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## Contents

Nature of Plant Sports. HAIG DERMEN.....	123
Forty illustrations from photographs furnished by the author	
Introduction by GEORGE M. DARROW	
A Book or Two.....	174
The Gardeners' Pocketbook	
<i>Meriania nobilis</i> . W. H. HODGE.....	177
A Technique for Growing Azaleas in Bermuda. JOHN KNOWLTON.....	179
Two Experiences with Tree Peony Propagation. MAUD R. JACOBS.....	181
Southern Viburnums. E. J. HORDER.....	182
<i>Spathicarpa sagittifolia</i> . D. G. HUTTLESTON.....	183
New Guinea Trumpet-Creeper. W. H. HODGE.....	184

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JULY COVER ILLUSTRATION

(G. HAMPFLER)

A flowering plant of *Spathicarpa sagittifolia* as grown under cultivation at Longwood Gardens, Kennett Square, Pennsylvania. The caterpillar plant is native to Brazil.  
... See details on Page 183

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G. HAMPLER

*Tecomanthe venusta*

*First flowering plant in the Western Hemisphere  
of the New Guinea Trumpet-Creeper.*

[See Page 184]



# Nature of Plant Sports

HAIG DERMEN

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## I. Introduction

GEORGE M. DARROW

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This article might have been entitled "A Key to the Mystery of Plant Sports" since it unravels so precisely the nature of variations or sporting in many plants that have puzzled horticulturists, plant breeders and plant hobbyists in general. The discussion on the *Nature of Plant Sports* by Dr. Dermen summarizes a part of his work in one field of botany in which he has been interested for much of the past twenty years. Dr. Dermen came to the fruit research group of the U. S. Department of Agriculture from Bussey Institution of Harvard University in 1937 to study cytological problems of fruits. He soon became the world authority on the cytogenetics of fruits and on the use of colchicine in obtaining polyploids or cytological sports. In most cases the polyploid plants proved to be chimera with only certain tissues being tetraploid, the rest being diploid.

In the following pages he tells clearly and simply what plant sports are. It will be a stimulating experience to the reader. By following his description and discussion, it is possible for a horticulturist to understand what a plant sport is and what to expect of a plant sport. The discussion is basic to the propagator of vegetative sports, such as color sports of apple, early and late maturing sports of peach, or thornless blackberry, as well as to the breeder who wishes to use a polyploid plant in breeding, to the horticulturist who is curious about variegations and all sorts of chimera forms, and to the teachers of botany and horticulture who are interested in the problems of specific origin of tissues in plants. This article also may be of particular interest to radiologists who attempt to induce mutations in plants, and to virologists who would be interested in the diagnosis of some plant defects whether they are symptoms of virus effect or are expressions of genetic vegetative mutations.

Although the approach of the article is toward an understanding of basic facts and the article itself may seem forbidding to non-professional botanists, this must not mislead the reader since Dr. Dermen has really made conscious effort to make all the essential facts as simple and clear as possible or practicable. However, this is not like a story to be read hurriedly. It will be slow reading for most people who wish a thorough understanding of the subject.

Cytological chimeras—termed cytochimeras—obtained from colchicine-treated peaches and naturally-occurring sports of apples are illustrated and explained. An understanding of these makes it possible to understand naturally-occurring vegetative sports such as color sports of fruits and leaf variegations. Many points of a basic nature in the article have not been reported previously.





Fig. 1. A variegated poinsettia leaf and a peach-nectarine fruit.

## II. The Anatomy and Cytology of Chimeras

The appearance of vegetative sports and their behavior have puzzled and intrigued plantmen and investigators for generations. The appearance of a fuzz-less peach or of a peach with patches of white and yellow flesh, or the development of branches with variegated leaves on a privet or holly plant is an example of a phenomenon recurring through the centuries that man has cultivated plants. Explanations in the literature on the subject of vegetative sports have not been fully adequate. A more precise explanation of sporting as described in this article has been possible only in recent years (6).<sup>\*</sup> Studies of *diploid* (sum of chromosomes of two sex cells, called gametes), and *polyploid* (a multiple of the number of chromosomes of diploid) *chimeras* (6, 26) in plants resulting from the use of the drug colchicine have given us a better understanding of the nature of vegetative sports.

The present article has been prepared to help readers of this Magazine understand the nature of common sports by describing the origin and make-up of a

few of them, such as leaf variegation and fruit sports (Fig. 1). It will also explain why some sports are fixed, and why and how others revert to their original forms. For example, when we examine variegated leaves of plants, such as privet, English ivy, or geranium, we will see that the pattern of the contrasting colors is never exactly the same in any two leaves. In extreme instances, some leaves would appear to have reverted to the original green color and others would have become completely colorless or may have taken entirely the sporting color. Similarly, on a tree of a red fruited sport of apple, a branch may be found with fruits with less color that resemble those of the original variety, while the fruits on the rest of the tree have the intense coloring, characteristic of the sport variety. This phenomenon is called reversion of sport to normal, an undesirable phenomenon, horticulturally speaking.

As we shall see, the story of sports is closely tied to the development of the *growing point* of the shoot. The growing point is also called the *shoot tip*, *shoot apex*, *apical meristem*, or *apical dome*. Therefore, a close study of this

<sup>\*</sup>See Numerical References on Page 172.



region of plants is very pertinent. When a prepared microscopic section of a bud or shoot tip is examined under a high-power microscope, we see at the tip a broad, usually curved area that grows rapidly from which new leaves, stem, flower, and fruit develop. Figure 2 shows a highly magnified section through a shoot tip of peach with the growing point indicated by an arrow. Masses of cells above and along the sides of the growing point represent sections of leaves and leaf stipules, while the mass of tissue just under the growing point is

the part of the twig from which stem tissues develop. When a plant is actively growing, the cells at the tip divide frequently, the shoot tip continuously grows outward, and leaves are initiated along its margin. A shoot tip, instead of growing into a twig with leaves, may also develop into a flower.

Generally speaking, vegetative plant sports are more or less permanent changes or variations from normal. They are brought about principally by a genetic change (mutation, sporting) in one or more genes or by chromosomal

**Fig. 2.** *A microscopic longitudinal section through a peach shoot tip. (Apical dome of shoot tip indicated by arrow.)*





changes occurring originally in the nucleus of a single cell at the very center of a growing point of a bud or shoot. Some sports are also known to have occurred from a mutation outside of the nucleus of a cell, in the cytoplasm. The first group of sports are of nuclear origin and those in the second group are of cytoplasmic origin.

Many mutations can be recognized when growing points have given rise to leaves, flowers, or fruits. Other mutations affect the physiology of the plant and may not be so easily recognized. As stated above, details of this phenomenon have become clearly evident only in recent years as a result of experiments in polyploidy (doubling of chromosomes), induced by use of the chemical colchicine to produce new varieties of plants. This induced polyploidy, termed *colchipoity*, often may result in giant forms of flowers and fruits, or it may change sterile species hybrids into fertile forms. The polyploidizing effect of colchicine occurs in rapidly dividing cells. Therefore, colchicine is applied to buds of actively growing plants. The polyploid effect of colchicine is observed first in the leaves developing from a treated bud and later in flowers and fruits (5, 14, 20).

*Cytochimeras in peach.*—In experiments performed at the Plant Industry Station, Beltsville, Maryland, first with cranberry plants (19) and later with peach (13) to induce doubling of chromosome numbers, it became evident that only rarely did chromosome doubling take place in all tissues in the new growth from a treated bud. Instead, we usually obtained *chimeras*. It meant that in some tissues of these plants the chromosome number had doubled once, becoming *tetraploid* (double of diploid); in other tissues, where no change had taken place, they remained *diploid*. The resulting plant (part tetraploid, part diploid) is known as a *periclinial chimera*. In order to understand this phenomenon, detailed microscopic examinations were made of growing points, leaves, stem, flowers, and fruits of both normal and chimeral materials at their early stages of growth (7, 11, 12, 13, 14, 18).

Figure 3 shows longitudinal sections through shoot tips of six peach twigs. The broad curved portion in these illus-

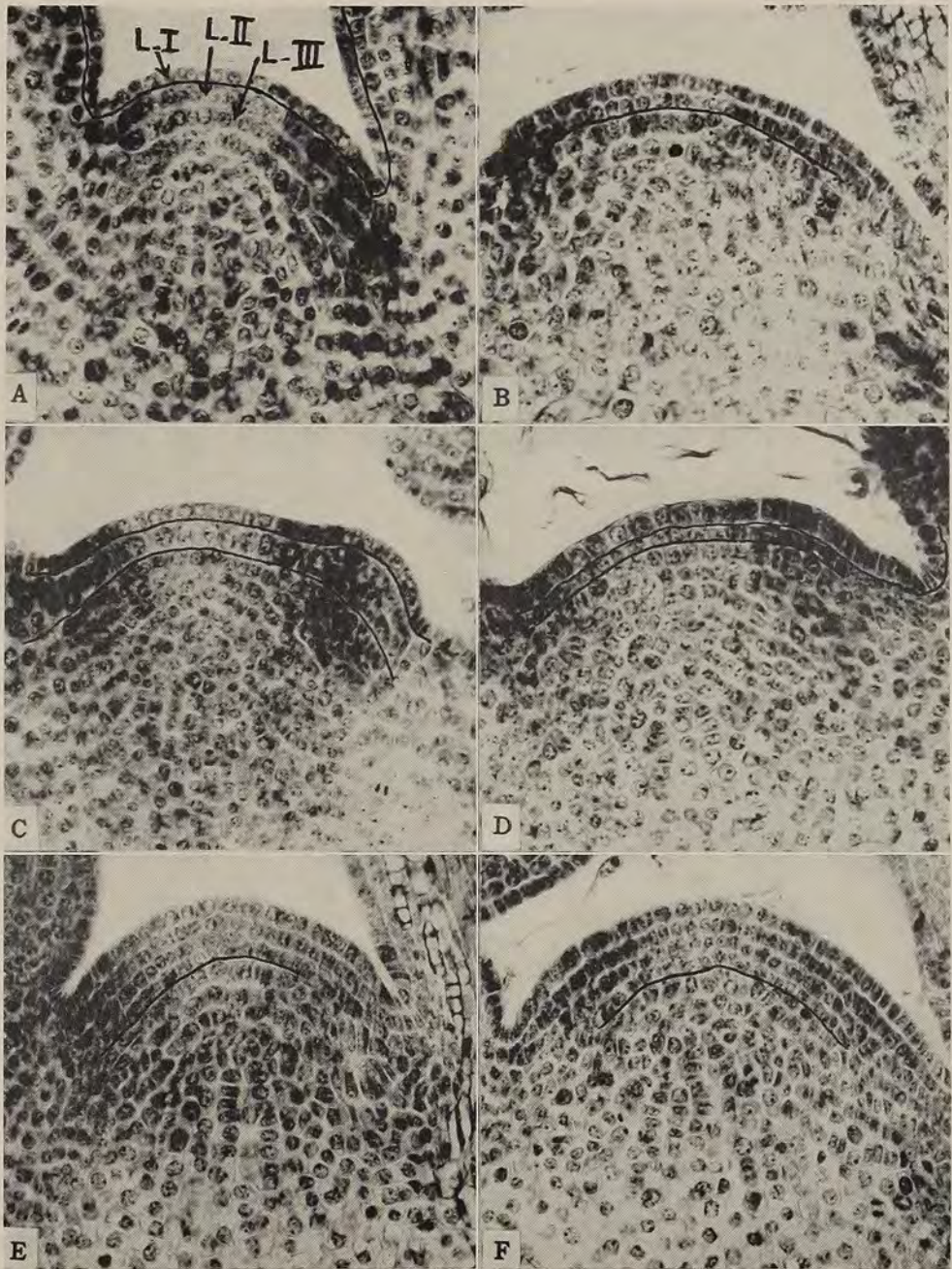
trations represent the very tip of a shoot, the same apical dome region as indicated in Fig. 2, but at a higher magnification. As the cells divide and the shoot grows forward, small bulges occur at the sides of the apical dome at definite intervals. One such bulge is seen at the right side of the dome in Fig. 3-C. Such bulges grow into leaves, and are the very beginning of leaf formation.

Since development of plant parts is initiated at the growing point of a bud or twig, chromosome doubling following colchicine treatments was looked for in the tip region of shoots. The tips in Fig. 3 represent six different types of partial polyploidy resulting from two different chromosome numbers in shoot tips. Significant features of these tips are: 1) cells are normally arranged pretty much in layers, and 2), if colchipoity is induced, it is usually limited initially to one of the layers in the shoot apex. Thus, as a result of colchipoity, we find the dual chromosome condition in a shoot apex to be precisely delimited. *The term chimera is given to such duality whether it represents a difference in chromosome number, as in the six growing points shown in Fig. 3, or simply a difference in genes in different layers of cells, expressed in color or otherwise.* The condition of duality in chromosome number is termed *cytochimera* (cyto—from cytology, the science of cells) or *periclinial* (parallel with the circumference, for example, of a stem)—*cytochimera*. Duality in color of leaves due to gene mutation or cytoplasmic mutation is termed *variegation*.

In the shoot apex the arrangement of cells in distinct layers is due to division of cells in the upper portion of the dome in a vertical plane, that is at right angles to the surface of the dome. Why the cells in the upper region of the dome divide predominantly in this manner is still unsolved. The cells located underneath the outer few rows divide in more haphazard fashion—vertically, horizontally, or diagonally, with respect to the surface. Consequently, twig growth is both in length and in width.

The upper illustrations in Fig. 3 show four different chimeral shoot tips of peach. Each represents a different kind of chromosomal-periclinial-chimera composed of diploid and tetraploid regions resulting from colchicine treatment.





**Fig. 3.** Microscopic longitudinal sections of six shoot tips of peaches, indicating variously diploid-tetraploid chimeras.



The lower two illustrations in Fig. 3 show tips of two twigs developed laterally on a shoot, the dome of which is illustrated in Fig. 3-B. These photomicrographic sections are magnified about four hundred times. They were examined at much higher magnification, however, in order to establish whether cells in certain regions were diploid or tetraploid. This cytological difference was determined mostly from the size of nuclei, but in part from differences in cell size and the chromosome number in cells in which chromosome number could be determined or estimated (for more detail, see references 12, 18). As the diploidy and tetraploidy of regions were determined under the microscope, an ink line was drawn between differing regions on the photographic prints. This was done so that different chromosomal regions could be identified at a glance.

Close observation of Fig. 3-A shows that the cells above the ink line are small and that the nuclei in cells of the single row designated L-I are small compared with those in layers of cells L-II and L-III. Thus L-I was determined to be diploid and L-II, L-III, and deeper tissue were tetraploid. L-I, L-II, and L-III are terms applied to layers of cells in all growing points described in this article. Fig. 3-B shows a dome in which the upper layers, L-I and L-II, are diploid and the rest of the tissue in the dome is tetraploid. In Fig. 3-C, L-II—between the two ink lines—is tetraploid and L-I, L-III and the tissue deeper in the dome are diploid. Fig. 3-D shows the reverse of the type illustrated in Fig. 3-C. Here L-II is diploid and L-I, L-III and the inner tissues are tetraploid. The chromosome number (ploidy) of all inner tissues was usually found to be the same as that of the third layer, L-III.

No type of chimera condition in the plants studied was strictly permanent. The most stable chimera condition was the type in which L-I differed from the inner tissues. It is obviously due to the fact that the plane of cell division becomes increasingly random in cells located farther away from the surface of the dome, as indicated previously, whereas the plane of cell division in L-I is varied seldom. As mentioned above, the two domes shown in Figs. 3-E and 3-F are from lateral twigs of a shoot, the dome of which is shown in Fig. 3-B. In

these two domes, the layers of cells above the ink line are diploid and the tissues beneath are tetraploid. As a tree with the chimera condition shown in Fig. 3-B grows and expands, some twigs will have this arrangement; a very few will be of the type shown in Figs. 3-E and 3-F; but some will be entirely diploid. Thus, a chimera of the type 2-2-4 (diploid-diploid-tetraploid) may become 2-2-2 (diploid in all three layers) and a chimera of type 2-4-2 may change to 2-4-4. Very rarely 2-4-4 type will change to 2-2-4 or 2-2-2. In one instance, an entirely diploid branch was found on a 2-4-4 chimera peach tree.

Study of chromosomal chimeras has been very useful. It has made it possible to learn the exact origin of tissues and tissue system or areas within leaves, stems, flowers, and fruits, and the relationship of each tissue, or tissue area inside each plant organ, or plant part, to a particular apical layer. Since all these plant organs or parts develop from the shoot apex, and are actually and directly transformations or differentiations of shoot or bud tips, it should be readily possible to trace the origin of any tissue or internal area in a plant organ back to a specific apical layer. A root is also a plant part but it is not considered here. (See page 167).

Microscopic sections of very young leaves of a vigorously growing peach twig are shown in Fig. 4. Fig. 4-A shows sections cut through young leaves (*a*, *b*, *c*, and *d*) at a level considerably above the dome area of a twig. Fig. 4-B shows a section through the same twig but at a point very close to the dome. Here are shown sections of two additional leaves, *e* and *f*. Leaf *a* is the oldest and *f* the youngest and the others are lettered in that order. The twig was from a plant that had the 4-2-4 chimera makeup. Determination of different ploidy in each tissue of the leaves in these sections showed that only the epidermal tissue of the leaves originated from L-I; the entire internal tissue of the leaf blade originated from L-II; and only the bulk of the midrib tissue originated from L-III. In the lower portion of leaf *a*, the 4x (tetraploid) epidermis is partially delimited with an ink line (shown by an arrow) and an island of 4x tissue in the midrib region of each leaf is also delimited with an ink line.





**Fig. 4.** Two cross sections of 4-2-4 chimera peach shoot at a little distance above the apical dome region to show details as to origin of tissues in leaves from apical layers L-I, L-II, and L-III.





**Fig. 5.** *Transverse sections of two twigs. Top, back of dome in Fig. 3-E. Bottom, back of dome in Fig. 3-F.*

Figure 5 shows cross sections of twigs cut a little distance back of the domes shown respectively in Figs. 3-E and 3-F. The tissue enclosed by the wavy ink line in both sections is 4x. This illustrates how irregular may be the patterns of 2x and 4x tissues in the stem. A study of stem (twig) sections of 2-4-2 and 4-2-4 chimera-type plants showed that the epidermal tissue of the stem originated

from L-I as in leaves; L-II gave rise to part of the cortical tissue under the epidermis to varying depths, sometimes even extending beyond cortical tissue deep into the vascular tissue system (the darkly stained band of tissue in the stem sections) and into the pith tissue in the center of the stem. L-III usually gave rise to the inner part of the cortical tissue, conductive tissue and pith.





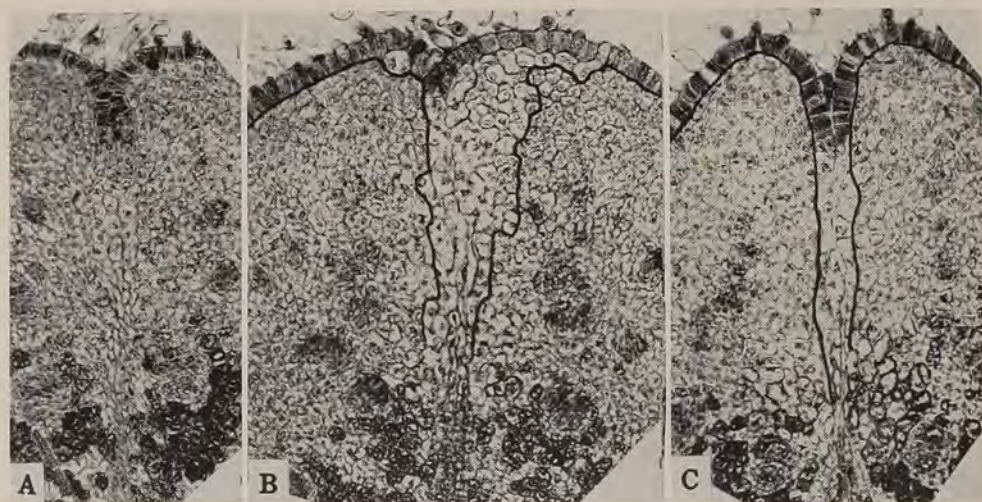
**Fig. 6.** *A section through an embryonic fruit of a 2-2-4 chimeral peach before opening of flower.*

Figure 6 shows a section through an embryonic fruit taken from inside of a flower bud. It was from a tree of 2-2-4 chimeral type, the dome of which is shown in Fig. 3-B. The white line in the fruit section was drawn to show the approximate boundary line of the pit. The tissue outside the white line grows into the fleshy part of the mature fruit and that inside into the hard pit tissue.

