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Evolution by Individuals, Plant-Herbivore Interactions, and Mosaics of Genetic Variability: The Adaptive Significance of Somatic Mutations in Plants

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Summary. Differences in the pattern of organization of organisms may lead to different patterns of evolution, genetics and ecology. Plants and animals differ in their fundamental patterns of organization. Plants consist of a series of repeating units that compete with one another, while animals consist of mutually interdependent systems that cannot compete. As a result, plants may be able to take advantage of somatic mutations in ways that are not available to animals. Somatic mutations arising in plants can be inherited by naturally occurring mechanisms of sexual and asexual reproduction. Long life span, large clone size, and the complete regeneration of buds each year may permit an individual plant or clone to evolve. Plants may even develop as mosaics of genetic variation. Evolution by individual plants and/or development as mosaics of genetic variation may prevent herbivores from breaking the defenses of their host plants. This evolution may also result in greater "fine tuning" to local environments leading to ecotypic variation.

Introduction

Although many horticulturists and botanists are familiar with the economic aspects and heritability of somatic mutations, the adaptive significance of this source of genetic variation has not been appreciated. The goal of this paper is to synthesize knowledge from rather diverse fields into an ecological framework of predictive value and to present an alternative hypothesis for some currently recognized field patterns. We argue here that somatic mutations may be an important source of heritable variation in plants by first presenting the known mechanisms and evidence for heritability, and secondly, by developing the evolutionary implications. The latter include the evolution or genetic change of individual clones through time, the development of mosaics in which the branches of an individual tree or parts of a clone represent an archipelago of similar but distinct genetic islands, and the effect of this genetic variability on the coevolutionary interactions of plants and herbivores.

Heritability of Somatic Mutations

Mechanisms of Inheritance

Gene and chromosome changes which occur in somatic or vegetative cells can lead to permanent changes in the plants in which they arise. Such changes can be caused by point mutations, deletions, duplications, inversions, aneuploidy, polyploidy and extrachromosomal mechanisms of inheritance (Hartmann and Kester 1975). Plant parts that arise from genetic changes in which all tissues have the same genetic makeup are termed "bud sports" (Edmond et al. 1975). If a somatic mutation arises in a meristematic cell of a bud, the derivative cells will also carry the mutation. Thus, a somatic mutation that occurs in the meristem of any bud can spread with the production of other derivative buds (year to year growth within a single plant). The mutation can be expressed in the gametes of sexual reproduction (Stewart and Dermen 1979), and/or develop into an independent plant through various naturally occurring modes of asexual reproduction.

Mutations often affect only a portion of the meristem. Plants or plant parts so derived are termed "chimeras" and are composed of two or more genetically distinct tissues growing adjacent to one another (Dermen 1960). Chimeras result from the layered structure of the meristem. Depending upon the plant group, the promeristem contains up to 3 layers of dividing cells with each layer giving rise to different plant tissues (Esau 1975). For example, with the stems of peach, the L-I layer produces the epidermis, the L-II layer gives rise to the outer cortex and part of the vascular cylinder (also the anthers and ovules), and the L-III produces the inner cortex, vascular cylinder and pith (Dermen 1953, 1960). Since chimeras are composed of genetically different tissues, a mutation must generally arise in a layer whose derivative cells are the floral parts of the plant for a somatic mutation to be expressed in the gametes of sexual reproduction (Neilson-Jones 1969, Grant 1975). However, with the formation of adventitious buds (which originate from tissues of different meristematic origin from most other buds), somatic mutations that would not normally be expressed in the gametes of chimeras may still be incorporated into the gene pool of the gametophyte generation. For example, Darrow (1928) and Howard (1970) demonstrated that adventitious buds of potatoes and blackberries may express a different genotype from the other buds of the plant. Another mechanism permitting gametic expression of mutations arising in meristematic layers not normally involved in production of gametes is described by Dermen (1960). In cytochimeras of peach and apple (i.e., diploid and tetraploid cells), the mutant cells of one meristematic layer may be incorporated into other layers depending on the plane of cell division. While horizontal divisions maintain the integrity of the meristematic layer, vertical divisions may effectively inject a cell from one layer into another. Thus, regardless of the meristematic layer in which a mutation arises, genetic expression is still possible.

