night is given in the accompanying table. A thermograph was tied immediately above the spadix, and gave an automatic record of the variation of temperature.

TABLE XXII.—SHOWING THE RATE OF EXUDATION FOR EVERY HOUR OF DAY AND NIGHT (*Palmyra Palm*)

Time	Temperature	Exudation	Time	Temperature	Exudation
Noon	36·5° C.	45 c.c.	Midnight	25·7° C.	112 c.c.
1 P.M.	38·5° C.	40 ,,	1 A.M.	25·7° C.	112 ,,
2 ,,	40·0° C.	37 ,,	2 ,,	25·3° C.	115 ,,
3 ,,	36·5° C.	44 ,,	3 ,,	25·0° C.	119 ,,
4 ,,	42·5° C.	88 ,,	4 ,,	24·7° C.	118 ,,
5 ,,	38·0° C.	65 ,,	5 ,,	24·8° C.	107 ,,
6 ,,	32·0° C.	73 ,,	6 ,,	25·2° C.	97 ,,
7 ,,	28·7° C.	86 ,,	7 ,,	26·2° C.	87 ,,
8 ,,	27·0° C.	97 ,,	8 ,,	28·0° C.	78 ,,
9 ,,	26·0° C.	110 ,,	9 ,,	30·0° C.	67 ,,
10 ,,	25·5° C.	113 ,,	10 ,,	32·0° C.	60 ,,
11 ,,	25·5° C.	114 ,,	11 ,,	34·0° C.	52 ,,
Midnight	25·7° C.	112 ,,	Noon	36·5° C.	45 ,,

From the data given in the above table we find that, as the temperature rose from 36·5° at noon to 40° C. at 2 P.M., the exudation *became lowered* from 45 c.c. to 37 c.c. After the attainment of the highest temperature at 2 P.M., thermal noon, the temperature fell at 3 P.M. to 36·5°, and the exudation was enhanced to 44 c.c. Ignoring for the present the disturbance produced at 4 P.M., the temperature underwent a decline from 6 P.M. to 4 A.M. next morning, the fall being from 32° to 24·7° C. This was attended by an increase in exudation from 73 c.c. to 118 c.c. All these variations in the exudation in the Palmyra Palm are characteristically similar to those in the Indian

Date Palm : that is to say, the minimum exudation takes place at thermal noon, and the maximum at thermal dawn.

The Action of Sunlight

A sudden disturbance in the record occurred, as mentioned above, when the temperature rose abruptly from 36·5° C. at 3 P.M. to 42·5° C. at 4 P.M. Hitherto the rise of temperature had been attended by a fall in exudation, but now there was an apparent anomaly in the sudden enhancement of exudation from 44 c.c. at 36·5° to 88 c.c. at 42·5° C.

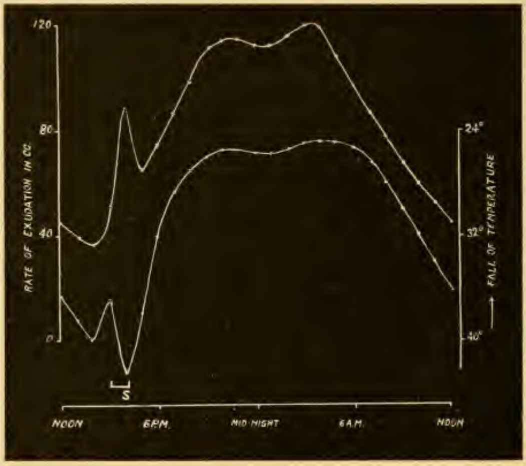

FIG. 63. The Upper Curve shows the Diurnal Variation of Exudation in Palmyra Palm, the Lower Curve the Diurnal Variation of Temperature; the Down-curve indicates a Rise and Up-curve a Fall

Note the general parallelism of the two curves which is disturbed by incidence of sunlight s on the spadix ; this induced local rise of temperature and enhancement of exudation.

The cause of this unexpected deviation at 4 P.M. was, however, found in the following observation. I was watching the record of exudation, when a sudden jump in it drew my attention to the intervention of some disturbing factor. On looking up at the tree, I found that sunlight had just fallen on the exuding spadix, which had previously been in the shade of the leaves overhead. Hitherto, the general rise of temperature had induced a relatively greater loss by transpiration, the result being a diminution of exudation with rise of temperature and *vice versâ* ; so that the curve of exudation had run a parallel course with that of temperature in which the down-curve indicates a rise and the up-curve a fall. But when the sunlight fell on the exuding spadix, the two curves diverged from each other (fig. 63).

The explanation of this is found in the fact that exudation is enhanced by a rise of temperature : the spadix had its temperature, and therefore also its exudation, suddenly increased by the sunlight which fell on it at 4 P.M. A parallel instance of enhanced exudation due to the thermal action of sunlight has already been noted in the ' weeping ' Mango-tree (p. 176).

The Absence of Root-Pressure

In Palms the exudation of sap appears to be quite independent of root-pressure. Molisch has, as stated before, failed to find any indication of it in *Arenga saccharifera.* The following investigation was undertaken to find out whether root-pressure is generally absent in Palms.

It should be remembered that the Indian Date Palm grows in a dry or even arid soil ; hence necessity compels the tree fully to exploit the scanty and precarious supply of water. For this it sends out numerous roots to a considerable distance. The number of roots was found to exceed a thousand, each about 1 cm. in diameter. I dug the ground to a depth of 12 feet (4 metres) without any prospect of reaching the end; the thickness of the individual roots remained almost unchanged. I followed another root to a lateral distance of 21 feet (7 metres) and yet the end was not in sight. The trunk of the tree is thus slowly charged with water absorbed by the enormously extended root-system. The fact that the tree is not entirely dependent on the immediate supply from the soil, but that it has a supply stored in reserve, is proved from results of two different experiments. I first tried the effect of copious irrigation; but it had no immediate effect in enhancing exudation. It is true that the exudation from trees growing near water-courses is relatively more abundant; but this is due not to any immediate action, but to the previous storage after slow and long-continued absorption of water from the soil.

I next cut down the Date Palm, which was exuding at the rate of 4 litres a day; the tree was therefore in a condition of vigorous exudation. After the felling of the tree, the cut ends of the stem did not, however, exude a single drop of sap; portions of the tissue taken from the interior of the trunk were found to be almost dry, and it was only after considerable compression that a small quantity of sap could be squeezed out. The above experiment proves that there is no root-pressure to cause exudation from the injured surface at the top of the tree, and that the sap is held in the trunk with great tenacity.

The result of the following observation is very striking and of much theoretical interest. After cutting down the tree, it was deprived of any supply of water from the soil. In spite of this the sliced stem in the upper portion of the tree continued to secrete sugar-containing sap for thirty-six hours. This shows that the exudation of sap is not immediately dependent on the absorption of water by the root, but that the secreting activity of the terminal wounded surface withdraws sap held in reserve in the trunk.

Stimulus for the Initiation of Exudation

We next consider the question of the active exudation from the surface of incision in the Palm. It has been shown that the exudation from the root-stock of *Cucurbita* is not solely due to root-pressure, but that the terminal layer at the cut surface also takes part in the process. The physiological activity of the terminal layer was demonstrated by the local action of dilute chloroform, which enhanced the rate of exudation (p. 141). The cells of the terminal layer also respond, as we have seen, to various agents such as light, temperature, and so on.

In the Palm the factor of root-pressure is absent; hence it is the layer of cells at or near the surface of incision that is specially concerned in the active secretion. This secretion of sugary liquid at the incised surface of Palm-stems resembles the secretion of a similar liquid by the nectaries of flowers and of digestive fluid by the glands of *Nepenthes*, since in all these cases the secretory energy is developed in the cells of the secreting tissue. But the secreting tissue of the Palm differs from the glandular tissues in that its activity is not spontaneous. The normal inactivity of the wounded surface is shown by the fact that there is no exudation when the vertical slices are first made in the upper part of the stem of the Date Palm, nor when a terminal section is made in the spadix of the Palmyra Palm. As already stated, exudation is initiated *in the former only after slicing the stem repeatedly for nearly a week, and in the latter, after special preliminary treatment of the spadix for several days.*

What now is the explanation of these facts? I have shown elsewhere that a living tissue may be roused from a state of inactivity to rhythmic or multiple activity by the action of an adequate stimulus. A very inactive tissue would naturally require a very strong stimulus, or a succession of stimuli which become effective by their cumulative effects. In moderately excitable tissues, on the other hand, a less intense stimulus would be sufficient. Thus the dormant activity of the pulvinule of *Desmodium* may be revived by the application of a moderate stimulus. Again, isolated cardiac tissue comes to a state of stand-still; when in this state, application of a prick is found to arouse the quiescent tissue to renewed multiple activity.

I now describe the special treatment to which the inflorescence of the Palm has to be subjected in order to induce exudation. For this purpose, two different processes have been elaborated in different countries, which may aptly be described as 'butting' and 'milking,' from the not very far-fetched analogy of the action of the calf to make the cow yield her milk.

For the exudation of the sap from the inflorescence of the *Arenga* Palm, very strong and repeated stimulus is essential; 'the Malayas, during four or five weeks previous to flowering, inflict repeated blows on the base of the bole with a wooden hammer; then, when the inflorescence is cut off, secretion begins at once.'[1]

In Bengal the practice with the inflorescence of the Palmyra Palm is a little different. The long spadix is held tightly between the fingers and kneaded from above downwards, the process being similar to the milking of a cow. This potential milking process is repeated day after day for more than a week. Section of the tip of the spadix is then followed by the exudation of sap.

The methods employed in inducing exudation from the previously inactive tissue of the Palm are thus seen to be fundamentally similar. They have one object in common, namely, the arousing of the dormant activity by the repeated application of a mechanical stimulus, which may be repeated cuts, repeated blows, or repeated kneading. As the result of this treatment, the inactive tissue becomes as active as the glandular tissue, and is thus able to maintain the exudation even though there is no root-pressure to urge it.

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[1] Jost, *Plant Physiology*, Supplement, p. 13.

With the exception of the stimulus necessary to initiate it, the process of exudation in Palms is in every way similar to that of the root-stock and of the tree with leaves. The diurnal curves of exudation of *Cucurbita* with side-branch (fig. 52), that of the Rain-tree (fig. 54), and those of the *Phœnix* and the Palmyra Palm are very much alike. The exudation, in all these cases, attains its maximum at thermal dawn, and its minimum at thermal noon.

Molecular and Cellular Model

The ascent of sap, the excretion by the leaf, and the exudation from the cut surface of a root-stock, are thus seen to be all brought about by cellular activity, which extends throughout the length of the tree. Under normal conditions, the tree as a whole may be regarded as having two poles, as it were, one at each end, the absorption by the root at one end being distinguished by a plus sign, and the excretion by the leaf at the opposite end by a minus sign. The plant may thus be compared to a bar-magnet with positive and negative poles, north and south, at the ends, the intermediate region being apparently neutral. According to the molecular theory of magnetism, the smallest particle in a bar-magnet is itself a magnet with two poles, the juxtaposition of two opposite poles producing the apparent neutralisation in the middle. The existence of the opposite poles which neutralise each other may easily be demonstrated by breaking the bar-magnet across at the horizontal line, when a positive or north pole will be found below the upper section and the opposite south pole above the lower section. A similar cut in the stem will bring

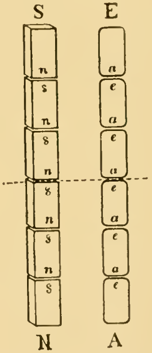

FIG. 64. The Molecular and Cellular Model: plant, right; magnet, left

out the opposite functional polarities above and below the line of separation. The lower end of the cut stem A will be found to absorb, and the upper end of the root-stock E to excrete water. In the limit each cell must exhibit this polarity, its lower end absorbing water and the upper end excreting it (fig. 64); without this, the one-directioned propulsion of sap would be an impossibility.

It will be seen that in the ascent of sap it is quite unnecessary to postulate two forces, one pulling from above, and the other forcing from below. For an identical cellular activity would appear as that of a suction-pump, or as that of a force-pump, according to the particular point in view. We thus arrive at the theoretical conception that it is the pulsation of the individual cell which is ultimately concerned in the maintenance of the ascent of sap. I go on, in the following chapters, to describe new experimental methods by which it has been possible, not only to detect, but also to record, the pulsation of an individual cell.

SUMMARY

The maximum secretion of sugar-containing sap by *Phœnix sylvestris* is 19 litres, and by the Palmyra Palm 20 litres per day. The total quantity of sap exuded by the Palmyra Palm during its lifetime may be as high as 120,000 litres, the quantity of sugar yielded being 12,000 kilograms.

The Palm-tree exhibits a diurnal periodicity of exudation, which follows the general law established in regard to leafy trees, that the minimum exudation occurs at thermal noon, and the maximum at thermal dawn.

Local rise of temperature, the result of temporary exposure to sunlight, induced an enhancement of exudation in the Palmyra Palm, the excretory tissue responding in the same manner as the cells which effect the ascent of sap.

There is no root-pressure in the Palms; the water absorbed by the extended system of roots is stored and held tenaciously in the trunk; after cutting down the tree the surface incision at the top of the trunk continues for a time to secrete sap. A layer of cells at or near the surface of incision is thus the seat of the secretory activity.

The secretory activity of the terminal layer is brought into play by the intense stimulation caused by repeated cuts, by repeated blows, and by repeated kneading.

CHAPTER XIV

DETERMINATION OF VELOCITY OF THE ASCENT BY THE ELECTRIC METHOD

Electric variation with change of turgor—Electrometric determination of velocity—Galvanometric determination—Shock-effect of the hydrostatic blow—Simultaneous determination of velocity of ascent by mechanical and electrical methods—Determination of velocity by the Di-phasic method—Summary.

In the investigation of the ascent of sap, we have hitherto employed only the method of Mechanical Response, in which advantage is taken of the erectile movement caused by the increase of turgor due to the ascent of sap. We turn now to an independent method for the detection and measurement of the rate of ascent of sap, which will be found to extend our scope of investigation and to lead to the discovery of many phenomena which are beyond the scope of the mechanical method.

This new method is electrical. I have shown in my work on Comparative Electro-Physiology that the electric condition of a tissue undergoes a definite variation under changes of turgor ; a *diminution* of turgor induces an electric change to galvanometric *negativity,* while an *increase* of turgor induces, on the other hand, an electric change to galvanometric *positivity.* The accompanying table shows the mechanical and electrical concomitants of the changes of turgor in the tissue. A sudden diminution of turgor with contraction occurs under excitation, and a slow diminution of turgor is produced under increasing drought. An increase of turgor is, on the other hand, produced by the ascent of sap after irrigation.

TABLE XXIII.—SHOWING THE EFFECTS INDUCED BY VARIATION OF TURGOR

Effects of diminution of turgor caused by drought or by stimulus	Effects of increase of turgor caused by the ascent of sap
Contraction	Expansion
Fall of the indicating leaf	Erection of the leaf
Induced galvanometric negativity	Induced galvanometric positivity

A plant under drought has its turgor diminished throughout its length. If now we make two electric contacts, A with the stem, and B with a distant leaf, the electric conditions of the two points will be more or less similar, and the galvanometric spot of light will remain stationary. Irrigation will, however, cause an ascent of sap, which will reach the lower contact A earlier, and induce an enhancement of turgor at that point. This will at once be signalled by a sudden electric change to positivity at A, represented in the record as an up-curve. This arrangement will be described as the Mono-phasic method. The second, the Di-phasic method, will be described later.