The black ink line indicates the boundary between 2x and 4x regions, a very wavy path at the outer portion of the fruit and a more or less straight line (not so visible because of darkly stained tissue in the region) by the seed cavity. The tissue enclosed by the black line was 4x, and that of other parts 2x.

At the very beginning of fruit development in the flower bud of peach and





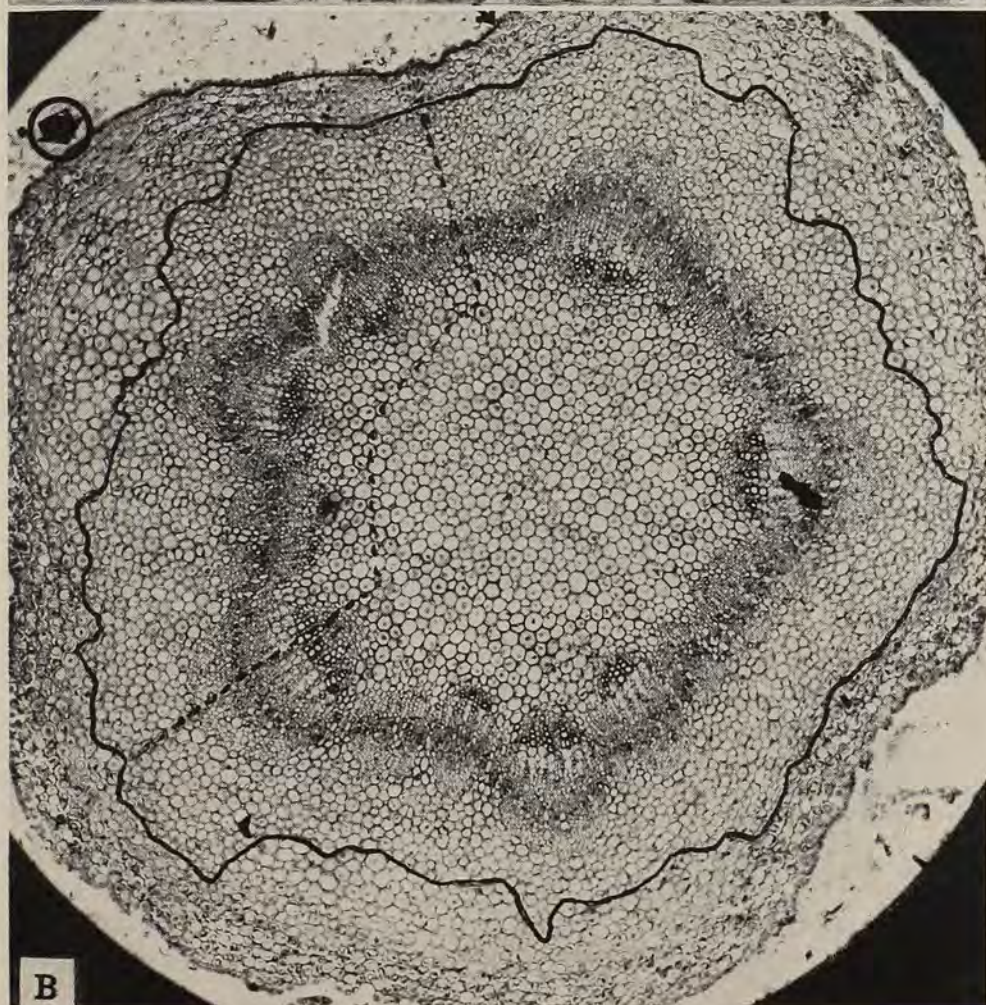
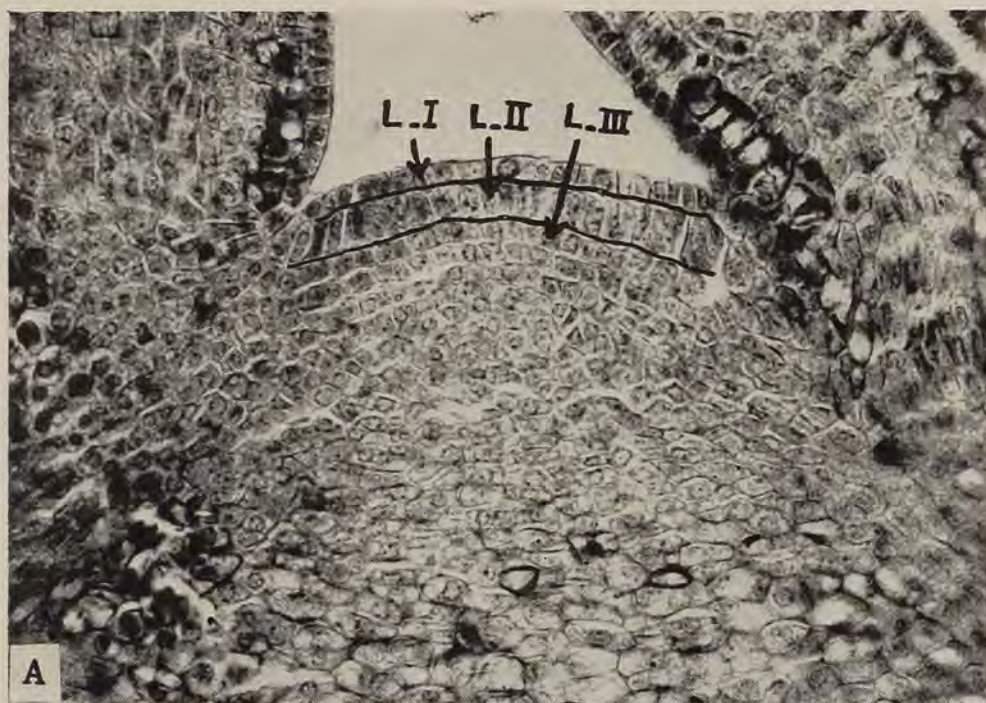
**Fig. 7.** Sections through suture area of three peach fruits. *A*, a diploid fruit; *B* and *C*, fruits of a 4-2-2 type chimera.

related stone fruits, the fruit looks somewhat *U*-shaped when viewed from the top or in a transverse section with the aid of a microscope, and changes with growth into a closed form like an "o." Therefore, when the two edges of the primordial fruit eventually meet, they fuse and form a deep line in stone fruits known as the suture. A slight dip in the upper part of the fruit section in Fig. 6 represents the suture. When the suture area of fruits of plants with 4-2-2 and 2-4-4 chimeras was studied microscopically, it was found that only occasionally had two layers of cells originated from L-I in the suture; usually six or more layers of cells at the suture were of L-I origin. In Fig. 7-A is shown the suture area of a fruit from a plant in which both L-I and L-II were 2x, therefore the whole tissue in the area of the suture is 2x as in Fig. 6. Fig. 7-B represents a suture area in a fruit of a 4-2-2 plant. Here the tissue in the suture area, about six cells wide, is 4x as is the epidermis. In Fig. 7-C is shown the suture tissue of another fruit, from the same 4-2-2 chimeral trees as in Fig. 7-B which is 4x and only two or three cells wide, a condition seldom found. Early and late ripening sports of peaches in which the suture area ripens later or earlier than the rest of the fruit, are evidence of the importance of the fact that suture tissue derived from L-I is usually several cells thick.

*Cytochimeras in apple.*—Studies similar to those in peach were made with a chimeral apple which had occurred naturally. Chimeral conditions in these two plants were alike in certain respects but they also had certain important differences. Fig. 8-A illustrates a shoot apex of the 2-4-2 type chimera in apple which is similar to that shown for peach in Fig. 3-C. Some other apples studied were of 2-4-4 and 2-2-4 types. Fig. 8-B shows a transverse section of the twig a little distance back of the dome shown in Fig. 8-A. In this stem section the central homogeneous appearing tissue is the pith. Around the pith the darkly stained band of tissue is the conductive tissue at the early stage of twig growth. Outside of this is the cortical tissue, and outside of the cortical tissue is a thin layer of cells, the epidermis. At the upper left portion of the section, an ink line was drawn part way (the area between two arrows) along the epidermis to indicate the dividing line between the diploid epidermis derived from the 2x L-I and the tetraploid outer portion of

**Fig. 8.** Shoot tip sections from a 2-4-2 chimeral McIntosh apple. *Top*, longisection of shoot apex. *Bottom*, transverse section of the twig, back of tip in top illustration.







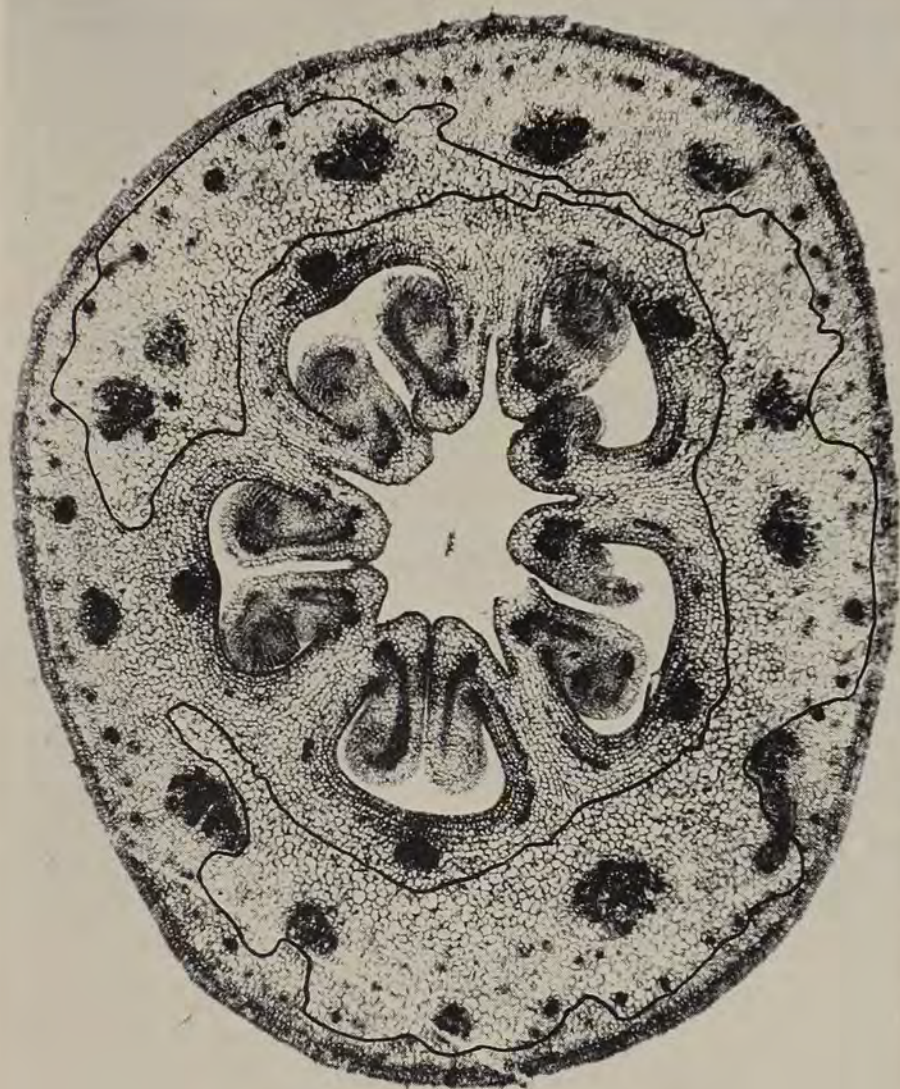


**Fig. 9.** *A transverse section of the marginal portion of a young leaf of a 2-2-4 chimeral Northern Spy apple.*

the cortical tissue derived from the 4x L-II. The continuous ink line in the cortical region separates the tetraploid part of the tissue (outer) from the diploid part (inner). Thus it was found that in the apple as in peach, a 2x L-I had given rise to a diploid epidermis alone. The cortical region is divided cytologically into two parts; an outer

tetraploid part derived from 4x L-II and inner diploid part derived from 2x L-III. The rest of the inner tissues of the stem were also diploid. The dotted line at the left portion of the stem section was drawn to indicate that at times tissue development from L-II may extend deeper in some parts of the stem, even into the pith region. The development-





**Fig. 10.** *A transverse section of a fruit of 2-2-4 chimeral Winesap apple before opening of flower.*

al process just indicated is discussed on Page 167 in connection with the problem of adventitious bud development.

Figure 9 represents a transverse section from the marginal one-quarter portion of a very young leaf of a 2-2-4 chimeral apple. As mentioned before, L-I gave rise to the epidermal tissue. But, in contrast to the situation in peach, usually only part of the internal tissue in the apple leaf originated from L-II. In the apple, tissue developed from

L-II consisted of one layer of cells immediately next to both upper and lower epidermises of the whole leaf and of all the inner tissue outside the ink line toward the margin of the leaf. Tissue developed from L-III comprised the remaining great bulk of the inner tissue of the leaf. In the peach only an inner portion of midrib tissue was derived from L-III. In Fig. 9 the inner tissue within the ink line represents the tetraploid area derived from 4x L-III. Out-





**Fig. 11.** *A longisection of a fruit of 2-2-4 chimera Winesap apple before opening of flower.*

side the line the tissue in the leaf section is diploid and derived from  $2x$  L-I (only the epidermis from L-I) and L-II.

Figure 10 represents a transverse section through the seed cavity of a young fruit of apple at the pink bud stage of flower development. This was from a 2-2-4 chimera plant, and the pattern of

the chimera condition in this fruit resembled remarkably that of peach illustrated in Fig. 6, although morphologically the two fruits differ. In Fig. 10 the tissue around which the ink line is drawn represents the tetraploid portion in this fruit; the ovular area and the outer portion of the fruit are diploid.



In Fig. 11 is shown a longitudinal section of an apple flower at a stage of fruit development similar to that in Fig. 10. This was also from the 2-2-4 chimeral plant. The portion enclosed by the ink line is tetraploid and the other parts are diploid. Flower parts were more intensively studied in chimeral apples than in peach. In apple no tissues or areas in tissues in any flower parts except in the fruit proper origi-

nated from L-III. The volume of tetraploid tissue in the fruits of 2-2-4 chimeras was variable. In some fruits the whole inner portion of the fruit, except the ovular tissue and a very narrow strip next to the epidermis, was 4x. In other fruits only a trace of 4x tissue could be found and in still others tetraploidy was entirely absent. In the latter case the branches bearing fruits with no 4x tissue in them had reverted to diploidy.



Fig. 12. *Variegated leaves of a citrus. Mutation in L-II.*

### III. Naturally Occurring Leaf Variegation and Fruit Sports and Their Propagation

In the preceding discussion, the manner in which plant sports, particularly chimeras, develop was explained on the basis of experimental findings. We now turn to the description of specific types of natural sports, vegetative variation, such as leaf variegation and fruit sports, and attempt to explain the way each may have originated by comparing them with the developmental processes of the experimentally derived chimeras.

*Variegation in citrus and poinsettia.*—A familiar type of variegation occurs in citrus leaves (Fig. 12) which is char-

acterized by several shades of green centrally and irregular areas of white marginally. Each color zone is sharply delimited and the pattern is restricted separately or independently on the two surfaces of each leaf. Thus the variegation on the upperside of each leaf differs from that on the lower surface. The difference in patterns between the two surfaces of leaves is very important characteristic of true variegations that are of genetic origin. The citrus leaf is comparatively thick and composed of about fifteen layers of cells. The number of





**Fig. 13.** *Variegated leaves of a poinsettia. Mutation in L-II.*

distinct shades of green in the variegated leaf appears to be related to its thickness which in turn is related to the number of layers of cells in a cross section of the leaf.

Variegation in poinsettia similar to citrus is shown in Fig. 13. In poinsettia with thinner leaves the number of distinct shades of color is less than in citrus.

Citrus and poinsettia leaves were cut crosswise in very thin sections to examine their structure from the upper to the lower epidermis. Figure 14-A represents a diagrammatic section of a citrus leaf, and B and C represent two sections of poinsettia leaves. The small rectangles, some cross-marked and others plain, represent cells. The small narrow rectangles at the upper and lower sides of the diagram represent cells of the leaf surface or epidermis. Areas with cross-marked cells represent colored portions of the variegated leaves and the areas without cross-marking the colorless portions. In the leaves of citrus, the two

layers of cylindrical cells under the upper epidermis make up the palisade tissue and are normally filled with disk shaped green bodies called chloroplasts. In the leaves of poinsettia and most other plants the palisade tissue is one cell layer wide. The region between the palisade tissue and the lower epidermis is the spongy tissue in which cells are actually more rounded or many-sided and contain fewer chloroplasts. Cells of the epidermal tissue, except the guard cells on each side of the oval shaped opening called stomata, or stomates (breathing pores), lack chloroplasts. Therefore the epidermal tissue of leaves appears colorless, whereas the inner tissue is green. In the diagram the layers representing colored cells are shown at different depths in the sections as is also variation in number of cell layers.

In the variegated citrus leaves more shades of green occur than in poinsettia. The degree of intensity of green (Fig. 12) is governed by the relative distance of the chlorophyll-bearing cells from the



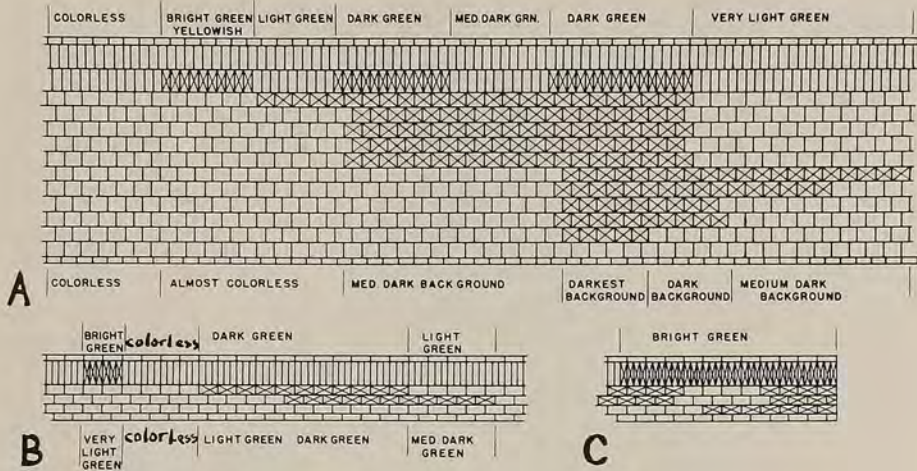


Fig. 14. *A*, diagram showing leaf thickness of citrus and varying shades of green in a variegated leaf. *B* and *C*, similar diagrams for poinsettia.

leaf surface, by the number of layers of cells in the green tissue and by the number of colorless layers of cells between epidermis and deeper green tissue. Thus, by careful examination of Fig. 14-A, the reader can readily understand the basis for this fact.

As pointed out earlier, the shoot apex of a bud or twig has three primary histogenic (giving origin to tissues) layers: L-I, L-II, and L-III. Studies of various types of diploid-tetraploid chimeral plants, particularly of apple, showed that the one-layered epidermal tissue is developed from L-I; a portion of tissue under the epidermis in leaf, stem and fruit is originated from L-II; and the central tissue in these organs is derived from L-III. Thus one might reason—and rightly so—that the variegation in leaves of citrus and poinsettia is due to a naturally occurring genetic color mutation in L-II at the apex of a shoot or bud. As thus interpreted, the tissue in the colorless areas in these leaves would correspond to the diploid portion of the tissue in the cytochimeral leaf of the apple shown in Fig. 9, and the colored area would correspond to the tetraploid tissue derived from L-III. Thus, leaf variegations just described would truly represent a chimera condition expressed as color variation, and are analogous to the cytological chimeras resulting from chromosome variation. Chromo-

somal chimeras can be studied cytologically in the earliest developmental stages of plant organs, such as a leaf; but the color chimeras can be studied usually in the more or less matured plant organs. They cannot be traced back to the growing point. Since color is not present or detectable in meristematic—embryonic—tissues, it is detected in mature tissues, in mature organs, such as leaves and fruits.

When variegated plants are observed closely we may find individual leaves or branches with leaves entirely colorless or entirely green. Occasionally we also find some leaves, as in poinsettia and in privet, which are marginally dark green but have a duller green central portion. A poinsettia leaf with such a make-up is shown in Fig. 15. These colored and non-colored tissues basically resemble certain diploid-tetraploid chimeral material.

