but in many cases it is practicable to select homozygote individuals of one sex. Fig. 6 shows the results that follow when all recessive females are discarded and only homozygote males are used. It is seen that after the second generation no recessives crop out, and that within ten generations the number of heterozygote individuals decreases to a very small proportion of the population.

It was Fig. 2 about which Dr. Shull, at the meeting of this association last year, stated that it illustrated the results obtained by Mr. Burbank by his method of selection, which in many cases consists of discarding undesirable forms.

It should be remembered that the principles here outlined apply only to Mendelian characters. We do not yet know whether all hereditary characters obey Mendel's law of segregation or not. If there are characters which do not obey Mendel's law then these formalæ would not apply to them.

CLONAL OR BUD VARIATION.

By Herbert J. Webber.

Contribution II, Laboratory Experimental Plant-Breeding, Cornell University.

LIMITED MEANING OF INDIVIDUALITY IN PLANTS.

Up to the present time breeders have been dealing primarily with the plant as an individual and as the unit in all considerations of variation evolution and breeding. This, however, from the standpoint of our cultivated plants is clearly an error as many of our varieties have originated as so-called bud sports or bud variations and it is clear that this type of variation must have its place in any system of plant-breeding. Animals, particularly the higher forms, are almost completely Autonomons. The animal has a definite number of legs, arms, ears, etc. It possesses almost complete bilateral symmetry. Each part is dependent on the other parts for its existence. All parts develop and grow together and die at the same time, having a more or less definite span of life. In all of the higher plants, however, there is a totally different condition. Every plant is made up of a certain number of largely independent units which may be said to be fighting with each other from birth for supremacy. Each node, internode and bud forming together a unit which is designated a phytomer is in considerable measure independent of every similar unit on the plant. To make this clear take as an illustration a tree of any sort. The first shoot produced is for a period simple and

unbranched. This shoot bears a number of buds, situated one above another and distributed around the twig in accordance with the regular order of sequence natural to the species. These buds which may all seem alike nevertheless do not develop alike, and the difference from the development in the animal kingdom becomes immediately apparent in the further development. Each of the buds is capable under certain conditions of growing into branches, but as a matter of fact only a limited number of them actually develop. Certain of the buds, apparently more favorably located as to the securing of nutrition from the general plant body than others, begin to push out branches and these grow rapidly and by their growth apparently absorb the available nutrition to such an extent that the buds near them from necessity remain dormant. These secondary branches which start immediately begin a competition with each other which is severe in the extreme. They must obtain light in order that their leaves may elaborate the necessary food. Certain ones of them from their more favored location get the full light, the shade some of their neighboring branches. These favored branches grow much more rapidly than the others and may come to entirely overshadow them. The branches thus overgrown and shaded usually carry on a precarious existence for a time and finally die and their death instead of injuring the main development of the plant body helps it as is well know.

REGENERATION THROUGH BODY PARTS.

It is also important to remember that the higher plants differ from the higher animals in the fact that almost any portion of the plant body may be used to propagate what in the general sense would be considered a new individual. Everyone knows that we regularly propagate certain plants by transplanted vegetative parts, without reference to sexual reproduction. Our potatoes are grown from tubers, our strawberries, pineapples, raspberries and blackberries from slips or suckers; our grapes from cuttings; our onions, tulips, gladiolus and lilies from bulbs, etc. The extensive use of this practice by gardeners and florists demonstrates conclusively that in very many cases buds or almost any part of any plant may be taken and lead to reproduce a new plant which will bear flowers and seeds and in practically every detail reproduce a new comparable with a seedling developed as a result of a definite sexual union. This power of vegetative regeneration is probably universal in all higher plants. Skillful propagators after extensive experience always claim that they can grow anything from vegetative parts. This power

of regeneration is not limited simply to growing buds and upper parts of the plant, but even roots are known in a very large number of cases to have the power of producing adventitious buds and growing into complete plants. The student will be familiar with this faculty of roots by having observed the numerous sprouts developed from roots of the silver leaf poplar and Aspen (Populus alba and Populus tremuloides). It will be recognized from the above statements that all parts of the plant must contain the entire heritage of the species as almost any part may be grown into a fully developed individual representing the type of the species and possessing all of the capabilities of sexual reproduction possessed by a seed propagated plant. It is well known that in a large majority of the lower groups of plants the inter-dependence of the different cells and parts of the plant is even less close than in the higher plants, and that almost any fragment of the plant body will under the proper condition continue to grow and reproduce. The lower down in the scale we go the more marked this factor becomes in general till we reach the unicellular types where each cell is to be considered an individual.