Electrometric Method of Determination of Velocity

As the electric resistance between the first and the second contacts is very great, it appeared to me that an electrometer might prove to be a suitable instrument for this research, since its indications are independent of the resistance of the circuit. I am not aware that the Quadrant Electrometer has ever yet been used for physiological investigations. The prevailing impression is that it is very difficult to maintain the high insulation of the circuit necessary for the maintenance of the electrification of the needle, and that the indication of the instrument is liable to be disturbed by external electric disturbances. I have, however, been able to render the method not only sensitive but free from external disturbances. No difficulty was experienced in maintaining the charge of the needle constant. The sensitiveness could be raised so as to give a deflection of 1 mm. for a difference of potential of 0·001 volt. The zero-position of the reflected spot of light was found to remain steady for days in succession.

FIG. 65. The Electrometric Record for the Determination of Velocity

Irrigation at arrow caused, after an interval of seven minutes, a sudden erection of the base line upwards, indicating induced electro-positivity of the first point of electric contact. [The time-marks are at intervals of twenty seconds.]

The advantage of this method is, that not only does it allow visual observation of the induced electric variation, but photographic records may be easily secured. The resistance of the circuit or its variation produces no change in the deflection; the latter, moreover, gives the absolute value of the induced electromotive force. The lower point of contact, A, is connected with the insulated pair of quadrants, the distant indifferent point being put in connection with the second pair, which is earthed.

The following is an account of a typical experiment for the determination of the velocity of the ascent in an intact specimen of *Impatiens* by the electrometric method. Suitable connections being made with the stem and the distant leaf, a continuous record was taken on a photographic plate. The record (fig. 65) exhibits certain feeble pulsations, the special significance of which will be explained in a subsequent chapter (p. 212). On irrigation at the point marked with an arrow, there was no immediate effect; but after an interval of seven minutes there was a sudden erection of the base-line towards electro-positivity, accompanied by two large pulsations. The increased turgor due to the ascent of sap to the first point of contact is thus signalled by a flexure of the base-line upwards. The absolute value of this induced positivity was found to be 0·04 volt.

The interval between the application of water and the hydro-electric response was, as stated before, seven minutes; the intervening length was 78 mm.; the velocity was therefore 11·2 mm. per minute, which we found to be the velocity of ascent in *Impatiens* in a 'moderate' condition (p. 41).

Galvanometric Determination of Velocity

Having determined the absolute value of the electromotive variation by the Quadrant Electrometer, we next employ the Galvanometer, with its relatively higher sensitiveness. In order to measure accurately the short interval of time, the reflected spot of light from the galvanometer is interrupted periodically at intervals of fifteen seconds. The record thus consists of a series of short vertical lines, and the successive spacings represent intervals of fifteen seconds. The dotted record is thus its own chronogram.

On irrigation of a particular specimen of *Impatiens*, a very strong positive response occurred after two minutes

Fig. 66. Galvanometric Determination of Velocity of Ascent

Irrigation at arrow. The galvanometric positivity indicative of arrival of hydraulic wave occurred after 11 dots, *i.e.*, 2′ 45″. Note the preliminary negative twitch due to hydrostatic blow. (Successive dots at intervals of 15″.)

and forty-five seconds. The length through which the sap ascended was 80 mm., the velocity of ascent being thus 29 mm. per minute, that is to say, nearly three times greater than in the previous case. In the record (fig. 66) the normal positive is seen to be preceded by a transient negative response, indicative of an excitatory contraction and diminution of turgor. This must have been brought about by the shock-effect of the hydrostatic blow which preceded the rapid ascent of sap.

Shock-effect of the Hydrostatic Blow

Whilst investigating the transmission of excitation in *Mimosa,* I became aware that under certain circumstances a sudden variation of hydrostatic pressure may act as a mechanical blow upon the sensitive pulvinus. Under moderate stimulation by electric shock applied at a distance, this hydrostatic disturbance does not occur, and the excitatory change proceeds with a definite velocity along the special conducting nerve. Thus in a given specimen the application of electric stimulus at a distance of 30 mm. from the responding pulvinus caused the fall of the leaf after an interval of 1·9 seconds, the velocity being thus 16 mm. per second. This velocity was found to be constant in successive experiments. If instead of the electric stimulus we employ a violent mode of stimulation, such as a cut or a burn, a hydrostatic disturbance occurs, which, travelling with great speed, delivers a mechanical blow on the sensitive pulvinus, causing a fall of the leaf almost instantaneously; this mechanical transmission is unlike the relatively slow point-to-point propagation of nervous excitation. The effect of the hydrostatic shock is thus an excitatory mechanical contraction, with the concomitant electric response of galvanometric negativity.

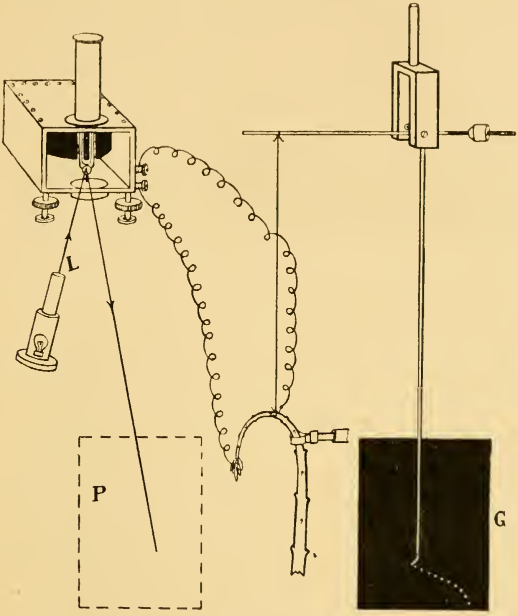

FIG. 67. The Method of Simultaneous Determination of the Velocity of Ascent by the Mechanical and Electric Methods

The mechanical lever-recorder is on the right with recording glass plate G; the galvanometer is to the left; light, L, reflected from its mirror falls on the photographic plate P. The curved part of the stem is connected by a string with the recording lever; the same point is in electric connection with the galvanometer.

A similar transmission of a hydrostatic blow may be expected in plants in which the roots on irrigation absorb water with great activity, which gives rise to a hydrostatic disturbance. This will travel with great rapidity, and by its shock-effect cause contraction and galvanometric negativity at the distant responding point. The quick hydrostatic impulse will be followed by the slow hydraulic wave with its positive electric response indicative of expansion. The preliminary negative and the consequent positive in fig. 66 are thus probably due to the hydrostatic and hydraulic effects respectively.

In the mechanical records of the ascent of sap hitherto obtained, no corresponding preliminary negative response had been noticed. The explanation of its absence may be either (1) that such contractile effect, even if it took place, was too small to be detected by the low magnification of the record ; or (2) that the response was transitory, and was therefore missed in the interval of the successive dots, which was usually one minute. I therefore undertook an investigation to find out whether, under the given conditions, an excitatory negative mechanical response occurred preceding the normal erectile response. For this the recording plate was maintained in oscillation at intervals of fifteen seconds, and the magnifying power of the recording lever was at the same time increased. I also arranged for the simultaneous record of the mechanical and electric responses.

Simultaneous Determination of Velocity by the Mechanical and the Electric Method

In the experiments hitherto described to determine the velocity either by the electric or by the mechanical method, the specimens employed were necessarily different. Since the physiological condition of any two plants is probably not identical, the values obtained by the two methods cannot be compared with each other. For testing the relative reliability of the two methods, we must so arrange matters that the two records, mechanical and electrical, are obtained from an identical specimen. The agreement of the two results will prove the accuracy and reliability of the two methods.

The Method of Record.—The experimental arrangements are as follows: the bent portion of the drooping stem is attached to the Mechanical Recorder by a thread, the oscillation of the smoked plate being once in fifteen seconds. Galvanometric connections are also made with two points, one on the curved portion of the stem, and the other on a distant leaf. The reflected spot of light from the galvanometer mirror falls on a photographic plate, which descends at the same rate as the smoked glass-plate of the Mechanical Recorder (fig. 67). The source of light for the galvanometer record is a 4-volt pea-lamp. The oscillating part of the Mechanical Recorder periodically

FIG. 68. Simultaneous Mechanical (lower curve) and Electric (upper curve) Records, in Determination of the Velocity of Ascent: irrigation at arrow

Note simultaneous negative and positive responses in both.

makes and breaks the electric light circuit. The successive dots in the two records represent the same interval of time, namely, fifteen seconds.

TABLE XXIV.—THE RATES OF TRANSMISSION OF HYDROSTATIC IMPULSE AND OF THE CONDUCTION OF SAP

Specimen	Length	Transmission period of hydrostatic impulse	Velocity of hydrostatic impulse	Period of water conduction	Velocity of ascent of sap
	mm.	secs.	mm. per min.	secs.	mm. per min.
I.	90	60	90	240	23
II.	80	45	106	195	24·5
III.	110	60	110	255	26

The specimen employed for the following experiment was in an optimum condition. The simultaneous records given in fig. 68 exhibit the very striking similarity between the mechanical and electrical responses. The hydrostatic shock-effect occurred simultaneously in the two, exhibited by a downward excitatory twitch in the mechanical, and a downward excitatory deflection in the electric curve, indicating galvanometric negativity. The shock-effect, due to transmission of hydrostatic impulse, occurred in both after 4 dots, or one minute after irrigation. As the intervening length of stem was 90 mm., the velocity of the hydrostatic impulse was 90 mm. per minute. There was a quick recovery from the excitatory effect. The conducted water next reached the responding region and gave rise simultaneously to positive responses in both—an erectile movement in the mechanical, and an upward deflection, indicating galvanometric positivity, in the electric record. As this hydraulic response occurred four minutes after the application of water, the velocity of ascent was 23 mm. per minute. The hydrostatic effect is thus seen to be sharply defined from the effect of the conduction of sap, the velocity of which has been determined by two different methods with identical results. I give in Table XXIV. the detailed results of several experimental determinations with different specimens, which, on account of their different physiological condition, exhibited different rates of conduction. The transmission period obtained by the mechanical and electrical response, as already stated, was the same.

Determination of Velocity by the Di-phasic Method

The employment of this method is of much theoretical interest. Instead of making the second electric contact at a distant indifferent point, we make it with the stem itself at a certain distance from the first. When the water of the ascending sap reaches the first contact, the electric signal is given of galvanometric positivity at that point. This deflection will remain constant for a certain length of time. But as the water, continuing its ascent, reaches the second contact, there will be produced a galvanometric positivity at that point which will cause a sudden reversal of the previous deflection of the galvanometer. Suppose the distance from the root to the first contact A is D, and the time-interval between the application of water and the first electric response is T, then

$$V = \frac{D}{T} \quad . \quad . \quad . \quad . \qquad (1)$$

If the interval of time between the first response and the subsequent reversal be t, and the distance between the two contacts l, then the velocity V' of transport between the two points will be

$$V' = \frac{l}{t} \quad . \quad . \quad . \quad . \qquad (2)$$

The distance from the root to the first contact cannot be determined as accurately as the distance between the two contacts. Hence the determination of the velocity by (2) will be the more accurate.

The specimen employed in the following experiment was not in an excitable condition, so the disturbing element of the hydrostatic blow was absent. The first positive electric response occurred two minutes and fifteen seconds after the application of water to the root. The distance D was 40 mm.

$$V = \frac{40}{2 \cdot 15} = 18 \text{ mm. per minute.}$$

The distance *l* between the first and the second electric contacts was 55 mm., and the electric reversal took place three minutes and fifteen seconds after the first electric response. The velocity is therefore

$$V' = \frac{55}{3 \cdot 15} = 17 \text{ mm. per minute.}$$

The two velocities are thus seen to be practically the same.

SUMMARY

Increase of turgor is attended by an electric change to galvanometric positivity, while diminution of turgor induces the opposite change to galvanometric negativity.

The ascent of sap to any point (causing an increase of turgor) is thus signalled by a deflection of galvanometric positivity.

Simultaneous records obtained by the mechanical and electric methods give identical values for the velocity of the ascent of sap.

When two electric contacts are made on the stem, one above the other, the positive electric response takes place first at the lower contact; the ascending water then reaches the upper contact and causes a reversal of the previous electrical response. The interval between the two responses is the time taken by the sap to travel through the intervening distance. The variable time lost in absorption by the root is thus eliminated in the Di-phasic method.

In plants in a vigorous condition there is a quick absorption of water which causes a hydrostatic impulse; this, travelling with great rapidity, delivers a mechanical blow at the distant responding point, causing an excitatory response of contraction and galvanometric negativity. The records of both mechanical and electrical response in an excitable specimen exhibit this preliminary negative, followed by the normal positive due to the ascent of sap.

CHAPTER XV

DISCOVERY AND RECORD OF THE PULSATION OF AN INDIVIDUAL CELL

The lectric Probe for detection of pulsation in the interior of the plant—Turgor and electric variation during a single pulsation—Electric pulsation of *Desmodium*—Periodic groupings of pulsations—Record of pulsation of a single cell—Cellular pulsation in herbaceous plants—Pulsating cells in trees—Pulsatory activity modified under variation of temperature—Record of pulsation by Einthoven galvanometer—The period of a single pulsation—Summary.

A DETAILED account has been given in the preceding pages of the ascent of sap and its diverse manifestations. The transport of sap has been shown to be brought about by the co-operating activity of numerous living cells, such activity being appropriately modified under physiological variations.

The plant, as a whole, may be regarded as a machine for pumping water from the soil and excreting it outside, in which the active cells concerned in the ascent of the sap act as a series of pumps arranged in a vertical row. We have a mechanical model of such a cellular pump in an india-rubber bulb, such as is used for spraying and other purposes : the contractile down-stroke causes an expulsion, and an expansive up-stroke brings about a suction of water. The cellular pumps may likewise be visualised in action, with alternate contractile down-stroke and expansive up-stroke. The former causes an expulsion of water from the cell with resulting diminution of turgor ; the expansive up-stroke sucks in water, with concomitant increase of turgor.

A steady propulsion of water may be maintained by the uniform rhythmic action of a vertical series of such cellular pumps. When the up-stroke is equal to the down-stroke, the absorption and expulsion will be equal, and the average turgor of the cell will remain constant, though after the completion of each up- or down-stroke a variation of turgor will occur above and below the mean value. Complications are likely to arise when the up- and down-strokes are unequal.

All life-movements must ultimately be due to the elementary activities of individual cells. As in the study of chemical phenomena we strive to get an insight into the molecular or atomic activities, so also in the investigation of the dynamics of life a very great advance will be assured if we can get access to the smallest unit of life, the individual cell, or the ‘ life-atom ’—a congregation of which constitutes the living organism.

But the pulsatory movement of a cell is ultra-microscopic, and its detection may well appear to be beyond the range of possibility. However, the detection of ultra-microscopic movements is not so hopeless as it has been assumed to be, for the Crescograph, which I have devised, enables us to obtain a magnification of from ten to a hundred million times. This would be sufficient to detect not merely cellular but also atomic movements. The difficulty of recording cellular pulsation does not therefore arise from a lack of sensitiveness in the instrument, but from the practical impossibility of attaching a single cell to the Crescograph.