In the leaf at the upper left in Fig. 13 there is a small separate patch of colored tissue. That patch was as bright green as normal green leaves. The coloring of the mutilated leaf at lower left, especially at its outer left margin, was also normal bright-green. When sections through the bright-green areas were studied it was found that there were normal green plastids in the palisade layer, whereas elsewhere in the leaf the palisade layer lacked normal plastids.





**Fig. 15.** *Reversed variegation in a poinsettia leaf.*



The relationship of the small bright-green patch to the rest of the leaf tissue is indicated in the upper left portion of the diagram B in Fig. 14. Diagram C in this figure shows the condition found in the mutilated leaf, though reversed.

When sections through the leaf shown in Fig. 15 were studied, it was found that in the marginal areas, where the color was dense, all internal tissues were green. In the central area, where the color was dull green, the palisade tissue contained normal chloroplasts, and a layer of cells next to the lower epidermis also had green plastids, but the cells of the inner so-called spongy tissue were colorless (diagrammatic partial representation in Fig. 14-C). At the lower left of the leaf (Fig. 15) there is a small area that shows the typical variegated leaf pattern illustrated in Fig. 13. If we compare this peculiar color relationship in the poinsettia leaf in Fig. 15 with the diploid-tetraploid tissue condition in the apple leaf in Fig. 9 we see more precisely that the patterns formed in these two leaves resemble each other closely. In the poinsettia leaf the marginal tissue is normal green and extends over a centrally colorless tissue. In the apple leaf the marginal tissue is diploid and extends over a centrally located tetraploid tissue. In both the pattern formed by two contrasting tissues is similar; in one the difference is genetic and in the other it is cytological.

It was pointed out that certain diploid-tetraploid chimera types are not permanently fixed or stable and that they may change. This is because the cell division plane in L-II in a growing point may change from vertical to horizontal. This change of position in cell division may also occur in L-I, very rarely in some plants and not so rarely in others. At the Plant Industry Station we found on a 2-2-4 chimera apple tree completely diploid branches and on 2-4-2 and 4-2-4 chimera peaches some branches that were 2-4-4 and 4-2-2 respectively. As mentioned before only once was a small peach branch found that showed a change from 2-4-4 to entirely 2-2-2 type, diploid condition. This was discovered because the peach was highly sterile in both 2-4-4 and 4-4-4 conditions. The branch that had become fully diploid was fully fertile.

In Medford, Oregon, Professor F. C.

Reimer showed the writer some changes in two sports of Bartlett pear. One was of the 2-4-4 giant fruited type. On some trees of this sport completely diploid branches had developed. The other Bartlett was a red colored sport. Breeding results from the red sport had shown that the color factor was in L-II. On some trees of this sport some branches bore normal colored fruits, developed on branches originating from L-I which was presumably genetically green. In the two pear sports and in the 2-4-4 chimera peach, buds that had given rise to branches which had reverted to normal had originated exclusively from L-I, not from all three histogenic layers, as generally occurs; or from L-I and L-II alone, as quite often happens. Horizontal cell division in epidermal cells, that would account for the origin of bud development from L-I alone, was observed in apple (10).

Whereas the development of the diploid-tetraploid chimeras was due to duplication of chromosome number in a given layer of cells in a growing point of shoot or bud, the origin of leaf variegation and some fruit sports has been mostly of a genetic, or mutational nature. We may now apply the concept of different cell layers in the shoot tips to the development or occurrence of leaf variegations and other sports to explain how they may have originated.

It may be concluded, according to the concept of chimera development, that variegation in the citrus and poinsettia studied is due to a mutation in L-II which has suppressed chlorophyll development of plastids in cells of tissues originating from L-II. In cases where the central area in the variegated leaves is green, L-III in the variegated plant is normal. The appearance of green patches over colorless tissue may be accepted as evidence that L-I, at least in poinsettia, is also normal and that cells of L-I in some leaves have divided laterally and given rise to green internal tissue. The appearance of leaves with a pattern similar to the one shown in Fig. 15 would result from division of a cell in a horizontal plane in L-I in the shoot apex. When this takes place, a cell in L-II next to the horizontally dividing L-I cells might then be forced to take a position in a cell deeper and thus take third rank position, so to speak.



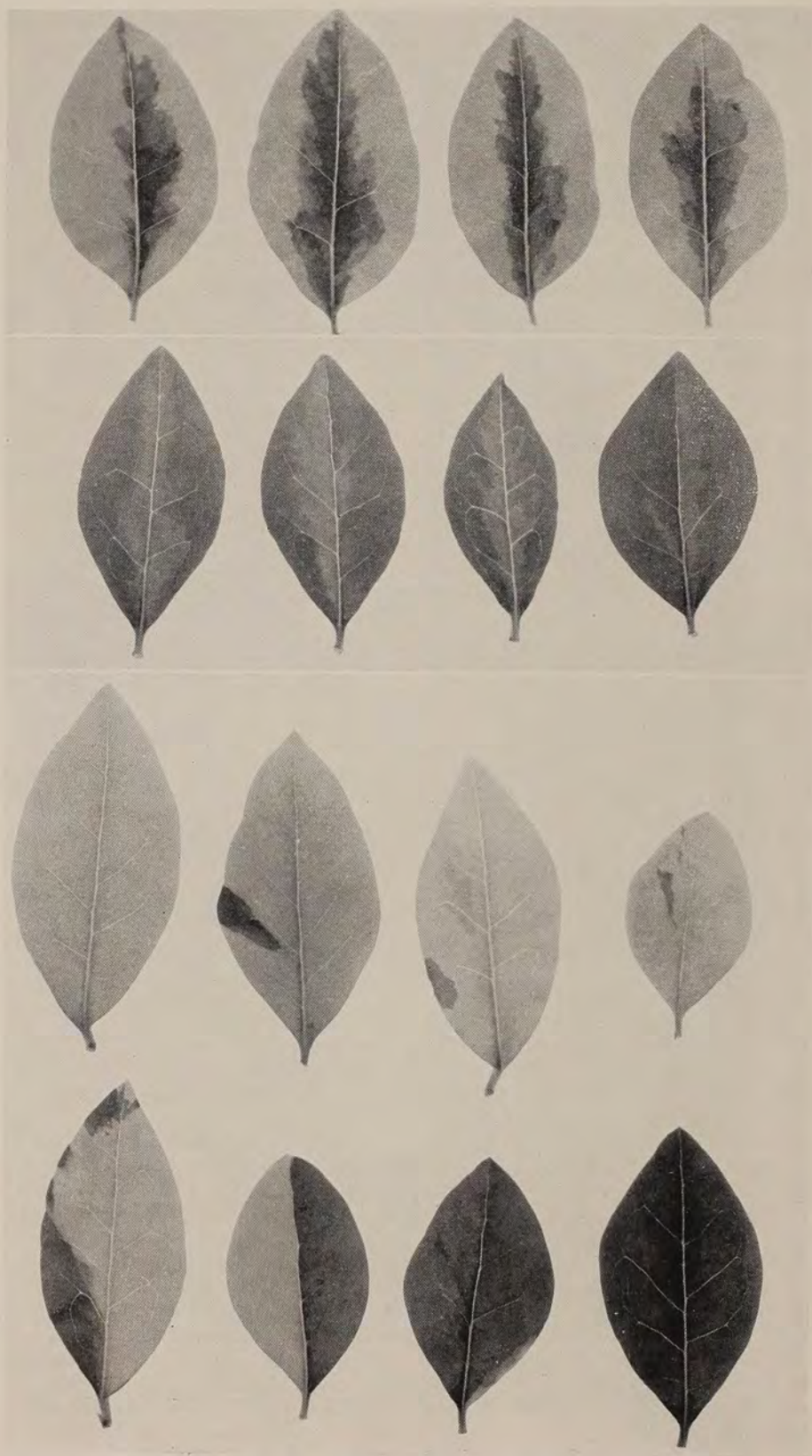


Fig. 16. *Variegation in privet.*



*Variegation in privet.*—Having two variegated shrubs of privet by my home has given me the opportunity to observe them closely and experiment with them. In Fig. 16 in the first row of leaves at the top are typical variegated leaves with colorless or yellow margins and green center in varying patterns and shades. The color density in the green areas, as in citrus and poinsettia, was related to the distance of green colored layers of cells from the epidermis and the number of colorless layers of cells between epidermis and green tissue. In privet the number of shades of green ranging from very pale to dense green was intermediate between the conditions in citrus and poinsettia, presumably because privet leaf has an intermediate number of layers of cells. In the second row in Fig. 16 are leaves with normal colored green margins and dull-green area in the center. They represent the reverse type of variegation similar to that in poinsettia (Fig. 15). In the third row one leaf is entirely colorless and the others have green patches of varying size developed from L-I. Green patches had occurred on either surface of the leaves. In the bottom row the first leaf at left has larger patches of green than the leaves in the third row; the second leaf is half yellow and half green; the third leaf is totally green except for a little yellow area at its lower right portion; and the fourth leaf is entirely normal green.

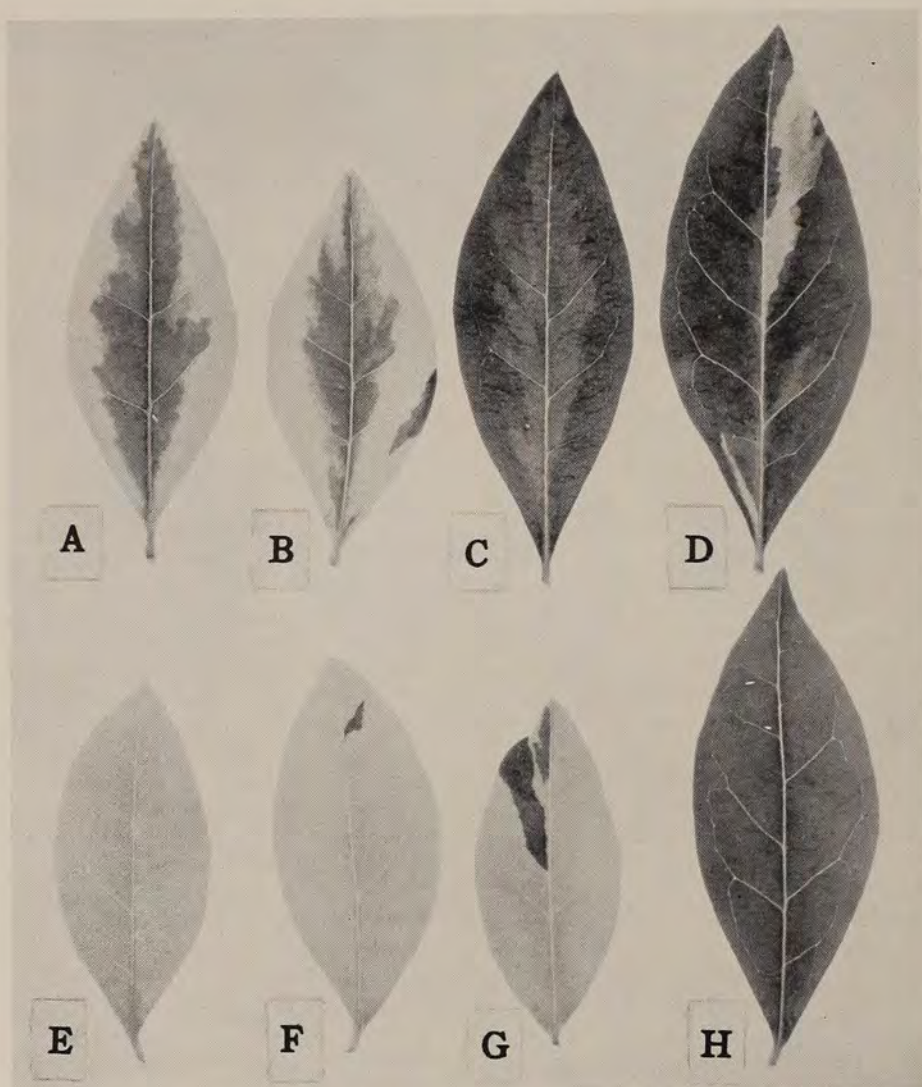
Shoot growth in privet is rapid; thus branches could be forced out during the growing season by cutting shoots back to a particular type of leaf to force out a branch from its axillary bud. This technique proved very helpful and was used repeatedly to determine what types of leaves would appear on the branches forced out from any given point. Generally, typically variegated leaves appeared on the twig forced out from a bud at the axil of a variegated leaf. But now and then on such a twig variegated leaves were interspersed with half-colorless and half-variegated leaves, or with leaves entirely colorless, or with yellow leaves with a patch or patches of normal color mostly marginally located. When a shoot was forced out from the axillary bud of a yellow leaf the leaves were all colorless, except for occasional normal green patches. From the buds of entirely green leaves only shoots with normal

green leaves appeared; thus a variegated form could be changed back, or reverted, permanently to the normal green form.

*Cell displacement phenomenon.*—An unexpected development was observed in variegated privet (also in *Euonymus*, see below). This was the appearance of colorless or yellow patches on the leaves with reverse type variegation. Branches developed from axillary buds of leaves with reverse-type variegation (Fig. 16, second row) bore mostly leaves with the same make-up and occasionally some leaves were entirely green. But in rare instances some colorless patches appeared on the reverse-type variegated leaves. A leaf with such a colorless patch is shown in Fig. 17-D. A typically variegated leaf A is shown for comparison. Leaf B has an additional green patch at right, derived from L-I. Leaf D has a large colorless area on the upper right side and a streak of colorless area on the lower left side. In extreme cases some leaves on twigs bearing mostly C-type leaves were half colorless and half green and some were even entirely colorless (leaf E). Some of the almost colorless leaves had in addition green patches developed from L-I, as shown on leaves F and G. Growth from L-I on twigs bearing such secondarily developed colorless leaves had resulted in the development of completely green leaves such as H. Figure 17, then, illustrates the sequence of changes from the typically variegated leaves through reverse variegation to development of normal green leaves.

All evidence indicates that variegation in the privet studied is due to a genetic change in L-II; and that L-I and L-III are genetically normal. Therefore the appearance of yellow tissue on the leaves with reverse-type variegation could be due either to a new mutation from green to yellow in some cell, or most likely as interpreted here, to one cell from a genetically colorless histogenic layer having gotten in between two normal cells of a genetically green layer. If that was possible, then a genetically colorless cell could give rise to a colorless patch, as that in leaf D, Fig. 17. The size of the colorless patch would depend on the developmental stage of a leaf at which this displacement or dislocation occurred. If this had occurred in a growing point before a leaf had started to





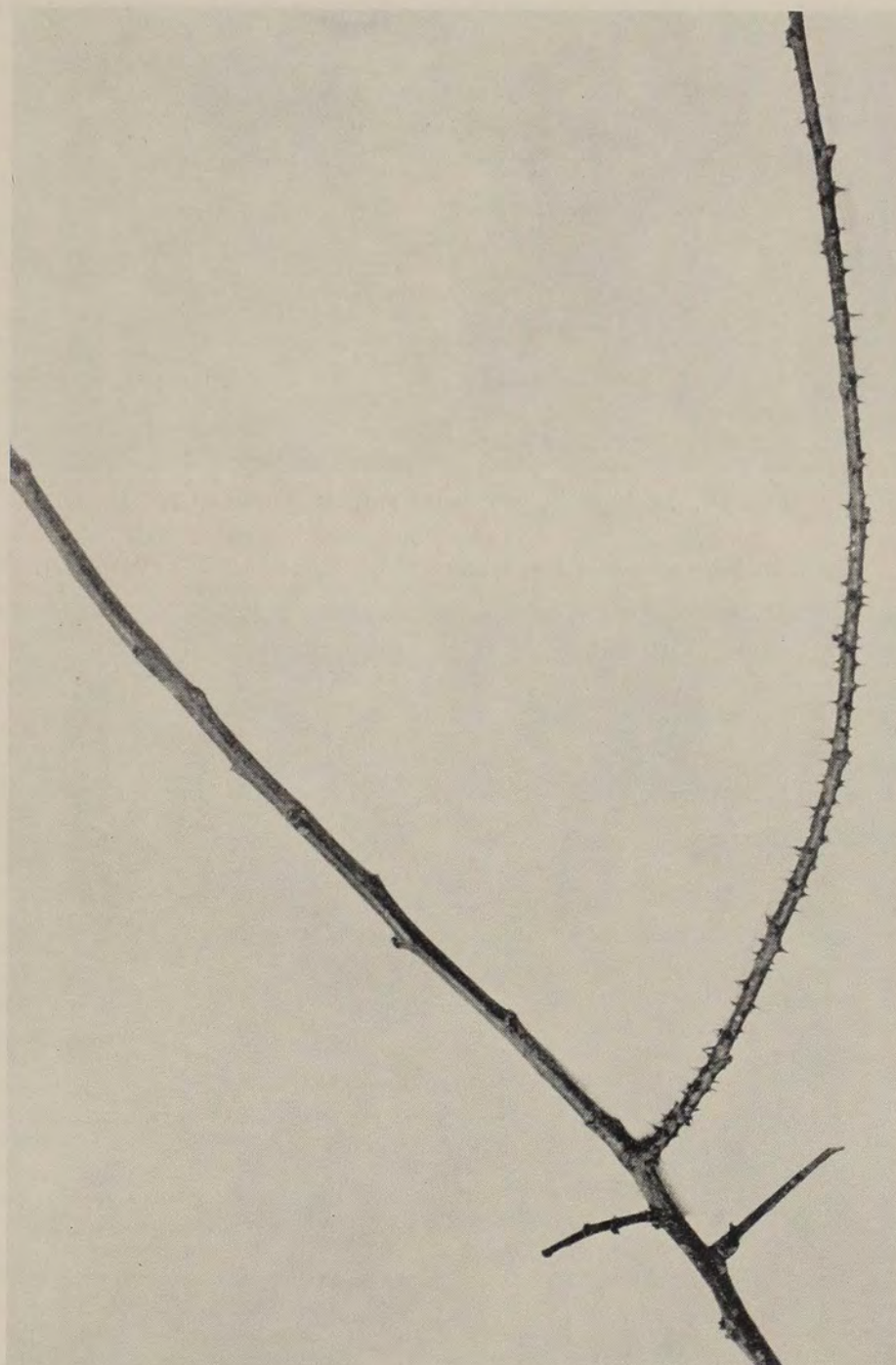
**Fig. 17.** *Changes in privet from variegation to yellow by cell replacement phenomenon.*

develop then a whole leaf, or a sector on a twig, might appear colorless. If the replacement, or displacement, had occurred when a leaf had only partly developed from the growing point then the size of a colorless patch would be only partial or limited.

