GENETICS AND MORPHOLOGICAL EVOLUTION IN PLANTS

L. D. GOTTlieb

Department of Genetics, University of California, Davis, California 95616

Submitted August 22, 1983; Accepted October 20, 1983

The first organism subjected to genetical analysis was a flowering plant, Mendel’s garden pea (Pisum sativum). The choice of a plant rather than an animal was favored by certain logistical advantages: true-breeding varieties were available, crosses between them were easy to make, and large hybrid progenies could be grown in uniform gardens. More importantly, plants furnished a remarkable array of morphological characters exhibiting discontinuous or discrete alternative expressions that could be recognized and scored in hybrid individuals. The mode of inheritance of numerous differences in structure and shape, as well as architectural arrangement or orientation, has since been examined in segregating progenies produced from hybrids within and between plant species. The evidence reviewed below shows that a significant proportion of these differences is governed by one or two gene loci. In contrast, other morphological characters in plants, particularly those of dimensions, weight, and number (the classical components of agricultural yield), generally exhibit continuous variation, and differences in their expression are usually governed by multiple gene systems. The difference between the two categories has not been widely appreciated. In regard to the evolutionary divergence of plants, differences in morphological structure, shape, and orientation appear to have particular significance although it is not now possible to state whether they are more or less important than quantitative characters.

In animals, most variation in characters of morphological structure is continuously distributed, and its genetic basis is best described by the multiple factor hypothesis which proposes that heritable differences are caused by the segregation of a large number of genetic factors with individually slight effects. Characters in animals that usually show discrete differences are those of color and pattern rather than structure or shape, for example, banding on snail shells, mimetic patterns on butterfly wings, coat color in rodents, spotting patterns on ladybug elytra, and color patterns in fish. Major differences in morphological structure brought about by single gene substitutions are known, but typically they exhibit deleterious pleiotropic effects involving reduced fertility and/or other developmental abnormalities (King 1975a, 1975b).

The greater prevalence of phenotypes which have discontinuous expressions
and simple patterns of inheritance in plants compared to animals may be a consequence of fundamental differences in their morphogenesis and development. If so, then explanations of the mode of origin and evolution of morphological characters in the two kingdoms require different hypotheses which in turn will have important implications, particularly for speciation theory.

Much of the evidence on the genetics of morphological characters in plants was obtained more than 40 yr ago, and is no longer widely known or appreciated. Information on the subject is now relevant, however, because of the recent controversies about macroevolution (Eldredge and Gould 1972; Gould 1980, 1982; Stebbins and Ayala 1981; Charlesworth et al. 1982). In this paper, I review the literature as a means of stimulating renewed interest in the genetic bases of morphological evolution in plants.

MORPHOGENESIS AND THE NUMBER OF GENES RESPONSIBLE FOR MORPHOLOGICAL EVOLUTION

Growth and differentiation in plants are normally initiated in meristems that occur at the apices of all shoots and roots (Esau 1953). Plants that increase in thickness have additional meristems, the vascular and cork cambia, which are responsible for secondary growth. Cell divisions in the shoot apical meristem increase shoot length and lead to the serial formation of lateral primordia from which leaves, buds, or floral parts develop. Divisions in the root apical meristem also increase length, but lateral root primordia are differentiated from cell lineages stacked behind the meristem. Other local meristems function as sites of cell division in actively growing organs such as the intercalary meristems in the internodes and leaf sheaths of many monocots and the marginal meristems of leaf blades.

The utilization of meristems has the consequence that different parts of the plant body are largely autonomous, permitting them to respond independently to different environmental conditions by forming root or shoot systems of various sizes or by remaining dormant. Such capability is critical for stationary organisms which must accommodate their environment and respond rapidly both to advantageous and deteriorating conditions. Local environmental differences are common features especially around large plants, for example, temperature differences on north versus south sides or at different elevations above the ground, differences in light intensity brought about by shading, and differential damage caused by herbivore predation or pathogens.

Plant tissues have many unique developmental features which facilitate adaptation to environmental fluctuations. Following predation or climatic change, new meristems can be regenerated from many plant parts. The responses of meristems to local external and internal environments appear to be mediated by locally synthesized growth substances, as well as those produced elsewhere in the plant body, and are not necessarily related to the responses of other meristems on the same individual (Trewavas 1981). In contrast, the animal body is more fully integrated by means of hormones which are synthesized in central sites and directed to receptive peripheral locations.

Another important developmental feature is the repetitive structure of the plant
body, with the same organ and tissue types differentiated in separate places and at separate times. This is rarely the case in higher animals in which most organs are differentiated only during embryogenesis according to highly regulated developmental schedules. Therefore a single change during embryogenesis has a high probability of affecting the differentiation of many structures. This critical distinction between plants and animals was noted by Sinnott and Dunn (1935, p. 210). "The time factor is of so much greater significance in animals than in plants as to constitute almost a new variable which disproportionately magnifies the complexities of development. Plants, by their ability to repeat in the meristematic tissues many of the steps of development which in animals are passed through but once, tend to escape from the domination of a time sequence."

Plants also have many fewer organs, tissues, and cell types than animals. It has been estimated that plants have only about 50 different cell types in contrast to earthworms with 66, insects with 100 to 150, and mammals with about 250 (Stebbins 1982, p. 210). Plants require fewer organs because much of their metabolism is partitioned at the cellular and subcellular levels rather than in spatially separated organs specialized for different functions.

These and other developmental features of plants must be taken into account when considering the evolution of morphological characters. I propose that the open, less integrative, and plastic pattern of morphogenesis in plants permits large changes in morphology on the basis of relatively few genetic changes. In animals, large morphological changes caused by mutations at one or two genes are less easily accommodated because typically disharmonious pleiotropic effects of the mutations must be buffered by changes in numerous other loci. In contrast, many mutations in plants cause marked changes in morphology without deleterious pleiotropic effects, for example, those that add or remove structures, change allometry, or rearrange the relative orientation of parts. Consequently the argument that mutations of large effect rarely serve as the basis for adaptive evolution (Lande 1981, 1983) is less applicable to plants. Evolutionary divergence among genera or families of flowering plants may reflect many fewer genetic changes than is the case for similar taxonomic levels of higher animals.

At least three factors held back the formulation of models of plant evolution that take into account the unique aspects of plant development: (1) unwarranted generalization of results from continuously varying characters of length, size, or yield to the many characters in plants which commonly exhibit discrete or discontinuous expressions; (2) inattention to the morphogenetic and developmental basis of character divergence with the result that inappropriate characters were often used for genetic analysis; and (3) neglect of ploidy level so that estimates obtained in tetraploids and hexaploids of the number of gene substitutions responsible for character divergence were widely applied even though the estimates were inflated because of genome addition.

**GENETIC STUDIES OF MORPHOLOGICAL DIFFERENCES WITHIN SPECIES**

Hundreds of genes that affect morphological structures and plant architecture have been identified by examining patterns of segregation following hybridization between different cultivars or species. The data for many major crops are avail-
able in recent summaries: maize (Coe and Neuffer 1977); barley (Nilan 1974); rice (Khush 1974); wheat (Sears 1974); pea (Yarnell 1962; Blixt 1974; Marx 1977);
tomato (Rick and Butler 1956; Rick 1974). The information for wild plant species
is more scattered and frequently is found in the older literature. The evidence for
the number of genes having major phenotypic effects comes primarily from the
proportions of parental phenotypes recovered in F2 generations and often does
not include data from F3 or backcross generations. Although particular examples
may not be up to contemporary standards of genetic analyses, in the aggregate,
the studies provide convincing evidence that numerous morphological differences
in plants show simple patterns of inheritance.

Table 1 presents a representative list of morphological differences within plant
species that are governed by one or two genes. Examples are available for many
plant organs including roots, stems, leaves, flower parts, fruits, and seeds as well
as branching patterns, phyllotaxy, position and type of inflorescence, and growth
pattern. None of the listed morphological changes is associated with either abnor-
mal development or reduced fertility.

