name are not "true to type" (that is, they are not identical to the original plant).

Conversely, to a breeder, or the alert horticulturist, phenotypic changes from the normal characteristics of a particular clone may offer opportunities for improvement of that clone or the species.

"Bud sport" types of mutations often have given rise to important commercial or interesting new clones (Table 1).

Dermen (3, 4, 5) and others (10, 12) have described the phenomena of chimeras and bud sports and discussed their possible induction and uses. Tissue-culture techniques also offer further possibilities for isolating new plant types from chimeral tissues by protoplast culture or other methods of chimeral tissue separation (1, 11). An unusual dahlia bud sport ('74-10D') could have exerted a significant impact on the dahlia world (Fig. 3) but was lost because of an inability to propagate it successfully. Perhaps better control over spontaneous and induced changes may be possible and such new types as '74-10D' may be preserved as we learn more about the fundamental concepts of clonal variability. The following papers are presented in an effort to help further our understanding of these concepts, to inspire new efforts, and to offer opportunities for synergistic interaction among plant propagators.

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**THE CLONE IN HORTICULTURE**

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The clone is one of the basic categories of cultivar (4) with extremely important applications in horticulture. "Cloning" can be defined as the vegetative regeneration of a single genotype as represented by a single plant, single growing point, single meristem, or single explant. More recently this term has been expanded to cover regeneration of a fragment of a chromosome or gene. Cloning is a powerful procedure both as a plant selection tool for breeding and as a plant propagation tool for reproduction. This paper focuses attention on the opportunities and problems in propagation as it relates to horticulture.

**Characteristics of clones**

The exploitation of cloning for the selection of superior individuals followed by vegetative propagation has been one of the consistent themes throughout horticultural history. The clone is one of the basic categories of cultivar as defined in the International Code of Nomenclature for Cultivated Plants (4). Clones exist in nature and with some species, vegetative multiplication is a major strategy for their adaptation (11). Such species reproduce by special vegetative structures such as root suckers (aspen), natural layering (creosote bush and black spruce), rhizomes (iris, lily-of-the-valley, various grasses, and huckleberry), and such structures as bulbs or corms (lily, onion, and tulip). Cultivation of various food and fiber crops (e.g., potato, yam, sugar cane, banana, and bamboo) are based on development of clones and utilize such naturally occurring vegetative structures combined with division.
The discovery that certain woody trees, shrubs, and vines could be propagated readily by hardwood cuttings was the basis for the selection of clones of early horticultural crops of grape, fig, and olive (53). Extension of cloning to the fruit tree species (apple, pear, cherry, plum, and citrus) required the development of techniques of grafting since such species were difficult to propagate by cuttings. Cultivar selection of these species through seed propagation would be impractical not only because they are characteristically heterozygous, cross-pollinated, and not true-breeding, but also because they tend to have long juvenile periods before flowering (23, 51). Even though various fruit and nut crops (e.g., peach, almond, walnut, and pistachio) have been grown extensively as seedlings in various parts of the world even to rather recent times, the modern era of production really began with the selection of specific clones. The ability to propagate clones by leafy cuttings became possible with the development of propagation technology, such as greenhouses, mist facilities, and rooting hormones. The consequence of these developments has been to extend the cloning process to everwidening lists of plants, particularly ornamentals (17).

Recent advances in breeding and propagation technology involving cell and tissue culture and micropropagation have produced an increasing, if not explosive, increase in selection and vegetative propagation of clones (15, 18, 33, 34, 39, 40). This trend is found not only in traditional crops where vegetative propagation is used, e.g., fruits and nuts (52) and ornamentals (19), but also in traditionally seed-propagated industries such as forestry (20) and vegetable and agronomic crops. These techniques promise new cultivar selections and rates of production undreamed of a few years ago (19). In vitro mass propagation has been useful in species and cultivars naturally slow or difficult to propagate vegetatively (orchid, fern, many foliage plants, and fruit tree root-stocks), but also in species where traditional vegetative methods exist (chrysanthemum, strawberry, and bulbs). In part, the application is for the development and maintenance of pathogen-free source plants (17).

Benefits. Cloning provides a powerful means of: 1) selecting specific genotypes of varying degrees of heterozygosity as cultivars; and 2) “fixing” them immediately for subsequent propagation. The result is maximum phenotypic uniformity among “superior” vegetatively propagated offspring and powerful tool to standardize modern horticulture to the minutest detail both in product and production methods.

