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1. PROPAGATION. PURPOSE IN THE PLANT WORLD. METHODS.

The power of reproduction is a ~~chara~~ characteristic possessed by all living organisms. It is a necessity for the continuance and multiplication of species. By this process in the plant world, the earth's surface is kept covered with vegetation. New areas are encroached upon, the old areas preserved. In the struggle for existence, those plants are most widely distributed, which ~~ha-~~ have successfully solved the problem of the propagation of their species.

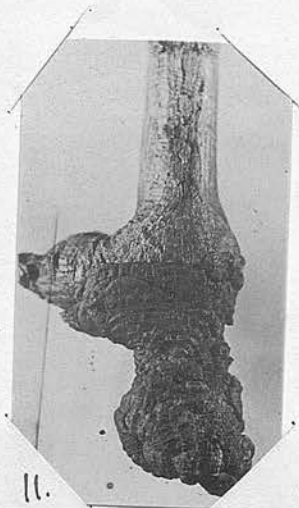
There are two distinct modes of propagation in the plant world:— 1. sexual, and 2. asexual.

A. Sexual Reproduction is reproduction of the plant by seed.

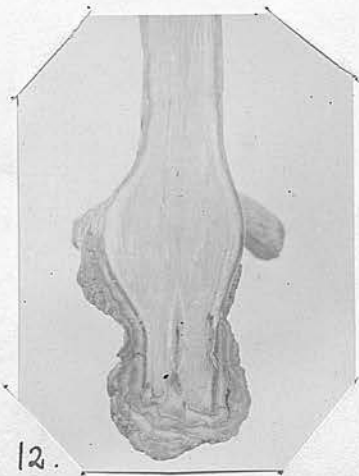
The essential aim is increase of the individual with no regard to area. The elaborate mechanisms for seed dispersal shew an adaptation and utilization of such agencies as wind, insects, birds, man, &c. In nature, this mode of reproduction is the more common and those plants that have highly perfected their seed dispersing mechanisms, are most widely distributed e.g. Compositae, Leguminosae, &c.

B. Asexual /

(17a.) Copy.



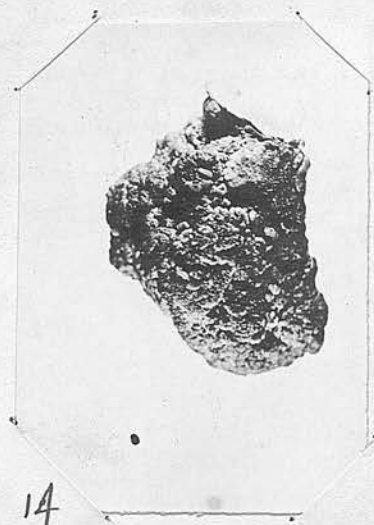
11.



12.



13



14

Fig. 11. + 14. - (*Anaerospaera racemosa*.)
Laminated appearance of forced callus, obtained by
successive excitations

Fig. 12 + 13. - Macroscopic sections of same.

(1) ~~H.~~ Henslow. 1906.

(2) MacDougal ~~B.~~ P. 1901.

Hall ~~J.~~ G. 1905.

Dale ~~M.~~ 1901. cp. also page 9 and 10.

(3) refs. (1) page 5.

(4) ~~M.~~ Burbidge. 1877. Preface.

Many of the methods included under Asexual Propagation in practice are not convenient for every plant. Only those methods which give the most rapid results have been utilized in commerce. Commercially speaking, other methods have not been worth while; but they have no right to be considered as impossible. Theoretically, as will be shown in the following paragraphs, vegetative reproduction is a capacity possessed not only by the plant as an individual, but by every portion of the plant. Therefore, in practice, as will also be shown, it is an ignorance of conditions that causes the failure of any portion of any plant to be reproduced.

2. MISCONCEPTION OF CAPACITY FOR VEGETATIVE PROPAGATION

Although the fact is sometimes not generally recognised, there is an unlimited capacity for vegetative regeneration in the plant world. Not only do individual plants possess this capacity, but even portions, attached or severed, a fact which is shown by a consideration of the various vegetative means of increase in nature.

A. Nature's methods of vegetative propagation.

a. The plant as a whole: vegetative organs serving for reproduction.

The plant as a whole has the power of reproducing itself by the production of specialized vegetative organs /

organs. These organs are modified to serve as storage organs. When, therefore, division of the plant, naturally or accidentally occurs these storage organs become detached from the plant. By reason of the reserve food material contained, life is however maintained, until the new organs (roots, shoots, or both) necessary to reconstitute a new individual are formed. Such modified vegetative organs arise normally and are:-

- Bulbs, bulbils, or bulb tubers. (modified buds)
- Fleshy leaves. (modified leaves)
- off sets, stolons, rhizomes, suckers, runners, stem tubers, fleshy stems. (modified stems)
- Root tubers, fleshy roots (modified roots)

Handwritten notes:
 not found
 bulbils
 bulbs
 ↓

Handwritten notes:
 Key has in
 w.p. of plants
 in flower
 ↓

Thus it is seen that every vegetative portion of the plant (stem, leaf and root - even in exceptional cases, parts of the flower) may become modified to act as reproductive organs. In the construction of these reproductive organs nature has followed a certain principle. Where there is a reserve store of food, the attachment to the parent plant is slight. The reproductive organ is easily detached, and by reason of the reserve food is at once able to support itself,

e.g. /

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(e.g. bulbils, fleshy leaves).

Where, however, there is little store of nourishment, the attachment to the mother plant is much closer, and the detachment is usually gradual (e.g. stolons, runners, rhizomes, &c.) (1) It follows from a consideration of this method of vegetative reproduction that a reserve of food material (either in the reproductive organ, or close at hand in the parent plant) is a factor favouring vegetative reproduction. This factor must therefore be taken into account in practice. (see p)

b. The plant as a whole. Adventitious organs formed for reproduction.

If the plant does not modify the normal vegetative organs for the purpose of reproduction, it may reproduce itself ^{by} for the formation of adventitious organs, which in contradistinction to the normal vegetative organs, arise abnormally. These adventitious organs are of two kinds:- adventitious shoots i.e. shoots occurring on roots either directly or as the result of wounding (see p. adventitious roots i.e. roots occurring on shoots either directly or as the result of wounding (see p. In this method of asexual propagation, no storage of food material /

(1) Aiken, 1906, Dale-1875, Duchartre 1875, Nye 1904, Vöchting (#) 1900. &c. 1901.
(ii)

material is made, but provision is made for reproduction of the portion by the formation, while still attached to the plant, of new organs, which after ^{yer} severing are at once able to function.

c. Severed portions of the plant.

The capacity for vegetative reproduction is an important asset to the plant, liable as it is to all forms of mechanical injury. Not only however does the plant as a whole possess this power, and provide for future detachment by the formation of modified vegetative organs, or adventitious organs, but even portions not intended by nature to propagate, having neither reserve of food material, or already formed roots or shoots. Such a portion, becoming detached either artificially or naturally, instead of dying, is often found to have re-established itself by the subsequent formation of new adventitious organs. The fact that vegetative regeneration in this way does not often occur in nature, is due to the lack of favourable conditions while roots and shoots are being formed.

In the case of a portion which becomes detached after adventitious roots have been formed, the formation of these

these organs is attended with no difficulty, the store of food material and life generally being maintained by the mother plant. (see B -

In the case of the modified vegetative ^{organs} too, the store of food material, (even though adventitious organs are not formed till after entire or partial detachment) is sufficient for life to be maintained, until these new ~~or~~ organs are produced. In this case, however, the severed portion has neither a store of food material, nor is it already in possession of adventitious roots and shoots, therefore the reproductive energy, while existing, is often not able to assert itself, owing to the unfavourable conditions under which life is maintained.

Handwritten notes:
Y...
M...

If, however, a certain amount of moisture, and an even temperature be present, reproduction is effected and new organs are formed. This is shewn by examples of detached portions (e.g. branches of willow &c.) which give rise to new organs in presence of moisture.

The phenomenon of the sprouting of old stools, after trees have been cut down, also shew that the portion remaining after the severing has taken place has the power under suitable conditions of regenerating.

When a part of a plant becomes not only wounded, but entirely severed in nature, the separative energy or reproductive power is first made evident in the formation /

formation of healing tissue termed callus. From this callus tissue, the adventitious organs may arise, though not necessarily. (see p

This fact of callus ^{formation} is also taken account of in practice. Nature's method of healing is utilized in the severing of the organ, and conditions are observed which will induce callus formation. (see p

In practice also adventitious roots and shoots are induced by mutilation &c. The portion on which these adventitious organs are desired, is either left as in nature, in connection with the parent plant, until they are formed. (e.g. layering, in arching &c. see next page. p 10.) or if the part of the plant is severed, due recompense is given for the loss of nutrition so occasioned. (e.g. cuttings &c. p 11.).

It is seen therefore that vegetative methods employed in practice, are derived directly from an observation of the methods occurring in nature. In vegetative reproduction, with regard to parts intended by nature to propagate, certain principles are followed. It is only when these principles are observed in practice that success is possible, in methods imitating those indicated by nature.

With regard to parts not intended by nature for propagation, the inherent tendency to reproduce is expressed only under those conditions which maintain life.

In /

In practice therefore, any part of the plant not intended by nature to propagate (e.g. cuttings) may be made to reproduce, if due consideration is given to conditions which will maintain life.

B. ARTIFICIAL METHODS OF VEGETATIVE REPRODUCTION

Among the various methods of vegetative reproduction the best known are the following. They follow naturally, from a consideration of the methods employed by nature.

a. Utilization of Vegetative reproductive organs.

Division. In this mode of vegetative reproduction (including propagation by stolons, runners, bulbs, tubers, &c.) the plant is artificially divided, and new plants obtained (cp. A. back).

Since in nature the conditions that favour seed formation are usually antagonistic ^{to} the formation of vegetative reproductive organs, in practice the one can usually be promoted by inhibition of the other. Luxuriance in growth is usually accompanied by barrenness. These observations have given rise in horticulture to the practice of checking in some manner the upward flow of the sap, that would otherwise go to the development of the seed. Thus the formation of vegetative organs are induced in artificial ways, such as, scarring the centre of bulbs; wounding the crown of a plant cutting /

Yes but you have to be careful of the points

Yes but if you cut the crown

cutting off terminal heads.

These methods are found, while preventing the formation^{of seed,} to promote the production of suckers and offsets, which may then be used for the vegetative propagation of the plant.

b. Reproduction by adventitious organs formed first: severing follows.

Layering:- In the methods of artificial layering, derived from the consideration of natural layering, the shoot of a plant is pegged down ^{to} and the soil in various ways to induce root formation, but is not severed from the plant, until after their formation. The method is en only convenient for low growing plants or branches that can easily be brought into contact with the soil.

Marcottage : The method of marcottage is really a special form of layering. When a branch is too high, or some factor makes it inconvenient or impossible to bring the branch to the soil, the soil (usually damp moss, damp earth &c) is conveyed to the branch.

Inarching : The method of inarching is also a special form of layering. The plant on its own roots is equivalent to the branch attached to the parent plant in layering and marcottage, and the special soil in this case is another plant. In this case /

case the new formation is the callus tissue - not necessarily roots and shoots. Inarching is also termed "grafting by approach";⁺ When for some reason or another it is inconvenient to avail oneself of the whole plant, for its increase by any of the foregoing methods, a part is entirely severed from the parent plant and reproduced in the following ways. While reproduction by natural cuttings takes place less frequently in nature, owing to the unfavourable conditions, this method from its convenience tends to become the most important in practice, since due regard can be paid to these conditions.

* new §.

c. Reproduction by first severing: production of organs follow

Cuttings ∴ In the method of reproduction by cuttings, some portion of the plant, not intended by nature to propagate - (root, stem and leaf) is severed. With the factor of callus, and with the necessary environmental conditions, these parts are artificially induced to grow. Roots or shoots (or both, in the case of leaves and topless stems cuttings) must be formed before the cutting can be said to have struck.

Grafting. The method of grafting is really that of cuttings on a special soil - bearing the same relation /

relation to cuttings as ⁱⁿarching to layering. Grafting is the transference of a part of a plant (scion) to another plant (stock). A callus tissue must be formed to unite scion and stock. (In this case the scion is equivalent to the cutting, the stock is the special soil)

Budding. The vegetative method of budding is also a particular form of grafting, and thus a special form of cutting. The method consists in the transferring of a single bud of one plant to the stem of another. (The bud in this case forms the cutting; the stock, as in grafting the special soil).

3. POSSIBILITY OF VEGETABLE PROPAGATION.

By a consideration of the means of vegetative reproduction in nature, and by the behaviour in practice of such a plant as Aeghthus montana, any part of which can be made to regenerate, one must conclude that the capacity for vegetative propagation is inherent in all plants, and in all parts of the plant. It is in fact as much a characteristic of the organism as is growth. The experience and researches of horticulturalists and botanists up to the present day, can only lead one to this conclusion.

In earlier times it was thought that stems were the only parts of the plant which bore buds on their surface ⁽¹⁾ but later investigations /

(1) Lindley 1855.&c.

Montana.

Theoretically, the principle of the universal capacity for vegetative reproduction follows from a study of the construction of the plant. The plant is a living organism composed (in the flowering plants) of root, and shoot and leaf. Experience and investigation of various metamorphoses and transitions from one organ to another show that these organs are not distinct, and that there is no strict limit between them as we are accustomed to place. (1) The difference in external appearance and internal structure have been evolved as a result of different conditions on parts with different functions. By reversing these conditions and functions, metamorphoses may be made to occur - e.g. roots into shoots &c. (2) If, therefore, reproduction is possible for one part, it should be possible for all parts, the only condition being the presence of undifferentiated cells, or cells whose destiny is not yet fixed, in order that growth and subsequent differentiation may follow. These undifferentiated cells may already be present or may be supplied in the new formation of callus.

Now, since the general construction of plants is the same, it follows therefore that the difficulty, in some cases inability, at the present day of many plants to reproduce themselves, is not real, but depends on conditions, extrinsic /

(1) McCallum 1905.
 (2) Philippi 1901.

extrinsic and intrinsic. The importance of this principle that the capability of vegetative reproduction is inherent in all plants, and in all parts of the plant, is very great in horticulture. It acts as a stimulus to finding the necessary conditions for vegetative propagation by careful notes of experiments, just as the best or only conditions for successful culture of plants have only been found by experience. (1)

4. GENERAL CONDITIONS OF REGENERATION

The general conditions that are necessary for regeneration (in its widest sense, see p 18.) are those which are essential to the support of life: viz. a certain amount of heat, moisture and food material. These conditions have been deduced from a consideration of nature's methods of propagation. Even the food material can to a great extent be dispensed with, since life can persist for some time and regeneration takes place, even when the plant is starving. (2)

In practice all these conditions must be supplied. Since the conditions of life vary for each individual plant, so will the conditions of regeneration. This fact has been sometimes neglected. In many plants it has been found that by a selection of a shoot of a different age or condition, by

(1) See notes on culture of plants in current gardening periodicals, e.g. Garden, Gardener's Chronicle &c

(2) McCallum 1905.

by the choice of a different season of year, according to the rest period of the plant for the insertion of the cutting, ⁽¹⁾ and in other ways by adapting the conditions to the nature of the plant, success has been achieved even in cases which were at first pronounced incapable of being reproduced vegetatively by means of cuttings.

In practice, the phenomena of regeneration are found to be promoted by additional artificial conditions, i.e. by the application of various stimuli. An increase of heat may be found to act as a stimulus in regeneration. An excess of moisture may give the same result. Other external conditions may be used as stimuli, but the chief stimulus in regeneration has been found to be undoubtedly that of the wound.

While in nature, reproduction often takes place directly without the intervention of a wound stimulus, or the formation of healing tissue, yet it is ^{far} more common even in nature to find new formations resulting from a wound. Thus the wounding, mutilation or entirely severing a part of a plant has been utilized in practice in order to induce new formations. The tissue callus, provided by nature to heal the wound, often acts as a starting point of differentiation, and subsequent root and shoot formation. Therefore in plants that are slow and obstinate in rooting, artificial stimuli have have been given by cutting or paring of the callus, in order to induce the formation of these organs. (see after)

Not /

Not all plants, however, make use of this callus tissue for the formation of new organs. The amount of callus formation is usually correlated with the ease of root and shoot formation, and according to the presence or absence of preexisting structures, new organs may or may not arise from the callus tissue. Thus in the stem, the pericycle is rarely active. New organs therefore usually appear from the callus tissue itself. In the root, however, the pericycle has the important function of producing lateral rootlets. Therefore under the conditions of severing the root and treating as a cutting, it is not surprising to find shoots are also formed by the pericycle - instead of arising always from the callus.

5. REGENERATION. MEANING OF TERM. CONTRIBUTIONS BY VARIOUS AUTHORS. &c.

In order to study Regeneration or Reproduction in all its aspects, especially its three main features, Callus, Root and Shoot formation, it is desirable to know what contributions have been made to the subject by various authors, especially during recent years.

At the outset, the term Regeneration has led to some confusion among investigators owing to the limited sense in which it has been used. It has, however, been generally agreed among modern writers, such as Göebel (perhaps the greatest exponent on the subject), ⁽¹⁾ Klebs, Küster, McCallum, Morgan &c. that the use of the term in its wider application is after all the /

(1) see bibliograghy under each author.

the only possible one, since the phenomena of regeneration are so closely intimate with those of ordinary vegetative growth. The following table has been drawn up in order to make the term as employed by the various writers intelligible at a glance.

Note (The subdivisions are necessarily somewhat arbitrary to make the meaning clearer. There is really no hard and fast line between the various processes).

Regeneration in the modern, or wide sense, includes the general phenomena connected with vegetative parts giving rise to new tissue, new organs, or parts of organs.

(see ^{under} Goebel, Klebs, Küster, Morgan &c.).

Regeneration therefore includes:-

- 1. Regeneration (limited sense)
- 2. Replacement or Substitution.
- 3. Restoration a. of organ
b. of individual.

1. Regeneration or Re-creation - limited sense

The formation of an organ 'de novo', exactly resembling in function and form the lost part. (This, as pointed out by Miss Kupfer, limits the use of the term, to the restoration of embryonic tissue in root and shoot).

(see ^{under Nemece} Nemece, Frank, Pfeffer, Pranté)

11. Replacement, or substitution

The substitution of another organ, the *primordia* of which are already in existence, for the organ or part which /

which has been lost. This may occur in two ways:-

- 1. By the modification of an organ which takes on as far as possible the external appearance and internal structure of the lost organ. The development is abnormal. {see Boirivant, on root and shoot}.
- 2. by the development of latent organs, which would not develop, but for the new conditions of severing or mutilation. The development is normal. (This is synonymous with vegetative growth under abnormal conditions).

See Vöchting, Morgan, and Klebs.

111. Restoration or re-creation

The development of an organ 'de novo' at a place or in conditions where normally it would not occur.

See Miss Kupfer.

6. CAUSES OF REGENERATION. VARIOUS THEORIES
ADVANCED. THE VITALISTIC THEORY.

The consideration of the term Regeneration, leads one naturally to consider the question of the Causes of Regeneration. This much vexed question has been dealt with by the different writers, according to the more or less limited conception they held of Regeneration. A brief summary of some of the causal factors advanced might be /

be given. (The views given are naturally by no means exhaustive (see literature under each). They only give an idea of the different lines which have been followed).

The causal factor or factors according to

Bratland Farmer	is, stimulus due to chemical and physical agencies.
Driesch	correlations
Goebel	partly wound stimulus, partly formative stuffs.
Klebs	Removal of part, acting like external conditions (against wound stimulus and polarity as causal factors).
Kupfer	ferments or enzymes (theory of formative stuffs in altered form)
Kuster	removal of hindrances to growth
McCallum	controlling influence of organism acting along protoplasmic connections.
Morgan	physical differences, tension of cell &c. (against theory of formative stuffs)
Noll	form disturbance as stimulus
Vöchling	polarity
Wiesner	wound stimulus from dead cells.
see also under:-	^{Nemec} <u>King</u> , <u>Hettlinger</u> , <u>Wakker</u> , <u>Winkler</u> , <u>Sachs</u> , &c.

Taking the term Regeneration in the wide sense, the difficulties which arise in the consideration of the causes of the phenomenon considered in its limited sense disappear. Since Regeneration is a characteristic of the /

the plant, the causes for its phenomena are the same as those which govern growth. Like growth, the capability for regeneration is an evidence of the life of the plant. This may be termed the Vitalistic Theory as opposed to the Formative stuff theories of Goebel, Sachs, Kupfer &c. or more materialistic theories of Morgan and others. It comprises the wound stimulus theories of Noll, Wiesner, Pfeffer and others.

Seeing that life is neither chemical or physical despite the simulation which many scientists would call (1) life, neither will the problems of Regeneration be solved in this direction. Life is an energy, a force, ^{analogous to} like electricity, the causes of which, scientifically we know nothing, but the evidences of which are manifest. Growth is an evidence of life, so also is Regeneration. Growth in the plant is a building up, or constructive process.

Regeneration is a rebuilding, a reconstructive, reproductive or reparative process.

Growth is development under normal conditions.

Reproduction is usually development under the abnormal conditions of mutilation or severing, though it may also occur in normal conditions..

Since /

(1) Address of Pres. Brit.Assoc. 1912

Since growth asserts itself in a certain form according to conditions, that is to say, the plant adapts itself to its environment, (Plant Ecology).

Regeneration also manifests itself in a certain form according to conditions. (1)

Too great an emphasis has often been laid by investigators on the form. (2) Whether the resulting organ is a root or shoot does not really matter, since there is no real limit between these organs. (3)

The end of Regeneration is reproduction, which in itself is usually the completion of a reparative process, and the form in which the phenomenon manifests itself depends on conditions. Since the capacity for Regeneration is latent in the plant, these conditions may be normal; Usually, however, since the natural tendency of the plant under normal conditions is to reproduce itself by seed (4) abnormal conditions such as wounding, mutilation or severing of the vegetative organs are usually necessary to call this energy into action. (5) The wound stimulus cannot however be said to be a causal factor. It is merely a stimulus /

(1) Bretland Farmer 1903.

