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A STUDY OF VARIEGATION IN CHLOROPHYTUM ELATUM

Thesis for the Degree of M. S.
MICHIGAN STATE COLLEGE
Charles L. Weddle
1938

THESIS

A STUDY OF VARIEGATION IN
CHLOROPHYTUM ELATUM

A Thesis Submitted to the Faculty of
Michigan State College of Agriculture
and Applied Science
in Partial Fulfillment of the
Requirements for the Degree of
Master of Science

By

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Division of Agriculture
1938

Approved May 27, 1938.
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THESIS

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Introduction

The great majority of plants are uniformly green. Some characteristically develop other colors due to development of anthocyanin pigments. Varieties of other species such as *Coleus blumei* may typically develop leaves with little chlorophyll in certain portions of their leaves. Still other species are normally green, but individuals occasionally develop leaves with white or yellow areas devoid of chlorophyll. The types of variegation commonly recognized are as follows:

1. Physiological. Often the leaves of plants present a more or less mottled or variegated appearance because of nutritional disorders, high water table, or injured root systems. Variegation of this type is greatly influenced, indeed caused, by environmental conditions and perhaps in the narrower sense of the term is not to be classed as true variegation.

2. Pathological. Virus diseases commonly interfere with chlorophyll development, usually resulting in mottled green and white, or green and yellow leaves. *Abutilon Thompsoni* is *Abutilon striatum*, infected with a virus which

causes a mottling of leaves. Such infection can be transmitted to healthy plants by grafting onto them scions of infected stock or by insect carriers of the virus.

3. Chimeral. Another type of variegated plant is the chimera, which is composed of tissue which is genetically green and tissue which is genetically without chlorophyll, arranged in various patterns depending upon the time and method of origin of the white tissue.

This study deals only with the latter type of variegation, some points concerning which it is hoped may be elucidated.

Review of Literature

Of equal interest to the geneticist, the cytologist, the physiologist, the morphologist and the horticulturist since the beginning of the twentieth century, and to some extent even before, has been the problem of chimeras. A plant chimera according to the newer and broader concept is any plant which is composed of two or more genetically different cells, or tissues, so combined as to form a single individual. The difference in the components may be little or great, involving a difference in a single gene or an entire chromosome complement, the limit being imposed only by species affinities. It follows that chimeras whose tissue components differ little are more numerous, and that those involving the greater differences between their components are not produced naturally, but are the result of grafting one species or genus upon another. Winkler first used the term chimera to describe a branch that arose which was composed of the tissues of two different plants. Since then the term has been used in a more restricted sense to indicate only the peri- and mericlinal and sectorial types, but now the term has acquired the broader concept given above.

The most simple method of obtaining a chimera is that of grafting one variety upon another. Although grafted plants are not usually considered to be chimeras, such individuals conform perfectly to the new definition for the term and serve to illustrate some of the features of all chimeras and many of the physiological problems found in most chimeras. And too, the periclinal, mericlinal and sectorial chimeras have been known to arise from grafted plants, in fact, have been produced experimentally by Winkler, whose work was partly responsible for Baur's chimeral hypothesis. Winkler saddle grafted two species of *Solanum* and after the union had formed severed the stem at the union, leaving a small strip of scion tissue. Adventitious buds were thus induced, some of which arose exactly at the point of union of stock and scion. Branches forming from such buds contained some tissues from the stock and some from the scion and the growing point was interpreted by Baur (1908) as being a composite (but a mosaic or coarse mixture rather than a blend) of both tissues. Darwin writes of grafting two halves of a hyacinth bulb together thus producing a flower stem whose flowers were half one color and half another. To this type of combination of tissues Baur gave the descriptive name of sectorial chimeras. Baur's chimeral hypothesis states that chimeral patterns met with in mature parts of plants are the result of chimeral growing points, i.e. the pattern found in the mature organ is merely a development of the pattern already present in the growing points.

Baur's work was begun with the idea of studying the old graft hybrid theory which had resulted from accidental chimeras which had arisen from routine grafting operations during the half century or more preceeding. These plants, the earliest of which was the Bizarria orange, were chimeras whose anomalous behavior was thought at the time to be the result of actual fusion of somatic cells following the grafting operation and to be vegetative hybrids. Winkler at first concurred with this opinion and designed his experiments to refute Baur's hypothesis. His work, however, yielded unexpected evidence in favor of the chimeral hypothesis. Baur's work, which was done with an irregular variegated strain of *Pelargonium zonale*, found what have become known as sectorial mereclinal, periclinal and mixed chimeras and elucidated for the first time some of the points which are discussed in the following paragraphs.

The Form and Recognition of Chimeras

The form which chimeras take depends upon the kind and the wideness of the differences between the component tissues and their anatomical distribution in the individual. Anatomical disposition of the components affects the genetical behavior and the appearance and recognition of the chimera. Chimeras arise in nature most frequently by somatic mutation, every such change resulting in a chimera, if the broader concept holds, though not always recognizable. These facts provide an interesting aspect to the problem when it is considered that a somatic mutation may involve a change in a single gene, a single chromosome, or may result in the doubling of a whole chromosome complement. Point and time (in ontogeny) of origin naturally affect the anatomical distribution of the mutant tissue. Plants with plastids mutating late in the development of the leaves would be characterized by relatively small areas devoid of chlorophyll, whereas, were the mutation to take place in the leaf primordium, practically the whole of the leaf might be affected; were the change to occur early in the ontogeny of the plant, many of the leaves would probably be affected. The first two types would not be perpetuated since there the mutant tissue does not include a growing point. Such late mutating genes are known in _Pharbitis_ (Imai 1927), _Polygonium_ (Imai 1927). Imai also found recurrently mutating strains of white-variegated barley and of Veronica Corallina, Capsicum, Plantago, Dianthus, Lespedeza, Pelargonium, Gentiana and Heliotropum. He classes mutations as auto- and exo-, automutations being those which take place independently of the gene complex, and exomutations being those which are stimulated by other genes. Chittenden (1927) observed strains of Pelargonium zonale which sported to white branches (mutation early in antogeny) with green ticks on the stipules (reversion occuring late in development).

