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The genetic basis of plant form

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Plant architecture is relevant to a number of questions in population biology because it affects the number, size, and fecundity of individuals. Architectural differences in wild plants have frequently been described and are presumed to have a genetic basis because the differences are maintained when the plants are grown in uniform gardens, but little genetic research has been done. Studies in crop plants, however, provide substantial information about how plant form can be genetically manipulated. They show that the architecture of many crops has been successfully modified by making a small number of genetic substitutions that affect shoot length, flowering node, branch presence and orientation, habit, and growth determinacy. The changes occur at the level of metamers (leaf–axillary bud–internode) and become multiplied by iteration into the characteristic architecture of the plant. Metamer growth and iteration are tightly coordinated by genetic factors that operate at the level of the whole plant. Evidence supporting this hypothesis includes single gene control of coordinated changes among successive internodes, genetic control of production of metabolites or signals that move from mature tissues to shoot growing points, and allometries connecting organs arising from the same meristem. Since different plant architectures are associated with differences in fitness, information on the genetic basis of the morphological and physiological characters that cause the architectural differences will elucidate how fitness characters evolve.

Introduction

The primary data in plant demography are counts of individual plants over time. In clone-forming plants (as many as two-thirds of the common perennial species in Great Britain according to Abrahamson (1980)) such counts have uncertain meaning because the number of individuals need not equal the number of genotypes. Since correct genotype assignment is essential for the analysis of population turnover, individual fitnesses, and the likelihood of adaptive response to environmental change, plant demographers have had to consider how shape or architecture affects the size, number, and distribution of individuals.

Much attention has been paid to the iterative or metameric structure of the plant body (White 1979, 1984; Harper & Bell 1979; Harper 1981) because it provides the architectural basis for the vegetative fragmentation of clonal plants and establishment of the ramets as separate individuals. The 'rapprochement' of morphology and ecology is significant because it may stimulate more intensive investigations to identify the morphological traits contributing to fitness differentials within populations and to the adaptive differences between geographically separate populations. To facilitate this effort, I review present knowledge of the genetic control of plant architecture, and discuss the usefulness of the concept of plant metamerism from the standpoints of genetics and development.

Morphological divergence and genetic analysis

Plant development is characterized by an open and plastic pattern of morphogenesis in which growth and organ differentiation are initiated at meristems that occur at the apices of all shoots and roots. Other meristems function in actively growing organs such as intercalary meristems in the internodes and leaf sheaths of many monocotyledons and the marginal meristems of dicotyledon leaf blades. In some plants new meristems can also be generated after predation or injury. Cell divisions in the shoot apical meristem lead to the serial formation of lateral primordia from which leaves, buds, or floral parts develop. Further cell divisions in the apical and subapical meristems contribute to the increase in shoot length.

The repetitive structure of the plant shoot, based on the node–leaf–axillary bud–internode complex (the metamer of White (1984)), permits the plant to adjust its morphology through time according to local environmental conditions. The responses appear to be mediated by locally synthesized growth substances as well as those produced elsewhere in the plant body and need not be related to the response or condition of other meristems on the same individual. The result is often a marked plasticity that can lead to many genotypes having a similar appearance or single genotypes displaying multiple phenotypes as a function of age, size, or microhabitat. Such capability is important for stationary organisms, which must adapt to their environment and respond rapidly to both advantageous and deteriorating conditions.

The central role of meristems in plant development may be a major factor facilitating the evolution of morphological differences which are discrete or discontinuous in expression rather than gradual (Gottlieb 1984). Thus many differences in morphological characters involve presence versus absence of structures, or sharp alternatives in shape, and architectural position or orientation. Other morphological characters differ in continuous fashion, showing changes in dimensions, mass, or numbers, the classical components of agricultural yield. The two categories of morphological change appear to involve different numbers of genetic changes (Gottlieb 1984). Discrete changes are governed by one or two genes. Continuous changes, which often involve end products of growth such as height, leaf length, or seed number, are influenced by numerous genes with slight effects individually, though many probably act only indirectly via general effects on growth and vigour. The categories are not exclusive alternatives but rather represent the extremes of a spectrum of morphological changes. Indeed in complex characters, the differences may include aspects that are discrete and others that are continuous. For example, in *Aquilegia* a single gene governs presence versus absence of petal spurs but the length of the spurs is influenced by numerous genes (Prazmo 1965). Before genetic studies of architectural differences are done, the specific underlying morphological changes must be identified.