(2) See results of investigators, e.g. Klebs, Vöschling, Goebel &c.

(3) see back par. 2. p. 14.

(4) see back par. 1 p. 1.

(5) see Hettlinger, Kitchen, King, 1894-1901.
under Hering, Townsend, Henslow,
 Burns, Goebel, Pfeffer.

stimulus, promoting Regeneration, which may and can take place without its aid. It is, however, undoubtedly the primary stimulus, altering as it does the function or activity of the whole or part of the plant. Under the new conditions, the plant so to speak has to readjust itself. Now, seeing that the activity or growth of the plant is governed by such factors as turgidity, chemical changes in the cell &c., it follows that these are all minor factors, (not primary factors) in the process of Regeneration. All these factors are necessary, but no one can be said to be the cause of Regeneration. The changes involved in these factors result from a disturbance of the activity of the plant, which itself is brought about by normal conditions during the life of the plant, or abnormal conditions of wound and other stimuli. Therefore these factors involved are in reality effects. They in their turn act as secondary stimuli, giving rise to secondary effects.

(A table has been drawn up to make the meaning clearer).

Regeneration #

Regeneration

inherent capacity in the plant usually called into being by primary stimulus, severing or mutilation. (in many plants this capacity is expressed, without a stimulus (Poplars).

Severing or Mutilation
or prevention from functioning.

(primary stimulus)

disturbance of activity and function of parts

(general effect) acting as - stimulus (Noll, Küster)

- difference in tension (Morgan)
- chem. and physical change (Bretland Farmer)
- nutritive matter (Coesel, Sachs, Kupfer) & enzymes
- Polarity changes (Klebs)

(Special effects) stimuli

First Results

- formation of meristem (callus)
- formation of other meristematic tissue
- stimulus to latent organs (buds)
- stimulus to existing organs (root & shoot)

Final Results dependent on conditions (see after) (external & Internal)

- Amount of callus - large or small
- Formation of new organs from callus or new meristem
- Development of latent organs (buds)
- Modification of existing organs (root and shoot)

The /

The variation in Final Results in cuttings and parts of the plants which have so often appeared so puzzling is quite comprehensible when one considers that Regeneration here is ^{most of ten} essentially a reparative process, and that the results will be conformed or adapted to the immediate need of the plant. This is by no means a teleological explanation as Miss Kupfer ⁽²⁾ considers. It is, as in ecology, the adaptation of the plant to its environment. This reparative process is manifested in:-

1. The healing of the wound (see on callus)
2. The formation of new, or the development of latent organs, which are necessary to the completion of the reparative process. The form of the organ will therefore be that which serves the reparative process best. Now since absorption and nutrition are essential functions in the life of the plant, the form of the organs will be that which best fulfil these functions. This explains why roots are usually formed first on severed leaves, and why roots are first formed even on roots, if they are old and unable to function perfectly.

The field of research in the subject of vegetative propagation is so vast, that an effort to systematise results has been made, and notes, original and otherwise, collected under

(1)

(1) Klebs 1903, Küster (ii) 1903., Goebel (iii) 1902, (iv) 1903, (vi) 1905 &c.
 (2) Kupfer 1907.

under the following headings:-

Vegetative Propagation: Generally considered, in the Flowering Plants.

Vegetative Propagation in Particular, by means of cuttings, (Root, Stem and Leaf) in the Flowering Plants.

By so doing, it was found that the essential phenomena connected with vegetative reproduction, callus, root, and shoot formation, would be considered. The same phenomena occur in the consideration of other vegetative methods, but not necessarily all together.

e.g. Grafting (callus formation is the chief phenomenon
Layering (callus and root formation are the chief phenomena. Shoot formation need not be considered, since branches not roots are usually layered).

It was found advisable to subdivide the subject into two parts.

Part I: dealing mainly with the theory of Vegetative Propagation in Dicotyledons, Monocotyledons, and Conifers.

Part II: containing articles, general and particular collected mainly from the current gardening periodicals, on the Propagation of the various plants in cultivation, arranged alphabetically in their natural orders.

CHAPTER II

DICOTYLEDONS. STEM-CUTTINGS.

I. RELATIVE IMPORTANCE OF VARIOUS METHODS OF VEGETATIVE PROPAGATION IN HORTICULTURE: Their General Practicability.

Vegetative propagation is important in Dicotyledons for many reasons -

a. When seed will not ripen in this country and must be imported, e.g. in many shrubs - Asimina.

. When seed that is produced is not good, e.g. Hamamelis.

When seed is good, but the resulting plant is not to be relied upon for purity of colour or form, e.g. Lobelia vars., Dianthus barbatus vars.

b. As a sure method of propagation where plants hybridise freely amongst themselves, e.g. Cistineae. Such plants as Cistus and Helianthemum raised from cuttings are often superior from the point of view of purity, to seedling plants.

True varieties are invariably increased by seed: propagation by cuttings, &c., is usually employed for hybrids, though these can also be raised from seed ⁽²⁷⁾

by/

by careful selection, when well established, e.g. Berberis (by seed), Mahonia (by cuttings). New hybrids are obtained from seed by Mendel's Law⁽¹⁾.

c. As a method of continuing a sport or juvenile ~~stage~~ stage as a distinct plant⁽²⁾, e.g. Laburnum Adami. Cuttings are also made of the best coloured shoots in order that the resulting plants may also be well coloured or variegated, e.g. many Euphorbiaceae (Phyllanthus, Groton).

d. For quick rooters, propagation by stem-cuttings is the general mode of increase, e.g. Mimulus, Veronica, Hydrangea, Fuchsia, &c.

e. Vegetative propagation by means of layering is employed when the plant is a shy rooter, and cuttings are difficult to strike, e.g. many shrubs - Chimonanthus, Rhododendron, Azales, Magnolia, &c.

f. The method of grafting is employed for many reasons -
To give a weakly variety the benefit of a strong stock.

For economy in valuable plants, which may be used as scions on stocks of less valuable nature.

To diminish or increase the height of a plant, and to/

(1) Bateson 1866 and 1870, and cp. recent literature on Hybridization by seed such as Burbank 1909. Blaringham 1909, Clark 1910, Green 1910 etc. also literature on Graft Hybrids (see f. footnote.)
(2) cp. also Conifer cuttings Chap. IX, page

to generally add to its beauty and symmetry⁽¹⁾.

To substitute choice varieties (particularly in fruit trees)⁽²⁾ without disturbing the original plant.

In recent years grafting has been experimented with for obtaining hybrids⁽³⁾.

g. Inarching - or grafting by approach - is sometimes more convenient than grafting proper, as the scion is half supported by the stock; by this means a much longer branch may be united than by grafting and also the plant is drawing nourishment from its own root till union takes place, e.g. valuable shrubs - Camellias, &c.

The advantages of the method of seedling inarching are -

Valuable for hard-wooded plants.

Simple and inexpensive and certain.

Flowering earlier.

Value of plants quickly determined. (4)

h. Budding: many ornamental trees are more conveniently propagated by budding than by grafting, as a large number of plants can be obtained from one scion.

It/

(1) cp. next heading (g).

(2) Ikeda 1911.

(3) Baur 1909, Heuer 1910, Hildebrand 1908, Hirschel 1909, Jost 1907 & 1910, Jouin 1900, Nienburg 1910, Richter 1910, Strassburger 1909, Thumm 1909, Winkler (v) 1907, vi 1908., Wittmack 1910. etc. etc.

(4) Oliver 1911.

It is thus a more economical method, and can be used with success for more delicate subjects, e.g. Roses (principally); many hard-wooded plants: Plums, Peaches, Nectarines, &c. Many fruit trees are propagated in the West by budding, but in the East, e.g. Japan, the older method of grafting is adhered to, except in the cases of Peaches and Nectarines⁽¹⁾, for which the newer method has been adopted.

II. CONSIDERATION OF THE METHOD OF VEGETATIVE PROPAGATION FROM STEM-CUTTINGS IN PARTICULAR.

1. ADVANTAGES and DISADVANTAGES of PLANTS RAISED from STEM-CUTTINGS as COMPARED to those RAISED from SEED.

The possibility of the method of propagation by stem-cuttings in Dicotyledons is unlimited. Nearly every plant known in horticulture may be propagated by means of cuttings made from their stems, though the method may not always be the most desirable one. In some cases the plant resulting from cuttings are not so good from the gardener's point of view as those raised from seed, that is to say -

1. They are stunted, ugly or unsymmetrical, e.g. Casuarina, Erodium, Ardisia.

2/
✓ (1) see Ikeda, 1944.

2. Cuttings do not flower so well as the seedlings although the cuttings increase easily, e.g. Myosotis vars.

3. Annual and biennial plants are, with few exceptions, e.g. Lobelia, Klugia, Saintpaulia (leaf-cuttings usual), raised from seed, and while the possibility of cuttings to strike in many other plants does exist, seed is so abundantly produced, and so easily obtainable that preference is naturally given to the sexual mode of reproduction, e.g. Berberis, Plantago, Compositas, &c.

4. Some plants, such as Aralia Veitchii, are poor rooters (though most Aralias are easily increased) and propagation by stem-cuttings, under the conditions that are at present known and practised, is a slow and tedious process. Grafting on common species is the best method of increase from a cultivator's point of view. Difficulty in striking is also found with many shrubs, but in nearly every case the difficulty has been, or may be overcome by repeated experiment.

In most cases, however, cuttings are much to be preferred, as -

1. The shape can usually be controlled to a very great extent, e.g. Eleagnus edulis, Bixa.

2. Plants get leggy and ragged at the foot, if cultivated/

cultivated from seedlings and allowed to grow on. It is found much better to take frequent cuttings from low symmetrical plants. Particularly is this the case with the Acanthads, e.g. Acanthus, Apheleandra. (See also Chapter IV. under Genera).

3. If a plant is dioecious, seedlings may often be chancy: the same sex may be obtained, cuttings are therefore more certain, e.g. Mimordica mixta.

4. Cuttings are speedier than seedlings although seeds may be abundantly produced, e.g. Crassulaceae. Flowering plants are obtained from cuttings next season usually, while three or four years elapse before the adult stage is reached from seed, e.g. Boniun calli-thyrsun.

2. PRACTICAL CONSIDERATIONS: Nature of Shoots employed.

The kind of cutting that is employed varies somewhat according to the experience of the propagator, but is dependent mainly on the nature of the plant, and in particular the season of the year in which it is inserted. That much of the success depends on a right choice of cutting is shown by the following examples:-

Combretum purpureum is a plant which was for a long time thought difficult to strike⁽¹⁾. Since the young shoots/

(1) cp. Garden vol. XXIV 1883, p. 66., also vol. XXXVI 1889 p. 22

shoots are somewhat pithy, with long intervals between the nodes, the cuttings are thus liable to damp off - and so it has been found better by experience to select shoots in summer of medium length, half-ripe, for the purpose of propagation⁽¹⁾. Pieces of half-ripe wood also propagate laid in a horizontal position on coconut fibre in a propagating frame - Temperature 80°.

Ipomoea horsfallia is another difficult subject for propagation, being very slow to root, and with I. batatas not producing seed easily under cultivation, but by right selection of wood and season, success is made possible. The preceding year's shoots immediately after flowering at the end of February have been found suitable for cuttings⁽²⁾.

Luculia gratissima has also been found difficult to propagate, possibly on account of the slow rooting, and of the disposition of the young shoots (from which cuttings are preferably made early in spring⁽³⁾) to flag.

List of other plants still considered difficult to propagate/

propagate from stem-cuttings. Are :-

Many other Leguminosae, e.g. Hovea,
Eutaxia, Kemedyia, Dillwynia, Eumacea.

Jacaratia dodecaphylla (Passifloraceae).

Schinus molle (Anacardiaceae).

Heritiera (Sterculiaceae).

Aralia Veitchii (Araliaceae).

Acacia spaerocephala (Leguminosae).

Daphniphyllum (Euphorbiaceae).

Ailanthus glandulosa (Simarubaceae).

Ghimonanthus fragrans (Calycanthaceae).

Magnolia (Magnoliaceae).

Azalea (Ericaceae).

Arbutus (Ericaceae).

Sp. of Banksia (Proteaceae)

Brownea (Leguminosae)

Hovea (Leguminosae).

Rhopala (Proteaceae)⁽¹⁾.

Seeing therefore that the state of the shoot is one of the main conditions of success in propagation by means of stem-cuttings⁽²⁾, an enquiry into the nature of shoots commonly employed is necessary.

According/

(1) cp. list in Van der Heede 1910 also Part IIA Progat of Dicots.

(2) Hemsley 1903.

According as cuttings are inserted in spring, summer or autumn they may be divided into three groups.

a. Cuttings inserted in spring or early summer.

Cuttings that are inserted in spring are usually of immature wood. They are soft in character, and are often found to give successful results when older and harder shoots taken as cuttings have resulted in failure, e.g. Mahogany, Cashew, Litchi, Luculia gratissima⁽¹⁾.

Some plants reproduce more easily from growing than from ripened wood, e.g. Nepenthes.

Young cuttings are taken for speedier propagation where exposure to the air is injurious to the plant, e.g. Theobroma.

They are also to be preferred in quick rooting plants, e.g. Allamanda, Ixora, &c.

The chief danger in this kind of cutting seems to be the tendency to damp or rot off. There is an absence of any thickened cuticle or bark, and transpiration is greater than in the case of hard wood cuttings, where the vegetation is dormant instead of active as in spring. For most soft young cuttings a warm moist and somewhat confined atmosphere seems to be necessary in order that regeneration may be as speedy as possible, the/

(1) Mr. L. Stewart.

the conditions of heat, light, and moisture naturally being adjusted to the hardiness of the plant.

b. Cuttings inserted in mid- or late summer.

The plant in summer is in its period of fullest activity before its rest period begins, and August⁽¹⁾ may be said to be one of the best months for propagation in the whole year. Some plants will not form meristematic tissue until their tissues are firmer, so that very young cuttings which would be liable to damp or rot off, cannot be chosen. Half-ripe cuttings are taken in this season for many hardy shrubs, e.g. Veronica, Epacris, &c.

c. Cuttings inserted in autumn.

The majority of hardy deciduous trees and shrubs are propagated by cuttings in autumn⁽²⁾. For this purpose cuttings are made of ripened wood, the better to withstand the period of winter. Cuttings of ripened wood succeed best with many plants, such as Cassia, several Araliaceae, many hardy shrubs such as Lilac, Privet. Callus forms during the winter and acts as a temporary root system, and roots are formed in the following spring.

As in young and half ripe cuttings success is dependent /

(1) Mr. L. Stewart.

(2) Cp. also Conifer Stem-Cuttings, Chapter IX, p .

dependent on the nature of the plant, and to a large extent on the conditions of soil temperature⁽¹⁾. As would be expected, the temperature needed for hardy plant cuttings is considerably lower than that needed for young tender cuttings. The ground in autumn is warmer than air, so that the base is kept warmer than the apex, a most desirable conditions for trees in winter. Too high a temperature would cause the dormant leaf-buds to burst, and the cutting to expend its energy in transpiration before roots are formed to balance the operation by absorption. The cuttings therefore are placed in sandy soil or merely sand in a cool greenhouse, or even outside with some protection (glass if necessary) for the winter weather.

The various kinds of cuttings, (cuttings without leaves, cuttings with heel, cuttings with slanted cut), are considered in V. den Heede's L'Art du Bouturer 1910, and also the plants which are commonly so treated.⁽²⁾ Also, for advantages of leaves being left at the base of a cutting⁽³⁾.

3. THEORETICAL CONSIDERATIONS: Changes after insertion of a stem-cutting.

The/

(1) cp. after page

(2) Stoepfke 1903.

(3) Bayley Balfour 1912.

The biological significance of regeneration and vegetative propagation, apart from its horticultural interest and importance, is very great to the plant, liable as it is to all forms of mechanical injury. Not only has the detached portion the power under suitable conditions of regenerating itself, but the injured plant from which the portion was detached has the power of healing itself by a loose tissue known as callus, and if necessary, of producing new organs from or near this callus tissue. The fact that the life of a tree, for example, does not suffer when injured artificially by pruning, or accidentally by wind, &c., is mainly due to its power of being able to form this protective tissue⁽¹⁾ (fig.). If it were not so, the tree might be seriously injured by the attack of fungi, &c. obtaining an entrance into the softer tissues laid bare by the wound (fig.).

In some cases when a branch is cut off a tree, due to careless pruning, in a season when the sap is active, to imperfect protecting with tar, the sap exudes, and in spite of the partial formation of callus, the tree continues to bleed. The bleeding may continue for years -
in/

(1) In trees the immediate protection is given by the formation of wound gum. For wound healing in trees see Hartig 1894, Jeffrey 1906, Krieg 1908, Potter 1906, Schürhoff 1906, Scrauer (i) 1895 & (ii) 1909.

in one case an elm bled, in spite of every effort to stop it, for six years⁽¹⁾. There is a more striking example⁽²⁾ - also an elm - in which bleeding has continued for upwards of thirty years. Figure shows a tree (also elm) in which bleeding is continuing (the exuding sap is shown on the bark). The only effective remedy to stop the bleeding of trees is to recut at the proper season (winter)⁽³⁾.

The economic value of this tissue therefore is very great to the plant generally, when it is in possession of both roots and shoots. In the case of cuttings, however, in which the plant has become deprived of some of its organs, the economic value of callus formation is even greater. The whole of the exposed tissues would rot away were it not for the temporary protection of the callus formed like a cushion in the region of the cut (figs.). On the formation of this tissue for the time being, to a greater or less extent hangs the life of the plant. Some plants that root easily and quickly have no great need for callus formation, and therefore produce but little, e.g. Misulus luteus, Lanium album.

If, therefore, the value of callus to the plant as

a complete organism, and in part, be great, and if the correlation of callus formation and regeneration be intimate, then a fuller and more systematic knowledge of the nature of callus, the conditions under which it is formed, and its relation to root and shoot formation, may lead to greater results in the matter of vegetative propagation by means of cuttings, grafting, &c.

A. Callus formation.

The first change noticeable after insertion at the basal end of a stem-cutting is the formation of callus tissue. This is the general rule in Dicotyledons, though in some instances the amount of callus formed is so small as to be almost negligible, e.g. Mimulus, Fuchsia.

The amount of callus is dependent on the time of rooting⁽¹⁾.

a. External macroscopic appearance.

The external appearance of callus varies considerably. In the healing of a tree the regular shape of the lip-like growth towards the centre of the wound is very characteristic (figs.). Slight variations occur, however, which serve to distinguish the callus formations of the different trees (cp. Ash, Holly, Beech). The extreme variation in the macroscopic appearance of callus in cuttings is to some extent accounted/

(1) See III, 4, p .

accounted for by the nature of the plant (internal factors)⁽¹⁾ to some extent by the conditions under which the plant is propagated (external factors)⁽²⁾. Thus at times the mass of soft callus tissue appears as a roundish knob: at other times as a protuberance divided up into smaller outgrowths. Invariably, however, the tissue is soft to the touch, and mammilated to a greater or less degree owing to unequal growth in various directions.

(1) See **IV, A**, p.
 (2) See **IV, B**, p.

(13).

III.
F. A. A. Contd.

The external appearance and development of callus tissue were early noticed and described by various authors. Among them Meyen (1) says "If cuttings are placed in the ground in the ordinary way, and the ends observed from time to time, it will be noticed that a more or less rapidly developing outgrowth is formed from the inner cortex. It soon assumes a yellowish appearance, and increases in size (sometimes very considerably especially in evergreens ^TMyrtaceae, Coniferae) so as to cover the end of the cutting with a knobbly, warty, mass which often breaks up into several outgrowths, and protrudes beyond the cut edge. This outgrowth is known among gardeners by the name of 'callus'. It consists merely in an outgrowth of the inner cortical parenchyma, the cells of which become corky on the exterior, and brown in colour, and exhibit a considerable thickening of their walls."

To these notes might be added that callus is produced by any meristematic tissue of the plant, not only by the inner cortex, as will be shown more fully in the microscopical examination of callus tissue. (2)

(1) Meyen 1839

(2) cp. III A c page 48

7. ~~Da~~ ~~3. A. a.~~ ~~8.~~
L. A. Contd.

The pith readily takes part in the formation of callus, and the callus cells may be seen to protrude from the rest of the tissue, like the cells from the inner cortex. e.g. Coccoloba, &c.

The wedge shaped medullary rays characteristic of the Bignoniaceae produce callus in cuttings which protrudes with that of the pith and inner cortex.

In order to examine the general mode and appearance of callus formation in Dicotyledons, shoots from a number of woody stove plants were selected, cut in pieces, and laid horizontally on damp fibre in a propagating frame. It would not have been a fair comparison, if some of the cuttings had been placed in a vertical position, others horizontally, as the horizontal position has a certain effect on the callus formation. (1) The horizontal position was here chosen for the purpose of convenience. Many of the specimens simply rotted off, but a number persisted for a considerable period, and produced callus at the cut ends. The time under which the specimens were under observation was from January 4th. to 30th. 1911. The following notes were recorded. (It will be noticed (2) that the notes are very general, and only

(1) See IV. 4. p. 4. b.

(2) Cp. IV. 1. C. p. 3. A. c. p. 48 &c.

3.A.a.
L. A. Contd.

indicate the development in the pith, and in the cortical region. In a more minute microscopical examination the ^{letter} might be divided into the callus produced from the cambium, and that from the cortex).

Adenocalymna nitida - callus in the outer region chiefly in inner cortex: callus from the wedge-shaped medullary rays, and from the pith.

