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Physiological consequences of modular growth in plants

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Modular plants are structurally stable systems. Perturbations in the genome that arise during growth (somatic mutations) are, it is conjectured, detected and eliminated by diplontic selection at the apical meristem. This requires accurate control, which, it is suggested, results in the accuracy of module arrangement, or phyllotaxy. During differentiation vegetative modules tend to retain autonomy and totipotency; the differentiated state is maintained by a constant flux of signals between parts. This enables damage to be repaired and differentiation to be adjusted to the availability of resources. The differentiation of modules to form flowers, on the other hand, is achieved by loss of totipotency, by hierarchical organization of the genotype, and by tissue-specific signals between parts. Elaborate, but fixed-function, structures can be produced in this way.

The physiology of modular plants is best described in terms of cooperation, not competition, between modules. The theory of multicomponent systems predicts that as plants increase in size, structural stability of growth will be lost unless the connectance between modules is kept below a critical value. Experiments confirm that the exchanges of assimilate between modules are limited, but not fixed (the system can adapt to damage). The distribution system is vulnerable to exchanges that might benefit individual modules but that would reduce the inclusive fitness of the genome. Such exchanges are controlled by the organized senescence of branches, leaves, fruit and ovules.

Introduction

Within the walls of each plant cell three genomes (nuclear, mitochondrial and chloroplast) cooperate for their mutual survival. For life in the open sea, the optimal phenotype can be constructed from a single planktonic cell, whose activities can be controlled by the diffusion of mRNAs from a single nucleus. In most other environments, small phenotypes are not optimal, and here multicellularity evolved. Small propagules were still required for dispersal, and since their parents were sessile, they needed mechanisms for autonomy. Modular growth enables the young plant to attain autonomy while it is still small, and yet, by repetition of parts, to reach a large final size. This paper considers the mechanisms involved in (i) initiation, (ii) differentiation, (iii) regulation, and (iv) death, of modules. The analysis is developed through a series of propositions.

Initiation of modules

I use the term module to refer to a repetitive unit of construction, for example, a single cell in a filamentous alga, leaf plus stem plus axillary bud in a higher plant.

Proposition. *An organized, modular, phenotype is the product of a set of organizing principles or rules.*
Lindenmayer (1982) has shown that the growth of various species of filamentous alga, such as *Chaetomorpha* and *Ulothrix*, can be simulated by a computer provided with a set of rules for 'cell' division, polarity sensing and differentiation. The rule for cell division requires that the

two daughter cells develop differently, one remaining mitotic, the other differentiating and becoming non-mitotic. This implies the existence in filamentous algae of a mechanism to determine the polarity of division and differentiation. Laboratory studies have identified such a mechanism; it involves electric fields (Jaffé & Nuticelli 1977; see also Trinci & Cutter, this symposium).

In the higher plants, cell division is largely confined to specialized regions, which constitute only a small proportion of the plant body. The meristematic growth habit enables delicate thin-walled dividing cells to be protected against drought, predators and mechanical collapse, at the cost of a substantial reduction in growth rate. While it is still in the ovary, the number of cells in an embryonic plant of *Daucus carota* L. (carrot) doubles every 24 h (Gray *et al.* 1984). If cell division continued to occur throughout the plant's body, an embryo would grow to maturity (about 2^{28} cells; C. C. Hole, personal communication) in 28 days. In another fortnight it would contain 2^{42} cells and weigh about 2.5 t. Localizing cell division to meristematic areas limits the plant's potential growth rate, a handicap in variable environments, but it opens the possibility of modular growth. Modular growth required, however, the evolution of further mechanisms.

PROPOSITION. *In multicellular plants, modular growth requires the repetitive establishment of autonomy and a secondary axis of polarity among the cells leaving the apical meristem.*

Division of labour can be achieved without such mechanisms. In the roots of modern Gymnosperms and Angiosperms, different functions are assigned to different ages of tissue; in the dimorphic root systems of some amphibious plants such as mangroves, *Typha* and *Ludwigia*, each meristem is assigned permanently to the production of a particular set of tissues. But such patterns are relatively inflexible. They have proved to have only a limited potential compared with the repetitive production of parts from a single apical meristem, that is, modular growth.