Architectural differences in wild plants are frequently described, and are presumed to have a genetic basis since the different phenotypes are maintained when grown in uniform gardens, but only a few genetic analyses have been made. These include studies in *Layia* on orientation of branches and presence versus absence of central stem (Clausen 1951) and prostrate or erect habit in several species (references in Gottlieb 1984). No studies appear to have been reported on clone-forming plants. The paucity of genetic research on wild (non-domesticated) plants reflects the complexity of the analysis, and the fact that most geneticists working with plants study agricultural species in which true-breeding lines are available (or can be constructed) and large progenies readily grown.

Consequently, it is necessary to study the results of research with crops to learn how genes affect plant architecture. Varietal differences within crop species include a large array of different architectural forms. Breeders have determined the genetic basis of these differences and have been able to design plants for particular environments by transferring genes and combining genes in novel combinations. Thus, although cultivated fields are not similar to natural habitats, the results with crops reveal how plant phenotypes can be genetically manipulated and thereby help to inform us about what is possible. Morphological changes in crops will certainly have counterparts in wild plants, and there is no reason to believe that the types of genetic control will be much different.

One of the most critical problems in a genetic analysis is the design of test environments that enhance or magnify the effects of particular genes or gene combinations that might otherwise be obscured by environmental variables. For example, flowering time in pea (*Pisum sativum*) was originally thought to be a quantitative trait affected by an additive polygenic system. However when F_2 plants from a cross, later shown to involve the *Sn*/*sn* allelic pair (see below), were grown under short days and mild temperatures, the segregation was sharp with *Sn* conditioning flowering at a high (late) node and *sn* at a low (early) node (Murfet 1977*a*). The segregation was blurred if cool temperatures were used or if the photoperiod was increased, and the allelic difference disappeared altogether if the plants were vernalized and exposed to continued cold nights. The incorrect conclusion that flowering was largely polygenic in pea resulted from growing plants under cool temperatures in field conditions. 'The problem is to devise methods and circumstances which will enable us to trek back from the phenotypic (visable) periphery of gene action, where the effects of many genes are often integrated into a single parameter, through the maze of interlocking biochemical wheels in the primary level of gene action where every gene has an individual effect' (Murfet 1977*a*).

Another profound problem is how to decide which phenotypic character is the correct one for genetic analysis. Plant demographers emphasize life-history traits such as survivorship, age of reproduction, and fecundity, and the plant breeder often measures only yield. Characters of this sort are abstract constructs that add up an uncertain number of genetic inputs and are closely affected by the environmental conditions in which the plants are examined. Some plant breeders are acutely aware of these problems. 'Genes do not exist for yield *per se*. Genetic control is indirect, through control of the physiological components . . .' (Wallace *et al.* 1972) and, one may add, the morphogenetic components. To make sense of genotypic diversity in wild plant populations it will be necessary to pay close attention to the primary components of morphological development and physiological performance.

One of the best examples of phenotypic analysis known to me is the identification of the primary determinant of shape difference between elongate and spherical fruits of *Capsicum annuum* (red pepper) by Sinnott & Kaiser (1934) and Kaiser (1935). They plotted increase in ovary length against increase in ovary diameter on a double logarithmic plot and found that the allometric line connecting length and diameter changed slope sharply following fertilization in the elongate type but maintained a constant slope in the spherical type (figure 1). The change in slope segregated as a single gene difference. But the mature fruits were continuously variable from elongate to spherical, depending on the duration of their growth (when allometric slope is greater than unity, the fruits become more elongate as growth continues), effectively masking the discrete allometric change (figure 2). Analysis of the mature fruits only, the likely procedure in most quantitative genetic studies, would fail to reveal the simple but significant developmental input to the shape difference.