Aristolochia tricaudata - small amount of callus in inner cortex.

Bombax pentandrum - callus from inner cortex and pith.

Brownea coccinea - callus formation in patches in cortical tissue: none in pith.

Catalpa guinensis (Fig. 6) - callus formation in a regular ring in cortex: none in pith.

Clusia sp. - a ring of callus from cortex and from pith.

Combretum purpureum - callus from inner cortex and pith.

Gmelina hystrix - callus formation from cortical tissue: none from pith, which had sunk considerably.

Heritiera macrophylla - callus formation in patches in cortical region: none in pith.

Norantea guinensis (Fig. 8) - beautifully clear callus from cortex: none from pith though soft.

Pachira aquatica (Fig. 9) - large formation of callus in inner and outer cortex amongst xylem in the medullary rays and from pith.

~~W.A.~~ ~~1.~~ 3. A. a.
 V. L. A. Contd.

Tabernamontana longiflora - callus from cortex: none
 from pith.

(p. 46a
 seq.) b Tectona grandis (Fig. 4) - callus formation somewhat
 patchy in inner cortex protruding over xylem:
 none from pith.

Vitis voivneriana - slight formation of callus in cortex:
 rotted off.

From these examples it will be noticed that callus formation varies very considerably according to the nature of the plant, though the conditions of heat, light, and moisture remain the same, and that callus is on the whole more easily produced from the cortical region, beginning from the cambium than from the pith. If the conditions are altered, the amount and ease of callus formation may also vary even in cuttings of the same species (p).

(1) See IV. 4. p. 4. B. p.

3. A. 7.

(17).

47.

~~3. A. 7.~~
4. 2. B.

Internal macroscopic appearance: undifferentiated callus.

As considerable variations occur in the external appearance of callus, so it might be expected that variation would occur in the general appearance of a section across various callus outgrowths. A macroscopic section of an ordinary callus outgrowth at the base of a shoot shows a mass of more or less undifferentiated tissue surrounding the cut end. (1).

^(p. 171 seq.) A case of forced callus (*Anaemaepaegma racemosa*) exhibited a laminated or ringed appearance (Figs. 12+). As the illustrations (Fig. 11 + 14) ^{13.} show, the cut was made at the internode 2-3 ins. above the swollen node. Callus formed in the usual way. By constantly keeping moist, and by persistently cutting, the callus was stimulated to further growth. In cutting the knife carefully followed the outline of the last growth. A laminated appearance was thus obtained. The more regular appearance of Fig. 14 was also obtained by subjection to successive excitations for the space of about two years. The internal macroscopic sections also show ^{the} laminations. (Figs. 12+) ^{13.} more clearly.

(1) cp. III A c Figs. also Figs in Sorauer 1909, Tittman 1895.

(18).

B.A.C.

A. 3.

IV. 1.6. Microscopical examination: structure of callus.

The microscopical examination of callus is of more interest, since we can learn which old tissues are most active in forming the new protective ^{tissue} and also in what manner new organs, viz. roots and shoots are formed. Among the early investigators of the internal structure of callus was Cruger.(1). The most important of his deductions were utilized by Stoll(2), who examined a large number of cuttings for the purpose of tracing the structure and development of callus. As three typical plants he took Hibiscus reginae, Passiflora quadrangularis and Giselina littoralis for his observations, partly on account of the clearness of their tissues, partly on account of their prolific callus production. From his observations he came to the following conclusions.

1. 'That every tissue of the plant excepting true wood, bast and epidermal cells, is capable of aiding in the construction of callus, the initial and chief growth being from the cambium.'

This statement has been confirmed by all later investigations.

As might be expected any undifferentiated tissue capable of rapid division will at once become meristematic under given conditions and form callus. If cambium be present, as Stoll

✓ (1) Crüger. 1860.

✓ (2) Stoll. 1874.

53. A.C.

W.A.
I.F.S. Contd.

says, the initial and chief growth will ^{be} from this point. But the presence of cambium is not necessary to start callus formation as will be seen from the results of Stoll(1), Frank(2) &c. and from the results of Miss Kupfer's experiments with the rind and central cylinder of the turnip (3) (Coulter and Chrysler) (4) found a similar development of shoots from isolated cortical regions of *Zamia*.). Epidermal cells rarely give rise to callus, at least in stem cuttings, though Jost(5) asserts that all cells containing protoplasm and nuclei, even epidermal cells are capable of forming callus.

'That the new tissue formed is a complex tissue called callus which has no similarity either in the form of cells or their arrangement with the old tissues.'

From the manner of the formation of callus it will be readily seen that the new tissue will differ in its appearance from the old: the old tissues which are permanent and are in connection with each other form a regular vascular system, and sharply divided from it by cells which were primarily exposed and withered is the new tissue of callus, which is at first undifferentiated. (6). The difference is due to the meristematic

- (1) Stoll 1874.
- (2) Frank 1895
- (3) Coulter and Chrysler 1904.
- (5) Jost 1907.
- (6) Stoll 1874 Fig X. cp. also Figs. in Sorauer & 1909, Tittmann. 1895.

3. A. c.
 W. A. c.
 IV. 2. C. Contd.

nature of callus as compared to that of the old tissue. In shape the cells differ; at first brickshaped like cambium cell they later assume a polygonal and rounded appearance. due to pressure from all sides. Where the pressure is less as in soft fleshy xerophytes it might be expected that the cells would be more regular in shape. This was found to be the case in the examination of plants such as Cotyledon, Crassula

iii 3. ' In the development of the callus tissue are formed meristematic patches.'

iv 4. These patches are different according to their activity. Either they become permanent tissue, as in the case of the periphery of the callus, and at the several phloem and xylem bundles, or else they keep their meristematic activity, and differentiate certain layers for the cutting. In the first case they are analogous to the formation of cork in wounds and are to be compared to the phellogen layer. In the second place they are analogous to the cambium, and its relation to secondary thickening in Dicotyledons.'

Callus formation in Dicot. stems is capable of forming secondary tissue, by the later development of a cambium which produces as in the stem, xylem to the inner side, phloem to the outer as will be shown more fully later. (i)

(i) ~~3. A. c.~~ 3. A. c. p. . also 4. A. p.

3.A.c.
 4.A.3
 4.3.C. Contd.

the power of forming primary tissues as in the case of regeneration of the root-tip⁽¹⁾. This power is almost confined to the root and seldom possessed by the stem.⁽²⁾

The researches of Crüger⁽³⁾ and ~~Koster~~^{+ others}⁽⁴⁾ have given us much information, regarding callus formation, but it is from the more recent work of Simon⁽⁴⁾ that we get a more minute knowledge of the differentiation of callus tissue. Not only has he distinguished the cambial callus from the pith and cortical callus, but he has studied in detail the development of Stoll's 'meristematic patches', showing the parts these various meristems play, and by what stages the vascular system of the new organ (root or shoot) developed in the callus is finally connected with that of the old stem.

His results, chiefly with Populus nigra are briefly the following. Except for a few points, they may be extended generally.

Callus by formed by a plant cutting at its base or apex, may be divided according to its origin into Cambial, Pith, or Cortical callus.

- (1) Simon (i) 1904.
 (2) Lopriore 1892 , 1895.
 (3) Crüger 1860.
 (4) Simon (ii) 1908.

B.A.C.

~~A.C.~~

A.C. Contd.

a. Cambial Callus.

The callus formed from the cambium is as all authors agree, the most fundamental. The first divisions are parallel to the wounded surface, so that the first tissue formed is made up of parallel rows. Development after this is very quick, for not only the cambial but the callus cells themselves are now meristematic, and these divide in all directions, so that the cells become larger and more irregular. A fan-shaped mass of callus is thus formed over the wound in the neighbourhood of the cambium. When the callus has reached a certain size, differentiation begins and various tissues are formed.

Differentiation of cambial callus.

i. Tracheids:- callus cells become thickened and form tracheids: they occur singly or in groups but not in any regular continuous series: a combination of these groups may take place by callus cells between them becoming tracheids, so that a certain continuity occurs.

(Fig. 1. Sunon p. 389).

ii. Sclerenchymatic cells:- these cells, like the tracheids occur isolated or connected into groups developed directly from callus cells, and are therefore as varied in form. They are easily distinguished from the tracheids, even when young, and their walls not very thick, by the characteristic lamination and the presence of

IV.1.C.Contd.

a.ii.contd.

round or oval pits. The older sclerenchyma are easily distinguished by their markedly thickened walls, and

Simon p. 360/361 narrow lumen. (Fig. 2/3)

iii. The Epidermis of the callus tissue is scarcely to be distinguished from the callus cells themselves except that the cells are somewhat larger and slightly thickened. They are capable of further development, but often die their contents disappearing. A cork layer is developed and the function of the epidermis is taken on by the

p. 362, living cells beneath them. (Fig. 4) Simon

iv. The Lenticel and cork formation occurs as in woody stems by the formation of a cork cambium, a row of callus cells

p. 369, becoming meristematic to perform this function. (Fig. 7)

b. Cortical callus.

The callus formed from the cortex cannot really be separated from the cambial callus, for it is formed simultaneously with it. Küster(1) who is the only author before Simon(2) who has worked minutely on the differentiation of callus, says that the secondary cortex also forms tracheids. Simon(2) shews further that numerous tracheids groups occur, which

(1) Kuster (iv) 1904.
(2) Simon 1908.

G. J. H. C.

1.0. Contd.

b. contd.

later lay down for themselves meristems through the activity of which isolated wood masses are formed. Sclerenchyma ^{is} developed in the primary cortex, and possibly tracheids though through intermingling of the callus from the two origins, this cannot definitely be observed.

c. Pith Callus.

The pith has not such a great capacity for the development of callus as the cambium or cortex. (1). But that it can produce callus has been shown by the various investigators, Stoll (for Passiflora and Hibiscus) (2), Maule (for Euonymus europaeus radicans) (3) and Krieg (for Vitis vinifera) (4). To these mi might be added Coccoloba, Pachira, &c. (Figs. 3, 9d. page 16a. etc. (5)).

Like the callus developed from the cambium, the first few rows are regular. Very soon growth becomes irregular, that from the outer edges of the pith being the greatest. Differentiation begins with the appearance of isolated tracheids, on the peripheries of which are formed new meristems. The resulting wood elements may exhibit various

- (1) cp. IV, 1 A page
- (2) Stoll 1874.
- (3) Maule 1896.
- (4) Krieg 1908.
- (5) cp. also 3 A a page 45.

c. contd.

forms and orientation. Generally the separated meristems meet, so that finally a continuous bent woody portion is formed. Small vascular strands often appear in the pith meristem which become connected to the vessels of the pith periphery. Under certain conditions a meristem is formed which runs right across the pith callus, in connection with this continuous woody portion. The meristem divides off xylem towards the centre; by continued growth bast elements may also occur to the outside but these only seem to be formed when the meristem from the pith grows into the meristem formed from the cambium, the differentiation thereafter becoming the same as that from the cambial meristem. As in cambial callus, sclerenchyma may also be formed in large or small groups in the pith callus. On the surface of this callus, too, under certain conditions, appear cork or lenticel formations. (1). As in cortical callus, the tendency to form the lenticel formations seems to be greater, a regular epidermis being scarcely met with. Differentiation of tissues in the pith callus is very ^{similar} and cannot really be separated from that in the callus developed from the cambium.

(1) cp. IV. 1. 6. seq. p.

B. Root formation in Stem-cuttings.

- a. Development of pre-existing primordia.
- b. Formation of entirely new roots. External appearance.
- c. Origin.

1. After a varying period after callus formation, roots are formed on the stem-cutting (figs. 21-31). The root formation is an evidence of the power of vegetative reproduction in the plant (cp. Introduction, par. 3, p. 24), and is a result following on the new conditions of severing. Root formation in a stem-cutting takes place either -

- a. as a development of pre-existing root primordia which in normal conditions would not develop.
- b. as the formation of entirely new roots.

a. Development of pre-existing root primordia. Few plants actually possess root primordia on their shoots, though in some cases this does occur, as in Salix viminalis, S. vitellina, S. pruinosa, &c. ⁽¹⁾ where the primordia are found under the cortex singly on both sides of the axillary bud or in numbers. These usually remain latent in the normal vegetation, but develop in cuttings. The early appearance of these adventitious root primordia in/

(1) Goebel (ii) 1905. vol. I sect. 4.

in the case of Salix⁽¹⁾ is the most probable explanation of the ease with which its cuttings develop. In other woody plants, where no such primordia exist, it may be that the development is slower or quicker according to the ease and quickness with which they are formed.

b. The formation of entirely new roots. The majority of stem-cuttings, possessing no root primordia, are obliged to form new roots on being severed from the parent plant.

The appearance of the basal end of a cutting is quite characteristic, so that it is possible in most dicotyledonous plants, as will be seen from the illustrations (figs. 15-20) to tell by the external appearance of the roots whether a plant has been raised from seed, or by means of a cutting. In the latter, callus formation is present, though sometimes indistinct (in a macroscopic examination) the basal cut is evident, and secondary roots only are present: in a plant raised from seed, on the other hand, a distinct tap-root is visible. The difference may at once be recognised by a comparison of two specimens of Terminalia angustifolia, the one raised from seed (fig. 15), the other from a cutting (fig. 16). The difference persists for some years (fig./

(1) Goebel (ii) vol. II. 1905. page 275.

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(fig. 18a & b).

c. Origin of roots. Macroscopical Examination.

Concerning the origin of roots Stoll states that "the formation of roots does not actually take place at the callus itself, but either immediately above the cut, or even in regions above, which have no direct connection with the callus formation".

This statement is not wholly correct, though it is generally true. Gruger found that roots could arise in the callus or above it; Wiesner, Hansen, Kupfer have confirmed Gruger's results, and there is no doubt that the roots may vary in their origin, as may be seen from the illustrations (figs. 21-31). Scabiosa pleroccephalum (fig. 10) is an example where the root actually proceeds from the callus tissue. In other examples, the roots also proceed from the cut surface (figs. 21, 22, 24, &c.). They are known to arise indifferently above or from the callus, but usually they proceed, especially the later formed roots, from the region above the cut surface and callus formation (figs. 23, 26, 30). The macroscopic sections (figs. 19 and 20) show more clearly the origin of the adventitious shoots and the cut across the base.

Microscopical Examination. Roots that arise

at/

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at the basal end of a stem-cutting are adventitious. Their origin is endogenetic.

When they arise from the permanent tissue of the stem above the callus, the general rule for the origin of adventitious roots in Spermophyta is adhered to, i.e. they proceed (with few exceptions) from the pericycle⁽¹⁾ like other lateral roots.

But in many cuttings roots actually proceed from the callus tissue. No pericycle as such is present.

In the cambial callus, the origin of the roots is from the meristematic layer developed directly from the cambium⁽²⁾. The formation of the roots from the callus is thus, according to Simon⁽³⁾, always dependent on the appearance of the said meristem, which possesses the same capabilities as the cambium. It thus follows that roots cannot arise from the callus formed by the primary or secondary cortex, and they have not been observed to do so.

The pith callus, under ordinary conditions, is also unable to produce roots.

If, however, the parts of the stem, cortex, pith, &c., be isolated, then the results will be different (as/

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- ✓ (1) see figs. 66-70: Scott. 1902.
 - ✓ (2) see ~~IV~~ 10, p. 3. A. c. p. 52.4.
 - ✓ (3) Simon 1908.

shown in Root-Cuttings): under these new conditions the pith and cortex may give rise to roots (Kupfer).

c. Shoot formation in Stem-Cuttings.

- a. Normal development of shoots and lateral buds.
- b. Abnormal development of pre-existing lateral buds.
- c. Formation of entirely new buds.
- d. External appearance, internal structure, and origin of foregoing.
- e. Literature.

Shoot formation is an evidence of growth in the plant. It is a further stage in its regeneration, as it occurs usually (though not always) after the production of roots.

Shoot formation on a stem-cutting may occur -

- a. When there is no severing of the apical end the terminal and lateral buds develop normally (normal vegetative growth).
- b. When the apical end is severed -
 - b. x. the lateral buds develop abnormally (vegetative growth resulting from stimulus) or modification of existing lateral shoots takes place.
 - c or d. entirely new shoots are formed.
- d. For apical stem-cuttings roots are the only organs that require to be reproduced in order that regeneration of /

of the individual may be complete (see Kupfer, &c.). New shoots arise from buds which are produced at the growing point in the axils of the leaves, in the same way as on the parent plant. There is no difference here between the production of shoots in the regenerated plant and normal vegetative growth. These normal shoot buds are exogenetic in origin (see Goebel, Scott, Jost, &c.)

b. If the apex of the cutting be severed or prevented from functioning (see Goebel, Jost, Vöchting, Klebs, &c.) a disturbance of growth relations takes place.

a. If lateral buds exist, their development usually takes place. Their development differs from that of ordinary vegetative growth, externally in that it is much stronger. A bushy habit can thus be induced in plants which would be inclined to grow tall and scraggy. The time of development after severing depends to a large extent on the nature of the plant. With many woody plants - Rubus, Sambucus, &c. - cuttings are made in this way, the tops being cut off and the lateral buds left to develop. The development is slower in these cases, as in most woody plants, than that of the terminal bud: if it were not so, the terminal bud would develop before roots were formed, and the cutting would be exhausted⁽¹⁾.

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(1) see III, c, p. 64

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The fact that the apices are taken off in order to get sufficiently ripe wood must also be taken into consideration.

Goebel, McCallum, Jost and other investigators⁽¹⁾ have shown that a distinct correlation exists between the development of the terminal and lateral buds. If the terminal bud be severed or prevented from functioning then the lateral buds develop. In the same way, if the apical lateral buds are prevented from functioning, the basal lateral buds develop. McCallum⁽²⁾ has shown that these dormant axillary buds will not develop as long as the growing point remains intact, no matter how vigorous and well-nourished the plant may be, or how abundant the water supply.

The phenomenon is therefore one of quantitative correlation, the development of the arrested buds being due to the severance or absence of function⁽³⁾ of the terminal shoot^{(3) (4)}.

The shoots may not only have been pre-existing as buds, but as shoots. In the case of the severing of the apex modification of these existing shoots takes place.

In/

- (1) see under Pfeffer, Vöchting etc.
- (2) McCallum. 1905.
- (3) Driesch 1901. also under Goebel various.
- (4)

(1)

In an interesting paper Boirivant has shown that the replacement of an axial shoot by the nearest lateral shoot has tended in a modification of structure, both external and internal. In his experiments he cut off the apex of the shoot at varying distances from the extremity, both transversely and obliquely. The lateral branch of replacement was then compared externally and internally to a normal lateral branch on the same level in a complete specimen, and also to the main shoot. Among the Dicotyledons from which he obtained his results were Phaseolus multiflorus, Ricinus communis, Faba vulgaris, Lupinus, Artemisia vulgaris, Urtica dioica, Chenopodium album.

The chief points he arrived at were:-

External modification took place in the branch of replacement -

1. the branch of replacement changed direction, bent, became vertical and lengthened.
2. the diameter of the branch became more considerable.
3. its lengthening was more rapid.
4. leaves were larger and more spaced out.

Internal modification also took place.

1. the meristems function^{ed} more actively in the modified branch than in the other branches.
2. the diameter of the stele was relatively larger/

* (1) Boirivant 1897.

larger, that of the cortex smaller. This was due to the greater quantity of fibro-vascular elements in the stele, and often to a larger quantity of pith.

- 3. the cellular elements in the modified branch were larger and stronger.
- 4. strengthening tissue was abundant, especially in the pericycle and of collenchyma.

Since by its internal structure and external appearance the modified lateral branch approaches more nearly to the parent axis than to a normal lateral branch, Boirivant concludes that it generates in a large extent by replacement or substitution the portion destroyed of the main axis.

The origin of these shoots is, as in normal vegetative shoots, exogenetic.

c. ♀. Where pieces of herbaceous stem without the apex, or pieces of stem without buds, i.e., internodal pieces, are used for stem-cuttings, the formation of terminal buds takes place. These shoots are not pre-existent as ^{such} but must be formed de novo. These are not normal but adventitious shoots (see fig.).

The origin of adventitious shoots was observed in Acanthus montana (a rapidly growing species and possessing in common with nearly all Acanthads the power of being easily reproduced from cuttings). At the apical end callus tissue was first formed.

Shoot formation has been considered, in the foregoing paragraph, with regard to stem-cuttings in particular. In connection with regeneration of the stem in general ^{also} ~~it~~ might be noted -

- 1. Regeneration as a result of wounding the cotyledons (see Jacobi, &c.), ^{1910.}
- 2. Regeneration of split stems (see Depriore, &c.), ^{1895.}
- 3. Regeneration of the epicotyl (see A. W. Clark, &c.), ^{1904.}
- 4. Regeneration of the hypocotyl (see Burns, Hedden, &c.), ^{1905. Burns 1907. 1906.}

and other points.

Literature. See under

Boirivant.	McCallum.
Goebel.	Pfeffer.
Jost.	Scott.
Kuster.	Vöchting.
&c. &c.	

4. CONDITIONS AFFECTING CALLUS, ROOT, AND SHOOT FORMATION.

Regeneration is a vital energy, closely bound up with the life and growth of the plant. Conditions have a modifying influence on the plant expression of this energy, but they are not the primary causes of regeneration. Conditions may be either external or internal.

A. /

A. Internal. Among internal conditions, the three main are:-

- a. nature of the plant: the "personal equation".
- b. polarity.
- c. correlations.

a. Nature of the plant. The regenerative power of the plant is naturally influenced by the nature of the individual. Where growth is difficult or slow, when the plant is delicate or in some obstinate to manage ("miffy" as they say in gardeners' books), then the individual will regenerate with difficulty. And conversely, where growth is rapid, abundant, where vitality is strong, the regenerative power of the individual is relatively stronger.

b. Polarity, or polar tendency is the tendency for roots to appear at the root pole, and shoots at the shoot pole. Many and far reaching have been the investigations on this vexed subject, but it has been generally agreed that polarity is a general inherent characteristic, possessed by all higher plants in greater or less degree.

