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Some life-history consequences of modular construction in plants

By A. R. Watkinson[1] and J. White[2]

[1] *School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, U.K.*
[2] *Department of Botany, University College Dublin, Dublin 4, Ireland*

The nature and life-history consequences of modular construction in plants are discussed with particular reference to growth, reproduction and survival. Plants grow by the iteration of modular units and as a consequence growth can be described in terms of the population dynamics of these structural units. Changes in size, whether positive or negative, depend on the birth and death rates of modules; however, if the births continue to exceed the deaths, plants then have the capability of attaining enormous sizes, especially if they are clonal. The population nature of plant growth also means that plants of the same age may show large variation in individual size if individuals differ in their relative growth rates. Correlations between age and size are often, therefore, very weak.

Constraints on the allocation of resources accumulated during growth have important implications for the reproductive schedules of plants, but the analysis of constraint functions has so far revealed little about the actual detail of these schedules. All the meristems of semelparous plants are involved in or die at reproduction and as a consequence death of the genet follows reproduction. For iteroparous plants, however, there are fundamental differences between the reproductive schedules of plants with a single shoot module and those with many shoot modules. The former demonstrate a relatively constant rate of reproduction from year to year following maturity whereas the latter show a continual increase in fecundity with size and age. The reproductive schedules of clonal plants are further discussed in relation to the allocation of meristems to either growth or reproduction.

The pattern of mortality is examined at both the level of the module and the genet. Particular attention is focused on the survival and senescence of leaves and shoots; there is no equivalent regular shedding of organs in unitary organisms. Whereas genet senescence and death are coincident with shoot module death in semelparous plants, there is no evident relation between them in iteroparous plants. The life span of the genet reflects the birth and death rates of its modules and both aclonal and clonal plants that are iteroparous may achieve considerable longevity. The longevity of aclonal plants often seems to be restricted by the accumulation of dead material and the problems of being large. Clonal plants are, in contrast, potentially immortal. It is questionable whether the genets of iteroparous plants show senescence as defined for unitary organisms since there is no separation of germ plasm from soma and since apical meristems do not appear to senesce. Insofar as they retain the capacity for rejuvenescence from apical meristems, genets of modular organisms do not senesce; it is only the constituent organs that show senescence, death and decay.

1. Introduction

The many and varied life histories of plants have traditionally been subdivided by the duration of life of the genetic individual (genet) into annual, biennial and perennial. Recent demographic research has increasingly cast doubt on the distinctiveness of the biennial life cycle. Very few plants are obligately biennial; most 'biennials' appear to be facultative (Kelly 1985). They

may either, like *Verbascum thapsus*, have annual, biennial or triennial geographical races (Reinhartz 1984) or, like *Digitalis purpurea* and *Senecio jacobaea*, exhibit biennial or perennial life cycles in response to environmental circumstances (van der Meijden & van der Waals-Kooi 1979). Most biennials are therefore probably best considered as short-lived perennials that may complete their life cycles within two years, given optimal conditions (Harper 1977).

A more recent subdivision of life histories by demographers has used another criterion, recognizing two fundamentally different patterns of reproduction as a function of age. These were named semelparous and iteroparous life histories by Cole (1954). The former has an obscure etymology, but refers to those organisms whose reproduction is confined to a single age class and followed by death. Iteroparous organisms reproduce (or are physiologically capable of reproducing) more than once. Botanists have traditionally referred to plants with such life histories as monocarpic and polycarpic, respectively. In seed plants a further useful distinction may also be made between shoots that have only one terminal and more or less synchronous reproductive episode, and shoots with more persistent and indeterminate vegetative expansion, bearing lateral reproductive structures over an indefinite period, often years.

A description of the life history of a plant in terms of the actively growing phase of the life cycle is, of course, only a partial description. Plant populations exist in two parts: the growing plants and the dormant seeds. Most species possess some form of seed dormancy and it is only at the time of germination, which is the formal equivalent of birth in animals (Harper & White 1974), that the embryo acquires independence from the parental tissue. The dormancy of seeds has three important consequences. First, by delaying germination it slows down the rate of increase of the population: only when one generation follows on directly from the next is the growth rate of the population maximized. Second, the longevity of seeds confers perenniality on many annual plants and produces populations in which the generations may overlap. In a sense annual plants with long-lived seeds can be considered as long-lived semelparous perennials. The dormancy of at least a fraction of the seed crop also provides a safeguard against unsuitable conditions in a variable environment (León 1985).

Among life-history phenomena it is the relationship of reproductive activity to age that has received most attention from evolutionary theorists, by consideration of the role of natural selection in moulding the forms of life histories, as described by the age-specific survival probabilities and relations of fecundity with age (Law 1979; Charlesworth 1980). Attention has been focused in particular on selection for iteroparity as opposed to semelparity and on such questions as the effects of selection on the age of first reproduction, reproductive effort and senescence. All of these studies have treated unitary and modular organisms as if they were equivalent. It is the aim of this paper to examine whether there are any life-history features that are particularly associated with the repetitive, modular construction characteristic of plants. And since the life history of an organism reflects the pattern of allocation of resources between reproduction, maintenance and growth with time, we shall consider some of the consequences of modular construction in plants as they affect growth, reproduction and survival.

2. Growth

(a) A demographic approach to growth

Populations of unitary organisms are composed of individuals, the genotypes of which specify a unitary morphology and a life cycle that proceeds remorselessly from the zygote through

juvenility and a reproductive phase to senility and death (Harper & Bell 1979). In contrast populations of *modular organisms* are composed of individual genets (individuals that develop from zygotes) each of which is made up of a collection of unit tissues (above the level of the cell, a distinction necessary unless all multicellular organisms are to be considered modular). In plants the zygote develops into an organism in which one or more structural tissue units are iterated by one or (usually) many growing points, themselves capable of self-perpetuation. For various types of morphological analysis the structural unit chosen may be a leaf with its axillary meristem, a bud, a metamer, a shoot, a branch system or ramet, indeed any structural tissue unit that is iterated. This is a very broad definition of modular growth which encompasses all vascular plants.

There is a more restricted definition: the term *module* is used by some morphologists (Hallé *et al.* 1978) to refer to a monopodial shoot which is produced by a single apical meristem and terminated by a reproductive structure. Thus, a talipot palm (*Coryphya umbraculifera*), nearly 20 m tall with a single apical meristem, would be regarded as a single module; but in our terms it shows modular growth or construction, growing by the repeated, sequential iteration of structural tissue units. We shall refer to modules in this stricter sense as *shoot modules*, but otherwise use the term unqualified for reiterated structural units.