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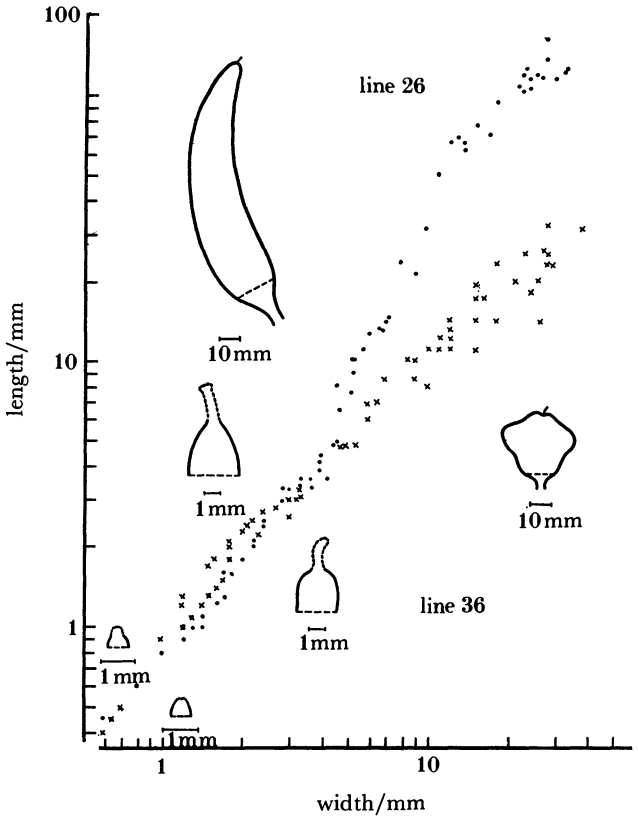

FIGURE 1. Double logarithmic plot of length against width from ovary primordia to mature fruit in two varieties of pepper (*Capsicum annuum*) with elongate and approximately spherical mature fruit shapes. Note change in allometry in the elongate variety, at an ovary width of approximately 5 mm, which is initiated shortly after anthesis (from Sinnott & Kaiser 1934).

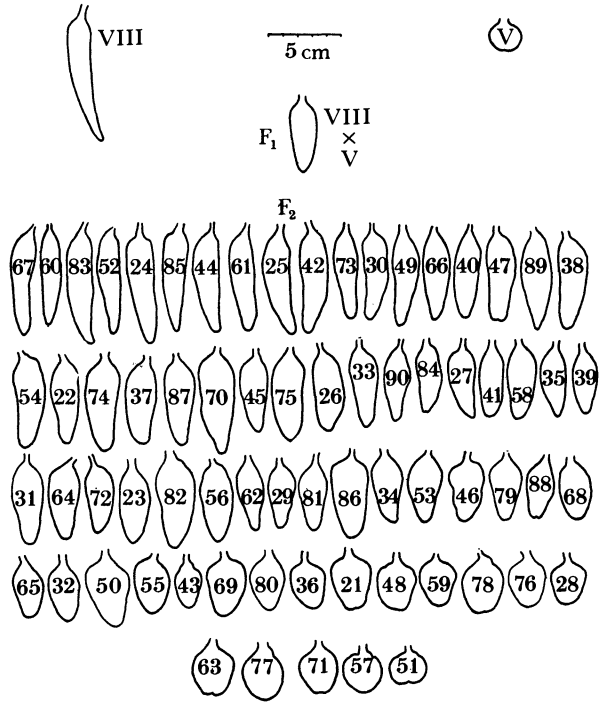

FIGURE 2. Trace drawings of typical mature elongate and spherical fruits from two varieties of pepper (*Capsicum annuum*), the F_1 hybrid between them, and F_2 progeny. Note absence of discrete segregation in shape (from Kaiser 1935).