In modular plants the repetitive processes at the apical meristem take place with remarkable precision and regularity, resulting in accurate phyllotaxies. Two approaches have been used to study the rule systems of phyllotaxy: geometry for the state-rules and computer simulation for the process-rules. Geometric analysis of the properties of regular lattices shows that the set of regular (stable) arrays on the surface of a cone or cylinder can be described by a function of two parameters, θ and h (Erickson 1983). θ is the angle subtended between two successive elements of the genetic spiral, h is the vertical distance between them. Phyllotaxies resemble a Feigenbaum system (Feigenbaum 1980) where h is the bifurcation parameter, and θ is the dependent variable. Stability is only attainable within rather narrow limits; for example, a regular 3:5 phyllotaxy can be maintained only between the points ($h = 0.11$, $\theta = 135.9°$) and ($h = 0.29$, $\theta = 142.1°$) (Erickson 1983). Thus close control is required of the parameters θ and h.

The computer simulations use reaction–diffusion equations to model the processes in shoot apical meristems. The apical meristem is represented as a two- or three-dimensional net of communicating cells, continually increasing in size. Some sort of morphogenetic signal, either mechanical (strain) or chemical (activator or inhibitor), is assumed to be generated in each cell and to be communicated across the net with a characteristic decay function. Local minima arise in the resulting morphogenetic field, and as growth continues it is possible, by appropriate choices of parameter values and boundary conditions, to make the successive minima adopt a regular configuration (Ridley 1982). Again, strong control of the parameters is a pre-requisite.

Phyllotaxy is a good taxonomic character; it is under strong genetic control and is little affected by perturbations in the environment. The value of θ is maintained with remarkable

precision; for example, in *Epilobium* the standard error in θ was 0.26° (Meicenheimer 1981). In a meristem of 100 μm diameter an angular deviation of 0.26° corresponds to a distance of only 0.2 μm, about the diameter of a single cell. This is probably an underestimate of the precision of the initiation process, for the fluctuations in θ are in part systematic, not random (Kumazawa & Kumazawa 1971).

In discussing the 'mysteries' of phyllotaxy, Thompson (1917) remarked that 'I, for my part, see no subtle mystery in the matter other than what lies in the steady production of similar growing parts similarly situated at similar successive intervals of time'. What can be the adaptive value of such steadiness? Since leaves can twist on their petioles, I suggest that if an accurate phyllotaxy has an adaptive value it is more likely to relate to conditions during the initiation of primordia, than to their subsequent life; it seems unlikely that accurate phyllotaxy is simply a means for optimizing light-interception. Now apical meristems, in addition to their main function of initiating modules, have various second-order functions:

PROPOSITION. *Extensive modular growth requires long-lived apical meristems. These require a mechanism for preserving the integrity of the genome, by removal of mutant cells from the germ line as they arise (that is, diplontic selection).*

The shoot apical meristem is the principal source of new nuclei within the phenotype. It is therefore largely responsible for maintaining the integrity of the genome. In tissue culture the plant genome is remarkably labile (Scowcroft 1984), but in the intact plant it is, with few exceptions (Durrant 1962; Whitham & Slobodchicoff 1981; Cherfas 1985) very stable; many cultivars that are vegetatively propagated appear to maintain their genetic integrity indefinitely. How is this stability achieved? Klekowski & Kazarinova-Fukshansky (1984) suggest that mutant cells are removed from the germline by a mechanism of diplontic selection, which operates at the apical meristem. Diplontic selection requires a means of determining the type (same or mutant) of young cells, for example by comparing the local value of a morphogenetic field with an internal reference value (Wolpert 1981). This leads to the following conjecture.

PROPOSITION. *The patterning of primordia at the apical meristem is the by-product of systems that regulate the value of h and θ with time. The primary function of these mechanisms is in diplontic selection; they maintain a stable morphogenetic field at the shoot apical meristem.*

According to this conjecture diplontic selection requires stable morphogenetic fields; and the occurrence of tightly regulated phyllotaxies in the shoots of modular plants reflects this stability. Since leaves, roots, etc., rarely contribute to the next generation they would not be expected to exhibit diplontic selection or accurate control of cell lineages.