White (1984) has used the term metamer for a structural unit below the level of shoot module and the phrase 'modular growth' may be more or less synonymous with 'metameric growth'; but the equivalence, so evident in plants, cannot be taken for granted for animals: not all metameric (segmented) animals are necessarily modular, particularly if they lack the capacity for proliferation of 'somatic replicas produced by budding or fission' (Hughes 1983), one of the most characteristic features of modular organisms. The taxonomic limit of modular construction in animals remains a moot point.

Unlike a unitary organism, the product of a zygote in a modular organism has population properties of its own. This is because the growth of a genet can be described in terms of the number of modules which in turn depends on the rate at which modules are born and the rate at which they die. The modular growth of a genet can be described by the equation

$$\eta_{t+1} = \eta_t + B - D, \tag{1}$$

where η is the number of modules, B is the number of module births and D is the number of module deaths (Noble *et al.* 1979; Harper 1981). While this equation takes no account of whether the modules are vegetative or reproductive it nevertheless provides a basis for the growth of individual plants to be studied at a demographic level (Bazzaz & Harper 1977). More complex models of individual plant growth involving matrices are described by Maillette (1982) and McGraw & Antonovics (1983). Clearly if the growth of an individual genet can be described in terms of the population dynamics of modules then the modules of each genet will have an age structure together with other population attributes such as expectation of life and age-specific mortality. As the birth and death rates of modules can be expected to vary with the conditions in which a genet finds itself then so can the age structure. For example the leaf population of *Linum usitatissimum* grown in deionized water for 100 days shows an age structure dominated by leaves that are less than 20 days old whereas the leaves live much longer on plants grown in a full nutrient solution (Harper 1981). Leaf senescence here is related to the withholding of nutrients.

Applying the concepts of population growth to a population of modules allows the rate of

growth of a genet to be calculated from one census to the next by subtracting η_t from both sides of (1) to give

$$\Delta\eta = B - D. \tag{2}$$

If $\Delta\eta$ is positive the population of modules will increase in number, whereas if $\Delta\eta$ is negative the number of modules will decline. Assuming that the number of module births and deaths does not change either with time or with the number of modules, then the genet will increase to an infinite size if $\Delta\eta$ is positive and die if $\Delta\eta$ is negative. Yet for plants where the modules remain part of a physiologically integrated whole and contact of the shoots with the soil is through a single axis (for example, most trees and annual herbs) an exponential phase of growth is typically followed by a period in which the rate of iteration of new modules and accumulation of biomass declines until a maximum size is reached (Franco 1985). The rate of production of new modules is in this case either dependent on time or the number of modules already present. If the latter, then competition between modules for a limited supply of resources around the base of the plant or the effect of overlapping leaves on each others' activity presumably results in either a decrease in the birth rate of modules, an increase in mortality or both. There is a clear analogy here with density-dependent population growth in unitary organisms. Alternatively, constructional constraints may well impose a limit on the size that an individual genet can attain. Interestingly, the branch modules of a tree get progressively smaller as the number of modules increases (Borchert & Honda 1984). This may reflect the most efficient way that a branching system can support a photosynthetic canopy. If the modules did not get smaller as the branching system developed it is likely that the whole plant (if dependent on a single trunk) would eventually collapse from biomechanical limitations.

In contrast clonal plants that spread laterally and root at the nodes have at least the potential capability (depending on the branching system) of increasing in size indefinitely; new resources can always be tapped as the genet forages into new areas. Clonal growth thus allows plants to escape from some biomechanical size constraints. Clones of bracken fern (*Pteridium aquilinum*) have commonly been observed up to 300 m in diameter (estimated to be about 700 years old) and a few clones reach almost 500 m across, probably about 1400 years old (Oinonen 1967). Various estimates have been made of the extent of clonal growth in quaking aspen (*Populus tremuloides*): two clones of 10.1 and 43.3 ha, containing about 15000 and 47000 ramets, respectively, have been described by Kemperman & Barnes (1976), who also suggest that some clones may approach 81 ha in area. A few other examples of the extent of clonal growth are given by Cook (1983). For these plants there is no decrease in the size of modules as the number of modules increases. Those genets that space their modules far apart can spread over an area quickly ('guerrilla' growth form) whereas those with short internodes will have a 'phalanx' growth form, where the modules are tightly packed (Lovett Doust 1981). Clearly the way in which the modules of a genet are packed and whether or not they remain connected can have major effects on the way a genet exploits environmental resources and interacts with neighbours (Harper 1981).

(b) Variation in plant size

Individual plant genets may attain enormous sizes but they may also show immense variation in size. Such plasticity is largely a consequence of modular growth and the number of modules iterated (Harper 1981). Small individuals are those in which few modules have been iterated or many have aborted or died. In contrast a high birth rate of modules or a low rate of modular

abortion and death, or both, results in vigorous growth and large individuals. Even individuals of the same age within a monoculture consist of a size hierarchy of individuals with a few large dominants and many relatively small individuals. Such hierarchies develop soon after seedling emergence and the inequality between individuals appears to become even greater as seedlings grow. Simple exponential growth is sufficient to cause such a shift from a symmetrical to a highly asymmetrical distribution with large size differentials if individuals differ slightly in their relative growth rates (Koyama & Kira 1956). As such it is tempting to suggest that greater size inequalities might develop in clonal plants where the phase of exponential growth might be expected to last for longer than in those plants with a single stem, especially if the individuals are widely spaced. But other factors may play a role. In high density stands where interference occurs between individuals asymmetric or one-sided competition may further exaggerate the difference between individuals leading to dominance and suppression (Aikman & Watkinson 1980). As reproductive output is generally highly correlated with plant size large individuals will typically be more fecund while small individuals will usually have higher mortality. Consequently, in sharp contrast with unitary organisms, there will often be a very weak correlation between age and the reproductive performance and mortality of many plants.

Dominance and suppression may lead to a decline in the size of some individuals since the death rate of modules (D) may exceed the birth rate (B), but it is not the only factor. Grazing and pathogen activity may also result in a decline in module number. With grazing the death rate of modules can be increased by animals removing them completely or by removing parts of them: the latter while not resulting in immediate module death does result in an increase in the death rate (Dirzo 1984). Where animals continue to remove modules at a rate greater than the birth rate the plant will decrease in size and perhaps die whereas if grazing is at a level such that $B > D$ the plant will continue to iterate and accumulate new modules. Animals that feed on seedlings may often cause death (Crawley 1983) but established plants are much more resistant to herbivory because most herbivores remove only parts of the plant or tap resources leaving other plant parts that are capable of regeneration through the iteration of new modules. Frequently the heavy grazing of a plant that results in a decrease in the number of modules may be followed by a recovery period in which new modules can be iterated as long as there are some undamaged meristems. For example, the cinnabar moth *Tyria jacobaceae* often defoliates ragwort *Senecio jacobaea* such that there is an apparent seed loss of 100%. On fertile soils the plants can compensate partly for this defoliation by the iteration of new modules and the production of a second crop of flowers (Islam & Crawley 1983). Seed yield is decreased and seed maturity delayed in comparison with ungrazed plants but the longevity of the plant may be increased because defoliation tends to increase the number of rosettes as damaged plants produce new rosettes from root buds and from the crown of the root stock.