Genetic modification of architecture in crop plants

Remarkable phenotypic changes have been made in the architecture of rice (*Oryza sativa*), tomato (*Lycopersicon esculentum*), pea (*Pisum sativum*), and wheat (*Triticum* spp.) by very simple genetic substitutions involving a few major genes. Subsequent analyses of the interactions of these genes in the diverse genetic backgrounds required for particular environments often led to incorporation of additional gene modifications. In the following case studies, I emphasize the consequences of the initial changes brought about by the genes that had large effects.

Rice

Probably the most significant genetic modification of plant architecture was the development in the early 1960s of the dwarf varieties of wheat and rice (Coyne 1980). In rice, three- to fourfold increases in yield were achieved by making use of a single recessive gene from Taichung Native 1, a Taiwanese Indica variety, which conferred a number of beneficial effects: a short, stiff, wide, upright leaf; short internodes; and a high number of short panicles (Aquino & Jennings 1966). The dwarf varieties averaged about half the height of standards. Dwarf stature had been previously known in rice, but the phenotype had not been useful because it invariably exhibited complex patterns of inheritance and was subject to marked environmental influence. The great value of the Taichung Native 1 gene was that it had a major effect on stature and was not correlated with undesirable agronomic traits. This made it possible to transfer the gene to already acceptable varieties (Aquino & Jennings 1966).

The increased yield associated with the gene was clearly related to the new architecture. The erect leaves permitted a more uniform distribution of incident radiant energy over the entire leaf canopy, including the lower leaves, which resulted in substantially higher accumulated dry seed mass per unit leaf area per unit time (reviewed by Wallace *et al.* 1972). The short plant stature also conditioned a strongly positive response to nitrogen fertilization, and without the lodging that nitrogen typically caused in tall varieties. In addition, the dwarfs partitioned a larger proportion of total photosynthate to their seed rather than to additional vegetative structures. But the yield advantage of dwarf stature did not simply reflect a novel plant form. The advantage became evident only with appropriate cultural practices and only in pure stand since the dwarf plants were unable to compete with tall plants for light.

Processing tomato

Most varieties of tomato normally have indeterminate growth and sprawl indefinitely, continuing to flower and mature fruits further and further out on the stem and branches. The decision in California in the 1950s to design machines to harvest tomatoes for the processing industry required major changes in tomato architecture and in the pattern of fruit set and ripening. The primary changes depended on the use of the recessive *sp* gene (Rick & Butler 1956) which confers a compact, orderly, and determinate growth form (Rick 1978), and makes possible the harvesting of an entire field at one time.

The stems of varieties with the *sp* gene develop only one or two leaves between successive inflorescences and terminate in an inflorescence whereas normal stems have three leaves between reproductive structures. Branches of such varieties terminate their growth at approximately equal distances from the central stem and the plant flowers abundantly in short time

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period. Both normal and *sp* plants produce a similar number of leaves before the first inflorescence and show similar rates of growth.

The *sp* gene is often used in conjunction with the recessive gene *j* which conditions the absence of the joint in the fruit pedicel, at which fruit abscission normally takes place. This causes the fruit to remain tightly attached to the calyx. The inflorescences of *j* also develop leaves in addition to flowers, resulting in plants with a dense proliferation of leaves, branches, attenuated stems, and frequent unfruitfulness (Rick & Savant 1955). However, both problems are relieved by combining *j* with *sp* and when this is done the attachment of the fruits remains sufficiently strong that the vibration associated with mechanical harvesting does not cause the fruit drop which may occur when *sp* is used alone.

Major genes controlling branching habit and fruit position in the related genus *Capsicum* (peppers) have also been identified and may prove useful to developing a mechanical harvesting system (McCammon & Honma 1984).