*A thornless blackberry sport.*—Darrow (4) reported the appearance of a thorny shoot on a branch of a thornless blackberry sport known as Cory Thornless

blackberry (Fig. 18). Breeding evidence showed that subepidermal tissue and the rest of tissues in the stem of this thornless sport were genetically thorny. Blackberry thorns are developed from the epidermal tissue, and mutation in L-I had suppressed thorn development in the sport. Thus in some instances replacement of epidermal cells by underlying cells may have taken place to account for the appearance of thorny





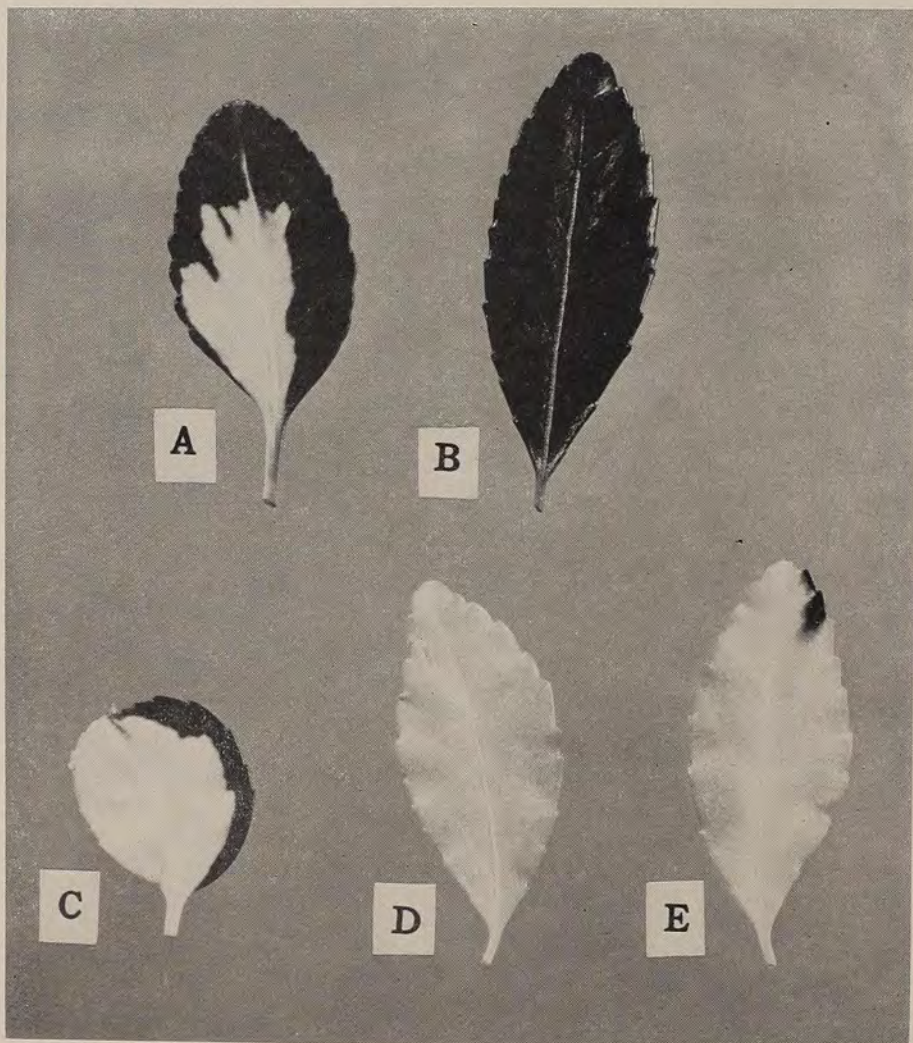
**Fig. 18.** *Recurrence of a thorny shoot on a cane of a thornless sport of blackberry. Mutation in L-I.*





**Fig. 19.** *Variegation in Euonymus. Mutation in L-III.*

**Fig. 20.** *Variegation in Euonymus changing to yellow as in privet.*





branches on thornless plants. Of course it could also be that in some cases a reverse mutation may occur in these sports and the sport reverts to normal. It was noticed, however, that in the case of variegated privet yellow patches kept recurring only in leaves on twigs bearing reverse-variegation, C type, leaves (Fig. 17); such patches never appeared in the entirely green leaves which had originated from normal L-I.

*Variegation in Euonymus.*—Leaves of *Euonymus japonicus* var. *mediopictus* (the spindle tree) are shown in Fig. 19. Leaf at left is normal green; middle leaf is variegated, being marginally green and centrally colorless; leaf at right is variegated but with a minimum of colorless area along the midrib. Mutation of the colorless form in this plant seems to be in L-III. A typically variegated leaf in this *Euonymus* plant should have resembled that of the poinsettia leaf shown in Fig. 15, the leaves of privet in the second row in Fig. 16, and leaf C in Fig. 17. Variegation in *Euonymus* is correctly genetical, judging from the fact that purely green leaves appear on a twig intermixed with variegated ones, and twigs bearing only green leaves occur along twigs bearing variegated leaves. Furthermore, when shoots are cut back to variegated leaves the new shoots bear variegated leaves almost entirely and occasionally completely green leaves. When shoots are cut back to green leaves, the shoots bear only green leaves. In the variegated leaves of *Euonymus* there is perhaps at least one layer of cells of palisade tissue derived from the genetically normal L-II over the colorless area. It may be that some substance which suppresses normal chloroplast development in the tissue derived from L-III diffuses into the adjacent genetically normal-green cells and affects the normal-green coloring there also, and thus a diffused coloration appears along the edges of colorless central areas. This phenomenon obviously is not present in leaves of poinsettia, privet, and other species considered herein; consequently the differently colored areas on these leaves appear sharply defined.

As this article was being written, the cell displacement phenomenon described above for variegated privet, and presumably in blackberry, was also found to occur in the variegated *Euonymus*.

As was pointed out, variegated bushes of *Euonymus* frequently displayed branches which had reverted to normal and bore green leaves entirely and permanently. Other branches, however, on the whole continued to bear variegated leaves with green margins and yellow centers. At the beginning of February 1959, at one of our greenhouses I saw many cuttings of variegated *Euonymus* being grown. Two of the young plants had *pure yellow-leaved shoots* along with branches with typically variegated leaves. These two plants were repotted and care was given to make them grow at a fast rate.

Since in privet the displacement of cells brought about a change in the composition of the chimera make up of variegated leaves, the possibility that a similar phenomenon also occurs in *Euonymus* was considered. If such is the case, I thought it possible that, as in privet, in *Euonymus* also green patches of growth may appear on some yellow leaves. Such a possibility would be contingent on the assumption that in some leaves of *Euonymus* a cell with a yellow factor from L-III has gotten between two genetically normal cells of L-II and that genetically normal L-I has remained intact in such a displacement process. In that event, some of the yellow leaves may be expected to show occasional patches of green originating from genetically green L-I. Two such leaves (on branches bearing yellow leaves), one with one patch of green tissue and another with two green patches, were actually found. Figure 20 illustrates the sequence of changes in the phenomenon of cell displacement in the variegated *Euonymus*. A represents a typical variegated leaf of this plant developed from genetically green L-I and L-II, and genetically yellow L-III. B is a leaf in which the internal tissue was derived completely from green L-II. Leaf C was found on the branch immediately below the point above which all the leaves were yellow; the lower leaves were typically variegated. In the yellow part at left of leaf C, L-III has replaced normal L-II and in the part at right the variegation pattern has remained unchanged. Leaf D is completely yellow. Leaf E is the one yellow leaf with a green patch. More leaves of such character were found as the branches with yellow leaves continued to grow. The appearance of green





**Fig. 21.** *Variegation in a tobacco plant. Mutation in L-II.*

patches on yellow leaves indicates that L-I in the yellow-leaved branch is normal. All these observations show that the variegation in *Euonymus* herein described is truly of a chimeral nature as in the other plants, and is due to a genetic mutation present in L-III; and that the displacement phenomenon is the cause of the change from the variegated form to the completely yellow.

So far these observations show that a cell from L-III can somehow migrate into L-II and thus change the chimeral arrangement of the apical layers. Whether in privet and *Euonymus* a cell

from L-II can similarly migrate into L-I remains to be determined. Such was assumed to have occurred in blackberry.

*Tobacco variegation and its genetic analysis.*—In this article the causes of variegations described earlier and others to be described farther on are considered to be of genetic, nuclear, origin. As we saw in each case variegation was directly associated with absence of normal chloroplastids in one particular histogenic layer. Therefore, it would be most instructive if each material that has been studied anatomically were also subjected to breeding tests.



As it is not practicable to carry on an extensive breeding experiment with each sport described, a variegated plant of commercially grown tobacco (*Nicotiana tabacum*) was chosen for such a test as an example, the result of which may apply to some cases of variegations, if not to all of them. Tobacco is herbaceous and an annual plant. Breeding results from it can be obtained in a comparatively short time.

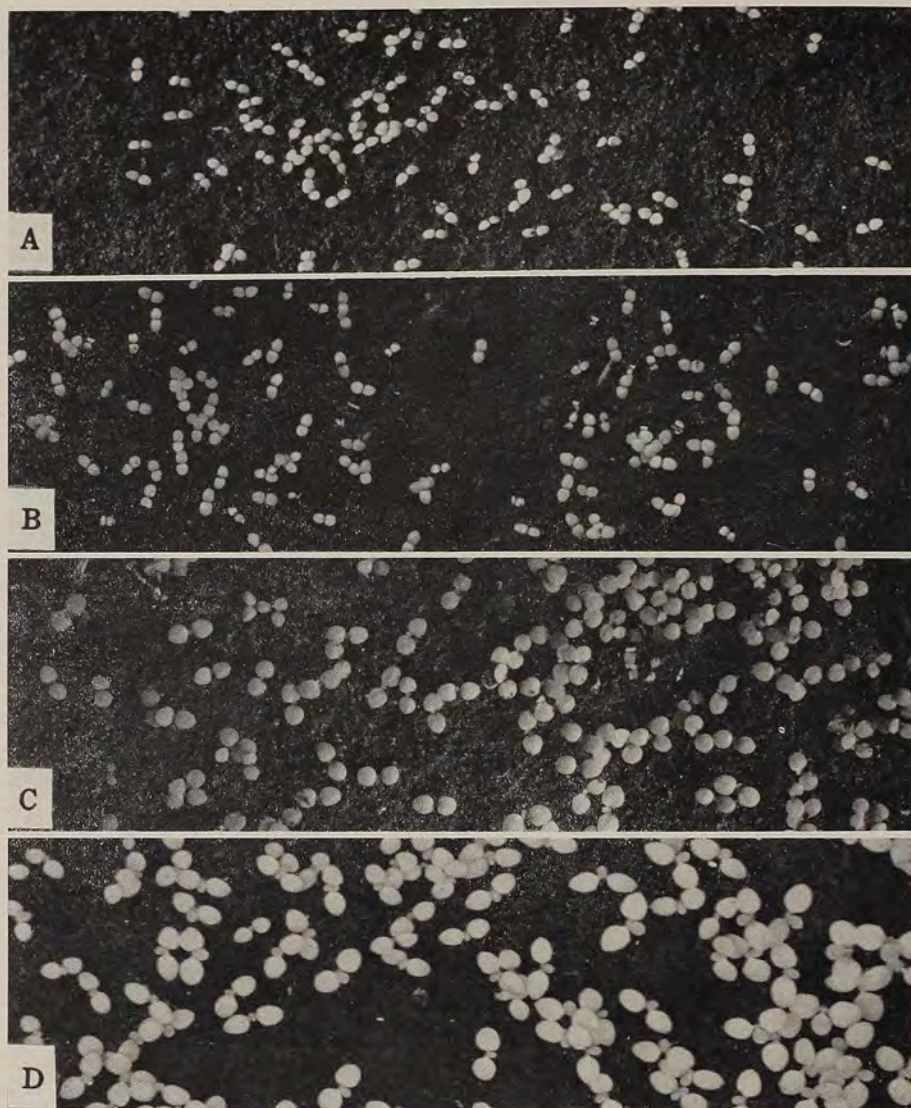
Two variegated leaves of tobacco are shown in Fig. 21. The variegation in these leaves appears similar to variegations in leaves of poinsettia and privet. In the tobacco plant besides leaves with a central green area surrounded by colorless tissue there were found two leaves, shown in Fig. 21, each with a normal green patch of tissue from L-I. Such a green tissue can be seen at the upper left side of leaf at left and a large patch at the upper right side of leaf at right. Therefore, as in other variegations described, the mutation resulting in marginally colorless tissue was considered to be present in L-II, and that L-I and L-III were normal.

Cytological studies of plants earlier discussed have shown that the pollen grains and the egg cells originate in the tissues developed from L-II. The evidence of that was determined from studies of 2-4-4 and 2-2-4 chimeral plants. The 2-4-4 plants functioned as tetraploid plants and produced large pollen grains because L-II in these plants was 4x. The 4-2-2 and 2-2-4 plants functioned as diploid, and produced normal small pollen grains because L-II in these plants was 2x. The nature of the diploidy or tetraploidy in the plants studied was determined by measuring the size of pollen grains, by microscopic studies of tissues in anthers and ovaries, and from breeding results with diverse types of chimera plants. As stated previously, occasionally L-I may give rise to internal tissue growth in leaves, and the same may happen in anthers and ovaries. Thus in rare instances some normal pollen grains may be produced in anthers and normal eggs in ovaries of a 2-4-4 chimera plant and tetraploid type pollen grains and eggs in a 4-2-2 plant. Such a happening may cause confusion when breeding results of some plants are analyzed. However, as a rule in dicotyledonous plants L-II is the layer from which sexual tissue in

anthers and ovaries is derived, although occasionally exceptions may occur. In monocotyledonous, grass-type, plants, however, the sexual tissue in anthers may develop quite regularly partly from L-I and partly from L-II. Such results were obtained in two cytochimera monocots produced by colchicine treatments. Emsweller and Stewart (21) obtained it in cytochimera lily (*Lilium longiflorum*) and Traub (28) in cytochimera daylily (*Heimerocallis*) hybrid varieties.

The variegated tobacco plant was used in breeding in a number of ways. In the first step a few of the flowers of the variegated plant were self-pollinated. From self-pollination, a normal set of seeds per seed-capsule was obtained. About 2,650 seeds were sown in a flat. Percentage of seed germination was normal for this particular variety and very high. All seedlings were lacking in chlorophyll, however, and reached only the cotyledonary stage (Fig. 22-A) and thereafter all the seedlings died. In the second test, a few flowers of the variegated plant were pollinated with pollen from a normal green plant of the same variety. Again a normal set of seeds was obtained, and about 2,000 seeds were planted. The germination was normal, but again all seedlings were colorless and reached only the cotyledon stage (Fig. 22-B) and died. In the third test a few flowers of a normal green plant were pollinated with pollen of the variegated plant. About 4,500 seeds from this cross were planted, germination was normal and all seedlings were green and continued to grow normally (Fig. 22-C). In a fourth test, a few plants from the third test were brought to flowering and some flowers of these plants were self-pollinated; thus a second generation of seedlings was raised. For this test, about 2,000 seeds were sown and the resulting seedlings were green and grew normally (Fig. 22-D). *Not one seedling in all four tests appeared as variegated.* This, the writer judged, was a case of mutation of cytoplasmic (non-genic and non-nuclear) origin occurring in L-II alone; and the defective nature of the L-II and the colorless tissue originating from it was entirely associated with the cytoplasm of the egg cells in the ovaries and was not carried by the pollen or male gametes.



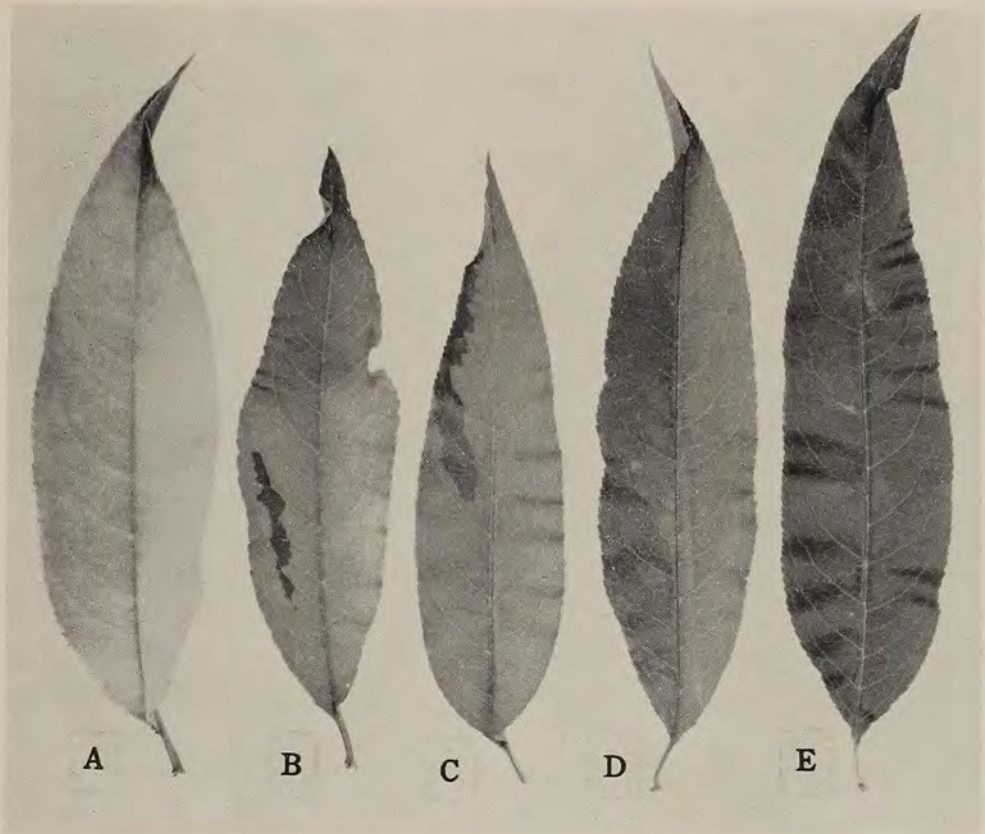


**Fig. 22.** *Four groups of tobacco seedlings from breeding result of variegated tobacco.*

It may be concluded from this breeding test with tobacco that variegation, as such, described in tobacco and in other plants is not an inherited character. Variegation in these plants appears as a vegetative expression due to certain chimeral conditions. The appear-

ance of patterns is the result of normal tissues originating from normal histogenic layers beside or above or below an abnormal colorless tissue. In the tobacco, breeding results show that the abnormal color was due to a cytoplasmic factor.





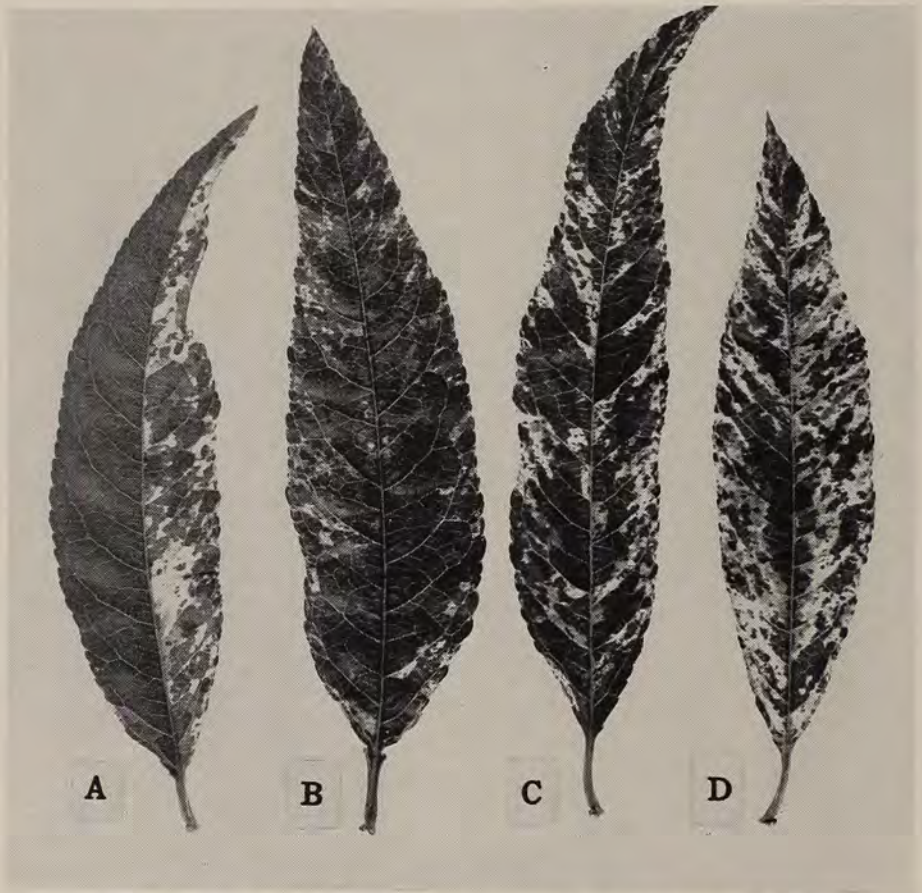
**Fig. 23.** *A yellow leaf sport in peach. Mutation in L-II.*

*Sports of peach leaf color.*—When cytochimeras of peach were studied (13), it was found that L-I gave rise to epidermal tissues in the leaf as in apple (11); but unlike apple, L-II gave rise to the whole internal tissue in the leaf reaching into the midrib; and L-III gave rise only to a part of the tissue, centrally located in the midrib. In peach, a mutation in L-II affecting chlorophyll development appears to affect the whole leaf blade instead of color-pattern development similar to that in poinsettia. In apple, L-II generally gave rise to the marginal part of the internal tissue of the leaf and L-III gave rise to the rest of the internal tissue. So far I have not seen a variegated apple leaf, but I would expect—based on the cytochimeral study—that if variegation did occur in apple and affected the color of tissues originating from L-II it might be basically similar to the variegation type found in poinsettia and privet.

Figure 23-A to D shows leaves of a yellow mutant of peach. On two trees about eight years old, propagated from buds of a yellow-leaf sport of a peach, almost all the leaves, numbered in several thousands, appeared yellow and only very rarely were leaves found with a patch of normal green. When the sport trees were three years old, one leaf on each was half green and half yellow. The shoots bearing these leaves were cut back to the half-colored leaves and in both cases a shoot grew with completely green leaves along one sector of the twig. Along the other sector of the twigs leaves were either yellow or partly yellow and partly green. These twigs were again cut back, but the cuts were made to entirely green leaves. This time two new twigs bore only completely green leaves and have continued to do so ever since they were forced out.

