Leaf Variegation and Plant Chimeras©

Garry K. Burge, Ed R. Morgan, and John F. Seelye
New Zealand Institute for Crop & Food Research Limited, Private Bag 11-600, Palmerston North, New Zealand

INTRODUCTION

Many of our ornamental cultivars have been selected for characteristics of their foliage. This includes foliage colour (e.g., golden *Ulmus glabra* and *Podocarpus totara* selections, purple *Fagus sylvatica* selections) and a wide range of leaf variegation patterns. These patterns include spots or maculations (e.g., *Begonia maculata*, *Zantedeschia elliottiana*), stripes (e.g., many *Phormium* selections), and differences in leaf colour between the leaf margin and mid region.

Leaf variegation can be induced by viruses (e.g., some *Abutilon* selections) and nutrient disorders. However, the leaf variegation observed in most of our ornamental cultivars selected for foliage characteristics is genetically controlled (Marcotrigiano, 1997). These variegation patterns can be divided into cell lineage or non-cell lineage types. It is important to understand these types of genetically controlled variegation, as their propagation requirements and stability are very different (Tilney-Bassett, 1986).

CELL OR NON-CELL LINEAGE

In plants with non-cell lineage variegation, all of the cells have the same genotype, but the genes responsible for the production of pigments or leaf blistering that alter leaf colour are only expressed in some of the cells. Examples include *Sansevieria trifasciata* and Rex begonias. The leaf patterns are due to differential gene expression between genetically identical cells. Such non-cell lineage variegation or pigmentation also occurs in flowers (e.g., petals of pansy) and fruit (e.g., striped tomato cultivars). Non-cell lineage variegation is sexually transmitted from one generation to the next.

Cell-lineage variegation is due to different genotypes within the same plant. These are often referred to as genetic mosaics or chimeras. The chimeras are usually formed by mutation of cells in the apical meristem. The variegation patterns of chimeras are related to the cell division planes of the histogenic layers in the apical meristem (Tilney-Bassett, 1986). Dicots usually have three layers, while monocots have two or three layers. There are several types of chimeras – sectorial, mericlinal, and periclinal. Sectorial chimeras have a sector of all layers that is genetically different from the other layers, whereas with mericlinal chimeras a sector of only one layer is genetically different. Sectorial and mericlinal chimeras are generally unstable and so of little commercial value. However, periclinal chimeras are more stable and have one or more complete cell layers that are genetically different (Tilney-Bassett, 1986). The orderly division planes in the apical meristem allow cell layers to remain autonomous. Each cell layer produces specific tissues in the leaves and other plant organs. For example, the epidermis is produced from the outer cell layer (L1). The second layer (L2) produces the palisade parenchyma and the spongy parenchyma of the leaf margin, and the third layer (L3) produces the upper and middle layers of the spongy parenchyma (Burk et al., 1964). Hence, when one of these layers has a plastid mutant that prevents the normal formation of green chlorophyll, a white or cream sector develops in the leaf.

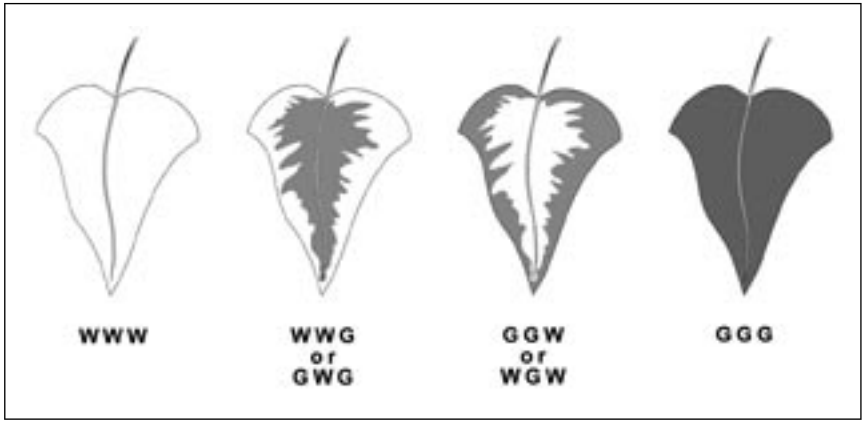

Figure 1. Leaf colour patterns of periclinal chimeras with white plastids in one or two of the cell layers.