Vöchting and his school assert that polarity is a stable quality, though it may be modified by such external conditions as light, moisture, &c.

Klebs and his followers, on the other hand, tried to prove by a series of experiments that while there exists/

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exists a polar tendency in cuttings, yet "it is highly probable that this polarity is reversible". Vöchting more recently (1906) disproved Klebs' results, and such investigators as Goebel (1907), Simon (1908), Y. Freund (1910), Dopescheg-Uhlar (1911), appear to have strengthened Vöchting's position, in the assertion that polarity is a stable quality in the higher plants.

Vöchting not only asserted the polarity of the plant or pieces of the plant, but also demonstrated the polarity of the individual (see also Niche). His assertion that every individual cell possesses a basal and apical pole would seem likely by the fact that normal transplantation results in a true union. Inverse transplantation however brings about no union of tissue, and hypertrophy is caused by the effort of the cells to regain their original position (see figs. in Jost).

The assumption of the individual polarity of the cell would also seem to have been proved by the experiments in copulation of callus of Simon (1908). This investigator found that when an apical callus was grafted on to a basal callus or vice versa, union took place by the formation of a complete vascular strand. If on the contrary two like ^a cells were placed together, no union took place, showing as in the former experiment that like polarity/

polarity repels like, but is attracted by polarity of the opposite kind.

Callus formation is usually the first evidence of regenerative power. Each of the undifferentiated cells will, according to Vöchting's hypothesis, exhibit a polar tendency. If then, division always takes place in the same direction, there should follow a marked difference between basal and apical calli. Tittmann⁽¹⁾ asserted that under equal conditions, callus formation is equal at both apical and basal ends of a cutting, but Küster⁽²⁾, Müller⁽³⁾, Kny⁽⁴⁾, &c., and the more recent researches of Deposcheg-Uhlar¹⁹¹¹ and Y. Freund¹⁹¹⁰, have shown that as a general rule callus production at the basal end of a cutting is greater than at the apical end. Simon⁽⁵⁾, too, has confirmed these results and has shown, moreover, that the apical and basal calli vary under different conditions, but always in a specific way. Under normal conditions differentiation proceeds on different lines. At the apical end of a cutting shoots are always produced, never roots. At the basal end, roots are produced, and in some cases shoots.

As will be noted from the foregoing paragraphs

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- ✓ (1) Tittmann 1895.
 - ✓ (2) Küster 1903, 4.
 - ✓ (3) Müller 1856
 - ✓ (4) Kny 1894, 1901.
 - ✓ (5) Simon 1908

the differentiation of callus may be divided in two groups, phases:-

1. The formation of tracheids, &c. and shoot formation.
2. The meristematic activity resulting chiefly in wood and wound tissue formation from the meristem proceeding from the cambium. From this wound tissue roots are formed.

At the apical pole, the first phase of differentiation is found to predominate. Meristems are formed to some extent but callus formation is predominant. With the appearance of the meristem from the cambium, the second phase of the differentiation begins, but usually does not proceed further. The meristems are irregular and form scattered vascular strands.

At the basal end, while the callus formation is more regular, the continuous meristem forms a real wound tissue. In older specimens the difference may not be so well marked, but the number of thin vascular strands in rays out to the periphery distinguishes an apical callus (fig. 16). In an older basal callus the outline is more irregular⁽¹⁾, which macroscopically makes the appearance very similar to an apical callus. But a microscopic section of even an old basal callus shows that the irregularities are due not to original callus formation, as in the/

(1) Simon 1908.

the apical end, but to new parenchymatous tissue developed on top of the old tissue. These new tissues are gradually differentiated into small or larger groups of wood elements, and the highest point of their development is reached in the production of shoots. Shoots therefore do not occur in the ordinary development of a basal cutting, but are a later production.

Thus, according to Simon, the basal end of a cutting exhibits -

- a relatively large callus formation, which is basal in character (see page before).
- from the differentiation of this callus, root formation occurs, as the primary formation.
- as a later or secondary formation, shoot formation occurs.

The apical pole of a cutting, on the other hand, exhibits -

- a smaller callus formation, which is apical in character.
- from the differentiation of this callus, shoot formation occurs as a primary function.
- root formation rarely or never occurs⁽¹⁾.

In youngseedling cuttings the basal and apical poles are further distinguished by the formation of a red coloration (anthocyan) at the root pole, and the appearance of/

(1) Unless primordia are already present, as in many of the Salices.

4/2

of the green coloration of chlorophyll at the shoot pole⁽¹⁾.

Since conditions have a modifying influence on the differentiation of callus, it will at once be seen that the secondary formation may become prominent, while the primary formation be inhibited.

Thus shoots may be exhibited and commonly at the root pole, while roots may be formed (though rarely) at the shoot pole. A seeming reversal of polarity may thus be obtained.

Vöchting, while asserting the polar tendency in plants, would also have it that it is the primary cause of regeneration.

But an effect cannot be said to be a cause and polarity is undoubtedly, in spite of Vöchting's transplantation experiments and Simon's grafting experiments, a characteristic not of the undifferentiated cell, but of the differentiated cell. It is therefore a result of differentiation and thereafter acts as a stimulus in regeneration (see table, Introduction).

If polarity were a characteristic of the undifferentiated cell, then division of the cells would be limited to two directions, the transverse and longitudinal, in the formation of callus, if basal and apical callus were to evince a polarity of their own.

But/

✓ (1) Freund. 1910

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But this is exactly what does not take place. The cells at first regular, become rapidly irregular, owing to division in every direction, especially at the edges. Therefore callus tissue while undifferentiated cannot be either basal or apical in character.

As soon, however, as differentiation begins, the ~~destiny~~ destiny of the cells becomes fixed and polarity becomes evident.

Simon's failure to graft like calli possibly depended on the fact that differentiation had already begun. If however two cuttings are grafted together the one in an inverse position, the other in normal position, before callus formation in either had begun, union would be found to be effected⁽¹⁾ and the callus formed to unite the two would be partly formed by each cutting⁽²⁾.

Polarity therefore cannot be said to be synonymous with the reparative energy or regenerative power which causes in the first place the formation of callus, though it is one of the chief stimuli in the formation of roots and shoots, a stimulus which may be, however, considerably modified by other conditions present.

c. Correlations. Another modifying internal influence is the fact of correlative growth. The development of pre-existing primordia or already existing organs will modify/

(1) Mr. L.B. Stewart . example of vine. grafting.

74.

length of the shoots that are formed.

In practice, experience has taught that in most cases temperature somewhat above that which the plant is naturally accustomed to, is the optimum temperature for regeneration.

b. Moisture. Since heat and moisture are the two greatest factors of growth generally, it is to be expected that, if the temperature is not lowered, a moist atmosphere will induce callus, root, and shoot formation.

Callus formation is greatly increased by moisture (Simon, Küster, Freund, &c.).

The amount of moisture induces the formation of hyperhydrisch tissue (see Simon). In a saturated atmosphere, this tissue is predominant, while that of real callus is small. Shoot formation is marked, as also is root production (see Simon).

2. Soil.

a. Solid media. The soil in which a plant is grown has undoubtedly an influence on its after development. Experience only has taught from an observation of natural conditions, and from series of experiments, which is the best soil for any one plant.

In the case of cuttings, it has been found that sand affords a good soil medium for stem-cuttings until the time of rooting.

Other/

Other solid mediums such as sphagnum, sawdust, charcoal, cotton, &c. have been experimented with, but the cuttings experimented with are found to decay with greater rapidity, owing to the greater difficulty of drainage, than in sand. Coconut fibre, though spongy in substance, is often apt to produce decay through the amount of water it can hold.

The effects of limy, clayey and other soils on cuttings have not been worked out in detail.

b. Liquid mediums. i. Water. Vöchting, Klebs, Goebel, McCallum and others have used water as a medium in regeneration experiments.

Callus formation generally is weaker in water, though the basal is still stronger than the apical. The cambium primarily, and cortex only slightly, and not the pith take part in the production of callus in the water. The want of transpiration is probably the real cause of the checking of callus formation in water (see Simon).

Root formation is favoured by contact with water (see Klebs, Vöchting, Simon, Tittmann, and Küster).

ii. Water cultures. The effect of growing plants in water cultures, either containing all ingredients or with the omission of some, has been noted. (see Jost, &c)

With regard to stem-cuttings, there is much more difficulty/

difficulty in estimating the effect. The cuttings, improved as they are with absorbing organs, and susceptible to unfavourable conditions, are very apt to decay. That the liquid medium has a marked effect on the rooting is shown by a comparison of cuttings of Coleus (see figs.), placed in acid, alkali, and full nutrient solution.

The experiment was suggested by Riehm's experiments with isolated leaves in various solutions. A consideration of these led to the supposition that quicker rooting might be obtained, even of difficult species, by cultivating in various solutions. The experiments for the most part were not a success. There are two great objections to this method of culture -

1. There is a great tendency for the submerged part to decay in the liquid medium.
2. When the formation does occur, the roots formed are very tender - the difficulty therefore of repotting is very great.

Another method might be devised, as of watering with different solutions, instead of cultivating in a liquid medium, which might give the desired result.

3. Light. Kuster found that in absence of light, callus formation was greater. Darkness seems also to favour root formation (see Vöchting).

Simon/ 1906.

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Simon finds no marked change, however, in the differentiation of callus.

4. Gravity. When a cutting is inversed, that is when the force of gravity is acting in opposition to that of polarity, retardation of callus formation usually takes place (Tittmann). Simon found also that in inverse position, the apical callus was strongly checked, and more slowly produced.

The basal callus was on the other hand, stimulated and was much larger than the apical. Shoots however were only produced in 10 per cent of the cuttings (of Populus nigra) and not at all in P. canadensis, therefore shoot formation in basal callus is not dependent on gravity.

In anatomical structure, the apical callus shows no marked difference from the normally placed cutting, but the basal shows a marked difference, approaching in character to the structure of the apical end. At the periphery more or less numerous callus mounds⁽¹⁾ appear, from the surface of which shoots are produced. These shoots are always weaker than those at the apical end.

In Simon's experiments no production of roots occurred, but these are also dependent not on the inverse or normal position of the cutting, but on the changes in the/

(1) ~~Wittmann~~^{Cp.} W. 4. A. p. 69.

78.
the basal callus⁽¹⁾.

5. NODAL AND INTERNODAL CUTTINGS.

The subject of the place of cuttings is of sufficient interest - practical and theoretical - ~~to~~ to be worth attention. It is a matter only to be determined by repeated experiment whether a particular plant will strike best cut actually at the node, just above, just below the node, or anywhere at the internode. In many plants which form little callus and are quick rooters, the mode of cutting makes little difference to the time of rooting. Soft-wooded plants are as a rule not greatly affected by the place of cutting, e.g. Lobelias, Geraniums, Pelargoniums, Acalyphas, &c., for they strike easily and quickly. Medinilla magnifica and other Melastomads were found to strike as easily at the internode as at the node.

In practice in the majority of cases cuttings are made at the nodes. In a few exceptional cases where rooting has been declared difficult cuttings at the internode have been successful, e.g. Oleandris, &c.

As a general rule, cuttings at the internode retard root formation. This was found to be the case with internodal cuttings of Fuchsia, Veronica, &c. Another curious/

(1) ~~See~~ 4. A. p. 69.

curious fact is that in many plants the natural tendency for cuttings is to form roots only at the node (see also fig. 30) (many plants themselves form adventitious roots also only at the nodes, e.g. Abobra), or to form roots at the node first, and later at the internode, no matter how the cuttings are made (fig. 36b).

A number of cuttings were made of Mimulus luteus at the node. They struck easily and quickly with little callus formation. Cuttings of the same plant cut at the internode rooted easily and quickly also, but only from the node (fig. 37).

A teleological explanation of the phenomenon might be offered, that since it is the tendency of the majority of plants to form adventitious roots at the node, this inherent tendency is continued in the cutting. For example, adventitious roots often occur in Labiates at the nodes, so that rooting at the node first, in a cutting, is to be expected, and in fact does occur (figs. 36a & b).

Sorauer⁽¹⁾ suggests that the greater amount of parenchyma and greater vitality of cells at the node may account for its efficacy in root production.

Regeneration would be expected to occur where the conditions were most favourable; at the node there is a greater/

(1) Sorauer. 1904.

greater amount of nutritive matter actually present, and a greater circulation of food, therefore root formation first and afterwards shoots will take place most easily from the node.

The following experiments are suggested --

- willow cut at node (apex)
or
poplar internode (base)
- willow node (apex)
or
poplar node (base)
- willow internode (apex)
or
poplar node (base)
- willow internode (apex)
or
poplar internode (apex)

Cp. Root and Shoot Formation.

(cp. Simon's results).

Chapter IIIDICOTYLEDONS. LEAF CUTTINGS.

HISTORICAL CONSIDERATIONS: VALUE OF METHOD.

The method of leaf cuttings is of great antiquity, though it has not been practised on a large scale till fairly recently. According to Vöchting, (1) who gives a short account of the investigators of leaf regeneration from the earliest times, Mandirola (X) 1652, and Agricola (~~1772~~) (X) seemed to have been the first investigators in this direction. Lindley (2) too quotes a passage from the translation of Agricola to shew that the fact of leaves propagating was no modern discovery. Curiously enough, (since they do not occur frequently in the list of plants most commonly propagated by means of leaf cuttings) citrons, lemons, laurels &c. seem to have among the first plants that are recorded to have been increased in this way. Isolated phenomena of adventitious root and shoot formation on leaves still attached, or severed from the parent plant were noticed by Thümmig (1781) Duh. du Monceau (1758) Bonnet (1779), Mustel (1781). In 1784 for example we find the following quaint assertion by Abercrombie, (3) "Among the succulent tribe (speaking of leaves) some sorts neither furnish seed in this country, nor afford any means of propagation by suckers, offsets, or shoots for cuttings &c. as frequently prevail in the chiding aloe, and some others; and which have thick fleshy leaves, cuttings

(1) Vöchting 1878, 1900.

(2) Lindley 1855 p. 271.

(3) Abercrombie 1784, p. 151.

(2).

thereof, assisted by a hotbed, will take root and grow."

In 1816, Knight examined the callus formation in isolated leaves of the potato. His observation of the lengthened life of isolated mint leaves is well known (1). Cassini (1816) and Muntz (1843) investigated the formation of adventitious buds on leaves of *Cardamine pratensis*, a phenomenon which Vöchting himself examined and which was worked ^{out} in greater detail more recently by Riehm (2). De Candolle (1827) described and made experiments with regard to adventitious bud formation on detached leaves of Bryophyllum calycinum. Dutrochet (1837) similarly investigated Ranunculus bulbosus, while Duchartre (1853) studied the leaves of Lycopersicon cerasiforme and pyriforme, on which adventitious buds were formed. Vöchting (1878) himself carried out a number of experiments with regard to leaf regeneration, chiefly with Begonia Rex and discolor Heterocentron diversifolium and Cardamine pratensis. The more recent work of Regel (1878) Beinling (1883), Lindemuth (1903) &c in connection with leaf regeneration will be mentioned later. (3).

The value of this mode of propagation is still perhaps underestimated. It is a matter of common knowledge that some plants e.g. Begonia, Bryophyllum etc. strike from their leaves with marvellous ease and rapidity, and the method is commonly employed in gardening ^{for} plants with fleshy or hairy leaves. Such plants as Crassula Cotyledon Sedum Portulaca Sempervivum Gesnera, Phyllogathis &c &c are easily propagated from leaf cuttings. Considerable variations

(1) Knight 1816.

Riehm 1905.

(3) cp. para. III p 96. also par c

(2)a.

have been found.

by experimenters in the ease and rapidity with which plants regenerate themselves by means of leaf cuttings, but ~~it is probable~~ as in shoot and root cuttings- this difficulty - in some cases inability- of the leaves of certain species to reproduce roots and shoots, (or having produced roots to produce shoots) is not real, but depends on conditions, extrinsic and intrinsic.

In late years some experimental work has been done with regard to the striking of leaf cuttings, (1) but particularly from the theoretical standpoint, and our practical knowledge is still far from systematic, and limited in extent. From the horticulturist's point of view, the fact that a leaf plant can be propagated after much trouble and difficulty is practically useless, unless certain conditions are found which render the propagation by this method far more easy and economical, especially if the plant, can be propagated otherwise. The nature of the resulting plant is also a consideration from the horticultural point of view. In the case of Begonias, plants struck from leaves are often more symmetrical, stronger, and more freely flowering than those raised from seed or from other cuttings (2). In the case of a rare plant, however, it stands to reason that the method of leaf propagation, if sure, even if slow and difficult, would be of value on account of its economy.

(1) See under Beinling 1833, Beusekom 1907, Goebel 1902, 1903, 1905, 1908, Kupfer 1907, Lindemath 1904, Regel 1878, Riehml 1905. &c .

(2) G.C.p266 III Ser. vol. XLIX 1911 also L1911p.298.

(5)

Even in ordinary plants, propagation by leaf cuttings is an economical method, for not only is less material cut away from the parent plant, but for each successful leaf cutting, a comparatively large number of resulting plants are obtained. Another interesting point is the matter of early flowering from leafcuttings. This important discovery was made by Sachs in 1893(1). He found that the new individual resulting from a leaf cutting differed according to the region of the old plant from which it had been taken. For example, a leaf cutting ~~differs~~ made from a Begonia in full bloom developed adventitious buds from which new flowers were quickly formed, but on the other hand, by taking a leaf from a plant that had not yet flowered, the new plant produced did not develop flowers until after some time. Goebel(2) obtained the same result with Achimenes, and Winkler(3) with Torenia asiatica. The point is not without its practical importance, as well as its as it theoretical interest. Miss Kupfer found too that in the case of Sedum Tortuosum which had not been known to flower before, a flower stalk appeared in regeneration experiments, and the true identity of the new species was discovered.(4) . The way is open here for more experiment, for the matter of early flowering is always one of interest and importance to the horticulturist.

- (1) Sachs 1892.
- (2) Goebel 1902, 1903, 1908.
- (3) Winkler 1903.
- (4) Kupfer.

(4).

II. PRACTICAL AND THEORETICAL CONSIDERATIONS.

A. Variation in results.

In practice, only those plants which reproduce themselves easily and quickly by means of leaf cuttings are propagated by this method. The majority of these are of a more or less hairy or succulent nature. Hard, leathery, or thin papery leaves are unsuitable. Many Dicotyledons plants not possessing succulent leaves are also capable of reproduction by these organs but though propagation by this method is possible, other methods are usually more speedy and profitable. If a series of plants are indiscriminately selected, as in the experiments of Lindemuth⁽¹⁾, to test the possibility of regeneration in leaves, the question of the great variation in results confronts us.

Seeing that the conditions of absorption and transpiration, carbon assimilation etc. affect the life and growth of the plant, the variation in results with leaf cuttings must be accounted for by the "personal equation".⁽⁴⁾ Not only must the personal peculiarities of the leaf itself be taken into consideration but also the general character of the parent plant. The inherent tendencies in a leaf cutting are as strong as in those of a stem cutting (for example, the formation of a tuber at the base of a leaf cutting of Gesnera cardinalis)⁽²⁾ and these tendencies must be taken into account

(1) Lindemuth 1903.. (2) Stingl. 1908.

(3) see para. Fig. 11 also Daposcheg-Uhlar 1911.

II.A.Contd.

in the treatment of a leaf cutting. For instance, more care is needed to be given to the leaves of a small rooster than to those of a free rooting plant, and so on. That the peculiar characteristics of the leaf which is used for a cutting bears a great influence on the success of the experiment is obvious. Soft succulent leaves like those of many xerophitic plants have within themselves a certain reserve of food material and water and they are consequently not so dependent on external conditions and are more likely to succeed. Thin leaves on the contrary, possess little water or food material and owing to their inactivity are slow of forming meristematic tissue, and are thus more liable to decay. Hard and leathery leaves too, although they possess a greater power of withstanding decay, are more liable to death owing to insufficient nutrition.

B. Method of putting in the Cutting.

The conditions usually observed by gardeners are ⁽¹⁾ that the leaf, not too young nor too old, be taken off with its petiole entire, laid on cocoanut fibre, moist sand, or sandy loam, usually face upwards, and the petiole inserted in the fibre or sand to a depth of one third to half an inch, according to the thickness, length, and texture of the leaf, and that both soil and atmosphere should be kept uniformly moist.

(1) Louden 1878, Lindley 1855, Fuller 1901 and modern gardening Textbooks.

(6).

B. Contd.

It is again obvious that the leaf must be rightly selected with regard to its age, so that a maximum amount of strength and reserve material may cope with the new conditions. The condition of the parent plant as regards flowering has already been referred to. (1) In order to accelerate the callus formation and consequent root formation, it is usual to cut the leaves transversely across the midrib. The flow of material is thus stopped, and a stimulus is given by the wound to form a healing tissue of cork or callus and afterwards roots and shoots. (2)

C. Results with whole or parts of

leaves; a
^{leaves}
 a. attached to the plant.

According to Jost (3) the plant as a general rule has no power of replacing leaves or parts of leaves. If a blade of a leaf be removed, the petiole still attached to the parent plant usually dies: but in the case of Cyclamen persicum, if a leaf blade of a young plant be cut off (only in a young plant is such an experiment successful) at a short distance from the wound a development of tissue takes place on both sides of the petiole, and this proceeds to form excrescences which both in outward form and internal structure, must be described as new leaf blades. (4)

(1) cp. para. I page 85.

(2) cp. Intro. also Figs. 1, 4, 6. also Beusekom 1907 page 169.