I have, however, been able to overcome the difficulty of securing contact with an individual cell by the employment of the Electric Probe, which I devised for my ‘ Investigation on the Localisation of the Geo-perceptive Organ.’[1] One terminal of a sensitive galvanometer is connected with the Probe, which is thrust into the geo-perceptive stem, step by step, the other terminal being connected with a distant indifferent point. When the stem is laid in a horizontal position, a particular layer becomes stimulated under geotropic action. As the Probe enters the stem, it begins feebly to pick up the excitatory electric change due to the geotropic stimulus. A sudden enhancement of this occurs when the Probe reaches the

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[1] *Life-Movements of Plants*, vol. ii, 1920, Longmans.

geo-perceptive layer itself, the response of galvanometric negativity being now at its maximum. As the Probe passes beyond the sensitive layer, the electric indication rapidly disappears. This method is extremely delicate, and it is thus possible to localise the particular layer of cells inside a plant which perceives and responds to a stimulus. I have also been able to localise by the Probe the particular strand in the interior of the petiole of *Mimosa* leaf which functions as a nerve along which excitatory impulse is being transmitted.[1]

We will now try to find out whether it is at all possible to localise by means of the Electric Probe the active cells in the interior of the plant which, by their rhythmic activity, cause the propulsion of the sap. The characteristic of such a pulsating cell is that it undergoes alternate expansion and contraction, the former being attended by the absorption of sap and increase of turgor, and the latter by expulsion of sap and diminution of turgor.

In an ordinary non-rhythmic cell, the state of turgor is normally constant, and its electric potential, therefore, remains unchanged. But in a pulsating cell there is a series of alternate expansions and contractions, an up-stroke followed by a down-stroke: consequently, the rhythmic cell will exhibit periodic fluctuations of turgor below and above the mean. I have already shown that an expansion and an increase of turgor may be electrically detected by galvanometric positivity, and a diminution of turgor by galvanometric negativity. It should therefore be theoretically possible to detect these pulsations by putting the rhythmic cell in connection with a galvanometer by means of the Electric Probe, the other contact being made with an indifferent point. The expansive up-stroke of the cell, with the phase of increased turgor, would be detected by a positive, and the contractile down-stroke, with diminution of turgor, by a negative electric variation. The galvanometer spot of light would reveal, by its alternate swings to the right and to the left, the

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[1] 'On Dia Heliotropic Adjustment of Leaves,' *Roy. Soc. Proc.*, B. vol. 93.

invisible pulsations of the active cells in the interior of the plant.

TABLE XXV.—TURGOR AND ELECTRIC VARIATION DURING ONE COMPLETE PULSATION

Phasic change	Turgor variation	Electric variation
Expansive up-stroke	Increase of turgor	Electro-positivity
Contractile down-stroke	Diminution of turgor	Electro-negativity

The tabular statement given above will explain the different phases of the pulsating cell, with their electric concomitants.

Electric Pulsation in the Desmodium Leaflet

Having explained the theory of the electric detection of pulsation in rhythmic cells, we shall next try to find out whether this can be rendered practicable for experimental purposes. In demonstration of this I will first give an account of the electric pulsations which were recorded with the leaflet of *Desmodium gyrans*. The pulsatory activity of its pulvinule is quite evident from the automatic up-and-down movements of the leaflet. The period of a single pulsation under favourable circumstances is as short as a minute ; in a sluggish condition the period may be lengthened to five minutes or so. In the mechanical record we notice various types, ranging from irregular to uniform pulsations ; the pulsation of a detached leaflet is often irregular, probably from the shock-effect of amputation. If the preparation is kept for a length of time under favourable conditions, the pulsations tend to become uniform ; they often exhibit periodic groupings similar to those seen in the record of pulsations of the isolated animal heart.

As regards the mechanics of the pulsatory movement of the leaflet of *Desmodium*, we may, for the purpose of simplicity, ignore the feeble action of the upper half of the pulvinule, the lower half being relatively far more effective.

In the periodic movement of the leaflet, the expansion and enhancement of turgor of the lower half cause the up-movement ; contraction and diminution of turgor, on the other hand, give rise to the down-movement. For the electric determination of these pulsations we make suitable connections with a sensitive galvanometer, the first contact being made with the lower half of the pulvinule, and the second contact with the inactive sub-petiole. After this we observe very remarkable manifestations of electric pulsation, in which the up-stroke of galvanometric positivity corresponds with the expansive up-movement, concomitant with increase of turgor, of the pulvinule. The down-stroke of the electric pulsation is, on the other hand, concomitant with the down-movement which results from contraction and diminution of turgor. It has to be borne in mind that the electric pulsation is not due to the mechanical pulsation as such, for if we hold the leaf and thus prevent its up-and-down movement, the electric pulsation is found to persist. Both the mechanical and electric pulsations are but different indications of the periodic changes of turgor of the active cells. I reproduce the galvanograph of the electric pulsations of the leaflet, which are here seen to exhibit periodic groupings (fig. 69), as is often found in the record of the mechanical pulsations of the leaflet. Other electric records exhibit different types ranging from the irregular to uniform pulsations.

FIG. 69. Record of Electric Pulsations of the Pulvinule of *Desmodium* exhibiting Periodic Groupings

Detection and Record of Cellular Pulsation

In attempting the detection and record of the pulsating cells in the stem, we follow the same procedure as in the case of the *Desmodium* leaflet. Of the two contacts with a sensitive galvanometer, one is made with a distant indifferent point, such as a dying or dead leaf in which all life-activity is arrested or abolished. The other contact is made with the stem in which ascent is taking place, by a fine platinum wire. As the wire is gradually thrust into the stem, the sub-epidermal cells give no indication of any pulsation ; but as soon as the point of the wire comes in contact with an active cell in the deeper tissue, the electric pulsations become very vigorous, as will be seen in the records obtained.

FIG. 70. Record of Cellular Pulsations in *Impatiens*
Note periodic groupings.

FIG. 71. Record of Regular Cellular Pulsations in *Musa*

The records of the cellular electric pulsations thus obtained exhibit characteristics similar to those shown in the records obtained with the *Desmodium* leaflet. There are both irregular and regular pulsations ; and they sometimes exhibit periodic groupings as in fig. 70, which is a record obtained from *Impatiens*. The remarkable similarity between this and the record of *Desmodium* (fig. 69) is very striking. The next record (fig. 71) shows the uniform pulsations given by the petiole of *Musa*.[1]

Cellular Pulsation in Trees

The first records which I attempted to obtain were from herbaceous plants, as they are easier to manipulate. A misgiving may exist that cellular activity is not operative in tall trees, other agencies being presumably concerned in the transport of sap to great heights. Three tall trees happen to grow in the grounds of the Institute, and these gave me an opportunity for investigating the subject. The first is a Mango-tree, the second is a *Ficus religiosa*, and the third a Cadamba (*Nauclea cordifolia*). The last two grow to a height of 30 feet (10 metres) or more. Suitable electric connections were made with a young branch near the top of the tree, and the wires were led to the recording galvanometer inside the laboratory. The cellular pulsations were found, under favourable conditions of light and warmth, to be very active, in fact even more vigorous than in herbaceous plants. In fig. 72 is seen the record of the uniform pulsations of the Mango-tree; fig. 73 gives the record of cellular pulsations of *Ficus*, in which we observe periodic groupings. The *Ficus* was in a state of disturbance owing to the action of the wind, which caused flutterings of its numerous leaves. The record of the pulsations is therefore not uniform, but is characterised by periodic groupings. Cadamba also gave similar results.

A very interesting fact in connection with the cellular pulsations is that their vigour is dependent on favourable physiological conditions. The records given above having been taken during winter, the pulsations were found to

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[1] The minor fluctuations in the electric record, fig. 65, of the velocity of ascent of sap, are now understood to have been due to cellular pulsations.

be very feeble in the cold morning. Satisfactory records could therefore be obtained only at midday, when warmth increased the cellular activity and thus enhanced the amplitude of pulsation. I had occasion to repeat the experiment in summer, when the temperature at midday was 40° C., which is above the optimum-point. This caused a great enfeeblement of the pulsation, so that it was only by experimenting early in the morning that it was possible to secure any satisfactory record during the summer.

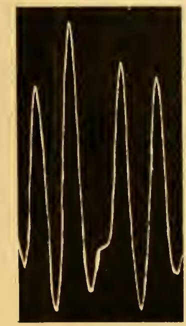
FIG. 72. Record of Cellular Pulsations of the Mango-tree


FIG. 73. Record of Cellular Pulsations of *Ficus religiosa*

Record of Cellular Pulsation by Einthoven Galvanometer

The electromotive variation induced by cellular pulsation is about a millivolt or so, and the resistance of the circuit is very high, being about a million ohms. For taking a record of cellular pulsation it was therefore necessary to use a very sensitive D'Arsonval galvanometer, which gave a deflection of 1 mm. for a current of 10^{-10} ampere. The inertia of the suspended coil was too great for very accurate determination of the period of a single pulsation. In this respect the Einthoven galvanometer offers a great advantage, since its exceedingly thin string follows the most rapid variation in the impressed electromotive variation Its disadvantage is that the sensitiveness of the instrument is very much less than that of the D'Arsonval galvanometer.

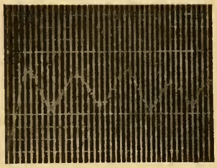

FIG. 74. Record of Cellular Pulsations in *Nauclea*, taken by the Einthoven Galvanometer

The successive horizontal lines represent the electromotive force, one small division being equal to 0·1 millivolt. The successive vertical lines represent intervals of a second. The period of complete pulsation is 13·5 seconds.

I hoped, however, to obtain a record of the pulsations even with the Einthoven galvanometer by taking advantage of conditions favourable to the pulsatory activity of the plant. Unfortunately the recording apparatus was ready only in May, when the prevailing high temperature had caused a depression in the cellular activity. In spite of this I was fortunate enough to obtain several records early in the morning which proved to be fairly satisfactory. The recording plate was allowed to drop at a rate of about 1 mm. per second; the sensitiveness of the apparatus was so adjusted that successive divisions in the vertical scale represented an electromotive variation of a tenth of a millivolt. The record was obtained with *Nauclea*; the electromotive variation of the pulsating cells is seen to be 0·4 millivolt; the periods of successive pulsations are practically the same, being 13·5 seconds (fig. 74).

SUMMARY

The pulvinule of the leaflet of *Desmodium* exhibits periodic electric pulsations corresponding to the mechanical pulsations. The up-movement due to the sudden increase of turgor has an electric concomitant of galvanometric positivity; the opposite electric change to galvanometric negativity occurs during the phase of sudden diminution of turgor and fall of leaflet. The period of a single pulsation varies under different circumstances from one to five minutes.

The discovery and record of pulsation of the cells active in the propulsion of sap was made by the employment of the Electric Probe, which during its passage detected pulsatory activity in a particular layer in the tissue of the stem.

The electrical records of alternate galvanometric deflections of positivity and negativity afford evidence of the occurrence in the tissue of cellular pulsations consisting of periodic increase and decrease of turgor due to alternating expansion and contraction.

These cellular pulsations are enhanced by favourable physiological conditions, and are depressed by unfavourable conditions. They exhibit all the characteristics of the pulsations of the *Desmodium* leaflet, and of those of the animal heart.

The records obtained with an Einthoven galvanometer show that the period of a single pulsation may be as short as 13·5 seconds: the period of pulsation is often lengthened under cold to about three minutes.

The electromotive variation under the less favourable condition of excessive heat in summer was found to be 0·4 millivolt: under favourable circumstances it may be as high as several millivolts.

CHAPTER XVI

LOCALISATION OF PULSATING CELLS AND DETERMINATION OF WAVE-LENGTH

Localisation of active layer of pulsating cells in *Impatiens*—Localisation in *Brassica*—Amplitude of pulsation at different depths—Theory of the electric determination of wave-length—Successive electric maxima and minima—Determination of wave-length in *Chrysanthemum* and in *Musa*—Change of wave-length under physiological variation—Upsetting of the phase-difference by passage of electric current—Summary.

Having demonstrated that a layer of cells in the stem is in a state of active pulsation, an attempt was next made to localise this layer by means of the Electric Probe. One of the galvanometer terminals is connected with the Probe, and the other with a distant indifferent point in the plant (fig. 75). The fine Probe, insulated except at the tip, is then thrust into the stem step by step ; its passage gives

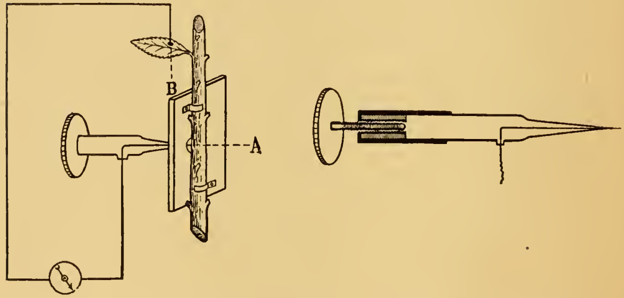

Fig. 75. The Electric Probe for the Localisation of the Active Layer

The point of the Probe enters the stem at A, the second electric contact being made with the distant leaf. The figure to the right is an enlarged view with the micrometric screw for the gradual introduction of the Probe into the tissues of the plant.

rise to a certain amount of irritation which causes a temporary abolition of the rhythmic activity of the cells. The protoplasmic recovery is, however, complete in the course of ten minutes or so. The record of cellular pulsation is then taken on a photographic plate, allowed to fall at an uniform rate by means of a clockwork.

Localisation of the Pulsating Cells in Impatiens

The Probe was introduced transversely into the stem by successive steps of 0·1 mm. No pulsation could be detected at the epidermis. As the Probe reached a depth of 0·1 mm. it detected a feeble pulsation: a similar result was obtained when it reached a depth of 0·2 mm. Owing to the residual after-effect caused by the insertion of the Probe, the base-line of the record was slightly displaced. At the next step, when the Probe reached a depth of 0·3 mm., the pulsations exhibited a sudden enhancement. This was so great that a part of the record went off the plate (fig. 76): evidently the Probe had come in contact with pulsating cells. As the Probe was thrust still deeper into the stem, the pulsating activity rapidly disappeared. When a transverse section of the stem was made at the

FIG. 76. Record showing the Amplitude of Electric Pulsations at Different Layers in *Impatiens*

Note the abrupt enhancement at a distance of 0·3 mm. from the surface, the particular layer being in the inner cortex; a portion of the record has gone out of the plate.

line of the passage of the Probe, it was found that the maximum activity had been detected when the Probe touched the internal layer of the cortex abutting upon the vascular tissue. The size of the active cells in *Impatiens* was found to be about 0·08 mm. in diameter. Contact of the Probe with the xylem did not cause any pulsation; this is highly interesting, proving that the dead xylem does not take any active part in the propulsion of sap.

The proper season for *Impatiens* was over by September, and all the specimens died by October. There were, however, other plants growing in the grounds of the Institute, among which were: Cauliflower (*Brassica oleracea* var.), Bean (*Vicia Faba*), Potato (*Solanum tuberosum*), and Tomato (*S. Lycopersicum esculentum*). I wished to find out whether it was possible to detect cellular pulsation in all these plants under normal field-conditions. The electric connections were made with the plant in the usual manner, the wires being led to the galvanometer inside the laboratory: they all gave evidence of cellular pulsation. In *Brassica* the electric pulsations were even more vigorous than those obtained with *Impatiens*: I will therefore describe in detail the experiment with this plant, the results obtained with others being given in a subsequent table.

