VEGETATIVE PROPAGATION*

Introduction.—The application of entirely vegetative methods of propagation has in recent years become of great importance in temperate orchard practice, and the researches of horticultural experimental stations in Europe and America have demonstrated the great advantages, both from a scientific and a commercial standpoint which have accrued from planting standardised material obtained by vegetative means. There seems every reason to believe that similar advantages might be anticipated from the application, in a wider field, of vegetative propagation to several tropical crops, but the realisation of this will depend primarily on the discovery of methods of vegetative propagation suitable to commercial application, and secondly in the interest shown by the planters themselves in the use of vegetatively raised stock. This article has been prepared to summarise and to afford a discussion of the most important work which has been done in recent years, as most of the literature may be unavailable to the tropical grower.

Seedling and Vegetative Propagation.—When a plant is propagated from seed, it stands in a different relation to the parent plant than do the other products of its growth, such as the leaves, twigs, roots, and buds. In nearly all plants the "germ" of the seed is a sexually formed structure, produced as the result of a fusion between two sexual cells known as gametes, one of which may have been contributed by another plant. This process involves a re-combination of inheritance factors and produces a new individual with characters usually differing from those of either parent. Even if a plant is self-pollinated, the seedling would not, in general, grow into a plant exactly duplicating the parent in all its characters. Actually, if a crop were habitually self-pollinated for several generations, the progeny would tend to come true to seed, but this systematic breeding rarely, if ever, occurs in orchard crops. Moreover, such pure lines would, with these crops, take many years to breed experimentally owing to the long generation periods.

This production of variation in the offspring is characteristic of sexual reproduction, and it is believed by some botanists to play an important part in the production of new forms in nature. The hybridisation made possible by sexual reproduction is of great importance to the horticulturist in the production of new types. Some new varieties arise as "bud sports" without any sexual process occurring, but the majority are the result of hybridisation. It is impracticable in slow-breeding plants such as most tree crops, to continue breeding from the initial hybrid until the desired new qualities are fixed so that they come true to seed. Instead, a method of multiplying the first hybrid unchanged must be used, and this may be achieved by one of the methods of vegetative propagation. Both vegetative propagation and seedling reproduction are processes in which either juvenile parts, or in vegetative propagation, parts capable of rejuvenation, are removed from a plant and used to establish another plant. The fundamental difference is that in seedling reproduction the new plant originates in a single fertilised cell, whereas in vegetative propagation the new plant develops from multicellular tissues in which no fertilisations take place. The vegetative propagation of a new plant takes place by the "germination" of almost any

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part of a plant except the seed, by placing the part selected in a suitable environment, either before or after severing it from the plant. There are several fundamental methods used, but not all are suitable for any particular type of plant. The practical details of technique differ considerably for different subjects, according to their capacities for regeneration, and each new variety tried may require its own special treatment.

A practical classification of methods may be made into:

(1) Rooting processes, and

(2) Grafting processes.

The first group of methods aims at the production of new roots and shoots upon plant parts such as stems, roots, or even leaves, the new root and shoot system being eventually established as a new plant. This group may be further sub-divided according to whether the new roots are formed while the organ is still retained on the parent plant, or after it has been removed as a cutting.

Thus there are:

(1) Layering, stooling and allied processes such as "bagging" or "marcotting".

(2) Cuttings, which may be either hardwood or softwood stem cuttings, root cuttings or leaf cuttings.

The second main group consists of the method of grafting, budding, and approach grafting, sometimes collected under the general term "graftage". There are many modifications of practical methods, but the basic principle is always that of inducing the tissues of two separate plants to grow together, in order to form one composite plant. In grafting and budding a part of one plant, either a small piece of stem or a piece of bark including a bud, is removed and placed in contact with the cambial tissue of the other plant, so that the tissues grow together. In approach grafting two plants are made to grow together while each is still on its own roots, by removing the bark from portions of the stems to expose the cambium, and binding the two stems together with the bared surfaces in contact. It is not necessary to enter into details of the different methods of vegetative propagation, as they are described in horticultural books on the subject. Unfortunately, the literature dealing with vegetative propagation of tropical crop plants is very scanty and is confined almost entirely to budding and grafting methods. The importance of the root stock on the performance of a fruit tree seems to have received practically no attention from tropical workers, and the problems of propagation of tropical root-stocks remain practically a virgin field.