Plants and crops can be considered as populations of modules (Bazzaz & Harper 1977; Hardwick & Milbourn 1967). In the analysis of the growth processes of such populations 'birth' comprises module initiation and emergence from the apical bud. The rate of initiation of primordia sometimes varies with age (Romberger & Gregory 1977) but it generally responds rather little to variations in the external environment (Berg & Cutter 1969). The rate of emergence of modules from the apical bud does vary with the environment (Milford *et al.* 1985). Hence the following:

PROPOSITION. *Accommodation of plant growth rate to the supply of environmental resources is achieved by variation in the rate of module growth and in the number of functional meristems, rather than in the rate at which modules are initiated at each apical meristem.*

Thus variation in, for example, nutrient availability results in variation in the size of the plant (that is, size and number of modules) at flowering and harvest; the dates of flowering

and harvest (a function of the rate of module initiation) remain relatively invariant. This is in accordance with predictions from models of life-cycle characteristics (Cohen 1971).

DIFFERENTIATION OF MODULES

In stable environments large phenotypes are at an advantage. A small phenotype can be enlarged by the dichotomous branching of one axis into two, each daughter being an identical copy of the parent axis. As the copying process continues, the dimensions of the overall structure will increase linearly; but the number of growing points will increase exponentially. So the growing points on the periphery of the plant will become increasingly, and impossibly, tightly packed. This leads to the following:

PROPOSITION. *A mechanism for differentiation, that is, a mechanism that ensures that the daughters of a branching do not all behave similarly, is an essential requirement in the production of large, branched, modular structures.*

A mechanism for meristem 'dormancy' meets this requirement. It also confers the ability to reconstruct damaged structures (see below). Growth of a modular structure without differentiation imposes other problems. A variety of analyses suggest the following.

PROPOSITION. *Module differentiation is organized in such a way as to optimize a cost–benefit function.*

This proposition is supported, for example, by cost–benefit analyses of branch disposition and light interception (Honda & Fisher 1978), of canopy height and light interception (Iwasa *et al.* 1984), of rhizome branching angle and soil exploration (Bell 1979), of the costs and benefits of sun or shade leaves (Bazzaz 1979), of vegetative or floral branches (Smith 1984), of long and short shoots (Wilson 1966), and of elastic versus geometric similarity in trees (MacMahon & Kronauer 1976).

Cost–benefit analyses have severe limitations: for example, it is mathematically impossible to maximize for more than one variable at the same time; in natural selection, history and chance and other unknowns also enter the equations. Nevertheless, it has proved easier to analyse the costs, benefits and trade-offs of various differentiation patterns than it has to identify the mechanisms by which they are achieved. In trees, two broad groups can be distinguished. The first group, typified by, for example, some species of *Araucaria*, are stoutly constructed trees; the tissues are long-lasting or 'evergreen' and the developmental sequences appropriate to each position in the structure are determinate and almost invariant. Invariant differentiation may be achieved by mechanisms such as topophysis (patterns of differentiation determined by position) and by hydraulic dominance (patterns of xylem flows determined by xylem resistance) (Zimmermann 1978).

The developmental processes that characterize the second group appear to have arisen later in evolution (Corner 1967). These plants rely less on mechanical strength and invariant patterns of development, and more on stand-by or 'dormant' buds and on conditional patterns of development. Dormant buds enable damage to be repaired (reiterative growth), and variation in the abundance of resources such as mineral nutrients or light to be accommodated ('opportunistic' growth (Tomlinson 1982)). Evidently a signalling system is involved, but the detailed mechanisms of 'apical dominance' and correlative inhibition are still obscure (Hillman 1984).

Studies of the abstract rules for form generation in higher plants are not as well advanced as they are in filamentous algae, although Lindenmayer (1984) has derived rules for simulating

the growth of certain complex inflorescences. The rules are position-dependent and require signalling between branches.

The experimental work on plant signalling systems can be summarized as follows.

PROPOSITION. *Discrete or 'pulse' signals for differentiation may pass between modules. Once differentiation has been achieved, it is maintained by a constant flux of signals from neighbouring cells or modules.*