Dried pea

The availability of two major recessive genes in pea that change leaf structure and thereby canopy structure has stimulated a number of studies to improve the yield in the dried pea crop (Hedley & Ambrose 1981). The pea leaf of normal plants is pinnately compound and composed of two large foliaceous stipules, one or more pairs of subterminal leaflets, and terminal tendrils. Incorporation of the *af* gene converts the leaflets into tendrils and the *st* gene reduces stipule size. When both genes are present in the homozygous state, the phenotype is said to be 'leafless', and when the *af* mutation is present by itself, the phenotype is designated 'semi-leafless'. Both types have improved standing ability compared with peas with the usual foliage because their greater number of tendrils interweave and provide support for the plants. The crop dries more rapidly and has a reduced risk of disease. Light penetration through the canopy is also improved.

Anatomical studies (Meicenheimer *et al.* 1983) showed that the multiple tendrils of *af* plants develop from numerous secondary primordia that form at the position of the leaflet primordia. The tendrils develop from radial marginal meristems like those of normal tendrils, and both adaxial and marginal meristems are absent. Thus the *af* gene appears to establish tendrils in new positions without causing changes in their appearance. The *st* gene reduces stipule size by reducing the duration of cell division in both the abaxial and adaxial stipule meristems. Knowledge of the ontogenetic basis of mutant development is important because it assigns the time and location at which the morphological changes are initiated.

The leafless plants appear to have efficient net CO_2 fixation and are able to translocate sufficient photosynthate to the developing pods (Hedley & Ambrose 1981). At relatively low planting densities (16 plants per square metre) canopies produced by leafless plants have half the total dry mass attained by leafed plants but at densities in excess of 100 plants per square metre the leafless canopies were more productive (Hedley & Ambrose 1981). The leafless phenotypes, however, showed a reduced relative growth rate compared with the leafed plants and as a result produced less biomass per unit area after 60 days, reducing their value as a crop (Pyke & Hedley 1983). In contrast growth of the semi-leafless type (with normal stipules) was similar to that of leafed plants, suggesting to Pyke & Hedley (1983) that it might provide a better crop phenotype than the double mutant. Their proposal has been supported by independent studies carried out in Wisconsin (Wehner & Gritton 1981).

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The attempt to define a crop phenotype for dried peas, like the research with dwarf rice and determinate processing tomatoes, has involved substantial analyses of interactions between plants and the environment in which they are grown. The genetic manipulations proved generally straightforward compared with the intensive investigations of the crop ecology that followed, since after the genes were incorporated into a wide range of genetic backgrounds the breeder had to assess how the new genotypes performed in different environments.

Population biologists who undertake genetic analysis of the differences between plants already growing in nature have to tackle the reverse problem. Because the plants they study could generally be considered successful, though perhaps divergent in fitness, their task is to identify the genetic basis of the morphological and physiological traits that confer success. This might be done by examining the relative performance of F_2 segregants and identifying the plants that differed greatly in fitness. Correlating the fitness differences with differences in specific characters would permit 'the character states to be "mapped" onto fitness', as suggested by Antonovics (1984).

Shoot elongation

Other studies in pea concern the effects of gene interaction on shoot elongation and furnish one of the most detailed genetic analyses of plant architecture. In this species, internode length is governed by five major loci and internode number by five additional loci. Most of the phenotypes produced by different combinations of alleles at the ten genes have been examined in a series of elegant studies reported in Murfet (1977*a*, *b*), Reid *et al.* (1983), and Reid & Murfet (1984).

The genes governing internode length are associated with gibberellin (GA) metabolism. The tall *Le*/dwarf *le* alternative was one of the classic traits studied by Mendel. Homozygosity of the recessive *le* allele reduces internode length by 40–60 % and causes the stem to have a zigzag appearance. Biochemical studies, making use of gas chromatography and mass spectrometry to identify GAs, established that *le le* plants cannot carry out the conversion of GA_{20} to GA_1 in the shoot apical region, presumably because they lack the necessary enzyme (Ingram *et al.* 1983, 1984). The unavailability of GA_1 is the specific cause of reduced internode length, but how this is accomplished is not understood. Of interest is that GA_{20}, which is an intermediate metabolite in the elongating shoot, is apparently the active GA in the elongating fruit pod. (GA_1 is not present in this organ.)