Types of Chimeras

Grafted plants and those chimeras resulting from late occurring or recurrent mutations being excluded, there are three types of chimeras with varying abilities for perpetuating themselves, viz., the sectorial, the mereclinal, and the periclinal.

The sectorial chimera is one in which the two tissues are united side by side in the stem and the growing point of the main stem or of a branch. A section of such a stem, were it possible to stain the two tissues differentially, would appear as a circle with one sector differing from the other as a pie in which one or more cuts had been replaced with another kind. In the branch in which it occurs, such an arrangement may be comparatively stable, but the lateral branches which arise will have the constitution of one or the other of the components. Only those buds arising at the junction of the two components will have a chimeral structure, and they will vary depending upon the proportion of each tissue entering in. In plants having several sectors of mutant tissues, however, the majority of lateral branches may have the sectorial arrangement, but very seldom will the exact composition of the original stem be repeated. In this discussion it has been assumed that in sectorials the mutant component comprises part, but not all, of each meristematic layer. Occasionally it happens that in addition to the sectorial structure one of the component tissues will have a thin strip overlapping the region of the other tissue. Such an arrangement, as will be seen later, often gives rise to the periclinal form. The sectorial type of chimera is then quite unstable within itself and in succeeding vegetatively propagated generations.

The mericlinal type appears much as the sectorial, the difference being that the differing sector does not extend all the way to the center. The differing tissue in this type consists of a skin one or more cell layers deep, which does not reach the center of the stem, and extends only part of the way around. The mericlinal type behaves in growth and vegetative propagation in the same manner as does the sectorial, except that branches arising on the side of the stem which is overlaid with the superficial strip of aberrant tissue, will give rise to the periclinal structure. Unless the strip overlying the parent tissue is several cell layers thick, branches pure for that type of tissue contained in the strip will seldom arise, the explanation being that deeper lying tissue will be drawn up, forming the 'core' of the branch resulting in a periclinal arrangement.

The periclinal chimera is like the mericlinal, except that the skin of one type completely surrounds and envelops a core of the other. As a rule no change of pattern occurs in the production of lateral shoots; therefore, the periclinal is the most stable type of chimera, since, as has been pointed out, the other two types tend to resolve themselves into branches pure for the component tissues, or into the periclinal arrangement.

The literature is replete with examples of the various types of chimeras. Many species have been involved. The majority of instances have dealt with variegated plants, obviously because of the ease of detecting a chimeral arrangement with the green and white pattern.

It is now suggested (Jones 1937) that the mericlinal type arises most frequently in nature and that many chimeras described in the literature as sectorials were probably in reality mericlinal arrangements.

Peri- and mericlinal chimeras, according to Baur's hypothesis, are made possible by the fact that angiosperms grow by division of cells in two or more self-perpetuating meristematic regions arranged in concentric rings or layers in the growing stem. Such an arrangement, it seems to this writer, precludes much of the possibility of true sectorials being formed naturally. Ferns grow from a single apical cell and therefore the only chimeral type possible to them is that in which somatic mutation occurs during development. Such cases have been known in both sporophytic and gametophytic generations. (Anderson-Kotto 1923). Gymnosperms grow from single meristematic regions.

Although there has been much controversy concerning the point of self-perpetuating meristematic layers being composed of different kinds of tissue, the existence of stable periclinal chimeras with one-, two-, and three-layered skins has confirmed the existence of such arrangements, (Krenke 1933). It must be kept in mind that a growing point consisting, for example, of two layers of potentially white tissue over a core of green tissue, will not reproduce exactly that arrangement in the leaves. And therein lies one of the most difficult problems dealing with chimeras, i.e. the problem of assigning the origin of a particular tissue to a certain layer of meristem. Another problem of importance is that concerning the number of meristems in the growing points of plants.

Not all chimeras are easily recognized and analyzed. as those the differences of whose tissue components are comparatively great. Ability to produce chlorophyll is easy enough to detect in the foliage, but impossible in the meristems. Many genetical characters such as those concerned with floral form and color express themselves over a comparatively short period of the life cycle and in a relatively small portion of the plant's anatomy. Such considerations emphasize the fact that chimeras are quite likely much more abundant than is realized.

Chimeras and Morphology

The study of chimeras has proved useful in many different lines of investigation. The morphologist has profited much from the study of chimeras, the most valuable information being a knowledge of the particular layer of the meristem concerned with the formation of the different tissues in the mature plant. That the carpels and hence the seed in angiosperms are produced by the subepidermal layer of meristem was thought before chimeras were understood. Seed production in many chimeral species has, however, confirmed this fact.

Relation of different mature leaf tissues to definite regions of the growing point has been difficult. Jones (1937) has competently treated this problem of chimeras in relation to morphology. Some of the more pertinent points of his discussion are given here.