Again the shrinkage of plants as a result of grazing and their potential for regrowth means that the age and size of a genet are poorly correlated. Since the fecundity and survival of plants is often much more closely related to size than age, a number of authors (for example, Werner & Caswell 1977; Kirkpatrick 1984) have argued that it is better to classify the life history characteristics of plants by size rather than age which is the most often used classification for unitary organisms. Population models based on size-related parameters that incorporate shrinkage and fragmentation, as well as the more familiar processes of growth, reproduction and death, are described by Hughes (1984). Others have argued for a classification based on age-state (Sarukhán & Gadgil 1974) which comprises a somewhat arbitrary classification of

plants into a number of categories (for example, seed, juvenile, young reproductive, senile) based partly on age and size. It would of course be preferable to monitor the fate of individual plants according to both their age and size (Law 1983) but this has seldom been attempted (see Werner & Caswell 1977). Such large samples and such detailed monitoring are required to calculate all the necessary transition probabilities between the various age and size classes that the labour involved is daunting. Nevertheless an understanding of the variance in life history characteristics that occurs both in relation to size and age is essential if one is to understand the evolution of life history patterns (Lacey *et al.* 1983).

3. REPRODUCTION

(a) *Constraints on the allocation of resources*

How does an organism allocate the resources that it accumulates during growth? If there were no constraints on the design of organisms one would expect natural selection to optimize growth, reproduction and survival irrespective of the age of the plant. In this case the organism with the highest absolute fitness would be immortal, start to produce progeny almost immediately after it was born and continue to produce large numbers of offspring at frequent intervals as it grew older; it would be a 'Darwinian demon' (Law 1979). No unitary organism of this type exists and the assumption that there is no relation between present reproduction and future survival or reproduction is clearly incorrect. There are constraints on the resources that can be accumulated over a given time interval and constraints on the way that these resources can be divided up between the competing demands of maintenance, growth and reproduction (Law 1979). Although a greater allocation of resources to reproduction might be expected to increase the number of offspring produced, fewer resources to maintenance might increase the risk of mortality and fewer resources to growth might reduce both survival and the potential for reproduction later in life. It seems reasonable to suppose, therefore, that reproduction early in life will vary inversely with reproduction and the chance of survival later in life.

The importance of the relation between present reproduction and subsequent reproduction and survival for the evolution of life histories has been extensively explored by using the notion of reproductive value (see Charlesworth 1980). By using this concept it has been shown that a knowledge of the form of the constraint functions between reproduction, growth and survival together with a knowledge of the factors affecting them is central to an understanding of the evolution of reproductive schedules. Unfortunately we have very little information on the nature of these constraint functions in plants except for a few plants such as *Agave* (Schaffer & Schaffer 1977), *Astrocaryum* (Piñero *et al.* 1982) and *Dipsacus* (Caswell & Werner 1978), which have one or few shoot modules. In *Poa annua* (Law 1979), which has an indeterminate pattern of growth, the variance in the data is so great that it is impossible to judge the exact nature of the constraint functions. There are too few data yet to generalize but this may well typify the problem in defining constraint functions for plants with many shoot modules and especially for clonal plants.

In iterating new modules plants are producing shoot systems that are partly capable of paying their own carbon costs (Watson 1984). This applies not only to vegetative modules but also to flowers and fruits (Bazzaz *et al.* 1979). These factors compound the problems of measuring reproductive effort and the determination of survival costs (Tuomi *et al.* 1983). In addition,

developmental constraints may influence the way in which apical meristems (considered as a resource) are allocated to either reproduction or growth (Armstrong 1982; Watson 1984) in a way quite unlike that in unitary organisms, where there is no separation of the germ plasm from the soma. A meristem may either generate new meristems allowing further growth or it may become a flower primordium that produces seed and dies (Harper 1981); once committed to flowering it is precluded from generating new meristems. Thus growth form, which reflects the sequential iteration of modules, imposes constraints on growth and reproduction. The exact significance of this for the reproductive schedule of a plant can be fully appreciated only if growth form and modular construction are taken into account in investigations of resource allocation.

(b) Reproductive schedules

(i) Semelparous plants

All the meristems of a semelparous or monocarpic plant are involved in (or die at) reproduction and as an inevitable consequence death of the genet follows (figure 1 a). Some authors (for example, Charlesworth 1980) regard all annual plants as semelparous, in that they reproduce within a single season, but many annuals (for example, *Poa annua*, *Senecio vulgaris*) have indeterminate growth and continue to form new shoots as long as conditions are favourable. Each individual shoot may be monocarpic but because all shoots do not flower synchronously the genet as a whole may be considered polycarpic or iteroparous. Indeed Kirkendall & Stenseth (1984) have questioned whether any annual plant is semelparous, on the somewhat restrictive criterion that organisms with true semelparity cluster their progeny in one, condensed reproductive phase. Most annual plants by their argument are uniseasonally iteroparous or polycarpic; this is due either to a succession of monocarpic shoots (for example, *Senecio vulgaris*) or to the persistent reproductive activity of polycarpic shoots (for example, *Cakile maritima*). Meusel (1955) had earlier made a distinction between annual plants that produce their shoots in one or more growth cycles, and there is undoubtedly a wide variety of
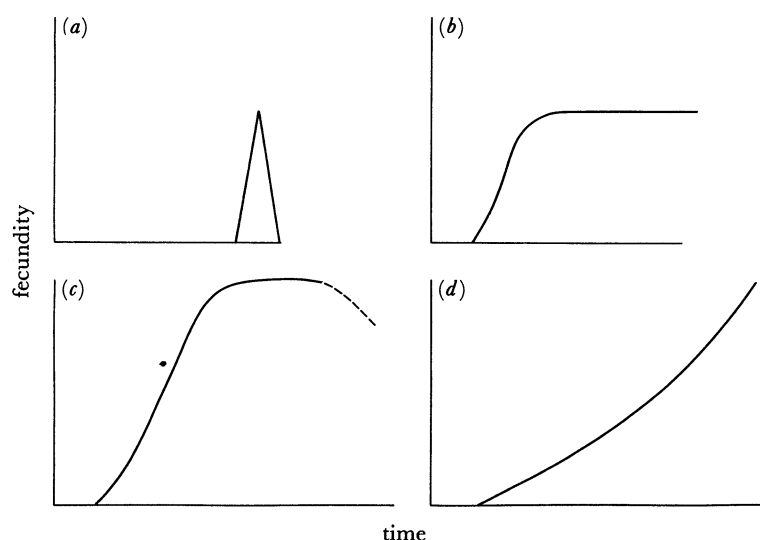