Localisation of the Active Layer in Brassica

In order to localise the pulsating layer with greater accuracy, the Probe was introduced by successive steps of 0·05 mm. As the intervening distance between the epidermis and the pith was about 0·7 mm., this necessitated twelve successive observations, each requiring fifteen minutes; the total period of the experiment was thus lengthened to about three hours. Fortunately, the plant, under field-conditions, was in a state of exceptional vigour. The experiments had, however, to be completed preferably before afternoon, for there is a depression of activity towards evening. The pulsation was found to be feeble to a depth of 0·25 mm., when it exhibited an abrupt increase, the amplitude of pulsation being now 68 mm. A microscopic section after the experiment showed that the most internal layer of the cortex abutting upon the endodermis was at a depth of 0·26 mm. When the Probe was pushed further in by 0·05 mm., it reached the phloem, and the pulsating activity of that layer was found to be very much less, the amplitude being reduced to 15 mm. When the Probe reached the xylem, pulsation had practically ceased, the amplitude being reduced to about 1 mm.: it should be borne in mind that living cells are not altogether absent from the xylem. The activity in the pith was found to be so feeble as to be negligible.

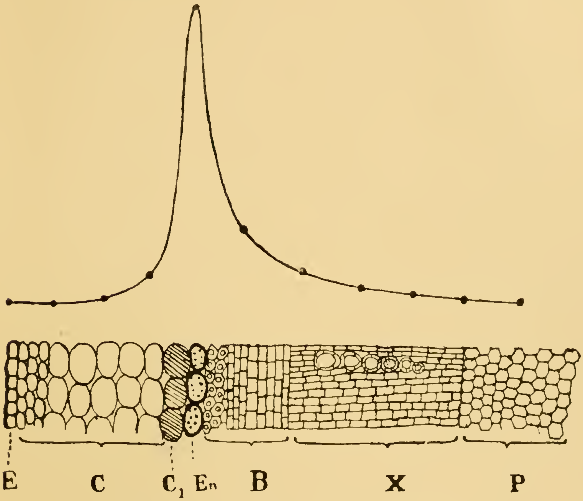

FIG. 77. Section of the Petiole of *Brassica*, and the Curve of Cellular Activity at Different Layers

E, epidermis; C, cortex; C_1, the active internal cortical layer; En, endodermis; B, phloem; X, xylem; P, pith. Note the sudden enhancement of activity at the layer C_1.

In the following table are given the quantitative values of the cellular activity of the different layers of cells. I also reproduce a drawing of the microscopic section, made along the line of passage of the probe, giving at the same time a curve representing the amplitude of pulsation at the different layers (fig. 77). The section, after being moistened slightly, must be examined immediately after the experiment; too long an immersion in water is apt to cause a swelling of the cells, which vitiates the measurements.

TABLE XXVI.—AMPLITUDE OF ELECTRIC PULSATION AT DIFFERENT LAYERS (*Brassica oleracea*)

Cells	Position of the Probe at different depths from surface	Amplitude of pulsation
Epidermal	Surface	0·0
Cortical	0·1 mm.	0·0
,,	0·15 ,, ...	1·0
,,	0·2 ,, ...	6·0
,,	0·25 ,, ...	65·0
Bast	0·3 ,, ...	15·0
,,	0·35 ,, ...	9·0
Xylem	0·4 ,, ...	5·0
,,	0·45 ,, ...	1·0
,,	0·5 ,, ...	0·0
Pith	0·7 ,, ...	0·0

Examination of the curve given in fig. 77 shows that the amplitude of pulsation attains a maximum at the most internal layer of cortical cells which abuts upon the endodermis, the curve undergoing an abrupt fall both outwards and inwards. The ascent of sap in the stem depends on cellular activity, which has been shown to be most marked in the internal cortex: we are therefore led to the conclusion that this innermost layer is the one that is specially active in the propulsion of the sap.

The experiment was repeated with *Lycopersicum*, *Vicia* and *Solanum*. The following is a tabular statement of the results. The active cells in *Solanum* were found at a relatively greater depth than in the other specimens.

TABLE XXVII.—AMPLITUDE OF ELECTRIC PULSATION AT DIFFERENT DEPTHS IN THE TISSUE OF THE STEM

Position of the Probe	Amplitude of pulsations of :		
	Lycopersicum	Vicia	Solanum
Surface	0	0	0
0·1 mm.	4 mm.	1 mm.	..
0·2 ,, ...	20 mm.	3 mm.	..
0·3 ,, ...	2 mm.	10 mm.	..
0·4 ,, ...	..	1 mm.	..
0·5 ,, ...	..	..	1 mm.
0·6 ,, ...	..	..	12 mm.
0·7 ,, - . . .	..	..	1 mm.

In all of these cases the cellular activity was localised in the innermost cortical layer ; in plants having an endodermis, the active layer abutted upon it ; in others it was contiguous to the phloem. Accurate localisation of the active layer is facilitated by the fact that the rise of activity detected by the Probe during its approach, and the fall of activity during its recession, are very abrupt. This will be understood from the mean results of observations upon four different species of plants. When the Probe was in contact with the active cortical layer, the mean amplitude of pulsation was 84 mm. ; at a centrifugal distance of 0·1 mm. from this layer, the amplitude showed a decline to 6 mm. ; and at a centripetal distance of 0·1 mm. it was only 5 mm.

All living cells may exhibit pulsation to a greater or less degree : the activity of the internal cortex is, however, exceptionally great. Thus there is, in the stem of dicotyledonous plants, a cylindrical sheath, a few cells thick, surrounding the vascular tissue, which subserves the rapid conduction of sap. For reasons shortly to be given, the cellular pulsations of this layer propel the sap preferentially upwards. The functional xylem-vessels are situated very near the active cortex, and in the case of *Brassica* are only 0·15 mm. distant from it. The injection of sap into the xylem may, therefore, be accomplished without difficulty or delay during the phase of expulsive contraction of the pulsating cells in the cortex. The inactive xylem may be regarded as a reservoir, the water being pumped in or withdrawn according to circumstances.

These results also bring out the important fact that some of the important physiological organs are grouped in the closest proximity to each other. Passing from the outside to the centre, we first encounter the active cortex which maintains the rapid ascent of the sap. The next layer is the endodermis, which may be regarded as the sense-organ for the perception of the stimulus of gravity : it is the falling starch-grains in the endodermis that initiate the reaction by which the plant orientates itself in relation to the vertical. The geo-perceptive endodermis, in its turn, is in contact with the phloem, and I have shown elsewhere that the phloem functions as the nerve of the plant. All the principal systems of tissues regulating growth and movement are thus found to be in close relation with each other.

Electric Determination of the Hydraulic Wave-length

Each pulsating cell in the active layer executes periodic contraction and expansion, and it is obvious that, if these phasic changes occurred simultaneously in all the cells, the propulsion of sap in a given direction would be an impossibility. There must, therefore, exist a phase-difference, a sequence of pulsation from cell to cell. Have we any proof that such phase-difference exists, and that there is a co-ordination of activity in a vertical row of cells along which the sap is being propelled? In order to determine if this sequence could be established, I employed the method of exploration with the Electric Probe. Let us imagine a vertical row of cells, c_1, c_2, c_3 . . . c_n. If there is sequence of activity, it would then follow that while c_1 is contracting, another cell, c_n, will be in the opposite phase of expansion ; c_1 will thus be expelling sap, while c_n will be absorbing it ; the direction of propulsion will thus be from c_1 to c_n. The difference of phase between one cell and the next will be slight, but at some particular distance from each other two cells will be in opposite phases of activity, that is to say, while one is contracting the other is expanding, and *vice versâ*.

In order to detect this phasic difference by means of the exploring Probe, one electric contact A, made with the stem, is permanent, while the distance of the second contact B from the first is gradually varied. When the contacts A and B are very near each other, the cells at the two contacts will be very nearly in the same phase, they will be expanding or contracting at about the same time. While contracting, A will indicate electro-negativity, so will the electrode B ; during expansion both the electrodes will indicate electro-positivity. There will be little or no electric difference at the two electrodes, and the galvanometer will be practically quiescent. The case will, however, be different when B is sufficiently separated from A, so that it is in contact with a cell the phase of which is opposite to that at A. When contraction is taking place in A, there will be expansion at B : the electric change at A will be negative, that at B positive, and the electric difference of the two electrodes will be a maximum. The same maximum difference will occur when the cell at A expands and that at B contracts : A will now be electro-positive and B electro-negative. The swing of the galvanometer spot of light will be now in the opposite direction. Thus by increasing the distance from B to A, we shall pass from an electric minimum to a maximum, and this in spite of the increasing electric resistance interposed in the circuit. As the distance is further increased the phase-difference will be diminished, and we shall arrive at a second minimum, followed by a second maximum, and so on.

We have here a case analogous to the propagation of the periodic disturbance of waves of light and of sound. The distance between the two successive points in opposite phases is half the length of the wave. The velocity of propagation of the wave is given by the formula $V = n\lambda$, where n is the number of pulsations in an unit time, and λ the length of the wave. We also know that when the distance between the two points of the propagated wave is increased from 0 to 2λ, to 3λ, etc., that is to say, by even multiples of half the wave-length, the two points will be in the same phase ; but if the distances are $\frac{\lambda}{2}$, $\frac{3\lambda}{2}$, $\frac{5\lambda}{2}$ (*i.e.* odd multiples of $\frac{\lambda}{2}$), then the two points will be at the maximum difference of phase.

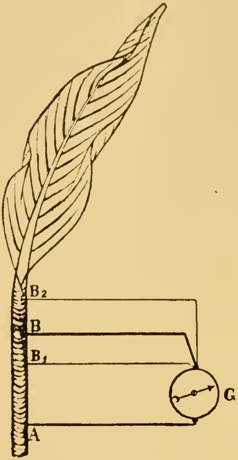

FIG. 78. The Method of Exploration by the Electric Probe for the Determination of the Hydraulic Wave-Length

A is the fixed, and B the exploring contact ; when B is at half the wave-length, the electric variation is maximum. This electric variation decreases as the second contact B is moved nearer to (B_1) or farther away (B_2) from A than the maximum point B.

Hence if the ascent of sap be due to periodic hydraulic waves, the fact will find its crucial demonstration in the detection of successive electric maxima and minima in the path of conduction. This demonstration will also prove that there is a sequence of propulsion from cell to cell.

The experimental difficulties in this demonstration are, however, considerable. The velocity of propagation, and therefore also the wave-length, are not the same in different specimens. Hence the position of the second electrode for the first maximum (where the phase-difference is opposite) can only be found by trial, by thrusting in the exploring Probe at gradually increasing distances from the first. But the numerous intervening wound-spots would undoubtedly modify the normal velocity of ascent. The procedure adopted to minimise this difficulty was to reverse the process of exploration, that is to say, gradually to diminish the distance between the two electrodes, instead of increasing it. The wound spots would then remain outside the region of exploration (see fig. 78).

Determination of Wave-length in Chrysanthemum

A preliminary series of experiments was carried out with specimens of stem of *Chrysanthemum*, which were in every respect alike. I thus obtained a definite idea of the position of the first electric maximum, which was found to be at a distance of 50 mm. This obviated to a great extent the fatigue which might occur from too many pricks with the exploring Probe. I give a detailed account of two typical experiments from the numerous determinations which gave similar results. In the first, the Probe was, to begin with, placed at a distance of 70 mm.; the response was found to be feeble. The Probe was then brought nearer, to a distance of 50 mm., and at once a great enhancement of the amplitude of pulsation was indicated. As the distance of the Probe was further reduced to 30 mm. the amplitude was much smaller; and at a distance of 5 mm. there was practically no electric difference (fig. 79). The distance from the maximum to the minimum is thus 50 mm., the wave-length being 100 mm.

In the second experiment, with a different specimen of *Chrysanthemum*, two probe-contacts were made: one at B at a distance of 50 mm., and one at B_1 at a distance of 5 mm. from the contact at A. The object of this was to make allowance for any variation that might conceivably occur during the experiment. The record was first taken with the contact at B_1; this gave a minimum amplitude. The next was taken with the contact at B, at a distance of 50 mm.; this gave the electric maximum.

FIG. 79. FIG. 80.

FIG. 79. Determination of the Wave-length in *Chrysanthemum*. The electric maximum is at 50 mm.

Note the enfeeblement of response as the probe is moved nearer to or farther away from the maximum point.

FIG. 80. The Cyclic Record with the Second Contact at 5 mm., at 50 mm., and once more at 5 mm.

The final record was taken with the probe-contact once more at B_1, and the record of the electric minimum was the same as at the beginning (fig. 80). The electric maximum is thus found to lie at the same distance as in the first experiment of the series. In certain other experiments I obtained a second minimum and a second maximum, the distance between the successive minima being the same as that between the successive maxima. Prolonged experiment is, however, apt to cause fatigue and abolish the response. The electric maximum is very definite at the exact distance of half

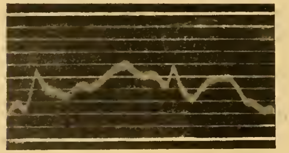

FIG. 81. The Einthoven Galvanometer Record exhibiting the Phenomenon of Interference

The recurrent 'beats' occur when the second point of contact is not exactly at half the wave-length.

the wave-length. Failure in securing this gives rise to the very interesting phenomenon of ‘beats’ seen in the record obtained with the Einthoven galvanometer (fig. 81).

Determination of the wave-length in Musa.—I employed the same method in the determination of the wave-length of the hydraulic wave in other plants. The following (fig. 82) is a record of the responses when the exploring electrode was placed at successive distances of 40 mm., 30 mm., 25 mm., and 20 mm. With diminishing distance the electric variation increased till it reached a maximum at a distance of 25 mm.; this is the point of the electric maximum, for further diminution of distance brought about a diminution of the electric variation. The phase-difference is maximal at a distance of 25 mm., which is therefore equal to half the wave-length.

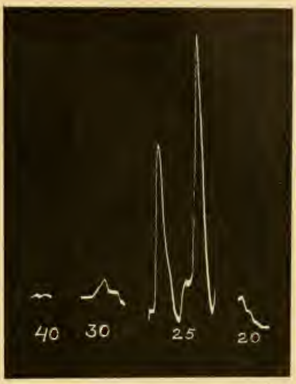

FIG. 82. Determination of wave-length of Cellular Pulsation in *Musa*

The Probe is gradually brought nearer from the fixed contact, from 40 to 20 mm. The electric maximum occurred at 25 mm., which is half the wave-length.

The wave-lengths of different species of plants under normal conditions and at a temperature of 30° C. are given below.

Chrysanthemum .	100 mm.
Musa . . .	50 mm.
Canna . . .	40 mm.