The experiment just described indicates that the yellow mutation in this





**Fig. 24.** *A mosaic leaf sport in peach. Mutation in L-II.*

sport is in L-II and that L-I which gave rise to occasional green tissue is normal. The status of L-III in the peach sport could not be determined because the leaf tissue developed from L-III would be in the central area of the midrib and would not be pigmented. This experiment confirms the cytological evidence that the whole internal tissue in the peach leaf, except a part of the central portion of midrib, is derived from L-II and that a pattern of variegation similar to the poinsettia type could not be expected to occur in peach.

The peach leaves shown in Fig. 23 range from entirely yellow to entirely green. Leaf A is the typical yellow leaf due to mutation in L-II. Leaves B and C are mostly yellow with patches of normal green tissues originating from normal L-I. Half of leaf D is normal green and half yellow. It was from the

bud in the axil of such a half and half leaf that a branch with normal green leaves grew as explained above. Leaf E from the green branch is entirely normal green. The coloration in leaves of this sport changed in intensity from light yellow to almost green under the effect of favorable light and nutritional conditions.

The leaf sport shown in Fig. 24 appeared on J. H. Hale peach variety. This sport may be compared with the familiar mosaic variegation of genetic origin in corn (maize) kernels and in flower color variegations of *Verbena* which the writer had observed several years ago. In severely mosaic areas of some leaves the tissue is mostly colorless with numerous detached, sharply defined, islands of green tissues in varying dimensions. The sporting in this peach appears as being due to an ever-mutating gene or some other



cytological factor in cells of L-II which, during the growth of the leaves, at times has no abnormal effect and at other times does affect unfavorably. Thus here and there cells carrying the gene for normal color give rise to normal patches of green tissue and cells carrying the mutated gene, or under some other cytological conditions, give rise to colorless areas. But again, L-I being normal, internal tissue occasionally developed from it would appear green. Leaf A appears to be developed internally half from normal L-I and half from abnormal L-II. This analysis was confirmed when a small twig with leaves totally green was forced out from the axial bud of the half green and half mosaic leaf.

The comments made in the above paragraph were based on the condition of variegation observed on two trees when they were one-year-old and had only a limited growth. In the second year of growth these trees branched out considerably and certain branches were cut back to force ample new growth in order to study possible changes in variegation as had been done in other variegated plants described earlier. One of the trees continued to produce predominantly leaves with extreme mosaic-variegation. As was indicated above, when a shoot was cut back to a bud subtended by half mosaic and half normal green leaf, a new shoot with a limited growth appeared to bear only normal green leaves. The normal appearing branch just referred to had proliferated during the second year's growth into several secondary and tertiary branches. But it turned out that the leaves on the new branches were *not* all normal green as had been expected, but all the twigs bore a mixture of leaves with varying degrees of mosaic-variegation, shown in Fig. 25. A number of times when twigs were cut back to a normal appearing leaf, the new twigs arising from the subtended bud consistently bore some normal appearing leaves; some of the other leaves were severely mosaic and some were in lesser degree mosaic.

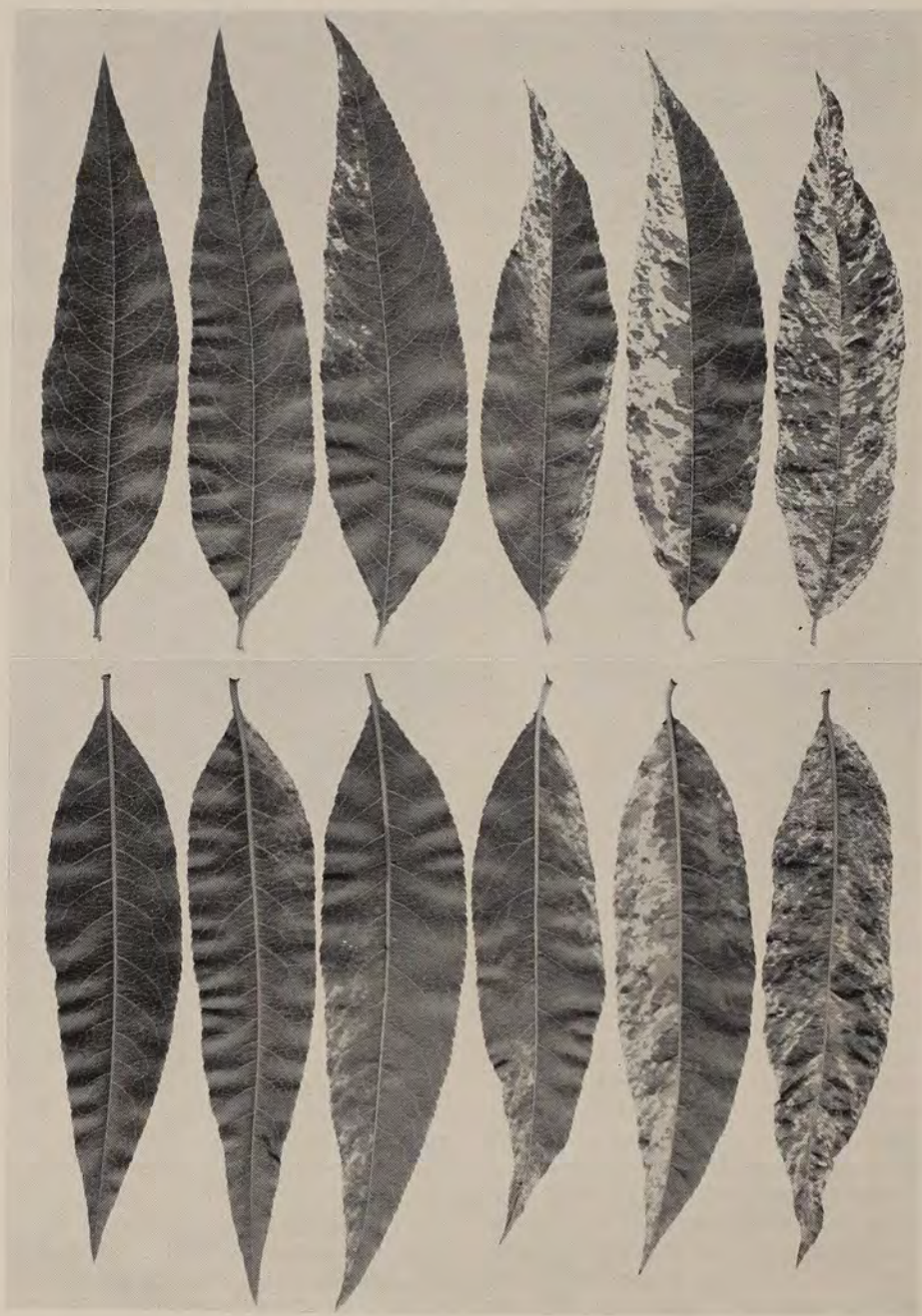
In Fig. 25, the upper row shows the upper surface view of six leaves, the lower row shows in corresponding order the under side of the same leaves. The first leaf at the left is entirely green; the second has a narrow mosaic area at right of the petiole; in the third, mosaic con-

dition is present toward the tip, strictly at the left of the midrib; in the fourth there are two separated mosaic areas, one at the lower edge near the petiole and the other toward the tip of the leaf; in the fifth, at one side of the midrib, the leaf is heavily mosaic and at the other side very lightly so, in an area confined near the petiole; and the sixth leaf is most severely mosaic as was shown earlier in Fig. 24.

Further noteworthy features observed in this mosaic variegation: 1) So far, during two growing seasons, no twigs appeared which bore only normal green leaves, although branches were developed from buds at the axils of normal-appearing leaves. 2) Twigs grown from buds at the axils of leaves with heavy mosaic usually bore similar leaves. 3) There appeared some mosaic areas which were at the very edge of leaves and separated from the midrib. 4) In some severely mosaic parts there were numerous small areas of tissues completely lacking in color, surrounding tissue being green; in some other leaves small islands of tissues were green and surrounding tissue was white. 5) In many mosaic variegated leaves green tissues were confined to certain depths, beneath or above which, as the case may be, tissues were colorless. Such a type of differential coloration can be clearly seen along the midrib in the fifth leaf (Fig. 25).

If this mosaic-variegated condition was due to a mutation confined to L-II, as the writer had thought previously, there should not have occurred isolated mosaic areas, often confined to the very edges of leaves, especially areas farther away from the petiole and away from the midrib. Such a development does not parallel the development in leaves of cytochimeral peaches. Odd location of some mosaic-areas suggests that this particular disorder may not be genetic. For such a variegation to be genetic, its development is expected to be more random in its distribution over the leaves. On the other hand, where normal green patches appeared and beneath or above them tissues are colorless, as along the edge of the fourth leaf in Fig. 25, it would suggest that this disorder may be genetic, as illustrated diagrammatically in Fig. 14. In order to fully understand the nature of this mosaicism, last fall (1959) a few buds from a normal green





**Fig. 25.** *Range in mosaic-variegation pattern.*





**Fig. 26.** *A true mosaic-variegation. An ever-sporting gene mutation from purple to green. Mutation in L-II.*





**Fig. 27.** *A yellow leaf sport in peach. Mutation in L-I.*

peach tree were grafted on twigs with leaves severely mosaic. These buds will be forced (in 1960) to growth in order to test whether this particular disorder may be transmissible and therefore be due to effects of a virus. Certain possible developmental features during further growth of these particular variegated trees may help to resolve the present case, and, incidentally, we may learn more fully how some variegational symptoms may be properly diagnosed to determine whether they are genetic or pathological.

Figure 26 illustrates a kind of mosaic-variegation in peach leaf which appears to be truly of genetic origin. It was found in 1959 on a purple colored seedling. The change in color is from purple to green. The mutation appears to be a so-called ever-sporting type, and it appears to be present in L-II. The variegated seedling when discovered showed solid colored leaves along one side and

mosaic-variegated leaves along the opposite side. Mutation in the seedling had occurred part way up the plant. This was judged from the fact that all the leaves at the lower part of the plant were of uniform color. On the uniformly colored side of the tree, new twigs bore similar leaves and the twigs on the variegated side continued to bear variegated leaves. In Fig. 26, the top row shows the upper surface of five leaves and the bottom row the corresponding lower surface of each leaf. In both groupings the leaves at the ends represent entirely purple ones, normal for this tree, and the three in between are representative samples of variegated types in which light colored areas represent green color, changed from purple. It can be seen that the pattern of variegation on the upper surface of each leaf definitely differs from that of its lower surface. Such a differential coloring almost consistently on the two surfaces of a variegated





**Fig. 28.** *A leaf sport of Aralia pennocki resembling chlorosis. Mutation in both L-II and L-III.*

leaf is considered as a very useful diagnostic point in judging whether a variegation is of genetic origin.

Figure 27 shows variegated leaves from a twig of a young peach tree resulting from a mutation originating in L-I. The sporting initially appeared as mosaic, but the mosaicism disappeared. When a twig was forced out from an axillary bud of a yellow leaf, like that shown at the far right in Fig. 27, all the leaves on that twig were uniformly yellow. Most of the leaves on the tree were green because L-II in this plant was normal and only occasionally a patch of pale green area appeared on some green leaves. Pale green color in such areas was due to yellow color over green, yellow tissue presumably having originated from L-I. Twigs bearing only yellow leaves were weak in growth and the leaves usually withered and died and none turned into green as in another sport earlier described. This account would indicate that this yellow mutation differed from the previously described yellow sport, since in that mutation the yellow leaves could become almost green and survive the whole growing season like the normal leaves.

*A sport of Aralia leaf color.*—Leaves shown in Fig. 28 are from a leaf sport of *Aralia pennocki* which was displayed at the 1960 National Flower Show in Washington, D. C. At first glance the leaves appeared to be either affected by a disease or to show some sort of nutritional deficiency. Close observation revealed that many leaves had patches of green tissue at their margins and a few were entirely green, while most appeared to be completely defective, being pale green with chlorotic condition along the veins. Presence of some leaves marginally green with chlorotic center and some leaves entirely green indicated that the clone at the Flower Show represented a type of sport quite different from the obviously variegated forms as described in this article. The sport in the *Aralia* plant is very instructive and helpful as a guide to the curious in the diagnosis of a plant symptom whether it is caused by an external factor, pathological or physiological, or by a mutation.

If the leaves of *Aralia* had shown only the chlorotic condition, it could be suspected that the symptom is of an external nature. But since some of the leaves appeared defective and some others were





Fig. 29

*Sansevieria*

Fig. 30

Showing variegations in  
*Pandanus*

Fig. 31

*Dracaena*

partly green and partly defective, similar in that respect to most variegations, and some appeared clearly normal, then the defective condition would be in the nature of a mutation. Therefore, the mutation in this plant must have originated in L-II and that L-I is genetically normal-green which accounts for the appearance of normal-green areas in some leaves and also for the development of some entirely green leaves. It may be assumed that L-III, like L-I was originally genetically green but has been replaced by a daughter layer of cells originating from the mutated L-II, hence defective appearance of the entire internal area of leaves of plants in the *Aralia* clone.

*Variegation in monocotyledonous plants.*—In most monocots leaves are elongated, as in grasses. Therefore when leaves of such plants become variegated, the variegation appears in linear form instead of irregularly patterned as in poinsettia. In Fig. 29 are shown a normal leaf (left) and a variegated (right) of congo-snake-sansevieria (*Sansevieria trifasciata* var. *laurentii*). The gray and

dark-green horizontal banding on both leaves is normal; it is due to larger and greener chloroplasts in cells in the dark bands and smaller and paler green chloroplasts in cells in the lighter bands. In the variegated leaf the factor for colorless tissue occurs in L-1. The width of colorless tissue at the margins of variegated leaves indicates the amount of tissue normally developed from L-1. It varies greatly as can be seen from the apparent complete lack of colorless tissue in the marginal areas of some leaves, in others from the presence of a slight amount of colorless tissue and in still others, as in the leaf to the right, very considerable amount of colorless tissue developed from L-1. No normal plastids could be seen in guard cells of the epidermis of variegated leaves, and the cells underneath the epidermis in green areas contained normal plastids.

Two leaves shown in Fig. 30 were from a variegated *Pandanus veitchii* (Veitch's screwpine). The one at left was a typical variegated leaf and that at right was a colorless type occasionally found. In this plant also the variegation





**Fig. 23.** *Chimeral colorless sport in juniper. Mutation in L-I.*

is due to a mutation in L-I. The forking in the green coloration in the middle of the variegated leaf would indicate that during the early stage of its growth, tissue development from the mutated L-I was both marginal and central, whereas the growth of the colorless leaf was entirely from the mutated L-I. The status of chloroplasts in the variegated *Pandanus* was similar to that in the variegated *Sansevieria*.

In Fig. 31 are shown two leaves of a variegated dracena (*Dracaena deremensis* var. *warneckii*). Leaf at left is a typical one with normal green margins, a narrow colorless strip next and a grey green at the center. A leaf like the one at right with colorless center is also found frequently. In this plant the mutation for colorlessness is in L-II. The guard cells in the epidermis of these leaves

contained green plastids. As in *Sansevieria* and *Pandanus*, L-I normally gives rise to varying amounts of tissue at the leaf margins. In some cases there was no noticeable marginal green tissue and in others this was considerable. Leaf at right represents a condition in which green tissue ordinarily developed from L-III in the variegated plants is eliminated and is replaced by colorless tissue derived from L-II. It is possible, I presume, for some leaves of the variegated *Dracaena* to develop as completely green, just as some leaves of the variegated *Pandanus* were completely colorless, by leaf development from L-I alone, but I did not find any in the limited number of variegated plants I have seen. The complex variegation system found in *Dracaena* would indicate monocots also may have three histogenic layers.





**Fig. 33.** Detail of colorless sport in juniper shown in Fig. 32.

*Variegation in conifers.*—Studies by Foster (22), his students and others have indicated that in the shoot apex of coniferous plants the cell division is random in contrast to that in the shoot apex of angiosperms where, as shown in this article, the cell division follows a certain pattern, and cells are arranged in layers in the shoot apex. In discussing this problem, the writer suggested in a previous article (8) that in the gymnosperms periclinal chimeral forms, such

as variegation in angiosperms, should not appear. Hejnowicz (23), however, reported a variegation in *Juniperus sabin*. In 1958, the writer saw a variegated form of juniper, *J. squarrosa*, at the National Flower Show in Washington, D. C. Also, John L. Creech, Plant Industry Station, obtained from England a variegated form of *J. expansa nana* of which branches are shown in Figs. 32 and 33. Variegation in all three junipers appears to be similar, in that each



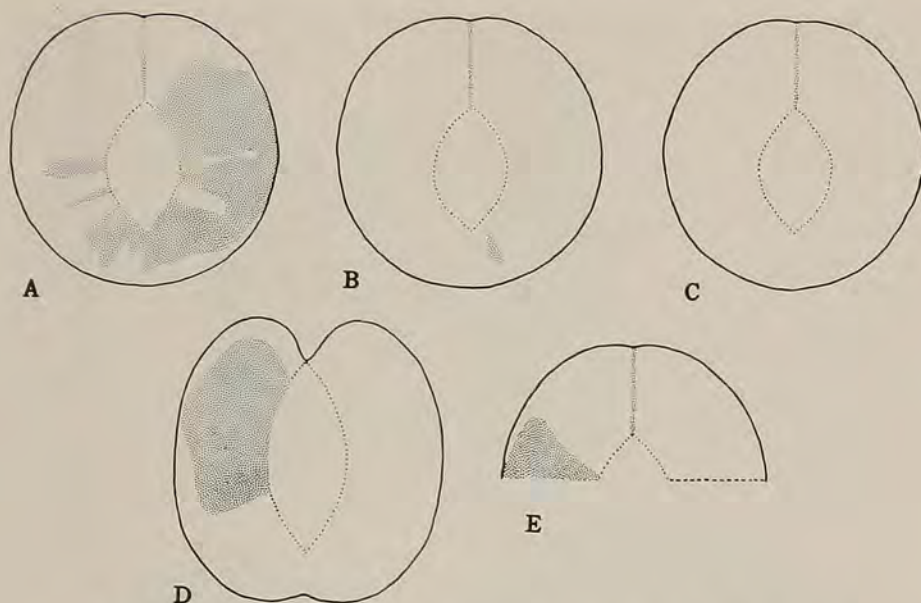


Fig. 34. White-flesh sport in fruits of normally yellow-fleshed Elberta peach variety. Mutation in L-II.

resulted from mutation in L-I. The variegated plant of *J. expansa nana* was only about twelve inches high and six inches wide when the writer saw it. Some small twigs of this plant were completely colorless while tips of other twigs and some areas along others were colorless.

The variegation, or the sport, in the juniper resembles leaf color sports of peach illustrated in Fig. 27, *Sansevieria* in Fig. 29 and *Pandanus* in Fig. 30, all with colorless mutation in L-I. In the monocot *Sansevieria* and *Pandanus* whenever L-I carries the mutation its effect is obvious, for generally considerable portions of tissue in the margins of the leaf blades originate from L-I. In the peach the presence of mutation in L-I is apparent only when internal tissue of a leaf is occasionally developed in part or totally from L-I. In this respect juniper seems to resemble more the peach, a dicot plant, than *Sansevieria* and *Pandanus*, monocot plants; except that in the shoot apices of the juniper, cell division must be occurring in horizontal plane more often than in peach.

In this respect juniper also resembles privet, for example, where cell division in a horizontal plane seems to occur rather frequently. This would account for the frequent appearance of internal tissue formation from L-I. The discovery of variegation in junipers indicates that some, if not all, gymnosperms and perhaps all angiosperms are characterized by primary histogenic—apical—layers, and that some gymnosperms are essentially like the angiosperms as to the cell activity in the shoot apices.

*Fruit sports of peach.*—Three fruit sports of peaches were brought to the writer's attention. One was a white-fleshed sport of the normally yellow-fleshed Elberta variety; the others were nectarine sports (fuzzless) of J. H. Hale and Elberta varieties. Full details of the first two sports were given in a previous publication (18). Here only the most pertinent points concerning the developmental features of the three sports are discussed.

When fruits of the white sport of Elberta were cut into, most of them were





**Fig. 35.** *Part-nectarine fruit sport of J. H. Hale peach variety.  
Mutation in L-III.*



bicolor and showed a pattern of white and yellow flesh coloration resembling leaf variegation of the poinsettia type. In some fruits the flesh color was entirely white except in the suture line which in all cases was colored yellow. Some others had only a very small amount of yellow flesh besides the yellow suture. In Fig. 34 are shown diagrams of four fruits with varying amounts of yellow and white flesh (the stippled areas of the flesh and sutures indicate yellow color). In A there are large areas of both yellow and white flesh; in B there is only a trace of yellow flesh, and in C all the flesh except the yellow suture is white. Diagram D shows a fruit cut in half longitudinally, and E the same half cut transversely.