FIGURE 1. Schematic diagrams for the reproductive schedules of semelparous plants (a) and iteroparous plants with a single shoot module (b) or multiple shoot modules which are in turn either aclonal (c) or clonal (d).

reproductive schedules among plants traditionally referred to as annuals. Relatively synchronous reproduction of shoots or meristems of a genet may perhaps be characteristic of some winter annuals (for example, *Vulpia fasciculata*, *Erophila verna*), but it is perhaps more conspicuous in many facultative biennials (for example, *Daucus carota*) once a critical size threshold for flowering is achieved (Gross 1981). These 'biennials' scarcely (if at all) propagate themselves vegetatively and often have only a single vegetative axis; this restricts the time span of genet reproduction. Maturation of the primary, secondary and tertiary umbels of *Pastinaca sativa*, for example, takes place within three or four weeks (Hendrix 1984). Such relatively synchronous monocarpy of meristems is, it seems invariably, soon followed by senescence and death. There are relatively few examples of semelparous plants among long-lived perennials. These include some bamboos, *Agave* spp., *Strobilanthes* spp. (Janzen 1976), *Frasera* spp. (Inouye & Taylor 1980; Threadgill *et al.* 1981), *Lobelia telekii* (Young 1984), and a few tropical trees (Veillon 1971; Tomlinson & Soderholm 1975; Foster 1977). The large majority of perennial plants are iteroparous, since after some shoots flower each genet retains the capacity for sequential reproduction by the formation of new meristems, themselves eventually capable of reproduction.

(ii) *Iteroparous plants*

Consideration of the reproductive schedules of iteroparous species shows that there are fundamental differences between plants with a single apical meristem and those with many apical meristems (figure 1 *b–d*). The latter may in turn be divided into those where the shoot modules remain part of a physiologically integrated whole (aclonal) and those with shoot modules that may become physiologically independent (clonal). The first category is typified by the coconut palm (*Cocos nucifera*) which has a single apical meristem and trunk. No visible trunk is formed until the palm is several years old and the apical meristem has attained its full diameter. At this point the diameter of the stem remains relatively constant and the trunk is gradually built up by the accumulation of modular units. An adult palm consists of 25–35 leaves; one leaf is usually shed as a new leaf unfurls, thus maintaining a constant leaf area and number. Flowering commences at 6–12 years of age and a typical plantation palm has 8–10 leaves from whose axils fruit bunches have been harvested, 10–14 leaves supporting fruit bunches in various stages of development and 10–12 opened leaves with axillary spadices in different stages of growth (Purseglove 1972). The seed production of a palm may therefore remain relatively constant over a large number of years (figure 2), since although the total mass of the tree is increasing the number of leaves remains relatively constant. *Astrocaryum mexicanum* similarly shows a relatively constant seed production for a given individual once it reaches reproductive maturity although there may be large year-to-year variation (Piñero & Sarukhán 1982). There appeared to be no decline in fecundity with age in natural populations of this understory palm, which if knocked flat by falling branches or trees has a remarkable capacity to recover by turning erect at the stem apex and continuing its growth (Sarukhán *et al.* 1985). Coconut trees in commercial plantations do, however, show a decline in reproductive capacity after about 60 years, although this may vary greatly between individuals and between various selected cultivars (Child 1964).

The fecundity of a plant with numerous apical meristems may generally be expected to increase over a much longer period of time after the onset of reproduction, as the number of shoot modules continues to increase. In those (aclonal) plants where modules remain part of
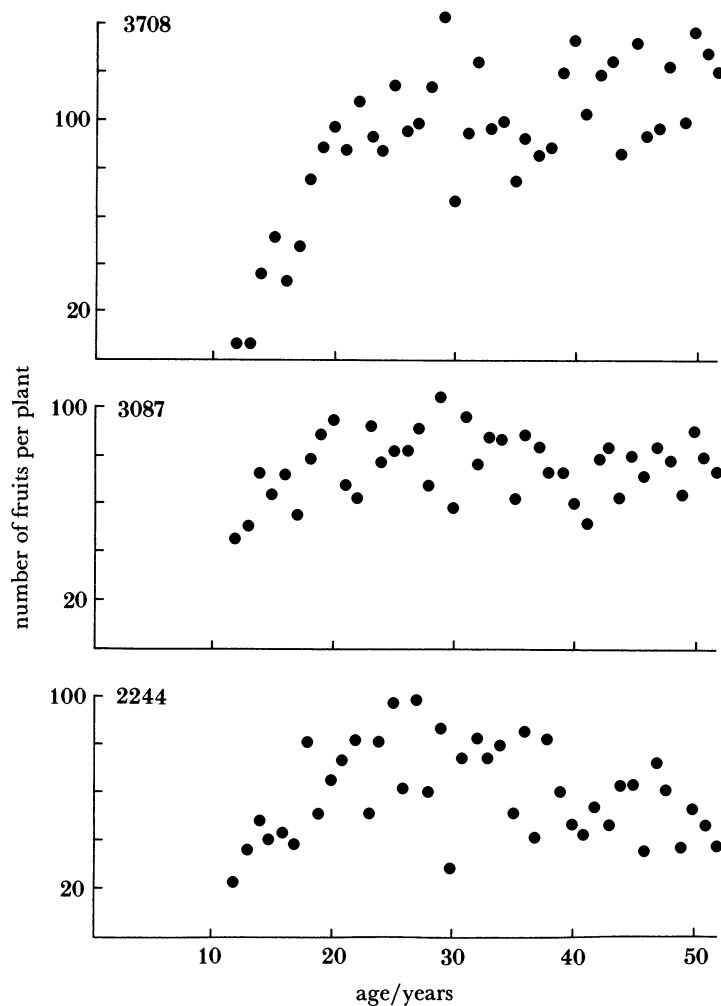
FIGURE 2. Fecundity as a function of age in *Cocos nucifera* (coconut): the reproductive output of three separate trees (cv. West Coast Tall) which were planted in 1917 and began fruiting in 1928. The total numbers of fruits during the period of observation are indicated for each tree; note year-to-year variation. (From data kindly supplied by E. V. Nelliat, Central Plantation Crops Research Institute, Kerala, India.)

a physiologically integrated whole (at least for some resources such as water, if not for others such as carbon (Watson & Casper 1984)), a maximum level or plateau of fecundity may be expected, followed by a decline as a result of disease, damage or senescence (figure 1*c*). Where shoot modules of a (clonal) genet achieve physiological independence, typically by making their own roots, genet fecundity may be expected to match the growth of the modular population and increase indefinitely, even exponentially (figure 1*d*). Under optimal conditions for modular expansion there is no reason to expect fecundity to decline. But the nature of gene flow between individuals may, however, change as the clone expands and this may affect fecundity, especially if genets are self-incompatible (Handel 1985).