EXTENT OF BUD VARIATION.

The fact that the developent of each bud, as pointed out in the preceding section, is influenced by its environment and that it possesses the same reproductive powers and capabilities of transmission of character as the sexually propagated seeds, would lead us to expect variations to occur in buds and bud propagated plants as well as in the seed propagated forms, and this is in fact the case. In general it is recognized that this so-called bud variation is less in degree but it is doubtful whether this is truly the case as many supposed variations in seedlings is doubtless the result of the seeds having come from different branches, which as a result of bud variation transmitted to the seed different tendencies. The validity of this doubt will be enforced by the further discussion. It is true that certain clonal varieties of fruits, apples, pears, grapes, etc., propagated entirely by buds and in general are considered to remain very constant. It is equally true that many such varieties are very old and have ever since their origin been propagated by buds, as witness for instance the Baldwin apple originated in 1842, Northern Spy 1800, Jonathan 1829, Catawba grape 1802 and Concord grape 1849. Such illustrations are liable to impress upon us unduly the stability of buds and clonal varieties. We forget meanwhile the reasons for this stability in comparison with what we consider to be the instability of races pro-

pagated by seed. When we consider the stability of clons we forget that we are largely deriving our concluslons from such instances as the above cited cases where the plants are perennial and live normally to an age of a half century or more. We forget that while there may be little careful selection of buds such as we should wish to have, yet there is scarcely ever a bud propagated which is not taken from a tree known to be true to the type of the variety. If a tree is noticed to be off in type that is in branching, color or otherwise, buds are not taken from it. Again buds or scions are cut almost wholly from the upper part of the tree and from good thrifty shoots of certain character. There is thus a continuous selection to keep the variety true. The buds are not taken as a whole and mixed together and sown like wheat. In races, on the contrary, which we consider to be shorter lived and which we interpret to be due to the greater inherent variability obtaining through seeds produced sexually, we are drawing our conclusions primarily from our experience with races of annual or at most possibly biennial plants such as corn, wheat, cotton, beets, cabbage, etc. True, the races of such short lived plants do not endure so long as the clons of apples and grapes as a whole. Yet if prevented from deterioration by crossing they may endure for many years. The Leaming corn having a very characteristic tapering ear was originated between 1850–1855 and where bred isolated has remained fairly true to the type and is extensively cultivated today. The same may be said of the Boone County White which originated about 1870. No plant is more variable or more difficult to keep pure than corn. The Fultz wheat originated in 1862 is cultivated extensively today, and is a fairly uniform sort after a lapse or nearly a half century. There is no indication that the Fultz is any more variable today than the Concord grape originated only a few years before. Indeed the Concord grape has shown many more recorded variations even of bud variation than the Fultz has of seedling variation. Wheat is self-fertilized it may be argued, but still it is sexually fertilized and gives the opportunity for a segregation and redistribution of matter in the formation of sex cells and a recombination in sexual union. There is no doubt but that a variety such as Fultz has a complex heritage and that many characters are latent in it which might be expected on our present lines of thought to be segregated and recombined in the course of sexual reproduction. Races in general are being crossed unquestionably with other and different races continuously, no matter what care is taken to present contamination and this brings in a different heritage which the most careful rogueing cannot entirely eradicate. In

seed propagation, therefore, much or probably the greater part of the variation is due to crossing with different races. Another factor of importance which must not be overlooked in this discussion is the fact that whatever bud variation occurs in races is having its influence on the variability of the seedlings and is being considered and classed as seed variation because the seed from different branches is all harvested together and planted without separation.