Studies of cytochimeral peach fruits showed that a strip of tissue in the suture area is derived from L-I and that it is contiguous with the epidermal tissue. They also showed that the flesh and pit are derived from both L-II and L-III. In the 2-2-4 chimeral fruit in Fig. 6 the pattern of tissue development from 4x L-III may now be compared with that of the yellow portion of fruit A in Fig. 34. In the cytochimeral fruit the 2x portion of flesh corresponds positionally to the white portion of the fruit of the color sport and the 4x portion to the yellow portion. A color variation in peach here described would indicate that in the white sport of Elberta the mutation occurred in L-II. In breeding tests, the gene for white flesh in peach is found dominant over that for yellow. In a normal diploid peach, the yellow color is due to two genes for yellow color. A change from one gene for yellow to one gene for white is sufficient to change yellow color of peach fruit to white. Since L-I in this sport was genetically normal yellow, the suture tissue derived from it had remained yellow. The yellow coloring at the suture appeared both internally and externally. Sports in stone fruits with a contrasting color in the suture area were often found and most of these could have had a genetic basis similar to the one here described to account for the distinct character in the suture. The sport here described was not simply a change in color. Texture and flavor of the fruit were also affected, so that the fruits of the sport had a much pleasanter taste than nor-

mal yellow fruits of the Elberta variety.

Genetically speaking, nectarine fruits are merely fuzzless peaches. Nectarine fruits are firmer than peaches and have a distinctive flavor. In Fig. 35 are shown fruits of a part-nectarine sport of the J. H. Hale peach variety. Trees propagated from this sport bore either entirely normal peach fruits or normal peaches on some branches and part-peach and part-nectarine fruits on other branches. No trees or branches bore all nectarine-type fruits.

In Fig. 35 the upper fruit appeared as being wholly nectarine except for a wide band of fuzz along the suture. The fruit at the lower left had a covering of fuzz over most of its surface with only small areas fuzzless. The fruit at the lower right was like a typical nectarine. The fruit shown in Fig. 1 was also from the same sport; it had normal fuzz on its left side and practically no fuzz on its right. Although most nectarine-like fruits appeared to be without fuzz, close observation revealed a limited amount of very short fuzz on most of them. The nectarine-type fruits were somewhat smaller than typical J. H. Hale peach fruits; their flesh was firm and tasted somewhat tart. This was also true of the flesh of the nectarine portion of part-peach and part-nectarine fruits. The over-all flavor of fruit of the sport was delectable and therefore this part-nectarine sport might well be worth maintaining as a variety. In such a case the branches on trees bearing only peach fruits could be pruned off and leave only branches bearing mostly nectarine or part-nectarines.

If this nectarine mutation had been in L-I, all fruits should have been fuzzless. If the sport of the J. H. Hale had occurred in L-II, all trees propagated from this sport should have borne nectarine fruits. From breeding of J. H. Hale variety and of the sport only typical peaches have been obtained. For this reason it was concluded that the sporting in J. H. Hale had occurred in L-III.

The fruits of the nectarine sport of the Elberta variety were entirely fuzzless at maturity, although fuzzy in the flower stage. All trees vegetatively propagated from it have borne only fuzzless fruits. In this sport the mutation was in L-I. The L-I origin of this sport has been confirmed by breeding tests. When



crosses were made between this sport and nectarine varieties the seedlings obtained produced typical fuzzy peaches. All the fruits of the Elberta sport cracked at the suture and remained considerably undersized.

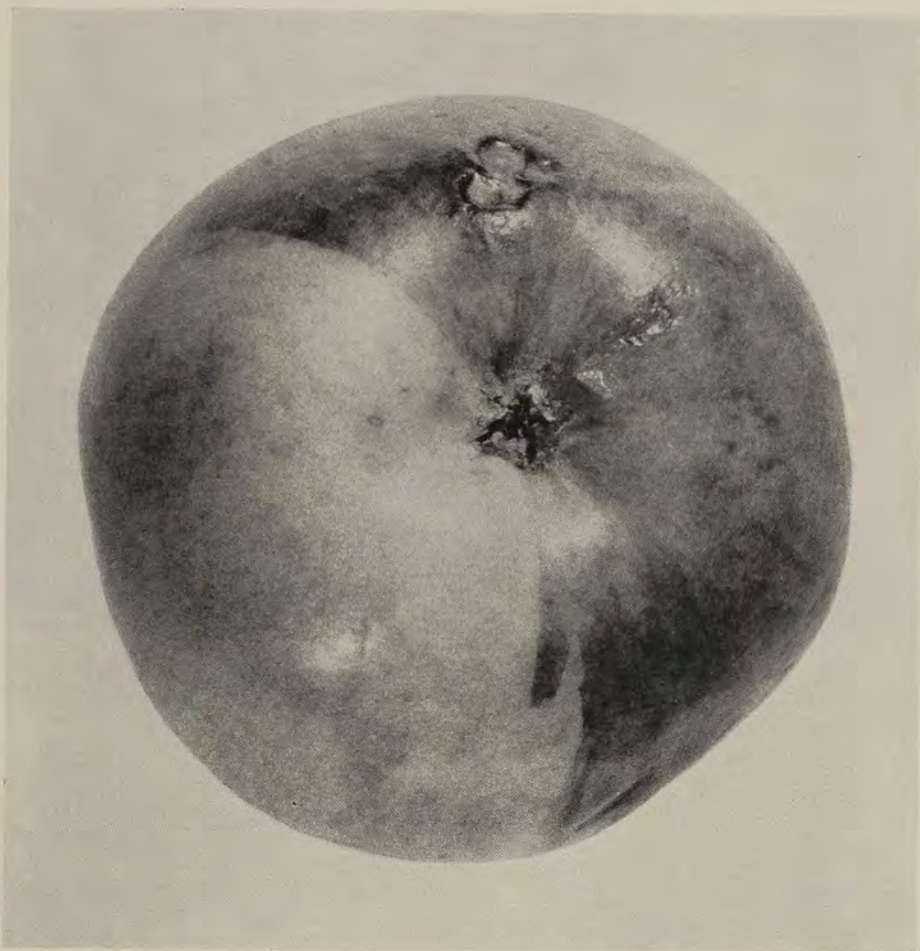
Breeding tests from the nectarine sport of J. H. Hale also resulted in a progeny of typical peaches as just mentioned. It was therefore assumed that in part-nectarine and part-peach fruits of J. H. Hale the tissue development may have paralleled that shown in Fig. 6. Positionally the "nectarine" tissue would correspond to the 4x tissue in the cytochimeral fruit developed from L-III (Fig. 6). On this basis the nectarine effect in some fruits of the J. H. Hale sport may be due to proximity to the epidermis of the tissue developed from the mutated L-III. It may be assumed that some substance from the "nectarine" tissue developed from L-III diffuses into the epidermal tissue and suppresses fuzz development by preventing normal growth of the epidermal cells into hairs (some chemical diffusion was also suggested in variegation of *Euonymus*). Where fuzz has developed it would indicate either that inner tissue in the fuzzy region of the fruit had developed entirely from normal L-II or that tissue developed from mutated L-III was located far deeper in the fruit.

*Fruit sports of apple.*—In the apple many color sports are known. It is suspected that most of these are of chimeral nature. In most colored apples the coloring matter is present in the subepidermal tissue. The content of cells of the epidermal tissue, especially in mature fruits, is practically destroyed, hence the epidermis is without coloring matter. In Fig. 36 is shown a fruit of one of the red color sports of Stayman variety. In this fruit, about two-thirds of the area was red colored and one-third was of the duller but lighter color, typical of the original variety. This may indicate that this red color sport of Stayman originated as a mutation in L-II and that the appearance of a normal colored sector on the left was from horizontal division of a cell of L-I which is normal and carries a gene or genes for normal, duller-red, color. It would seem that in the case of the fruit shown in Fig. 36, at or before the time when a growing point was differentiating from

the vegetative to the reproductive stage, that is into a flower bud, one of a group of three (see reference 6) centrally located cells in the apical dome of L-I divided horizontally instead of vertically, and the remaining cells continued to divide vertically. Thus, in one-third of the fruit the subepidermal tissue must have originated from the one genetically normal cell of L-I and this sector showed the normal dull color of the original variety, while in two-thirds of the fruit the red color of the genetically red L-II showed. It may also be that the appearance of a normal colored sector in this fruit was due to a reverse mutation from darker red color of the sport. This change in coloring may more readily be compared with changes in sports of Bartlett pear described elsewhere. It would seem if a mutation for red color in apple occurred in L-I, it would have no effect on coloring of fruits, since the content of cells of the epidermis is practically destroyed in mature fruits as pointed out above. A color mutation in L-I may be apparent, or expressed, only when internal tissue in the fruit is developed from L-I. The presence of red color mutation in L-I may be suspected in some cases when fruits with bright red sectors occasionally appear among fruits of a variety that normally is of dull-red color. Color sports derived from a mutation in L-I, which consequently has given rise to tissue growth from L-I, may be expected to remain constant and not revert to normal color.

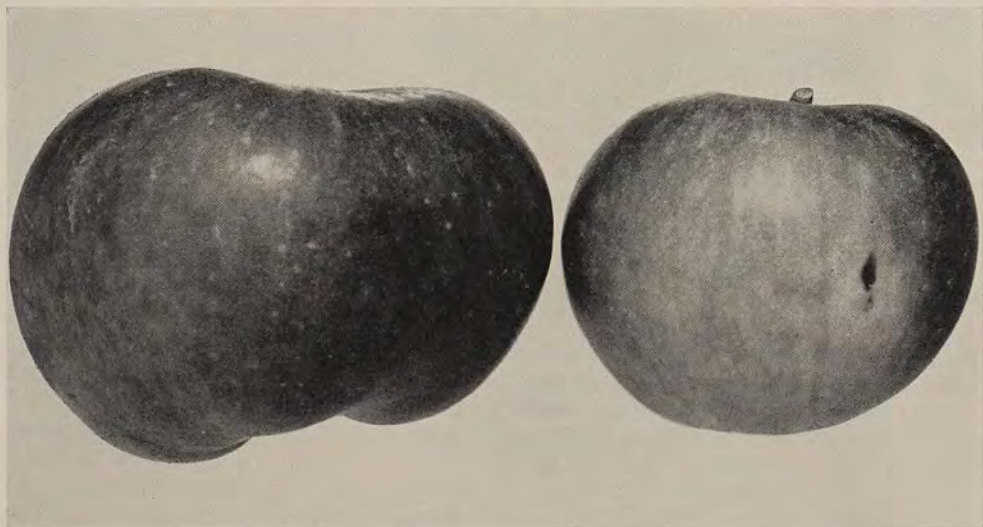
The two apple fruits shown in Fig. 37, one large and one of normal size, were from a tree of Winesap variety. The large-sized fruits on this tree were mostly asymmetrical in shape. Cytological examination of growing points of twigs from branches bearing oversize fruits showed a 2-2-4 type chimeral condition, whereas the growing points of twigs of branches bearing normal size fruits were 2-2-2, entirely diploid. Thus the sport would breed as a diploid since L-II is diploid. The enlarged portion of the fruit (Fig. 37) may be mostly tetraploid and the shallower portion mostly diploid. This can be understood when the giant fruit shown in Fig. 37 is compared with the cytochimeral makeup of the fruit shown in Fig. 10. Such asymmetry of fruits was also found in 2-2-4 type peach chimeras.



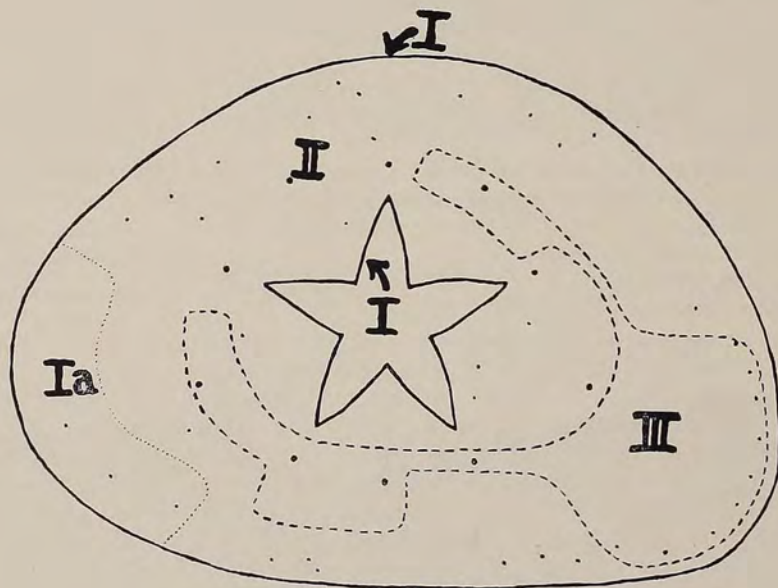
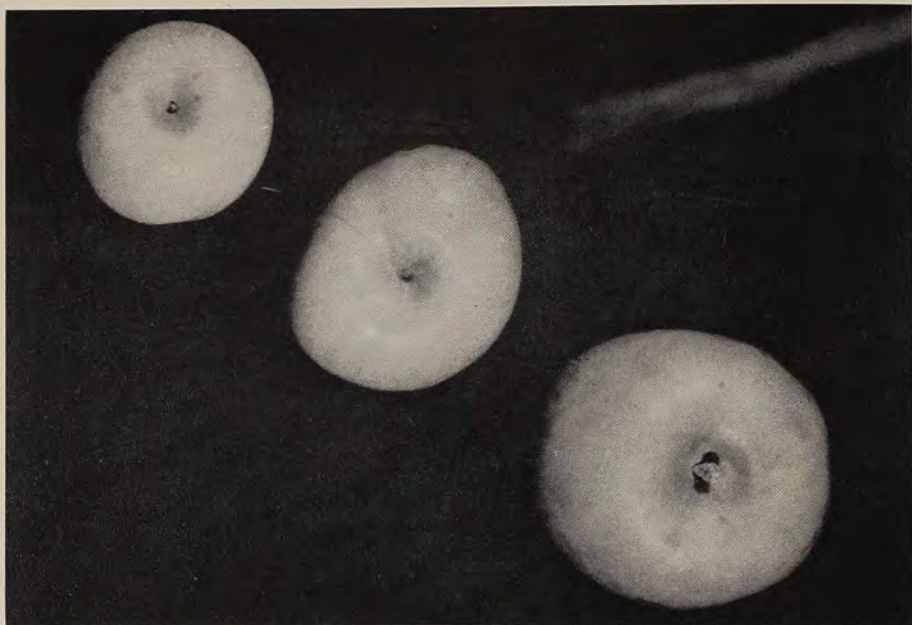


**Fig. 36.** *Light color sector on a fruit of a possibly dark red chimeral sport of Stayman apple. Mutation possible in L-II.*

**Fig. 37.** *Two fruits from a 2-2-4 chimeral Winesap apple; left is from a 2-2-4 branch; right is from a diploid branch and shows the normal size fruit.*







**Fig. 38.** Largest of three fruits from Rhode Island Greening apple variety. The other two are from a sport of Rhode Island Greening called "Sweet-and-Sour." Diagram of sweet and sour portions of the large fruit of "Sweet-and-Sour" sport. Mutation in L-LL.



Figure 38 represents an old pomological curiosity, the "Sweet-and-Sour" apple sport of the Rhode Island Greening variety. The bottom fruit, largest of the three fruits in this figure, is Rhode Island Greening, a tart apple; the other two are from a Sweet-and-Sour tree. The middle fruit, asymmetrical in shape, medium in size is typical of the sport. Some parts of the asymmetrical fruit when tasted were either sweet or sour. The top fruit smaller, evenly shaped, was entirely sweet. The mutation in this case had been a change in the factor for sour taste to sweet, but the mutation also had affected size of fruits. This mutation parallels the mutation of the nectarine sport of peach and the diplo-tetraploid chimera of the Winesap apple. The diagram in Fig. 38 was constructed on the supposition that in this sport L-I and L-III are normal and L-II carried the mutation. Tissues marked I are derived from L-I; II represents sweet flesh of the sport fruit derived from L-II; and III represents sour flesh derived from L-III. On the left side of the diagram an area is marked Ia to indicate that in some cases a part of flesh may be derived from L-I and will be sour. In actual tests, it was found that the bulged out parts of the fruits tasted sour and the shallow parts sweet. All the small, even-shaped fruits were sweet.

*Propagation of sports.* — Most of the vegetative-type sports described herein present problems in propagation since at least initially they affect only a portion of the plant tissues. Thus they differ from mutations occurring in egg cells or pollen grains in flowers, which will affect all tissues of a plant resulting from breeding.

When a mutation occurs in a plant it is present first in a single cell and affects only that cell and tissues derived from it. If the change occurs in a central cell of a growing point (6), it affects only one layer or a sector of a layer and consequently, as we saw in the various sports discussed herein, it involves only one tissue or a region in the internal tissues. The other tissues or areas remain normal. These facts must be taken into consideration when attempts are made to maintain or propagate sports of a chimeral nature.

Methods of vegetative propagation vary with the nature of particular plants.

The chief methods of propagation are a) bud grafts, b) shoot grafts, c) rooting of stem cuttings, d) rooting of leaves or leaf segments, and e) growing of shoots from root cuttings. By use of methods a, b, and c, which permit a bud of the sport to develop into the new plant, the chimeral form of a sport may be maintained. It was shown previously that, although most buds of a sport reproduce that particular sport, not every bud may do so. It was explained that such a result was due to a change in the usual characteristic mode of division of cells in histogenic layers, L-I and L-II. Propagation by methods d and e may be used to produce plants originating from L-III, as will be pointed out below.

The value of some sports depends on whether they remain constant or revert to the normal type as may happen in color or giant sports of fruits. Some color and giant sports may be made homogeneous throughout their tissues by forcing the development of adventitious buds or through root propagation if either of these methods is feasible.

In 1946, the writer observed (9) that adventitious buds, originating inside of bark, may be induced to develop on the stem of some apple varieties. The experiment was performed by cutting back one-year-old apple trees to about twelve inches from the soil level and destroying all lateral buds by digging them out with a knife. It resulted in adventitious bud development along the stem. Such buds originated in the phloem region inside the bark.

By developing adventitious buds pure color sports were obtained from two color sports of apple varieties: Improved All Red McIntosh (a sport of McIntosh) and Scarlet Staymared (a sport of Stayman); these sports had probably originated from a mutation in L-II. It is not known whether these sports are stable for the color or have shown a tendency to revert to the original lighter red color of the varieties from which they had originated. A number of such color sports in apples have shown a tendency to revert to original colors.

In order that certain problems involved in propagation of sport plants may be clearly understood, we need to reexamine the apple stem section shown in Fig. 8. There we find that the epidermal tissue is derived only from L-I,





**Fig. 39.** *Adventitious shoot development. Pure diploid and pure tetraploid shoots obtained adventitiously from a 2-4-2 chimeral McIntosh apple.*

the outer portion of cortical tissue generally from L-II and the inner cortical tissue, the conductive tissue [phloem, cambium and xylem (wood)] and pith are mainly from L-III. When stem cuttings are rooted, the roots originate from inside the bark, presumably also from the phloem region as the adventitious buds in the stems. Consequently when certain sports are propagated by root cuttings or by adventitious buds we may obtain some unexpected results.

Results obtained when shoots from adventitious buds were forced out of the stem of one-year-old trees of a 2-4-2 type McIntosh giant-fruited sport illustrate the case indicated above (16). Six one-year-old trees of Giant McIntosh were obtained from the Massachusetts Agricultural Experiment Station. On the basis of cytological examination of a shoot tip of one tree, this sport was considered to be a 2-4-4 type chimeral sport. Hence an effort was made to obtain



shoots entirely 4x by forcing out adventitious buds on the stem of the one-year-old trees.

Figure 39 shows adventitious shoot growth on the stem of a one-year-old tree of the Giant McIntosh sport. In Fig. 39-A, four bud swellings on the stem are marked a, b, c, and d. The first three buds are located along one side of the stem, almost on a straight line; the fourth, d, is lower on the right. Fig. 39-B shows the same tree with shoot growth from buds a and d; no growth occurred from b and c. On cytological examination shoots from a were found to be *entirely diploid* contrary to expectation since, as pointed out in the preceding paragraph, the preliminary cytological examination of this McIntosh sport showed it to be a 2-4-4 type chimera; therefore, all adventitious growth should have been homogeneously tetraploid. The result thus obtained suggested, as was later proved (16), that the sport had originated initially as a 2-4-2 type chimera and that the 2-4-4 chimeral plant earlier reported (10) was derived from a change in the 2-4-2 chimera. The branch from bud d was also examined and was found to be *entirely tetraploid*. It was "luck," so to speak, that bud d had not developed along the line of buds a, b and c. In that case if a shoot had grown from it, it would have undoubtedly been diploid.