Advantages: (*a*) *Uniformity*.—Vegetative propagation essentially extends a genetic type unchanged, no sexual process intervening. Thus, no matter how hybrid the individual selected for propagation may be, the vegetative offspring preserves its identical genetic constitution. Such a family of plants, all of one genetic type, is called a clone (Gr. klonos, a twig). Hence, in a clonal plantation, the variability between the plants, due to differences in genetic constitution, is eliminated and the only variability is that due to the environment. In some crops, notably cacao, it is known that the variability in a normal seedling population is very high owing to the very hybrid constitution of the plants, and a considerably smaller variability is to be expected in a clonal population. On the other hand, some crops which possess a purer genetic make-up, show a comparatively small variability in a seedling population, but such crops are rare among tropical perennials.

In practice, two aspects of variability are to be considered, firstly, variability in *type of crop*, and secondly, variability in *yield of crop*. The fixation of fruit type by some form of vegetative propagation is essential in temperate fruit crops such as apples and pears, in which seedlings produce fruit of very poor quality. The variety to be propagated is usually budded or grafted on to a stock. In tropical fruit crops, similar methods are sometimes used, but the practice is not uinversal. Certain types of citrus are propagated by budding, and "improved" mango and avocado pear varieties also are vegetatively propagated. In cacao, which does not produce a directly edible fruit, the necessity of a uniform fruit type is less obvious but equally certain. The propagation of a uniform good bean type would be of great value, as cacao, after picking, undergoes a series of technical processes in which uniformity of bean in size, chemical composition, texture, thickness of shell, etc., is highly desirable. It cannot be too much stressed, that in cacao, uniformity may represent an important factor of quality.

The reduction of variability in yield is probably quite as important, as reliable scientific work is greatly complicated by a crop showing high variability. The lay-out of a manurial trial, for example, is made very much similar and cheaper if the material to be worked with is as uniform as possible. This can only be realised by having clonal material throughout. The advantages to the commercial grower are no less. The poor bearing trees in a plantation may be regarded as being merely a load upon the more productive trees; their presence increase production costs per acre, and renders intensive cultivation impossible. This is particularly the case with cacao, where a large proportion of the trees consists of poor, or very poor, bearers.

The root-stock upon which a variety is budded often has a marked influence upon the yielding capacity of the scion. In fact the variation of yield when seedling stocks are employed may actually be as great as if the trees were entirely seedlings. If uniform yielding material is required, the variety must either be established on its own roots by rooting cuttings or stool shoots, or else it must be budded on to a clonal root-stock. Only if the root system is clonal can a reasonable uniformity of yield be obtained.

(*b*) *Extension of Environmental Range of a Crop.*—The propagation of uniform types may enable a crop to be grown under conditions of soil and climate which would be unsuitable for the growth of the majority of the original mixed seedling population. Thus, a particular plant may be noticeable by its greater resistance to drought, cold, or disease than its neighbours and will on propagation yield a clone, incorporating this property, and capable of successful cultivation in a situation where the original types would fail. When top-worked varieties are considered, there is additional control over environment in the possibility of selecting a suitable clonal root-stock. Hanson dealing with apple growing in the prairie north-west of United States of America and Canada, where the winter conditions are very trying for fruit trees gives two factors for success with orchard fruits:

(i) A hardy variety.
(ii) A hardy stock for budding and grafting.

The ordinary commercial seedling apple stocks were found to be subject to root killing. Seedling stocks of the Siberian Crab, "Pyrus baccata" were found to be much more resistant and certain "Pyrus baccata" seedling hybrids were very satisfactory. However, Hansen emphasises the advantages of being able to obtain a clonal root-stock of a hardy type: "It would be a great advance over the present method of growing seedlings, to root these vigorous "Pyrus baccata" hybrids from cuttings. The ideal future apple stock may be some f[1] hybrid derived in part from "Pyrus baccata" grown from cuttings to ensure uniformity".

Tropical crops do not have to contend with winter cold, but the similar problem of drought resistance occurs. A series of clonal root-stocks in cacao, for example, worked with scion clones, would yield valuable information on the question of the degree of drought resistance of different cacaos, and its correlation with cropping and premature wilting of crop.