Alleles at the *La*, *Cry*, *Lm*, and *Na* loci also affect internode length and, in different combinations with *Le* or *le*, produce a series of length phenotypes. The anatomical effects of *La* and *Cry* mimic the effects of applied GA, which is thought to mean that they are also involved in GA metabolism (Reid *et al.* 1983). The *na* allele eliminates the phenotypic difference between *Le* and *le* and may block an early step in GA biosynthesis (see below). The five genes illustrate both the complexity of genetic control of internode length and the ease with which single gene substitutions can change the phenotype.

A comparable set of genes affecting internode lengths has been identified in maize (*Zea mays*). Mutants at these genes cause dwarfing by reducing internode lengths as much as five- to tenfold, and at least four of them appear to block particular steps in the pathway leading to synthesis of GA_1, which Phinney & Spray (1982) believe is the only active GA in maize shoot elongation. One of these mutants (d_1) prevents the conversion of GA_{20} to GA_1 (Spray *et al.* 1984). Its resemblance to *le* in pea suggests the two gene loci may be homologous.

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Node number also affects shoot length. In pea, five loci govern node number by affecting the time of transition from vegetative to reproductive growth. The loci act to determine whether plants are early developing (flowering at a low node), intermediate, or late developing (flowering at a high node) (Murfet 1977*b*; Reid & Murfet 1984). Separation of the phenotypes governed by the five loci depended on close attention to conditions of cultivation. Complete diagnosis required growth under both short and long days and particular temperature régimes. *Sn* and *Hr* govern response to photoperiod perhaps by controlling the synthesis of a flowering inhibitor in the shoot. Gene *E* promotes flowering by reducing expression of *Sn* in the cotyledons. The four alleles identified at *Lf*, in homozygous condition, result in a minimum flowering node of 15, 11, 8, or 5, respectively, indicating a remarkable precision of effect, postulated to occur by influencing the sensitivity of the shoot apex to flowering stimuli (Murfet 1975). The *veg* gene at the fifth locus prevents flowering over a wide range of photoperiod and temperature régimes and overrides the effects of the other loci. However, segregation at *Sn* and *Hr* was still identifiable in *veg* plants by attention to pleiotropic effects other than flowering such as the appearance of the apical bud, production of lateral branches, or change in growth rates. The differences among the *Lf* alleles, however, were completely obliterated by *veg* (Reid & Murfet 1984).

It is not unusual for architectural traits to be affected by genes that govern the expression of a number of characters. It is sometimes possible to separate the several effects of these genes by placing them on different genetic backgrounds (Williams 1960). Such experiments probably occur in nature frequently following hybridization and could be studied once major genes are identified.

In contrast to the mutants that block the synthesis of GA in the pea shoot, an apparent lesion in the GA-sensing mechanism or the presence of GA antagonists may be responsible for the semidwarf stature of many high yielding wheats. In the 1950s dwarfing genes from the Japanese variety Norin 10 were incorporated into many wheat cultivars. Initial attempts to determine the number of genes conditioning the dwarf phenotype were not successful because final plant height was influenced by many genes in addition to the dwarfing ones (Law & Gale 1979). The situation was clarified when it was shown that Norin 10 and related strains exhibited a modified response to exogenous GA, which in other wheats causes stem and leaf elongation, but in these strains stimulated tillering without affecting elongation (Gale & Marshall 1975). The semidwarf plants were found to have high endogenous levels of GA. The recognition that they were insensitive to applied GA led to the identification of the responsible genes, now designated *Rht1* and *Rht2*. The result demonstrated that the quantitative difference in plant height was actually a qualitative difference in response to GA (Law & Gale 1979).