The signalling systems must match, in terms of information content or variety, the processes they control. It seems unlikely that the recognized plant growth substances can provide this variety; polysaccharide moieties may also be involved (Canny 1985). But morphogenetic signals are not necessarily chemical. Changes in electrical membrane potential accompany many developmental processes. Strain, which is a function of the mass of distal modules, is a signal for the differentiation of reaction wood, and hence for the adjustment of branch angle (Fisher & Stevenson 1981). Other mechanical stimuli such as wind loading and plant–plant contact, which elicit adaptive morphological responses, also appear to be sensed as mechanical strain (Biddington 1986). Mechanical strain generated by cell expansion determines the direction of the division plane in cytokinesis (Lintilhac & Vesecky 1984). The red:far-red ratio in the light at the base of the canopy is a function of presence of upper leaves as light filters (Holmes 1983), and is a signal for the release or initiation of axillary buds (Deregibus *et al.* 1985; see also Franco, this symposium). Short range 'pulse' signals between modules occur in the differentiation of successive perianth components (Heslop-Harrison 1964). A long-range, continuous flux of signals (auxin) is maintained from shoot apex to root tip, overriding local fluctuations in availability of nutrients and by its logarithmic dose–response characteristics 'smoothing out' the processes of differentiation (Trewavas 1982). Local variations in this flux of auxin appear to be responsible for the characteristic pattern of xylem differentiation along the stem (Ewers & Zimmerman 1984), and hence for the differential growth of buds (Salleo *et al.* 1985) and the development of characteristic branching patterns (Honda *et al.* 1981).

A continuous flux of signals also passes upwards from root to shoot, indicating the current availability of mineral nutrients (de Wit & Penning de Vries 1983) and of water (Blackman & Davies 1985). The root-signals are a function of the root's genotype; the growth of the shoot systems of fruit trees can be regulated by appropriate choice of rootstock (Rogers & Beakbane 1957).

In a number of cases the signal for differentiation remains obscure. The branches of some gymnosperms exhibit topophysis, each retaining its characteristic angle of growth even when the others have all been removed, or even when the branch is taken from the plant and grown on as a cutting (Worrall 1984). Some plants, for example peas (*Pisum sativum*), switch from initiating vegetative modules to initiating flowers after a precisely counted number of nodes (Hardwick 1985). Diffusates, probably gibberellins, from the cotyledons are implicated (Murfet & Reid 1985). In other species the following is possible.

PROPOSITION. *Meristem size is an autonomous signal for differentiation.*

The size of the shoot apical meristem gradually increases during ontogeny. It has been suggested that this provides a signal for the mechanisms that control branching (Thornley 1977) and the switch to floral growth (Battey & Lyndon 1984). We do not know how the parameter h, and meristem size, are controlled (Charles-Edwards 1984), but the apical meristem is a potential site of accumulation for various materials that are carried in the vascular system (Sheldrake 1973) and it has been suggested that the tendency of materials such as boron to accumulate at the shoot apex of primitive plants may have provided the necessary opportunity

for localizing cytokinesis and building an apical meristem there, by the evolution of a mechanism that made cytokinesis critically dependent on the ambient level of boron (Lovatt 1985). Elaborations of such mechanisms may be involved in the control of meristem size.

During vegetative growth, plant cells tend to retain totipotency; irreversible determination is uncommon (Sussex 1983). This contrasts with the situation in many animals, where totipotency is rare, and differentiation seems to reflect a hierarchical organization of the genome (Britten & Davidson 1969). It seems that:

PROPOSITION. *Modular organization of the phenotype imposes a non-hierarchical organization on the genotype; totipotency is a consequence of modular growth.*

In unitary organisms (such as vertebrates and insects), the phenotype is reliably entire and even-aged, and differentiation can be achieved by a hierarchically organized genome, dependent on tightly controlled flows of signals between parts. The benefit is that very complex patterns of differentiation can be achieved, but the cost is a loss of totipotency. In the development and differentiation of modular, uneven-aged, organisms, on the other hand, a degree of local autonomy and totipotency is valuable as insurance against accident and because it enables the size, type and number of modules to be adjusted to the resources available. Such adjustments are appropriate during vegetative growth, when the function of each module is the exploitation of resources. For modules concerned with reproduction (that is, sepals, petals, etc.) function and therefore structure are fixed. Here we tend to find a hierarchical organization of the genome, tissue-specific signals, and loss of totipotency.

Studies of abnormal patterns of differentiation of the inflorescence of *Plantago lanceolata* by van Groenendael (1984) suggest that in this plant differentiation of reproductive structures occurs by commitment to a defined sequence of events. Various abnormal inflorescences of *Plantago* can be explained in terms of the substitution at a late stage in the sequence of 'instructions' appropriate to an earlier stage. The system is reminiscent of the homeotic box system in animal segmentation. In other species gene transfer experiments demonstrate that the expression of at least some plant genes is tissue-specific. For example, the gene for production of the seed protein phaseolin has been transferred from beans to tobacco. In its new host the gene is preferentially expressed in the appropriate tissue, that is, the seed (Netzer 1984). The nature of the tissue-specific signal or signals is not known.