The shoot apex consists of an inner core which contributes most to the growth in volume, covered by one or more layers of cells which form the tunica, each layer of which is self-perpetuating. Jones (1937) interprets work by Krenke as indicating a whole series of such layers, and makes the statement that "the existence of such self-perpetuating layers is confirmed by the occurrence of stable periclinal chimeras with one-, two-, and three-layered skins." Quoting Jones, "The leaf primordia originate as folds on the stem meristem, the formation of these resulting from the occurrence of periclinal divisions in certain layers. No general statement can be made as to how many layers are involved.

"Even when the origin of the leaf primordium is known, the problem of tracing which part of the mature leaf is related to a particular layer of stem meristem is solved only in part. The primordium is a protuberance having the form of a tapering cone flattened on the adaxial side and represents the future petiolar-midrib region. Two phases of development now occur."

1. The two phases listed by Jones are an increase in radial thickness, due to activity of the sub-epidermal layer resulting in a wedge of newly formed tissue on the adaxial side. Chittenden (1925) described two dichlamydious (the two outermost layers of the tunica differing from the type tissue) periclinal chimeras in *Pelargonium*, transverse sections of the petioles of which showed just such a wedge-shaped strip of tissue. In these green-over-white and white-over-green chimeras this strip stands out in the contrasting green and white tissue.

2. By organization of two marginal ridges of meristem, the leaf lamina differentiates from the upper portion of the primordium, here as with development of the leaf primordium there seems, according to Jones to be great variation in the number of meristematic layers taking part. Jones cites Renner as having found that the edge of the leaf of *Sambucus nigra* results from periclinal divisions of the dermatogen, and work by Pottier who found this the case in certain monocotyledons. Foster (1937) confirms this with his study of *Rhododendron*. Chittenden (1925 and 1927) again confirms these findings by a study of two chimeras, *Pelargonium* "Freak of Nature" and *Hydrangea hortensis nivalis*. In *Pelargonium* "Freak of Nature" the stems, petioles, peduncles and centers of the leaves are pure white with stipules, leaves and calyx having green margins. Were the sub-epidermal layer responsible for the green in the marginal mesophyll of the leaves, a sub-epidermal layer of green cells would extend over the centers of the leaves giving them pale green; therefore, it is considered that the dermatogen is responsible for the marginal mesophyll in this variety of *Pelargonium*. "Freak of Nature" is perfectly analagous with the medioalbinata variety of *Chlorophytum elatum* studied in the present work. The above examples in which the dermatogen gives rise to the marginal meristem are not considered normal by Jones, who writes, "....the outer layer of the tunica normally

gives rise only to the epidermis of the mature plant...."

Imai makes the generalization that most, but not all, dicotyledons arise from three meristematic zones and that all monocotyledons have only two. He does not consider that dicotyledons may have more than three. It is doubtful, however, that with all the enormous diversity and versatility in the plant kingdom any such broad generalizations can be made.

Chimeras and Cytology

Cytology has made a contribution to the study of chimeras and is receiving in return answers to some problems. Cytological study contributed much to the analysis of Winkler's Solanum chimeras. Chromosomal chimeras in crepis have been studied by Hollingshead (1928), and in tobacco by Kostov (1930). The behavior of plastids in the inheritance and development of variegated plants has been a source of information to the cytologist concerning these seemingly inconsistent cell inclusions. White tissue of variegated plants contain plastid differing apparently only in their ability to produce chlorophyll. The cause of the inability of plastids to produce chlorophyll and their propagation and transmission has been the concern of cytologists. Three theories concerning reasons for this inability of plastids have been advanced, vix., (a) an inhibitory action of the cytoplasm of one parent on the plastids of the other, (b) inability within the plastid itself, and (c) nuclear (genetic) factors controlling chlorophyll production, these usually being simple recessives. If both types of plastids are found in the same cell, Yashui (1929), it is considered that the second is the case, whereas, if white and green plastids are never found together, the first explanation is advanced. The several instances in which variegated plants have arisen from crosses of normal green varieties or species, Clausen (1929), Harland (1937), Love and Craig, Dalgreen as reviewed by Chittenden (1927), are accounted for by the first explanation. Sharp thinks that the difference in green and white plastids is entirely developmental, not inherent in the plastid itself, but conditioned by "some invisible differentiation" on "one type of initial body being carried out in the cytoplasm. He does not mention the possibility of green and white plastids occurring in the same cell. This writer finds only one direct mention, Yashui (1929), of such a condition, though Imai (1937) strongly postulates it. Baur, as reviewed by Jones (1934), seems not to doubt that such a condition exists, although cytological proof is impossible, due to the difficulty of distinguishing between undeveloped chloroplasts and chondriosomes or leucoplasts.

Cytological evidence of plastids passing into the egg along with the male gamete is meagre, Correns (1928). Such is indicated, however, by bi-parental, non-Mendelian inheritance of variegation. The few instances of such inheritance tend to indicate that in some plants passage of paternal cytoplasm with plastid primordia into the egg occurs; but in the majority of cases, as indicated by the greater number of cases of purely maternal inheritance of chlorophyll, this does not occur. The relationship between cytological processes and the problem of chimeras and variegation is thus quite apparent.

Chimeras and Genetics

It is the field of genetics primarily which has concerned itself with the problem of plant chimeras. This is explicable by the facts that chimeras arise from somatic mutations and that inheritance in chimeras is often non-Mendelian. An understanding of the chimeral hypothesis has clarified many problems concerning bud variations and somatic mutations, e.g. Clausen and Goodspeed account for the nectarine sporting to peach with the hypothesis that the nectarine is a chimera. Theoretically, nectarine, the recessive condition, would not be likely to mutate to peach, the dominant condition, but were the nectarine a monochlamydius chimera with a core of peach and a skin with the factor for the smooth skin, the peach core would be expected to break through occasionally reverting to peach, such reversion actually occurring rather frequently.