Increasing fecundity with increasing plant size has been recorded frequently by plant demographers in recent years. Two general patterns are apparent, as Kohyama (1982) indicated for trees. The first shows an increase in reproductive output with size or age, followed by a plateau at maturity and perhaps a later decline. So far this pattern is only known for
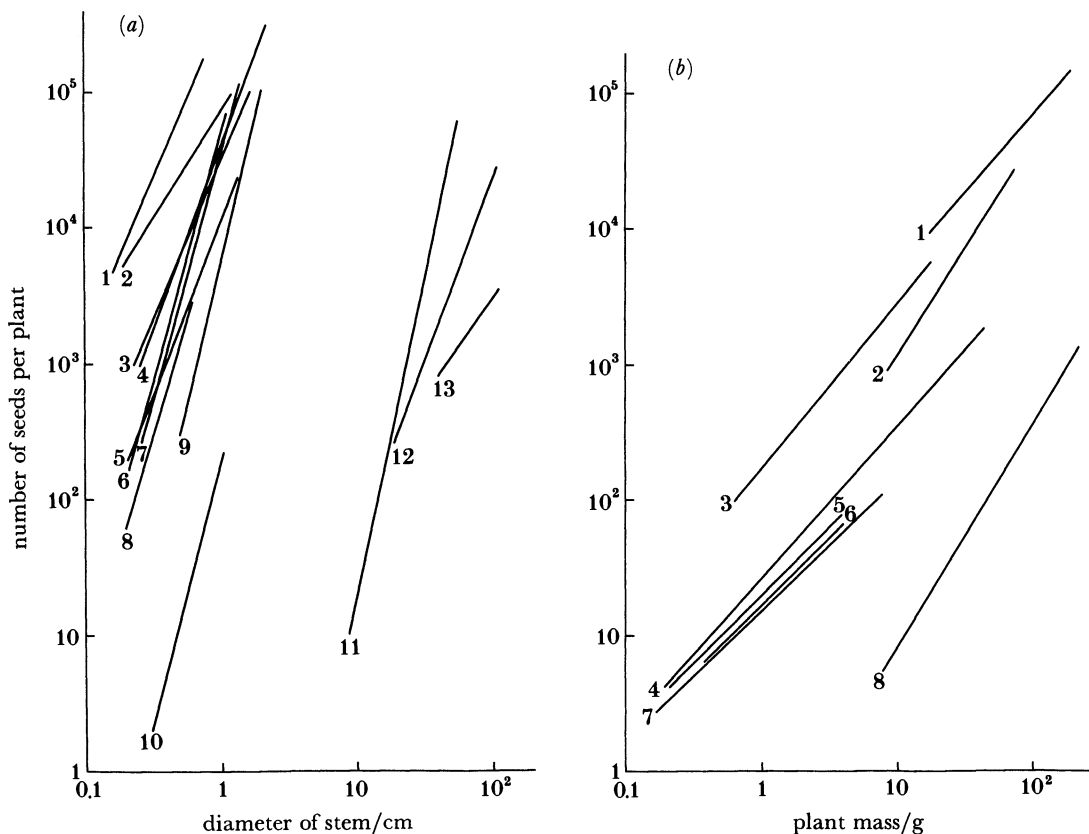
FIGURE 3. Fecundity as a function of size in seed plants. (a) Size expressed as basal stem diameter for herbs (1–9) and a shrub (10) or diameter at breast height for trees (11–13). (1) *Erigeron canadensis* (Hayashi & Numata 1968); (2) *E. annuus* and *E. strigosus* (Hayashi 1984a); (3) *Oenothera parviflora* (Hayashi & Numata 1968); (4) *Chenopodium album* (Fukuda & Hayashi 1982); (5) *Polygonum persicaria* (Hayashi 1984a); (6) *Chenopodium album* (Hayashi & Numata 1984); (7) *Artemisia princeps* (Hayashi 1984a); (8) *Daucus carota* (Holt 1972); (9) *Lactuca virosa* (Boorman & Fuller 1984); (10) *Symphoricarpos occidentalis* (Pelton 1953); (11) *Bursera simaruba* (Hubbell 1980); (12) *Quercus crispula* (Kanazawa 1982); (13) *Pentaclethra macrolobata* (Hartshorn 1975).

(b) Size expressed as above-ground plant mass, for perennial (1–3) and annual (4–8) herbs. (1) *Solidago sempervirens* (Cartica & Quinn 1982); (2) *Rumex crispus* and *R. obtusifolius* (Weaver & Cavers 1980); (3) *Plantago asiatica* (Kawano & Matsuo 1983; figure 12); (4) *Bromus sterilis* (Firbank et al. 1984); (5) *Vulpia fasciculata* (Watkinson 1982); (6) *Setaria faberi* (Kawano & Miyake 1983); (7) *S. pallide-fusca* (Kawano & Miyake 1983); (8) *Ambrosia trifida* (Abul-Fatih et al. 1979). The lines for *Setaria* spp. and *Plantago asiatica* are samples from a wider range of data given by the authors.

Note that the slopes of the lines in (a) and (b) are a function of the size parameter given in the source literature; but since plant mass (w) is typically related to stem diameter (d) by the power function $w \propto d^{\alpha}$, where α is approximately 2.5 for both trees (White 1981) and herbs (Hayashi 1984b), the difference between them is more apparent than real.

(aclonal) trees and for the shrub *Staavia dodii* (Moll & Gubb 1981). There is reasonably sound evidence for it in *Pinus ponderosa*, *Abies concolor* (Fowells & Schubert 1956) and *Abies veitchii* (Kohyama 1982), though some other reports, such as those for *Quercus* spp. (Downs & McQuilkin 1944; see Silvertown 1982), are based on inadequate evidence.

Far more general is the second pattern of reproductive output as a function of size or age: a sustained exponential increase, truncated only by death of the plant (figure 3). Most of the evidence for this comes not from clonal plants, where one might expect best to find it, but from aclonal plants. These examples (which include several semelparous plants) provide botanical

counterparts of the size- and age-related reproductive output of the gorgonian coral illustrated by Harper & Bell (1979). The data on which figure 3 is based sometimes have a high variance (as for *Bursera simarouba*), but the general trend in all cases is an exponential increase with size. The exponential relationships recorded for trees (figure 3a: 11–13) are not likely to be maintained indefinitely, if they live long enough to become senescent through disease or disintegration. But it is questionable how often trees ever become senescent through physiological decline, before they are simply destroyed by natural forces such as windthrow (Harper 1977; Ogden 1985). It is clear, however, that the largest (and possibly, sometimes, chronologically the oldest) individuals in a population contribute disproportionately to reproductive output and have a preponderant influence on the recruitment of the young, as Harper (1977) suggested. The genetic basis of such differential reproduction remains almost unknown, though there is recent evidence for it in *Pinus ponderosa* (Linhart *et al.* 1979). But it seems that long-lived modular organisms whose reproductive output not only remains undiminished, but *increases* with age, may have much more profound and lasting influence on the genetic structure of local populations than long-lived unitary organisms.