Even if a somatic mutation is not incorporated into a cell line that differentiates as gametes, it can still be perpetuated

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by cloning. Asexual reproduction via tubers, tubercles, tuberous roots, bulbs, pseudobulbs, cormels, stolons, runners, rhizomes, offsets, root crowns, stem joints, layering of lower branches, inflorescence bulbils, apomictic seeds, and adventitious embryony is widespread among plants. Because no genetic recombination is involved in asexual reproduction, the genetic composition of the parent plant tissues is maintained and somatic mutations arising in all plant parts (e.g., roots, stem, inflorescences) can become independent of the parent plant (Grant 1975). Quaking aspen *(Populus tremuloides)*, black locust *(Robinia pseudoacacia)*, subalpine fir *(Abies lasiocarpa)*, Gambel oak *(Quercus gambelii)*, jumping cholla *(Opuntia fulgida)*, and century plant *(Agave deserti)* are a few of the long lived species in which the formation of clones is common (Peattie 1953, Fowells 1965, Gentry 1972, Benson 1974).

Horticultural Evidence

The bulk of the evidence for somatic mutations in plants comes from the horticultural literature where cultivated crops and ornamentals have been intensively studied. Although we are aware of the problems in dealing with cultivated plants, we would like to remind the reader that Darwin's *Origin of Species* relied heavily on such literature. Somatic mutations arise naturally in many plant groups and are used by horticulturists in developing new cultivars that are superior to the parent stock. Many of these mutants have become a major source of commercially important fruits and ornamental plants. For example, before chemicals were commonly used to induce mutations, 33% of the plant patents issued by the U.S. Patent Office were for plants originating as somatic bud mutations (Shamel and Pomeroy 1936). Furthermore, Cramer (1907, cited in Shamel and Pomeroy 1936) estimated that of the 8,800 varieties cultivated in Europe in 1899, 5,000 originated as bud sports. To maintain the genetic order which might otherwise be broken up or lost by sexual reproduction, most varieties are propagated asexually by horticulturists (grafting, layering, cuttings, division of tubers, etc.). For example, in 1906, a bud sport was discovered in which the grapefuit from only one branch of a tree possessed pink flesh (Hartmann and Kester 1975). This single branch has since served as the parent stock for all the pink-fleshed grapefruit grown in the United States. In cultivated bananas, all plant parts produce viable somatic mutants. There are 50 known somatic banana mutants which include black stems, pink fruit, dwarf growth form, drooping leaves, inflorescence characters, resistance to disease and crop yield (Simmonds 1966). Somatic mutations have occurred in all potato varieties, some of which have been so superior that they nearly replaced the parent stock. In the United Kingdom in 1968, there were 20,000 cultivated acres of the somatic mutant, Red Craigs Royal potato, compared to 6,000 cultivated acres of the parent stock (Howard 1970). These examples represent just a few of the thousands of heritable somatic mutations that have been selected an maintained by man for various commercial and/or aesthetic reasons.

It should be emphasized that the great majority of somatic mutations probably go unnoticed because they don't visibly affect the color and growth form of the plant (Hartmann and Kester 1975). Soost et al. (1961) relate an example involving citrus in which a mutation was detected too late to prevent economic loss. A bud sport arose in the propagation stock in which fruit acid concentration increased; it was propagated unknowingly and detected only years later when the trees began producing inedible fruits. Citrus are particularly difficult to maintain as pure clones even by accepted methods of asexual reproduction. In examining more than 100 orange orchards in California, Shamel (1943) showed that in the average orchard, 25% of the trees exhibited striking entire-tree variants (i.e., the whole tree is affected), and in some orchards, it was as high as 75%. As of 1936 (before the use of mutagens), over 1,660 bud mutations of citrus were recorded (Shamel and Pomeroy 1936).

High variation within asexually propagated plants is common in such diverse plants as cherry, lemon, grape, sweet potato, chrysanthemum, dahlia, coleus and others from different plant families. Horticulturists state that the progeny of these asexually propagated crops are no more uniform than that of seed propagated crops (Edmond et al. 1975). Harrison and Fincham (1964), using *Antirrhinum majus*, demonstrated that for the same locus, somatic mutation rates were correlated with germinal mutation rates, and both types of mutation rates were similarly affected by changes in environment. Comparisons of the limited data on mutation rates further support the above observations of high variation within clones. The average rate of appearance per locus for specific somatic mutations in eight potato varieties (between 10^{-3} and 10^{-5}) is similar to or greater than the average germinal mutation rates for any one locus of *Drosophila* (between 10^{-5} and 10^{-7}) or maize (between 10^{-4} and 10^{-6}) (Heiken 1958, Howard 1970). Although such comparisons are admittedly highly incomplete, they do suggest that somatic mutations provide an important source of heritable variation in plants.