The developmental story of 2x and 4x shoots in the giant sport of McIntosh can be better understood if we again take a close look at Fig. 8. As stated previously, adventitious buds originate in the phloem region. If the stem in Fig. 39 had had the chimeral makeup shown in Fig. 8-B, shoot growth from all adventitious buds would have been diploid. Therefore, it was most likely that the stem or shoot in Fig. 39-A originated from a bud with a dome which in part was 2-4-2 and in part 2-4-4 (derived from 2-4-2). As a result in a larger part of the stem the phloem and xylem tissue must have originated from 2x L-II, and in a limited part from 4x L-III. This sort of thing also occurred in peaches shown in Fig. 5. (Incidentally, attempts made to induce adventitious bud growth on over fifty young peach trees of Elberta and Golden Jubilee failed. The writer, however, has seen adventitious buds develop on some chance peach

seedlings). In Fig. 8-B the dotted line was drawn to indicate the possible origin of a portion of deeper tissue in the stem from 4x L-III, derived from 4x L-II. It seems correct to assume that the stem shown in Fig. 39 had the diploid-tetraploid makeup illustrated in Fig. 8-B; and that the buds a, b, and c had risen from the region of phloem which was 2x, and bud d had risen from the region of the phloem which had become 4x.

By the adventitious bud-method pure tetraploid forms have been obtained also from 2-4-4 chimeral Delicious, Ontario, Wrixparent (15) and from 2-2-4 chimeral Winesap apple (17, 25) varieties. Adventitious buds along the internodal regions on the stems of Delicious, McIntosh, Ontario and Wrixparent were developed with varying frequency on six trees of each variety in the experiments. No such buds occurred on the stems of six Winesap apples when it was first attempted, or on the stems of twenty-four trees used in a second experiment. Finally a larger number, sixty plants, were used in the hope that an "accident" might happen and that a pure tetraploid form of Winesap would develop. Six months after all sixty trees were disbudded, a swelling appeared in the calused region on one tree shown by an arrow in Fig. 40-A, and two swellings on a second tree (not shown). On both trees the swellings gave rise to branches. Fig. 40-B shows the emerging of a shoot from the first tree and Fig. 40-C its later development into a branch: *the shoot was pure tetraploid*. The branches on the second tree were both pure diploids, presumably because this particular tree had developed from a completely diploid bud, as the 2-2-4 condition in this chimeral Winesap frequently changes to 2-2-2, or 2x, as previously described.

As is well known, in some red color sports of apples, there is a tendency to revert to normal color. A red color sport of Bartlett pear has shown such reversion. Here it would suggest that these red sports may be made color-stable if adventitious shoots are developed from them. It should be kept in mind, however, that adventitious buds from some varieties may be obtained with ease and from others with considerable difficulty, if at all.





**Fig. 40.** *A pure tetraploid shoot obtained adventitiously from a 2-2-4 chimeral Winesap apple.*

In stem cuttings, when rooted, the roots, as stated earlier, arise from the phloem region as the adventitious buds. Buds that develop normally at the nodes of shoots arise usually from all three histogenic layers. Hence, leaf variegations and certain fruit sports as described in this article are maintained through normal bud propagation. But adventitious buds originate from cells in the phloem; they will have the genetic or cytological constitution of the phloem and usually therefore of L-III from

which phloem tissue normally arises. Similarly, as roots arise adventitiously, they also may have the genetic or cytological makeup of L-III. When L-III has a different genetic or cytological makeup from other histogenic layers of the plants, shoots developed from root cuttings may have only the characteristics inherent in L-III of the particular chimeral plants, if in the meantime no replacement of tissue developed from L-II had taken place in the chimeral plant.



#### IV. "Graft-hybrids" and "Graft-chimeras"

Some of the readers may have come across references to plants known as *graft-hybrids* or *graft-chimeras*. In each case these are supposed to have originated by adventitious growth from the area of the graft union between two different species, most of them belonging to two closely related genera. Some of the famous ones are *Bizzarria* orange, *Cytisus* (or *Laburnum*) *adami*, *Crataego-mespilus*, *Pyro-cydonia*, *Amygdalo-persica*, and perhaps a few more. These are described in a small book by Jones entitled *Plant-Chimaeras and Graft-Hybrids* (24). A very good discussion with a long bibliography on the subject was published by Swingle (27). This topic has also been discussed interestingly by Weiss (29) and Clowes (3). In recent years, Bergann (1, 2) has been studying some of these forms very intensively.

These plants when discovered were first accepted as being graft-hybrids. Winkler (30) appears to have set himself to prove experimentally that these were truly *graft-hybrids*. This he attempted to show by grafting nightshade (*Solanum nigrum*) on tomato (*S. lycopersicum*) and tomato on nightshade, and by forcing adventitious bud growth from the grafts. He cut off the grafted plants at the point of their graft-union. From the callused surface of the decapitated plants he obtained some shoots that had the immediate appearance of the two components. He thought that these odd-looking plants were truly graft-hybrids. Later Winkler (31) himself was able to determine through cytological study that these were not graft-hybrids but were in fact graft-chimeras. After graft-hybridity of tomato-nightshade mixed plants was resolved in favor of graft-chimera, the idea became current that *Bizzarria* orange, *Crataego-mespilus*, etc., also were graft-chimeras.

It is surprising that even now the terms graft-hybrid and graft-chimera are used loosely as if they mean the same thing. For a specimen to qualify as a graft-hybrid it must be assumed (a) that union has actually taken place between two somatic (vegetative) cells, one from

the scion and the other from the root-stock; (b) that the nuclei of the two cells have fused where scion and root-stock have made a union; (c) that from the united cell has developed an endogenous (internally developed), adventitious bud which has grown into a branch. The course of these events would require that the vegetative hybrid thus originated contains the sum of the somatic (body) chromosomes of the parent stocks. The graft-hybrid would then really be a true hybrid with a double chromosome number. It should here be emphasized that at present we have very precise histological, cytological, genetical and horticultural methods that should be used to determine the exact nature of such plant forms before conclusions concerning these plants are to be accepted at all.

It appears that authentic graft-chimeras have been obtained experimentally only between Solonaceous plants (*Lycopersicum* and *Solanum*), plants which are herbaceous with succulent stems. To this day, there has been *no* authenticated record of anyone's having produced graft-chimeras *experimentally* between *woody* plants. The writer strongly suspects that most, perhaps all, woody "graft-chimeras" that have been reported to have originated by chance may not be really graft-chimeras, but are mutational chimeras originated in the manner described in this article for a few fruit (for example, the nectarine sort of peach) and leaf sports. Bergann (1, 2) and a number of other investigators (see references 1-2) believe, however, that in three well known forms they are truly graft-chimeras. These are *Crataegus asnierei* and *C. dardari* and *Laburnum adami*. The first two forms are known as *Crataego-mespilus*, are considered to have been derived from grafts of *Mespilus germanica* over *Crataegus monogyna*, and the third is considered to have been derived from a graft of *Cytisus purpureus* over *Laburnum anagyroides*. Bergann reports (1, 2 and personal correspondence) having observed the appearance of *Mespilus*



branches on *C. asnierei* and *C. dardari*, and branches of *Cytisus* on *Laburnum adami*; and that he has been able experimentally to force out adventitious branches resembling the rootstock parent in all three graft forms. It would be most desirable if Dr. Bergann could publish such results with suitable illustrations. These might include initiation of adventitious bud development on the stems of the supposed chimeral material, details of comparative vegetative growth and certain gametophytic developments, for instance, comparative pollen grain size and percentage of normal and abnormal pollen. A publication of such a character would be most welcome so that serious doubts about the origin of such forms may be fully resolved.

One more comment: The term "hybrid" is used in the science of cytology, genetics, horticulture, and taxonomy to connote union of two nuclei. In some Russian and other scientific literature we find reference to both "graft-hybrid" and "vegetative-hybrid." In reading these reports, we do not find evidence that anyone has succeeded in demonstrating the development of new forms

of plants which may have resulted from union of two vegetative nuclei. These reports usually contain references to some suspected influence of rootstock on the scion of grafted plants; and often these reports carry genetic implications, and such results are given as indication or grft—or vegetative-hybridity. If such influence is all that is implied by the terms "vegetative-hybridity" and "graft-hybridity" then the authors of such works should find another word to express this kind of influence or phenomenon. In order to avoid confusion and unnecessary misunderstanding the word *hybrid* and any other words conveying similar meaning should be strictly reserved for the specific meaning just pointed out. The term graft-chimera has a valid meaning when applied to the two herbaceous solanaceous plants mentioned, but it should not be used with reference to woody plants, until all doubts concerning such forms are fully cleared. As to the terms "graft-hybrid" and "vegetative-hybrid," they are fictional and should have no place in scientific literature.

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# A Book or Two

## **The Home Book of Flower Arrangements**

*Using Oriental, European, and Colonial Containers*

Estelle G. Easterby. Chilton Company, Book Division, 56th and Chestnut Streets, Philadelphia 39, Pennsylvania. 1960. 156 pages. Illustrated. \$3.50. (Library).

This book states in its foreword that the author intends to teach young people the real fundamentals of flower arranging. In the first 17 or 18 pages it attempts to give a background of Egyptian, Grecian, Gothic, Roman, Persian, Dutch and Flemish, French, Georgian, Victorian, Colonial Chinese and Japanese arrangements. The information conveyed is sketchily dangerous to a novice arranger because it is much too brief and treated so lightly. There are many complete books on historical arrangements of various periods that could be referred to as further study aids for young people.

The accompanying photographs of interpreted Japanese arrangements are quite good and seem well thought out and executed, although there is a mixture of Japanese and Chinese in containers and accessories, which is completely acceptable for home arrangements. Some very interesting and easy to execute designs are pictured in a short chapter entitled Modern Arrangements.

Discussed, but all too briefly, are the subjects of growing suitable material for arranging, containers, mechanics and accessories. Treated lightly also are the Elements of Design, Color and The Principles of Design. The reviewer feels that these points would be much clearer to the arranger were they related to direct examples using photographs of arrangements, especially where color is concerned.

Twelve lovely color plates occupy the center of the book. To the critical judge some would have a few design flaws, but nothing serious enough to discourage the intended young reader. The section on Suitable Arrangements for Different Areas of the Home pictures some lovely arrangements. The majority of these are simple vertical or nearly vertical arrangements using but a few flowers. A chapter on Church Arrangements pictures one good one. Lastly in this book there is a rather incomplete discussion on dried materials; how to preserve materials and inanimate objects that might be used by the floral arranger.

VICTORIA K. ANGEL

## **Orchids In Australia**

Fred Moulen. Charles T. Branford Company, 69 Union Street, Newton Centre 59, Massachusetts. (June 1958) (Printed in Switzerland by Imprimerie Centrale Lusanne for Edita S. A., Lausanne.) 148 pages. Illustrated. \$15.00. (Library). AHS Members' Price \$12.75.

The author, an Australian orchid grower, lecturer and color photographer, has combined these talents to produce this book. The book contains only eight pages of text, as such, but it also contains a hundred excellently rendered color reproductions of flowers in the orchid family as grown (cultivated) in Australia. Some of the color plates are full page reproductions; all have lengthy captions on facing pages, almost tantamount to text. The volume includes perfect color photographs of species and hybrids of Cymbidiums, Cattleyas, Vandas, Cypripediums, Dendrobiums, Miltonias, Odontoglossums, and others.

It is an excellent book of color photographs of some of the better known orchids, but it is shy on much that the commercial grower and hobbyist seeks to know about the Australian orchids, such as cultural practices, and especially information on and pictures of the orchids endemic to that country.

E. G.

## **Tree Fruit Production**

James S. Shoemaker and Benjamin J. E. Teskey. John Wiley & Sons, Inc., 440 Fourth Avenue, New York 16, New York. 1959. 456 pages. Illustrated. \$6.95. (Library).

This new text deals with the propagation, culture, and handling of tree fruits in the United States and Canada. Suitable for the beginners' course in pomology, it will also serve as a general reference book on orcharding. Considerable emphasis is placed on recent scientific developments. Such fields as spraying for fruit thinning are included. There is somewhat of a tendency to include too many subjects at the expense of adequate discussion. The text is well illustrated and many references are suggested for supplemental reading.

H. W.

(Books available **for loan** to the Membership are designated: (Library). Those not so designated are in private collections and are not available for loan. Books available **for sale** to the Membership are designated with the special reduced price and are subject to the usual change of price without notice. Orders must be sent through the American Horticultural Society accompanied by the proper payment. Please allow two to three weeks for delivery. Those not designated for sale to the Membership at reduced prices can be purchased through the Society, however, at the retail prices given. In these instances the full profit is received by the Society to be used for increased services and benefits of the Membership.)



## ***The Book of Planters***

Robert Scharff. M. Barrows and Company, Inc., 425 Fourth Avenue, New York 16, New York. 1960. 191 pages. Illustrated. \$3.50. (Library.)

A detailed and well-illustrated guide on interior and exterior planting boxes. Informative and well-written, the book covers all important phases of this increasingly popular form of gardening and should serve adequately as a ready reference for planter construction, plant materials, and planter problems.

C. N. JOHNSON

## ***Camellias For Everyone***

Claude Chidamian. Doubleday & Company, Inc., 575 Madison Avenue, New York 22, New York. 1959. 191 pages. Illustrated. \$3.95. (Library.)

This book is especially beneficial for persons just becoming interested in growing camellias. The author has gone to some length to convince the reader that camellia growing is easy, simple, and requires little time and effort. He attempts to break down the barrier of legend and myth that camellias are fragile, rare, and exotic. In this attempt, he somewhat over-emphasizes the ease with which these plants can be grown in different locations and under different conditions. In a later chapter, however, he gives a thorough discussion of how the camellia can be adapted to conditions which will induce favorable growth under varied climatic conditions.

A list of the most important species, varieties, and mutations is given with descriptions of flower form and color. This useful guide also gives information as to the time and length of blooming period and landscape value.

The author has done a superb job of bringing to the reader's attention new and interesting ways to use camellias in the landscape. The chapter covering uses of the glamorous camellia as a valuable landscape plant is one of the highlights of the book.

Information is also given on growing camellias under glass. Culture and growing habits are discussed in detail.

A chapter is devoted to ways camellias can be used to beautify the interior of the home. Used either as bonsai or arrangements to spotlight a gorgeous bloom, camellias are excellent for indoor use. The author goes further in giving step-by-step instructions for making camellia corsages.

The chapter devoted to collecting, buying, and propagating contains profitable information for those who are planning additional purchases. A valuable discussion on camellia culture is presented. The author points out that camellias must be adapted to conditions similar to their native environment to insure successful growth.

Adequate information is given on the maintenance, pests, and diseases of camellias.

The final chapter on camellia literature is especially valuable to the reader. A brief discussion of the most informative literature is presented.

This book should encourage many to grow camellias for the first time and should encourage many others to find new ways to use the plant in the landscape. The book is interesting, well illustrated and provides profitable information for all persons interested in camellias.

LEMOYNE HOGAN

## ***The American Camellia Yearbook, 1959***

Edited by Herbert S. Wolfe. American Camellia Society, Box 2398 University Station, Gainesville, Florida. 1959. 388 pages. Illustrated. \$6.00. (Including Membership). (Library.)

The 1959 Camellia Yearbook is a fine collection of articles on the camellia which are grouped together into five major sections; Relatives, Species and Varieties; Diseases and Insects; General Culture; Plantings and Gardens; and Awards, Shows and Varietal Registrations. In each of these sections there is an article, or two, that has lasting information in the better understanding of this plant. In the first section, these would be articles such as those dealing with the possible cause of false hybrids, the chromosome numbers or the description of new types.

The sections on Pests and on Culture each have articles that report on the research findings with this plant. These are reporting on pest controls, cold hardiness, nutrition, and propagation. They will interest the serious student of this plant as well as some written in a more popular manner that will appeal to the hobbyist.

Several gardens or collections of camellias are described, as well as varieties growing on the outer edges of the camellia "belt." Reports of this kind give help and encouragement to those active fanciers of this flower.

Society information is included as the annual report of new varieties registered, show awards, and membership list. It even includes a none horticultural item; a poem on the camellia. There are articles to appeal to all interested in the camellia. A good yearbook.

CONRAD B. LINK

## ***Peonies, Outdoors and In***

Arno & Irene Nehrling. Hearthside Press, Inc., 118 East 28th Street, New York 16, New York. 1960. 288 pages. Illustrated. \$5.95. (Library). AHS Members' Price \$5.06.

This most effective presentation of the peony is marked by three impressive characteristics: the extensive scope of the book, embracing a many-faceted approach to one of the great ornaments of the garden; the authoritative grasp of the subject shown by the writers; and their own enthusiasm which they communicate so happily



to their readers whether connoisseurs or beginners in peony culture who can do little more than recognize that Festive Maxima is a peony.

The subjects embraced are all-inclusive: historical background; graphically clear botanical classifications; the peony calendar; design in the garden; characteristics and cross-classification of varieties; culture; many aspects of indoor use and practice; and a supplement covering peony gardens, private, public, and commercial.

It is difficult to choose which sections are most successfully done. The presentation of varieties by many classifications form an excellent handbook for selection: by color, height, time of flowering, foliage, fragrance, and garden purpose. It is good to see the hybrids getting the attention that their new world of brilliant, clear colors deserves. Interest would be added for many collectors if the hybridizers names had been used more freely after varieties. The authors have been careful not to overpower the reader by presenting an all-inclusive list of varieties, but have exercised restraint and discrimination in their choice.

In noting the carefully detailed steps in culture and garden design with peonies, one needs to remember that actually few flowers produce with less drudgery "an attractive garden with a minimum of work."

Collectors in many horticultural fields have learned the incalculable value of visiting other gardens to see new and coveted varieties. It is hoped that many garden books will emulate this volume in its supplement that locates geographically and gives pertinent data on many gardens where peonies can be seen at their best.

The text is written in clear, effective prose, but illumined with touches of imagery that are appealing—"red stems and sea-green leaflets," "the peony, that peacock among flowers." The many well-chosen pictures, with some brilliant color inserts, tend to make the text much more graphic and usable.

If a negative note must be struck, it might be that too much space is devoted to working out combinations with other flowers, something that perhaps most gardeners prefer to achieve under their own inspiration.

It will probably be many years before there is issued another volume that will take away from the Nehrlings their distinction of having given the peony world its definitive text.

FRANK J. GILLIAM

### **Religious Themes In Flower Arrangement**

Ruth E. Mullins. Hearthside Press, Inc., 118 East 28th Street, New York 16, New York. 1959. 122 pages. Illustrated. \$5.95. (Library). AHS Members' Price \$5.06.

In the beginning of this book the author attempts to cover (but does so very inadequately) the Great Religions of the World in eight half-pages of text. Each page is accompanied by an arrangement, many of which incorporate driftwood, small accessories, and dried materials, and some are placed on painted wooden bases.

Of the 64 or so arrangements pictured, more than half make use of driftwood, dried ma-

terials, containers, and accessories that seem to lack the elegance, grace, and dignity associated with and traditional to religious floral arrangements.

A chapter on Church Arrangements pictures six arrangements of predominantly fresh materials of only moderately good design. All seem again to lack the grace, charm, and purity of balance so appropriate and fitting to the religious theme or church setting for floral decoration.

The all important phase of design in the arrangements is discussed briefly, but the many flaws are apparent; most noticeably in the Scale, Proportion, and in many cases the size of the accessories used.

Included is a brief Reference List; a list entitled Symbolism of Flowers, Leaves and Fruits with common names of the materials used. Also included is a list, again with common names only, of some flowers, foliages and fruits of the Bible.

VICTORIA K. ANGEL

### **Form and Space of Japanese Architecture**

Norman F. Carver, Jr. Published by Shokoku Publishing Company; distributed by Charles E. Tuttle Company, Rutland, Vermont. 1955. 200 pages. 164 illustrations. \$12.00.

This bi-lingual book, addressed primarily to architects, concerns itself with two elements of design—Form and Space. These are defined and discussed, important since the concepts as presented must have determined the illustrations.

