Understanding Foliar Variegation as it Relates to Propagation

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Variegation can be defined as "varied in appearance as in one item possessing more than one color". Animals and plants can be variegated. In plants, variegation is manifested as streaks, spots, stripes, and blotches and is most apparent when it occurs on leaves and petals In many cases, the ornamental appeal of a plant is entirely based on its variegation pattern. For example, coleus hybrids (*Coleus* × *hybridus*) and rex begonias (*Begonia* × *rex-cultorum*) would not be considered ornamental if their leaves were entirely green Unfortunately, for many species the genetic and physiological control of variegation is poorly understood as most of our experience with variegation has come from casual observations of cultivated ornamental plants. Scientists do know, however, that the variegation is frequently caused by differences in the type or amount of pigments in cells The most conspicuous leaf pigments are generally the green chlorophylls and the red or purple pigments (generally anthocyanins).

For the plant propagator, knowing what controls variegation pattern in a given plant can be critical if offspring which are "true-to-type" are to be obtained I will not attempt to explain the complex genetics associated with the many forms of variegation nor will I discuss physiological problems such as mineral deficiencies and unwanted diseases, conditions whose symptoms can be described as "artificial" variegation Instead, I will outline the control of variegation patterns as it relates to both sexual and asexual (i.e. vegetative) plant propagation. For some of the described examples, there are no detailed scientific studies to verify the nature of the variegation. Nevertheless, this author has taken the liberty to list plants which he is confident fall into the category described.

There are two basic types of variegation, **cell lineage variegation** and **non-cell lineage variegation** (Kirk and Tilney-Bassett, 1978) Cell lineage variegation occurs when a plant is made up of two or more genetically distinct cell types (i.e. the plant is a genetic mosaic). The cells within the colony of uniquely-colored leaf cells are related to each other in that they are descendants by successive cell divisions of the original cell in which the color change occurred. The extent of variegation can be dependent on the stage of leaf development when the color change occurred. For example, if a cell's color change (i.e. genetic change) occurs when the leaf is very immature the uniquely-colored sector will be large, whereas if the color change happens very late in cell development only a tiny patch of uniquely-colored cells will be evident. As you will see with the description of chimeras below, the biological "rules" which govern the angles of cell divisions can have a large impact on the pattern of variegation in cases of cell lineage variegation.

In non-cell lineage variegation all of the cells in the leaf have the same genotype but only some of them express the genes responsible for certain pigments. There appears to be no relationship between the pattern of leaf cell division and the patterns of colors on the leaf. In most cases of non-cell lineage variegation it is the "geographic" location of a cell on the leaf, and not from which cell it descended, that determines its color. Therefore, within a given plant the patterns of variegation tend to be somewhat predictable (e g. all leaves possessing white veins on a green background).

CAUSES FOR CELL LINEAGE VARIEGATION

Chimeras

The most common cause for cell lineage variegation is chimerism Chimeras are genetic mosaics in that they are plants which possess more than one genotype In plants, chimeras owe their existence to the orderly patterns of cell division in the shoot apical meristem (i.e. shoot tip or terminal growing point). Most higher plants possess shoot apical meristems which have a layered arrangement of cells. Cells tend to divide perpendicularly to the surface of the meristem Because of this, cell layers tend to remain independent of each other and their appearance can best be described as rows of bricks on a wall Chimeras can arise when a mutation occurs in one cell in one layer but not in other cells in other layers With time, a whole cell layer becomes populated with mutant cells When this occurs a periclinal chimera is formed. It is only when an entire cell layer is uniform in genotype and genetically unique that a chimera which is stable enough to be propagated as "true-to-type" is formed.

Organs such as leaves have their origin in the shoot apex. If the shoot apex is composed of layers of mutant and normal cells, so too are the organs which arise from the apex The most common chimeras are those with white leaf edges on green leaves (Fig. 1). Since chlorophyll is not phenotypically expressed in the apical meristem, we tend to overlook the fact that the leaf's variegation pattern is a reflection of the arrangement of genetically green and genetically white cell layers in the shoot apical meristem.