Since each somatic mutation results in the plant becoming a chimera, the problems of bud variation and of chimeras are closely associated. The chance of a somatic mutation becoming known at once is necessarily slight, since the change may occur anywhere in the deeply laid tissue of the plant, or arising in the epidermis of the plant may perpetuate itself for many vegetatively propagated generations before being involved in a tissue where it may express itself. Asexual propagation tends to reveal any aberrant tissue that may be concealed in a species. Thus considerable error is involved in calculating rates of mutation in vegetatively propagated plants. Shamel, Scott, and Pomeroy (1918-1920) found that in citrus, the frequency of bud variation is sufficient to necessitate constant bud selection in maintaining varieties. Many prominent varieties of fruits, vegetables and flowers have originated by so-called bud mutation, which in many cases is really somatic rearrangement of tissue components already there as the result of former mutations.

Many cases of chimeral arrangement in fruits and flowers, Woodcock (1930), Stout (1920), Robinson and Darrow, illustrate the chimeral beginning of bud variations. A white chrysanthemum flower having a sector of yellow in it was sent to Mr. Frost of the Michigan State College Department of Horticulture recently.

Sporting in recognized chimeras is frequent, usually involving only somatic rearrangement. As has been pointed out, it is most frequent in sectorials. Periclinals, Chittenden (1927), most frequently sport to tissues comprising the core; but often there are variations in the number of layers in the skin, and sometimes, Bateson (1919), is found a reversal of core and skin components; and when three tissues are present, one may be omitted, Chittenden (1927).

Chromosome chimeras are those plants in which one or more meristems do not have the usual somatic chromosome complement, e.g. the normal somatic complement in tomato is 24; a plant in which the core tissues contained 48 (tetraploid number) with a skin of 24 chromosomes would be considered to be a chromosome chimera. Chromosome chimeras have been found by Blakeslee and Belling in *Datura*, by Kostov in *Nicotiana*, by Leslie in tomato, and by Hollingshead in *Crepis*.

Chimeras and Physiology

Physiologists have found few phases of the study of chimeras of interest to them, since the waning of interest in the problem of reciprocal effect of stock and scion. Kostov (1928, 1929) has treated immunity relations in plants, and Jones (1934) treats briefly their bearing on chimeras. Spillman (1909) makes the statement that the white cells from *Pelargonium zonale* can manufacture starch.

Variegation

Since the original work of this paper is concerned with the constancy of variegation in a periclinal variety of *Chlorophytum*, a few words of summary concerning variegateds should be included here. In the majority of cases the factor responsible for the inability of a cell to develop chlorophyll is a single recessive gene. Instances of such are too numerous to cite here, since many are included in the bibliography. The cases of maternal inheritance account for most instances of non-Mendelian inheritance, instances again being too numerous to cite. Non-Mendelian-bi-parental inheritance postulates contribution of plastids through the pollen tube from the paternal parent and their joint control with those included in the egg cell of development of chlorophyll in the progeny. One of the commonly cited examples of the above (Ikeno 1917) proved to be an infectious chlorosis. Jones (1934) cites Collins (1922) as having found non-Mendelian-bi-parental inheritance in *Chlorophytum elatum*, the variegated plant with which this study deals. Repeated examination of the work, however, fails to disclose any such statement by Collins, or any grounds for such interpretation by Jones or Chittenden, who also cites Collin's *Chlorophytum* as an example of this type of plastid inheritance. This writer has not had opportunity to examine the original work of the other examples, Baur (1908) and Renner (1924), as cited by Jones and Chittenden of this type of inheritance.

Variegation sometimes is found in the offspring of species crosses. Chittenden assumes this the result of the plastids of one species not being functional in the cytoplasm of the other. It is not clear, however, why complementary factors for chlorophyll deficiency, one located in each of the species, and both being necessary for expression, could not be responsible in this case. Harland, working with two species of cotton, found double recessives for chlorophyll deficient.

No class of chimeras other than the variegated plants prized for their ornamental value, and bud sports, and a few others such as *Cytissus Adami* and the *Crataego-Mespili*, cultivated as oddities, has as yet achieved economic importance. Imai states that cultivation of periclinal forms of *Pelargonium* became a fad in Japan and that plants of named varieties have sold for very high prices. Jorgensen and Crane (1927), however, have tried using Winkler's grafting methods to produce a potato with periclinal skin of tomato which would be resistant to *Phytophthora*. Such is theoretically possible, but Jorgensen failed to get the right combination. Asseeva (1927), however, found that several varieties of potatoes in cultivation were periclinal chimeras, both tissues in some cases being of well known varieties, and that bud sports in potatoes were often the result of somatic rearrangement of chimeras.

EXPERIMENTAL

Introduction

Species and varieties of Chlorophytum long have been grown and admired by gardeners and florists. One species, C. comosum, Hope (1873), was admired and given literary significance by Goethe in 1828, who wrote a letter concerning this plant in which he praised its beauty. The most popular of the chlorophytums are the variegated forms of C. elatum and C. comosum, with the former of which this paper deals. Two forms of each of these species are admired for their attractive green and white leaves and their graceful flowering scapes. Of the two types, both of which are represented in each species, one (the medio-albinata variety) has the white tissue in bands down the centers of the leaves and the leaves of the other (the albo-marginata variety) have white margins, the green tissue being in the center of the leaf in this case. They are considered, in fact, to be reciprocal forms of periclinal chimeras. The medio-albinata form of C. elatum was studied in this work.