Sands gives a good example of the increase of the environmental range of a tropical crop by vegetative propagation in the cultivation of cinchona in Java: "The 'Ledgeriana' types of cinchona can only be successfully grown on their own roots on virgin land, of which there is a very limited area now available. Practically all the fields when replanted are put under selected 'Ledgeriana' strains grafted on *Cinchona succirubra*, which has a much stronger root system than 'Ledgeriana' and grows well over a wider range of territory and poorer soils".

(*c*) *Increase of Vigour of Weakly Types by Working on to Suitable Clonal Root-stocks.*—In a budded grafted plant, that is a worked plant, the root-stock frequently has a marked effect on the performance of the scion. The growth of any plant may be regarded as a balanced process between vegetative and reproductive activity, and under given conditions, a definite ratio exists in the expenditure of effort between these two activities. In worked stocks the type of root-stock seems to be an important controlling factor of this balance; in difference root-stocks with the same scion variety produce quite different growth habits and fruiting capacities in the scion. A variety which does not do very well on its own roots in a certain situation may be improved in general vigour by a root-stock which modifies any tendency to produce too much "wood" or fruit. The work of the breeder often produces such types, which possess valuable qualities, but which are not sufficiently vigorous to be grown well on their own roots, and requires the assistance of a suitable root-stock. Thus the apple variety "Cox's Orange Pippin" is a delicate subject on its own roots and neither crops well nor makes good vegetative growth; in particular, it is readily attacked by apple canker. If worked on to a suitable dwarfing stock, however, the habit of growth is made more sturdy and the tree also crops better. In tropical crops, at the present day, delicate "improved varieties" are rare, the plants are all very near to the "wild" form. Improvement by selection and breeding has not been going on for centuries, as in the temperate pome fruits. Hence, most of the types one might select for varieties would be hardy. However, breeding work will soon bring out the necessity for the mothering of new varieties by sturdy root-stocks. In cacao, the more delicate types such as *Theobroma Cacao*, var. *Criollo*, *Th. pentagona*, and possible *Th. Cacao.* × *Th. pentagona* hybrids, may be rendered hardier by working on to clonal root-stocks.

(*d*) *Propagation of Sterile Types.*—A sterile type may be defined as one which cannot be propagated by seed. Either no seed at all may be produced, or the seeds, if formed, may be incapable of germination or further growth. If such a variety is to be propagated, some vegetative method must be used.

An edible fruit variety may be esteemed on account of its absence of seeds. Seedless oranges, grapefruit, sapodillas, etc., are well-known. In the citrus fruits such types have frequently been propagated as clones, such as the Marsh seedless grapefruit and the Washington navel orange. Although seedless sapodillas sometimes occur, no method of vegetative propagation has so far been used to extend such varieties.

(*e*) *Early Maturity.*—Frequently a vegetatively raised sapling will come into bearing sooner than a seedling of corresponding age. Also, a bud from a seedling, "mothered" by budding on to an older stock often bears much sooner than the seedling itself. This is not always the case, however; in some crops, notably apples, each fertilisation seems to introduce a "juvenile period" of a definite time, during which the variety will not fruit, whatever the nutritional conditions. If the juvenile period of a seedling can be shortened by working on to a stock, it is of great value in breeding investigations, as fruit is produced earlier and the delay between generations is appreciably lessened.

Disadvantages of Vegetative Propagation: *(Initial Cost)*.—The view is often expressed that it would cost much more to plant up a plantation of a crop, such as cacao, for example, with vegetatively propagated plants, than with seedlings. This question of initial cost, strictly speaking, is purely an economic one and cannot legitimately be brought against vegetative propagation as a horticultural method. At present with a plantation crop such as cacao, planting is usually done by putting in seeds at stake, which certainly establishes a plant very cheaply. Nursery plants could never be produced sufficiently cheaply to compete in first cost with this method of planting, and also contract planting, as practised in Trinidad would not probably be satisfactory in establishing these expensive plants. However, it is unfair to quote increased cost per acre in planting as an argument against planting up with a high-yielding clonal stock instead of with seed, for if the clonal material yields consistently a higher crop than the seedlings, it will in consequence yield a higher rate of interest. In general the overhead costs of an estate are little affected, if at all, by the type of material planted, and since it costs about the same to maintain good stock as to maintain bad, it is generally the accepted principle of horticulture that adequate expenditure on planting material is the truest economy in the long run.