Unfortunately, a plant's sex cells (i e the eggs and pollen) are derived from single cells which are ultimately derived from only one of the cell layers in the shoot apical meristem. Therefore, plant chimeras cannot be maintained by seed propagation. Seedlings of self—pollinated white and green chimeras will be either green or white depending on the position of the white and green cells in the tissue layers of the apical meristem. The white seedlings die soon after germination because they use up their stored sugars and cannot produce sugar without chlorophyll. In some yellow and green chimeras (e g. *Hosta sieboldiana* 'Frances Williams'), the yellow cells do possess a limited amount of chlorophyll and yellow seedlings would survive and grow more slowly (but would not be variegated).

Some vegetative propagation techniques can be used to perpetuate a chimeral plant. However, if the technique relies on adventitious shoots, the chimera will separate into its component genotypes. For example, leaf cuttings normally produced adventitious shoots from only one cell layer. Therefore, leaf cuttings from variegated leaves (e.g *Sansevieria trifasciata* 'Laurentii') will produce non-chimeral shoots. Chimeral separation also occurs when root cuttings are used and to some extent with most micropropagation techniques. The only way to propagate a true chimera so that the new plants are "true-to-type" is a technique which includes the terminal or axillary vegetative buds. Axillary buds contain the same layering arrangement as the terminal bud from which they arose (Marcotrigiano, 1990).