Problems. These rosy potentialities should not blind us to some potential costs or problems associated with cloning. The fact that essentially all plants of a single clonal cultivar are identical genetically makes all plants equally susceptible to an old or introduced pest, to some environmental stress, or to other conditions. Industries such as fruit and nut crops are examples, par excellence, of monocultures (14). The concentration of large-scale production into a single genotype or at least a relatively few genotypes, usually from a more or less common origin, may lead to pressures to eliminate other less horticulturally useful genotypes from our inventories, with the potential loss of much genetic diversity present in the species. Perhaps most important in propagation of a clone is the potential for variation that may develop through inadvertent selection of the wrong clone, development of an inferior variant, or introduction of a systemic pathogen. The occurrence of any of these problems early in the multiplication process may result in production of thousands of copies before discovery.

Variation within clones

Sources of within-clone variation can be divided into 4 broad categories: 1) genetic mutations (spontaneous and/or induced); 2) chimeral rearrangements of pre-existing mutants; 3) epigenetic changes; and 4) systemic infection by pathogens. The occurrence of such variation can have either useful or detrimental effects and thus provides great, new opportunities in horticultural improvement or undesirable conditions that will create problems in propagation.

Somatic mutations. Somatic variations can arise at the cell level by modification in the chromosomes, plastids, or mitochondria (16). Opportunities to exploit such variation, either spontaneous or induced, is made possible by the cloning of such variants. Selection of spontaneous desirable “bud sports” or bud-mutations has played a major role in cultivar improvement in such crops as citrus or apple. More recently, the potentiality to induce variation or to select for variation at the cell level in suspension cultures followed by cloning has been exploited extensively by many horticultural researchers and genetic engineering firms (17, 28, 34, 40, 41). Procedures and concepts such as somaclonal variation, protoplast culture, protoplast fusion, transformation, and organelle transfer have become part of the horticultural scene (17). On the other hand, the opportunity for the development and selection of undesirable unwanted variation is also great (8, 13).

Chimeras. Most genetic variants that occur in somatic tissue are chimeral, which means that mutant and nonmutant cells and tissue occur in combination (6, 35). Many horticultural novelties, such as variegated foliage or flowers, color fruit sports, and thornlessness owe their uniqueness to their chimeral nature. Such chimeras may not be stable with various kinds of propagation and their uniqueness may be lost unless the growing points used for propagation contain both mutant and nonmutant tissue (17).

The effect of a mutation in a single cell on the phenotypic expression of a cultivar is complex and depends on the prominence of the characters affected, the subsequent extent of the “cloned” sector of the mutated cells in the growing points, and the selection of growing points for propagation (35). Consequently, the effect of the initial (primary) mutational event in a plant is not likely to be observed immediately in the plant. The mutation may occur later among the cloned progeny plants of the first or 2nd vegetative generations. If the plant is used as a source for propagation, then detection of the mutant in the clone may be only in the secondary propagation source, not in the primary source. Pruning to force lateral buds to grow and/or extensive propagation of individual growing points or buds is utilized in mutation breeding programs to detect mutants (6). Rearrangements of chimeral and nonchimeral tissue from previous mutations can account for the appearance of bud-sports and somatic variability in clonally propagated cultivars, whether desirable or undesirable.

Epigenetic. The term “epigenetic” has become used to indicate variation in phenotypic expression that is perpetuated by cloning but does not involve permanent changes in the genotype (10, 27, 28, 29). On the one hand, all of the ontogenetic and phenological changes that occur in the development of an individual can be considered as epigenetic (38). On the other hand, from an operational and experimental standpoint, one needs to demonstrate the existence of such variation by comparative cloning within populations of asexually propagated buds or cells. Such a procedure to identify variation would be analogous to segregation studies of gene markers within seedling populations.

Epigenetic variation has been identified at a descriptive level in cells, tissues, organs, and individuals. Examples at the cell or tissue level include such phenomena as habitation (27, 28), production of embryogenic callus (48), and comparative callus growth from juvenile and mature ivy (37). Cloning from individual nodes of rice or tobacco produced shoots or flowers depending upon location (24, 46). Isolated cells taken sequentially from different parts of the stem can produce roots or shoots (42). The most conspicuous phenomena at the level of the individual are “phase changes” associated with juvenile and adult forms of woody plants where phenotypic variation can be shown by age of first flowering, ease of rooting, growth form, and various morphological and physiological characteristics (5).