Since this review is primarily concerned with changes in structure and shape,
table 1 does not reference studies of the expression of color or color pattern, even
though extensive research has been done on these traits beginning with Mendel’s
analysis (which included 3 color characters among the 7 examined). The table is
divided into three categories (though these may not always be exclusive): A,
presence versus absence; B, changes in structure or shape; and C, changes in
architecture.

The first category includes floral structures involved in pollinator attraction
such as ray florets on the reproductive heads of Senecio which, when present,
markedly increase outcrossing rates (Marshall and Abbott 1982), and structures
involved in seed dispersal, for example, elongate scales (paleae) on the floral
receptacles of Crepis and pappus on achenes of Layia. Another group of presence/
absence characters includes epidermal structures that presumably reduce or pre-
vent herbivore damage such as spines on the fruits of Datura, Ricinus (castor
bean), and Cucumis (cucumber), papillae on seed coats, and various types of
pubescence, the latter also implicated in the maintenance of proper leaf tempera-
ture for photosynthesis, for example, Ehleringer and Bjorkman (1978).

Included in category B are many single-gene traits essential to the domest-
ication of crop plants, such as nonshattering rachis in cereal grasses and indehis-
cent pods in legumes, both of which permitted harvests to continue over longer
time periods and served to increase the amount of seed actually obtained (Pickers-
gill and Heiser 1976). Other changes governed by one or two gene loci are those
that affect the configuration of flower parts which may influence pollinator service
(Collinsia, Eschscholzia, Lathyrus, Phlox, Primula), and features of fruits im-
plicated in dispersal (Crepis, Cucurbita, Layia, Medicago, Pisum) or seed number
(Lycopersicon, Sesamum).

The most interesting examples of coordinated morphogenetic and genetic anal-
yses were carried out on fruit shape, a particularly favorable character because
the entire process of enlargement can often be followed from the earliest ovary
primordium to maturity, sometimes involving a many thousandfold increase in
TABLE 1

MORPHOLOGICAL AND ARCHITECTURAL DIFFERENCES GOVERNED BY ONE OR TWO GENES IN NATURAL POPULATIONS OR CULTIVARS. (Tetraploid and hexaploid taxa designated by 4X and 6X, respectively.)

A. Presence versus absence of structure
   Ray florets: Senecio squalidus (Ingram and Taylor 1982)
   S. vulgaris (4X) (Trow 1912)
   Paleae (scales) on floral receptacles: Crepis capillaris (Collins 1924)
   Spines on fruits: Ricinis communis (castor bean) (Harland 1920)
   Cucumis sativus (cucumber) (Crane and Lawrence 1952)
   Datura stramonium (Avery et al. 1959)
   Fruit bractlets smooth vs. horned: Spinacia oleracea (spinach) (Nohara cited in Matsuura 1933)
   Pubescence on leaf midrib: Crepis capillaris (2 loci) (Collins 1924)
   Glandular pubescence on involucres and peduncles: C. capillaris (Collins 1924)
   Pubescence on fruits: Dithyrea wisitzenii (Rollins 1958)
   Papillae on seed coats: Spargula arvensis (New 1959)
   Pappus on achenes: Layia chrysanthemoides (Clausen 1951)
   Glands on petiole base reniform, round, or absent: Prunus persica (peach) (Crane and Lawrence 1952)
   Glandular pubescence on leaves: Gossypium hirsutum (4X) (2–3 loci) (Lee 1968)

B. Differences in structure and shape
   Leaflets vs. tendrils: Pisum sativum (garden pea) (Marx 1977)
   Cotyledons “rolled” or not: Collinsia heterophylla (Gorscic 1957)
   Leaves “droopy” or not: C. heterophylla (Gorscic 1957)
   Leaf margin entire vs. lobed: Lactuca serriola (Whitaker 1950)
   Pharbitis nil (Imai 1930)
   Petioles and other organs elongate or not: Nicotiana tabacum (4X) (Stebbins 1959)
   Calyx enclosing vs. not enclosing fruit base: Capscium anuum (red pepper) (Lippert et al. 1966)
   Upper corolla lip reflexed or not: Collinsia heterophylla (Gorscic 1957)
   Flower erect vs. hooded: Lathyrus odoratus (sweet pea) (Bateson cited in Crane and Lawrence 1952)
   Flower keel clamped vs. open: L. odoratus (Bateson cited in Crane and Lawrence 1952)
   Corolla shape differences: Primula sinensis (DeWinton and Haldane 1933; Anderson and DeWinton 1935)
   Normal vs. long pistil: Eschscholzia californica (Beatty 1936)
   Pollen long (3-pored) vs. round (2-pored): Lathyrus odoratus (Bateson cited in Crane and Lawrence 1952)
   Flower petal fan-shaped vs. lobed with “tooth” in sinus: Clarkia amoena (Hiorth cited in Lewis and Lewis 1955)
   Petal margin entire vs. laciniate: Phlox drummondii (Kelly 1920)
   Eschscholzia californica (Beatty 1936)
   Papaver alpinum (Fáberge 1943)
   Corolla salver- vs. funnel-shaped: Phlox drummondii (Kelly 1920)
   Fruit locule number two vs. multiple: Lycopersicon esculentum (tomato) (Lindstrom cited in Rick and Butler 1956)
   Sesamum indicum (sesame) (Abe cited in Matsuura 1933)
   Fruit surface smooth vs. warty: Cucurbita pepo (squash) (Whitaker 1974)
   Fruit rind hard vs. soft: C. pepo (Whitaker 1974)
   Fruit straight vs. concavely curved: Pisum sativum (Blixt 1974)
   Fruit pod coiling clockwise vs. anticlockwise: Medicago truncatula (Simon 1965)
   Fruit spherical vs. pear-shaped: Lycopersicon esculentum (Lindstrom 1927)
   Fruit elongated vs. spherical: Capsicum anuum (Kaiser, 1935b)
   Fruit disk-shaped vs. spherical: Cucurbita pepo (Sinnott 1935)
   Fruit conical vs. tumari (transversely constricted above middle): Lagenaria leucantha (Pathak and Singh 1950)
   Fruit winged vs. wingless: Plectritis congesta (Ganders et al. 1977)
   Achenes winged vs. wingless: Coreopsis tinctoria (Smith and Parker 1971)
   Achene wings entire vs. fimbriate: Coreopsis grandiflora var. saxicola (Smith 1973)
   Fruit triple-keeled and pubescent vs. keelless and without pubescence: Valerianella ozarkana (Eggers Ware 1983)
size. In the summer squash, *Cucurbita pepo*, Sinnott (1935) found that the difference in shape between a flattened disk type (greater equatorial than polar diameter) and an isodiametric or spherical type was governed by a single gene.

The diversity of shape in the mature fruits was already evident in the very small ovary primordia (Sinnott and Durham 1929). Double logarithmic plots of length and width at numerous stages of development revealed that fruits that grew to different final shapes had similar allometric constants \( k \) throughout their enlargement. This suggests that even though the starting and end points were different, many of the intervening growth processes were similar (Sinnott and Kaiser 1934).

The genetic control of shape appeared to be independent of that for size (Sinnott 1935, 1958). The evidence came from the results of a cross between a variety with a large disk and one with a small sphere. The size of the F\(_1\) was close to the geometric mean of the parents. The means of the F\(_2\) disks and spheres were similar to each other and close to that of the F\(_1\). Although the F\(_2\) segregation for
shape was clearcut, mature fruit sizes were continuously variable, suggesting that additional genes operated on size.

Genetic analyses were also conducted on gourds of the genera *Lagenaria* and *Trichosanthes* which differ in shape from long and narrow through to flattish (Sinnott 1960). In contrast to *Cucurbita*, the primordia of these fruits had similar shapes but their allometric constants differed with some types showing greater relative increase in length during enlargement and others the reverse (Sinnott 1936). In a cross between the Zucca and Bottle races of *Lagenaria*, which differed in the slope of the allometric lines correlating their length and width (1.3 vs. 0.8, respectively), the F1 resembled the Zucca parent, and the F2 segregated cleanly into two groups, one with the allometry of one parent and the other with that of the other parent, indicating a single gene difference for the allometric constant itself (Sinnott 1958). Since the constants were not 1.0, the final shape of the fruits depended on the size to which they grew, a feature which appeared to be influenced by a number of genes as well as environmental factors.