In animal differentiation, morphogenetic signals may be amplified by the cAMP–adenyl cyclase mechanism. In the higher plants the mechanism appears to be less well developed (Brown & Newton 1981). Evidence is accumulating that:

PROPOSITION. *Stable (canalized) patterns of differentiation can be established in a tissue of totipotent cells by driving reactions to completion by autocatalysis.*

Instances of autocatalytic (or positive feedback or flow facilitation) mechanisms in plant morphogenesis include, for cytokinin, the habituation of tobacco pith cells (Meins & Foster 1985), and, for auxin, the two-cell developmental model of Stange (1984), auxin enhancement of the synthesis or activity of its own binding sites (Starling 1984), and the auxin-enhanced differentiation of auxin-transporting (vascular) tissues in stems (Sachs 1981). A computer model of autocatalytic processes in a laminar tissue provides a convincing simulation of the development of leaf venation (Mitchison 1980).

The vegetative parts of modular plants are, then, at least potentially, totipotent and autonomous. The ways in which relationships between such units are regulated is discussed in the next section.

Relationships between modules

The cell plate is not entire but perforate, so that syncytial connections extend throughout the plant body, linking cells to one another in a three-dimensional network. Modules are linked to one another by a 'superapoplast' (xylem) and 'supersyncytium' (phloem) (Raven 1977). As the number of modules, n, in the system increases, the potential number of flows of substrate between modules increases rather rapidly (as n^2). Yet the growth of higher plants is characterized by 'harmonious relationships' (Münch 1938), or 'functional equilibria' (Brouwer 1983). How is this achieved?

Consider a simple two-component system, for example, shoot and root. We are interested in the rules for allocating increments in mass between components, that is in the form of the relations $\mathrm{d}S/\mathrm{d}t = f(S, R, t)$; $\mathrm{d}R/\mathrm{d}t = f'(R, S, t)$, where R is mass per root, S is mass per shoot and t is time. A particularly simple case occurs when f and f' are defined by (1) and (2):

$$\mathrm{d}S/\mathrm{d}t = g_{ss} S + g_{sr} R, \tag{1}$$

$$\mathrm{d}R/\mathrm{d}t = g_{rs} S + g_{rr} R, \tag{2}$$

where the values of the coefficients g_{ss} and g_{rr} are fixed and where $g_{sr} = g_{rs} = 0$. Then

$$S = bR^a,$$

and growth is allometric. Allometry has often been claimed, but usually on somewhat inadequate data. Critical analysis of a particularly large and well structured data set (Currah & Barnes 1979) confirmed that the estimated value of the coefficient a $(= g_{ss}/g_{rr})$ was more or less constant over time and over treatments. A physiological explanation of this constancy, which has often been observed, is not as yet available. The estimated value of the coefficient b was constant with plant spacing, but its value decreased with time: that is, growth in time was not allometric. This too appears to be a general phenomenon (for an explanation see Barnes (1979)).

Equations (1) and (2) could, in principle, be extended to describe the growth in mass of a plant of n modules. This would require n differential equations and n^2 coefficients. The analysis of such equation systems shows that in large, randomly connected sets of n interacting components, stability is critically dependent on the degree of connectance (the percentage of non-zero values of the coefficients g_{ij}). If connectance is greater than about 15% the system will almost certainly be unstable to perturbations (Gardner & Ashby 1970). Large values of connectance strength will also cause instability (May 1972). Two propositions follow from these theoretical studies. The first is:

PROPOSITION. *To avoid instability of growth, the phloem connectance between modules must be less than about* 15%.

The proposition is in accordance with 'Canny's rules' (Canny 1984). Labelled assimilates can move along single strands of phloem for hundreds of centimetres and all connections between modules appear to be potentially available, but (unless the system is perturbed) it seems that each module serves as 'source' to, or draws as 'sink' from, only a few of its nearest neighbours; interaction strength (g_{ij}) decreases sharply as the distance between source and sink increases (Cook & Evans 1983). Experiments with labelled assimilates confirm that in modular plants, phloem connectance is maintained at a low value.