(*b*) *The Root System*.—It is a wide-spread belief among planters that a tree raised from rooted cutting or sucker fails to form a good system, and that in consequence, the sapling does not develop into a healthy bearing tree. In particular, with cacao trees, it is stated that when they have been raised from detached basal suckers—"chupons"—they do not develop a tap-root, and that therefore they will be of no value, as, for some reason, great importance seems to be placed on the presence of a tap-root. Granted that no vegetatively raised individual can develop a true tap-root, in cacao the supposition that basal suckers do not develop main roots which function exactly similarly, is untrue; most "chupons" which have rooted on the trees have a main root when they are young, and if this subsequently decays it must indicate that the soil conditions are not suited to its persistence.

In work at the Imperial College of Tropical Agriculture on the vegetative propagation of cacao, both rooted shoots from stools and from layered stems, have been found to develop sturdy main roots, similar to the tap-roots of seedlings. Plants raised from this material form quite as good root systems as nursery seedlings.

Recent work at East Malling has shown that the type of root system developed by a stock is constant, irrespective of any particular method of propagation, under uniform soil conditions. Even in different soils, in an experiment with some of the East Malling apple stocks it was found that each stock still developed its characteristic type of root system with sufficient constancy to be identifiable in the different soils. Only the extent of development of the root systems was markedly affected by the type of soil. It is true that the layered stocks used did not develop tap-roots, but adequate root systems, both for assimilation and anchorage, were formed—"the main scaffolding of roots spread out in the top 18 inches of soil; but vertical roots often descend from these scaffold roots to a depth of many feet".

(c) *Senescence and Degeneration.*—This heading covers the remaining major criticism which must be considered. Does continued vegetative propagation necessarily result in any lack of vigour, either vegetative or sexual, in the plant? On *a priori* grounds one would think that it must do so, for in vegetative propagation there is no sexual act to intervene with the production of a new individual; the act of vegetative propagation merely extends in space an individual which normally has a finite existence, for every tree seems to become feeble with age, and eventually to die. How can this act be expected to result also in an indefinite extension in time? The conception is not difficult when the probable causes of senescence in a perennial plant are considered. Even in a tree which reckoned to be 1,000 years old, the canopy of leaves is renewed every year or every few years, and most of the active root system is of young growth. There is no need to postulate any degeneration or tiring of the protoplasm of the meristems to explain the general moribund aspect of an old tree, the explanation probably lies in the difficulty which the tree finds in nourishing its young growing parts—the conducting path for the sap is long and much of it is rendered inefficient by air blocks. The cambium of the trunk cannot form new tissue sufficient to overcome the difficulty, and is itself working under stressed conditions, for respiration must be a serious problem in an old encrusted trunk. Further, fungi enter the trunk and limbs of the tree *via* broken branches or pruning wounds and cause decay, first in the pith and eventually in the more vital tissues. Thus the senility may be brought on by a progressive failure of the separate parts of the organism to work harmoniously together, and eventually, when one part breaks down, the whole tree as an organism dies. If young tissue from an old tree is removed and put in a favourable environment (the act of vegetative propagation) the resulting growth, after a time, is in every way comparable to that of similar tissue taken from a tree in the prime of life. Stout gives examples of the persistence of vigour upon vegetative propagation. Cuttings of Lombardy poplar taken from slow-growing twigs of a large tree, root poorly, and those which do root, grow poorly for a time. But after two or three years of nursery treatment the stock becomes vigorous and makes fine sucker branches that are excellent for propagation as cuttings.

Cacao is a tree which may be regenerated from basal suckers even though the old tree be moribund. There seem to be no grounds for supposing that these "secondary" trees are less vigorous or fruitful than the original seedlings; in fact many of the best bearing trees in the older Trinidad orchards are probably regenerated "chupons" themselves many decades old, from trees which would now be aged at least 150 years.