Anatomical studies showed that the shape of the fruits was not related to the form of the cells, which were essentially isodiametric in the fundamental tissues of both elongate and flattened types. The two fruit shapes did differ in the planes of mitotic divisions with the elongate ones showing a preponderance of divisions at right angles to the ovary axis, and the flattened ones having division figures in all planes (Sinnott 1958).

Important studies were also carried out on fruits of *Capsicum annuum* (red pepper). Sinnott and Kaiser (1934) found that varieties with elongate fruits and those with nearly spherical ones had similar ovary shapes until fertilization. Then, in the elongate type, the allometric line relating length to diameter changed slope sharply whereas the spherical one maintained a constant line throughout its enlargement. Kaiser (1935a) reported that the F2 progeny segregated into two parental classes: 31 plants showed the allometric change and 9 plants maintained the constant rate, suggesting a single locus. Thus, the genetic effect in *Capsicum* acted at a specific developmental stage during the course of fruit enlargement. Particularly interesting was that in the F2 the mature fruits were continuously variable from elongate to spherical so that the discrete event which gave rise to the allometric change was effectively masked. This occurred because the fruits also differed in the size to which they grew, the result of differences in additional genetic and environmental factors. Kaiser (1935a) pointed out that when the allometric slope was greater than unity, fruits became more elongated as they grew larger. The results showed that information about morphogenesis was essential to identify particular genetic contributions. Analysis of only the mature fruit would not have revealed the simple genetic basis of the allometric change that took place after fertilization, yet this change was the primary determinant of the shape difference.

Several striking differences in fruits of wild plants have been shown to have a simple genetic basis (fig. 1). Two interesting cases come from the Valerianaceae. Natural populations of the winter annual *Plectritis congesta*, which grows on rocky headlands in British Columbia, were found to contain plants bearing either winged or wingless fruits, a dimorphism subsequently shown to be controlled by a
single locus with the allele for winged dominant to that for wingless (Ganders et al. 1977). The wings more than triple the size of the individual fruits. Under experimental conditions, plants heterozygous at the locus were taller, heavier, and more branched suggesting that the polymorphism may be maintained by heterozygote advantage at the locus itself or at a linkage group marked by the locus (Carey and Ganders 1980). Similar fruit polymorphism also characterizes natural populations of Valerianella ozarkana, native to the central and southern U.S. (Eggers Ware 1983). The fruits of this species are either triple-keeled with prominent cilia along each keel or they lack the keels and are fusiform in shape without any pubescence (fig. 1). As in the related Plectritis, the two morphs appear to be governed by alternate alleles at a single locus with triple-keeled dominant to keelless (Eggers Ware 1983). The presence versus absence of “wings” on the fruits (achenes) of species of Coreopsis, in the Compositae, and whether the wings have an entire margin or are fimbriate (fig. 1) are also under monogenic control (Smith and Parker 1971; Smith 1973). In each of these cases, plants having the different fruit morphs have been assigned species status, but the genetic information led to changed taxonomic rankings.

Certain differences in plant architecture are also frequently attributable to one or two gene substitutions. Among these are changes in growth habit from determinate to indeterminate or vice versa, a characteristic change in many cultivated species (table 1). Another common phenotypic alternative is that between prostrate and erect habit, particularly in wild plants. Many maritime ecotypes are prostrate or procumbent, a habit considered adaptive to frequent high winds and salt spray common near coastal sites, whereas the inland populations are erect.
This alternative, which may be achieved by several genetic routes, is often governed by one or two gene loci (table 1).

Suppression of lateral buds by the action of two or three loci in the common sunflower *Helianthus annuus* (a tetraploid species) results in the development of the single massive central head of commerce (Hockett and Knowles 1970). The difference between erect and pendent fruit in *Capsicum* is controlled by a single gene (table 1); the same dichotomy also characterizes flowers of different species of *Aquilegia* and young heads of *Crepis* species, and in both cases is also monogenic (table 2).

Many single genes, mostly in cultivated varieties, have been identified that have correlated and presumably pleiotropic effects on more than one organ, usually leaves and petals or sepals. For example, in the Japanese morning glory *Pharbitis nil*, which normally has a three-lobed leaf and a funnel-shaped corolla, homozygosity for the recessive "maple-leaf" gene results in the development of a deeply incised five-lobed leaf and a division of the corolla into five petals: similarly the "willow" mutant has a very narrow leaf and the corolla is divided into five narrow petals (Imai 1930). Some of these pleiotropic genes also affect other leaf homologues (stamens and ovaries), often severely reducing fertility. Other genes in the species affect only one or the other organ.

Genes that affect both leaves and petals have also been identified in *Primula sinensis* such as "oak" which governs an increase in the depth of the sinuses on both organs, and "crimp" which changes the margins of the leaves, sepals, and corolla (Anderson and DeWinton 1935). As in *Pharbitis nil*, other genes affected one but not the other organ.

Different alleles of the S1 locus in *Nicotiana tabacum* affect the form of a number of plant organs. The dominant allele leads to the differentiation of long petals, long calyx teeth, points on the corolla lobes, long anthers, and elongated capsules, whereas plants homozygous for the recessive allele exhibit near opposite conditions (Stebbins 1959). The recessive *compacta* allele in *Aquilegia vulgaris* (European columbine) causes precocious secondary thickening of cell walls, which apparently inhibits cell elongation and brings about a compact bushy growth habit with brittle stems and unusual erect flowers (Anderson and Abbe 1933). The possibility remains in these examples that the character correlation results from tightly linked genes rather than a single locus. An unambiguous genetic test to discriminate very tight linkage from pleiotropy requires the recovery of a crossover product between the putative genetic units, but the appropriate test calls for the growing out of a very large number of progeny, often not possible with wild plants. Zohary and Imber (1963), however, were able to demonstrate that the differences between the longer, awned apical spikelets, and nonshattering spike of *Aegilops speltoides*, one of the presumed diploid parents of bread wheat, and the shorter *ligustica* spike (with its awned lateral spikelets that disperse individually) was governed by a tightly linked gene cluster since they found rare intermediate morphs in otherwise dimorphic natural populations.

Among the most divergent morphologies that characterize varieties within a single plant species are the six vegetables that have been developed from *Brassica oleracea* (Thompson 1976). Cabbage has numerous leaves overlapping its terminal
bud, Brussels sprouts have enlarged axillary buds, the kohlrabi has a swollen cormlike stem, kale has a fleshy marrow stem, and cauliflower and broccoli have thickened inflorescences and fleshy flower buds. Many of these differences appear to be controlled by two major genes as well as several loci with modifying effects (Yarnell 1956). Thus F2 segregations from a cross between kohlrabi and cabbage included both parental types and were readily accounted for by two major loci and a minor or modifying locus (Pease 1927). Hearting versus nonhearting cabbages differed by two loci with the latter trait dominant (Pease 1926).

Numerous other examples of discontinuous morphological phenotypes within single plant species, including both wild and cultivated plants, have been described in various summaries and reviews (Matsuura 1933; Knight 1947; Crane and Lawrence 1952; Yarnell 1956, 1965; Pelton 1964; Lippert et al. 1966; Meyer 1966; Rahcie and Roberts 1974; Janick and Moore 1975). The general findings were that character differences such as those listed in table 1 were governed by one or two genes with major effects; additional modifying loci were sometimes also identified.

GENETIC STUDIES OF MORPHOLOGICAL DIFFERENCES BETWEEN SPECIES

The genetic basis of morphological differences between species has been less amenable to analysis because incompatibility generally prevents the production of interspecific hybrids and, even when these are synthesized, they usually are fully or partly sterile. However, it has been possible to obtain segregating progenies from hybrids between a number of species that show marked morphological differences (table 2).