Change of Wave-length under Physiological Variation

The velocity of the ascent of sap caused by the propagated hydraulic wave is, as we have seen, modified under physiological variation; it is increased by the application of warm water at the root, or at the cut end of the stem. We have further seen that the velocity of the wave-propagation is $V = n\lambda$, where λ is the length of the wave. But the increase of velocity on the application of warm water may be due either to increase of frequency or to increase of wave-length, or to both. That the wave-length is increased will be seen from the results of the following experiment. I took a petiole of *Musa* and made two contacts, A and B, at a distance of half a wave-length, which was found in this and in the previous experiment to be 25 mm. Application of warm water at the cut end enhanced the velocity, the result being that the existing electric difference between A and B was found to have undergone a great diminution, so that it was necessary to increase the distance from the original 25 mm. to 35 mm. in order to obtain the new electric maximum: the wave-length thus increased from 50 mm. to 70 mm. The increased cellular activity is also shown by the enhanced amplitude of pulsation (fig. 83).

FIG. 83. Effect of Rise of Temperature in increasing the Wave-length

The pulsation at maximum point of 25 mm. had become irregular and diminished in amplitude as seen in second pair of records. The transfer of second contact to 35 mm. gave the new maximum with its enhanced amplitude of pulsation.

Upsetting of Phase-difference by Passage of a Constant Electric Current

Another very interesting method of upsetting the existing phase-difference through the agency of an external agent is that of the passage of a constant electric current. I have shown elsewhere that the intensity and the velocity of a propagated physiological impulse are modified by the action of a constant current. With a current of moderate intensity the speed of the propagated wave *is enhanced against the direction of the current, whilst it is retarded in the same direction as the current.*[1] We take a stem of *Canna* and make a longitudinal slit which extends nearly to the top: the two halves are separated from each other by the insertion of a piece of mica, and the separated ends of

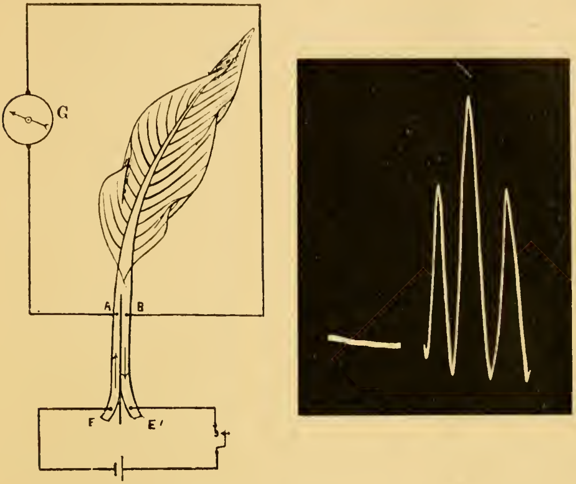

FIG. 84. Translocation of the Point of Electric Minimum by Passage of Electric Current

The figure to the left represents the experimental arrangement. The record to the right shows the effect of passage of current in the translocation of the electric minimum.

Note the first record exhibiting the minimum due to similar phase in the two contacts. Phase-difference increased by passage of current as indicated by the enhanced response in the second part of the record (see text).

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[1] *Proc. Roy. Soc.*, B. vol. 88, 1915.

the cut stem are wrapped with pieces of moist cloth. The electrodes are placed on two points, A and B, which are in the same horizontal line and are in the same phase before the passage of the current, as is independently demonstrated by the horizontal line shown in the record (fig. 84) indicating an electric minimum. A constant current is now sent into the lower end of the stem at EE^1, *ascending* along the left half and *descending* by the right half. The hydraulic wave is retarded on one side and accelerated on the other : hence a *difference of phase is induced at* A *and* B, as shown in the resulting pulsating record. The passage of the current produced a displacement of the base-line (not shown in the figure) ; but this static displacement does not explain the pulsations, which are due to the induced phase-difference. On the stoppage of the constant current, the induced phase-difference disappeared and the record became once more horizontal.

SUMMARY

The experiments described show that there is a definite layer in the stem which by its pulsatory activity maintains the ascent of sap : this layer has been localised by the Electric Probe. In dicotyledonous plants it is the innermost layer of the cortex abutting on the vascular tissue.

The dead xylem exhibits no pulsation. The vascular tissue of the xylem is, however, injected with sap by the pulsating activity of the cortex, the intervening distance being very small.

For the uni-directional propulsion of sap, the further condition of sequence of pulsation or phase-difference is necessary. This has been demonstrated by the method of electric exploration by which the points of electric maxima and minima have been determined. The distance between successive points of electric minima or maxima is half the wave-length of the hydraulic wave. The length of the wave is found to be increased by a rise of temperature, which also enhances the velocity of the ascent of sap.

The cellular pulsations cause a pumping action ; and the sequence of pulsation from cell to cell brings about the unidirectioned flow of the sap. The sap expelled during the contraction of one cell is absorbed by the cell higher up during its phase of expansion. There is a propagation of a wave of contraction, preceded by one of expansion ; in consequence of this the sap is, as it were, squeezed forward. A succession of such waves maintains the continuous ascent of sap.

CHAPTER XVII

THE CELLULAR MECHANISM IN THE TRANSPORT OF SAP

Initiation of pulsation—Effect of stimulus—Effect of differential hydrostatic pressure—Effect of constant electric current—Effect of variation of temperature on pulsation—Effect of anæsthetics—Effect of diminished internal pressure—Summary.

In the endeavour to obtain a clearer general conception of the ascent of sap, as effected by the pulsating cellular mechanism discussed in previous chapters, it may now be enquired, how is the pulsation initiated ?

It has been demonstrated that certain agents enhance the rate of ascent, with consequent increase of turgor of the tissue ; whilst other agents induce a depression or arrest of ascent with a resulting diminution of turgor. These diverse effects must ultimately be due to induced variations in the pulsation of the active cells. The final analysis would be reached if we could record the waxing and waning of the pulse-throbs of an individual cell under varying changes in the environment.

The pulsating cell has been compared to a pump with alternate expansive up-stroke and contractile down-stroke. The rate of propulsion of water will thus be increased by enhanced frequency or increased amplitude of pulsation ; diminished frequency or amplitude will, on the other hand, cause a diminished rate of propulsion.

A more complex effect will be produced when the up- and down-strokes are unequal. It is the up-stroke that sucks in water : hence with a relatively enhanced up-stroke an accumulation of sap will occur in the cell, which will become distended and more turgid. If, on the other hand, the up-stroke is reduced and the down-stroke increased, the result will be a diminution of turgor.

With these preliminary considerations, we proceed to study the effects of external agents on the pulsation of the individual cell, and thus to obtain an insight into the mechanism by which the rate of propulsion of sap is enhanced or depressed. Nothing, indeed, could be more impressive than the responding movement of the galvanometer spot of light, revealing the working of the invisible cellular machinery. Under a stimulating agent, for example, the responding spot of light is violently thrown in one direction (beyond the recording plate), and the heightened activity is manifested by the quickened rate or enhanced amplitude of pulsation. Unfortunately, the recording spot of light, on account of its extreme rapidity or great range of movement, leaves little or no trace on the photographic plate. It is only after the first violent outburst has abated a little that the impression made by the moving spot of light can be found on the plate. The record therefore exhibits the character of the change, though not its full extent.

The effects of the following external agencies on cellular pulsation have been studied:

i. The effect of stimulus in initiation or enhancement of cellular pulsation.
ii. The effect of differential hydrostatic pressure.
iii. The effect of constant electrical current.
iv. The effect of variation of temperature.
v. The effect of anæsthetics.
vi. The effect of diminished internal pressure.

The Effect of Stimulus on Pulsation

A clue to the initiation of pulsation in the ascent of sap may be found in the cell-to-cell propagation of pulsation in cardiac muscular tissue which has become quiescent after isolation. On applying the mechanical stimulus of a prick, the irritation causes an excitatory impulse which is propagated from cell to cell onwards. This is apparently what happens in the pulsating layer in the plant; and we will now endeavour to determine what is the stimulus that initiates the multiple activity of the cells.

The pulsating activity of the root-cells may be produced in two ways: first, by an increase of internal pressure; and secondly, by the continued action of an external stimulus. The increase of turgor of the root-cells by absorption of water from the soil is partially due to osmotic action; but the mere increase of turgor by absorption will not suffice to ensure the continuous maintenance of pulsation. For we found that the ascent of sap is arrested when the plant, with its root in water, is kept in darkness: under these unfavourable conditions, the cells pass from the active to the inactive state. We also found that the application of a stimulus renews their activity, with the concomitant renewal of the ascent of sap (p. 57).

The root, under normal conditions, is shielded from the stimulus of light, so that source of stimulation is eliminated. It may be stimulated by chemical substances present in the soil; but of this there is no evidence. The remaining possible source of stimulation, which would appear to be the most important, is the mechanical; the root and rootlets, in boring their way through the soil, are subjected to the constant stimulus of friction. The total surface stimulated is thus very large. Timiriazeff[1] found from calculation that the total length of the root-hairs of a wheat-plant grown in a flower-pot was twenty kilometres (twelve and a half miles). The stimulation over this enormous surface must be considerable, and capable of initiating and maintaining the activity of the root-cells.

This explanation is based upon the results already obtained concerning the effects of stimulus upon rhythmic activity. It has been shown that, while a strong stimulus applied to a highly excitable tissue inhibits its activity, a stimulus of moderate intensity applied to a sub-tonic

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[1] Timiriazeff, *The Life of the Plant*, p. 110. Longmans.

tissue initiates and maintains its activity. Further experiments on the effect of strong stimulus on cellular pulsation were carried out in the following manner. Thermal or mechanical stimulus was applied to a lateral leaf by application of a hot wire, or by the section of the leaf. There was no immediate effect on normal pulsation, but after an interval of about a minute, required for the excitation to reach the pulsating cells, a very violent contractile response occurred, exhibited by the down-stroke, which went off the recording plate (fig. 85). The recovery to the normal is seen to have taken place after a certain interval of time. It will now be clear that the cellular activity in the interior of the plant may be affected by the stimulation of the leaf by light, or by such mechanical stimulation as that caused by the wind, and that the effect of such a stimulation may affect distant organs through an induced variation in the ascent of sap.

FIG. 85. Effect of External Stimulus inducing Cellular Contraction

Note the resulting down-stroke, which went off the recording plate.

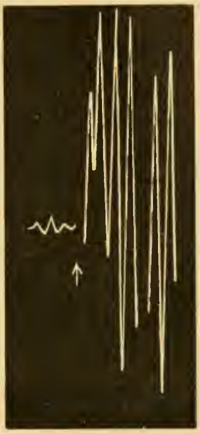

FIG. 86. The Effect of Electric Stimulus on Cellular Pulsation of a Sub-tonic Specimen

Note the very marked enhancement of activity after application of stimulus at arrow.

The converse process is that of the depletion of stored energy causing a stoppage of cellular pulsation, and of the restoration of activity by the application of stimulus. The experimental specimen was kept inside a dark room for several hours; the cellular pulsations were now found to have become very much enfeebled. In order to ascertain that this was caused by the lack of stimulus, I subjected the specimen to the electric stimulation of an induction shock of moderate intensity, which was passed along its length. The galvanometer was disconnected during the process, the connection being re-made a minute after the cessation of stimulus. The record (fig. 86) shows the very great enhancement in the cellular activity which persisted for a considerable length of time. The experiment demonstrates once more that it is physiological activity which effects the ascent of sap, and that this activity is maintained by the action of stimulus.

The Effect of Differential Hydrostatic Pressure

The second factor in the initiation of rhythmic activity is an increased internal hydrostatic pressure. Diminution of pressure inhibits the pulsatory activity of the *Desmodium* leaflet, and also of growth in growing organs: increased pressure, on the other hand, enhances the activity. Similar effects are observed in the cellular pulsation which maintains the ascent of sap. In normal conditions, the root-cells absorb water from the soil, with resulting increase of turgor and of internal hydrostatic pressure. The top of the stem is, however, in a state of diminished turgor and internal pressure, due to the transpiration from the leaves. The cellular activity is therefore greater at the root than at the top of the shoot. In cut stems placed in water, a similar difference of activity exists between the lower and upper ends of the stem. This difference is a contributory factor in the determination of the direction of the propulsion of sap, from a place of greater to a place of lesser activity. As regards the underlying cellular pulsation, it will presently be shown how the diminution of internal pressure causes a depression culminating in an arrest of pulsation.

The Effect of Constant Electric Current

It has been shown how a quiescent rhythmic tissue is roused to activity by the application of stimulus. The passage of a constant current often acts as a stimulating agent; a very striking illustration of this I found in the initiation of rhythmic activity of the leaflets of *Biophytum*, originally at standstill, by the passage of a constant electric current along the petiole.[1]

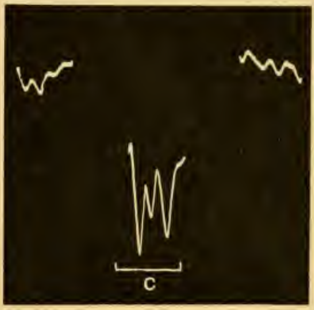

FIG. 87. Effect of Electric Current on Cellular Pulsation

The upper records are of pulsations before the commencement and after the cessation of current. c, enhanced pulsation during the passage of the current.

The cellular pulsation which causes the ascent of sap is sometimes found to be greatly enfeebled or even arrested. The experiment demonstrating the renewal or enhancement of pulsation by the passage of a constant current was carried out in the following manner. The lamina of a lateral leaf of *Impatiens* was made the indifferent point for the second electric contact. The first contact was made on the stem, at exactly the same level as the lateral leaf, so that the passage of a constant current through the stem should not give rise to a difference of potential between the two contacts. In practice there was a very

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[1] *Irritability of Plants*, p. 249.

small difference which caused the displacement of the base-line. A constant electric current was then led through the length of the plant, one electrode being applied at the tip of the shoot, and the other to the soil in which the root is buried. The current is turned on and off by means of a key. A second reversing key enables us to change the direction of the current.

The record given in fig. 87 shows the stimulating effect of the passage of a constant current on cellular pulsation. The normal pulsation was very feeble, but passage of the current is seen to have induced a marked enhancement. The starting of the current is independently exhibited by a displacement of the base-line ; the stoppage of the current is followed by the cessation of enhanced pulsation. It is thus seen how it is possible not only to record the elementary pulses, but also put them under external control, the natural condition being resumed immediately on the cessation of the stimulating current. It may be stated here that the stimulating effect of a constant current is modified by the direction and intensity of the current.[1]

The Effect of Variation of Temperature

The enhanced rate of ascent of sap under rising temperature has already been demonstrated by the increased rate of suction and quickened rate of the Erectile Response ; the converse effect of cold has also been shown in the depression or arrest of the Suctional and the Erectile Response (p. 63).

Temperature variation has also a very marked effect on the amplitude or the frequency of pulsation. I have been able to diminish or enhance the amplitude by alternate application of cold and warmth. In fig. 88 it is seen that

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[1] Bose, 'The Influence of Homodromous and Heterodromous Electric Current on Transmission of Excitation in Plant and Animal,' *Proc. R. S.*, B. Vol. 88, 1915.

the amplitude of pulsation is very greatly enhanced by a rise of temperature, the activity of the cellular pump being thereby increased. A rise of temperature is often found to produce also an enhancement of the frequency of pulsation. Thus from the record of the Einthoven galvanometer, the period of a single pulsation in a particular specimen at ordinary temperature was found to be twenty-five seconds. After raising the temperature through 5° C. the period was found to be quickened to fourteen seconds.

FIG. 88. Effect of rise of Temperature in Enhancement of the Amplitude of Pulsation

Normal pulsation before application of warmth is seen to the left.