The fruit production of *Opuntia* species on the Galapagos Islands also increases exponentially with plant size, since fecundity is determined by the number of flowers per pad (flattened shoot module); reproduction begins when plants have accumulated about 20 pads (Racine & Downhower 1974). This particular example is an instructive illustration of the real morphological basis of the fecundity patterns for various species illustrated in figure 3: plant size is a derived parameter which hides this basis, the number of modules of which the plant is constructed. This may be further exemplified by the data for *Lactuca virosa*: the exponential relationship between fecundity and stem basal diameter (figure 3a) can be expressed also as an exponential relationship between fecundity and the number of nodes (or metamers), since node number and basal diameter are almost isometrically related (Boorman & Fuller 1984). Several other investigators have tried to relate fecundity to morphological parameters directly: for example, 'degree of branchiness' in *Xanthium strumarium* (Lechowicz 1984); branch number in *Salicornia* (Jefferies *et al.* 1983) and *Staavia dodii* (Moll & Gubb 1981); node number in *Ceratiola ericoides* (Johnson 1982).

The preceding discussion shows that most iteroparous plants demonstrate an increase in fecundity with size and age. This contrasts strongly with the reproductive schedules of iteroparous unitary organisms as illustrated, for example, by *Drosophila* and man where different design constraints are involved. For these species there is a rapid rise in fecundity to a maximum early in life once reproduction has been initiated followed by a slow decline (Charlesworth 1980). This pattern is not exhibited by plants. Other unitary organisms such as many small birds and mammals that maintain a constant size following reproductive maturity show a relatively constant rate of reproduction from year to year. This pattern of allocation is similar to that in plants with a single apical meristem. It is perhaps the cold-blooded vertebrates that continue to grow in size throughout their reproductive life and show a positive correlation between fecundity and age that are most similar to the large majority of plants.

(c) Meristem allocation in clonal plants

Although the life cycles and reproductive systems of clonal plants are becoming well understood (see, for example, Kawano 1985) their reproductive schedules remain almost unknown. It is nevertheless possible to examine how modular construction in clonal plants
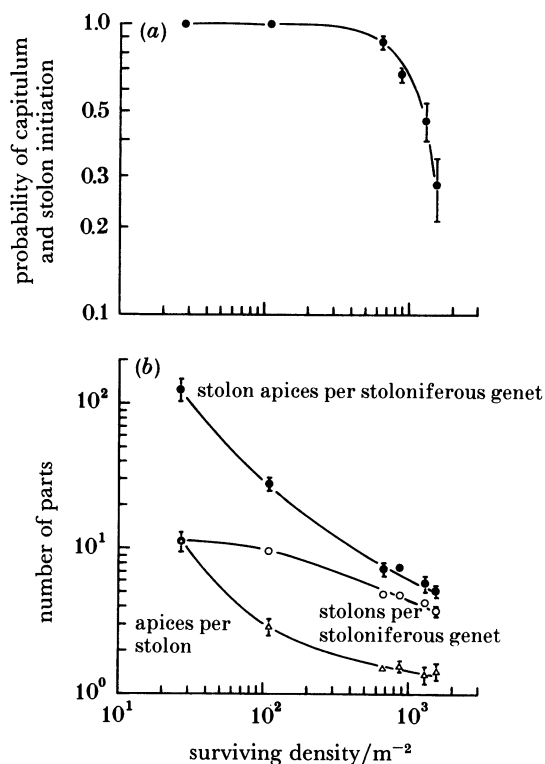
FIGURE 4. (a) Probability of a genet of *Hieracium pilosella* forming a capitulum and stolons in relation to surviving genet density. (b) The number of apices and stolons per genet and the number of apices per stolon in relation to surviving genet density. (From Bishop & Davy 1985.)

imposes constraints on reproduction, through the allocation of meristems to either reproduction or growth. Three recent studies on *Eichhornia crassipes* (Watson 1984), *Hieracium pilosella* (Bishop & Davy 1985) and *Potentilla anserina* (Eriksson 1985) demonstrate the power of this approach. For example, *Hieracium pilosella* is a rosette-forming stoloniferous herb with a close physiological coupling between the evocation of the terminal inflorescence bud and the development of one or more axillary buds into stolons. Only after floral evocation will one or more of the axillary buds develop into stolons and even if the capitulum then aborts or is grazed off stolon development continues. Despite the close coupling of flower and stolon production there is nevertheless considerable scope for plasticity in the allocation of meristems to reproduction and clonal growth since flowers may abort, and the number of stolon apices depends on the number of stolons initiated and the number of stolon branches. How then does intraspecific competition affect apical meristem allocation? Bishop & Davy (1985) showed that the number of reproductive and stolon apices per genet declined with density but that the form of the plastic response was rather different (figure 4). Moreover, the number of apices allocated to reproduction on a per unit area basis rose to a peak and then declined as the density of genets increased, a finding that contradicts the linear models of Williams (1975) and Abrahamson (1980) that predict a shift from growth to reproduction with increasing population density. Neither does this finding support the model of Armstrong (1982, 1984) which predicts a constant reproductive effort irrespective of conditions. Certainly the geometry of growth strongly influences the allocation of resources to growth and reproduction in *Hieracium pilosella* but so do the conditions in which the plants find themselves.

Moreover, the growth form of *H. pilosella* has important implications for its demography, as shown by Bishop & Davy (1984) in a study on a nutrient-poor grassland. There the exclusion of rabbits from the sward had little impact on the rosette density of *H. pilosella* compared with grazed plots but it significantly reduced the rate of turnover of rosettes resulting from clonal growth. The death of rosettes was related to rabbit grazing in a rather complex way since only 11 % of losses could be attributed directly to rabbit activity. In fact the single most important cause of death in both the grazed and ungrazed areas was senescence following flower initiation, since *H. pilosella* rosettes are semelparous. The probability of flower initiation was, however, higher in the grazed areas and as a consequence mortality was greater too. The higher mortality in the grazed areas was thus inextricably linked to the higher rates of flower initiation as was the recruitment of rosettes, since clonal growth is also coupled to flower initiation. This example beautifully illustrates the complex constraints that growth form may impose not only on the reproductive schedules of modular organisms but also on their population dynamics.