The mechanisms by which epigenetic changes are produced and controlled are not clear but apparently involve information transfer from gene to enzyme (10). One of the characteristics of epigenetic change, cited by various authors, is that these changes are induced by internal or external agents, such as ontogenetic stage, hormones, and environmental factors (temperature, light). Once induced, they continue to manifest the phenotypic expression in the absence of the inducing agent.

Accumulation of viruses and other pathogens. A characteristic of clones in horticulture is their tendency to accumulate various pathogens and to maintain them during subsequent propagation. The accumulation of pathogens, primarily viruses and virus-like organisms in propagation stock of clonally propagated crops such as fruit
trees, berries, and potatoes, is detrimental and has been recognized as the main cause of deterioration and so-called “running-out” of various plant cultivars (8, 41).

On the other hand, addition of virus can be beneficial in some cases. Certain “strains” of citrus exocortis viroid have been potentially useful in dwarfing citrus (10). Viruses and other pathogens have been vectors to introduce useful genes into clones (31).

Seedling and clonal developmental cycles

Knowledge of the genetic principles and concepts controlling variation of seed-propagated plants has been attained through study of transmission and segregation of marker genes through sexual reproduction. Such knowledge has come primarily from annuals or other plants with short life cycles. The genetic and epigenetic concepts and principles involved in somatic variability involve the understanding of transmission during mitosis of genetic and epigenetic information during the ontogenetic life cycle of the individual.

An individual plant starts its life cycle either as a seed or from some vegetative propagule such as a cutting, bud, scion, explant, or bulb or some other naturally detachable structure. Concepts of 3 kinds of individual life cycles are presented: 1) sexual seedlings; 2) apomictic seedlings; and 3) clones. Horticulturally and biologically, populations of individuals with these life cycles represent fundamentally different kinds of cultivars.

Sexual cycle. The propagule is the seed which is produced as a result of meiosis and fertilization of male and female gametes. A model for the developmental cycle of a seedling plant (23) is shown in Fig. 1. The cycle begins with the zygote and ends with seed production. A new cycle then starts with a new zygote produced within this individual. This developmental (ontogenetic) cycle includes a more or less continuous shift in the “epigenetic potentiality” of shoot apices from purely vegetative to reproductive. What can often be recognized phenotypically as juvenile, transition, and adult phases occur in the course of this change (51). These phase variations can be expressed as distinct morphological or physiological phases in different parts of the plant “topophysis” (17).

One of the basic expressions of these epigenetic changes is the control of flowering age in different species. If a plant is annual or biennial, the developmental cycle is completed in one or two seasons and the plant dies since no growing points remain vegetative. New vegetative shoots are produced continually if the plant is perennial, but flowering and seed production occur each year or season, usually from upper or outer extremities of the plant.

The seedling cycle can be characterized in terms of the transmissibility during propagation of the 4 kinds of somatic variability:

1. Genetic. The genotype of the individual plant is not reproduced exactly with seed propagation (in the absence of apomixis) but genetic variability, including any new, mutant genes that may have appeared during that cycle, will be redistributed to the next seedling generation, depending on the degree of homozygosity or heterozygosity.

2. Chimeral. If the mutant involves the L₅ layer in the plant, then segregation of the new allele should be demonstrated in the offspring.

3. Epigenetic. Epigenetic changes that have developed in the shift from juvenile to adult are reversed during the sexual processes that lead to the formation of the zygote. This shift represents an epigenetic reversion back to some earlier stage of ontogeny.

4. Virus. Most of the virus load in plants is lost and not transmitted to the next generation, although exceptions exist. Seedlings have been important sources of “virus-free” plants and were considered at one time to be necessary to bring about the rejuvenation of “aged” clones (41). Viroids, however, may be transmitted readily to seeds (17, 47).

Apomictic cycle. The 2nd basic cycle is the “apomictic seedling cycle” (Fig. 2), where embryo formation occurs without meiosis and fertilization (recurrent apomixis, adventitious embryony) or with meiosis and no fertilization (nonrecurrent apomixis) (4, 17, 43).