The Effect of Anæsthetics

The very great enhancement of the rate of ascent of sap by the application of dilute chloroform has already been described (p. 70). The following experiments were carried out to determine the responsive variation of pulsation by the application of chloroform to the root.

In the first experiment of the series, a small dose of chloroform was applied. The normal pulsations were feeble; but the stimulating effect of a small dose of the anæsthetic was so great that the record went off the plate in an upward direction, that is, towards expansion and enhanced suction.

FIG. 89. Effect of Chloroform, applied at Arrow, on Cellular Pulsation

Note preliminary enhancement of pulsation, with prolonged up-stroke; pulsation arrested on continued application.

The up-stroke was very much longer than the down-stroke, with the result that the base-line was displaced upwards beyond the plate: consequently, the propulsion of water upwards became very rapid.

In the second experiment, I applied a larger dose of chloroform. The preliminary effect of the anæsthetic was stimulatory and the amplitude of pulsation became greatly enhanced; the up-stroke was longer than the down-stroke, and the base-line was raised towards increased positivity, indicative of enhanced turgor. Continued action of chloroform, however, caused a depression, which culminated in the final arrest of pulsation (fig. 89).

The Effect of Diminished Internal Pressure

It has been shown (p. 54) that the effect of diminished internal pressure, due to the application of a plasmolytic solution to the root, is to induce retardation or arrest of the ascent of sap. I will now describe the effect of diminished pressure on cellular pulsation. In the experiment to determine the effect of diminished pressure induced by a plasmolysing agent, the first part of the record (fig. 90) shows that the normal pulsation, though feeble, was uniform. On application of a dilute KNO_3 solution to the root, at the point marked with an arrow, we observe a responsive variation in the pulsation which is very characteristic. The down-stroke, which represents contraction, becomes greatly increased, while the up-stroke, which represents suction, is relatively decreased; the base-line thus declines downwards, indicating a persistent diminution of turgor. The final result is an arrest of pulsation and a throttling of the channel for propulsion, with the consequent arrest of the ascent of sap.

FIG. 90. Effect of Diminished Internal Pressure on the Cellular Pulsations

Note down-stroke being longer than the up-stroke.

TABLE XXVIII.—SHOWING THE DEPENDENCE OF THE ASCENT OF SAP ON CELLULAR ACTIVITY

External agent	Effect on cellular pulsation	Effect on the rate of ascent
Warm water . .	Enhancement	Enhancement
Cold water . . .	Diminution or arrest	Depression or arrest
Stimulus on sub-tonic tissues . . .	Renewal or enhancement	Renewal or enhancement
Chloroform (small dose)	Enhancement	Enhancement
Chloroform (large dose) .	Depression or arrest	Depression or arrest
Plasmolytic solution .	Arrest	Arrest

Table XXVIII. on the previous page shows at a glance how the ascent of sap is dependent on the pulsation of active cells in the tissues of the plant.

SUMMARY

Cellular pulsation is initiated and maintained under the action of stimulus of moderate intensity. It is probable that pulsation is initiated in the root, which is stimulated by mechanical friction against the soil. The direction of the excitatory impulse is from the root upwards, giving rise to the sequence of pulsation from cell to cell.

Cellular activity is enhanced by increased hydrostatic pressure. On account of the loss of water by transpiration, a differential hydrostatic pressure exists between the cells of the root and those at the top of the shoot. This is a co-operating factor in determining the direction of propulsion of sap from the region of greater cellular activity in the root to that of lesser activity at the top of the shoot.

A constant electric current of moderate intensity is found, under certain conditions, to enhance the amplitude of cellular pulsation.

A fall of temperature causes a depression in the cellular pulsation, culminating in arrest and the consequent stoppage of the ascent of sap. Rise of temperature, on the other hand, enhances the frequency or the amplitude of pulsation. The activity of the cellular pump is thus greatly increased, with a resulting enhancement of the rate of ascent.

The effect of a small dose of chloroform is to induce a very great enhancement of the amplitude of the cellular pulsation ; in the first stage of its action the up-stroke, which represents suction, is relatively long ; the vertically situated cellular pumps serially take up this enhanced suction, and the propulsion of water upwards becomes very rapid. Continued action of the anæsthetic causes a stoppage of pulsation, with the consequent arrest of the ascent of sap.

A diminution of hydrostatic pressure by application of a plasmolysing solution to the root induces an arrest of cellular activity. The characteristic effect on cellular pulsation is that the down-stroke, which represents contraction and expulsion, becomes greatly increased; while the up-stroke, representing expansion and suction, is reduced. The general result is a throttling of the channel for the conduction of water, with the consequent arrest of the ascent of sap.

CHAPTER XVIII

THE HYDRAULIC AND THE NERVOUS REFLEXES

Interaction between distant organs—Sachs's experiment of the growth of a branch inside a dark box—Hydraulic convection and nervous conduction—Importance of stimulus in maintenance of life-activity—The Leaf a catchment-basin for reception of stimulus—Stimulation of internal cortex by transmitted excitation of sunlight—Antagonistic action of hydraulic and nerve reflexes—Dual impulses under stimulus—Opposite effects of direct and indirect stimulus—Explanation of opposite geotropic responses in shoot and in root—The co-ordination of nervous reflexes—Dia-heliotropic attitude of leaves—Summary.

One of the most difficult problems in plant-physiology is that of finding an explanation of the interaction between distant organs. What are the links by which they are connected with each other? Numerous examples may be cited of the influence of one part of the plant on a distant part; I may refer to a very interesting instance described by Sachs. A plant kept in darkness becomes abnormal in its growth, and the motility of its sensitive organs disappears; but in Sachs's experiment, a long shoot of *Cucurbita* was made to grow inside a dark box, the rest of the plant being exposed to light. The covered part of the plant, in these circumstances, showed normal growth of stem and leaves, and produced normal flowers and a large fruit. The tendrils inside the box, moreover, were found to be fully as sensitive as those outside. Some chemical substance or substances must therefore have been conveyed from the organs outside, causing a regulation of the normal growth of the organs inside the dark chamber.

Hydraulic Convection and Nervous Conduction

It is a well-known and important fact in the physiology of animals, that certain chemical substances, termed hormones, produced in certain organs, are carried in the circulating blood to other organs or parts of the body in which their regulatory action becomes manifested. There is no doubt that hormones are likewise produced in plants ; and that these chemical substances, produced in one organ, are conveyed to distant organs in the sap distributed by cellular activity. This transfer of matter may be distinguished as the hydraulic *convection* associated with circulation.

The distant members of the plant-body are also put in communication with each other by nerve-connections ; for I have shown elsewhere that a nervous system exists in plants, by which excitatory or nervous impulses are transmitted with a definite velocity which in different plants varies from 30 mm. to less than 1 mm. per second.

Importance of Stimulus in the Maintenance of Life-activity

There is a particular aspect of the action of stimulus which is of fundamental importance in the life of the plant. The continuance of its normal functions depends on external stimulus to maintain the tissues in an optimum tonic condition ; for deprivation of stimulus reduces the plant to an atonic condition, in which all life-activities are brought to a standstill. Turning our attention to particular instances, we find that growth and movement in plants depend on the turgid condition of the tissue, which is determined by the cellular activity which maintains the ascent of sap.

We have seen that all rhythmic activities are maintained by the action of stimulus. We observe here a regulatory process which is met with in all physiological actions. Beginning with the tissue at the lowest tonic level (due to prolonged deprivation of stimulus), the incidence of stimulus initiates and enhances the activity to a maximum, the tonic condition of the tissue being raised at the same time to an optimum. Continued stimulation above this point causes a partial inhibition, but this need not be regarded as a permanent depression, for the after-effect of such stimulation is often to cause an enhancement of activity. These effects have been illustrated in various modes of rhythmic activity ; in the pulsation of *Desmodium,* in growth (p. 15), and in the cellular pulsation effecting the ascent of sap (p. 236).

It is thus clear that for the maintenance of the ascent of sap in a tree, the internal cortex should be excited throughout its length either by direct or by transmitted stimulation. The root-cells are locally stimulated by mechanical irritation of friction against the soil. As for the great length of the cortex in the trunk of the tree, covered as it is by the thick bark, direct stimulation of the active internal cells by external stimulus is impossible ; it can only be effected by transmitted stimulation. There thus arise two questions : the first relates to the external stimulus which by its transmitted excitation maintains the cellular activity of the internal cortex ; the second relates to the nervous path by which the excitation reaches that active layer.

Among the external stimuli, none is more potent than light. All the conditions favour the transmission of its stimulating effect to a distance by the nervous channel, which is the phloem in the vascular tissue. The expanded lamina of the leaf, in which the vascular bundles are spread out in fine ramifications, is not merely a specialised structure for photo-synthesis, but also a catchment-basin for the stimulus of light, the excitatory effect of which is gathered into larger and larger nerve-trunks for transmission to the interior of the plant. It is very significant that the internal cortex in which pulsatory activity is to be maintained abuts upon the phloem through which excitation from outside is conducted.

In the interior of the plant the distribution of the vascular bundles is such that no mass of living tissue is too remote to be excited by the stimulus conducted by the nervous channels. How reticulated they may often be, even in the trunk, is seen in the photograph of the distribution of the vascular bundles in the main stem of *Papaya* (fig. 91). This network, of which only a small portion is seen in the photograph, girdles the stem throughout its whole length, and in this particular case there were as many as twenty such layers, one within the other.

FIG. 91. Photograph of a Layer of Fibro-vascular Tissue in the Stem of *Papaya*

It is contended that all parts of the plant are, by means of nerve-conduction, maintained in the most intimate communication with each other. It can only be in virtue of the existence of a system of nerves that the plant constitutes a single organised whole, each of whose parts is affected by every influence that falls upon any other.

The Hydraulic and the Nerve Reflex

We have seen that two different impulses are transmitted to a distance, the hydraulic impulse propelling the sap, and the nervous impulse conveying the excitatory disturbance. Both these impulses, the hydraulic and the nervous, also produce movements at a distance. Thus irrigation of the root of *Mimosa* gives rise to the *erectile response* of the distant leaf. If, instead of irrigation, we apply a strong stimulus to the root, say a prick with a pin or an electric shock from an induction coil, the transmitted nervous impulse induces a *fall* of the leaf. *The hydraulic impulse is thus antagonistic to the nervous impulse.* Even in ordinary response and recovery we observe these opposite actions The erectile movement of the leaf is due to the ascent of sap to the pulvinus along a definite channel. Stimulation of the leaf induces a contraction and expulsion of water from the pulvinus which escapes by the same channel through which the ascent took place, but this time in a reverse direction. The two phases of the normal response, viz. the excitatory down-movement followed by erectile recovery, are thus brought about by the excitatory and hydraulic actions respectively. The fact that the hydraulic expansion opposes, and may even neutralise, the excitatory action is seen in the response of *Mimosa*. The apparent insensitiveness of the plant early in the morning is partly due to the excessive turgor of the pulvinus at that time of the day. Again, application of water to the pulvinus induces an expansion and inhibition of response which may be restored by the withdrawal of the excess of water by glycerin.[1]

The phenomena of movement in plants present innumerable difficulties. Hardly any responsive movement has been observed of which an example directly to the contrary may not also be found. It has therefore appeared hopeless to unify these very diverse phenomena, and there has been a tendency towards a belief that it is not any definite physiological action, but the individuality of the plant that determines movements which are for its own advantage. The teleological argument thus advanced is, however, no true explanation ; it rather confuses the real issue and diverts attention from the discovery of the efficient cause. The complexity that baffles us arises from the combination of numerous reflexes, sometimes concordant, and at other times in antagonism to each other.

The term 'reflex' has been defined as the 'reaction in which there follows on an initiating reaction, an end-effect reached through the mediation of a conductor itself incapable of the end-effect.'[2]

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[1] *Irritability of Plants*, p. 88.

[2] C. S. Sherrington, *The Integrative Action of the Nervous System*, p. 6.

Now the invisible hydraulic impulse initiated by the irrigation of the root causes an end-effect, namely the erectile response of the leaf at a distance ; we may therefore regard this particular effect produced at a distance as the *hydraulic reflex.* There is a different end-effect, due to transmission through the plant-nerve of excitation which causes the fall of leaf ; this is the *nervous reflex* ; the hydraulic reflex induces, as already stated, an expansive and the nerve-reflex a contractile end-effect. A complexity thus arises in the motile response of growing and of pulvinated organs due to the two reflexes antagonising each other. The recognition of the existence of these two distinct reflexes makes it possible to offer a full explanation of various effects which have hitherto appeared to be anomalous.

Dual Impulses under the Action of Stimulus

Response in Pulvinated Organs.—Stimulus applied at one end of the long petiole of *Averrhoa Carambola* causes successive fall of the sensitive leaflets. There is, however, a preliminary effect which had not been noticed, but which comes out very clearly in the mechanical record obtained by a magnifying lever. The record given in fig. 92 exhibits response to the stimulus of an electric shock applied at a distance of 50 mm. from the responding leaflet. It is seen that it gives rise to two distinct impulses, one positive and the other negative. The hydraulic positive produced an *erectile* response of the leaflet shown by the down-curve, while the excitatory negative caused a rapid *fall* of the leaflet. This negative impulse reached the leaflet forty-four seconds after the application of stimulus ; the velocity of the excitatory impulse is in the present case 1·1 mm. per second, which is slower than the positive impulse.

I obtained similar double responses with *Biophytum* and other sensitive plants under modes of stimulation as diverse as electrical, chemical and thermal. Stimulation causes local contraction of the excited cells, with expulsion of water which gives rise to a hydraulic wave, the velocity of which is generally greater than the propagation of the excitatory protoplasmic change constituting the nervous impulse. The hydraulic wave gives rise to the preliminary erectile response ; the subsequent excitatory fall is brought about by the nervous impulse.

FIG. 92. Positive followed by Negative Response in *Averrhoa*

Down-curve represents erectile response ; and the up-curve exhibits the responsive fall.

In the record of the two reflexes given in fig. 92, the excitatory response is more intense than the hydraulic ; hence if the two impulses reach the responding organ at about the same time (which will be the case when the stimulus is applied at or near the responding point), the positive becomes masked by the predominant negative. Application of stimulus at a distance causes the slow-moving negative impulse to lag sufficiently behind the positive so as not to mask it.[1]

In semi-conducting tissues, the excitatory impulse undergoes rapid diminution or abolition with the distance ; hence a stimulus of moderate intensity applied at a distance induces only the positive response. It thus happens that while direct application of stimulus causes contraction, application of the same stimulus at a distance induces the opposite effect of expansion.[2]

Responsive Movements in Growth.—I obtained parallel effects in experiments on growth. Direct stimulation of the growing region was found to induce a retardation in the rate of growth which culminated in actual contraction. Strong stimulus applied at a distance from the growing region gave rise to a diphasic response, an acceleration followed by retardation. When the stimulus is moderate or feeble, the excitatory impulse is unable to reach the distant responding region ; the hydraulic impulse is transmitted, the resulting reflex being an expansion, an enhancement of turgor, and an increase in the rate of growth. The positive tropic curvature in growing organs is due to the contraction of the proximal side by direct stimulation, and the expansion caused by the positive hydraulic impulse transmitted to the distal side.