However, it must be granted that the question as to whether senile degeneration does or does not occur in clones, is not satisfactorily answered even to-day. For over a century the "Degeneration" problem has been discussed, without conclusive evidence coming forward either for or against, but, as in most controversial subjects, the field of enquiry has been littered with much unsatisfactory evidence, based on faulty observations or faulty deductions, or both. On the whole, true cases of senile degeneration remain unproved. The cases cited have always had some explanation in terms of disease or environmental unsuitability. Even if work of the future does show that, for certain crops at least, some degeneration must occur on continued vegetative propagation, the fact will not be of much importance.

Even if the old varieties were still as vigorous as ever, the public taste would forsake them for new ones, the admirable properties of which would be supplemented by new varietal names, which, suitably chosen, would most probably enhance the appeal to novelty.'

The subject of senile degeneration as it stands today, is admirably discussed by A. P. C. Bijhouwer in a review of the literature recently published by the Imperial Bureau of Fruit Production.

Apparent Senescence.—This is quite a different thing from the true senescence discussed above, but is much more likely to occur in practice with large-scale vegetative propagation. It is often called "reversion", "running out", and other terms suggestive of degeneration. The deterioration may arise, in general, in two ways, although both may play a part. The first way is by the infection of the clone with some disease, which is passed on by vegetative propagation. The virus diseases are the ones which must be especially looked for to cause this trouble; they are systemic, cause morphological and physiological changes, often indeed suggestive of a reversion to the wild state, and they exhibit no trace of any organic parasite. The classic example, of a virus disease causing a general deterioration of a vegetatively propagated crop, is the "reversion" disease of black currants. This virus is transmitted by a Mite, which itself causes the malformity known as "big-bud". The virus also spreads through the branches of the black currant bushes, and cuttings taken from affected twigs spread the disease. By this means the disease was generally disseminated in England, causing immense loss to the growers. The only remedy was found to lie in establishing fresh propagation nurseries from carefully selected healthy material, together with rigorous "rogueing" of any diseased shoots which might appear.

The other way in which deterioration of a stock may occur is by the accidental introduction of extraneous stocks, usually chance seedlings, when the nursery plants are lifted; this is likely to occur in a plant which fruits in the nursery, such as the raspberry. With raspberry the canes fruit, and seedlings spring up, which may not be obviously different in appearance from the clonal stock, but which develop into plants with poorer fruiting capacities. Prevention of this contamination must also be sought by clean cultivation and rogueing. In addition to these seedling rogues, objectionable types may appear even in rigidly maintained clones of some plants, by the production in the clone of bud sports or branch mutations. This is particularly liable to occur in some citrus types such as grapefruit. Shamel notes the occurrence of undesirable branch mutations in various citrus fruits, and stresses the danger of the propagation of such poor types. There is always the possibility in a variety which is unsuitable, such as the Marsh seedless grapefruit, or the Washington Navel orange, that special "improved" forms might be sold which would be merely unstable chimaeras, liable to revert, on part or whole of the tree, to the normal form.

(*d*) *Problems of Sterility within a Clone and between Clones.*—The planting up of an orchard with uniform clonal material may introduce problems of sterility which would not arise in a plantation of seedlings. Many cultivated clonal varieties of orchard crops are partly or wholly self-sterile, that is, they do not set fruit with their own pollen. Vegetative propagation of such a type does not remove this condition; all the members of the clone will have the same degree of fertility or sterility to one another as the original plant possessed when self-pollinated. With such sterilities as male sterility, and self-incompatibility seed production depends on a suitable cross-pollination, which would not take place if self-incompatible clonal material were planted up in blocks away from other types. Thus, unless a clone is found to be reasonably self-fertile, it should not be planted exclusively in blocks, but with rows of some other cross-fertile variety chosen to ensure successful mutual cross-fertilisation. In a crop, such as cacao, where the seed is the part required, partial sterility is serious in that few seeds are developed. On the other hand, in most fruit crops the edible portion is not the seed, and is often developed in the absence of seeds, as in bananas and seedless citrus fruits, and in these cases self-incompatibility may not matter.