(3) Jost ~~1910~~ 1907, page 329.

(4) Hildebrand 1898., Goebel 1902, page 435.. 1908, page 203.

(5) Regel 1878.

In the same way, by artificial stimulus, regeneration of leaves was obtained on Aristolochia Siphoc (1).

On the other hand, the whole leaf, while still attached to the plant, has the power in many genera of regenerating tissue, in a wound injured portion and also possesses the power of forming adventitious buds without any wound stimulus.

Regeneration of Wound Tissue.

In a series of investigations on the leaves of flowering plants Freundlich (2) found that in Dicotyledons, regeneration of ~~wound~~ wound tissue was common. The regeneration was not dependent on leaf venation. (cp. Monocotyledons), (as he had at first thought in a comparison of Monocotyledons and Dicotyledons) but \neq is a general characteristic of Dicotyledous plants. There is obviously here a connection between the power of regenerating leaf tissue and leaf fall in Monocotyledons and Dicotyledons. In Dicotyledons as is well known the leaf prepares a special layer (absciss layer) for the coming leaf fall of the leaf. In Monocots, however no such layer is formed and leaf fall is usually gradual, caused by the rotting of one or successive layers of tissue. Thus a greater activity of the leaf seems

(1). Leavitt R. J. 1906.

(2) Freundlich. H. F. 1909.

to be the nature of the ~~plant~~ Dicotyledonous plant as compared with the Monocotyledon and must be taken into account in the consideration of regeneration results (cp. Monocotyledonous leaves: also ~~on~~ conditions internal Chapter I. n par. 4).

Freundlich has also shown that if the midrib be severed, or the nerves of the 1st, 2nd, or 3rd order, the wound reaction sets in at the basal end. The apical end gives little or no reaction. The intensity of the reaction is always dependent on the strength of the nerve.

4. Formation of adventitious buds on leaves.

There are many Dicotyledonous plants that exhibit the power of regeneration in their leaves by forming buds without any wounding. ⁽¹⁾ Regel and others give a list of such of such plants, among which Cardamine, pratensis

/ and other species.

(1) Regel. 1878.

C. Contd.

and other species, ^{~~Sisyrinchium~~} Nasturtium, Bryophyllum calycinum are typical examples. Such plants that have the power of forming buds during their normal life, ^{Vöchtling (1)} Wakker (2) has put into one group, while those plants that only produce buds after separation from the parent plant form another group, such as Peperonias, some Crassulas, Gesneraceae &c. It is obvious that ^{if} conditions be favourable, members of the first group will also be included in the second, as ^{Vöchtling (1)} Riehm ^{Hein} (3) found in his experiments with Cardamine pratensis, which produced roots and shoots easily when it was severed from the plant. The predisposition to regenerate while on the plant was completed by the detached leaf. Wakker furthermore states that in the first group buds can only be formed in distinct positions, and if these be removed no adventitious buds are removed. ⁽⁴⁾ Miss Kupfer disproved this statement in one example, Leptaxis Menziesii, in which new buds were formed after a period of four to five months after the old ones had been removed. There seems to be however some misconception concerning the normal buds produced in the leaf axil, and adventitious buds such as occur in Begonia phyllomanica. These buds ^{Wakker (2)} states occur on the stems and on the leaf stalks, and even on the blades, though these only in a meristematic condition, quite independent of the leaves.

- (1) Vöchtling 1878.
- (2) Wakker 1887.
- (3) Riehm 1905..
- (4) Kupfer 1907.

7. Detached Leaves.

Although a leaf or part of a leaf while still attached to the plant may have difficulty in the majority of cases in reproducing the lost part, this is not the case, as might be expected, with leaves or parts of leaves that have been detached from the parent stem. The conditions of sustenance and growth are entirely changed (1). From his experiments with *Cardamine pratensis* Richm (2) found that roots and shoots could be formed over all the surface, over the nerves of even very small pieces of the leaf. Vöchting (3) and others (4) have also made experiments with detached leaves. Among the results obtained at the present are briefly the following;—

Whole Leaf.

Entire leaves of a great number of Dicotyledons regenerate easily. (see list p. 110) in others less easily. Callus and roots are first formed, followed by formation of shoots. The roots are most plentiful on the under side of the petiole and cut surface but occur also on the upper. Callus root, and shoot

(1) op. 2 p. 26.
(2) Richm. 1905.
(3) Vöchting 1878
(4) Kupfer, 1897

formation are called forth by extra transverse cuts in the lamina. The callus formed is greatest in quantity at the base of the leaf. The root formation is usually on the under of the leaf, the shoot formation on the upper.

Part of a leaf.

Petiole. The isolated petiole of most Dicotyledonous leaves has been found under the conditions of severing to exert little or no power of regeneration. The tendency is very great, and the part usually succumbs before new organs can be formed. Roots however been formed on leaves of *Begonia* in the experiment of Vöchting (1), always at the basal end. Even shoots were obtained, also at the basal end before entire decomposition occurred. Vöchtings results shew therefore that regeneration of the isolated petiole may occur under suitable conditions.

Entire Lamina. Miss Kupfer (2) found that when the petiole of a leaf is largely or entirely cut away, roots form additional or entirely from the underside of the lamina e.g. *Begonia*, *Peperomia*, *Iresine*. Roots may be called forth as in the case of the entire severed leaf by extra transverse cuts

(1) Vöchting. l.c. 1878
 (2) Kupfer. l.c. 1907

in the lamina, and by longitudinal cuts e.g. Euphorbia nivalis. Vöchting found that the capability of regeneration in a lamina with no petiole, was expressed in an equal measure by isolated parts of the lamina. The regeneration was always greatest at the base. (1).
 Roots appeared usually on the under side, shoots on the upper, at the basal end of the leaf. Various experiments mainly with leaves of Begonias and Peperomias were made to confirm Vöchting's results. It was found that;—

Base of the Lamina. produced roots plentifully at the petiolar end; shoots were also formed at the junction of the nerves.

Central portion of the Lamina. Produced roots and shoots in the same way, the regeneration being greater toward the base.

Tip or apex. Isolated tips like isolated petioles rarely give good results, decay setting in before new organs are can be formed. The difficulty of root and shoot formation is much greater than at the base of the leaf

In practice, and in the plants selected as examples (see Figs) the phenomenon is one of regeneration of the individual since (the petiole being usually severed above

(1). Cp. Freundlich, H.F. 1909.

the axil) no shoot or root primordia are preexistent, and new organs must be formed. If however the leaf is detached with bud still adhering, (1) the regeneration process has already been given a start, and roots only need to be formed. Propagation is correspondingly speedier. Since to make a leaf cutting with bud still adhering, a portion of the stem is often cut with it, the leaf cutting becomes practically a stem cutting, and ~~follows~~ ^{much} develops in the same way. (2).

(1) ex. Kupfer & 1907.

(2) ex. p. Chap. 1. - § 3.

III. CHANGES TAKING PLACE IN THE REGENERATION OF A LEAF.

MACROSCOPICAL AND MICROSCOPICAL EXAMINATION.

As in the stem, there may be said to be three stages in the regeneration of a Dicotyledonous leaf. The formation of

- A. a healing tissue- either cork or callus.
- B. roots. and
- C. shoots.

A. Callus Formation.

The first change when the leaf has been separated from the parent plant and laid on a suitable, is the formation of a healing tissue at the base of the petiole, and at any cut surface. (1). (Figs. 1, 2) Usually this tissue is "Callus" but in many cases e.g. Peperomia &c. (2) a cork tissue (Wund-cork) is merely formed as in Monocots.

Comparing the internal structure of a leaf petiole or midrib to that of the stem (3) it will be seen that the bundles are closed, and typically Monocotyledonous in type (4), and that the potentiality for callus formation lies not in the cambium, for this is absent, but in the meristematic cells of pith and leaf parenchyma. The majority of Dicot. stem cuttings do produce a callus tissue at the base: almost invariably Monocots do not (5) but instead, the cells become

(1) cp. Chap. I. para. III.A.
 (2) Beinhling 1883. Taf. IV & V.
 (3). cp. Chap. I para III.
 (4) Scott 1902, page 66.
 (5) cp Chap. V.

III.A.Contd.

corky and brown (1). The fact that the majority of leaves produce callus like a Dicot. cutting rather than a mere cork formation like a Monocot. stem cutting, in spite of the absence of cambium, must be taken into consideration with their somewhat altered function when separated from the parent plant. For the time being, until roots and shoots are formed, they add to their own function that of a stem. This statement may be correlated with the fact that secondary thickening sometimes occurs in isolated leaves, a phenomenon which has attracted the notice of many investigators (2). The life of the leaf, which under the new conditions of separation and placing in heat and moisture, is often maintained for a considerable period beyond its normal duration, is thus able to be prolonged for a still greater length of time. When roots and shoots are quickly and easily formed as in Begonia, the essential characteristics of the stem are not necessary, nor in fact are they defined.

The phenomenon of callus formation in ^{Dicot} leaves ~~generally~~, might also be attributed to the fact that it occurs ~~is~~ usually as a seat of origin for the roots and shoots. Roots appear at the cut surfaces of leaf stalk and lamina only (as in the case of Peperomia(3)) or on the leaf surface generally (4). ~~In Monocots.~~

- (1) cp. Chap. V. para.
- (2) ~~Knight~~ Goebel 1907, Knight 1816, Kupfer 1907 etc.
- (3) Beinhling 1883.
- (4) Riehm 1905.

Where healing occurs by cork formation only, as in Peperomia (2) the exposed cells die. Active division takes place in the ~~exp~~ ~~posed~~ living cells above the dead layer, especially in the leaf pith and parenchyma. The epidermis for the most part remains unchanged.

When callus formation does occur, there may be various centre of activity, beginning from the pith until the whole cut surface is covered (3). Callus formation may occur from the epidermal cells outwards themselves (4). Regel (5) seems however to be disinclined to call the tissue formed in this way callus, just because the epidermal cells take part in its formation. But there seems no reason why epidermal cells ~~do~~ though not taking part in the formation of callus in the stem, (6) should not do so in the leaf.

As in stem cuttings, the amount of callus formation is variable (Figs. 1&2, 6&7.) The quantity depends on conditions ~~of~~ external and internal, the nature and inherent tendencies of the plant, and/

- (1). Chap. V
- (2) Beiling. 1883.
- (3). Kupfer. 1907.
- (4) Jost. p. 329. - 1907.
- (5). Regel. - 1848.
- (6). Chap. 1. para.

III. A. Contd.

and is intimately connected with its power of forming roots and shoots. If with Kuster (1) all cataplasms of a parenchymatal character resulting from wound stimuli are termed "Callus" then the intumescences Beusekom (2) has examined on leaves of *Gnetum Gneton* come also under this category: and these he has proved also to occur only in heat and moisture, the two most favourable factors in callus formation. (3).

A microscopical section across the base of the petiole of a regenerating leaf shews the same appearance as that of a stem cutting. ~~Fig.~~

B. Root Formation.

After the formation of callus, at the end of a varying period, roots are produced. (Figs. ³⁻⁸) In the generality of cases, these roots arise only from the cut surface. Their origin follows the rule for all adventitious roots, i.e. the origin is endogenetic.

The pseudo root hairs (*Pseudowurzelhaare*) or trichomes produced in many species of *Begonia* must be distinguished from true roots: These were observed and described by Regel (5) and shewn by him to really form part of the callus development: their origin is exogenetic, arising as outgrowths from the epidermis in the neighbourhood of the cut surface

(1) Küster 1906.

(2) Beusekom 1907.

(3) cp. Chap. I para.

(4) See also Figs. in Tittmann 1895, Soraue 1909.

(5) ~~cp. Chap.~~ Regel 1878.

III.B.Contd.

as well as on the petiole and on the cut lamina. Their function is merely that of anchoring, as in the *Silices*(¹). These pseudoroot hairs (Fig.) are however not characteristic of all leaves in regeneration, and are not to be found in *Peperomia*.(²)

Beinling (²) in his minute examination of the origin of adventitious roots on leaf cuttings of *Peperomia*, came to the following conclusions with regard to the formation of these organs in that genus. The origin of the roots are always endogenous, the plerome is at first differentiated from the cambial layer, which has been formed in the vascular bundle, the periblem and dermatogen from the succeeding divisions of the plerome. The roots are almost invariably found to find their way to the exterior by the cut surface, not through the epidermis. Normally the origin of adventitious roots is from the pericycle(³) Where this layer does not exist, as in the case of leaf cutting they take their origin in the cambial layer which is formed in the vascular bundles for the purpose.

(1) Goebel 1905 ii. page 264.

(2) Beinling 1883.

(3) Van Tieghem and Douliot.

III. B. Contd.

Regel has also proved that the origin of adventitious roots in leaf cuttings are endogenous, arising from the cambium developed in the vascular bundle. Wakker (2) confirms the endogenous origin of adventitious roots arising on detached leaves.

C. Shoot Formation

After some time in most succulents, shoots are produced. (see Figs.) These adventitious shoots on leaf cuttings are exogenetic in origin wherever possible. They are not preexisting structures on leaves, but are formed in the outer leaf parenchyma immediately below the surface and

(1) Regel. 1878.

(2) Wakker.

(4) cp. also Goebel II. 274. 1905.

.Contd.

and independently of the vascular^{system}(1). Wakker⁽²⁾ also confirms the exogenous origin for adventitious buds. According to Regel⁽³⁾ Peter-petershausen seems to claim an endogenetic origin for the adventitious bud on detached leaves of Begonia coriacea, a statement which in face of his general examination of the phenomenon in of regeneration in Begonias, Regel is very much inclined to doubt. A truly endogenetic origin has been proved recently by Van Beusekom⁽⁴⁾ in the case above mentioned, of adventitious buds arising on the leaves of Gnetum Gasoni L. The whole formation in this instance- the intumescence resulting naturally from the wound of the insect Aspidiotus Dictyospermi. Morg. and artificially from very small wounds - the yellow colouration of the leaf tip, and the internal disturbances in the leaf, with the ultimate formation of buds from a meristem in which the epidermal cells do not take part, must however be regarded as an exceptional occurrence. *Other workers e.g.* Mohl⁽⁵⁾ Carnel⁽⁶⁾ Berge⁽⁷⁾ confirm the exogenous origin of shoots on leaves.

After a varying period (in Beinling's experiments the old Peperonias leaves lasted a year, with the new shoots attached,) the new plant cuts itself by a cork layer, as in the formation

- (1) Beinling 1883.
- (2) Wakker 1887.
- (3) Regel 1878 footnote.
- (4) Beusekom 1907.

III.C.Contd.

of an absciss layer layer in leaf fall from the parent plant and is nourished by adventitious roots of its own, arising from the base of the new stem, and thus regeneration of the new individual is completed. Thus no structural communication is formed between the new shoots and the old leaf. Robinson (1) who examined adventitious buds formed naturally on Drosera rotundifolia, also found no vascular connection between them and the parent plant. (2). (29)

III.D.Co Difficulty of Shoot Formation
as compared with that of root formation ; Theoretical
Considerations .

It is a well known fact that practically any leaf if it is separated from the parent plant, and laid on a suitable medium, will form roots, some leaves doing this with the greatest ease, but from the experiments that have so far been out carried out with regard to leaf cuttings there seems an universal agreement as to the difficulty of shoot

(1) Robinson 1908.

(2) Dixon 1901.

III.D.Contd.

formation, as compared to root formation. *Ficus elastica*, *Camellias*, *Hoya carnososa* &c are examples of plants which produce roots easily on their leaf cuttings, but form no bud except after a considerable period. It is interesting to note in this connection that while other species of *Hoya*, *bella* &c. are propagated by means of their leaves quite easily, and while *Hoya carnososa* possesses in common with many other *Asclepiads* (*Ceropegia*, *Stapelia*, *Tylophora*) a thick fleshy leaf, from the appearance and texture of which regeneration would seem likely, yet this species is the more obstinate in rooting (1). If the internal structure of an organ, as well as other conditions bears some relation to its regenerative power (2), then the leaf of *Hoya carnososa* should differ in its structure from the majority of *Asclepiads*. This was found by examination to be the case, *Hoya carnososa* possessing peculiarities which are quite distinctive. De Vesque (3) has shown that the typical *Asclepiad* leaf as exemplified by *Ceropegia*, *Stapelia*, *Cryptostegia* &c ~~if~~ differs in little or no respect from the Cruciferous type

- (1) Lindley 1855 etc.
 (2) cp. Chap. I. para. IV.
 (3) Vesque 1885.



(1) Liriodendron tulipifera
(2) Magnolia speciosa
(3) Magnolia speciosa

III.D.Contd.

In all the species studied, the petiole exhibited a single bowshaped bundle with little or no mechanical fibres present. Sometimes small lateral bundles are to be found. Mechanical elements are equally rare in the median nerve. These characteristics were confirmed, and are shown in a transverse section of a leaf of Ceropegia, (Fig.). A transverse section of Hoya bella is almost identical. A transverse section of the leaf of Hoya carnosa petiole (Fig.) on the other hand shows the presence of marked patches of sclerenchyma irregularly scattered in the mesophyll. These patches are very numerous in the vicinity of the bundle but somewhat diminish towards the periphery of the section. A transverse of the lamina shows the median bundle surrounded by these sclerenchyma fibres accompanied by numbers of crystals. The sclerenchyma elements gradually disappear towards the tip of the leaf. Our knowledge is limited in this direction, but it would seem a likely conclusion that the presence of sclerenchyma offers a hindrance to some extent to shoot formation. ✓

III.D Contd.

For the difficulty of shoot formation as compared with root formation most clearly exhibited in leaf cuttings, many various suggestions have offered. (1). Goebel offers as a suggestion the absence of budforming materials in the leaf. Morgan asserts here as in other regeneration phenomena that even the idea of food stuffs fails to explain some of the simplest phenomena, and while it need not be denied, that under un certain conditions, the presence of or accumulation of food material may produce certain definite results, yet such food stuffs seem to play a very subordinate part as compared with other internal or innate factors.

It cannot be too strongly urged that regeneration like life or growth does not depend on one factor alone, external or internal, but that the capacity for regeneration in a plant is hindered or increased by a combination of factors acting and interacting with one another. (2).

In the leaf, even more than in the stem or root, food stuffs seem to play an important part in regeneration--

- (1) cp. also Intro. para V page Regeneration Theories.
 (2) Goebel 1907.
 (3) Morgan. 1901.
 (4) Mc.Callum. 1905.

III.D.Contd.

and this is not surprising, since it is the function of the work of photosynthesis and transpiration. Morgan (1) admits that the presence of a food material in larger or smaller quantities may determine the potentiality of a special part. One might proceed but little further and assert that shoot formation in the leaf depends partly upon the quantity and quality of the food material present to be utilised in the formation of the bud, while root formation depends to a greater extent upon the moisture, with little regard to the food material. This would seem a likely suggestion since under conditions of heat and moisture, if the plant is placed in water or on damp moss adventitious roots are developed rather than adventitious shoots... Richm's investigations (2) with regard to the development of roots and shoots on Cardamine pratensis seem also to bear the statement that the development of buds is dependent to a great extent on the quality and quantity of food material present. A brief summary of his results, which are most interesting and worth extending to other leaves, are as follows:-

✓ (1).Morgan. 1901. ,1903.
 ✓ (2).Richm. 1905

M.D. Contd.

With single solutions such as NaCl, K_3PO_4 &c. shoot formation takes place first, root production being greater the weaker the solution.

Water. - Both roots & shoots produced. Root Production very great.

With alkaline solutions a marked difference was noticed between root formation and shoot formation. Root formation was normal but shoot formation was hindered.

In sugar solutions (Cane and Grape) regeneration phenomena were very similar to that in water.

In mixed solutions (KN_3 & $MgSO_4$ NaCl KN_3 $MgSO_4$ &c.) shoot formation occurred but no roots were formed.

In acid solutions, shoots were formed but no roots.

(cp stem cuttings).

The following conclusions were therefore reached. Root formation is suppressed when leaves are immersed in acid solutions. Shoot formation on the other hand is suppressed or very seriously hindered when the isolated are under the effect of weak poisons or alkalis, or if the cell complex at the forking of a nerve has been injured. (1). Riehm(2) shows that the cell complex is always present where adventitious shoots are produced (). When these adventitious buds are produced while the leaf is attached to the plant (X) then the cell complex is also to be found between the forks of dividing nerves. If on the other hand, adventitious

(1) Vochting. 1878.

(2) Riehm 1905.

III.D.Contd.

buds are produced only after ^{pe}separation from the parent plant then the cell complex is produced by the division of several cells on the periphery of the wounded surface .

If Riehm's results with Cardamine pratensis can be extended to other leaves then a solution to the difficulty of shoot-formation might be found. It may be that the leaf has not sufficient acid food which seems more favourable to shoot formation, and that this consequently must be supplied in some form. By repeated experiment the optimum concentration of acid solution (mixed or otherwise) could therefore be ascertained for the particular plant.

IV. LIST OF PLANTS COMMONLY AT THE PRESENT DAY BY MEANS OF THEIR LEAVES.

The following is a list of plants commonly propagated at the present day by means of cuttings made from their leaves. (The list only includes those species that are increased by this method in practice. For a fuller list of plants from which it is possible to obtain new plants, but which are more interesting from a theoretical standpoint than a practical one, see under ^eAgel &c.) As this writer points out in the Begoniaceae Crassulaceae and Gesneraceae propagation by leaf cuttings is characteristic of the orders and is possible for nearly every member. In other orders as yet only isolated plants are propagated by this method.

- Begoniaceae. Begonias, especially the varieties
 - Gloire de lorraine
 - Winter cheer
 - Mrs Heal.
 - Ensign.
 - Gloire de sceaux.
 - All Rex varieties.

- Crassulaceae. Bryophyllum calycinum
 - pinnatum
 - crenatum.
 - Crassula
 - Cotyledon.
 - Echeveria.
 - Sedum.
 - Sempervivum.