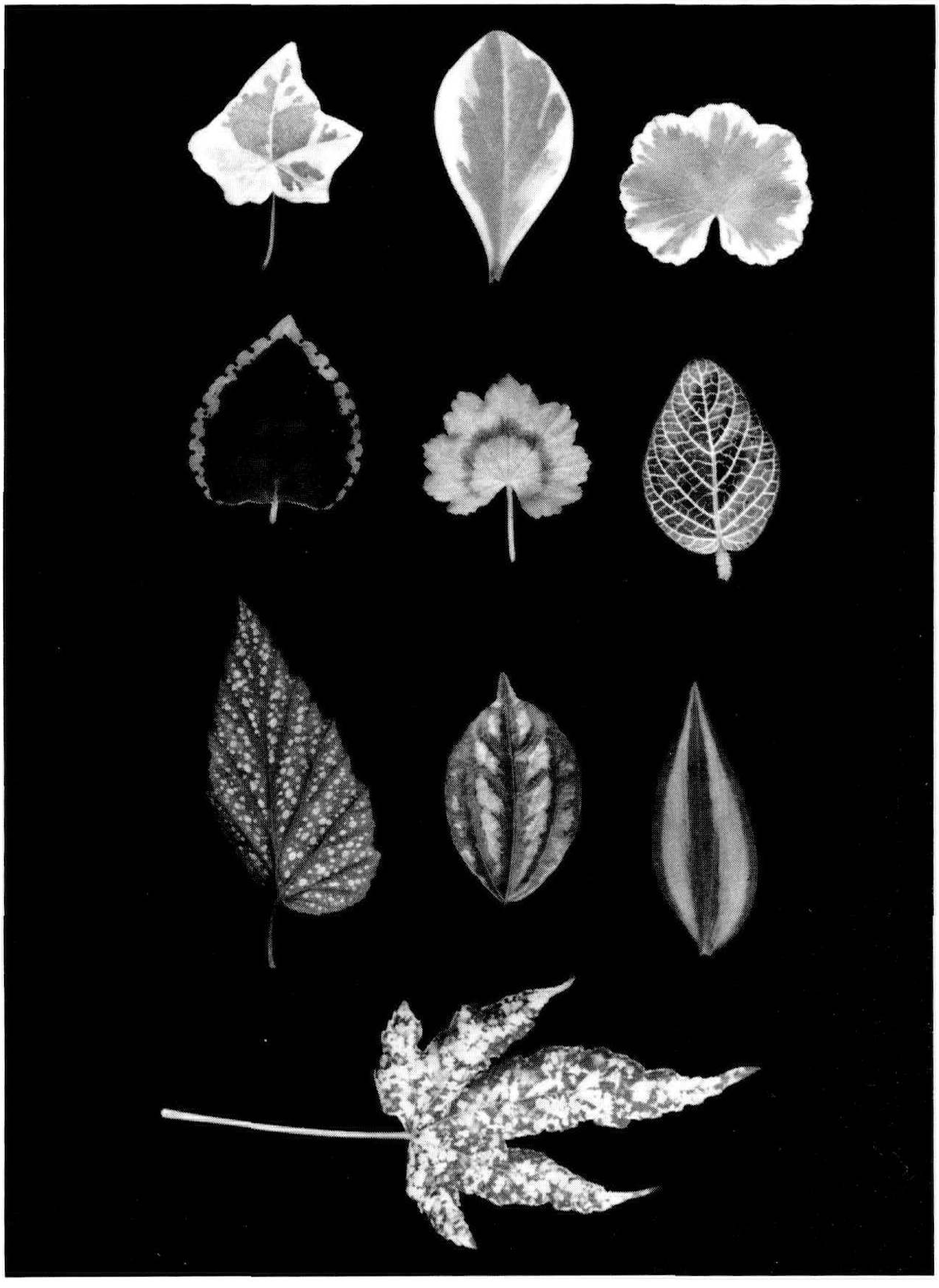

Figure 1. Variegated leaves. Top row: leaves taken from periclinal chimeras. They are (left to right) *Hedera helix* 'Glacier', *Peperomia obtusifolia* 'Albo-marginata', and *Pelargonum* x *hortorum* (cultivar?). Second row are leaves taken from plants where variegation is caused by gene expression for certain pigments in only some cells. They are (left to right), *Coleus* x *hybridus* 'Rose Wizard', *P.* x *hortorum* 'Alpha', and *Fittonia verschaffeltii* var. *argyroneura*. Third row are leaves from plants which sporadically produced leaf "blisters" or entire stripes of "blistered" tissue. They are (left to right) *B.* x *argenteo-guttata*, *Pilea cadierei*, and *Zebrina pendula*. Bottom row is a leaf of the virally infected ornamental abutilon, *Abutilon pictum* 'Thompsonii'.

Therefore, budding, stem grafting, leaf-bud cuttings, stem cuttings (including a bud), or whole plant divisions can be used to maintain chimerally variegated plants.

"Jumping Genes"

The scientific term "transposable genetic elements" refers to genes which have the ability to leave their position on the chromosome and relocate to another position. When they do this they often insert themselves into critical positions of other genes which effectively inactivates the other genes. The most familiar example of this effect is Indian dried corn which frequently possess small streaks and color blotches on the kernels. These streaks appear randomly (i.e. in no particular pattern) whenever gene action is blocked. So for example, if a gene which normally suppresses red pigment production is interfered with by the insertion of a "jumping gene", the red pigment can be produced The result is a colony of related red cells on a yellow background. The earlier this occurs in the development of the kernel the longer and wider the red streak. It is clearly documented that "jumping genes" can be sexually inherited On the practical side, there seems to be very little that one can do to control such genes. Recently, it has been proven that these genes result in color instabilities in snapdragon and petunia flowers. There are only a few documented cases where "jumping genes" effect leaf variegation. 'Jingle Bells' poinsettia bracts (actually modified leaves) appear to display the unstable variegation pattern typical of "jumping genes", although there has yet to be a thorough scientific study of this plant. With regard to maintaining the "jumping gene" variegation pattern, care should be taken to eliminate non-variegated sports since the variegation may not return in future generations even in cutting-propagated plants Tissue culture systems have been known to increase the activity of "jumping genes" and can lead to a wide range of unstable phenotypes (Marcotrigiano et al , 1990; Peschke et al., 1988).