Transmission of the 4 kinds of somatic variability during seed propagation with the apomict:

1. Genetic. The genotype of the individual plant is maintained and the seedling offspring retain the same genetic characteristics as the parent since an asexual process is involved. A new genotype...
would appear in the offspring if a mutation has occurred in the plant during or prior to flowering.

2. Chimeras. These mutant genes may or may not be transmitted depending on whether the L1, LII, or LIII, layers of the growing point were involved. If the mutant involves LII, then the new genotype will appear in the offspring.

3. Epigenetic. Epigenetically controlled changes would be reversed as with the sexual seedling. Apomictic seedling individuals that result proceed to develop through the same ontogenetic cycle as sexually produced seedlings. This indicates that epigenetic reversion of phase changes is not dependent upon the meiotic process itself but results from changes in the cells or the cellular environment of those tissues from which they originate. Apomictically produced seedlings show the same kinds of juvenility phases and characteristics as the sexually produced seedlings.

4. Virus. Most of the virus load in apomictic seedlings is lost or reduced, as with sexual seedlings. Consequently, apomictic seedlings have been utilized extensively in the production of "virus-free" cultivars of such crops as citrus (8, 17).

Clonal cycle. The 3rd kind of life cycle is the "clonal cycle," produced by the vegetative propagation of a perennial plant (23). The consequences of ontogenetic development in terms of the various growth phases—juvenility, transition, and adult—shown in the sexual and the apomictic cycles depends upon at which phase in the developmental cycle the vegetative propagules were taken for propagation. The appearance and behavior of plants propagated from seedling plants may vary depending on the prominence of the pheno-typic expressions of the separate phases and the rapidity of change. The plant should initially exhibit juvenile characteristics if propagated from the juvenile phase, but continue to develop towards maturation. The plant may initially show intermediate characteristics if propagated from transition (or reversion tissue) and come into flowering somewhat sooner. If from adult tissue, the plants may show growth habits and characteristics distinct from that of the juvenile habit. The growth cycle of a cultivar-clone that has been propagated repeatedly should be better represented as in Fig. 3 where the growth phases are vegetative → reproductive rather than juvenile → adult.

Plants in the clonal cycles may be difficult-to-root and come into flowering at an earlier age than comparable seedling plants. The interplay of these 2 characteristics can account for the need of budding and grafting techniques with pomological crops where fruit and nut production is the aim.

The 4 types of somatic variability have dramatic effects on the clonal cycle:

1. Genetic mutations. The genotype of the cells of the particular growing points of the source plant used in vegetative propagation is retained, including any expressed or latent mutants. Consequently, the discovery of so-called "bud-sports" which affect some obviously desirable phenotypic changes, such as color, growth habit, time of bloom, or time of harvest, have given rise to important new cultivars. [e.g., red (pink) color sports of apple or pear, or pink-fleshed grapefruit]. The possibility of small or large changes that reduce productivity, however, is more likely since most mutations have adverse effects.

Different propagation sources within the same cultivar may show differences in time in vigor, productivity, and reaction to particular environments because of accumulative mutation. Such differences may be difficult to document and to differentiate from virus effects (44, 49).

2. Chimeras. Reproduction of chimeras during vegetative propagation depends upon the nature of the chimera and the method of propagation (17). If the growing points contain tissues of both components of the chimera in the same arrangement as the source plant, then the basic chimera should be reproduced. If the growing point arises adventitiously, then the chimera is likely to revert to one or the other component.

3. Epigenetic. The significance of epigenetic mechanisms in controlling vegetative propagation, flowering, growth form, and other characteristics in plants has only recently been recognized as more than a horticultural oddity exhibited by a few plants. In nature, phase changes (juvenility → adult) control the life cycles of seedling plants and are major factors in adapting particular species to specific environments. Juvenility is expressed perhaps most strongly in woody trees and various bulb and corm producers, and less in shrubs (which tend to regenerate from bases) and vines.

Vegetative propagation has obscured the role of such epigenetic controls in horticulture (17) since changes are progressive and repeated vegetative propagation leads to stabilized adult forms. This pattern has occurred with tree fruit and nut species and bulbous and related plants, which then flower in a relatively short time compared to the seedling plants.

Selection of specific juvenile source material and its maintenance by repeated pruning of the stock plants can produce and maintain plants in an arrested stage of specific phases (e.g., juvenile forms, vines, easy-to-root, and bush-type plants).