- Gesneraceae. Gloxinia varieties.
- Achimenes.
- Columnnea.
- Chiririta sinensis
- Aeschynanthus.
- Leptandra. bicolor.
- Saintpaulia. &c.

See under Orders in Part II. A. General Notes on the Propagation of Dicots,

Chap. IV. Dicotyledons, Root Cuttings

(111)
in Conteeby 12.

1. POSSIBILITY OF DICOTYLEDONOUS ROOTS TO FORM SHOOTS.

a. Roots attached to the parent plant.

Under normal conditions, the majority of Spermophyta do not bear buds on their roots. The stem was formerly as t regarded as the only organ which bore buds, but as has been indicated(1) this power of bud formation is by no means confined to one particular part of the plant. As Beijerinck(2) has shown in his extensive paper on the subject, adventitious buds may occur on roots without previous wounding, as distinguished from callus buds, or those arising as a result of wounding, in a very great number of Dicotyledons. (3) From his own investigations, Beijerinck has extended the list of such plants, given by older investigators such as Warming, Irmisch, Wittrock(4). He has shown that normal shoot buds are to be found on the roots of members of Cupuliferae, Myricaceae, Urticaceae, Salicicaceae and a number of isolated plants in other families such as Geranium, Nasturtium, Anemone &c. In many trees, this power of shoot formation is habituale.g. in Limes, Chestnuts, Poplars, Alders, The young saplings round the mother tree owing their origin to this characteristic.

(1) see Intro. p. 2. p. 3. also p.

✓ (2) Beijerinck. 1886.

(3) see para. b.

✓ (4) see lit. under Beijerinck. 1886

The production of adventitious shoots on roots appears to be a subsidiary function of many plants, but in some cases, as for instance in the Podostemaceae, it has become the chief function. (1). That the roots, at least of some of the species (2) are also chlorophyllous and assimilating, is a fact which may result from the power in this order (3). Roots of certain genera, such as Pelargonium Radulum have been found to produce buds when pot-bound (4).

Generally speaking, however the power of forming shoots is exhibited in the root while still attached to the parent plant, only when it has been injured in some way. (5). The fact that most of the common weeds multiply so rapidly is due to the great power of regeneration of their roots, as well as that of the root stock (6). The roots of many Composites especially seem to possess this power in a remarkable degree. In *Cardamine pratensis* for example, the roots when cut into pieces near the surface by the plough send up multiplied stems. In *Leontodon taraxacum* the fleshy tap-root also retains its vitality and produces new stems when injured.

(1) Goebel.

(2) *Dicraea*. *sp. bengalā + D. algaeformis*. 1905. II. 250

(3) Goebel. *Organography*. 1905. II.

(4) Kunfer. 1907.

(5) equivalent to 'reparative shoots' see Wittrock. 1884

(6) MacAlpine. ?

Scorzonera hispanica, Chicorium intybus, Taraxacum officinale are also capable of easily producing new stems from their stems amputated roots. In Docks, especially in Rumex obtusifolius and acetosella any bit of the fleshy root is capable of regeneration. In Plantago lanceolata too, the ~~fl~~ fleshy taproot is fleshy and full of vitality.

Beijerinck mentions the formation of callus buds furthermore in Eryngium canestru and other Umbelliferae. Many trees such as Cratoegus and others also bear buds on their roots when injured. In Wittrock's list of reparative shoots formed as a result of wounding of the roots, such plants as Centaurea scabiosa, Agrimonia Eupatoria, Crambe maritima &c are given.

b. Severed Roots.

Many Dicotyledonous roots that do not normally produce shoot buds, while attached to the parent plant, may however, be induced to do so, by severing, and subjecting to environmental conditions as cuttings. (Some confusion has arisen among writers here, as in Monocotyledons (1). owing to the loose usage of the word 'root' with reference to cuttings, when rhizomes e.g. Primroses &c. subterranean branches e.g. corms Cyclamens, and tubers e.g. Potatoes have been implied.

(1). see page. Chap - V.

These are not true roots, but stem modifications, which bear buds in a regular manner just like the aerial stems. Roots however when they do bear buds, bear them irregularly. True root cuttings are a more important mode of propagation in Dicotyledons, than in Monocotyledons, where the rhizomatous stem effects the same purpose. It is a curious fact that many plants particularly shrubs, which are slow or difficult to propagate by means of stem cuttings, strike with comparative ease from cuttings made from the roots. It might seem from the frequent occurrence of this phenomenon, that a definite relation such as that which exists between the formation of seed, and the formation of vegetative organs, (1) also exists between the bud formation by the stem and that of the root. (2). Many shrubs such as *Calycanthus*, *Cladrastis*, *Ailanthus* (3), increase readily from cuttings made of pieces of their roots, and propagation by this method has become the common one.

(1). op. Intro. p. 9. B.
 (2) Cp. also Kny. 1894, 1901.
 (3). see notes under each genus part. II. p.

2. PRACTICAL CONSIDERATIONS. Advantages and disadvantages of the method. nature of the resulting plant ; temperagure&c.

As a method of propagation, root cuttings are not greatly in favour among horticulturists, and are ususally employed as a la t resort. Bouvardias (1) used at one time to be propagated a great deal from root cuttings, which strike fr& freely, but the more modern method is by stem cuttings though these must be chosen with care. In many cases e.g. Arnebia (1) root cuttings are the usual nodes as the shoots suitable for stem cuttings are produced in no very great number; the same occurs in Cephaelis, where root cuttings are also employed with success.

From the horticulturist's point of view, the end in propagation is not merely to increase the plant, but to get as the result, he best plant possible. From the point of view of economy, Root cuttings are not perhaps so economical as leafcuttings. In the case of a rare plant, such as Jacaratia dodocaphylla, a cultivator might hesitate to m&k& cuttings of the roots, for fear of killing his specimen, and yet try leaf or stem cuttings , if thease were available in any quantity. But on the other hand, the method of root

(1). see note under Bouvardias. partII. p.

cuttings are a more economical method than increase by stem cuttings, if the result be considered, since while each stem cutting will only give one resulting plant, (1) each root may be cut into moderately small pieces, each piece producing a new plant.

The resulting plant does not differ materially in most cases from that raised from a stem cutting, except in the point of time. A root cutting of Spathodia campanulata for example gives a plant earlier than a cutting of the stem does. In other cases the resulting plant may be producing later.

In the case of sucker plants, however a plant raised from roots is often superior to that raised from the sucker, e.g. in Raspberry, Blackberry, and the Currants (2). A plant constantly reproduced from suckers often intensifies the suckerlike habit and generally degenerates. (An analogous degeneration occurs with plants propagated by means of single scale leaves instead of whole bulbs) (3).

In the case of plants with fibrous roots, e.g. Sparganium &c. the impracticability of the method of root cuttings is obvious but in all cases of plants with thick fleshy roots, as in

(1). cp. Chap. I. Stem Cuttings. *ib.*
(2). see Fuller. 1901.
(3). see Chap. V. Leaf cuttings. Monocots.

Senecio, Lactuca, Clerodendron, &c. the method is possible and indeed may often prove to be the most advantageous, especially under conditions where propagating frames and such devices for the reduction of transpiration are not available. And this is a point in favour of root cuttings. For root or pieces of roots may be buried in the soil and thus suffer little or nothing from excessive transpiration, while absorption is still continuing. Stem and leaf cuttings, on the other hand, have for the time being, no means of absorption, and are also, in consequence of their exposed surfaces, in danger of excessive transpiration and resulting death, and thus need a higher temperature than do root cuttings. Root cuttings may be a natural mode of vegetative propagation. Root cuttings are nearly always artificial. The conditions in each case must therefore be very different.

Propagation by root cuttings is to be recommended for many perennials. The method is found to be quicker than increase by seed, and requires no great skill on the part of the operator. If the cuttings are inserted in January, a good stock of plants will be ready by June. The mode of increase is specially to be recommended for Japanese Anemones, Gaillardias, Acanthus, Eryngium &c. (1).

✓ (1). G.C. 24.1.85. Vol. XXIII. p. 113. 1885.

3. THEORETICAL CONSIDERATIONS.

For examination of the changes taking place in a root cutting after insertion, Spathodia campanulata, (Bignoniaceae) which is easily increased by cuttings made from the roots was observed.

A. Callus Formation.

Though so much work has been done with regard to the formation and differentiation of callus in stem cuttings (1) little detailed work has been done with regard to root cuttings in particular. Goebel (2) and Vöchting (3) are perhaps among the chief investigators in this direction. The cambium is, as in shoots, the main origin of the callus formation (4). In Spathodia campanulata the callus was formed very quickly after a few days. (Fig.) The central portion of the root seems to take no part in the formation of the tissue. With regard to the function of callus formation in root cuttings, Reehinger (5) states that -callus tissue, as in stem cuttings (6) in addition

(1)cp. Chap. I. §3. A.

(2).Goebel. *various*.

(3) Vöchting. *various*.

(4)Cp. Chap. I. §3. A.

✓ (5).Reehinger. 1894.

(6).Cp. Chap. I.

to its function of healing the wound, and thus protecting the plant from too great a transpiration, also forms a necessary transition tissue between the permanent cell tissue of the old plant to the newly formed tissue of the new organs. As in stem cuttings, also callus tissue in root cuttings may become assimilating and develop chlorophyll (1). The phenomenon happens particularly when the roots are exposed to light, and cultivated in a moisture saturated atmosphere as for example in Taraxacum officinale, and Armoracia rustica. The function may disappear, when new roots and shoots appear, or it may be retained, as in Armoracia. Callus formed in root cuttings may as in Conifers (2) pass into a resting stage, becoming as Reehinger puts it, a 'resting callus.' Callus formation after proceeding to some extent becomes in these instances covered with a periderm, and remains dormant, until a further stimulus causes it to form new organs as in Beta vulgaris, Medicago sativa. The callus cells often contain nutritive matter for the nourishment of the new organs, e.g. the callus in root cuttings of Armoracia rustica contains much starch, while that of Beta vulgaris contains sugar.

(1). This was also observed in the forced callus of Anacapaeg-na racemosa, see Chap. I.

(2). Chap. VI. p.

Differentiation of callus .

The callus formed in root cuttings differs in no respect from that produced in stem cuttings. It is at first undifferentiated. Later as in the stem, (1) various centres of differentiation appear, until finally new organs are produced. As in stem cuttings, the amount of callus formed at the cut ends of a root cutting is variable being mainly dependent on conditions of moisture and heat.

Lenticel expansion.

To be noticed with the callus formation in root cuttings is the marked activity of the cells in the vicinity of the lenticels. Under the influence of heat and moisture, these cells divide actively and form small liplike projections around the opening of the lenticel, thus enlarging the space occupied by them and causing them to be very noticeable. (2). These lenticels, as will be seen, serve as outlets for the secondary roots. (Fig.). In some plants e.g. Ficus elastica the lenticel expansion is shown much more clearly than in others e.g. Spathodia as the whitish colour of the enlarged lenticel stands out in strong contrast to the darker colour of the root. The origin of the roots from the lenticels has also been noticed for stem cuttings (3.)

(1)ep. Chap. I. p. 3.

(2).see Para.

(3).see Do. p.

B. Root Formation.

Vöchting (1) states that in a plant, different parts tend to give rise to unlike structures with considerable more ease than to like structures. Miss Kupfer (2) found, however, that secondary roots arise more generally and more quickly than shoots, even in root cuttings. When shoots were formed in the species she investigated, she found that the appearance of roots antedated that of shoots by a considerable period. The comparative time of root and shoot formation was therefore noted in the plants under observation for callus formation. As far as observed, there seemed to be ^{no} definite rule; sometimes the shoots appeared first e.g. Kennydea prostrata, sometimes the roots, e.g. Myriocarpa longipes.

In regeneration phenomena, root formation on Root cuttings may occur in different ways. (3).

a. No further severing of the root takes place.

If the root is small, it might be used as a cutting, without any further cutting. This is rarely, however, done in practice, as the roots used for propagation are essentially large thick and fleshy (4), and for economy

(1) Vöchting. 1926. etc.

(2) Kupfer. 1907.

(3) op. Shoot Formation on Stem Cuttings. Chap. I. p. 3. C.

(4) see para. 2. p. 117.

each root is cut into several pieces. If a whole root however is used, the production of new roots is identical with that of a root attached to the plant, in ordinary vegetative growth. Lateral roots are produced, most abundantly at the root pole. Their origin is endogenetic from the the pericycle.

b. Further severing of the root takes place.

At the tip;- Much work has been done with regard to the regeneration of the root tip, while the root is still in connection with the plant. (1), but little in regard to the regeneration of the tip in a root cutting. The capability of the root is however the same. Regeneration of the root takes place, but more slowly owing to the more difficult conditions under which the root is placed. According to the place of section, which may be made at actively growing tissue or further back at already differentiated tissue,) regeneration of new tissue will take place, or the formation of new roots.(2).

(1) see Goebel 1907, 1908 & c, Lopriore 1892, 1896, Warner 1908, Nemec 1905, Simon 1908 & c.

(2) Nemec 1905, Goebel 1907 & c.

the root cutting is cut into pieces;-.

This treatment of a root cutting, is as indicated(1).
the usual mode of procedure in practice.

Entirely new roots are found to form at the basal pole though if the primordia of lateral roots are already in existence on the piece, these naturally take preference in the matter of time. The origin of these new roots may be either above the callus, where their origin is from the pericycle, or they may arise from the cut end, from the callus tissue (2). The origin is also endogenetic. Though not investigated in detail, the differentiation of the callus tissue previous to root and shoot formation is probably identical with that described by Simon(3) for root and shoot formation in a stem cutting.

The effect of severing the main root, and leaving the lateral roots intact on the plant, though not strictly a question of root cuttings, is yet connected sufficiently with the whole subject of Regeneration, to be considered. Boirivant (4), has shown that when the main root of a plant is severed, the nearest lateral root or rootlets become considerably modified in structure and appearance. The lateral roots in general develop largely(5) In particular one or two lateral roots develop considerably

(1). see above para. 3. B. p. 122.

(2). cf. Chap I. § 3. C.

(3). cf. Simon 1904.

(4). Boirivant. 1897

and take on the character of the axis. They lengthen, thicken, and branch, and even become tuberous in character.

Internally, these lateral roots of replacement approach more nearly to the mother root, than to the lateral roots. The number of the vascular bundles is usually greater in the principal root than in the lateral roots. It was observed that after severing of the main root, the number of vascular bundles in these lateral roots of replacement became greater than in the normal lateral roots. In these modified roots, too, the vessels were larger, and more numerous than in the lateral roots- the central cylinder, the secondary tissues formed were larger in character and more abundant. It would be interesting to observe if the relation is the same, between the new secondary roots produced at the base of a piece of a root used as a cutting and the lateral rootlets existing on the root, as Boirivant has shown exists between the lateral and modified lateral roots attached to the plant.

If on the other hand, the main root is allowed to remain, but the lateral root severed, a modification of the main root resulting from the disturbance of activity (1) takes. The root was found to lengthen much more rapidly than a corresponding

(1) see Intro. p. 56. p. 24

principal root possessing lateral rootlets. It attempted to form fresh lateral roots and the resulting number of these roots were often in excess of those in the control plant.

Thus injuring had a stimulating effect both on the development of the existing roots and the formation of new roots. (1).

Internally the structure of the main root was also modified. It was found to possess a much greater lignification of tissue than was present in the main root of the control plant.

C. Shoot Formation.

In some plants (Cyrilla, Acanthus &c.) adventitious shoots are produced first, before secondary lateral roots are formed. This seems to occur when the root cutting is comparatively young and soft. In the case of old roots, young lateral roots are first formed to carry on the work of absorption, of which the old hard root is incapable.
Origin of roots.

a. From the callus tissue itself.

Where the shoots arise directly from the callus tissue, their origin is quite normally exogenetic, as in stem cuttings. (2)

b. Otherwise than from the callus tissue.

Where shoots arise on roots otherwise than from the callus

(1). *Recap.* cp. *Instr.* § 6. p. 24
(2). *Op. Chap. I.* § 3 B.

tissue, their origin is not definite, as is usually the case with roots (1), but varies according to the nature and age of the root cutting employed. In old woody pieces, e.g. in *Spatholobium* it would be expected that the origin would be endogenetic. Goebel (2) states that adventitious shoots arise as endogenetic structures at the position where the normal lateral roots may arise, and frequently their position bears some relation to that of the lateral rootlets, as in *Linaria vulgaris*, *Solanum dulcamara*, *Pyrola* &c.

The normal origin of shoots on stems and on leaves is exogenetic, but the presence of the actively functioning pericycle, acts in roots as a considerably modifying influence. The pericycle, which is the normal origin of lateral roots becomes also the origin of shoots. Trecul (3) has worked out the origin of rootbuds on woody plants, such as *Maclura aurantiaca*, *Ailanthus glandulosa* and others, and shown them to be endogenetic. But the origin of roots is not always so. They may arise independently in the medullary rays of *Pyrus japonica*, *Rubus* and others. In *Aristolochia clematidis* the shoots are developed from the deeper layers of the cortex (4)

(1) op. chap. I. para. 3 B.

(2) Goebel, 1905 etc.

(3) Trecul, 1847.

(4) Goebel l.c.

4. CONDITIONS AFFECTING CALLUS, ROOT AND SHOOT FORMATION IN A ROOT CUTTING.

The conditions, external and internal affecting the phenomena of regeneration act in the same way in a root cutting as in the case of a stem cutting (1). An increase of temperature, moisture &c. usually act as stimuli. With regard to Polarity, one point seems worthy of notice. While shoot and root formation take place at the shoot and root pole and is retarded by the inverse position, development takes place in the majority of cases most quickly in the horizontal position in root cuttings. (see Figs. of Spathodia If the point be considered, this might be expected, as the position is the natural one for roots. After descending vertically for a short distance into the earth, the roots spread horizontally, in order to carry out the function of fixation and nutrition more completely.

In the experiments which were being carried out with root cuttings, another interesting point was observed. It has been shown that in a stem cutting, the age of the shoot chose

(1).cy. Chap. I. para. 4. A+B.

is to a large extent responsible for the success in propagation. In a leaf cutting, moreover the choice of the leaf will influence the resulting plant. (1). In the same way, the age of a root cutting was found to have a marked effect on the resulting plant. If a young root were chosen (as in Acanthus montana) the resulting plant is more backward and approaches nearer the seedling stage, than if an old root cutting were chosen. It is to be noticed that in the young root cutting, the leaves that eventually appear on the shoot are more similar to the seedleaves of Acanthus montana, while those that are formed on the shoot of an older root cutting are more like the leaves of a mature plant. The difference in Acanthus montana is easily recognized, owing to the prickly nature of the mature leaves.

(1) ~~Coebel 1907 & Winkler, 1905 and others. also op. chap. II para. 2 p. 86.~~

5. LIST OF PLANTS COMMONLY PROPAGATED BY MEANS OF ROOT CUTTINGS.

- Acacia; (Leguminosae). (1).
grandis, *pubescens*, *pulchella*.
- Acalypha; (Euphorbiaceae).
- Acanthus; (Acanthaceae).
arboreus mollis and varieties especially *n. latifolius*,
n. longifolius, *n. spinosissimus*.
- Acanthopanax; ()
Quinquefolium variegatum &c.
- Achillea; (Compositae).
- Ailanthus ; (Simarubaceae).
glandulosa.
- Anchusa; (Boraginaceae).
italica.
- Anemone; (Ranunculaceae).
japonica, *alpina*, *sulphurea*, *pulsatilla* &c.
- Antidesma; (Euphorbiaceae).
sp.
- Aralia; (Araliaceae).
japonica &c.
- Aristolochia; (Aristolochiaceae).
Goldiana.
- Arnebia; (Boraginaceae).
echinoides.

(1). see notes under each genus in part II. 'General Note on the propagation of Dicot. Orders.

Note;—The list here given only includes plants commonly propagated by root cuttings. See also lists of

Beijerinck &c.
 1886.

- Asclepias; (Asclepiadaceae).
Cornuti. (Kerner and Oliver.)
- Bignonia; (Bignoniaceae).
venusta. (G. 22. 4. 82., G. 26. 2. 98.)
radicans. (G. 18. 11. 99.)
- Bouvardias; (Rubiaceae).
- Brownea; (Leguminosae).
- Caragana; (Leguminosae).
arborescens.
- Carya; ()
- Cassia; (Leguminosae).
- Catalpa; (Bignoniaceae).
guinensis.
- Cephaelis; (Rubiaceae).
ipocacuanha.
- Cephalotus; (Saxifragaceae).
- Cladrastis; (Leguminosae.)
amurensis.
- Clematis; (Ranunculaceae)
- Clerodendron; (Verbenaceae)
fallax, fragrans, trichotomum.
- Compositae; e.g. Scyrzenera, Lactuca &c.
- Coronilla; (Leguminosae).
glauca.
- Crambe; (Cruciferae).
- Croton; (Euphorbiaceae).