Ecological Implications

Somatic Mutations in Plants and Animals

The role of somatic mutations in plants and animals are fundamentally different. A plant is composed of many repeating modules, each capable of reproduction (Harper 1977). A beneficial somatic mutation that occurs in any bud can spread by the sexual and/or asexual mechanisms already described. On the other hand, if the mutation is a harmful one, as are most mutations, the death of a single bud should have little effect upon the survival of the whole plant due to the highly repetitive nature of plant structure. If we compare these plant features with the anatomy of animals (insects, mammals, etc.), just the opposite is true. Since most animals are not composed of repeating modules at the organ level of organization (exceptions include the echinoderms, proiferans, cnidarians and platyhelminths), the capacity to reproduce is restricted to a single organ system. Because reproduction is limited to a single organ system, somatic mutations have no known mechanism of being preserved, either sexually or asexually, beyond the life of the individual. Harmful somatic mutations may result in the death of the animal and have been implicated in the process of ageing (Kirkwood 1977). Thus, animals should evolve mechanisms which reduce somatic mutation rates to lower rates than in plants (Novitski 1977). Because of these basic differences, somatic mutations may enable plants to be better than animals at "fine tuning" themselves to local environments.

Mutations arising somatically in plants have a greater probability of being incorporated into the gene pool than mutations that arise in the gametes of either plants or animals. The most important advantage allowing superior somatic mutations to survive in plants is that stochastic elements are greatly reduced. For example, in animals, if a single sperm contains a superior mutation, the probability of it fertilizing an egg and the zygote surviving to sexual maturity is exceedingly small. Furthermore, in the recombination process of subsequent sexual reproduction,

successful combinations of interacting genes may be lost. In comparison, if a superior somatic mutation arises in the promeristem of a single bud, the probability of its surviving is much higher. The mutation will, at the very least, survive for the lifetime of the resultant twig, branch or other plant part, which could be many years in long lived perennials. During that time period, the mutation may be expressed in the gametes of sexual reproduction and/or perpetuated by the various naturally occurring methods of asexual reproduction. In the latter case, since no recombination occurs, as in meiosis, superior combinations of interacting genes would be maintained.

Because of the potentially greater survivability of somatic mutations already discussed, one might suspect that the cost of the mutational load of plants (Crow 1970) could be very high. This need not be so. The developing buds of a plant compete for sunlight, nutrients and apical dominance. The poorest competitors lose out and eventually die. Nurserymen have long known that buds compete with one another, because when a portion of the plant buds are removed, the remaining buds produce more and larger leaves than they could have otherwise (Kozlowski 1973, Addicott 1978). Thinning of flower buds in orchards is an important practice used to increase fruit size (Edgerton 1973). In nature, due to the elimination of poorer competing buds within a single plant, buds with inferior genetic combinations or mutations can be lost with little cost to the plant. Natural pruning, at least to the degree occurring in plants, is not known to exist in animals. This pruning ability should allow plants to lessen the genetic load that might otherwise exist.

Evolution by Individuals

In addition to providing a source of heritable variation for selection to act upon in future generations, somatic mutations may confer direct advantages upon the individuals in which they arise. If a superior somatic mutation arises, the branch or shoot carrying the mutation can potentially outcompete all others of the parent genotype. Since a plant is a population of competing buds which grow at different rates and regenerate each year (Harper 1977), the gene frequency of the plant or clone can change over a period of years and the parent genotype may be completely lost. For example, the horticultural variety, variegated maple, *Acer platanoides drummondi,* shows how such a process might occur. The leaf margins of variegated maple are white and the growth rate is approximately $^1/_3$ the growth rate of the parent stock, Norway maple. Occasionally, a single bud develops in which the leaves are entirely green like the parent stock, and it grows faster than all the other variegated buds on the tree. Because of the faster growth rate, regardless of where this bud appears on the tree, it soon becomes apically dominant. If nurserymen don't remove these wild type buds, the tree reverts over a period of years to the parent genotype and all variegated branches are lost via the process of natural pruning of the lower and less apically dominant branches (unpublished observations of T.G. Whitham and L.A. Whitham). Reversal time is primarily a function of the size of the tree when the wild type bud appears. The smaller the tree, the faster the changeover. Over a period of 40 years of observation at Whitham Nurseries, Agency, Iowa, we estimate that with the first appearance of a single wild type bud in a 5 m variegated tree, within 10 years, 95% of all the foliage would be of the wild type. Although variegated maple is probably a chimera in which both mutant and parent tissues are present in tissues of different meristematic origin, it does demonstrate that the gene frequencies of the living plant tissues change over the life of the plant or bud population. Such examples are common in the horticultural literature and occur in many plant groups (Dermen 1960, Neilson-Jones 1969, Hartmann and Kester 1975).