The data indicate that the genetic basis of morphological differences between species are of the same nature as those within species. However, an important problem often emerges in attempts to estimate the number of loci determining the genetic basis of particular interspecific differences. The finding that a character difference segregates simply does not mean that only one or two genetic changes were responsible for the production of the difference. A character which evolved by several steps from the ancestral expression can often be switched back to it by a single allelic substitution, for example, the reversion to hermaphroditism from dioecy (Westergaard 1958), and peloric mutants in Antirrhinum which mimic floral features of related genera (Stubbe 1959; and see below). Thus, in many cases, the available evidence does not permit the claim that a morphological difference necessarily evolved by only one or two genetic changes, although the potential for such evolution is clearly demonstrated.

The genetic studies of the columbine genus Aquilegia (Ranunculaceae) are particularly significant because only a few loci govern species differences in floral morphology, and these differences can be directly interpreted as adaptations to specific groups of pollinators (Prazmo 1965). The genus is divided into five species groups primarily on the basis of the position, length, shape, and color of petals and sepals. The characteristic floral structure of the columbines, found in all but one species, is the nectar-containing spur on each of the five petals. The spurs are
TABLE 2

MORPHOLOGICAL AND ARCHITECTURAL DIFFERENCES GOVERNED BY ONE OR TWO GENES WHICH DISTINGUISH SPECIES AND OTHER TAXA

<table>
<thead>
<tr>
<th>Species/Genus</th>
<th>Characteristic Differences</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aquilegia species groups</td>
<td>(Prazmo 1965)</td>
</tr>
<tr>
<td></td>
<td>- Spars hooked vs. straight</td>
</tr>
<tr>
<td></td>
<td>- Flower erect vs. nodding</td>
</tr>
<tr>
<td>Carthamus flavescens and C. tinctiorius</td>
<td>(cultivated safflower) (Imrie and Knowles 1970)</td>
</tr>
<tr>
<td></td>
<td>- Rosette growth duration short vs. long</td>
</tr>
<tr>
<td></td>
<td>- Leaf margin entire vs. lobed</td>
</tr>
<tr>
<td></td>
<td>- Seed heads shattering vs. nonshattering</td>
</tr>
<tr>
<td></td>
<td>- Achenes with vs. without pappus</td>
</tr>
<tr>
<td>Caryophyllaceae subfamilies</td>
<td>(Turrill 1940)</td>
</tr>
<tr>
<td></td>
<td>- Sepals free vs. united</td>
</tr>
<tr>
<td>Crepis eritensis and C. thomsonii</td>
<td>(Babcock and Cave 1938)</td>
</tr>
<tr>
<td></td>
<td>- Heads erect vs. nodding</td>
</tr>
<tr>
<td></td>
<td>- Achenes on the same head monomorphic vs. dimorphic</td>
</tr>
<tr>
<td>C. foetida and C. rubra</td>
<td>(Poole 1932)</td>
</tr>
<tr>
<td></td>
<td>- Heads erect vs. nodding</td>
</tr>
<tr>
<td>C. foetida ssp. foetida and ssp. commutata</td>
<td>(Babcock and Cave 1938)</td>
</tr>
<tr>
<td></td>
<td>- Paleae on floral receptacles present vs. absent (2 loci)</td>
</tr>
<tr>
<td>Galeopsis tetrahit and G. bifida</td>
<td>(both 4X) (Muntzing 1930)</td>
</tr>
<tr>
<td></td>
<td>- Incision in middle lap of lower flower petal present vs. absent (2 loci)</td>
</tr>
<tr>
<td></td>
<td>- Vasculature pattern differences in above structure (2 loci)</td>
</tr>
<tr>
<td>Haplopappus aureus and H. venetus</td>
<td>(Jackson and Dimas 1981)</td>
</tr>
<tr>
<td></td>
<td>- Ray florets present vs. absent</td>
</tr>
<tr>
<td>Lactuca graminifolia and L. canadensis</td>
<td>(both 4X) (Whitaker 1944)</td>
</tr>
<tr>
<td></td>
<td>- Leaf margin lobed vs. entire</td>
</tr>
<tr>
<td></td>
<td>- Life form annual vs. biennial</td>
</tr>
<tr>
<td>L. sativa and L. serriola</td>
<td>(Whitaker and McCollum 1954)</td>
</tr>
<tr>
<td></td>
<td>- Seed heads shattering vs. nonshattering</td>
</tr>
<tr>
<td>Layia discoidea and L. glandulosa</td>
<td>(Clausen et al. 1947; Clausen 1951)</td>
</tr>
<tr>
<td></td>
<td>- Ray florets absent vs. present (2 loci)</td>
</tr>
<tr>
<td>Lycopersicon esculentum and Solanum pennellii</td>
<td>(Tal 1967)</td>
</tr>
<tr>
<td></td>
<td>- Anther tip sterile or not (2 loci)</td>
</tr>
<tr>
<td></td>
<td>- Number of floral parts greater than 5 or 5</td>
</tr>
<tr>
<td></td>
<td>- Pedicel abscission zone intermediate in position or at base (2 loci)</td>
</tr>
<tr>
<td>Potentilla glandulosa ssp. nevadensis and ssp. reflexa</td>
<td>(Clausen and Hiesey 1958)</td>
</tr>
<tr>
<td></td>
<td>- Leaflets on leaf at base of inflorescence 3 vs. 5−7</td>
</tr>
<tr>
<td></td>
<td>- Branching pattern erect vs. divaricate (1−2 loci)</td>
</tr>
<tr>
<td></td>
<td>- Inflorescence open vs. dense</td>
</tr>
<tr>
<td></td>
<td>- Petals erect vs. reflexed (3 loci)</td>
</tr>
<tr>
<td></td>
<td>- Leaf rosette compact and drought tolerant vs. not so (3 loci) (Teeri 1978)</td>
</tr>
<tr>
<td></td>
<td>(This is probably the same character difference as winter-dormant or not according to Teeri [1978])</td>
</tr>
<tr>
<td>Streptocarpus subgen. eustreptocarpus, unifoliata and rosulata</td>
<td>species groups: (4X) (Oehlkers cited in Lawrence 1958)</td>
</tr>
<tr>
<td></td>
<td>- Rosette leaves single vs. many (2 loci)</td>
</tr>
<tr>
<td>Tropaeolum majus and T. peltophorum</td>
<td>(Whaley and Whaley 1942)</td>
</tr>
<tr>
<td></td>
<td>- Leaves orbicular vs. five-lobed (2 loci)</td>
</tr>
<tr>
<td>Ulmus glabra and U. montana</td>
<td>(Henry 1910)</td>
</tr>
<tr>
<td></td>
<td>- Leaves alternate vs. opposite</td>
</tr>
<tr>
<td>Urtica pilulifera and U. dodartii</td>
<td>(Correns cited in Sirks 1956)</td>
</tr>
<tr>
<td></td>
<td>- Leaf margin indented vs. entire</td>
</tr>
<tr>
<td>Viola tricolor and V. arvensis</td>
<td>(both 4X) (Clausen 1926)</td>
</tr>
<tr>
<td></td>
<td>- Growth habit erect vs. prostrate (2 loci)</td>
</tr>
<tr>
<td></td>
<td>- Labellum present vs. absent</td>
</tr>
<tr>
<td></td>
<td>- Petal large vs. small</td>
</tr>
</tbody>
</table>

This content downloaded from 142.150.190.39 on Fri, 16 Jan 2015 11:21:47 AM
All use subject to JSTOR Terms and Conditions
TABLE 2  
(Continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td>Viola pedatifida and V. sororia (both 4X) (Clausen 1951)</td>
<td>Leaf margin entire vs. highly dissected (2 loci)</td>
</tr>
<tr>
<td>Zea: maize and teosinte; (Galinat 1971)</td>
<td>Female spikelet paired vs. single (1–2 loci)</td>
</tr>
<tr>
<td></td>
<td>Phyllotaxy 4-ranked vs. 2-ranked (1–2 loci)</td>
</tr>
<tr>
<td></td>
<td>Female spikelet pedicellate vs. sessile (2 loci)</td>
</tr>
</tbody>
</table>

absent from the primitive A. ecalcarata, which instead has small nectar-containing “pockets” on its petals.