The mechanical equivalent of connectance is cross-bracing. Trees, unlike most man-made structures of similar size, are not cross-braced. It might seem that cross-bracing would offer a substantial increase in mechanical strength for little extra cost. But the connectance result predicts that in an artificially cross-braced tree (which could be constructed by making a large number of approach grafts between branches), patterns of growth would not be stable. The same is predicted to occur if connections develop between stilt roots and natural roots in plants such as *Ficus benghalensis*. Where connections develop between individual plants, such as in the hemiparasite *Bartsia* (which parasitizes its own species) the result of more than 15% connectance would be expected to be a loss of stability of growth of the ensemble and the emergence of a few very large individuals.

The open vascular system and primitive eustele of the stems of late Devonian plants soon evolved into a closed system, allowing lateral transfer between leaf traces (Beck *et al.* 1982). Lateral connections allow the system to compensate for damage and to smooth out variations in fluxes between modules. A significant percentage of fixed nitrogen imported by a module (a leaf) from the roots tends to be re-exported in the phloem to the roots, and the same appears to be true of carbon assimilates passing from shoot to root (Lambers 1983). These mechanisms may help confer functional stability on the system.

The second stability condition was that the average strength of interactions between modules should not exceed a critical value. This requirement is met relatively easily if all the modules of a plant have the same genotype but:

PROPOSITION. *If connections develop between modules of different genotypes, strong interactions may ensue, threatening the stability of growth of the system as a whole.*

In angiosperms, functional mixtures of modules of two (or more) different genotypes occur (i) in somatic mosaics; (ii) in periclinal chimeras; (iii) in plants attacked by a vascular parasite; (iv) in plants joined by root or shoot grafts; and (v) in the angiosperm ovary after outcrossing.

Somatic mosaics may arise by amplification of gene copy during growth or by the failure of diplontic selection during growth; the phenomena do not seem to be widespread and there have been few physiological investigations on the growth of mosaic plants, or of plant chimeras. The physiology of vascular parasites and their hosts, on the other hand, has received detailed attention. Modules of two markedly different genotypes develop intimate (but apoplastic) connections, and the resulting imbalance is such that the parasite modules increase at the expense of those of the host. Mistletoes (*Viscaceae*) maintain lower transpiration resistances, and higher transpiration fluxes, than in the neighbouring tissues of the host and thereby obtain a disproportionate share of the solutes dissolved in the host's xylem sap (Ehleringer *et al.* 1985). Dodders (*Cuscutaceae*) maintain a low concentration of organic solutes in the apoplast around their haustoria; the result is an enhanced rate of phloem unloading and of phloem translocation by the host to that area (Wolswinkel *et al.* 1984). A dramatic variant of vascular parasitism occurs in some naturally root-grafted plants: Epstein (1978) discusses a case in which 22 years after a forest of Douglas firs was selectively felled, 23% of stumps were still alive, preserved by translocates reaching them via root grafts to the remaining trees.

These examples suggest that the system of connections between modules, both xylem and phloem, is not strongly protected against the development of strong interactions and exploitation by 'selfish' individuals. Why have such vulnerabilities not been eliminated during evolution?

PROPOSITION. *A parsimonious strategy by every module towards its neighbours (that is, minimizing the values of g_{ij}) would change the general nature of the interactions in the internal environment from 'mutualistic' to 'antagonistic'.*

Law (1985) suggests that an environment of 'antagonistic' relationships is less stable than one of 'mutualistic' relationships. The proposition suggests that the same is true of interactions within the plant. A non-antagonistic rule system allows modules to cooperate in exploiting a patchy distribution of resources (for example, of sun flecks, or mineral nutrients) as in *Linnea borealis* (Antos & Zobel 1985) and to support injured modules (tillers of the tundra grass *Dupontia fischeri* that are injured by grazing lemmings appear to draw assimilates from less severely damaged neighbours (Mattheis *et al.* 1976)). However,

PROPOSITION. *Strong pressures for selection against 'selfish' interactions would be expected where these pose a consistent threat to the inclusive fitness of the genome, that is, where they are strongly expressed (large values of the parameters g_{ij}) and occur in every generation.*

Attack by a phloem parasite is a relatively rare event: as a result phloem parasites do not exert any great selective pressures for change in the phloem unloading system. The mechanism of unloading across the apoplast to the parasite *Cuscuta* is, however, very similar to the physiology of phloem unloading to ovules (Wolswinkel 1984); ovules have a different genotype to the mother plant, and are produced in every generation. It has been suggested that the result of these pressures has been the evolution by the seed plants of the integuments and the endosperm, whose function, it is suggested, is to control phloem unloading from parent to offspring, offset the trend towards 'selfishness' in the offspring, and organize the death of 'surplus' ovules (Queller 1984). Thus to avoid large values of g_{ij}, a module may be 'aborted'. This leads to the following proposition.