With cacao, as it exists at present, the question of self-sterility would not appear to be of much importance, for the crop seems to have a high degree of self-fertility, according to Harland and Frechville, about 70 per cent of the pods set are self-pollinated. However, cacao must be considered to be a virtually wild crop, and the best yielding trees which exist at present probably would not bear comparison with so-called "improved varieties", which will no doubt be produced as systematic selection and breeding work progresses. These improved varieties may be expected to exhibit various degrees of self-incompatibility and even, in some cases, imperfect cross-compatibility amongst each other, due to doubled incompatibility factors. In varieties where these effects occur, suitable mutually compatible varieties must be planted with them to obtain effective fertilisation.

Summary.—(1) A fresh plant may generally be raised by two methods: from seed, or from some fragment of a parent plant other than a seed, or as in budded seedling stocks, by a combination of both methods. Seed propagation involves a sexual act, and produces a definitely new individual which may or may not closely resemble the parent type. In most orchard crops, the offspring usually show considerable variation. Vegetative propagation is not a sexual process, and does not produce a new type, it merely extends the original parental type.

(2) Vegetative methods may be used to propagate either a complete plant or a scion plant which is worked on to another stock. Complete plants or root-stocks are raised from rooted cuttings, stool shoots or layers. Scion clones may be raised by budding or grafting the desired variety on to stocks, which may be either seedlings or members of a clone.

(3) The extension of a type by vegetative propagation makes possible a degree of crop uniformity, both of yield and of quality which is rarely attained in a seedling population. This uniformity is of great advantage both in the scientific and the commercial fields. In scientific work a high intrinsic variability in the experimental material obscures the variability caused by the experimental conditions; for the grower, the presence of low-yielding types increases the overhead costs of the plantation. To obtain the highest degree of uniformity of yield, the plants should be entirely clonal, both stock and scion.

(4) The isolation of individual plants, chosen for special qualities, such as cold or drought tolerance, and their subsequent vegetative propagation, can increase the range of cultivation of a crop by bringing in districts which are unsuited to the average type. This is analogous to the breeding of hardy strains of wheat, where however, vegetative propagation is not necessary to fix a type, as pure genetic lines are readily raised.

(5) In temperate horticulture it is a standard practice to work certain varieties on to vigorous stocks, thus improving either their vegetative growth or cropping capacity, or both. In tropical crops modern breeding work will probably produce similar delicate varieties which require the assistance of a hardy root-stock.

(6) Some desirable fruit varieties are highly sterile and thus cannot be propagated by seed. In these fruits, vegetative propagation must be used to extend the variety.

(7) A bud from a seedling may often be made to grow and bear fruit sooner than the original seedling, by working it on to a stock. This hastening of maturity would be of great value in speeding up genetic work on an orchard crop.

(8) The first cost of a vegetatively raised nursery plant will usually be higher than that of a seedling planted at stake. However, the increased yield expected from such nursery plants should amply justify the initial increased expenditure.

(9) A tap-root is by definition an organ peculiar to a seedling. However, exactly similarly functioning roots can grow on vegetatively raised plants. It is highly probable that in most orchard crops, after a certain age, the root systems of trees which grew from seedling root-stocks and those which grew from vegetative root-stocks will be found to be indistinguishable. Even in seedlings it is doubtful whether the primary tap-root is persistent in a mature tree.

(10) The question of senescence always arises in connection with the vegetative extension of varieties. At the present day the occurrence of true senescence in clones on continued vegetative propagation is neither proved nor disproved. However, even if some senescence were proved to occur, it would not affect very much the policy of orchard crop growers, who normally would wish to plant new varieties from time to time rather than to replant with old varieties which had begun to wane in popular favour.

There is however, the problem of contamination of clonal varieties by rogue plants, either of seedling or clonal origin, or by diseased plants. This contamination may materially reduce the yield from a plantation and give the impression of a senile change, or "running-out" in a variety. The solution must lie in the prevention of the propagation of rogue types by care in taking budwood or cuttings and by vigilance in the nursery.

(11) Self-sterility occurs in many varieties of fruit crops. Even different varieties may not be sufficiently cross-fertile to ensure sufficient setting. Some edible fruits develop with a low percentage of ovules fertilised, and in these, high degrees of sterility can occur without affecting yield. In a seed crop, however, a high percentage of ovules must be fertilised, as seed is rarley produced without fertilisation. In such crops, therefore, precautions must be taken against sterility by planting mutually cross-fertile varieties together.