In his brief preface, the author writes: "I have assumed, therefore, some basic acquaintance with Japanese architecture \* \* \* and proceeded above and beyond these particulars to define the general organization of Japanese architectural design and its implications for modern architecture. Such an approach, of course, is concerned not with fact alone, but interpretation of fact."

For readers of this Magazine, who may not have the "basic acquaintance," the reviewer presumes to remind them that the materials shown are primarily wood, and in lessening degrees, stone, tile, plaster, bamboo, straw, and paper. Wood shows every degree of finish, from raw forms to hand polished; stone, from natural forms, particularly river worn gravel, sand, to carefully cut. For many of these old buildings, only the most primitive tools were available and no modern means for lifting great weights; also, that hand labor of incredible skill carried out the work.

One might remind himself also, that Japan, an island country, has torrential rains, in the areas reported, not much snow, brilliant sunshine. These, too, affect design.

The reader interested in gardens will find nothing of plant materials, but a wealth of study of the relations between building and garden as they relate to one another and interpenetrate.

Mr. Carver has shared his great experience with a purpose, but any one may reap his own particular harvest of ideas and inspirations.

B. Y. M.



## The Gardeners' Pocketbook



W. H. HODGE

### *Meriania nobilis*

While residing in Medellín, Colombia, during 1945 and 1946, I had occasion to become acquainted with what is undoubtedly one of the most showy of small flowering trees native to the American tropics. This is *Meriania nobilis*, more familiarly known to the people of the Department of Antioquia where it is endemic as *amarraboyo* or *marraboyo*. Although a member of a prominent tropical family, the MELASTOMATACEAE, which can boast of a number of showy plants (e.g. *Tibouchina semidecandra*), few, if any, can compare in beauty of flower with this species.

The publication of a color photograph of *Meriania nobilis* (*Natural History*, Vol. 56, June, 1947) evoked comment concerning the possibility of cultivating the species and because this in-

terest still continues, it seems worthwhile to summarize what is known about this endemic Colombian tree and particularly about its potential as an ornamental.

The genus *Meriania* (honoring the German naturalist-traveler Maria Sybil Merian) includes some thirty or more species of tropical American trees of the West Indies and northern South America. *Meriania nobilis* was first named by the botanist, Triana, in 1871 from plants collected near Rio Negro, an agricultural community lying to the southeast of Medellín, capital city of Antioquia.

*Meriania nobilis*, as observed by this writer in the classical area, is a small tree seldom more than several inches in diameter and ranging upwards to fifteen or twenty feet tall. Its growth habit is not particularly ornamental, being open and even rather straggly. The large ovate leaves are, however, very attractive with their dark-green upper surfaces strongly nerved with palmate venation so characteristic of the Melastoma



Family. When in flower the *amarraboyó* makes up for all its vegetative deficiencies. The large flowers (up to three inches across) are beautiful not only in form but also in color, the buds and newly opened blossoms being a gorgeous pink (nearest to RHS Peony Purple 729/2-3), changing to rose as they become older. The yellow stamens with their characteristic dark horn-like appendages made a striking pattern at the center of each open bloom. Several flowers are borne in each cluster to form rather large, stalked racemes.

As desirable as the *amarraboyó* would appear to be as an ornamental, all attempts to cultivate this species have apparently failed. To help future attempts, a few remarks about its native habitat may be in order. The tree thrives in the low, open forests or woodlands which still cover the rather precipitous ridges of the central Andean ranges surrounding the valley in which the mile-high city of Medellín is located. These ridges lie at elevations of from seven to eight thousand feet where the climate is cool-temperate rather than warm-tropical. Because of the low latitude the annual and daily range in temperature is not great, but probably would run between fifty-five to seventy-five degrees Fahrenheit. At this elevation precipitation is considerably greater than in the Medellín valley, but the pattern of precipitation is the same with two dry seasons and two wet seasons each year.

A decade ago the species was quite common around Santa Elena lying near the height of land on the road between Medellín and Rio Negro. Here it could be observed in flower during the Fall, particularly in the month of October. In its native haunts it associates with such sister melastomaceous species as the magenta-flowered *Tibouchina lepidota* (*Siete Cueros*) and the white-flowered *Miconia theaezans*, common shrubs or small trees of the rather open woodland borders fringing the road. The presence of a number of ericaceous genera in the same plant communities seems to indicate that soil conditions are on the acid side.

During my sojourn in Colombia, I could learn of no one who had successfully grown the *amarraboyó* as an ornamental although some unsuccessful attempts had apparently been made to

transplant the trees to local gardens. Nor did I learn of anyone who had tried to grow this tree from seed. There must have been efforts made, for the local opinion was that the plants were mycorrhizic and would not grow in the absence of certain soil fungi.

Believing that it might be worthwhile to see whether *Meriania nobilis* could be grown from seed under cool greenhouse conditions, I wrote a good friend and former colleague, Carlos Garces O. of the Facultad de Agronomía at Medellín. Three ounces of the very fine seed were received in September, 1956. This was divided with several other botanic gardens and arboreetums both in this country and abroad. At the same time, a small quantity of soil collected from beneath trees in the wild was forwarded to the United States Department of Agriculture with the hope that it might be of advantage in supplying the necessary soil fungus for seedlings to be grown at the Plant Introduction Station at Glenn Dale, Maryland.

At Longwood Gardens seed was planted on several acid media including a peaty compost as well as the standard shredded sphagnum mix. Germination was excellent in both cases although the young seedlings subsequently made better progress in the sphagnum. During the next two years a few of the seedlings attained a height of ten to twelve inches, but most of them seemed to be unhappy and eventually all were lost in the fall of 1959. Similar results were attained at Glenn Dale, though they were unable to maintain plants after 1958.

In spite of these failures the *amarraboyó* still warrants further trial. The best spot to initiate controlled cultural trials would be in Medellín, Colombia, at the Facultad de Agronomía where proper facilities exist for horticultural testing. At the same time it would be worthwhile to try this plant again in this country. Keeping in mind that *Meriania nobilis* is an acidophile, that it inhabits the cool, moist Andes where it suffers neither high temperature nor frost, it would seem that the most likely spot for successful trial outdoors in this country would be in the San Francisco Bay area or in greenhouses under glass anywhere where summer temperatures can be kept under seventy-five.—W. H. HODGE, *Longwood Gardens, Kennett Square, Penna.*





W. H. HODGE

*Azaleas flourishing in raised bed of acid soil in Warwick, Bermuda.*

### **A Technique for Growing Azaleas in Bermuda**

Except in the marshes, the soil of Bermuda has been formed entirely from the weathering of a thick limestone cap. It is, therefore, alkaline with a pH ranging from 7.5 to 8. Many kinds of plants luxuriate in its rich, warm, red-brown loam, but hardly azaleas. And the soil contains far too much lime for a substantial lowering of the pH by means of sulphur or peat.

In attempting to develop a successful azalea technique for Bermuda the first

problem to be solved is then quite obvious:—to provide a suitable acid soil. Assuming a suitable soil, the next problem is where and how to use it. Finally, since azaleas are extremely climate-conscious, many requiring an uninterrupted winter dormancy, there is the further problem:—what azaleas to try, considering the comparative mildness of the Bermuda winter and the long, warm summer.

My first attempt at arriving at a satisfactory technique was to make up a soil from a mixture of imported peat moss, composting materials and local sawdust with fertilizers added plus a chemical





W. H. HODGE

*Luchu azalea* (*Rhododendron scabrum*) in Bermuda growing on a mound of acid soil separated from limestone soil beneath by a sheet of aluminum. (see lower right corner)

for speeding the breaking-down process. After a few months the "soil" was placed on top of the ground as a raised bed about ten inches deep and held in place by upended logs of Bermuda cedar sunk into the ground. It was felt that holes dug in the ground and filled with acidic material would not be satisfactory in this climate since lime would leach into the holes with every heavy rain. For about half the day the bed would receive full sun. Then my friend, Walter H. Hodge, who at the time was with the U. S. Department of Agriculture, Plant Exploration and Introduction Section, Beltsville, Maryland, kindly had sent to me a small consignment of azaleas for trial:—six

florist's azaleas; three plants listed as *Rhododendron* sp., "China" bearing the federal Plant Introduction No. 199,300; and three plants representing P. I. No. 199,302.

Avid invading roots from nearby shrubbery, an impaired pH due to a careless workman's shovel, and absence from Bermuda during the summer did not help this first experiment. In something less than the fullness of time the florist azaleas died, and so eventually did the three representatives of P. I. No. 199,300, though for awhile they looked promising. But the three plants of P. I. No. 199,302 survived the tough conditions, and when one of them put out its



first flowers, I was amazed at their intense beauty. This gorgeous red azalea from Formosa, with its distinctive glossy dark-green foliage and attractive lax habit of growth, has recently been identified by B. Y. Morrison, creator of the Glenn Dale Hybrid Azaleas, as undoubtedly a form of *Rhododendron scabrum*, the Luchu azalea, and not *R. linearifolium* var. *macrosepalum*, the name given P. I. No. 199,302 in Frederic P. Lee's *The Azalea Book* (somewhere along the line there seems to have been a clerical error). In flower, the Luchu azalea is surely among the world's most handsome and dramatically beautiful shrubs.

When our family moved to a new house, the brave Luchu azaleas and made-up soil went with us. One was planted in the garden on a mound with a 4 by 4-foot sheet of aluminum beneath to discourage unwanted invaders. The other two went into a slathouse in raised masonry beds. Then several *indica* type azaleas were imported from Florida, a dozen each of the clones 'George Lindley Taber,' 'Formosa,' 'Southern Charm,' and 'President Claeys.' They, too, went into the slathouse in raised beds planted in a fibrous marsh soil (with a low pH) which seemed worth trying. The pH was fine, but there was much osmunda fiber and precious little soil. Despite the use of appropriate fertilizers, none of the plants inside the slathouse did well. For one thing, there was too little light. But the Luchu azalea atop the sheet of aluminum outside in the sun grew and flowered nicely.

Now came a lucky break. In a part of a local marsh, which supports a scrubby mixed woodland of several acres, I finally discovered just what I had been hoping to find:—a highly acidic organic soil, twelve inches of it above the water level of the marsh. Transplanted to this true soil in raised masonry beds built for me by a kind landlady, in sun outside the slathouse, the Luchu azaleas and most of the *indicas* came to life! These beds measured eighteen inches high with a planting width of about three feet. At the bottom there is a thick layer of sawdust, then about ten inches of the marsh soil protected by a sawdust mulch. A little fertilizer has been used.

At present, nearly two years from the transplanting, all azaleas are doing well

—except 'President Claeys,' which is not satisfactory. In particular, the gorgeous Luchu azalea and *indica* clone 'George Lindley Taber' appear to be perfectly adapted to the Bermuda climate. Both are very fine indeed. Eventually the proximity of the masonry may adversely affect the soil pH, but it will probably take a long time.—JOHN KNOWLTON, *Marine Villa, Warwick, Bermuda.*

### Two Experiences with Tree Peony Propagation

Years ago, a nine year old plant of Reine Elizabeth seemed so unhappy that I transplanted it, setting it several inches deeper than it had been growing. The top died back. The following spring the roots sent up eight shoots that made quick growth. I tried layering the plant by the method used for gooseberries, piling garden soil around and through the clump, separating the shoots as widely as possible without breaking, and allowing only the tips to show above the soil. After firming the soil I covered the mound with old burlap and kept it well watered all summer. A year later each shoot was well rooted, was cut off near the ground, and was successfully planted. I realize that one experience does not prove much. I feel sure that some varieties will layer much more readily than others and that the same variety that may layer successfully in the south may not in the north. Even so, when I read some of the reports of poor results with layering tree peonies I wonder whether the gardener doing the reporting used mound layering or the type that my neighbors speak of as laying down a branch.

More recently I tried growing tree peonies from seed. Over a period of several years I secured several hundred seeds from five different sources. I shared the seed with a gardener in Illinois and with a Kentucky neighbor because the care I give seed is not a fair test. Unfortunately, I kept no records, being sure at the time that I could not possibly forget anything of so much interest. Of a hundred seeds secured from one grower I think not one came up, though they were healthy looking seeds. Each of three other



lots produced few seedlings. A lot of twenty seeds received packed in damp sphagnum and allegedly so packed as soon as removed from the seedpod gave almost perfect germination. The seedlings varied greatly in appearance and in apparent strength. Many of them disappeared before the second summer, presumably leaving only the strongest. Results in Illinois and Kentucky were much the same. Surprisingly enough, the seed that I planted in late summer and never saw again until I returned home in June produced fully as high a percentage of seedlings as the seed given conventional care and attention. So far only two seedlings have flowered, and only one for its second year. The interesting point there is that the second year flowers were much superior to the first year's flower in both form and size, suggesting that tree peonies may share the herbaceous peony's tendency toward variable bloom during its first years.—MAUD R. JACOBS, *South Carrollton, Kentucky*.

### Southern Viburnums

Many garden enthusiasts in the United States are "taken" with the Genus *Viburnum* and I am not an exception to this, collecting as many species as possible and growing them under garden conditions here on the northern Gulf Coast.

The familiar kinds need no introduction and very little comment in this article. They are all fine ornamental plants which lend themselves beautifully to the landscape planting plan: *Viburnum tinus* for corners and portals, *V. suspensum* where a more spreading plant is wanted, and *V. japonicum* where heavy texture is in order. For large buildings there is *V. odoratissimum* to add to the previous species, all from other countries.

The point of this note is to say something about the lesser known and appreciated native species.

One of these is a very small deciduous type that inhabits wooded hillsides in west Florida and Alabama on the Coastal Plain. J. K. Small calls this *Viburnum densiflorum*, and its lobed maple-like leaves make it look very much like *V.*

*acerifolium* to which it must be closely related. At any rate, with some pruning it makes a good subject for drought-troubled soils where a small plant is needed.

A much larger and more vigorous species is *V. semitomentosum* that is said to grow in low ground from Florida to Texas, and up to Pennsylvania. This one grows big, almost into a small tree, but all I have grown I have managed to keep as a dense shrub by frequent prunings. My plants are grown from cuttings, as it roots easily, from a single specimen in the woods near Gainesville, Florida, and as yet I have not found it in southern Alabama or west Florida, but without too serious searching. . . .

The ubiquitous species here is *V. nudum*, present in almost every creek bottom. This, I think, is less ornamental than the others but it seems to be accompanied by a variety that is very showy, one called *angustifolium* by Dr. Small, named for its narrower leaves. These are a dark shining green, and persistent. The plant itself has great possibilities in cultivation with its great masses of white flowers contrasted with the fine foliage.

Where a tree viburnum is wanted, there is none better than *V. rufidulum*. This seems rare in these parts and with me is deciduous. My plant is only seven feet high but it is reported to grow to twenty-five feet.

I am especially enthusiastic about the species I have saved till the last because it would seem that certain of its characteristics offer great possibilities as an ornamental. This is *Viburnum ovatum*, sometimes called Walters viburnum. This species has tiny, bright shining evergreen leaves, one-half to one inch in size, obvate in shape with blunt teeth on the sides and wedge-shaped bases. If allowed to grow naturally, it becomes a thin-trunked twenty-foot tree, but if sheared, it becomes a beautiful dense broadleaf evergreen shrub strongly resembling some variety of *Ilex crenata*, but with opposite leaves. It apparently grows on the Atlantic seaboard and into peninsular Florida and is said to reach its largest size in the Suwannee River Basin. My plants are seedlings from a tree, near Bradenton, Florida. Cuttings root very easily.—E. J. HORDER, *Mobile, Alabama*.





*An enlarged leaf showing the flowers that resemble caterpillar legs.*

### *Spathicarpa sagittifolia*

*Spathicarpa sagittifolia*, which has been rather aptly named the caterpillar plant, is a very interesting greenhouse aroid from Brazil that should also do well as a houseplant. Although its inflorescences are not showy, they are attractive and the plant's habit of flowering continuously is a strong point in its favor.

The glossy green, arrowhead-shaped leaves stand but three to four inches in height and are surmounted by the inflorescences, seven to eight inches high, consisting of narrow light-green spathes to which the spadix is completely fused. Thus the tiny, petal-less flowers form a

yellow-green fringe somewhat resembling the legs of a caterpillar along the axis of the spathe.

It has not been observed to set seed in the green-house, although the plant grows steadily, sending up new shoots from the underground crown, and can be divided with the utmost ease. *Spathicarpa* is not exacting as to soil requirements, doing well in any good potting soil that is kept moist. It seems, however, to do best in pure sphagnum which is not allowed to dry out. A night temperature of sixty degrees Fahrenheit and a day temperature of seventy seem to be optimum.—D. G. HUTTLESTON, *Longwood Gardens, Kennett Square, Penna.*



### New Guinea Trumpet-Creeper

During March, 1960, Longwood Gardens flowered for the first time in this country a beautiful bignoniaceous vine, *Tecomanthe venusta*, a new introduction into the Americas (P.I. 253223) having been obtained as a result of the fourth cooperative Longwood Gardens-U.S.D.A. exploration for ornamentals, conducted in Australia during 1958-1959. [See *The Nat. Hort. Mag.* 38:164-167, July, 1959.] For want of a common name and to indicate its place of origin, *Tecomanthe venusta* is being called the New Guinea Trumpet-Creeper.

A native of Australian New Guinea, *Tecomanthe venusta* is a vigorous woody dextrorse vine, under native conditions probably climbing high into the tops of forest trees. Although its dark-green, compound (five leaflets) leaves are attractive, the main ornamental feature of the plant lies in the beautiful, pendant, trumpet-shaped flowers which appear in axillary, umbel-like clusters (up to sixteen in a cluster on our specimen) on the old wood of the climbing stems. The tubular flowers are a light magenta-rose on the outside of the tube (closest to RHS Spinel Red 0023) fading to a paler rose (0023/3) and creamy-yellow on the inner surfaces of the spreading lobes and the inside of the tube, which also sports numerous narrow lines of Spinel Red running down to its base. Maximum over-all length of the individual flowers is about three and a half inches and each is about two inches across the flaring, somewhat irregular lobes. Although abundant nectar is produced at the base of each tube, the flowers are without apparent fragrance. Flower production on plants grown from rooted cuttings is fairly rapid. At Longwood Gardens such plants produced flowers in about a year's time. The first clusters to bloom appeared in early March, 1960, on the stem only a few inches above ground level, and subsequent blooming proceeded up the woody main stem to a height of fifteen feet or more from the ground. Under glasshouse conditions, it appears that the full flowering season may extend from three to four weeks.

*Tecomanthe venusta* appears to be easily propagated from simple three-node hardwood cuttings rooted in standard media at optimum temperatures of

seventy-five to eighty degrees Fahrenheit. Observations made under glasshouse conditions at the Botanic Gardens at Adelaide, South Australia, where the plant has also been successfully grown since 1952, indicate that this species is on the tender side and may require winter protection under subtropical or warm temperate conditions. At the Botanic Garden at Brisbane, Queensland (latitude approximately 27° south latitude, or the equivalent of Miami, Florida, with 27° north latitude) where this species has been grown outdoors, *Tecomanthe venusta* is perfectly hardy. On the basis of these Australian records, the vine is recommended for trial outdoors in subtropical Florida, throughout the West Indies and tropical America and in Hawaii. Where occasional frosts are to be expected, it has been suggested that the New Guinea Trumpet-Creeper might be grown successfully in pots, being moved outdoors during the warm season and under some protection during the winter. This procedure has been effective in the Botanic Garden at Adelaide where an annual top dressing has been sufficient to keep plants in top growing and flowering condition.

The Longwood Gardens' material of *Tecomanthe venusta* was collected as cuttings by the writer in October, 1958, from plants growing at the Botanic Garden, Brisbane, Queensland, Australia. Original plants cultivated in Australia were grown from propagations obtained from the Department of Forests at Lae, New Guinea. A first account of the culture of the New Guinea Trumpet-Creeper in Australia appeared in the *Journal of the Royal Horticultural Society* [T. R. N. Lothian, *Tecomanthe dendrophila*, *Jour. Royal Hort. Soc.* LXXXIII, Pt. 7, July, 1958], under the name *Tecomanthe dendrophila*. Comparison of living plants grown at the Botanic Garden at Brisbane and at Longwood Gardens indicates that the species in culture is not *Tecomanthe dendrophila* but rather *Tecomanthe venusta*, as herein described. Confirmation of this identification has come through the courtesy of Australian colleagues and in particular H. W. Caulfield, Curator of the Garden at Brisbane, and S. Blake, Queensland Government Botanist. — W. H. HODGE, *Longwood Gardens, Kennett Square, Pennsylvania.*





LILIAN A. GUERNSEY

*Styrax obassia*