In clons, on the contrary, only the variations classifiable directly as bud variations are ever considered. In clonal varieties we have no variation due to the continuous crossing of different clons, as there are no intervening sexual propagations. Clons of annual plants are rarely so stable or last so long as the clons of perennials. They seldom break up entirely but the usual history is that they apparently deteriorate in vitality or at least are after a time found to be inferior to newer clons and are discarded. This supposed deterioration and consequent discarding of the old clons is probably due in part to deterioration and partially to the actual advance made by breeders in producing better sorts. It is undeniable that in many cases there is actual advance shown in the new clon entirely aside from rejuvenescence. In the case of the Carnation: Scott, Portia and McGowan, excellent varieties in their time, have given way to Lawson, Enchantress, White Enchantress, etc. Scott and Portia were said by growers to have deteriorated and become unprofitable for culture. Yet no grower would claim that they were ever as good so far as size and beauty is concerned, if judged by our present standard of excellence. However this may be these clons have been discarded and in some measure at least due to degeneration. The life of a carnation clon is seldom more than 10 years and the same may be said of the life of our races of annual vegetables ordinarily. When the varieties are discarded in either case, however, it is not because they have segregated into other types but because they have lost vigor and have become superseded by newer and better sorts. The potato clons now cultivated are practically all new sorts. Even the world famous Early Rose, originated in 1861, has been almost wholly superseded and is now but very rarely found in cultivation. With reference to the apparent stability of clons of perennials it should further be emphasized that those apple clons referred to as so long of life are by no means at the present time the same as the old original trees. The Baldwin cultivated under varying conditions has become so changed that in many instances the fruit cannot be recognized as the same. Any one who has had the opportunity of examining fruit of this variety

from widely distinct regions—such for instance as from New York, Washington, Colorado and Arizona—is familiar with their differences. The Newton Pippin originated on Long Island has, according to Bailey, varied in Virginia into the Albemarle Pippin. In the extreme North West it has varied into a longer fruit bearing distinct ridges about the apex, and in New South Wales the ridges are more marked and other characters have appeared so that the variety has come to be known as the Five-crowned Pippin.

The evidence from the stability of clons in comparison with races, the writer would thus conclude, cannot be taken as indicating in any degree any greater inherent tendency for variation to occur more generally in seedlings than in clons. Freeing our minds from any preconceived ideas of this sort we are then in position to consider the extent of variation in buds or from any part of the soma or body of the plant.

ORIGIN OF BUD VARIATION.

Bud variation is a somewhat unfortunate term to apply to this general type of variation, as strictly interpreted the term is erroneous. By bud variation we mean not simply that variation which occurs in the bud, but any variation that takes place in the soma of the plant as distinct from the variation which is apparently caused during sexual reproduction and becomes first manifest in the seedlings. The cause of a bud variation probably has its origin in changes occurring in a certain growing cell or possibily in a group of cells and these cells which are apparently first changed or at least which first show the variation may be in some other member or part of the body. It would seem from the studies of Beijerinck[1] on *Cytissus Adami* that in this case at least the change took place over a considerable tissue part instead of being limited to the single apical cell of the bud, as might be supposed. The evidence on this subject is, however, very meagre. If the change took place in a single cell and cell multiplication continued, as would have to be the case if the variation is to become visible, we would, at the time the variation first becomes discernible, have a group of cells which would have been developed from the single cell first changed. From our present knowledge of the cytology of heredity we would assume that hereditary changes such as those manifested by bud variation as well as seedling variations are due to rearrangements of the hereditary units or anlagen which

[1] Beijerinck, "Beobachtung ueber die Entstehung von Cytissus purpureus aus Cytissus Adami." Ber. d. Deut. Bot. Gesell. 26a: 137–147. (1908).

occur during cell-division. In the case of seedling variation we assume that this rearrangement takes place primarily during the progress of the reduction division that precedes the formation of the sexual cells. So far as microscopic investigations go we have no evidence that would strengthen the idea of such a redistribution of characters ever taking place in the somatic cells. However, we have the strongest of all possible proofs that it does occur in the fact that in bud variation we get segregations of character analogous to the segregation in seedlings. In hybrids the characters very frequently segregate in the somatic cells giving branches resembling the pure parental characters which reproduce these characters through the seeds. Cytological evidence against the possibility or probability of such an occurrence is of no value in the face of its actual occurrence. The segregation of characters in hybrids was recognized before we had any knowledge of the occurrence of a reducing division. Xenia was known to occur before double fertilization was discovered. From the nature of the case in point cytological explanation must follow and must accord with the facts observed. The fact that a redistribution of characters occurs in somatic cells in the case of hybrids reverting back to their parental characters is thus certain. What occurs, however, in the case of what may be termed bud mutations where no hybridization occurs? East states, "We must admit that if mutation is due to some shuffling and distribution beyond the normal, of the cell units that are the bases of somatic characters, then the same stresses and strains that produce such changes upon the germ cell, should produce analogous changes upon the somatic cells that lay down certain plant organs.[1]