Reversions from adult to juvenile forms, with parallel shifts from hard-to-root to easy-to-root phases, provides a major tool in development of vegetative propagation systems for plants which have been particularly difficult to propagate up to now. Such reversions can occur through the formation of adventitious growing points in which new shoots are characteristically more juvenile than the original plant (32). Reversions also seem to be taking place with repeated subculturing of shoot tips in culture (26, 30) and with consecutive grafting onto seedling plants (15).

A question that must be answered in such studies is whether the new lateral shoots arise from axillary growing points or from adventitious growing points, either de novo on the stem or from callus (1, 17).

Another example of changes in epigenetic potential appears to be in the formation of embryogenic callus and the formation of somatic embryos (48). The potentiality in manipulating growth phases and other nongenetic changes in plants both in vivo and in vitro requires better knowledge of the epigenetic processes involved in their control.

4. Virus. Viruses and virus-like organisms (e.g., mycoplasma, viroids, etc.) have been the cause of much clonal variability. Once introduced into a clone the pathogen remains, although perhaps in a masked or latent form. Vegetative reproduction retains the virus in most methods of propagation unless very small pieces of the shoot tip near the apical meristem are used. The propagator has been a primary source of such pathogens among commercial sources.

One of the major achievements of recent years has been the elucidation of these virus—plant relationships and the concurrent development of so-called "clean stock" programs (7, 16, 17, 44).

Selection of "clean" sources has been achieved with a reselection within the cultivar by cloning from individual plants, buds, or meristem-tips. One can either identify individuals as "virus-free" through
index testing or use such techniques as heat treatment (thermo-
therapy) and/or ‘meristemming,’ where the smallest part of the
shoot tip capable of regeneration is propagated (36).

Sources of variability in vegetative-propagation systems

Elements of a vegetative propagation system are shown in Fig.
4. Primary effort in propagation of vegetatively propagated cultivars
has gone into establishing systems for distribution of “clean” prop-
agation stock to control viruses and other systemic pathogens. Such
programs include: a) identification of existing “clean” sources by
indexing and/or their development of “clean” sources by “meri-
stemming” or heat treatment; b) cloning from such sources through
selection of single growing points; c) maintenance of new source
plants in isolation to prevent recontamination; d) multiplication of
stock plants; e) propagation under conditions to prevent reinfection;
and f) distribution of “clean” plants to a planting site. Identity must be
maintained from source to planting stock, a function of Regis-
tration and Certification programs (7, 44).

In addition to monitoring the pathological status of the plant,
genetic continuity must be monitored to be certain that the product
emerging has the genetic and horticultural characteristics of the
cultivar that entered the system. Avoiding genetic variants is par-
pecially important when cloning is made from a single tree or a
single meristem.

Source material. Examples of problems include: a) collection
from the wrong source plant and an incorrect cultivar; and
b) propagation material of different origins within cultivars grown
extensively for long periods of time (i.e., in grape, apple, or citrus)
which develop variants that affect production (8, 37).

Certain disorders in particular plants are caused by unique genetic
systems that involve innate instability or change within the clone.
Some examples include noninfectious bud-failure in almond (22),
leaf crinkle disorders in cherry (21), June yellows in strawberry (50)
and lime bark disease in citrus (8, 47). With improved detection
techniques many of these may yet turn out to be pathogenic in origin,
but selection of suitable propagation sources is essential.

With modern agricultural and horticultural methods of production,
horticultural plants are being exposed, either in the field, green-
house, orchard, or test tube, to chemicals which are a new and
recently emerging has the genetic and horticultural characteristics of the
plant. Avoiding genetic variants is particularly important when cloning is made from a single tree or a
single meristem.

Propagation system. The vegetative propagation system itself
can influence variability. Segregation among chimera components
or reversion to original forms may occur (e.g., in adventitious shoot
formation on leaf or root cuttings). Chimeras are particularly
unstable with tissue-culture techniques involving adventitious devel-
opment of meristems or a callus phase.

Various micropropagation and tissue-culture techniques that have
been applied now to so many species with such large rates of mul-
tiplication create a new situation with inherent risks of genetic and
epigenetic modifications. Consequently, the effects of various types
of micropropagation on their potential role in creating genetic and
epigenetic instability must be considered (17).

Plant performance. Plant performance can be affected by prop-
agation system. Removal of viruses or other pathogens may increase
vigor such that the new plants may require different management
than the traditional culture.