4. Senescence and survival

There are no qualitative differences between the survivorship curves of genets in populations of semelparous plants and those of organisms with unitary construction (see, for example, Watkinson 1981). However, the modular construction of plants calls for a more detailed demography of the constituent parts of each genet: growth by accretion of modular units may be offset by their death and loss. There is no equivalent of regular shedding of organs in unitary organisms. What influence then has the senescence and loss of organs such as leaves and shoots on the survival of genets?

(a) The senescence of leaves and semelparous plants

The pattern of mortality has now been examined both at the level of the modular unit and the genet for a large number of plant species. Particular attention has been focused on the survival of leaves. Leaves often show sequential or asynchronous senescence: each leaf has only a limited life span so that as the shoot continues to grow the older leaves senesce and die progressively. This pattern is well illustrated by the survivorship schedules of overlapping leaf cohorts in evergreen trees such as *Pseudotsuga menziesii* (Mitchell 1974) and herbaceous plants such as *Ammophila arenaria* (Huiskes & Harper 1979). In contrast there is a relatively synchronous annual senescence of leaves at the onset of winter in some deciduous forest trees (Kikuzawa 1983) and many hemicryptophyte herbs (for example, *Mercurialis perennis, Urtica dioica*). Whatever the causes of leaf senescence and whether these are controlled by factors internal or external to the plant it is clear that it is a tightly controlled process at the modular level and that the sequence of events is usually highly ordered until the terminal stages are underway (Sexton & Woolhouse 1984).

In perennial, iteroparous plants with multiple shoot modules, whether aclonal (for example, trees) or clonal, leaf senescence and abscission are not directly associated with genet senescence. Indeed, by permitting the recovery of nutrients from leaves that have become shaded and suppressed by prolonged modular growth of the shoot system or damaged by herbivores and pathogens, leaf senescence may have benefits for genet survival: photosynthetically inefficient organs are abscised as new ones are formed (Leopold 1961). This contrasts with aclonal plants which have one or few monocarpic shoot modules where the terminal stages of leaf senescence are often coincident with death of the whole genet (characteristically annuals and 'biennials').

Many studies of senescence in plants have been conducted with such semelparous plants where senescence is typically associated with flower and fruit formation. The association of flowering and seed-filling with senescence in semelparous plants has led to the suggestion that death results from the mobilization of nutrients by developing seeds and exhaustion of the rest of the plant as resources are diverted to maximize the production of seed. This view of senescence is, however, too simple and the process of senescence in semelparous plants remains poorly understood (Sexton & Woolhouse 1984). Even among semelparous plants most attention has been focused on annuals, biennials and facultative biennials which are by far the most common forms of plant that demonstrate synchronous reproduction. No attention has been given to the senescence of semelparous plants that are long-lived perennials. These include those with one or a few shoot modules (for example, most *Agave* spp.), aclonal plants with numerous shoot modules (for example, *Tachigalia versicolor*) and clonal plants (for example, some bamboos, *Strobilanthes* spp.). Rather than a physiological interpretation of senescence, predator satiation has sometimes been advanced (Janzen 1976) as the reason for the evolution of semelparity in long-lived, clonal perennials; whatever the reason it would appear that it is a life history restricted to plants as we are not aware of any animals that demonstrate it.

(b) Shoot dynamics and the longevity of aclonal plants

Whereas genet senescence and death are coincident with shoot module death in semelparous plants, there is no evident relationship between them in iteroparous plants. Among aclonal plants individual shoot modules may be monocarpic (for example, species of *Aesculus*, *Magnolia*, *Rhododendron* and *Rhus*), but within the genet they are markedly asynchronous in reproductive activity, with well defined annual flushes of flowering of some but not all shoots. Formation of new shoots occurs by the continued modular growth of the genet for an indefinite and sometimes prolonged period of hundreds of years. Monocarpic shoots may be incorporated into the permanent framework of the plant (for example, *Rhododendron*) or abscised (for example, *Pinus*). Here shoot senescence and abscission enhances the structural properties of the crown by allowing new shoots to be accommodated: this is especially true in trees where crown architecture may change considerably during plant ontogeny (for example, Borchert & Honda 1984).

Shoot death and abscission appear to have no detrimental effect on the survival probability of the genet in iteroparous aclonal species (Millington & Chaney 1973). Rather death of the genet in adult plants seems to be associated with the accumulation of dead material and the problems of being large. Many trees and bushes exhibit considerable longevity. For example, *Pinus aristata* may attain ages of approximately 4900 years while *Quercus robur* may reach an age of 1200 years (Harper & White 1974). There is nevertheless considerable variation between species. Among trees conifers generally appear to attain greater ages than angiosperms while among bushes some species may live only a few years (for example, *Daphne mezereum*) and others over 200 years (for example, *Salix arctica*).

(c) Shoot dynamics and the longevity of clonal plants

Even more spectacular are the age of clonal plants whether they are trees, shrubs or herbs. Estimates for the longevity of clonal plants (see Cook 1983) include *Larrea tridentata* (11000+ years), *Populus tremuloides* (10000+ years), *Convallaria majalis* (670+ years) and *Pteridium aquilinum* (1400 years). The causes of death in old genets are many and various. Among extrinsic

factors fire, disease and competition may all cause the death of plants but a noticeable feature of clonal plants where the shoot modules lose physiological contact is that the death risk of the genet decreases with increasing clonal proliferation (Cook 1983) as a result, for example, of a reduction in the risk of systemic infection by pathogens.

The life span of the genet reflects the birth and death rates of its modules. Hence if the birth rate of modules continues to exceed the death rate the genet is potentially immortal. Our knowledge of the shoot module dynamics of clonal perennials is now considerable (Harper 1977; Silvertown 1982) but remains piecemeal: monocotyledonous herbs have received particular attention (see, for example, Noble *et al.* 1979; Callaghan 1984). For example, Noble *et al.* (1979) found that the shoots of *Carex arenaria*, which remain connected by rhizomes, show an increase in the probability of death with time. The life expectancy of a shoot varies depending on the time of recruitment into the population and the phase of sand dune development in which it is found, but most shoots are typically biennial. The rhizome segments associated with the shoots are, however, much longer lived, resulting in age structures of above and below ground parts that are quite different. While older parts of the rhizome eventually die, resulting in fragmentation of the genet, the continuous iteration of new shoot modules means that the genet may be extremely long-lived and potentially immortal. This conjunction of short life-span of shoot modules and long-life or even potential immortality of the genet is a noticeable feature of clonal plants. The life expectancy of individual tillers of *Eriophorum vaginatum* is about seven years under favourable conditions (Fetcher & Shaver 1983) but the estimated ages of mature tussocks range from 122 to 187 years (Mark *et al.* 1985). For *Ranunculus repens* most shoot modules have a half-life of only one year while the half-life of genets has been estimated at approximately eight-and-a-half years (Soane & Watkinson 1979). Much more dramatic, however, are the individual, non-fragmented clumps of creosote bush (*Larrea tridentata*) of seedling origin which may achieve ages of 60 years (and exceptionally up to 90 years) compared with the clones into which they eventually fragment, which may live for several thousand years (Vasek 1980).