Segregation patterns in the F2 progenies between A. ecalcarata and other species revealed that modification of the pocket into a spur was determined by a single gene, with spurred dominant to spurless (Prazmo 1965). My observations indicate that the spurs grow outward from the petal only after the other floral parts (stamens, styles, etc.) have differentiated. In A. formosa, for example, the ellipsoid-shaped bud attains approximately 6–8 mm in length before spur elongation begins. It may be that the addition of the spur was “feasible” because the gene action which initiates it occurs very late in the differentiation of the flower and, consequently, does not interrupt earlier processes of organ formation.

A second gene locus was found which governed whether the spurs were straight or curved at their tip, a characteristic which distinguishes species groups. Yet a third locus controlled the orientation of the entire flower, nodding or erect, a significant factor in pollination since flowers which are more or less nodding are visited by bees and bumblebees or by hummingbirds whereas erect flowers are visited by moths and butterflies.

In marked contrast to the mode of inheritance of these traits, the length of the spurs and the degree of their curvature showed continuous variation in the F2, presumably reflecting the action of a large number of genes. Other characters of size and length (stamen length, fruit length, and seed weight) also showed polygenic inheritance. This result reveals that different categories of morphological characters in plants have distinct modes of genetic control. Structural or architectural changes tend to be monogenic whereas changes in length or weight are polygenic.

The Aquilegia example also illustrates how certain genetic changes may acquire ecological significance and lead to effective reproductive isolation. Subsequent selection for specific matches between particular pollinators and spur length and curvature was presumably based on additional modifying loci. But such possibilities emerged because of the simple genetic changes that initiated the structures. The situation may be formally similar to the major mutations in mimetic butterflies which are later “improved” by numerous minor genetic modifications (Turner 1981).

A second important example concerns the evolution of the massive ear of maize (Zea mays) often considered to represent the most radical structural departure in the higher plants. Thus, “No one at the conference (1981 Chicago Macroevolution...
Conference) was prepared to challenge Stebbins’ remark that the most striking morphological novelty among the higher plants was the flower head of *Zea mays*, which is largely the result of selective breeding under domestication and is known to be under the control of many genes with small effects” (J. M. Smith 1981). The quotation reflects the widespread presumption that large changes in phenotype are evidence of similarly large changes in genotype. However, the novel morphology of the maize ear apparently evolved as a result of changes in a small number of characters, each governed by one or two genes.

Maize appears to have evolved from annual teosinte, a closely related grass native to Mexico, with which it shares the same chromosome number and homology and with which it is fully interfertile (Galinat 1971; Beadle 1980). Very recent electrophoretic studies have shown that maize (*Zea mays subsp. mays*) is essentially indistinguishable from one of the annual teosintes (*Zea mays subsp. parviglumis*; Doebley et al. 1984). Teosintes and maize have similar vegetative structure but have strikingly different female inflorescences (Weatherwax 1955). In teosinte, the seeds are produced from sessile female flowers (spikelets) which are borne singly in individual cavities formed within segments of a short rachis. In maize, the large ear terminates a short lateral branch thought to have resulted from extreme shortening and condensation of the lateral teosinte spikes into a single massive structure (Galinat 1971).

The remarkable transformation of teosinte to maize seems to have been accomplished by a small number of genetic changes. Beadle (1980) suggested that an early step involved a dominant mutation at the tunicate locus which reduced the hard teosinte fruit cases to a series of shallow cupules with the kernels enclosed within soft husklike glumes. In the tunicate form, the rachis has less tendency to shatter on ripening and the kernels can be threshed free of the chaffy bracts. Galinat (1971, 1977) described several genes linked to the tunicate locus that control additional traits affecting cupule development such as orientation of the spikelets, and the formation of abscission layers. He proposed that only three further genetic changes were necessary to complete the essential morphological transformation to maize, each governed by one or two loci (Galinat 1971). The domestication of maize also involved other changes such as increases in kernel size, increase in row number, and changes in leaf width, tillering, and height, but these changes are considered by Galinat (1971) to have only secondary significance in a developmental sense.

Beadle (1980) showed that it was possible to recover plants bearing the parental types of female inflorescence in a very large F2 progeny (nearly 50,000 plants) grown from a hybrid between teosinte and maize. He found that approximately 1/500 segregants resembled one or the other parent, suggesting that about five major and independently inherited factors could account for their differences. Unfortunately, this possibility was not validated by growing out F3 progenies.

Parental types for most of the individual characters had also been recovered in an earlier small F2 progeny (n = 127; Collins and Kempton 1920) between maize and the more distantly related Guatemalan teosinte, now called *Zea luxurians* (Doebley and Iltis 1980). Collins and Kempton noted that the characters “showed the greatest freedom of recombination . . . all combinations of characters ap-
peared . . . there appeared to be no incompatible combinations” (p. 36). This observation suggests that many developmental patterns in maize and teosinte must be closely similar even though their mature female inflorescences appear very different. However, the appropriate morphogenetic studies have not been carried out which might test this possibility.

Perhaps the most ambitious attempt to estimate a total number of genes responsible for morphological differences between two plant taxa was the monumental study by Clausen and Hiesey (1958) on the genetics and ecological responses of subspecies of *Potentilla glandulosa*. The study involved growing out clones of parents, F₁ hybrids, and F₂ segregants in three Californian transplant gardens at sea level (Stanford), 1,400 m (Mather), and 3,050 m (Timberline), and measuring 19 characters on each individual clone over a period of years. The cross reported in fullest detail was that between a subalpine form of ssp. *nevadensis* originating from the east slope of the Sierra Nevada Mountains of California (3,050 m) and a foothill form of ssp. *reflexa* (760 m). The estimates of gene number were based on the assumption that the phenotypic differences between the parents were governed by multiple genes with equal and additive effects so that F₂ segregation frequencies could be matched to the expansion of the binomial formula.

The analysis suffers from a number of technical problems such as inadequate partitioning of environmental and genotypic components of variance, frequent transgressive segregation indicating that the additivity assumption was violated, inadequate character definition leading to problems in scoring, and likely character overlap (length was measured on 4 different organs). Although these problems limit the validity of the estimates of the total number of genes involved, the study provides an immense amount of usable information. The most relevant result for the present review was the finding that the apparent number of gene loci governing a given character difference reflected its morphological category. Thus the F₂ segregation frequencies revealed that the five characters which are important in the taxonomy are each governed by one to three loci (table 2). These “key” characters involved discrete phenotypic alternatives: petals erect versus reflexed; branching pattern erect versus spreading; and inflorescence open versus dense. In contrast, differences in weight of the fruit and length of the petals, sepals, leaf, and stem showed continuous F₂ variation and seemed to be controlled by large numbers of loci, results similar to those in *Aquilegia*.

A similar finding was also evident in the analysis of hybrid progenies between *Lycopersicon esculentum* (cultivated tomato) and the wild *Solanum pennellii* (Tal 1967). These species differ in many morphological characters, but they can be readily hybridized and their hybrids are partly fertile. Tal reported the mode of inheritance of eight morphological differences, including three taxonomically significant characters: whether the anthers terminate in a long sterile tip (*Lycopersicon*) or are blunt and terminate in a small round pore (*Solanum*); the location of the pedicel abscission zone (intermediate in *Lycopersicon* or at the base in *Solanum*); and the number of flower parts (variable in *Lycopersicon* or always five in *Solanum*).

The different expressions in the former two characters were found to be con-
trolled by two loci each, and the difference in the latter character by a single locus. However, four “ratio” characters (style length/anther length; corolla lobe width/length; sepal length/corolla lobe length; and terminal leaf segment width/length) had complex inheritance patterns suggesting control by five to nine loci, depending on the particular character. The increase in estimated gene number for these characters almost certainly reflects their artificiality in a developmental sense, and underlines the importance of character definition.