CAUSES FOR NON-CELL LINEAGE VARIEGATION

Gene Expression

The most common cause for non-cell lineage variegation is differences in the expression of genes. Somehow, cells "know" in what position they are on a leaf. While all cells may have the genes necessary to make a pigment only those in the correct location will do so. Therefore, gene expression variegation usually results in a somewhat predictable variegation pattern from leaf to leaf. Gene expression variegation is common in animals For example, panda bears and bald eagles are variegated because cells in some positions are white while others are black, even though all the cells contain the necessary genetic information to contain pigment Their offspring inherit the same variegation pattern as their parents. In plants, there are a large number of species which display variegation due to gene expression. Some common examples are *C* x *hybridus*, *B.* x *rex-cultorvm*, and *Caladium* x *hortulanum* (Fig 1) Since all of the cells in the plant have the genetic information necessary to produce such striking patterns, the patterns are generally passed to offspring following seed propagation. However, in some plants the patterns caused by gene expression are somewhat variable just as height and skin tone vary in man, i e. there is a range of possibilities within the pattern. These slight variations can be due to the degree of expression of the genes responsible for the trait So, for example, some bald eagles may have whiter heads than others, although the basic pattern is the same for all bald eagles. If variation in offspring is undesirable, a selected desirable individual can be asexually propagated. Since all cells possess the same genetic potential, any asexual technique can be used to maintain the desired phenotype of the individual, even if it results in adventitious shoots rather than axillary shoots. Because asexual propagation is too costly in some species, breeders have selected plants which are fairly consistent in their expression of patterns even when seed propagated (e.g. many bicolored petunias).

"Blisters"

Several of the variegated plants which have silver specks, spots, and streaks on their leaves do not possess cells which are lacking the ability to produce chlorophyll. Instead, these plants go through unusual leaf development. In certain regions of the leaf, cells will pull away from the cells below them leaving what can best be described as a "blister" (Fig 1). This trait is actually a gene expression phenomenon (Hoch, 1980) and likewise poses no problems during propagation since it is passed on to sexual offspring or to plants propagated by any vegetative technique. Examples are *Pulmonaria officinalis* and many begonias (e.g. *B. maculata*).

"Beneficial" Virus

Most viruses, such as tobacco mosaic virus, which cause mosaic leaves are extremely detrimental to the health of the plant. In rare cases, the virus affects pigment production causing attractive variegation patterns without severely impairing the growth of the plant. For most viruses, infected plants do not transmit the virus to seed The most obvious foliar virus that causes attractive variegation is abutilon mosaic which in certain abutilon species (e.g. *Abutilon pictum* 'Thompsonii') causes a bright yellow and cream variegation pattern delineated by the veins of the leaf (Holmes, 1964) (Fig. 1) This virus can be seed or graft transmitted (Fulton, 1964). Many of the cultivars of florally striped tulips have a virus which create color 'breaks" (Fulton, 1964) Tulip "breaking" in some cultivars of tulip (*Tulipa* spp.) also causes leaf mottling and some stunting. This virus is naturally transmitted to daughter bulbs thereby perpetuating the phenotype It is possible that other uncharacterized variegated plants possess virus. Since seed transmission is rare, one way of testing is to propagate by seed and see if the pattern is maintained Grafting to non-variegated plants of the same species may also indicate whether or not a virus is present since viruses normally transmit through the graft union

CONCLUSIONS

The above discussion attempts to summarize some of the causes of foliar variegation. It is important to note that all variegated plants are not chimeras (Marcotrigiano and Stewart, 1984). Variegation can be influenced to some extent by environment (e.g. light levels) since gene expression is influenced by environment. In addition, whether variegation is caused by gene expression, virus, "jumping genes", "blisters", or chimerism, it should be noted that plants may possess more than one type of variegation. For example, *Pelargonium* × *hortorum* 'Mrs. Henry Cox', a zonal geranium, possesses tricolored leaves of green, white, and purple The purple ring is caused by gene expression and is stable through sexual propagation. The white leaf edge is caused by chimerism and if this pattern is desirable it can only be maintained by taking stem cuttings.

Determining the cause of variegation is best achieved by practical experience and utilization of the literature (Marcotrigiano, 1990, Peschke et al.; 1988). Fortunately, most forms of variegation can be maintained by any propagation technique. Chimerism is the only cause of variegation which imposes severe restrictions on the propagation technique used.

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