- Cydonia; (Rosaceae)
japonica.
- Cyrilla; (Cyrilleae).
- Cytisus; (Leguminosae).
- Dais; (Thymeliaceae)
cotinifolia.
- Dimorphanthus; ()
- Dionaea; (Droseraceae).
- Doronicum; (Compositae).
- Drosera; (Droseraceae).
- Echinops; (Compositae)
- Eryngium; (Compositae).
- Euphorbia; (Euphorbiaceae).
- Fatsia; (Araliaceae).
japonica, papyrifera. (see Aralia).
- Gaillardia; (Colpositae).
- Greyia; (Sapindaceae)
Sutherlandii.
- Gynocladus; (Leguminosae).
canadensis.
- Halesia; (Styraceae).
- Harpalum; see Helianthus.
- Helianthus; (Colpositae)
- Helleboris; (Ranunculaceae)
- Hormannia; (Sterculiaceae)

- Hippophae; (Elaeagnaceae).
rhannoides.
- Hypericum; (Hypericaceae)
adpressum, calycinum.
- Idesia; (Bixineae).
polycarpa.
- Jaborosa; (Solanaceae).
integrifolia.
- Jasminum; (Oleaceae).
- Lepidium; (Cruciferae).
latifolium.
- Linaria; (Scrophulariaceae).
pallida, genistaeifolia, vulgaris.
- Kennydea; (Leguminosae).
- Kigelia; (Bignoniaceae).
- Maclura; (Urticaceae).
aurantiaca, tinctoria.
- Monsonia; (Geraniaceae).
lobata.
- Morisia; (Cruciferae).
hypogea.
- Nerantea; (Ternstroemiaceae).
guinensis.
- Panax; (Araliaceae).
plumatum.
- Papaver; (Papaveraceae).
bracteatum, orientale and Eastern varieties.
- Passiflora; (Passifloraceae).
- Passiflora; (Scrophulariaceae).
imperialis.

Pelargonium; (Geraniaceae).

Petreaea; (Verbenaceae).
volubilis.

Plumbago; (Plumbaginaceae).

Poenia; (Ranunculaceae).
montana.

Primula; (Primulaceae).
acaulis rubra plena.

Pulsatilla; (Ranunculaceae).
bracteata. see Anemone pulsatilla.

Rosa; (Rosaceae.)
especially Manetti Roses.

Rhus; (Anacardiaceae).

Salix; (Salicaceae.)

Sambucus; (Oleaceae).
obulus.

Scopolymus; (Compositae).
grandiflorus.

Scorzonera; (Compositae).
hispanica.

Senecio; (Compositae).
pulcher.

Shepherdia; (Elaeagnaceae).
argentea.

Sophora; (Leguminosae).
alopocuroides.

Spathodia; (Bignoniaceae).
campanulata.

Statice; (Plumbaginaceae).
Holfordii, profusa.

Stokesia; (Compositae).
cyanea.

Symphytum; (Compositae). (Boraginaceae).

Tecoma; (Bignoniaceae).
capensis. radicans.

Terminalia; (Combretaceae).

Trichinium; (Amarantaceae) .
Manglesii.

Vicia; (Leguminosae).
faba.

Wigandia; (Hydrophyllaceae).

Xanthoceras; (Sapindaceae).
sorbifolia.

Xanthoxylon; (Rutaceae).

or

Xanthoxylum

Zauschneria; (Onagraceae).
californica.

(136)
in Contents. 137

CHAPTER IV.

MONOCOTYLEDONS. STEM CUTTINGS.

1. IMPORTANCE OF VEGETATIVE METHODS IN GENERAL.

The vegetative or asexual mode of propagation is perhaps of greater importance in the Monocotyledons than even in the Dicotyledons. It is important for the greater security and rapidity of result which it offers as compared to propagation by seed⁽¹⁾, but the method becomes of greater importance, since when seed is not obtainable, or produced with difficulty, it becomes the only satisfactory mode of increase.

Increase by seed is of course the only method when hybrids are wished, e.g. Orchids, Irises, &c., for the propagation of annuals such as Gramineae, &c.; and it is usually more convenient for water plants, e.g. Hydrocharidaceae, &c.

When however it is considered that the majority of Monocotyledonous plants represented in horticulture are either characterised by the possession of bulbs (Amaryllidaceae, Liliaceae, &c.) or creeping rhizomatous stems (Iridaceae, &c.) or else are upright tropical plants/

(1) see Introduction and Chapter I, p. 2 and p. 28.

plants cultivated chiefly for their foliage (Palms, Agaves, Bromeliads) and rarely flowering or seeding in cultivation, it will be seen at once that vegetative propagation is the characteristic mode of increase.

In the plants characterised by bulbs, corms, and fleshy rhizomes, the method of asexual propagation by the utilization of these modified vegetative organs is obvious, the more so since seed is rarely set. A definite relation exists between the formation of seed and that of reproductive vegetative organs⁽¹⁾. Particularly does this appear to be the case in Monocotyledons. Goebel⁽²⁾ says "Many Monocotyledons never set seed because their vegetative reproductive organs, for instance, bulbs and corms under ground, exercise a stronger influence upon the plastic materials than do the ovules after fertilization has taken place, e.g. Lilium candidum, Lachenalia, &c. In other plants also in nature, particularly Orchids, e.g. Microstylis ophioglossoides,⁽³⁾ also in Erythronium americanum⁽⁴⁾, Saffron Crocus⁽⁵⁾, and others the asexual method of propagation has completely taken/

(1) Intro. and chap. I. p2, p28.

(2) Goebel 1905.

(3) Nye 1904, and Pope 1906.

(4) Dandeno 1907.

(5) Henslow 1902.

taken the place of propagation by seed. In such bulbous plants, even if seed were obtainable, reproduction by the reserve organs would be preferable on account of the relative rapidity of development.

In the case of tropical ornamental plants, seeds must be imported (as in the Palms), or when obtainable, they are slow of growth (as in the Aroids). Thus the utilization of the thick spreading rhizomes, or the aerial stems (in the upright growing species) is usually the more practicable mode of increase.

While the method of cuttings of stems, or modifications of stems is largely used in Monocotyledons, the other methods such as grafting, layering, inarching, &c. are little employed. In all these methods, the part played by callus, or healing tissue, is important to effect a union, or to induce formation of new organs. The characteristic differences in structure between Monocotyledons and Dicotyledons, the absence of cambium in the stem, which is usually the impetus to callus formation, the slower growth of most Monocotyledons compared to Dicotyledons, make these other methods unsuitable (except for Dracaena⁽¹⁾). While scientifically/

(1) Dracaena species can be easily grafted.

scientifically possible, as in Dicotyledons, those methods which are most convenient are those which have become the most often employed.

2. CONSIDERATION of METHOD of STEM-CUTTINGS in PARTICULAR.

The stem in the Monocotyledons seems peculiarly suitable for reproduction, since it is usually present in a modified form as an underground portion.

It may be either a fleshy rhizome, as in Iris, many Dracaenas, &c., or a perennial rhizome of definite growth such as characterise Sedges, Grasses, Maram Grass, &c.

The stem may also be modified as -

A corn - as in the Orcus and Gladiolus,

in which the stem is the swollen portion: or

A bulb - as in Lily, Onion, &c.,

in which the stem is short, and the swollen portion is due to the arrangement of fleshy leaves overlapping one another.

In many tropical species an upright aerial stem is characteristic as in Cannas, Marantas, Dracaenas, &c. As in those plants characterised by a rhizome, the aerial stem is often soft instead of woody, and may/

may be used as cuttings for the increase of the plant. Whenever the modified stem is present however it is used in preference to the upright aerial stem, as producing quicker results.

The advantage of the method of stem-cuttings has already been indicated. It is quick and sure, and often the only available method of increase. In practice the conditions observed in the treatment of these stem-cuttings (both normal and modified) are very similar to those in the treatment of pieces of stem and root for cuttings in Dicotyledons (which see), the temperature, moisture, &c., being naturally adjusted to the nature of the plant.

3. THEORETICAL CONDITIONS.

Changes after insertion of Monocotyledonous stem-cutting.

In order to observe the change in regeneration taking place after the insertion of a Monocotyledonous stem-cutting, notes were made on the development of:

- a. An upright aerial stem-cutting with apex - (such as might be taken in a Dicotyledonous plant), inserted vertically, e.g. Asparagus madagascariensis.

b./

*

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rule in Monocotyledons.

After a short period, the bud at the lowest node generally develops, becoming swollen and the scale leaves (kataphylls) at its base are split. Usually the buds at two or three nodes above simultaneously develop. The development of these arrested buds is due to the disturbance of the whole vital activity brought about by severing from the parent plant, and by placing in conditions of heat and moisture⁽¹⁾. Usually the mode of development is the following:- Two protuberances appear at the base of the bud (fig.). These are the first two adventitious roots. They develop very rapidly, the one slightly in advance of the other. Usually they appear immediately under each kataphyll as in fig. but they may both appear under the same kataphyll (fig.). At the apex of bud, three growing points are to be distinguished even with the naked eye (fig.). The central one of these develops leaving the other two at its base. Thereafter development is in the ordinary way⁽²⁾. In its turn the bud at/

(1) Pfeffer 1903.

(2) Evans 1909.

at the base of the new shoot is developed and adventitious roots arise as before on the under side and a shoot on the upper. In this way a rhizome is produced exactly as in the development of the seedling⁽¹⁾ the main stem of the new plant being those produced from adventitious shoots and not the original stem from which the cutting was made. In quite a developed plant of *Asparagus* grown from a cutting, the new shoots developed from adventitious buds and the withered original stem or stems are usually distinctly discernible.

Two interesting points which clearly mark off a Monocotyledonous stem-cutting from a Dicotyledonous stem-cutting thus arise⁽²⁾ -

- a. Monocotyledonous cuttings as a general rule produce little or no callus. (see exceptions p.).
- b. The stem-cutting does not persist as the main stem of the plant, but the new stems are formed in succession from adventitious buds.
 1. To correlate these results distinguishing the Monocotyledonous cutting from that of a Dicotyledonous/

(1) Evans, 1904.

(2) op. Chapter I. §3. B. B. C.

Dicotyledonous one must first note the essential difference in the structure of the stem in the two groups. As is seen in the microscopical examination of callus tissue⁽¹⁾ the cambium is the most active factor in the formation although other parenchymatous tissue may take part. In a Monocotyledonous stem the vascular bundles are closed and there is no cambium. Moreover the fact that a thick-walled pericycle is usually present and undifferentiated cells occur only in patches in the pith, and to a small extent in the cortex, may also account for the absence of callus formation. *Dracaena* and *Yucca*, in which increase in thickness does take place owing to the formation of successive layers of cambium in the fundamental tissue from which the vascular bundles are developed, also form callus, though not invariably⁽²⁾ (fig.).

2. The new plant proceeds from an adventitious bud and the original stem-cutting dies away. Comparing also the figures (figs.) showing the macroscopic appearance of callus in a Dicotyledonous stem-cutting, the original stem there persists as the main stem of the new plant, and the development/

(1) Chapter I, par. §3. A.

(2) See also p. 151.

development of new buds gives rise in the ordinary way to secondary branches. In a typical Monocotyledonous stem-cutting, on the other hand, the main shoot is lateral, not terminal. If the terminal germination is compared with the behaviour of the cuttings in each group it will be noticed that the development of the lateral shoot in the case of the Monocotyledon and the persistence of the main shoot in the case of the Dicotyledon, is really a preservation of inherited tendencies! In the Monocotyledonous embryo the plumule is lateral while it is terminal in the Dicotyledon.

- b. It was found that the development of root and shoot in a Monocotyledonous stem modification used as a cutting was really identical with that in a true stem-cutting. Cuttings of the rhizome of *Dracaena* sp. were selected as examples for the examination, and pieces of their rhizome laid in a horizontal position on cocoanut fibre in stove temperature until development began. The adventitious buds developed as in the *Asparagus* series⁽¹⁾ obtaining nourishment from the rhizome, which does not/

(1) Op. p. 143. on.

not usually heal the cut surface by any callus tissue⁽¹⁾ but gradually withers away when the new shoot and adventitious roots are fully developed. While the development of the buds at the alternate nodes seems to be regular, the roots are produced irregularly, sometimes instead of an adventitious bud at the node, or opposite the bud at the same node, or not at the node at all, but indifferently at any part of the stem⁽²⁾. The regularity of bud development is shown in a figure of *Dracaena*, the irregularity of root production in a portion of stem of *Dieffenbachia*. *Dracaena* and other apical genera may be propagated also from apical stem-cuttings.

To be noticed in comparison with a Dicotyledonous cutting is the development of pre-existing shoot primordia to the exclusion of new shoot formation, even in the absence of the apex, (cp. Dicotyledonous shoot-cutting with severed apex). This phenomenon was observed even in pieces of aerial stems (cp. *Dracaena* sp.) the apex of which was severed, and inserted vertically in the propagating frame. No new shoots appeared from the/

(1) Op. P. ^{Chap. I.} § 3. A.
 (2) Op. P. Chap. I. § 3 B.

the apex, the new main axis being formed from a development of the buds already existent (cp. Acanthus montana). The lateral inherited tendency of shoot formation is thus shown in the non-development of new shoots.

The development of an apical stem-cutting thus really differs in no marked respect from the development of a cutting made of a rhizome or modified stem.

It seemed of interest however to compare the time of development of roots and shoots in an apical stem-cutting to that in a rhizome. For this purpose pieces of true stem and of rhizome were selected and placed under the same conditions of heat and moisture in the propagating frame and their comparative development noted -

a. in autumn or early winter.

b. in spring.

a. Notes on the comparative development of rhizome and stem in autumn.

For the purpose of comparison *Dracaena* sp. was taken. The rhizome in this species is characterised by a brilliant red colour, the true apical stem portion is white covered with the green leaves. The intermediate portion between rhizome and true stem is half/

half red half white, becoming more the one colour or the other as it approaches the rhizome or apical end.

1. Pieces of rhizome were cut up and laid horizontally in the propagating frame (80°), October 20th. November 16th the buds were well developed, but there were no roots at the time of examination, and no development of callus.
2. Pieces of intermediate portion were subjected to the same conditions. As figure shows, the buds towards the rhizome end were well developed, the buds at the stem end were poorly developed, but better than on the apical portion (cp. fig.).
3. True apical portions covered with the sheathing leaves were also cut up and placed in the fibre, October 20th. In all the pieces examined (October 20th)—a bud near the apex of the piece had developed, but very slightly compared to the buds on the rhizome pieces. At the root end a root was invariably about to appear, or had already appeared (fig.).

b. Notes on comparative development of rhizome and stem in spring.

The cuttings were examined on April 19th and examined May 15th.

1./

1. In the pieces of rhizome a bud was found to be well developed at the apical portion, while roots were formed in some cases at the base (see fig.).
2. In the intermediate portions the bud developed was found to be as large as that in the rhizome portion and a root or roots were found to be formed at the base. In one case a distinct development of callus covered the basal end.
3. The apical portions were inserted vertically. Buds were also found to be well developed. Roots were not found to be well developed. In one case where well developed roots appeared at the base from the cut surface and above (fig.) no development of shoots had taken place.

General Conclusions.

From a comparison of the two sets of experiments with true stem and rhizome cuttings, it is to be noticed that -

- a. in autumn the rhizome is the more active in the development of buds. This was to be expected, since the store of food material in the plant in the rhizome is greater than in the apical portion at a season when growth is inactive.
- b. in spring there is little difference between the size/

size of buds produced on rhizome and apical portion. In spring when growth recommences, the sap moves with greater vigour. The stream of plastic materials must therefore move from the rhizome up to the stem to supply the conditions of growth.

c. A callus formation may take place, though usually there is no formation of callus - as is typical of Monocotyledons. The callus formation is never in very great quantity, but is very marked, as it gives the cut end a rounded appearance. In the cases where no callus is formed decay of the softer tissues sets in, and the cut end presents the appearance of a bundle of fibry threads.

The conditions for the formation of callus and its non-formation in *Dracaena* have, however, not been investigated.

In all the experiments dealing with Monocotyledonous stems, cuttings were made of stems and stem modifications with buds or 'eyes' already existing. The resulting development is therefore not 'regeneration' in the limited sense⁽¹⁾ since roots are the only new organs produced. Monocotyledonous stem pieces without buds/

(1) see Introduction table. p. 18.

buds seem to possess, as far as experiments up to now have proved, little or no power of regeneration⁽¹⁾ and are therefore useless in practice. Theoretically, however, there is no reason why regeneration of budless pieces should not take place in the Monocotyledon as well as in the Dicotyledon if the conditions under which life could be maintained were known. As it is, a Monocotyledonous plant being usually characterised by a slower growth and a less vitality (see leaves) - it usually succumbs before reproduction takes place.

B. The microscopical examination of adventitious shoots in the regeneration of Monocotyledonous stem and rhizome-cuttings show that the origin of these organs is quite regular, and does not differ from their origin on the parent plant. The already existing buds, which were exogenous in origin develop. At the base of these buds adventitious roots are developed quite normally from the pericycle⁽²⁾. Sometimes adventitious roots are developed not only from the bud but from the old stem or rhizome (cp. Root-cuttings - Dicotyledons Chapter III.

This appears only to be the case in an old stem-cutting/

✓ (1) Kupfer, E. 1907.
 ✓ (2) see Scott, - 1902.

cuttings, or in a rhizome placed in a horizontal position, not in an apical or vertical cutting as in *Asparagus* and *Bamboo* (see figs.).

The formation of buds exogenetically at the vegetative point is the normal procedure⁽¹⁾. After their formation, the buds exist as latent organs until conditions such as severing from the parent plant and placing in conditions of heat and moisture causes them to develop. The roots on the other hand are not pre-existing organs. They are endogenetic in origin like lateral roots⁽²⁾ but may appear at any part of the stem (see figs.).

Notes on culture and propagation, general and particular, have been collected in *Monocotyledonous Orders* with references and bibliography. Special notes on the propagation of the following species are given (see Part II, B. Notes on the Propagation of Monocotyledons):-

Amaryllis and *Orinum*.
Bamboo and *Sugar Cane*.
Curculigo.
Cyperus alternifolius.
Eichornea.
Limnolobos hogothasis.
Xiphidium albicum.
Malaxis monophyllos, *M. paludosa*.
Restio subverticillatus.
Orchis.
 and others.

(1) Goebel 1905.

(2) Scott, 1902.

(154)
in Contents. 135

CHAPTER V.

MONOCOTYLEDONS. LEAF-CUTTINGS.
ROOT-CUTTINGS.

LEAF-CUTTINGS.

1. POSSIBILITY OF MONOCOTYLEDONOUS LEAVES TO REGENERATE.

Importance of method of increase in practice.

A. Attached leaves.

In Monocotyledons as in Dicotyledons nature has formed a provision for reproduction in leaves by the production of leaf-buds. These leaf-buds are found in such plants as Cuculigo orchidiosa, Malaxis paludosa, Aetherurus ternatus and others⁽¹⁾.

The Monocotyledonous leaf however as an organ, unless modified for the storage of food, shows little aptitude for regeneration. This is characteristic of the ^{group.} family - for vegetative reproduction takes place in the Monocotyledons rather by the modification and development of already existing organs than the formation of new organs (cp. also stem). (This is especially true of shoots, since adventitious roots are easily formed.)

That the Monocotyledonous leaf has a weak vitality/

(1) see Beijerinck, 1886.

vitality which will inhibit its powers of regeneration, is shown by its relation to leaf-fall. The leaf is inactive and simply rots away. The Dicotyledonous leaf-fall, on the other hand, is provided for by the preparation of a special absciss layer. Moreover, whenever a Dicotyledonous leaf has been wounded, without severing from the plant, the vascular tissue so injured has the power of regeneration. Freundlich in his paper on the power of regeneration in leaves, tried experiments with Monocotyledonous plants such as Potamogeton crispus, Hydrocharis morsus, Tradescantia fluminensis, T. Rheo, and T. virginica, Avena sativa, and Zea Mays. He made cuts across veins of their leaves, but no effort, except the slightest on the part of Zea Mays by the formation of a few tracheids, was made to regenerate the tissue injured by the wound. As he had obtained positive results with the leaves of Dicotyledons ⁽¹⁾ (~~which cp. p.~~), he thought that the venation of the leaves might have some relation to their power of regeneration. He therefore took plants with a leaf similar in appearance to that of Dicotyledons for his experiments, e.g. Philodendron erubescens, Monstera pertusa, Pinellia tubifera, Dioscorea villosa, and Arum maculatum. The leaves of the/

(1) see Chap. II 62. p. 89.

the three first mentioned species are like a Monocotyledon in that few of the nerves end blindly - a meshwork of interlacing veins are characteristic. Dioscorea is more like a Dicotyledonous leaf, both in appearance and in the fact that some of the veins end blindly; but most similar to a Dicotyledonous leaf is Arum maculatum which possesses a thick midrib and many free ends to the nerves. These leaves were treated in the same way, as were the others, but no success followed. Since however positive regeneration results were obtained on leaves of Plantago, a Dicotyledonous plant with Monocotyledonous venation, the author concluded that the venation of the leaf was not a factor in regeneration, but that the character or nature of the leaf was. (Sp. stem-cuttings, Chapter I.)

B. Detached leaves.

a. ordinary foliage leaves.

When leaves become detached, naturally or artificially, the conditions of life become changed, and the stimulus of the wound may be sufficient to call forth the power of regeneration under the new conditions. Ordinary Monocotyledonous foliage leaves however possess little or no reserve of food material, a low vitality, and little or no power of healing tissue. All these have been shown to be conditions inhibiting regeneration (see Chapter I. Introduction).

The/

The phenomenon of regeneration in Monocotyledonous foliage leaves is therefore rarely found in nature, and can with difficulty be induced in practice.

To demonstrate the possibility of regeneration in Monocotyledonous foliage leaves, experiments were tried with leaves of Dracaena, Dioscorea, and others. The leaves were detached and inserted under the same conditions of heat and moisture as the leaves of the Dicotyledons, e.g. Begonia, &c. The leaves persisted for some weeks without withering but no roots were formed, and finally the leaves faded.

Stingl⁽¹⁾ tried leaf-cuttings of plants in the following Monocotyledonous orders:- Alismaceae, Amaryllidaceae, Dioscorideae, Haemadoraceae, Hydrocharidaceae, Gramineae, Iridaceae, Liliaceae, Orchidaceae, and Pontederiaceae. With the exception of the Liliaceae and the Haemadoreaceae all the leaves that were inserted as cuttings withered without rooting, some very quickly, after a few days only as in Galanthus nivalis (Amaryllidaceae) and Zea Mays. (Gramineae), others remained fresh for a longer period.