One of the few coordinated genetic and developmental studies of a species difference was carried out on the leaf shape of *Tropaeolum*, the garden nasturtium (Whaley and Whaley 1942). The leaf of *T. majus* is broadly orbicular in outline whereas that of *T. peltophorum* is five-lobed and smaller than that of *T. majus*. Analysis of an F₂ progeny between them revealed that the leaf shape difference was controlled by two gene loci designated L/1 and U/u. Plants with the double recessive genotype llUu were acutely lobed like the *T. peltophorum* parent, and plants with either L-u or L uu genotypes were orbicular. Plants with llU- exhibited a novel, round-lobed outline.

The juvenile leaves in all four types were identical in appearance: acute-lobed and miniature. Double-log plot comparisons of growth along the midline of each leaf lobe against that along each sinus demonstrated that the several genotypes had different allometric constants correlating growth in the lobes and sinuses. In the round-lobed type, the sinuses grew faster than the lobes, and in the orbicular types, the sinuses grew very much faster than the lobes. In the acute-lobed leaf, the allometric constants established in the juvenile leaf were simply maintained until maturity. The increased growth of the sinus regions in the orbicular leaves also resulted in their attaining a larger size compared to the other leaf types. Anatomical studies revealed differences in cell size in the juvenile leaves which correlated with the differences in mature leaf shape. Regions destined to have greater proportional growth such as the sinuses in the orbicular leaf had many more cells (smaller in size) than other regions. Since all cells expanded to similar final size, those parts of the leaf with more cells expanded further.

In several cases, morphological differences that initially seemed to delimit genera were later shown to be controlled by one or two gene loci. One case involved the presence of paleae (bracts) on the receptacles of reproductive heads of *Rodrigia commutata* (Asteraceae) (Babcock and Cave 1938). *Rodrigia* proved to be interfertile with *Crepis foetida* which lacks paleae, and the presence versus absence of the paleae to result from allele substitutions at two loci (table 2). The crossing evidence was used to reduce the taxonomic rank of *Rodrigia* to that of a subspecies of *C. foetida*. A similar character difference is also known in *Crepis capillaris* (table 1). Receptacular bracts are unusual in *Crepis* and are regarded as primitive features in the family. Their presence in taxonomically advanced species such as *C. foetida* suggests they represent atavistic mutations (Stebbins 1950, p. 493).

A second case is that of a rare serpentine endemic in California, *Roxira serpen-
tina*, also a member of the Asteraceae, which lacks ray florets and consequently does not have ray achenes enfolded in the phyllaries, a feature which excluded it
from known genera. However, *Roxira* proved to have the same chromosome number and to be interfertile with *Layia glandulosa*, a widespread Californian species with eight large and showy ray florets (Clausen et al. 1947; Clausen 1951). Analysis of an F2 progeny grown from their hybrid revealed that presence versus absence of the ray florets was controlled by two gene loci. Thus, the unusual morphology of *Roxira* did not justify a generic status and it was assigned to *Layia* (*L. discoidea*). The rayless form also differed from its relative in several other morphological traits, suggesting it had a lengthy period of evolutionary independence. The *Rodrigia* and *Roxira* examples document how certain morphological differences may be very misleading in the absence of genetic data.

Monogenic control of the presence versus absence of ray florets has been documented in *Haploappus aureus* and *H. venetus* (Jackson and Dimas 1981). In this example, the genetic information led to the inclusion of both species in the same section, whereas previously they had been assigned to different sections of the genus. Of greater genetic interest was that the presence versus absence of the rays was monogenic, whereas the length of the rays behaved as a quantitative trait.

Genetic information about other types of floral characters used to distinguish genera has also been obtained from study of induced mutations, particularly in the garden snapdragon *Antirrhinum majus* (Stubbe 1959). Known as peloric mutants, they cause modifications of stamen number, both increases and decreases, and/or changes in floral symmetry, usually from zygomorphic (bilateral or irregular) to actinomorphic (radial). Mutants of this type were known to Linnaeus (Gustafsson 1979).

The snapdragon mutant *transcendens* has stamen number reduced from four to two and also a reduced number of petal lobes, character changes which have taxonomic significance in other genera of the family. The mutant *neohemiradialis* has an increased stamen number and radial symmetry, both characters typical of *Verbascum*. The mutant *fistulata* has a reduced corolla limb with a tubular configuration similar to that characteristic of the related genus *Rhinanthus*. These and other mutants isolated by Stubbe generally showed substantial variability in their initial phenotypic expressions. However, backcrossing to wild races of *Antirrhinum*, followed by selection for the mutant character, yielded stabilized types in only a few generations.

Such changes in floral symmetry, even from strongly zygomorphic to radial types, can occasionally be found on single individuals, especially toward the end of growing seasons, suggesting that genes of this type may act to overcome developmental thresholds (Wardlaw 1968). Their evolutionary significance is obvious since they might provide the first step toward novel morphology. Grant (1975, p. 98) offered a reasonable assessment of them. “An adaptively valuable macromutation appearing in a natural population, and showing variable expressivity in the early generations, might mark the beginning but only the beginning of an important deviation from the ancestral stock. Selection for the mutant phenotype would necessarily involve selection not only for the macromutation gene but also for additional modifier genes which stabilize its expression.”
QUANTITATIVE VARIATION AND GENE NUMBER

In addition to the many discrete morphological differences which are simply inherited in plants, other traits show continuous variability and appear to be influenced by large numbers of loci with individually slight effects. These traits are often measured as components of yield, particularly in agricultural contexts, and have to do with size, weight, and number. Many of them represent end products of growth such as height, leaf length, fruit size, and seed number or weight. Characters of this type are often responsive to factors which affect the general physiological state of the plant; consequently, genes which affect whole plant development often influence their expression.

Breeders are well aware of these general interactions on yield and its components. Wallace et al. (1972, p. 124) state, “A maximum estimate of gene number affecting yield is to assume that all genes of a plant affect yield. This maximum estimate is probably closer to reality than the minimum estimate. About any gene which affects photosynthesis or partitions photosynthate by diverting it from one metabolic pathway to another, which includes almost all genes, influences yield to some extent.” The realization that yield components are influenced by diverse physiological and morphological processes leads the quantitative geneticist to assess all loci in a population that contribute to the genetic variance of such characters even though many of them do so only as a consequence of their general effects on growth and vigor. Thus it is not unexpected that metric characters are found to be typically influenced by five to ten or more genes (Lande 1981).

Plant evolutionists also wish to identify how many genes contribute to the difference in a particular trait that distinguishes two populations or taxa. But they emphasize the developmental and physiological bases of the trait itself, and seek to identify particular ontogenetic steps which are responsible for specific differences in character expression rather than factors which operate through general influences at the whole plant or whole organ levels.

Important evidence regarding how genes affect metric or otherwise complex characters has been obtained by developmental studies. A recent analysis in bread wheat has identified a direct biochemical input to a quantitative morphological difference. In the 1950s, “dwarfing” genes from the variety Norin 10 were incorporated into many high-yielding wheat lines, but the initial attempts to determine the numbers and chromosomal locations of the genes were unsuccessful because final plant height was found to be influenced by many genes in addition to the dwarfing ones (Law and Gale 1979). The situation was clarified when it was shown that Norin 10 and related strains were insensitive to exogenous applications of gibberellins, the opposite of most other wheats in which its application leads to marked elongation of stems and leaves. The semidwarf plants were found to have high endogenous levels of the growth substance, suggesting its metabolism was blocked. This caused the applied gibberellin to stimulate tillering rather than elongation (Gale and Marshall 1975). Insensitivity to gibberellin led to the identification of the responsible genes and thereby redefined the quantitative difference in height as a qualitative response to a particular growth substance (Law and Gale 1979).
A different problem has been to distinguish the action of a novel mutation from the subsequent utilization of genetic and developmental information already available in the genome. For example, in "hooded" barley, the presence of a single dominant mutation leads to the development on the lemma of two extra florets separated by a rachislike structure bearing two lateral appendages, with the lower floret having inverted polarity (Stebbins and Yagil 1966). Prior to the genetic analysis, this complex structure, designated a "hood," had been thought to reflect numerous genetic changes.