Opposite Geotropic Responses in the Shoot and in the Root

The opposite responses of the shoot and the root to the stimulus of gravity find their explanation in the fact that in the former stimulation is direct and in the latter indirect. In the shoot the perceptive and the responding region is one and the same ; but in the root, it is the tip of the organ

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[1] I obtained similar diphasic effects in electric responses, a galvanometric positivity followed by negativity. This would explain the positive electric response in animal tissues which is often found to precede the normal negative.

[2] *Life Movements in Plants*, vol. ii. p. 286.

which alone is sensitive, while response takes place in a region at some distance from it. It has been shown in the previous paragraph that the movements in response to direct and to indirect stimulation are opposite to each other. From the fact that the geotropic stimulation of the shoot is direct, and of the root indirect, it is inevitable that an identical stimulus should in the two cases induce responses of opposite sign.

The Co-ordination of Reflexes

We have seen how the hydraulic and the nervous reflexes antagonise each other, and how the resultant movement is due to the algebraical summation of the two effects. There are again various nerve-reflexes, which by their co-ordinated action produce what is usually regarded as a specific response for the advantage of the plant. As an example of this we find that the leaves of *Mimosa*, subjected to one-sided illumination, place themselves at right angles to the direction of the stimulus, apparently for the purpose of absorbing the largest amount of light. This directive action even takes place when the motile pulvinus is kept shaded, whilst the four sub-petioles carrying the numerous leaflets are exposed to light. The result must evidently be due to a nervous impulse transmitted from the four sub-petioles, bearing the leaflets, to the pulvinus at the base of the main petiole.

Detailed analysis shows that the pulvinus itself is a complex organ whose four quadrants act as four distinct effectors with characteristic responsive movements (fig. 93). When the left flank of the pulvinus (1) is alone stimulated by light, the result is a left-handed torsion or movement against the hands of the clock. Stimulation of the lower quadrant (2) by light gives rise to a responsive movement which is downwards. Stimulation of the right flank (4) by light induces a right-handed torsion. The action of light on the upper quadrant (3) causes an up-movement. This is what takes place when the stimulus is localised at each of the four quadrants: whereas strong and diffuse stimulation gives rise to the fall of the leaf due to the predominant response of the lower half of the pulvinus.

Moreover, the same effects are induced by the separate stimulation of the four sub-petioles bearing the leaflets. When light is thrown on the left sub-petiole (1) the response is a left-handed torsion: stimulation of sub-petiole (2) induces a down-movement; that of sub-petiole (3) causes an up-movement; and, finally, stimulation of the right sub-petiole (4) induces a right-handed torsion.

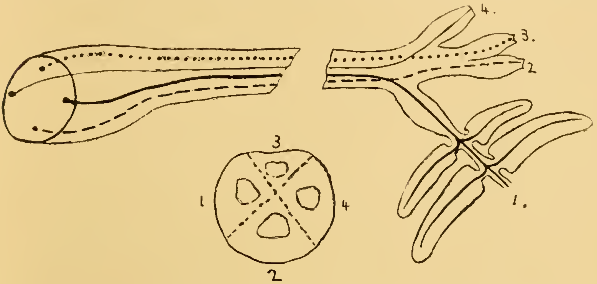

Fig. 93. Transverse Section of the Pulvinus of *Mimosa* (lower figure) showing the Quadrants which are in Nervous Communication with the Four Sub-petioles bearing the Leaflets (upper figure).

I have also found by the Electric Probe that it is the phloem in the vascular strand in the main petiole which transmits excitation initiated in each of the four sub-petioles. There are thus four separate nerve-strands which connect the four sub-petioles with the four effectors in the pulvinus.

A single reflex caused by the stimulation of one of the sub-petioles gives rise to a purposeless movement in a direction which carries the plane of the leaflets away from the position perpendicular to the incident light. But when the two sub-petioles (1) and (4) are simultaneously exposed to light of the same intensity, the two resulting torsions balance each other. Hence the lateral adjustments of the leaf as a whole are made by the two sub-petioles (1) and (4) which are situated outside. The balancing adjustments, up or down, are made, in response to the excitations transmitted, by the two middle sub-petioles (2) and (3). It is thus seen that equilibrium is only possible when the entire leaf-surface (consisting of the rows of leaflets carried by the four sub-petioles) is equally illuminated ; and this can only occur when the leaf-surface as a whole is perpendicular to the incident light. The leaf is adjusted in space by the co-ordinated action of the four reflexes. The dia-heliotropic attitude of the leaves is thus brought about by distinct nervous impulses, initiated at the perceptive region actuating the different effectors at a distance.[1]

There are additional reflexes caused by other modes of stimulation, such as that of gravity. The geotropic response is modified by thermal variation ; rise of temperature diminishes the geotropic response, while fall of temperature, within limits, enhances it.[2]

Thus even in such an apparently simple case as the adjustment of the leaf of *Mimosa*, there are the following variable factors : (1) the hydraulic reflex ; (2) the nervous reflex caused by the stimulus of light, in which there are four variables depending on the relative intensities of excitation transmitted by the four different receptors of stimulus ; (3) the geotropic action ; and (4) the effect of thermal variation in modifying the geotropic action.

It will be understood how, by the permutation and combination of these factors, numerous variations will be produced in the resulting response. This accounts for the complexity of life-movements, which are by no means capricious, but are capable of rational explanation on the investigation and the discovery of the numerous factors underlying their manifestations.

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[1] 'The Dia-Heliotropic Attitude of Leaves as determined by Transmitted Nervous Excitation,' *Proc. Roy. Soc.*, B. vol. 93, 1922.

[2] *Life Movements of Plants*, vol. ii. p. 513.

SUMMARY

The plant is an organised whole, there being interaction between distant organs.

There are two modes of inter-communication : (1) the hydraulic convection of fluids by cellular activity ; and (2) the nervous conduction of excitatory protoplasmic change.

Regulation of growth may take place by hydraulic convection of chemical substances (hormones) from one part of the plant to another.

Direct or transmitted stimulation is necessary for the maintenance of all modes of rhythmic activity, including the cellular pulsation in the ascent of sap.

Excitatory impulse reaches the interior of the plant along the phloem which functions as the nerve of the plant. The active cortex abuts upon the phloem, and is thus stimulated by the transmitted excitation from outside.

The leaf is a catchment-basin for the reception of the stimulus of light. The excitatory effect produced in the nervous elements present in the veins is gathered into larger and larger nerve-trunks and transmitted to the interior of the plant.

The hydraulic and nerve reflexes are antagonistic to each other. The former induces an end-effect of expansion, increase of turgor, galvanometric positivity, and erectile movement of the leaf. The nerve-reflex gives rise to the opposite effect of contraction, diminution of turgor, galvanometric negativity, and the fall of the leaf.

Stimulus applied at a distance gives rise to dual impulses, hydraulic and nervous. The hydraulic travels the faster, and induces the preliminary erectile response ; the nervous impulse which follows gives rise to the subsequent excitatory fall of the leaf. Of the two effects, the excitatory is the more intense.

In a semi-conducting tissue, the excitatory impulse undergoes diminution with distance, and may thus become extinguished. The result is that while direct stimulus causes contraction, fall of the leaf and retardation of the growth, a stimulus applied at a distance induces expansion, erectile movement of the leaf and enhancement of the rate of growth. The effects of direct and indirect stimulus are thus of opposite sign.

This explains the opposite effects of the stimulus of gravity in the shoot and in the root. In the shoot the stimulus is direct; in the root it is indirect, since the sensitive root-tip for perception of stimulus is separated from the region of response.

The dia-heliotropic attitude of the leaves of *Mimosa* and other plants is the result of the co-ordination of nervous reflexes. The pulvinus of *Mimosa* has four distinct effectors: the left and right quadrants respond by left-handed and right-handed torsions; the upper quadrant responds by an up-movement, and the lower quadrant by a down-movement. These four quadrants are in nervous connection with the four sub-petioles bearing the leaflets, which are the receptors for the stimulus of light. The leaf is adjusted in space by the co-ordinated action of four reflexes, equilibrium being only possible when the leaf-surface as a whole is perpendicular to the incident light. The dia-heliotropic attitude of leaves is thus brought about by distinct nervous impulses initiated at the perceptive region actuating the different effectors.

Additional reflexes are caused by other modes of stimulation.

The complexity of the life-movements arises from the presence of numerous reflexes sometimes concordant with, sometimes in antagonism to, each other.

CHAPTER XIX

GENERAL SURVEY

THE various theories that have been proposed in explanation of the ascent of sap are admittedly inadequate. The generally accepted view is that the motive power for the ascent is supplied to some extent by the root-pressure, which acts like a force-pump, but chiefly by the backwardly transmitted pull resulting from transpiration by the leaves.

It has, however, been conclusively proved that neither root-pressure nor transpiration from the leaves is essential for the ascent of sap, by the experiment in which the root and the leaves were removed, the stem being coated with an impermeable varnish ; on application of water to the cut end of the stem the ascent was found to take place with a velocity of more than 18 metres per hour (p. 36). This high rate of ascent was thus attained in the complete absence of root-pressure and of transpiration. Slow osmotic action, moreover, could not possibly ensure such a rapid ascent. As the movement of sap takes place even in small pieces of cut stem, it follows that the activity underlying the propulsion of sap is not confined to any particular region of the plant, but exists throughout its whole length. Further, the investigations described in the present work prove that the ascent of sap is due to the pulsatory activity of definite layers of cells in all parts of the body of the plant, the exact position of which has been localised. The investigations have included the three regions of the plant—the absorbing root, the conducting stem, and the excreting leaf.

The Ascent of Sap in the Stem

Investigations on the effect of physiological change on the ascent of sap have been carried out by the determination of the normal rate of ascent and its induced variations. Three accurate methods have been devised for this purpose: (1) that of the Erectile Response of the drooping leaf; (2) that of the Erectile Response of the drooping stem, and (3) that of the Electric Response (pp. 25, 195). The Mechanical and Electric Methods give results which are identical. The velocity of ascent is found to be modified by the physiological condition of the tissue, and may vary from 0·3 mm. to about 1000 mm. per minute.

The Pulsatory Activity in the Ascent of Sap

The rhythmic activity which underlies the propulsion of sap has been demonstrated by the comparative method. Any agent which modifies the pulsations of the leaflet of *Desmodium gyrans*, or the autonomous movement of growth, has been shown to induce corresponding modifications in the ascent of sap. The characteristic effects of various accelerating or inhibiting agencies not only offer crucial proofs of the essentially physiological nature of the action which maintains the water-transport, but also demonstrate that rhythmic activity is the most important factor in the process.

That the action of external agents induces identical effects in all modes of pulsatory activity, including the ascent of sap, has been demonstrated in a variety of cases, such as (1) diminution of internal pressure; (2) stimulation of tissues in a normal condition; (3) stimulation of tissues in a sub-tonic condition; (4) variation of temperature; (5) the arrest of rhythmic activity at a critical temperature; (6) action of anæsthetics; and (7) of poison.

1. *Effect of Diminution of Internal Pressure.*—Diminished internal pressure, due to drought or to the action of a plasmolytic solution, induces an arrest of movement in *Desmodium*, the arrest of growth (p. 12) and equally the arrest of the ascent of sap (p. 54): the cellular pulsations

on which the propulsion of water depends are, under these conditions, brought to a state of standstill (p. 241).

Excessive transpiration does not, as is commonly held, increase the rate of the ascent of sap: on the contrary, it has been shown that a condition of drought diminishes the rate of ascent, owing to the reduced activity of the pulsating cells.

As pulsatory activity depends on internal hydrostatic pressure, the pulsating cells are relatively more active in the more turgid portion of the plant. The direction of propulsion of sap thus follows the 'turgor-gradient,' normally, from the root, absorbing water, to the top of the shoot, in which partial drought is produced by transpiration from the leaves. On supplying water to the leaves and withholding it from the root, the turgor-gradient is reversed; the flow of sap now takes place downwards. The relative velocity of movement of sap in normal 'up,' reversed 'down,' and in transverse directions, has been found, in typical cases, to be as 27 : 4 : 1 (p. 49).

2. *Effect of Stimulus on Normal Tissues.*—Strong stimulus inhibits rhythmic activity; the pulsations of the *Desmodium* leaflet, and also the rate of growth, are diminished or arrested by it (p. 14): similarly it diminishes or arrests the ascent of sap (p. 56). Sunlight acts as a stimulus on herbaceous stems in which there is no thick bark to obstruct the light. The after-effect of long-continued action of light on these plants is to produce a persistent diminution of the rate of ascent, in consequence of which a physiological anisotropy is induced between the sunlit and the shaded sides of the plant. The velocity of ascent on the sunlit side is markedly lower than on the shaded side (p. 47). In trees with thick bark, the incident sunlight causes a rise of temperature and thus enhances the activity of the side exposed to the sun (p. 176).

3. *Effect of Stimulus on Sub-tonic Tissues.*—Rhythmic activity is enfeebled or arrested under the condition of sub-tonicity. The application of stimulus to a tissue in

that condition restores its activity ; it renews the arrested pulsation of *Desmodium* (p. 16), the activity of growth (p. 17), and the ascent of sap (p. 57).

4. *Effect of Variation of Temperature.*—A rise of temperature up to an optimum enhances the frequency of pulsation in the *Desmodium* leaflet, in the rate of growth (p. 17), and in the rate of ascent of sap (p. 58). A rise of temperature of 5° C., from 30° to 35°, doubles the rate of growth and of the ascent of sap. Fall of temperature has the opposite effect of lowering all pulsatory activities.

5. *The Critical Minimum Temperature.* — Pulsatory activity is arrested at a minimum temperature. In mature organs of several tropical plants this is about 14° C. The pulsation of the *Desmodium* leaflet and the ascent of sap in cut stems are arrested at this temperature. Growth is arrested at about 22° C., which is also the critical temperature for arrest of ascent of sap through growing roots (p. 68). One and the same tissue thus becomes a conductor or a non-conductor for the ascent of sap in accordance with the alternate rise or fall of temperature above and below the critical point.

6. *Effect of Anæsthetics.*—A small dose of anæsthetic has a stimulating effect, while a large dose brings about an arrest of activity, culminating in the death of the organism. The preliminary effect of chloroform is an enhancement of the amplitude of pulsation in *Desmodium* (p. 19), an enhancement of the rate of growth (p. 20), and an enhancement of the rate of ascent (p. 69).

7. *Effect of Poison.*—As the rhythmic tissue which maintains the ascent is continuous throughout the length of the plant, the death of a particular zone by poisoning or scalding does not arrest the suctional activity of the unkilled portions above. The suction may therefore persist till the whole length is killed (p. 22). The effect of poison is manifested in the arrest of ascent (p. 71) ; in the condition of the plant before and after poisoning (p. 74) ; and, in the case of seedlings of Wheat, by the simultaneous

stoppage of growth and of the exudation of water-drops from the tips of the leaves (p. 72).

The above experiments afford conclusive proof that the ascent of sap is due to pulsatory activity of living tissue. As the effects produced in cut stems are the same as those in intact plants with roots, the activity which maintains the ascent is not confined to any one part of the plant but exists throughout its whole length.

Localisation of the Active Layer for the Propulsion of the Sap

The generally accepted view is that the conduction of the sap takes place only through the dead xylem, and it is based upon two different experiments. The first is the 'ringing-experiment,' the inconclusiveness of which has been explained (p. 34). The second is the supposed abolition of the ascent of sap in the stem when its cut end is exposed for a short time to the air. Though the injected air blocks the xylem-vessels, yet in spite of this the ascent of sap has been found to persist (p. 37). This shows that the xylem is by no means essential for the conduction of sap. Other experiments already described offer, on the other hand, conclusive proof that the propulsion of sap is a physiological process of a pulsatory character, carried on by a living rhythmic tissue.