Long life span, large clone size, and the complete yearly regeneration of all the plant buds increase the probability that somatic mutations will arise in an individual, clone or population. For example, individual clones of bracken, *Pteridium aquilinum,* may be 1,400 years old and cover an area of 138,400 m^2 (Oinonen 1967a, b). Mutations arising in the rhizomes or underground stems of such plants are likely to become quickly established since each would have its own root system. Using rate of spread of circular clones to estimate the age of goldenrods, *Solidago missouriensis,* growing in virgin prairie, William J. Platt (pers. comm.) calculated the average age of clones to be 200–400 years, with some clones as old as 1,000 years. Since the largest clones contain upwards of 10,000 ramets, each of which is renewed annually, the potential for genetic change over the life span of the clone is high. With the desert shrub, creosote bush, *Larrea tridentata,* which grows in concentric rings, Vasek (1980) used field growth rates and radiocarbon dating techniques in estimating the age of the oldest clones to range between 9,400 and 11,700 years. Similarly, with 4,000 year old individuals of bristlecone pine, *Pinus longaeva,* somatic mutations are likely to have accumulated due to age (Libby et al. 1969). R.W. Allard (pers. comm.), in examining several enzyme systems in the meristematic tissues or bristlecone pine, found differences, in two cases, within the same tree, indicating genetic variation from one branch to another. Since so many herbaceous and woody plants clone, examples of this type are probably far more common than previously suspected. It would appear that the size and age of the clones in the above examples would allow the individual clone or plant to span evolutionary time.

Adaptation to local conditions might occur very rapidly via somatic mutations and lead to ecotypic variation. Platt (pers. comm.) has suggested that the tight packing of prairie goldenrods (Werner and Platt 1976) may have been greatly facilitated by somatic mutations. Considering the 200–1,000 year age of goldenrod clones, there have been only 8–25 generations since the last glaciation. This begs the question: "Could sexual reproduction through this limited number of generations account for the local adaptations of the goldenrod community?" Even if selection coefficients were very high, it would still be insufficient to explain how the populations evolved so rapidly. Alternatively, an entire community that was preadapted to local conditions could have migrated in with the retreat of the glaciers. This is highly unlikely, however, because the community is composed of a mixture of species with different geographic ranges. It would seem that somatic mutations represent a reasonable source of heritable variation that would permit adaptation to local conditions and the coevolution of closely related species.

Plants as Mosaics of Genetic Variation

Through several mechanisms, plants can develop as mosaics in which different branches or other structures of the same plant vary greatly in their genetic composition. Such variation within a single plant or clone could have a substantial impact upon its herbivores, and be adaptive.

Any branch on which a somatic mutation occurs will be genetically different from the other branches of the same plant. This is particularly relevant for genes or gene complexes that are unstable and mutate with high frequency to two or more relatively stable states. Such mutability to alternative states has

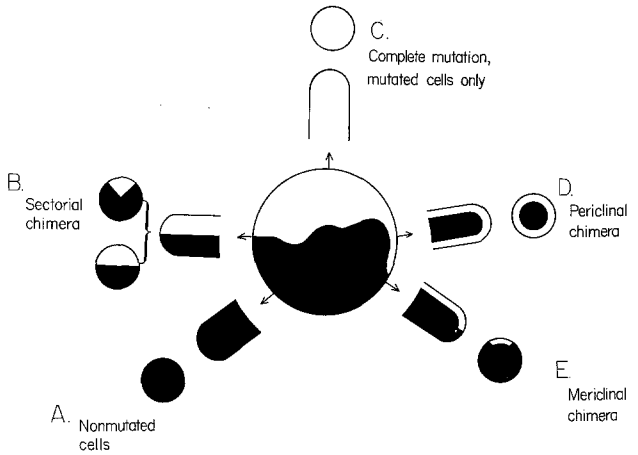

Fig. 1. Due to their point of origin, buds derived from chimeras can vary greatly in their genetic composition. Adapted from W. Neilson-Jones (1969)

been shown in *Antirrhinum* (Harrison and Fincham 1964) and maize (Peterson 1963). In the context that mosaics are adaptive, genetic instability may be favored evolutionarily, particularly in unstable environments.