Stebbins and Yagil found that the entire structure appears to be differentiated from a proliferation of relatively small epidermal and subepidermal cells on the lemma surface which are oriented in several planes rather than parallel to the lemma axis as in normal development. The unoriented cells form a meristematic dome or cushion that resembles an early stage in the normal development of spikelet primordia. By identifying these histological attributes, they demonstrated that the mutant gene interferes with the timing and orientation of cell divisions in the lemma, and that this leads to the formation of the primordiumlike tissue mass. Presumably its presence calls into play already available epigenetic information that carries out the differentiation of the unusual hood structure. The mutant gene itself does not in any sense specify the additional florets and appendages.

Corolla size in Nicotiana has been a favorite quantitative character since East (1916) used it to establish the rules of quantitative inheritance. In 1950, H. Smith presented an important analysis of hybrid progenies between the small-flowered N. langsdorfii and the large-flowered N. sanderae. In both species, corolla development proceeds in two stages. Initially, elongation of the corolla tube greatly exceeds that of the corolla limb. Shortly after anthesis, a definite turning point is reached after which tube elongation nearly stops and limb elongation accelerates. By plotting limb and tube lengths on a double-logarithmic grid, Smith found that in both species each elongation step was characterized by the same relative growth rate for the two dimensions (fig. 2). However, the species differed in the proportion of tube to limb in the early bud stage, and in the extent of tube elongation that occurred prior to the turning point.

A very large F2 progeny (N = 931) was grown which segregated for these parental differences, although parental corolla sizes were not recovered. Both the F1 and F2 progenies exhibited the same relative growth rates for the two stages of elongation (before and after the turning point), indicating that the genetic basis of this aspect of their development was the same. Smith presented the complete data set for 20 representative F2 plants as well as the F1 and both parents, making it possible to look for additional relationships not discussed in his paper. I found that the ratios of tube length to limb length at the turning point and at maturity were recovered in the F2 (fig. 3). This suggests a genetic control of the close correlation between them and, although F3 data were not presented, the difference between the species in this trait is probably governed by few loci. The finding is significant because it reveals that even though the parental differences in mature corolla size were not recovered, several developmental inputs to the difference were recovered. In addition it shows that corolla size is a composite character and this is why it is influenced by a large number of genes.
PLANT MORPHOLOGY AND GENETICS

80

70

60

50

/ 30

20

/ 10

Fig. 2.—Relative growth curves for corollas of *Nicotiana langsdorfii* (L), *N. sanderae* (S), and their F₁ hybrid (modified from Smith [1950]).

4.0

4.0

Y = 0.509x + 0.545

r = 0.794

3.0

3.0

Fig. 3.—Ratio of corolla tube length to corolla limb length at turning point on abscissa plotted against the same ratio at maturity on the ordinate. Those for *N. langsdorfii* (L), *N. sanderae* (S), and their F₁ are identified on grid; the remaining 20 points are F₂ plants. Calculations made from raw data provided in Smith (1950).
Many of the F2 plants displayed corollas with novel sizes and configurations, for example, short tubes and long limbs, which arose from new combinations of tube/limb proportions in the bud and relative durations of the two stages of expansion. The genes from the two species could be recombined in the F2 without apparent disharmony suggesting developmental similarities between their corollas “in spite of the markedly different phenotypes” (Smith 1950, p. 210). Smith also pointed out that the corolla size and configuration in other species of Nicotiana reflected changes in the same developmental inputs: bud proportions, allometries, extent of elongation before and after the turning point. Information of this type is valuable because it can be used to identify which developmental process may have been modified during the evolution of the corollas of different species.

Certain results of Anderson and Ownbey (1939) revealed a likely input to the corolla size differences. They examined anatomical features in N. langsdorffii and N. alata which is one of the parents of N. sanderae and similar to it in morphology. A close correlation was discovered between cell and organ size; the smaller flowered N. langsdorffii had smaller cells and did not respond to exogenous applications of auxin whereas N. alata had larger cells and longer organs and exhibited additional elongation upon auxin treatment (Nagel 1939). Unfortunately, coordinated analyses utilizing both genetic and developmental perspectives have not been carried out in Nicotiana, yet exactly this is required to elucidate the evolution of new morphologies.

In contrast to the results of such studies, limited as they are, conclusions about gene number derived solely from statistical analyses of means and variances of yield components in segregating progenies seem less helpful in understanding evolutionary divergence. For example, Lande (1981) used data from the classic long-term selection experiment for high and low oil and protein contents in maize kernels to support the hypothesis that large evolutionary changes usually occur by the accumulation of multiple genetic factors with relatively small effects. He concluded that 16 to 22 genetic factors and probably many more contributed to the divergence between the high and low oil lines. Dudley (1977), using different calculations and data from additional generations, estimated that 54 effective factors were responsible for the same divergence. Such calculations cannot elucidate the nature of the factors involved, but it is not unlikely that the effects of a very high proportion of them operate through many different metabolic processes of biosynthesis, transport, and partitioning. It is not clear that a similar multiplicity of factors should be expected in cases of large morphological changes.

Lande (1981) also used data from Powers’ (1942) study of the inheritance of fruit size difference between two varieties of tomato and suggested that at least 10 genetic factors were involved. Tomato fruit weight is an extremely complex character that is influenced by many environmental and developmental processes. Rick and Butler (1956) presented a thorough and lucid discussion of the measurement and estimation problems. They pointed out that fruit weight varies on the same plant, with most of the variance between fruits within the same cluster, probably reflecting competition for available nutrients. Fruit weight is also affected by the number of clusters per plant, the number of locules per fruit, pollination and seed development, and other factors. They noted that Powers
probably used too few fruits per plant (only 1 in the segregating progenies) for accurate representation of its fruit size, thereby increasing variance estimates.

Houghtaling (1935) found that varietal differences in tomato fruit sizes were already established in the very early ovary primordia since large-fruited varieties had larger primordia with more cells than small-fruited ones. Later Whaley (1939) showed that the size of the ovary primordium depended on the size of the apical meristem on which it was initiated, with larger primordia developing on larger apices and smaller ones on smaller apices. Both large and small fruits were similar in several aspects of their development. In both, anthesis marked the end of cell division and the beginning of cell enlargement, and the two phases had similar relative durations in both varieties (Houghtaling 1935). The varieties differed in that the two phases were carried on longer in the large-fruited ones (Sinnott and Dunn 1935).

Developmental information of this sort is relevant to the analysis of fruit size inheritance. Rick and Butler (1956) reported that parental ovary sizes but not fruit sizes were recovered in a large F2 progeny from a hybrid between varieties differing more than 100-fold in mature fruit size. This suggested that the ontogenetically earlier trait was controlled by fewer genes. The finding is consistent with the previously described results of Kaiser (1935a) on Capsicum. These examples illustrate that fruits and seeds as measured at the end of their developmental pathways are influenced by genetic factors that affect growth of the entire plant as well as particular processes during their own often lengthy maturation. While statistical analysis can lead only to the conclusion that many factors have small effects, developmental analysis can resolve many of the discrete components which contribute to the final product and can demonstrate, at least in some favorable cases, that these discrete components can generate large changes having evolutionary significance.

**PLOIDY AND GENE NUMBER**

Estimates of the number of gene changes governing morphological divergence also depend on the ploidy level of the species examined. Nilsson-Ehle, who is credited along with East for having formulated the multiple factor hypothesis, studied the intensity of pigmentation of bread wheat kernels which vary from white to very dark red, and showed that three loci were responsible for expression of the maximum difference between full red and white. Any one of the genes segregating by itself gave a 3:1 ratio of red to white, two loci gave a 15:1 ratio, and all three a 63:1 ratio. Progeny tests revealed a clear association between the number of genes for redness and the relative intensity of the red color. The study became the textbook example of genes which cause similar and cumulative effects, thereby providing a Mendelian interpretation of continuous phenotypic variation.

An important aspect of Nilsson-Ehle’s pioneering study which is often neglected is that bread wheat has three gene loci affecting kernel color because the species is a hexaploid that combines the genomes of three diploid species. The three loci are presumably orthologous copies of a single ancestral locus. Poly-
ploids are expected to have more genes than diploids and consequently the ploidy level of species utilized for gene number estimates must be specified.