It must be admitted that we have as yet little evidence as to the actual causes which lead to the production of seedling mutations, whether of progressive, retrogressive or degressive nature. That a change must take place in the hereditary matter, unit anlagen, or whatever we may call the hereditary plasm would seem indisputable and self evident. There would furthermore seem to be no reasonable ground to doubt that the changes taking place in the somatic cells resulting in similar mutations to those produced through sexual reproduction must be considered as of the same nature and to owe their origin to the same forces or causes. The writer does not propose to review the cytological evidence relative to this matter at the present

[1] East, Edw. M., Suggestions concerning Certain Bud Variations. Plant World 11 (1908), p. 77.

but it is at least interesting to note that Farmer, Moore and Walker[1] found cell divisions resembling reducing division taking place in abnormal cancerous or tumerous growths in man where only somatic tissue was concerned, and various investigations have found irregularities in chromosome distribution in somatic cells of plants and animals, such irregularities becoming very frequent as the cells approach the stage of differentiation where they lose the power of dividing and reproducing. That the so-called germ plasm is changed in a bud variation is shown by the fact that in some and probably in very many instances, the variation is transmitted through sexual reproduction.

If we accept Professor Morgan's conception (see article in this Report) that the apparent segregation of characters is the outcome of alternative states of stability (or of conditions), we would account for bud or somatic variations as caused by local conditions that so influenced or affected a certain cell or group of cells as to lead the recessive character to gain the ascendency and become manifest. It must be admitted that in the light of our present cytological evidence this would be the simpler explanation most easily accounting for the phenomenon. It should be remembered that the crucial point of difference of Morgan's view from the Mendelian factor conception lies in the fact that in Mendelian explanation it is assumed that in the formation of the germ cells the unit representing characters segregate while according to the latter Morgan's view at this time they enter into a more intimate relation so that the state that will produce one character has established itself. A factor strikingly in favor of Morgan's idea is that by selection we lead a character to increase until it finally becomes dominant and entirely overshadows the other character, though it does not exclude the reappearance of the other character. This is shown by the case of doubling. If we had a definite unit for doubling, to once obtain that character should fix it as permanent, while as a matter of fact there is always continual reversion in greater or less degree.

TYPES OF BUD VARIATION, AND THEIR USE IN BREEDING.

At the present time the writer does not contemplate a full discussion of the types of bud variation. It is well recognized by practically all investigators that we have in bud variation the same types of variation

[1] Farmer, Moore and Walker. "On the Resemblances exhibited between Cells of Malignant Growths in Man and those of Normal Reproductive Tissues." Proceedings Royal Soc. London, Vol. 72, pp. 499–504 (1904).

that are found in seedlings, namely, fluctuations, mutations and segregation of characters following hybridization. We also have just as markedly as in seedlings, the type of variation which Darwin called definite variations, where all of the plants of a kind grown under a certain environment, respond in the same definite way to the stimulation of this environment.

Are these variations of use to the breeder? It seems reasonable to suppose that they would have in breeding the same value which similar variations in seedlings have and the experimental data so far as the writer is informed seem to uphold this conclusion. The so-called definite variations, which are direct effects of the environment are apparently in no sense inherited in clonal propagation and are at least usually valueless. It may be that in some cases the environment causing the direct variation may also in some measure affect the heritage of the plant but in this case the variation would be of different nature and would be classifiable as a fluctuation or mutation.

Bud mutations are known in many instances to, in general, transmit their qualities in further bud propapations and this indeed is fundamental, as the branch showing the variation usually exhibits the change in many twigs which have been produced from the original bud after the change took place. Many such bud mutations, as for instance, cut-leaved sorts, have been propagated for many generations as clonal varieties.

It is also well known that bud variations or bud-segregations following hybridization are of great value to the breeder as a very large number of the bud-sports, so-called, in roses, carnations and chryanthemums are to be explained as bud-segregations following hybridization, and have been propagated as clons through many bud generations.