With chimeras, gene expressions can change rapidly. As discussed earlier, the meristems of plants are layered, with each layer giving rise to different tissues. If a tetraploid cell arises in the L-II layer of a diploid peach tree, it is referred to as a 2-4-2 cytochimera. Depending upon the plane of cell division, with further plant growth the tetraploid condition may spread to the L-III layer, giving a 2-4-4. Thus, on the same plant, one can have meristems with 2-2-2, 2-4-2, 2-4-4 or other combinations depending on which layer the tetraploid first arose (Dermen 1960).

With "sectorial" chimeras, entire sections of the stem differ such that the L-I, L-II, and L-III layers on one side of the stem are genetically different from the same layers on the opposite side (Fig. 1). The genetic composition of buds arising from sectorial chimeras is highly dependent upon their position of origin on the stem. Buds arising wholly on one side (A and C) are composed of totally normal wild type cells or totally mutated cells. Buds arising at the margins may be sectorial, periclinal or mericlinal chimeras (B, D and E, respectively), each having its own different pattern of arrangement of mutated and wild type cells (Neilson-Jones 1969). Chimeras of *Pelargonium* produce this kind of variation which is subsequently transferred to the seedlings after sexual reproduction (Baur 1930). Self-pollinated flowers arising on totally green branches give rise to only green seedlings and self-pollinated flowers arising on totally colorless branches produce only colorless seedlings. If a flower on a green branch is cross-pollinated with a flower from a colorless branch, some of the resulting seedlings develop to produce green, colorless and chimeral branches.

The above variation can be increased further by the development of adventitious shoot buds and roots. From the stem or roots of dicotyledonous plants, adventitious shoot buds and roots may originate from phloem, vascular rays, cambium, pith, lenticels and wound callus. On leaves, they may originate from the epidermis and cortex, cells between vascular bundles, and from wound callus (Hartmann and Kester 1975). Although this list is incomplete, it is obvious that adventitious shoot buds and roots may arise from tissues of different meristematic origin (L-I, L-II, L-III).

While the first source of variation depends upon somatic mutation rates, the last three are mechanical mechanisms that merely increase the existing variation. Taken in combination, an individual plant or clone may develop as a mosaic of genetic expressions, and such variation may be inherited by both sexual and asexual means. From an evolutionary perspective, mosaics may also offer an explanation for the higher degree of hybridization found in plants. Plant species are well known to hybridize far more frequently than animal species (Mayr 1970). An evolutionary consequence of mosaicism may be the lowering of the threshold of acceptibility for pollen having a radically different genotype from that of the accepting ovule.

Coevolution with Herbivores

Because of shorter generation times and greater recombination potential, herbivores (e.g., insects) should be able to break the defenses of long-lived plants and thus have an advantage in any evolutionary race. Because plants consist of populations of self-replicating buds, via somatic mutations they may be able to counter the adaptations of their herbivores or at least change as rapidly as their herbivores. Animals, on the other hand, are not systems of duplicating buds, but instead, are systems of mutually interdependent units (e.g., organs, tissues all having specialized functions that are interdependent). For this reason, animals must rely on gametic mechanisms of variability (gametic mutations, recombination, chromosomal changes) to cope with plant defenses. Changes in genotypic ability to cope with plant defenses must be transgenerational in animals (e.g., phytophagous insects). Plants, on the other hand, can afford the strategy of a long generation time, as long as they can stay ahead of their herbivores. Perennial plants have available to them, as a long term strategy, the gametic transgenerational mechanisms (available also to animals) that allow the plants to produce genotypes with superior defenses and competitive ability. They also have available the shorter term strategy of somatic mutations, which allows an intragenerational response to herbivore pressure and competition.

Slight changes in genotype may be highly effective against herbivores. Hatchett and Gallun (1970) have shown with the Hessian fly, *Mayetiola destructor,* that a gene-for-gene relationship exists in the interactions of this pest and wheat. Successful Hessian fly attack requires that for every resistant gene in wheat, the fly must possess a corresponding gene for virulence. A less than perfect genetic matchup usually results in the death of the fly larvae and as the number of resistant genes increases, the probability that any given fly has the correct genetic match for virulence declines. These important findings suggest that changes at single loci can have a dramatic effect upon plant-herbivore interactions. In a coevolved system with a gene-for-gene correspondence between plant and herbivore, somatic mutations, chimeras, and mosaics of genetic variability could play a very important role in the resistance of long lived plants by making it difficult for herbivores to achieve the required genetic matchup for successful host attack.