CONCLUSIONS

The present review of genetic studies of morphological characters in flowering plants establishes the following points. (1) Many differences, particularly those of presence versus absence, and those of changed structure, shape, or architectural orientation, are frequently governed by one or two genes; discrete phenotypic alternatives are common. (2) Differences in length, width, weight, and number (yield components) generally show continuous patterns of variation in segregating progenies and have been accounted for by many genes often with individually slight effects; however, a significant though unknown proportion of these genes probably influences character difference only indirectly via general effects at the whole organ or whole plant levels. (3) Differences in the mature expression of single structures can be independently influenced by genes that affect allometric constants, growth durations, or other discrete features during their development, and by genes that affect size and weight. (4) Differences that are expressed early in ontogeny may exhibit simple patterns of inheritance even when the mature expression shows complex inheritance. (5) Genes may affect only the structure or orientation of single organs or their parts or may affect more than one organ, though whether the latter correlations reflect pleiotropy or tight linkage of genes with slightly diverged functions remains difficult to assess. (6) Genes (and chromosome segments) from different species or differently adapted populations may frequently be recombined without disharmony in morphogenesis. (7) Estimates of gene number are expected to be higher in polyploid than diploid species.

Few rules have previously been formulated to describe the genetic basis of morphological evolution in plants. This is because character differences in natural populations were generally examined on a one-by-one basis, usually only in terms of their mature expressions, and without consideration of their ontogeny. In general, botanists did not make use of the important results of Sinnott and his colleagues which showed that genes control growth schedules and that complex divergence between mature features may result from a simple change early in their development.

Plant evolutionists also had a priori expectations about the genetic basis of character divergence which came from the NeoDarwinian consensus that evolution was mostly gradual and reflected selection of mutations having relatively slight effects on the phenotype. Since this perspective was coupled with vigorous rejection of models such as Goldschmidt’s (1940), which advocated that species differences depended on mutations with large and dramatic phenotypic effects, there was little interest in developmental timetables or their genetic basis. Although mutations that lead to large morphological differences appear to be more common in plants than previously acknowledged (e.g., Stebbins 1950, p. 102; 1974, p. 7), perhaps reflecting the unique developmental features of plant morphogenesis, as proposed in this review, this does not mean that the establishment of such divergence is accomplished by only few genetic events. Considera-
tion of the establishment phase, a problem in ecology, suggests that novel morphological features that initially provide imperfect adaptations are likely to be refined by selection at additional modifying loci.

Many appropriate studies are feasible in plants because morphologically diverse species can be hybridized. Indeed one of the most interesting aspects of higher plant evolution is the very great extent of natural hybridization (Raven 1976; Raven and Axelrod 1978; Grant 1981). The developmental similarity underlying divergent morphological phenotypes is evident in the vigor and fertility often observed in segregating progenies from hybrids between ecological races and perennial species. The classic examples include the hybrids in *Achillea millefolium* between the dwarf race from the Aleutian Islands and the giant Selma (central California) race (Hiesey and Nobs 1970), the well-known hybrids in *Potentilla glandulosa* (Clausen and Hiesey 1958), *Ceanothus* (Nobs 1963), Hawaiian species of *Bidens* (Gillett and Lim 1970), and *Dubautia* and other tarweeds (Carr and Kyhos 1981).

Also indicative of similar developmental patterns are the multiple examples of independent evolution of traits such as annuality from herbaceous perennials, hummingbird-pollinated species from bee-pollinated ones (Grant 1959; Raven 1979), predominant self-pollination with its frequent reduction of flower size and proportions from larger-flowered outcrossing species (Stebbins 1957), and secondary woodiness including small trees from herbaceous colonizers, particularly on islands (Carlquist 1974). Grant (1981, p. 486) comments, “The proneness of plant lineages to change over from one adaptive zone to another is correlated with the relative simplicity of the gene systems involved. Contrasting character combinations adapted to different ecological niches may be found at the racial level of divergence in some instances. Therefore change-overs or quantum shifts which are major in ecological terms but relatively minor in genetic terms, can occur repeatedly in different phyletic lines under the guiding influence of parallel selection alone.”

That perhaps 40% to 50% of the flowering plants are allopolyploids (Lewis 1980) constitutes additional evidence of widespread developmental similarity. The ability of two diploid genomes which govern divergent morphology, physiology, and biochemical attributes to occupy a common tetraploid nucleus, without upsetting processes of gene regulation and morphogenesis, cannot easily be interpreted otherwise.

In summary, many recent statements that morphological differences between species reflect large numbers of genetic changes are often misleading when applied to plants. The number of genes depends on the specific character examined, and accurate estimates require precise statements describing the ontogenetic basis of character divergence. A clear distinction is called for between genes that have direct effect on the development of character differences and those with indirect effects. In plants many characters of interest in evolution represent presence versus absence of structures, or changes in structure, shape, or position. Divergence may be initiated by changes in one or two genes; additional genes may act to modify the expression of such traits. Extrapolation from the events and processes that take place within species to those between species seems clearly warranted in
plants. There is no evidence of genetic revolution at any level; genes from different species or ecologically diverse races may frequently be recombined without disrupting morphogenetic processes.

Accurate specification of the number of genes making major contributions to character divergence is prerequisite for estimating rates of evolution and the extent of genetic divergence at different taxonomic levels. Although it is premature to require biochemical specifications because of our ignorance of genetic and developmental interactions, substantial information can be obtained in plants by studies of the ontogenetic and anatomical details of character expression when these are coordinated with genetic analyses. General inferences about the number of genetic changes responsible for morphological diversity will remain unreliable in the absence of such evidence.

SUMMARY

The genetic basis of differences in morphology within and between flowering plant species is reviewed in order to elucidate how many genetic changes are responsible for the evolution of new characters. Two broad morphological categories are evident. Differences in structure, shape, orientation, and presence versus absence are frequently discrete and appear to be governed by one or two genes. Differences in dimensions, weight, and number usually exhibit continuous variation and are influenced by numerous genes, though many of them probably act only indirectly via general effects at the whole organ or whole plant levels. Although it is difficult to specify the relative contributions of the two morphological categories during evolutionary divergence, it is clear that discrete character differences are more common in plants than in animals. I propose that their prevalence in plants is a direct consequence of the open, less integrative, and plastic patterns of plant morphogenesis which permit large changes in morphology on the basis of relatively few genetic changes. Morphological divergence among genera or families of flowering plants may reflect many fewer genetic changes than is the case for similar taxonomic levels of higher animals. Accurate estimates of the number of genes responsible for character divergence require knowledge of the ontogenetic and anatomical details of character development and these must be coordinated with genetic analyses. Until this knowledge becomes available, general conclusions about the number of genetic changes responsible for morphological diversity are premature.

ACKNOWLEDGMENTS

Much of the research for this article was done while I was on sabbatical leave and visiting the Botany Department, Duke University. I am grateful to the faculty of the department for their stimulation and hospitality and particularly to Janis Antonovics. Some of the material of the review was presented in symposium papers given at the AIBS Meetings in State College, Pennsylvania, in August 1982, and at the Darwin Centennial held at the University of London, in November 1982. I am grateful to Vera S. Ford for her competent, careful, and useful comments which helped to clarify many parts of the article.
LITERATURE CITED


DeWinton, D., and J. B. S. Haldane. 1933. The genetics of Primula sinensis. II. Segregation and interaction of factors in the diploid. J. Genet. 27:1–44.


Goldschmidt, R. B. 1940. The material basis of evolution. Yale University Press, New Haven, Conn.


PLANT MORPHOLOGY AND GENETICS

Lande, R. 1981. The minimum number of genes contributing to quantitative variation between and within populations. Genetics 99:541–553.
Matsura, H. 1933. A bibliographical monograph on plant genetics. 2d ed. Hokkaido Imperial University, Sapporo.


——. 1982. Darwin to DNA, molecules to humanity. Freeman, San Francisco.