Collins (1922) studied both forms of both species of this plant anatomically and genetically, determining their structural nature and finding that the chlorophyll production is maternally inherited, invariably, no matter what the source of the pollen, reproducing in the seedling the type of tissue which bore the ovule. The young capsules when borne on normal tissue are green and when borne on chlorophylless tissue are white, thus making it possible to determine which type of tissue bore the ovule.

The literature dealing with variegated plants recognizes the fact that there is considerable variation in the proportions of green and white in the variegated tissue. Apparently, however, little attention has been paid to this aspect of the subject which is a matter of both academic and practical interest. It was therefore decided to make a study of both the quantitative relationships of the two kinds of tissue found in the leaves of a variegated plant and of the permanency of such quantitative differences from one vegetative generation to another.

Chlorophytum is a liliaceous plant belonging to the tribe Asphodeleae. The species forms are pure green, origin of the variegated tissue being unknown. Small white flowers are borne in the spring on slender terete scapes, which after the flowering season produce vegetative shoots that under moist conditions produce roots. New basal crowns develop, thus furnishing two types of material for vegetative propagation. This writer has noted toward the end of the flowering season small vegetative shoots near the apex of the scape arising from what appeared at first to be a flower, i.e. one or two petals or sepals and perhaps a stamen being produced at the point which was producing a vegetative shoot. Thus the plant in some instances appears to be viviparious. After the flowers are produced the old crowns gradually die down and are replaced by new ones. In the green forms the scape is green, scape leaves, scape borne shoots, and young capsules being green also. In the W.C. (white center) form the scape is white, the scape leaves and the vegetative shoots borne on the scape have the white center pattern of the leaves, and the ovary of the young flower is white.

As observed by Collins the white portions of older plants often become comparatively green. Young plants, however, placed in a shady house are found also to develop chlorophyll in the ordinarily white tissue. The white tissue then seems to be what Lindstrom (1924) calls a 'virescent albino'. Collins postulated a bleaching or inhibitory factor present in the white tissue which weakened with age. In view of the fact that young plants also show a greening of the white tissue, it would seem better to assume absence of a factor to produce chlorophyll in intense light, but presence of another which produces it in diffuse light. Lindstrom (1924) found 8 factors for the production of chlorophyll in maize, thus making the conception of two factors for chlorophyll production in chlorophytum an easy matter. The above hypothesis is borne out, too, by the fact that normal green tissue in intense light is noticeably lighter in color than when grown in partial shade. Plants growing in a greenhouse with no whitewash applied for shade retain their healthy green color until longer, brighter days begin, when their color begins to fade. Albino seedlings borne by W.C. plants survive longer if grown in the shade and some appear to be developing chlorophyll. It is too early yet, though, to be sure that they will survive.*

The following observations on the general anatomy of the leaf of the W.C. form were made by Collins and confirmed by this work.

Guard cells in upper and lower epidermis over white areas were found, as were those of the epidermis of the white flowering shaft, to contain chloroplasts.

During the course of the experiment seeds, totaling near a hundred were germinated, all of which produced albino seedlings. A few seeds were gathered from totally green plants, but for some reason none germinated.

No pure white or pure green shoots or leaves were noted. A few leaves, however, were noted in which the white tissue extended to the edge of the leaf, i.e. the green edge was not continuous.

Collins, as if he doubts the hypothesis, says little concerning the chimeral nature of his chlorophytum, but theorizes at length about a 'rhythmic somatic segregation'. In speaking of Chodat's _Funkia Sieboldiana_, he says, "In it the sub-epidermal layer is green but the epidermis is albinotic. This appears from the fact that the guard cells whether taken from above the white or from above the green parts of the leaf, are devoid of chlorophyll. On the contrary, he found that in the form with the white center--

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* All the seedlings died.

F. Sieboldiana var. medio-variegata--the guard cells are green whether taken from the green or the white parts. Hence in consideration of the condition of the epidermis, each variety may be spoken of as a periclinal chimera. It was this observation which led me to examine the guard cells in detail, and the investigation of the leaves of *Chlorophytum* has shown that in all essential respects *Chlorophytum* agrees with *Funkia*."

Later, however, Collins makes the statement that, "In *Chlorophytum* the leaves originate as successive collars pushed off as it were from the rim of the meristematic zone," as though admitting only one meristematic layer. After discussing peculiar types of variegation patterns in *Tradescantia*, *Reineckia*, and *Dactylis*, he says, "No doubt in the variegated forms of *Chlorophytum*, blocks of albinotic cells occur in the apical meristem, but how these contrive to originate the orderly segregation of the chlorotic condition to the centers or edges of the leaves having regard to leaf origin is not clearly evident."

It is thus obvious that Collins does not think of the variegated forms of *Chlorophytum* as belonging to the common type of periclinal whose component tissues comprise different self-perpetuating meristems. It, however, does not seem necessary to postulate any rhythmic segregation of green and albinotic cells from a mixed growing point considering in the case of the white centered plant, the green guard cells over the white central areas of the leaf, and inheritance of the characters belonging to the sub-epidermal layer. Collins, too, mentions irregular chimeras from seed borne on green striped flowering scapes which (obviously being sectorials or periclinals) resolved themselves into the stable periclinal arrangement.