Other genes affecting plant form

A number of other genes that affect architecture in various crop plants have been identified: determinacy in soybean (*Glycine max*) (Hartung *et al.* 1981; Bernard 1972); climbing in dry bean (*Phaseolus vulgaris*) (Kretchmer *et al.* 1979); growth habit in lentil (*Lens culinaris*) (Ladizinsky 1979); determinacy in muskmelon (*Cucumis melo*) (Paris *et al.* 1984); leaf number and determinacy in cucumber (*Cucumis sativus*) (Miller & George 1979); internode length in watermelon (*Citrullis lanatus*) (Liu & Loy 1972); and branching in sunflower (*Helianthus annuus*) (Hockett & Knowles 1970). For a general review of other genes modifying crop plant architecture see Coyne (1980).

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Discussion

The studies described above demonstrate that the architecture of many crop plants has been successfully modified by changing only a few morphological traits such as length and number of internodes, presence and orientation of branches, habit, and determinacy. Breeders have studied these traits because genes that affected them in large ways were available and they could be placed into a range of different genetic backgrounds to assess how they affected yield. But the characters examined represent only a small proportion of those that influence plant architecture. Little or no information, for example, is available about the genetic basis of branch angle, location of abscission zones, pattern (relative timing) of lateral bud release, relative rates of branch and stem elongation, orientation of parts (nodding, horizontal, erect), or ability to form adventitious roots.

Genetic analyses of the differences in expression of these and other characters will have to be done to understand how changes that operate at the level of particular metamers are multiplied into the architecture of the whole plant. Interactions between the two phenotypic levels were not directly addressed in the crop studies. Nevertheless, they do furnish important evidence. Nearly all of it was consistent with the hypothesis that the growth and differentiation of metamers are tightly coordinated by factors that operate at the whole plant level. Evidence for the lack of metamer independence can be found in the studies of changes in internode length, graft transmissibility, and also from considerations of allometric correlations.

Reid & Murfet (1984) described a cross in pea between a 'cryptodwarf' with genotype *le la cry*^{c} *Na Lm* and a tall line with genotype *Le La cry*^{c} *Na Lm* which segregated four distinct height classes in the F_2 in the 9:3:3:1 ratio expected for two independently assorting loci. The stem internodes of plants in each of the four classes showed different patterns of length increase (figure 3). The significant point is that within each pattern, successive internodes elongated in a regular and correlated fashion until a particular maximum length was attained, and then successive internodes maintained this same length. Thus the effect of a single gene was able to coordinate changes involving many internodes. Similar correlated increases in successive stem

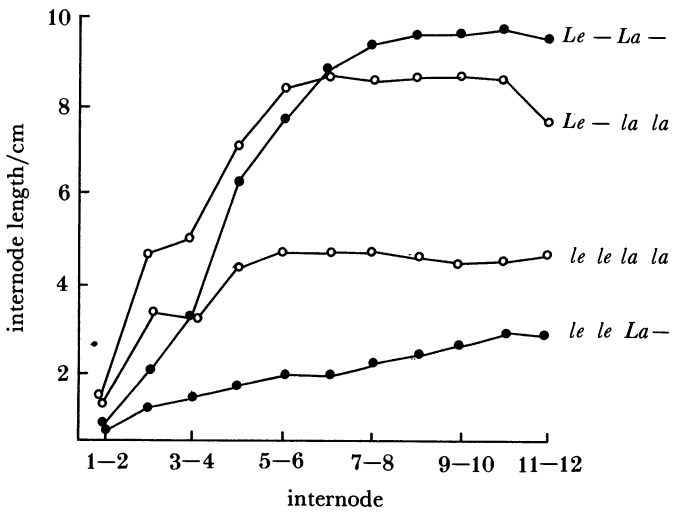

Figure 3. Mean internode length against internode number in an F_2 progeny in pea (*Pisum sativum*) segregating for *Le/le* and *La/la* loci (modified from Reid *et al.* 1983, figure 2).

internode lengths of different genotypes were also documented in *Cucumis melo* (Paris *et al.* 1984) and *Trifolium repens* (Booysen & Laude 1964). But in these latter examples the genetic situation is less certain.