The only type of bud variation, the value of which in breeding is in doubt, is what we term bud fluctuations. This doubt, it seems to the writer, is of exactly the same nature and based on practically the same evidence as the doubt which exists regarding the value of fluctuations in seedlings from the breeder's standpoint, or the standpoint of the evolutionist. Can we by the continuous selection of maximum fluctuations in any direction, change the mode or increase the maximum? All readers conversant with recent literature will recognize that further evidence on this question is necessary before any definite statement can be made. It would seem to the writer, however, that we are justified, from the evidence in hand, in believing that by continuous selection and the isolation of the selected strain, the mean of the variation

in the selected population may be raised much nearer to the maximum exhibition of the character in the race. This the writer belives to be equally true whether we select seedling variations or bud variations. Galloway and Dorsett, of the U. S. Department of Agriculture, by selecting violet cuttings from productive plants, greatly increased the general yield of their entire stock. Many experimenters have claimed to have secured marked increases in yield of potatoes, by the selection of seed from high-yielding hills. Sugar beets have been increased in sugar content by selecting as mother beets those having the highest percentage of sugar. Corn has been increased in yield and in number by selecting seed from individuals exhibiting these variations in the highest degree.

In these familiar cases of the selection of bud variations and seedling variations, the type of variation used is supposed to be what we would term fluctuations. In each case the mean of the variation in the selected population has been increased nearer to the maximum and maintained there apparently as long as the selection was continued. In each case apparently no new race has been established with permanent new mode, but the selection must be continued if the improvement is to be maintained. The writer believes this to be equally true whether we are dealing with seedling fluctuations or bud fluctuations. This fact, however, does not render such variations and their selection valueless to the breeder and cultivator. They desire the highest yielding strains of the variety or race they are cultivating and in many instances the profits accruing from the use of such strains will doubtless pay for the expense of the continuous selection. Seed breeders all over the country are now selecting corn in this way and the sugar beet industry is based and founded on the continuance of such a selection.

Such a continuous selection of fluctuations has proven valuable in many of our seed-propagated crops, but in no case except in the potato has the selection of clonal varieties been undertaken in a commercial way. The writer believes this to be a fundamental error in horticultural practice which should be remedied. It is well known among horticulturists that in an orchard of Baldwin apples we may find one tree that will produce well regularly while another immediately beside it may be a light or irregular producer; both trees have the characteristics of the Baldwin, but one is a good producer and the other is not. Such differences in yield of bud propagated plants are well known in carnations, violets, strawberries, apples, peaches, oranges and practically all clonal varieties. The evidence thus far accumulated indicates that these good and bad characteristics are in a large measure transmitted to the bud pro-

geny, yet we pay almost no attention to the plants from which we select buds or cuttings. An apple orchard will last for a hundred years and we could well afford to use the highest selected bud progeny possible to obtain in such a case. It seems to the writer that there is here an opening for breeders equal to the production of pedigree seed for sale. It is clearly as easy to take cuttings and buds for propagation from known good producers as it is to take seed from such good plants. In the case of seed propagated plants it is impractical to sell the seed direct from the breeding patch and seed breeders have adopted the policy of having multiplication or increase plots for the select strain so that the pedigree seed usually sold is from two to three generations removed from the selection. In the case of an exceptional Baldwin apple tree from which a nurseryman desires to take buds for propagation, it is just as feasible to top graft a number of the buds from such a tree on to another stock to quickly test the bud transmission of the characters, and then, if found, a good number of nursery trees may be grafted directly from the original tree and the buds or scions for propagating stock for sale may be taken from these nursery trees. Here the buds are not taken direct from the selected tree but are no farther removed from the selection than is the seed from increase patches in the case of corn.

Again, a continuous bud selection could readily be carried out with apples, peaches or any similar fruit, though a number of years would necessarily be required between each selection. A nurseryman having selected and taken buds from a specially good tree could readily follow certain orchards planted with such trees and, when they came into bearing, arrange to again take propagating buds from the best trees.

This field of plant-breeding is a much neglected one and certainly should receive much more careful consideration.

INFLUENCE OF FOOD SUPPLY ON VARIATION.

By Harry H. Love.

Contribution I. Laboratory Experimental Plant-Breeding, Cornell University.

The question of the effect of food supply on variation in plants has long been discussed. Thomas A. Knight was the first to state the law that excess of food supply is the chief cause of variation. He says "nutrition reigns supreme in the whole realm of variability. The amount of useful nutrition is the all important factor." Darwin also says, "of all the causes which induce variability, excess of food, whether or not changed in nature, is probably the most powerful." However