He had the greatest success however with foliage leaves of Liliaceae, e.g. Hyacinthus orientalis, &c.

Roots/

^{Stingl}
(1) 1908.

Roots were obtained after twelve days and after nine weeks a number of little bulbs appeared on the morphologically upper side at the base of the leaf, in the immediate neighbourhood of the cut surface over a nerve (cp. Chapter II.) His experiments with Hyacinthus orientalis, with H. candidans and Muscari racemosum, showed that splitting the leaf reduced its power of regeneration, and also that old leaves or small parts of leaves produced roots only, withering before bulbs were able to be reproduced.

So far therefore as experiments have gone up to the present, the possibility of leaves to regenerate in the Monocotyledons is very limited. This is to be expected from the greater difficulties to be contended with. The results of Stingl and others working in the same direction are important however because they show that monocotyledonous leaves do possess the power of regeneration, and the fact that up to the present monocotyledonous foliage leaves have not been found to regenerate is due to an ignorance of those conditions that would artificially induce regeneration. The method is interesting theoretically, and offers field experiment, but under the present conditions is not practicable since it is slow; also a ready means of vegetative/

vegetative increase is usually at hand, by division of the plant, or by cuttings of the rhizomatous stem.

It is a well-known fact in horticulture, however, that the leaves of the Bowstring Hemp (Sansevieria cylindrica) treated as cuttings will easily give new plants. Stingl⁽¹⁾ showed that leaves of this and also of S. guinensis made copious roots and shoots.

Mention must be made too of the unique case of Zamioculcas Loddigesii. Like Gonolobus, this plant is an exceptional Aroid, possessing deciduous articulate leaflets - ^T These leaflets are thick in texture, and fall away separately from the rachis. Professor Engler (1) mentions that Mr. Hild of Kiel University first observed the development of these fallen leaflets. At the end of the petiole little swellings appeared, developing into bulbets. Put into the ground, these bulbets formed two buds and rootlets around and beneath them. The buds first develop some scaly leaves which are succeeded by a pinnate leaf bearing one pair of leaflets. Soon after this mode of reproduction was made use of at Kew, and is the reason for the rapid distribution of the plant.(2)

(1) (X) Engler, 1880.

(2) (2) Stingl 1908.

(3) G.C. vol. XIV. 28.7.80. and 18.8.80.

The leaflet in question is not fleshy but rather shiny and leathery looking like a laurel leaf. Regeneration in this plant is all the more unique since it contains no perceptible store of food material (cp. Dicotyledonous leaves).

b. modified leaves: detached.

The power of regeneration in Monocotyledonous leaves is confined mainly to modified leaves acting as reserve organs. These leaves are usually the scale leaves of a bulb, are soft and fleshy, and contain reserve food material, conditions which are favourable to maintaining the life of the leaf while the process of reproduction is being carried on. In practice the utilization of modified scale leaves is a common mode of increase especially among the Liliaceae. The single scale leaf of the lily reproduces as easily as does the whole reproductive vegetative organ the bulb, and may be practised for nearly every species, e.g. L. myriasefolium, L. primulinum, L. tigrinum, &c. The method of increase by scale leaves has long been practised by Dutch bulb growers with Hyacinthus. It is said however to possess one disadvantage, and that is that degeneration of the whole bulb formed occurs if the method is continued successively year after year. The advantage of economy on/

on the other hand is obvious.

2. CHANGES IN REGENERATION.

The changes that occur after the insertion of a detached Monocotyledonous leaf bear a greater similarity to the normal development of the plant than in the Dicotyledons (cp. also Monocotyledonous stem-cutting).

a. In the ordinary foliage leaf when regeneration does occur, in bulbous plants, the development of the bulb takes place in the same way as that in a modified leaf (see 6). In the exceptional case of Zamioculcas Loddigesii, development is different. An increasing knob of callus is formed at the basal end of the leaf, from which roots and shoots are produced exactly as in the Dicotyledons (see figures).

b. The development of roots and shoots and the formation of the new bulb on a modified scale leaf used as a cutting proceeds in very much the same way as the normal development of the bulb, roots and shoots from the seed. It will be remembered that in a lily, the development from the seed was shortly as follows:- The cotyledon was developed and was of the nature of a foliar leaf; its base became bulbous: the upper foliage portion died off: from a slit in the base the first leaf appeared/

appeared: its base too became bulbous: a bud in its axil formed the next foliage leaf: in the axil of the second leaf the bud of the third leaf appeared, and so on.

The primary root that was first formed ¹early dies, its place being taken by adventitious roots developed at the base of the bulb formed by the fleshy bases of the overlapping leaves (see Duchartre, Scott, Evans on development). The changes in the regeneration of a scale leaf closely follow this development. Scales of Lilium primulinum were taken as examples.

The development started from the edge of the old leaf with the exogenous formation of the first leaf (instead of its formation from the base of the cotyledon, the old leaf here acts as the part of the cotyledon). The leaf is bulbous in character; in its axil another leaf is formed which in its turn bears an axillary leaf and so on.

Adventitious roots only appear at the base of the bulb so formed. Thus the appearance (when detached from the old leaf) is exactly that of a seedling after the cotyledon and primary root have died off. It is noticeable, too, that in a leaf-cutting, the adventitious roots are contractile. The contraction of the inner cortex/

cortex causes the wrinkles on the thick upper portion of the root (see ⁽¹⁾ Scott). This character is to provide for the drawing down of the bulb into the ground.

The microscopical sections show no features other than those described by authors in the normal development ⁽²⁾ (~~see Duchartre, Scott, Evans, &c.~~)

3. LIST OF MONOCOTYLEDONOUS PLANTS USUALLY PROPAGATED FROM THEIR LEAVES. These are mainly Liliaceae.

Bomarea volubilis (Liliaceae).

Fritillaria (Liliaceae).

Casteria (Liliaceae).

Haworthia (Liliaceae).

Hippeastrum (Liliaceae).

Hyacinthus (Liliaceae).

Lilium (Liliaceae).

Ornithogalum (Liliaceae).

See details of propagation under each in orders in Part II. (cp. Index. Chapter IV), GENERAL NOTES ON PROPAGATION OF MONOCOTYLEDONOUS ORDERS.

(1) Scott, 1902.

(2) Duchartre 1875. Evans 1909, Scott 1902.

ROOT-CUTTINGS.

4. Since Beijerinck wrote his paper on "Root-shoots and adventitious Roots", many instances have been recorded of Monocotyledons being able to be reproduced, either naturally or artificially from their roots.

In nature the phenomenon of shoots being produced by the roots is not uncommon, and serves as a mode of increase. The Orchids, many of which possess fleshy roots, seem particularly fitted for reproduction in this way. Among ordinary Orchids, as Hall has shown, seedlings are difficult to find, possibly because the plants have adapted themselves for vegetative means of increase⁽¹⁾. Arethusa, Jalopogon, Microstylis produce bulbs, a modification of the stem, but in others the roots are specialized for increase, e.g. Habenaria: a system of long branching roots occur as in Pogonia ophioglossoides, and P. verticillata, bearing at intervals adventitious buds. Very marked is the vegetative reproduction in Spiranthes cernua. Root-shoots are also to be found in Malaxis paludosa (a plant that also increases itself vegetatively by the formation of leaf-buds⁽²⁾), Cephalanthera rubra and other species. Adventitious shoots have also been noted/

(1) cp. Introduction. p. 2.
(2) see Leaf-cuttings. p. 155.

noted to arise on the aerial roots of Phalaenopsis Schilleriana⁽¹⁾, also on roots of Erythronium americanum. Goebel too has noted and investigated shoots arising from roots in Anthurium longifolium.

In practice the method of increasing Monocotyledons from their roots is rare. From the very nature of the roots in most plants of this family it would not be expected that propagation could be effected by means of these organs: the primary root is early lost and replaced by adventitious roots⁽²⁾ which are usually thin and fibrous, in contrast to the typical tap root of the Dicotyledons.

In gardening handbooks and in notes on propagation, the word "root" is often used where the rhizome or underground stem is implied. The rhizome is a true stem as its structure indicates and like the stem it bears true latent buds which may give rise to new shoots if the occasion requires. The mode of propagation from these rhizomes has already been discussed in the propagation of Monocotyledons from cuttings of stems and stem modifications⁽³⁾.

But all true roots in Monocotyledons are not necessarily/

(1) see reference: in Beijerinck 1886.

(2) see Duchartre, Scott, & C.

(3) see Stem-cuttings. Chap. IV.

necessarily thin and fibrous. Many like the Orchids possess thick fleshy roots. The plants that produce buds on their roots naturally may be propagated from cuttings made of their roots. Such has been found to be the case with Neottia, Spiranthes vars. &c. Pope⁽¹⁾ recommends the propagation of Phalaenopsis Stuartiana from root-cuttings as a quicker method of obtaining a plant than from seed. Root-cuttings of Phalaenopsis Schilleriana do not develop so quickly.

5. CALLUS, ROOT AND SHOOT FORMATION.

A. Callus Formation. - As in Stem-cuttings, the phenomenon of callus formation in monocotyledonous root-cuttings seems to be non-existent.

B. Root Formation. - Roots are formed adventitiously after the formation of the new shoots, in the usual way (see development of roots in leaves).

C. Shoot Formation. - The new shoots that are formed on roots may be ordinary foliar shoots (Anthurium, Pogonium, &c.), or modified to form bulbs, &c. (Scilla, &c.)

Shoot formation may take place on a root-cutting in two ways -

- 1./

(1) Pope. 1906.

1. They may arise as lateral buds. In this case they usually take the place of the roots.

2. They may arise as a modification of the root-tip itself.

Shoot formation, ^{on roots} which ^{rarely} never takes place in the ordinary way in the Dicotyledons (see Shoot formation), is not uncommon in the Monocotyledons. The two best known examples are Neottia nidus-avis and Anthurium longifolium. While Irmisch has shown that the shoots of the former are developed underground and rarely attain to a flowering stage, Goebel has noted that in Anthurium the shoots on the roots are produced near the surface and form strong branched plants. An anatomical examination of the plant in question showed that the tip of the root passed directly into that of the stem, the collateral structure of the stem being formed from a combination of the various parts of the root vascular system.

1. NATURAL AND ARTIFICIAL METHODS OF REPRODUCTION IN CONIFERS

A. Natural Methods.

The conifers are naturally slow growing trees. They will therefore reproduce themselves slowly. The vegetative means of increase in nature is very limited. Very occasionally, but in enough instances to shew that the power of regeneration does exist, shoots are found springing from old stools (see stem cutting), or shoot buds are produced on roots (root cuttings). The fact is however of little or no use in arboriculture.

If subjected to injury, the various organs shew a greater power of regeneration (see under stem and root). The natural mode of increase among the conifers is however by seed, and it is to this method of reproduction that natural woods and forests of conifers owe their origin and development. (1)

2. B. Artificial Methods

As in other classes of plants, both sexual and asexual methods of propagation are employed in practice amongst the Conifers. Since artificial methods are deduced from natural methods, the sexual has become the most important mode of increase. In some /

(1) See Forestry Text Books, ^{Eq.} Nisbet, Webster, Groom, & Co. 1894. 1896 - 1907.

some cases, as in Abies, Pinus, Picea (see notes under each) it is the only satisfactory one. In the case of new and rare varieties, or when seed cannot be easily procured, or is very slow in germinating, vegetative propagation by means of cuttings, layers, and grafting is resorted to.

- a. Layering is a method of vegetative propagation rarely carried out in Conifers since erect plants are not to be obtained by this means. Picea may be increased by layers, and the method has been employed for Juniper varieties.
- b. Grafting is also an unsatisfactory method, as the tendency is to produce a lateral rather than a terminal shoot. Unless carefully performed, it is not a method usually recommended. The operation is performed early in Spring or about the middle of August. For a detailed selection of stocks see (1) and (2). It may be mentioned that the common varieties are usually used as the stock for the particular variety, thus Juniperus /

√(1) Fuller 1901.
 √(2) A.D. Webster 1896

Juniperus communis for the Junipers, Cupressus Lawsoniana for the Cypresses, Tsuga canadensis for the Hemlock Firs &c.

- c. Cuttings. Although the value of the method of increase by means of cuttings is not so great as that by seed, still it is the most satisfactory of the vegetative methods, and the common mode of propagation for common and dwarf varieties, e.g. Thuja, Juniperus Cupressus &c. (see notes under each). The possibility of stem cuttings to strike in Conifers is not so limited as it is generally supposed to be (see under stem cuttings).

2. PRACTICAL CONSIDERATIONS

Stem cuttings of Conifers should be chosen from the exposed branches as these are found to strike more easily than shoots from the inner and shaded parts, which are apt to damp off, as are also succulent portions of leading shoots and branch tips. The length of the cuttings are recommended to be from 3 to 6 inches of the current year's growth, preferably with a portion of still riper wood or a heel attached. After cleaning the base of the cuttings of leaves, unless these are scalelike, with a sharp knife, they are inserted into the ground or pans in prepared soil of nearly equal proportions of sharp sand /

sand, peat and loam. Pure sand may also be used. It is preferred by many: it was in this soil that the specimens in the illustrations were grown. The cuttings should be pressed firmly in the sand, over the surface of which a little silver sand is sprinkled, and then moistened lightly. If inserted early that callus may form before winter, and if in the spring, while the roots are forming, the cuttings are shielded from the direct rays of the sun, they will give successful results. (1) Cuttings are made usually from terminal shoots. In dwarf varieties or conifers with no marked laterality of growth, lateral shoots may be used equally as well. In other cases, the terminal shoot is the only cutting that will give a successful result (see under conditions).

3. THEORETICAL CONSIDERATIONS. CHANGES FOLLOWING THE INSERTION OF A CONIFER CUTTING.

A. Callus Formation

In nature the power of Conifers to heal wounds caused by injuring or severing of their organs, is expressed in a different way to that of Dicotyledonous plants. If a branch of a Conifer for example be cut off, the wound may be covered to some extent by the characteristic lip like encroaching form of callus (see fig.) but mainly the wound is covered with a large excretion of resin. In some existing /

(1) See A.D. Webster

existing Conifers resin canals are present as a normal feature in the woody axis of the cone, as in Abies magnifica, Cedrus Libani, as well as a result of injury to the wood. But in others (e.g. Abies balsamea, Lequoia sempervirens, Cedrus atlantica) it is interesting to note (1) as Jeffrey has pointed out the resin canals do not appear even in the reproductive axis, except as the result of injury. The Sequoia gigantea, resin canals though occurring only as the result of injury in the older wood, are found normally in the first annual ring of branches which bear the cones, male and female, as well as in the woody axis of the female cone.

Thus resin formation to a large extent takes the place of, and obscures the formation of callus in nature in the cone-bearing plants. (2) Resin formation is also a hindrance to propagation. (3)

Gallus is formed after a period varying from a few weeks to some months, differing somewhat according to the lateness of the season in which the cuttings are inserted and persists during the winter. Fig. 1. shows a specimen of Sequoia sempervirens inserted in August 1909 and examined October 12th 1910. The basal end of the knob /

(1) cp. Anatomy of Conifers. see also Hartig 1894, Soraue 1909.

Jeffrey 1906.

(3) Bayley Balfour 1912, 1913.

knob cutting is covered with a knob of callus tissue, but no roots had appeared.

The formation of callus may be correlated with the stem structure of a Conifer. As the presence of cambium and consequent secondary growth is very similar to that of a dicot. stem, it would be expected that the callus and root formation would also be very similar. This is found to be the case. Callus tissue is formed from the cambium, cortex and pith and the external appearance is very similar to that of a Dicot. The callus formed in a conifer stem cutting soon, however, becomes hard woody and dark in colour, owing partly to the simultaneous formation of resin and also a protective periderm, and passes into the resting stage ⁽¹⁾ for the winter. The illustrations (figs. 1-4) show examples of callus formation in Conifers. In his investigations of callus formation, Stoll ⁽²⁾ observed Ce phalotaxus Fortunei Wellingtonia gigantea and Thuja orientalis and found no variation from the Dicot. type.

A microscopical section also shows no marked differences from that of a Dicot. cutting. Similar centres of wood and bast are formed in the loose tissue of callus cells, which is formed first from the cambium and then from the cortex until a large protruding mass is formed. There is usually little callus formation from the /

(1) Reehinger 1894.
 (2) Stoll 1874.

the central portion of the stem as pith and meristematic cells are in small amount.

B. Root Formation

Normally the power in conifers to produce adventitious roots is limited. When, however, a shoot is severed, roots are formed with greater or less difficulty according to conditions (see after). In the cuttings under observation, the roots appeared in spring, or after a period after insertion varying from some weeks to six months. The origin of these roots is invariably from the callus knob developed at the base of the cuttings and is normally endogenetic.

Root formation takes place easily on the dwarf varieties of Conifers, such as Juniperus Thuja &c. but with exceedingly great difficulty on other such, as Abies, Pinus Varieties. Miss Kupfer obtained a single root on a seedling used as a cutting of Pinus Laricio, and in apical cuttings of a three year old plant of the same pine, a single root was again obtained. The result is interesting, as it shews a tendency in this pine to form only one root from the callus produced as a result of injury. (1) Roots have not been recorded to have been formed in P. sylvestris cuttings till recently, however, when /

(1) Kupfer. Regeneration

when roots were obtained in the R.B.C. Edinburgh on a stem cutting .

O. Shoot Formation

In nature, the occurrences of stool, shoots is rarely found in Conifers. It is said to occur occasionally in young specimens of the Larch, and in three needled species of Pinus. Usually, however, as in Monocots shoot formation occurs as the result of development of preexisting primordia, rather than the formation of new organs. In an apical stem cutting of a Conifer, new shoots are formed from terminal and lateral buds in the ordinary manner of development, sometimes before roots are formed. (see fig. of Sequoia). Cuttings deprived of their stem apex, have not been examined for the development of new shoots primordia. It would seem probable that in such stem-cuttings, development and subsequent modification of the lateral bud would take place, as it does on the entire plant, instead of the formation of a new terminal bud .

Boisrivan in his study of replacement shoots has confirmed this,

In /

In horticulture, the development of the terminal bud in Conifers is naturally always aimed at in order to obtain symmetrical plants. It is for this reason that only apical cuttings are taken in the majority of cases. If the apices were removed, and cuttings made of pieces of the stem the lateral tendency (Laterality) which is always strong in vegetative propagation in the Conifers, would be intensified. For this reason seedling plants are preferable on the whole. In some genera, where propagation is effected by cuttings, the development of the terminal bud is forced by continual care and pruning. (1)

As in the Dicotyledon and contrasting with the Monocotyledon it is to be noticed that it is the original cutting that persists as the main stem, even when lateral branches are formed, the roots being produced from the base of the original cutting, not from the base of the new bud. (2) This fact can again be accounted for by the persistence of inherent tendencies, as in the Conifer seedling the plumule is terminal the cotyledons not less and usually more than two.

4. INDEX /

(1) Vochting 1884, 1904. Goebel 1907. Beijerinck 1886. on L Lateritat.
 (2) cp. Dicot. and Monocot. Stem cuttings chaps. I and IV.

4. LIST OF CONIFERS - CONSIDERED IN Part II. C.
(General Notes on the Culture of Propagation of
Conifers - p.)

- | | |
|---------------|--------------|
| Abies | Keteleeria |
| Actinostrobus | Larix |
| Agathis | Libocedrus |
| Araucaria | Phyllocladus |
| Athrotaxis | Pinus |
| Biota | Podocarpus |
| Callitris | Prumnopitys |
| Cedrus | Pseudolarix |
| Cephalotaxus | Pseudotsuga |
| Chamaecyparis | Retinospora |
| Cryptomeria | Saxegothia |
| Cunninghamia | Sciadopitys |
| Cupressus | Sequoia |
| Dacrydium | Taxodium |
| Fitzroya | Taxus |
| Ginkgo | Thuja |
| Gyptostrobus | Thuyopsis |
| Juniperus | |

LEAF CUTTINGS

The reduction of the leaf surface, and the structure of the leaf itself clearly indicates the xerophytic habit of the Coniferae. It goes without saying, therefore, that these leaves generally small in size (except some species e.g. *Podocarpus neriifolia* &c) and hard in texture, are unsuited for the propagation of the plant. (see under Dicot. leaves Chap. 2). It would be expected that, if separated from the plant, they would soon wither, under ordinary conditions. To ascertain the capability of regeneration some experiments might be carried out with the Conifer leaves. For this purpose Taxus Podocarpus &c might be chosen on account of the comparatively large size of their leaves. No investigation has yet taken place.

ROOT CUTTINGS

Bejerinisk⁽¹⁾ states in his study on root buds and adventitious shoots that normally no root buds are found on the Conifers. Cunninghamia sinensis seems however an exception. When, however, roots of Arancaria Cunninghamia and Ginkgo biloba ^{were severed + treated as} cuttings, root shoots appear. Few other genera have been investigated.

For /

(1) Bejerinisk 1886.

For six years M. Newmann tried to grow Araucaria from root cuttings without success, but eventually obtained roots and shoots on Araucaria Cunninghamia. He attributed his failure to the fact that the cuttings were closely covered with glass and that the consequent humidity of the atmosphere had caused them to perish. His opinion, ~~was~~ that all Conifers may be propagated from root cuttings is not however generally entertained; Even if this were the case (and the inability to regenerate has been shown to be dependent on conditions at present unknown) (see Introduction and Chap. 1.) the method is neither practicable nor economical. For from the experience of Mr L. Stewart (1) who has obtained plants from root cuttings of Podocarpus and Pinus sylvestris, only weak or knarled specimens are produced and these only after a protracted period of six months or more. The method, if not of horticultural value, is nevertheless interesting from the botanical point of view and is worthy of examination.

(1). Prop. R. B. G. Edinburgh.

1.

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