Chlorophyll is usually not present in the epidermal cells (L1 layer origin) except in the guard cells and trichomes of some species. Hence a periclinal chimera with a L1 albino plastid mutant (W) and L2 and L3 layers with normal plastids (G) (so 3 layers of chimera can be represented as WGG) usually has green leaves (Tilney-Bassett, 1986; Marcotriango, 1997). Periclinal chimeras with L2 albino mutants (WWG or GWG) have variegated leaves with a white edge and green mid region, while chimeras with normal plastids in the L2 layer and mutant plastids in L3 (GGW or WGW) have the normal green leaf colour on the leaf edge and a paler green colour in the mid region (Fig. 1).

Chimeras cannot be maintained by seed propagation because gametes (pollen and eggs) are usually produced by the L2 layer (Stewart and Burk, 1970; Marcotriango and Bernatzky, 1995). Therefore, plants with chimeral leaf variegation do not persist for long in the wild as they cannot be propagated from seed and frequently there is a selective disadvantage due to the lower photosynthetic rate of the leaf layer containing the plastid mutants.

The best known chimeras are ornamental plants with white to pale green sectors on their leaves. However, horticulturalists have selected many other chimeras including many red skinned apple (*Malus)* and pear (*Pyrus communis*) selections (Pratt et al., 1975), many poinsettia (*Euphorbia pulcherrima*) selections (Stewart and Arisumi, 1966), some chrysanthemum (*Chrysanthemum*) and carnation (*Dianthus*) selections (Melquist et al., 1954; Tilney-Bassett, 1986), some thornless blackberry (*Rubus* sp.) selections, and many potato (*Solanum tuberosum*) cultivars (Tilney-Bassett, 1986).

STABILITY OF CHIMERAS

Instability of periclinal chimeras that have differences in colour between the leaf margin and mid region is quite common (e.g., in hedges of variegated *Phebalium squameum* or *Ligustrum ovalifolium* cultivars). This results in loss of leaf variegation and production of green-leaved or white-leaved branches. This loss of variegation is due to "layer switching". Cells of one layer can divide periclinally and establish a new cell line in a different layer. Cells in the L1 layer nearly always

divide anticlinally, whereas cells in the L2 and L3 layers divide anticlinally and periclinally. These differences in cell division are the reason for the greater instability of chimeras with different genotypes in the L2 and L3 layers (e.g., chimeras with variegated leaf patterns) than the very stable chimeras with an L1 layer of a different genotype (e.g., many red-coloured apple cultivars) (Pratt et al., 1975; Burge et al., 2002).

The chimeral structure of a plant can be lost with the development of adventitious buds as these usually develop from a single cell in one of the cell layers. Hence, care is required when pruning bushes and trees as severe pruning sometimes forces adventitious bud development. Similarly, the chimeral layer structure can be lost in tissue culture if shoots develop from adventitious buds.

SYNTHETIC CHIMERAS

The periclinal chimeras described above are due to a mutation in one of the cell layers in the apical meristem. This can be a natural mutation or induced by mutagenic agents (e.g., irradiation or chemicals). Interspecific chimeras have also been produced accidentally from graft unions (Neilson-Jones, 1969; Tilney-Bassett, 1986). These include graft chimeras between:

- *Citrus medica* and *C. aurantium*
- *Citrus unshiu* (mandarin) and *C. natsudaidai* or *C. obovoidea*
- *Laburnum anagyroides* and *Chamaecytisus purpureus* (syn. *Cytisus purpureus*)
- *Crataegus monogyna* (hawthorn) and *Mespilus germanica* (medlar)
- *Camellia sasanqua* and *C. japonica*

Winkler (1907) was the first person to develop an interspecific chimera using grafting techniques. Nightshade (*Solanum nigrum*) was grafted onto tomato (*Lycopersicon esculentum*) plants and after union the junction was cut through transversely. A mixed callus derived from both species developed at the wound site, and from this callus adventitious shoots formed, some of which were found to be interspecific chimeras. Since then researchers have developed a number of mixed cell or protoplast systems to produce synthetic chimeras (Burge et al., 2002). Synthetic chimeral breeding provides an opportunity to develop cultivars with novel phenotypes. Examples include flower shape, size, and colour (Marcotrigiano, 1986; Stewart et al., 1972); disease or pest resistance (Goffreda et al., 1990); and fruit skin characteristics (Neilson-Jones, 1969; Jwamasa et al., 1977). The synthetic chimeral breeding techniques developed have been successful on Solanaceae species but to a lesser extent on other plants. However, the accidentally produced interspecific chimeras are from a wide range of plant families, indicating the potential to develop novel cultivars using synthetic chimeral breeding.