DEATH OF MODULES

PROPOSITION. *The threat of 'selfish' interactions is controlled by organized senescence of meristems or modules.*

In tree stumps supported by root grafts, a disadvantaged individual can apparently be maintained by phloem translocates indefinitely (Epstein 1978). Interactions between advantaged and disadvantaged modules of the same plant are organized more strongly. The first analyses of the development of the leaf canopy assumed that shaded leaves at the bottom of the canopy would be retained indefinitely, and that the increasing drain of resources would set an upper limit to the effective leaf area index. But observation showed that leaves that have been shaded do not persist: their maintenance respiration reduces, and eventually they senesce and die. Similarly, the lower branches of forest trees do not persist indefinitely; they 'age', in response to the shifting pattern of distribution of mineral nutrients within the tree (Moorby & Wareing 1963), itself a function of the tree's hydraulic architecture. Eventually, branches die, in an organized fashion, falling from a pre-existing collar and leaving an articulation zone or socket. Branches of a large tree may die in light intensities in which small trees of the same species stay alive (Went 1973) (this establishes a clean trunk below the morphological inversion point (Hallé *et al.* 1978)). In *Lolium multiflorum*, dependent tillers are maintained only for a short time, then they die (Ong & Marshall 1979). Climbing plants continually move their substance upwards so as to reach the light, the lower leaves dying in an organized fashion. In these and other cases of organized senescence there may appear to be a link with other processes, such as the development of self-shading, or of internal shortages of resources; but the correlation is not necessarily causal. It seems rather that module death is a canalysed and adaptive feature, conferring fitness on the genome, and that any correlation with other events is coincidental (Hardwick 1983).

From the point of view of plants as populations of modules (Bazzaz & Harper 1977), the death of meristems and modules is an important determinant of growth. Plant structure and agricultural yield in species as diverse as *Coffea* and *Pisum* can be described as a function of meristem and module death rates (Reffye 1981; Hardwick 1985). Leaf senescence is under nuclear control (Woolhouse 1982), but is subject to internal regulation; for example, the rate of leaf senescence can be accelerated or retarded by exogenous application of growth regulators, calcium and polyamines. In many species leaf longevity is either invariant or varies smoothly along the axis, so that zones of senescing and abscissing leaves tend to progress smoothly along each axis (sequential senescence). In monocarpic senescence, on the other hand, all leaves tend to senesce more or less simultaneously. Here a close correlation has often been demonstrated between leaf longevity (leaf area duration) and yield. As in other aspects of modular growth, we have only a poor understanding of the mechanisms involved.

Discussion

In this paper I have attempted to explore the rule systems, and derive some principles, of modular growth. Many details are still lacking, so that at present the propositions have the status of conjecture or hypothesis, rather than axiom or law. A recurring feature has been that modular plants exhibit 'structural stability' (Thom 1972). The result is that plants grown in the same environment are 'similar but not the same' (Nishida 1980). If the modular plant is a physiologically stable system, how should interactions between modules be described? Many plant physiologists have applied the notion of competition and competitiveness to describe relationships between modules. But successive modules have the same genome and are means to the same end, that is, the propagation of that genome. It may therefore not be helpful to imply that modules 'strive' against one another. Even where one module appears to obtain material benefit at the expense of a second (for example an upper leaf benefits, a lower one abscisses; a proximal fruit grows, a distal fruit aborts) it is arguable that the interaction should be described in terms of 'cooperation' rather than 'competition' (cooperative interactions maximize the inclusive fitness of the two modules involved).

'Modularizing the small detached house', concluded the visionary architect Albert Farwell Bemiss (1936) 'will give not only the benefits of mass production but those of superior architectural talent to the hundreds of thousands who will live in these homes ... Mass productive methods have come to stay, because they are simply the further development of the division of labour'. In higher plants, as in houses, it seems there were benefits to be gained from 'superior architectural talent', and from 'division of labour'; mass production through modularity of construction arose early in evolution and has evidently come to stay. To the question *cui bono*? (who profits by it? who is most likely to have brought it about?), the answer is that modular growth is brought about by the genome, and the profits of modular architecture accrue to the genome. Physiological mechanisms provide the means by which the genome achieves and maintains a modular phenotype; the end is evolutionary fitness.

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