Plants produced by micropropagation may display differences
such as changes in growth habit or time of flowering, as compared
to plants produced by standard methods. For example, the repro-
ductive potential of strawberry plants produced directly in micro-
propagation differs somewhat from that of conventional, field-produced
plants (3, 12). Such an effect appears to be transitory and the original
vigor such that the new plants may require different management
than the traditional culture.

Terminology

One of the requirements of a program dealing with the clone as
a horticultural entity is consistent terminology. Plants arising from
different propagation origins within a clone may constitute a group
whose identity must be maintained yet does not necessarily represent
a new genetic entity. Terms that have been used in the literature
to denote such groups have included “source,” “clone,” “sub-clone,”
“microclone,” “selection,” “strain,” “variant,” and “mutant” (45).
The terms “mericlone” (29) “calliclone,” (33) and “soma-
culture” (7, 36) have appeared in the literature. Plant breeders
have used the term “selection” to indicate a candidate cultivar prior to its
formal release. The term “clone” has been applied to different
accessions (sources) of the same cultivar in Repositories or Founda-
tion orchards (16).

A recent symposium on “Genetic Variability in Apples and Pears”
(45) recommended that the term “clone” only be used to designate
the original variety or cultivar, whereas the term “source” is to be
used to designate different origins within the clone. A plant different
from another within the clone is a “variant”; if the difference is
genetic in nature, then the plant is a “mutant”. Its progeny become a
new clone if they are stable after vegetative propagation.

The International Code of Nomenclature for Cultivated Plants (4)
defines the clone as one of the basic categories of cultivar, designated
as “a genetically uniform assemblage of individuals (which may be
chimeral in nature) derived originally from a single individual by
sexual propagation, for example by cuttings, division, grafts, or
obligate apomixis. Individuals propagated from a distinguishable
bud mutation form a cultivar distinct from the parent plant.”

This distinction between “clone” and “source” appears to go a
long way to resolve some nomenclature problems. A “source” can
be identified by name or number referring to a nursery block or
orchard; this is often done in practice. Thus its unique identity is
maintained distinct from other sources of different origins of that
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cultivar.

Fruit tree nurseries in different years often select budwood from
separate “source-orchards” which are related through consecutive
propagation. Such “nursery sources” may be in existence for many
years. Similarly, distinct “source blocks” may be used in orna-
mental nurseries for rooting.

A source originating from a single plant (growing point) within
the clone is a special case and might be designated appropriately as
a “source-clone”. The potential risks or benefits from a variant
either being selected as the original source-clone or appearing early
in the propagation sequence is significantly greater in this case than
from a multiple plant source (or block) where presence of some
variants might be tolerated. Furthermore, clean stock programs might
include a designation of “specific-pathogen-tested” (or “specific-
pathogen-tested”) source-clones, meaning specific source clones
selected for freedom from specific pathogens. ("Tested" is preferred
here rather than "free," but this distinction needs further expla-
nation.) This term could be shortened to SPT (SVT) source clones,
as suggested by Hartmann and Kester (17), and given a unique
number or name designation.
Programs to monitor genetic stability

Establish genetic identity of source plants. It is a truism expressed in horticultural literature and practice that the source plant one uses in propagation should not only be the correct cultivar but also should be "true-to-type" and not represent some inferior variant of that cultivar. These 2 aspects—"true-to-cultivar" and "true-to-type."—as they refer to a particular propagation source—are somewhat different concepts but in practice have been used more or less interchangeably. Visual inspection under proper conditions of both vegetative and reproductive structures by a person familiar with the cultivar is the first step in selection. Identification of many cultivars can be made by this means. In practice, this requirement of source selection may be difficult to achieve. Source plants used for propagation may not be grown under ideal conditions for verifying identity but in special blocks pruned to produce propagation material rather than fruited material. Supplementing this subjective inspection by objective biochemical, serological, or other tests would be useful and perhaps essential, as a kind of "genetic indexing" in future programs. Biochemical "fingerprinting" systems for a number of crops have much promise to identify relatively large genetic differences between clones. On the other hand, they may have much less potentiality in identifying genetic variation within clones.