Experiments with the Electric Probe have demonstrated (1) that a definite layer of tissue, namely (in dicotyledonous plants) the innermost layer of the cortex, is in a state of active pulsation which consists of alternate contraction and expansion: (2) that there is no such pulsatory activity in the dead wood (p. 218): (3) that the physiological agents which enhance cellular pulsation also increase the rate of ascent of sap; and, conversely, that agents which depress or inhibit pulsation induce a lowering of the rate, or an arrest of the ascent (p. 241).

The active cortex abuts upon the phloem, which is the conductor of the nervous excitation initiated by external stimulation. This is significant, since direct or transmitted stimulation is essential for the maintenance of cellular pulsation (p. 245).

Function of the Xylem

The alburnum is within a fraction of a millimetre of the cortex, and the water expelled during active contraction of the pulsating layer can be readily injected into the wood-vessels. That this is what actually takes place is shown by the ‘ weeping ’ Mango-tree in which a cavity had been formed by the decomposition of the alburnum on the right side of the trunk, the cortex being uninjured. The lateral injection of water by the active cortex filled the cavity and forced out the plug of mucilage which periodically closed the vent. The outflow took place when the cellular activity was at its maximum at thermal noon. The effect exhibited on the opposite side of the trunk, containing the alburnum intact, was quite different. There was no exudation from a hole drilled into that side. The intra-vascular pressure was, as shown by an attached manometer, at its *minimum* at midday owing to the water injected into the alburnum being rapidly removed by transpiration. These results afford conclusive proof (1) that the pulsatory activity of the cortex forces water not only upwards in the physiological conduction of sap, but also in a lateral direction into the contiguous alburnum, and (2) that the alburnum is the channel for the *mechanical* transport of water, the force of injection being supplied by the active cortex (p. 175). The bulk of the xylem serves as a reservoir, the water being pumped into or withdrawn from it, according to circumstances.

Physiological Continuity in the Plant

The fact that the ascent of sap is maintained by coordinated cellular activity throughout the length of the plant has been demonstrated by showing that the effects in different regions are correlated with each other. The activity of the ascent of sap has been estimated (1) from the relative rapidity of ascent determined by methods already described; (2) from the pressure exerted, as measured by the Recording Manometer; (3) from the rate of excretion from the leaves, as indicated by the Bubbler or by the Micro-Transpirograph; and (4) from the rate of exudation from the root-stock or from wounded plants, as shown in the automatic records given by the Tilting Electric Recorder.

Physiological continuity is manifested (1) *in the effect of drought*, natural or artificially produced, which diminishes not only the rate of ascent (p. 45) but also the exudation from the root-stock (p. 137) and the transpiration from the leaves (p. 102);

(2) *in the effect of the removal of the root* in increasing the rate of ascent of sap (p. 79) and enhancing the rate of transpiration (p. 11). The increase of transpiration thus produced was more than 70 per cent.;

(3) *in the effect of stimulus*, which retards the rate of ascent in the stem (p. 56), the exudation from the root-stock (p. 138), and the transpiration from leaves (p. 102). The retardation of transpiration is induced not only by direct stimulation of the lamina but also by stimulation of the mid-rib and of the petiole (p. 93);

(4) *in the effect of warmth* in enhancing the rate of ascent (p. 59), in increasing the rate of exudation (p. 142), and in enhancing transpiration (p. 92). It has been shown that the effect of local rise of temperature due to sunlight caused increased exudation from the Mango-stem (p. 176), and also of sugar-containing sap from the spadix of the Palmyra Palm (p. 187);

(5) *in the effect of anæsthetics*, a small dose of which induces an enhancement of activity, while a large dose retards or arrests it; whether it be the rate of ascent of sap (p. 69), or the exudation from the root-stock (p. 140), or the transpiration from the leaves (p. 114).

There is thus a continuity of physiological mechanism in virtue of which each region of the plant controls and is controlled by the rest.

Phenomenon of Excretion

It has been explained that there is no strict line of demarcation between the excretion of leaves, of glands, and of injured surfaces. In all alike, excretion is effected by the pulsatory activity of the terminal layer ; the apparent difference between them is a question of degree and not of kind. The difference is, in fact, the same as that which exists between the so-called autonomous pulsations of the *Desmodium* leaflet and the multiple pulsations induced in *Biophytum* and *Averrhoa* by the application of a strong or repeated stimulation. The pulsatory activity is autonomous in the terminal glandular layer in *Nepenthes* ; at the opposite extreme is the excretion from the relatively inactive layer of the wounded Palm. In the latter, the cut surface is at first inactive, and there is no root-pressure to cause any 'bleeding.' It is by the strong stimulation of the repeated wounds, of the repeated hammering and repeated kneading, that the pulsatory activity of the terminal layer becomes sufficiently aroused to cause active excretion (p. 190).

The excretion from the leaves and that from the cut end of the root-stock may be regarded as intermediate cases between the two above extremes. In the leaves the excretion from the terminal layer of cells is modified by the state of turgor, since the pulsatory activity of the cells depends on internal hydrostatic pressure. The turgor of the terminal cells is increased by the water *conveyed* and *conducted* into them respectively by the vessels in the veins of the leaves and by the cortex that surrounds them. When the ascent of sap is retarded by drought or by plasmolysis, the pulsatory activity of the terminal layer undergoes a decline, with a resulting diminution of transpiration (p. 102).

The physiological mechanism of the active excretion of water-drops from leaves is not essentially different from the above. Here the terminal layer is often supplied with water under pressure by means of the vessels, these being in their turn filled with water by the activity of the surrounding cortex.

In the root-stock of herbaceous plants (where the wood element is relatively slight), the excretion from the cut end is due, in part, to the activity of the terminal layer. For it has been shown that when the terminal cells are locally stimulated by dilute chloroform the rate of excretion becomes greatly enhanced (p. 141). Local rise of temperature also causes an enhancement of excretion (p. 142). These facts prove that every portion of the plant takes its share in bringing about the excretion by the terminal vent, whether this be the leaf or the cut surface of the root-stock. It has been supposed that the exudation from the cut end is a passive process brought about by root-pressure acting from below. But the source of the pressure is not localised; it is the result of the co-ordinated pumping activity of cells throughout the length of the plant, including the layer of cells at the cut surface.

Transpiration

That transpiration is a physiological process of excretion by the leaf-cells, the excreted water being removed by the physical process of evaporation, has been demonstrated by balancing evaporation, from an equivalent surface of water, against transpiration. The balance is upset during rise of temperature up to an optimum, transpiration being relatively more active than physical evaporation. The converse effect takes place during fall of temperature. Separate experiments with the Bubbler showed that, in the leaf of *Thunbergia*, the optimum temperature for transpiration is 33° C., which undergoes a decline on further rise of temperature (p. 128). We thus arrive at a discriminating test by which transpiration is distinguishable from evaporation. Evaporation is continuously increased with rise of temperature; transpiration exhibits, on the other hand, an optimum above which there is a decline.

The physiological activity underlying transpiration is further demonstrated by the following experimental results. Transpiration is depressed by diminution of turgor, is arrested by the action of stimulus, and is enhanced by a rise of temperature; under anæsthetics it undergoes an enhancement or depression according to the strength of the dose.

That the excretion of water from the leaf is an active physiological process is further shown by the fact that it continues even after the abolition of evaporation by smearing both the upper and the lower surfaces of the leaf with vaseline. The actively excreted water-drops are then found collected under the film of vaseline (p. 90).

Transpiration exhibits a diurnal variation, the maximum being attained at thermal noon, about 2 P.M.; the minimum transpiration occurs at thermal dawn, early in the morning.

Thermal radiation, by raising the temperature, enhances transpiration. Light-rays of the more refrangible blue-violet region, acting on the more sensitive lower surface of the leaf, cause a diminution of transpiration which amounts to about 36 per cent. The effect of red light is opposite, being an increase of 68 per cent. (p. 111).

Automatic Regulation of the Ascent of Sap

Excessive loss of water by too rapid ascent and transpiration, which would endanger the life of the plant, is automatically checked by physiological regulation. During excessive drought in summer the cellular activity is depressed, which causes a great diminution in the velocity of ascent (p. 45). The stimulus of sunlight retards the conduction in the stem (p. 46). Finally, while evaporation is continuously increased with the rise of temperature, transpiration undergoes a decline as the temperature rises above the optimum (p. 128), and this acts as a physiological check.

Relation between Root-pressure and Exudation

The ascent of sap has been explained as due to physiological conduction along the cortex and to mechanical convection along the xylem. The lateral pumping by the cortex fills the xylem-vessels with water and causes an intravascular pressure. When the amount of water forced in is greater than what is lost in transpiration, the pressure becomes positive ; when the vessels are losing more liquid by transpiration from the leaves than is being pumped into them by the cortex, the intravascular pressure becomes negative. There are thus two different possible cases, typified by (1) the root-stock without leaves, or the leafless deciduous tree ; and by (2) the root-stock with a side-branch bearing leaves, or the tree with leaves.

The maximum cellular activity in the ascent of sap occurs when the temperature is highest at thermal noon ; but this gain is counterbalanced in trees with leaves by the loss by transpiration, which is relatively greater. In the root-stock without leaves, and in the leafless tree, the intravascular pressure is at its maximum at thermal noon. Exudation from the cut end of the root-stock, or from a hole drilled in the tree, is also at its maximum at this period. The hole, reaching the wood, drains all the water that is being actively pumped by the cortex into the whole length of the conducting tissue below the hole. The 'bleeding' produced is therefore considerable. But in the root-stock with a side-branch bearing leaves, and in leafy trees, the loss by transpiration at thermal noon is, as already stated, relatively greater ; a maximum negative pressure thus occurs at thermal noon, and the side-tube sucks in water that is supplied to it. *The diurnal variation of pressure and exudation in the root-stock without leaves,* *or in the leafless deciduous tree, is determined by the daily variation of temperature, the maximum being attained at thermal noon, and the minimum at thermal dawn. The converse takes place in the root-stock with leaves and in the leafy tree* (p. 156).

The Cellular Mechanism

Discovery has been made of the pulsations of individual cells ; they have been automatically recorded by electric means, which show that the active cells concerned in the ascent of sap execute alternate expansion and contraction, the period of a single pulsation varying, under different circumstances, from fourteen seconds to several minutes. Deprivation of the stimulating action of the environment brings the pulsation to a state of standstill ; but application of stimulus is now found to renew the pulsating activity. Rise of temperature, which enhances the rate of ascent, increases the amplitude or the frequency of pulsation ; lowering the temperature arrests the pulsation and the ascent of sap. The preliminary effect of dilute chloroform is to enhance the amplitude of pulsation, so that the up-stroke in the pulsation, indicative of suction, is relatively greater than the down-stroke ; the rate of ascent of sap also undergoes a corresponding increase. Continued action of the anæsthetic arrests the pulsation, with corresponding arrest of ascent. Diminished internal pressure, induced by the action of a plasmolytic solution of KNO_3, gives rise to a characteristic change in the pulsation ; the down-stroke, which represents contraction, becomes greatly increased, while the up-stroke, which represents suction, is reduced ; the base-line declines downwards, indicating a persistent diminution of turgor. The final result is an arrest of pulsation and a throttling of the channel for propulsion, with the consequent arrest of the ascent of the sap (p. 241).

The uni-directioned propulsion of sap depends upon a sequence of pulsation from cell to cell. This has been demonstrated by the occurrence of definite electric maxima and minima in the path of conduction, the distance between the maximum and minimum being half the wave-length (p. 225). The sap expelled during the contraction of any one cell is absorbed by a cell higher up during its phase of expansion (pp. 142, 191). There is thus a propagation of a wave of contraction preceded by one of expansion, in consequence of which the sap is, as it were, squeezed forward. A succession of such waves maintains the continuous ascent of sap.

Mutual Control and Interaction between Distant Organs

The plant is a multicellular organism, and hence necessity arises for intercommunication and interaction between more or less distant organs. This is accomplished in two different ways : by *transfer of matter*, and by *transmission of motion*. The first is exemplified by the hydraulic convection of liquids carrying chemical substances in solution, such as occurs in the circulation of sap ; the second, in the conduction of excitatory change along nerves. The tissue for the cell-to-cell propagation of hydraulic impulse in the propulsion of sap is the internal cortex which abuts on the phloem ; this latter is the tissue for the conduction of nervous impulses. The two different conducting channels are thus in close proximity to each other.

For the continued maintenance of cellular pulsation in the ascent of sap, direct or transmitted stimulation is essential. When the plant is cut off from the stimulus of the environment, the cellular pulsation is stopped and the ascent of sap becomes arrested. Fresh stimulation renews the pulsation and the ascent. The roots are stimulated by friction against the soil. In the body of the plant, the distribution of the vascular bundles (containing the nervous phloem) is such that no mass of living tissue is too remote to be excited by stimulus transmitted from the receptive region. The leaf is a catchment-basin for the reception of the stimulus of light. The excitatory effect produced in the nervous elements present in the veins is gathered into larger nerve-trunks and transmitted to the interior of the plant (p. 246).

Stimulus gives rise to dual impulses (p. 249). The contraction of the excited cells is attended with expulsion of water: the hydraulic impulse thus produced gives rise to an erectile response of the distant leaflet. The excitatory impulse, which travels at a relatively slower rate, causes the opposite movement of a fall. The hydraulic and the nervous reflexes thus act antagonistically to each other (p. 247). The existence of these dual impulses, and the suppression of the nervous impulse when transmitted through a considerable length of semi-conducting channel, explain the various tropic curvatures, and the opposite geotropic responses given by the root and by the shoot (p. 251).

Co-ordinated action is often met with in the nervous reflex. The four quadrants in the pulvinus of *Mimosa* act as four different effectors with torsional movements to the right or to the left, and vertical movements up or down. These four quadrants are controlled by separate nervous impulses transmitted from the four sub-petioles bearing the leaflets when stimulated by light. The leaf as a whole is adjusted in space by the co-ordinated action of the four reflexes. The dia-heliotropic attitude of the leaf is thus brought about by distinct nervous impulses, initiated at the perceptive region actuating the different effectors at a distance (p. 254).

There are other modes of stimulation with corresponding nervous reflexes; and it is the permutation and combination of all these factors, some concordant and others antagonistic, that give rise to the innumerable variations of the resulting responses. This is the secret of the great complexity of the life-movements, which are by no means capricious, but are capable of rational explanation.

The ultimate result of investigations such as these is the establishment of the important generalisation of the unity of physiological mechanism in all life. For we find, in the plant and in the animal, similar contractile movement in response to stimulus, similar cell-to-cell propagation of pulsatory movement, similar circulation of fluid by pumping action, similar nervous mechanism for the transmission of excitation, and similar reflex movements at the distant effector. The simpler type of plant-organisation offers an unique advantage in investigation, the pursuit of which will no doubt lead to the solution of many perplexing problems of animal life.

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Printed in England at THE BALLANTYNE PRESS
SPOTTISWOODE, BALLANTYNE & CO. LTD.
Colchester, London & Eton