Feeding preferences of herbivores, resistance to disease, and hardiness are just a few of the many factors which may affect and/or accentuate the differential survival of buds present on a single plant or clone. If the buds vary in genotype due to sporting, selection should occur. For example, in the case of various perennials studied under field conditions, tissue loss to herbivores can be as high as 20 to 60% (Varley and Gradwell 1962, Dixon 1971, Morrow and LaMarche 1978). Due to selective feeding by herbivores, a resistant bud sport should suffer

less damage than other buds. Over a period of years, the genotype of the bud population may shift and allow the plant or clone to evolve away from the feeding preferences of its herbivores.

If all parameters affecting the tree are held constant, then the most superior single genotype within a tree should predominate. This tendency should be most pronounced in plants that exhibit a high degree of apical dominance and rarely clone (e.g., many conifers). In these trees genetic variability should be minimized because only the dominant apical meristem survives. As the stand of trees ages and the canopy rises, most of the lateral branches are naturally pruned. Thus, only one meristem survives for the whole life of the plant. This may be the case in *Pinus ponderosa*. The experiments of Edmunds and Alstad (1978) indicate that scale insects adapt to individual ponderosa pine trees.

If, however, environmental parameters, herbivores or any other factors affecting genotypic success vary, a balanced population of buds varying in genotype may prove most stable. Mosaics of this type are most likely to exist in plants that have multiple apical meristems and/or exhibit a propensity for cloning (e.g., many grasses, shrubs and examples of trees already given). In this case, as the plant ages and somatic mutations accumulate, the genetic distance between buds, branches or other plant parts may increase so that two branches at opposite ends of the canopy may be genetically distantly related to each other. These same selection pressures may also favor the development of periclinal chimeras in which the development of adventitious buds can quickly express another genotype. Interestingly, in nature, adventitious buds are usually formed after a plant suffers biological or physical environmental damage. This suggests that the derivation of these buds from a different meristematic layer may be an adaptive response in that it presents an alternative genotype in a changing environment.

A single plant or clone may represent a mosaic of genotypes that effectively prevents herbivores from evolving specific metabolic pathways to overcome plant defenses. For example, if we hypothesize that the genetic coding for a plant toxin mutates to a different but effective state to form a sectorial chimera, we can easily imagine that the resulting mature plant could be highly variable in both toxins and dosage. Faced with a mosaic of plant defenses in different dosages, herbivores may be forced to remain generalists or become extreme specialists. In such cases, plants with genes or gene complexes that are easily mutable into alternative resistant genotypes may be evolutionarily favored. Such a situation would further increase the likelihood that long lived plants or clones develop as mosaics.

Recent evidence shows that adjacent branches of the same tree can vary greatly in their suitability to herbivores. Whitham (1981, 1982) showed that colonizing gall aphids, *Pemphigus betae*, clearly respond to individual trees of narrowleaf cottonwood, *Populus angustifolia*, as if they were mosaics of varying susceptibility to attack. On adjacent branches of the same tree, aphid mortality during gall formation (a highly coevolved interaction) varied from 28% to 63% of the colonizing population. Aphids preferentially settled on those branches where survival was highest. The most preferred branch was colonized by 27 times more aphids, and subsequent reproductive success of survivors was nearly twice as great as that achieved on the adjacent less favorable branches. In addition, the variation between branches of the same tree can be nearly as great as the variation between the extreme trees in the population. Although the mechanisms that cause variation in suitability or resistance within or between these plants are unknown, these data demonstrate real differences within and between host plants to which herbivores must respond if they are to make appropriate settling decisions. In addition to somatic mutations and chimeras, these results could be caused by developmental patterns of plant growth, pest-induced plant defenses, and/or epigenetic factors (see Whitham 1982 for a discussion of these alternative sources of variation).

Individual plants or clones as mosaics of genetic variability may account for the correlation of species richness of plant parasites and the growth form of their hosts. Lawton and Schroder (1977) and Strong and Levin (1979) observed that per unit of geographical area, trees tend to have more pest species than shrubs, and shrubs have more pest species than herbs. Associated with this trend, Hamrick (1979) found that woody plants contain about three times more heterozygosity than herbaceous plants. We suggest that growth form and its associated size and age of the bud population may be closely related to the development of mosaics. Thus, individual plants or clones are not a single island as viewed by Janzen (1968), but an archipelago of similar but distinct islands to which pests may become adapted, depending upon island size.

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