"True-to-type" applied to a propagation source implies not only the correct cultivar but also the absence of a variant that might affect the future productivity and performance of that cultivar. Verification of this attribute in practice may not be possible by visual inspection of the source plant unless an obvious mutant has occurred. Particular traits, such as productivity, may not be measurable except with vegetative progeny tests (49). Source traits depend on particular environments for expression. Genetically mutant cells may be latent in the plant and not exposed except in future vegetative generations. Biochemical fingerprinting tests will have to be more sensitive to separate variants within clones than those between cultivars.

Vegetative progeny tests for horticultural and genetic verification. Performance testing under standard conditions is part of the selection and development process prior to release of a new cultivar. Vegetative progeny testing likewise may be needed where a new source clone is to be used (as in selection of pathogen-free stock). Once this step is completed, the clonal principle indicates that future propagation might be made with considerable confidence. Visual inspections of source plants should continue and in some cases, periodic monitoring by progeny testing might be appropriate. The term "true-to-type" might be applied then only to specific sources where this verification step has been concluded. Thus, the concept of "true-to-type" is distinguished from "true-to-cultivar.

The first could be identified by visual inspection or specific tests carried out on the original source plant, the latter by vegetative progeny tests. Vegetative progeny testing depends on the specific crop and application must be tempered with reason based on the time and conditions required to carry out the step.

Maintaining source identity. Despite the above suggestions for programs to monitor genetic identity, one can never predict when a new variant might unexpectedly appear somewhere in the sequence of operations. One needs to be able to determine promptly where this initiation of any variant to a particular source or to one of the phases of propagation and make early corrections with such records. This information would constitute a continuing vegetative progeny test of propagation sources in use.

Summary

The clone has major significance in horticulture because specific, superior individuals can be selected as cultivars and maintained through vegetative propagation as uniform genotypes with stable epigenetic phases (clonal life cycles). This contrasts with seed-propagated cultivars which either redistribute genetic factors and reverse epigenetic potentialities (sexual life cycles) or maintain genetic factors and reverse epigenetic potentialities (apomictic life cycles). Somatic variation can include epigenetic reversion, genetic changes, chimeral rearrangements and infection by various viruses and other pathogens. These conditions may develop at various stages of the propagation sequence. Four terms are suggested to refer to horticultural attributes of somatic variation: "clone", "source", "variant", and "mutant." The term "source-clone" is suggested for the specific cases where a single meristem within the clone is selected primarly for production of specific-pathogen-tested (SPT) plants for propagation. Three aspects of genetic control are suggested: 1) visual inspection and biochemical indexing for "true-to-type," 2) progeny tests for "true-to-type," and 3) maintenance of source identity for monitoring sources of variation.

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VARIATION AT THE CELLULAR LEVEL

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Certain plant species have been propagated clonally over long periods of time using classical techniques. Variants occasionally appear, but usually in relatively low frequencies (31). Thus, “carbon copies” of the parent plant might have been expected when tissue explants and single cells were first isolated and regenerated into plants by cell-culture techniques. Most regenerated plants are, in fact, apparent exact copies of the parent plant (40, 41). However, some culture systems now available for commercial propagation and research purposes appear to produce cell cultures and regenerated plants with considerable phenotypic variability.

The relatively high incidence of variation in ploidy and chromosome number among cultured cells and in regenerated plants led D’Amato (7) to conclude that propagation by means of the true shoot apex is the only procedure that ensures varietal purity and genetic stability among in vitro-propagated plants. Some vegetatively propagated plants are known to exist as periclinal chimeras (33, 34), or genetic mosaics (4, 7, 15, 33). Variation among regenerated plants from cells or tissues of such plants would be anticipated. Conversely, instances of high-frequency variation among plants (protoclones) derived from populations of single cells (protoplasts), which are supposed to be genetically uniform, are indeed surprising (21, 29, 37).

Variation among plants derived from protoplasts isolated from a single leaf raises penetrating questions about the genetic homogeneity of somatic cells (4, 9, 31) and the nature of genetic modifications that may possibly be occurring during the cell-culture and regeneration processes (1, 2, 8, 33, 36). The wide range in frequency of variants recovered from various cell-culture and regeneration systems indicates that several, perhaps many, factors can affect the degree of variation at the cellular level and/or expression of cellular variation in regenerated plants, e.g., species, cultivar, culture medium, duration of culture, and cell source.

Variation among plants from cloned cell-cultures could pose problems for those seeking to use such technology for the rapid propagation of disease-free plants (3, 7, 8, 22). On the other hand, the

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