This author therefore considers the albo-marginata and medio-variegata forms of Chlorophytum elatum and C. comosum to be simple, stable, periclinal monochlamydious (having one-layered skins) chimeras. The leaves, it would seem, are formed, as is found to be the case with Sambucus and certain monocotyledons by Renner and Pottier, as cited by Jones (1937), and in Pelargonium "Freak of Nature" and Hydrangea hortensis nivalis by Chittenden (1925), from the two outermost layers of the tunica. These workers found in these plants that the dermatogen gave rise to epidermis and by periclinal division to the marginal mesophyll of the leaves. Thus the green dermatogen in Chlorophytum elatum medio-albinata produces the green edges to the leaves. That the second layer of he meristematic tunica is not concerned in the formation of the marginal mesophyll is shown by the fact that seed borne by the plant are albinotic, the sub-epidermal layer of the tunica having been proved by Baur (1909), as cited by Bateson (1926), to be responsible for the production of the carpellary leaves. That the green tissue is only one cell layer thick in the tunica is proved also by the fact that chlorophyll is produced in several layers of the scape mesophyll in the green plant and is confined to the guard cells of the epidermis in the scape of the flowering plant. Collin's theory of an 'arc of albinoc[1] cells so travelling in segregation' "that they will trace out a spiral band passing around the apex in correlation with the spiral of leaf origin" presupposes areas on the stem free to produce totally green and totally white plants. Such plants, as has been mentioned, never occur. Since lateral shoots are axillary in origin it is possible that they too correlate with Collin's supposed spiral arrangement of the segregating albinotic or green tissue. In the course of this experiment, however, several plants were decapitated at random and all buds formed, whether adventitious or not, produced the typical arrangement of the white-centered green leaves. Had there been any areas of potentially white tissue reaching to the epidermis of the stem, it seems that some white shoots would have been produced from adventitious buds in this region. Another proof of the periclinal structure of the plant, could it be accomplished, would be production of white shoots from root cuttings. This was attempted but with no success.

Another phase of this study concerned itself with investigating the constancy in amounts of green, white and intermediate tissues in lines propagated asexually. Gardner,

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[1] In the case of the albo-marginata variety.

working with *Pelargonium* "Mme. Saleroi," an albo-marginata variety, (unpublished results) has been able to separate out strains of comparatively green and comparatively white plants in the course of several vegetative generations. By selection of cuttings Gardner is able to produce a strain in which the white margin of the leaf is very narrow and another in which the margin is fairly wide, the white area comprising perhaps half the leaf. Sports (somatic rearrangements in which either the green or the white tissue is omitted) are comparatively frequent.

Such studies have theoretical value, since in the proposed disease resistent chimeral potatoes of Jorgensen (1928), it will be necessary to maintain an optimum depth to the skin of tomato tissue. To be certain of resistence, the skin will need to be two or more cell layers thick in the leaves, but not thick enough in the stem to interfere with tuber formation. Studies of the amounts of tissue formed by the skin components in variegated plants, if large enough numbers of plants are used, should indicate the number of layers of meristem concerned in the formation of leaves in a species or variety. If within a variety the distribution of the amounts of skin tissue had a single mode, the interpretation would be that two layers of the meristem were involved in the formation of the leaves, only monochlamydius forms being present; if a bi-modal distribution indicating presence of both mono- and dichlamydius

forms were obtained three layers of meristem could be assumed to be concerned.

Methods

In January 1937 thirty-four plants of *Chlorophytum* which apparently varied considerably in amount of green were selected from those growing in the horticultural greenhouse at East Lansing. Four of these plants were the normal green type of *C. elatum*, two were *C. comosum* var. medio-albinata, and twenty-eight were of *C. elatum* variety medio-albinata. Later one plant was observed among those not selected which was of the albo-marginata type. Measurements in millimeters of each tissue type in each leaf of sufficient size were made in all plants. The measurements were recorded as mm. of green, mm. of white, and mm. of intermediate tissue, intermediate tissue, as indicated by a lighter shade of green, being that in which green did not compose the entire thickness of the leaf. The plants were then propagated as rapidly as possible both from division of the crowns and from the vegetative shoots produced on the scapes. The parent plants were numbered from 1 to 34 in no particular order with reference to apparent width of the green and white strips. The progeny resulting from crown divisions were designated as 1A, 1B, 2A, 2B, etc., the number indicating the parent plant and the capital letter signifying a crown division. Progeny resulting

from scape offshoots were designated similarly, a small letter being used to indicate scape origin. It was thought at first to compare amounts of green produced by each type of shoot, but insufficient numbers of plants prevented this comparison.

Considerable difficulty was had at first in determining the amounts of white and intermediate tissue since they in most cases were somewhat intermixed. After several trials, however, it was found the quickest and most accurate method was first to determine the combined width of the green and intermediate portions and with the ruler still held in place to estimate as closely as possible the width of each of the white and intermediate strips. This was found by comparison with results obtained by separate, very careful measurement of each minute strip of intermediate tissue to be relatively accurate. The combined width of the green margins on each side of the leaf was calculated, subtracting the combined widths of the intermediate and white bands from the total width of the leaf. This remainder method proved to be more rapid and as accurate as measuring each individual and separate strip of tissue and totaling them. Obviously, due to the varying width along the length of a given leaf of, for example, the green margins, considerable error would be involved in any method of estimating relative amounts of green, white and intermediate tissue. Since, however, we are interested in comparative values for amounts of the different tissue components, the methods used seem as satisfactory as any.

Results

The green plants. As was expected, all progeny of the green plants were green.