SUMMARY

An understanding of leaf variegation and chimeras is essential for plant propagators. This understanding is also essential for breeders interested in developing cultivars with leaf variegation or other characteristics that are controlled by cell lineage.

LITERATURE CITED

Burge, G.K., E.R. Morgan, and **J.F. Seelye.** 2002. Opportunities for synthetic chimeral breeding: Past and future. Plant, Cell Tissue and Organ Culture 70:13-21.

Burk, L.G., R.N. Stewart, and **H. Dermen.** 1964. Histogenesis and genetics of a plastid-controlled chlorophyll variegation in tobacco. Amer. J. Bot. 51:713-724.
Goffreda, J.C., E.J. Szymkowiak, I.M Sussex, and **M.A. Mutschler**. 1990. Chimeric tomato plants show that aphid resistance and triacylglucose production are epidermal autonomous characters. Plant Cell 2: 643-649.
Jwamasa M., M. Nishiura, N. Okudal, and **D. Ishiuchi.** 1977. Characteristics due to chimeras and their stability in citrus cultivars. Proc. Intl. Soc. Citriculture 2:571-574.
Marcotrigiano, M. 1986. Experimentally synthesized plant chimeras 3. Qualitative and quantitative characteristics of the flowers of interspecific *Nicotiana* chimeras. Ann. Bot. 57:435-442
Marcotrigiano, M. 1997. Chimeras and variegation: Patterns of deceit. HortScience 32: 773-784.
Marcotrigiano, M. and **R. Bernatzky.** 1995. Arrangement of cell layers in the shoot apical meristem of periclinal chimeras influences cell fate. Plant J. 7:193-202.
Melquist, G.A.L., D. Ober, and **Y. Sagawa.** 1954. Somatic mutations in the carnation, *Dianthus caryophyllus* L. Proc. Natl. Acad. Sci. (USA) 40:432-436.
Neilson-Jones, W. 1969. Plant chimeras. 2nd ed. Methuen, London.
Pratt, C., R.D. Way, and **J. Einset.** 1975. Chimeral structure of red sports of 'Northern Spy' apple. J. Amer. Soc. Hort. Sci. 100:419-422.
Stewart, R.N. and **T. Arisumi.** 1966. Genetic and histogenic determination of pink bract colour in poinsettia. J. Heredity 57:216-220.
Stewart, R.N. and **L.G. Burk.** 1970. Independence of tissues derived from apical layers in ontogeny of the tobacco leaf and ovary. Amer. J. Bot. 57:1010-1016.
Stewart, R.N., F.G. Meyer, and **H. Dermen.** 1972. Camellia + 'Daisy Eagleson', a graft chimera of *Camellia sasanqua* and *C. japonica*. Amer. J. Bot. 59:515-524.
Tilney-Bassett, R.A.E. 1986. Plant chimeras. Edward Arnold, London.
Winkler, H. 1907. Über propfbastarde und pflanzliche chimaeren. Ber. Dtsch. Bot. Ges. 25: 568-576.

The Cultivar Naming Code©

Chris Barnaby
Plant Variety Rights Office, P O Box 130, Lincoln, Canterbury

INTRODUCTION

Plant breeders and selectors routinely name their new creations and this includes those involved in plant propagation and production. At some point a plant propagator may need to name a new clonal selection or a seedling that comes up in a propagation tray. This may occur almost by accident such as the appearance of a different or "better" form of a commonly propagated species. This new form may then be developed into a new cultivar and possibly given a name. Is the name just something you dream up and go with or is there actually some guidelines or system to follow? You certainly can just pick a name and commercialise with it, this happens all of the time, but another option is to take a more systematic and considered approach utilising the International Code of Nomenclature for Cultivated Plants (the Code) and the appropriate International Cultivar Registration Authority (ICRA). It should be clear that The Code and ICRAs do not provide a new cultivar with any legal or official status. If you wish to obtain legal protection for a new cultivar and the name then you would need to make an application for variety protection to your national authority. For New Zealand, this would be the Plant Variety Rights (PVR) Office. The naming of cultivars with respect to PVR has specific requirements and will not be covered in depth in this paper as it has been covered in previous years.