We have established that the 'partial senescence' (Turner 1950) or 'asynchronous senescence' (Palumbi & Jackson 1983) of modules has no necessary effect on the senescence or death risk of the genet. This is a striking feature of modular organisms, not confined to plants (Palumbi & Jackson 1983; Potts 1984; Hughes & Jackson 1985) and calls into question Hamilton's (1966) argument that 'senescence is an inevitable consequence of the working of natural selection'. Hamilton asserted that the concept of a non-senescing organism demanded a mortality risk that does not change with age and a fertility schedule which increases exponentially as the organism grows older. Both of these criteria may be met by modular organisms, where senescence is *localized* within the genet and does not necessarily involve the entire organism. There is undoubtedly evidence that the probability of genet death is independent of age among established plants for some species (for example, Antonovics 1972) and we have already shown that fecundity may be expected to increase with both age and size for many plants.

(d) Senescence in iteroparous plants

What role does senescence play in the death of iteroparous species with modular construction? Plants are usually ignored or mentioned only in passing in general considerations of senescence (Comfort 1979; Charlesworth 1980), while specific discussions of plant senescence consider only the senescence of modules and semelparous plants (see, for example, Sexton & Woolhouse 1984).

Most theories of senescence include either evolutionary or physiological explanations (Bell 1984) and definitions of senescence reflect these two viewpoints. For example, Charlesworth (1980) regards senescence as the tendency for age-specific survival probabilities and age-specific fecundities to decline with increasing age for individuals of sufficiently advanced age. This definition is then qualified by the statement that the senescent decline in fecundity and survival should reflect the decline in performance of many different physiological functions with age. This implies that senescence is an inherent characteristic of the plant and yet the increased probability of death with age in plants is usually connected with extrinsic factors. The increased probability of wind-fall and lightning strikes in trees that results from an increase in size, death from interference in a successional environment, and the increased susceptibility to disease that results from mechanical damage surely cannot be regarded as reflections of senescence.

Certainly there are examples of a decline in reproductive output with age, as in *Staavia dodii* (Moll & Gubb 1981), and a decline in life expectancy with age has been reported for *Astrocaryum mexicanum* (Sarukhán 1980). Declines in the physiological activity of plants with age in general reflect the accumulating burden of respiratory tissue, vascular transport problems associated with ever-increasing distances that water and nutrients need to be moved, and increased susceptibility to pathogens and herbivores. These declines in physiological performance relate predominantly to aclonal plants, however, and are primarily side consequences of being large (Harper 1977). Whether the genets of clonal plants show senescence is not at all clear. There is a continuous turnover of shoot modules and in contrast with aclonal plants there are no tissues as old as the genet. It has been suggested that the decline in vigour of *Ammophila arenaria* in the later stages of sand-dune succession represents senescence (Eldred & Maun 1982) but it can also be interpreted in terms of interference (Watkinson *et al.* 1979). Similarly, examples of senescence among clonally propagated crop plants or forest trees ('senile degeneration') are probably in most cases due to more or less simultaneous epidemic infection, probably by viruses (Bijhouwer 1931; Wangermann 1965). Indeed it has been suggested that 'immunity to mosaic virus is the key to immortality in the potato' (Salaman, quoted by Bijhouwer 1931).

Although there may be a decline in physiological activity of genets, particularly if shoot modules remain physiologically connected, it must be questioned whether apical meristems senesce at all. They may cease to function in shoot extension (a process referred to as parenchymatization) or differentiate in their growth potential (Hallé *et al.* 1978), but they seem to show little evidence of senility. The continued and undiminished potential for vegetative propagation of distinctive cultivars of fruit trees has been cited as evidence to rebut the notion of senility in meristems (Schaffalitzky de Muckadell 1959). In genets with pronounced differences in juvenile and mature growth expression (for example, *Citrus, Eucalyptus, Hedera*), some meristems may 'age', but other meristems may remain undifferentiated and 'juvenile', even in mature plants. The continued capacity of meristems for rejuvenescence of the genet is especially well recorded in trees, where, somewhat paradoxically perhaps, those at the base of the trunk, the oldest part of the genet, retain the capacity to reiterate new shoots; this may be related to their proximity to the root system (Nozeran *et al.* 1982). Insofar as it retains the capacity for rejuvenescence from apical meristems, a genet of a modular organism does not show senescence, despite the senescence, death and decay of constituent organs. A clone of *Lemna*, for example, does not age. Individual fronds and the meristems they bear age and die, but rejuvenation takes place during clonal growth, as a result of which the average physiological age of the clone remains constant (Wangermann 1965). Advancing age of a parent frond affects

bud size but has little or no effect on the lifespan or budding capacity of the offspring (Claus 1972).

Thus in modular organisms senescence of some organs is associated with rejuvenescence and continued genet survival: partial senescence of the genet has replaced the senescence and death of unitary organisms (Turner 1950). Charlesworth (1980) argued that senescence was 'almost certain to evolve whenever there is separation of soma and germ plasm'. Modular organisms, however, show no such separation of soma and germ plasm (Buss 1983) and many remain capable of rejuvenescence indefinitely. Moreover, where fecundity increases with age there should be relatively low rates of senescence with respect to survival since increasing fecundity tends to reduce the selective differential between different age classes. These characteristics are particularly evident in iteroparous plants with numerous shoot modules. For these plants fecundity increases with age and size and the apical meristems retain the capacity for somatic maintenance and expansion by modular growth. Since there is no separation of germ plasm from soma this also allows the potential for the individual genet to evolve in relation to changing conditions. Somatic mutations in the apical meristem may, if they confer higher fitness, be incorporated in all subsequent modular units that are iterated thus allowing selection to occur between different modules of the same genet (Whitham *et al.* 1984). It is still quite unclear how important somatic mutation is in the evolution of modular organisms. In this volume Hardwick argues that the organization of meristems may be such as to weed out mutant cell lines. Most observed somatic mutations in higher plants appear to be cytoplasmic or sometimes due to virus infections. Great somaclonal variation is displayed in plants regenerated from potato meristems but in normal cultivation potato varieties seem to show high stability. If somatic mutation of the genome is a frequent feature in modular organisms, natural selection is to be expected *within* genets and between modules. We still lack the evidence from which to argue this case.

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