Chlorophytum comosum. Only two plants of this species were observed. The leaves of *C. comosum* are much narrower than those of *C. elatum*, the white tissue being in a narrow band down the midrib of the leaf, the white tissue constituting a much smaller portion of the leaf than in *C. elatum*. In the leaves of the two plants on which measurements were taken it is interesting to note that the average widths of the white strips was for plant 14 1.47 mm., the average width of all the leaves being 13 mm. In plant 14a the average width of the albinotic strip was 1.56 mm., average width of the leaves being 9 mm. Plants of this species being too few, no further data was taken.

Chlorophytum elatum variety *albo-marginata*. Of the 28 plants to begin with, only 10 yielded progenies large enough to provide sufficient data with which to work. Since the green tissue comprises the skin of the chimera, final results were tabulated in terms of amount of green tissue.

Analysis of Data. In analyzing the data, totals for each of the three tissue types (green, intermediate, and white) were prepared for each parent plant and each of the progenies. Percentages of each tissue type for each parent plant and each of the progenies were calculated. Since averages of percentages are not mathematically correct, these values gave no value representing the entire progeny with which to compare the percentages of green in the parents. It was therefore thought best to determine the average width of green per leaf for each parent plant and each of the progenies and the mean average width of the leaves of each of the progenies. These last two values were then comparable. Standard deviations were then calculated for the mean average width of each of the progenies.

TABLE I

PLANTS IN DESCENDING ORDER OF AMOUNT
OF GREEN OF PARENTS

No. of Parent	% Green in Parent	Av. Width Green Per Leaf in Parent	Mean Av. Width Green Per Leaf in Progeny	Standard Deviation of Col. 4
29	37.13	6.31	6.51	1.146
19	36.13	5.38	6.15	1.381
8	32.29	6.20	6.35	1.105
28	32.14	5.40	5.72	1.199
34	29.73	5.39	6.52	1.042
20	28.54	5.96	5.63	.692
22	28.41	4.81	5.63	1.015
25	27.48	5.19	6.52	.977
9	26.15	4.55	6.23	1.310
16	24.73	5.70	7.66	1.161

In Table I the ten parents having the largest number of progeny are listed in order of their descending percentage of green. The third column lists the average width of green per leaf in the parents, and were the average widths of the leaves equal in all cases, these figures would correlate perfectly with those in column 2. Column 4 lists the mean average width of green in the progenies, and column 5 presents the standard deviations of these values.

Examination of the figures in column 4 of Table I shows that, although the parents are arranged in order of descending percentages of green, mean average width of green in the progeny shows no such trend. There is obviously no significant relation then between mean average width of green in the progeny and percentage of green in the parents, nor with the average width of green in the parents. High standard deviations further emphasize this fact.

In Table II the percentages of each type of tissue for the parents are presented, followed by like values for each of the progeny. Parents with their progeny are listed in descending order of the percentages of green in the parents, and the progeny following each parent are in like order.

TABLE II

PARENT PLANTS WITH OFFSPRING IN ORDER OF AMOUNT OF GREEN

Plant	Green %	Int. %	White %
Par.29	37.13	25.74	37.13
29c	50.00	33.33	16.67
29b	50.00	21.74	28.26
29f	48.39	29.03	22.58
29e	45.76	30.51	23.73
29a	45.45	27.27	27.28
29A	35.71	33.33	30.96
29B	29.38	45.76	24.86
Par.19	36.13	28.57	35.29
19Fb	51.06	29.79	19.15
19Hc	50.00	18.75	31.25
19Ha	49.02	17.65	33.33
19Fa	47.46	27.12	25.42
19Fc	46.51	32.56	20.93
19Aa	42.98	32.23	24.79
19Hb	42.31	28.85	28.84
19E	32.17	32.88	34.96
19Da	30.95	34.52	34.53
19D	29.95	31.47	38.58
19G	29.66	28.06	42.28
19C	25.74	37.04	37.22
19F	23.83	35.27	40.90
19A	19.67	32.22	48.11
19H	19.21	25.66	55.17
Par. 8	32.29	20.83	46.88
8b	55.00	25.00	20.00
8Cd	53.33	24.44	22.23
8a	49.09	27.27	23.64
8Bc	45.45	27.27	27.27
8Ce	43.48	26.09	30.43
8Be	41.98	23.46	34.56
8Ba	40.91	25.00	34.09
8Cf	38.10	26.19	35.71
8Bd	37.76	26.57	35.67
8Cg	37.04	29.63	33.33
8E	36.22	24.05	39.72
8Ca	34.96	28.71	35.33
8C	33.41	25.27	41.32
8D	33.26	25.89	40.85
8Cb	32.30	17.70	50.00
8Db	31.35	36.36	32.29
8Da	31.33	23.61	45.06
8H	30.25	20.17	49.58
8Cc	28.21	31.47	40.32
8B	27.18	25.50	47.32
8F	26.22	20.12	53.66
8A	21.85	37.41	40.74
8G	19.42	28.64	51.94
Par.28	32.14	26.19	41.66
28F	41.63	33.01	25.36
28M	38.21	37.16	34.63
28E	37.73	32.23	30.04
28D	35.86	36.87	27.27
28H	35.12	32.35	32.53
28L	30.73	33.72	35.55
28I	30.23	50.58	19.19
28B	26.32	22.63	51.05
28G	14.29	64.29	21.42
Par.34	29.73	27.82	42.45
34e	58.18	14.55	27.27
34f	53.66	31.71	14.63
34a	53.57	25.00	21.43
34h	44.44	37.04	18.52
34b	44.16	25.97	29.87
34g	44.07	30.51	25.42
34c	40.54	24.32	35.14
34d	37.04	33.33	29.63
Par.20	28.54	35.53	35.93
20d	51.72	20.69	27.59
20a	50.00	16.66	33.34
20Aa	50.00	16.67	33.33
20c	44.68	36.17	19.15
20Ab	41.86	32.56	25.58
20e	40.74	22.22	37.04
20E	35.22	23.91	40.87
20b	34.85	19.70	45.45
20D	32.33	38.79	28.87
20A	27.87	30.44	41.69
Par.22	28.41	25.00	46.59
22b	42.86	21.43	35.71
22c	42.50	30.00	27.50
22a	38.46	32.69	28.85
22Aa	32.91	26.71	40.38
22A	24.31	24.81	50.88