I am aware of only a single example in which the length of a particular internode is controlled by a gene locus independently of other internodes on the same stem. The recessive gene *eui* (elongated uppermost internode) in rice nearly doubles the length of the uppermost internode but has no affect on other internodes (Rutger & Carnahan 1981). Since panicle length is also increased in plants with the *eui* gene, it is possible that the increase in uppermost internode length is a pleiotropic consequence of increased levels of GA produced in the larger panicles. The unusual rice internode is in the same position as the long internode basipetal to the flowering node in *Trifolium repens* which was shown to be subject to GA influence (Booysen & Laude 1964). GA biosynthesis presumably generally uses substrates from different parts of the plant.

A second example of correlative differentiation is the study of graft-transmissibility associated with the *Na* locus in pea (Reid *et al.* 1983; Ingram *et al.* 1983). *Na* was found to be transmissible across grafts but its effect was lost when the recessive allele *na* was substituted. In contrast, transmissible effects were not found for any alleles at the *Le*, *La*, and *Cry* loci. The transmissible substance in *Na* plants, which is produced in largest quantities in mature stem and leaf tissues, was able to promote elongation in dwarf *na* scions. Since the addition of *na* eliminates the phenotypic difference between *Le* and *le* plants (long versus short internodes), and since *Le* is responsible for the specific conversion of GA_{20} to GA_1 in the upper shoot, a final step in GA biosynthesis, it is likely that the *na* allele blocks the transmission or synthesis of a signal or a substrate that comes from the mature tissues. Thus *na* appears to govern an early step in GA metabolism. Such evidence also suggests whole-plant correlation.

Consideration of allometric relationships reveals additional examples of developmental correlations. A remarkable allometry is that between leaf number and trunk diameter in trees (Rothacher *et al.* 1954; see also White 1979). Among tree species, for trunks of a given diameter leaf number is inversely related to leaf size (White 1979). A more apparent allometry is that between the size of a plant organ and the size of the meristem from which it develops, a relationship first noted by Sinnott, according to Grafius (1978). Grafius (1978) added the valuable addendum that organs that develop from the same meristem are less subject to genetic manipulation than those arising from different meristems. For example, the areas of successive leaves on a single culm of barley show strong positive correlations, with the coefficients decreasing with distance between leaves (Fowler & Rasmusson 1969). Grafius (1978) pointed out that the area of such leaves could not be changed independently by breeding. Likewise the rate of growth in length and width of the same organ (fruit shape or leaf shape) could not be independently selected. Their shapes might be changed by selecting a different allometric constant between length and width or by changing the duration of growth. In contrast allometries between organs arising on different meristems are more readily changed by genetic manipulations because they are largely physiological (hormonal control, source–sink, inhibitory, etc.) and change with the environment. Grafius (1978) gives the example from a breeding programme in barley in which he was able to uncouple number of tillers per unit area from number of seeds per head. The developmental evidence in these examples suggests that although 'a plant is a population of parts' (Harper 1984), the growth and differentiation of the parts are coordinated to a large extent.

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The primary reason why plant population biologists should study the genetic basis of architectural differences is to find out the number of gene changes they represent. This information is necessary to account for differences in fitness that can be assigned to architectural characters. The literature contains many excellent examples of such fitness differences (Dirzo & Sarukhán 1984) but, since the genotypes that exhibit them have not been intercrossed in a genetic design, the number and type of differences among the genotypes are not known. Our ignorance in this area is nearly complete.

The many studies in crop plants indicate that genetic analyses can also be done in wild plants. Since the expression of architectural differences is often discrete, many of them may prove to have simple patterns of inheritance (this review and Gottlieb 1984). The likelihood of detecting genes with large phenotypic effects will be increased by careful attention to the morphological components including their anatomy and development as well as to devising environmental conditions that maximize genotypic differences in response.

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