TABLE II (con't)

Plant	Green %	Int. %	White %
Par.25	27.48	32.12	40.40
25h	51.85	24.07	24.08
25b	51.67	31.67	16.66
25a	50.79	25.40	23.81
25f	50.00	25.00	25.00
25c	48.78	26.83	24.39
25e	47.73	25.00	27.27
25g	38.18	36.36	25.46
25A	34.96	23.62	41.42
25d	22.22	22.23	18.52
Par. 9	26.15	21.84	52.01
9h	57.45	21.28	21.27
9e	55.00	25.00	20.00
9g	45.95	8.11	45.94
9c	43.18	27.27	29.55
9f	41.38	37.93	20.69
9i	41.38	20.69	37.93
9a	40.00	24.00	36.00
9j	38.10	30.16	31.74
9d	34.54	30.91	34.55
Par.16	24.73	31.80	44.47
16c	68.97	6.89	24.13
16f	52.00	24.00	24.00
16e	51.02	26.53	22.45
16d	47.61	30.95	21.43
16Aa	44.23	28.92	26.92
16g	43.18	22.73	34.09
16A	39.25	28.33	32.42
16a	33.75	32.18	34.07
16b	33.41	24.63	41.95

This table is presented merely to show the range of variation for the progenies. The range of variation is noticeably greater in the larger progenies.

Although the percentage of green tissue in the parents is more indicative of the comparative amount of green tissue, this measure being free from the effect of varying width in the leaves, it is perhaps not as comparable with the mean average widths of the leaves of the respective progenies as is the figure for the average width of green. Table III therefore presents the parents in order of decreasing average width of green in the leaves for comparison with the mean average widths of green in the progenies. Here again, however, there is no detectable trend in the values for the progenies and hence no significant relation of amount of green tissue in the parents to amounts green in the progenies.

TABLE III

PARENTS IN DESCENDING ORDER OF AVERAGE WIDTH OF LEAVES COMPARED WITH MEAN AVERAGE WIDTH OF LEAVES IN PROGENY

Plant	Av. Width G. mm.	Progeny Mean Av. Width G. mm.
29	6.31	6.51
8	6.20	6.35
20	5.96	5.63
16	5.70	7.66
28	5.40	5.72
34	5.39	6.52
19	5.38	6.15
25	5.19	6.52
22	4.81	5.63
9	4.55	6.23

Discussion

On the basis of results obtained in this study of a small number of plants, there would seem to be no point to selection in Chlorophytum variegateds in order to obtain strains of comparatively green and comparatively white plants, as Gardner has been able to do with Pelargonium Mme. Saleroi. Although it is recognized that different results might have been obtained had a larger number of plants with a wider range of variation been observed, and had the study extended over a longer period of time, this is consistent with the idea that the variegated plants of this species are monochlamydius periclinal chimeras in which the leaves are produced by the two outer layers of the meristematic tunica. If, as supposed, the outer layer of the tunica is responsible for the epidermis and the margin-mesophyll of the leaf, in this medio-albinata variety of C. elatum, periclinal divisions in the dermatogen are responsible for all the green tissue of the leaf margins. It is easy, therefore, to understand why the proportion of green produced, i.e. the relative width of the green margins, is not constant. The number of periclinal divisions is probably affected by a number of factors such as the general growth rate of the plant, or varying growth rates at the times when the length of the leaf is increasing and the time when the leaf lamina differentiates and grows from the leaf primordium. That such assumptions are true is indicated by the observation made by Collins and confirmed here that young rapidly growing plants appear to have wider bands of white tissue and comparatively narrower margins of green tissue.

With the exception of "Freak of Nature", leaves of Pelargoniums are thought to be formed by the action of three or more layers of the meristematic tunica, mono-, di- and even trichlamydius forms being possible. Efficacy of selection in this species can possibly then be attributed to the ease of segregation of plants with different numbers of layers in the skin tissue component.

Summary

1. The purpose of this study was to verify the periclinal chimeral nature of Chlorophytum elatum, variety medio-albinata, and to determine the efficacy of selecting for plants with more or less green in the leaves.

2. Thirty-four plants were studied, four of which were the green type form of C. elatum and two were C. comosum var. medio-albinata.

3. Measurements were made of the width of the green margins, of the white center strips and of the strips of mixed green and white tissue called intermediate in each of the parents and the progeny as derived from vegetative propagation.

4. Anatomical and genetical evidence gathered by Collins and confirmed by this work indicates a monochlamydius periclinal structure of these varieties of *Chlorophytum*.

5. No significant relation was found between amount of green tissue in the parents and the progeny.

ACKNOWLEDGMENT

The writer is very grateful to Professor V. R. Gardner for invaluable aid in the organization and pursuit of this work.

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