

## EIGHT

# Growth and Development in Clonal Plant Populations

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### INTRODUCTION

Ecological interest in the biology of plant clones originally derived from horticultural and taxonomic concerns with classification. Since antiquity certain higher plants have been propagated by means of cuttings; the term *clone* was coined shortly after the turn of the century to refer to cultivated plants that derived from such vegetative multiplication (Krikorian 1982). There soon followed considerable debate on terminology, but the official code of nomenclature of cultivated plants eventually defined a clone as "a genetically uniform assemblage of individuals (which may be chimeral in nature), derived originally from a single individual by asexual propagation, for example by cuttings, divisions, grafts, or obligate apomixis. Individuals propagated from a distinguishable bud-mutation form a cultivar distinct from the parent plant" (Gilmore et al. 1969). A ramet, from the Latin, "branch," loosely refers to the individual plant that constitutes a member of a clone.

Since the turn of this century, the existence of clones in natural populations of wild species has been primarily the concern of evolutionary systematists interested in natural variation and the factors affecting the process of speciation (Grant 1981). Clones may result from two processes: asexual formation of seeds without fertilization and the development of vegetative offshoots from the parent plant through the growth of a coordinated group of cells that form a meristem. Stebbins (1950) lumped these two processes together under the term *apomixis* (see glossary) and considered them forms of variation in the breeding systems of species. The frequency of asexual propagation among different populations was then interpreted in terms of its effects on the maintenance of

genetic variation and the formation of taxonomically distinct clones that might be considered asexual species.

This work led to certain general conclusions within which lay a paradox. First, some of the most widespread and successful plant groups appear to be obligately or exclusively asexual. Large continental areas with a diversity of habitat conditions have been rapidly colonized by such genera as *Rubus*, *Hieracium*, *Poa*, and *Taraxacum*, each of which contains a plethora of clones. Two genetic factors appear correlated with the high frequency of asexual reproduction: such groups often display high levels of ploidy compared with sexual relatives, and detailed examination of their evolutionary history often reveals a pattern of hybridization and heterozygosity. Thus the apparent adaptive success of such groups may derive from two aspects of asexual propagation: the capacity of clonal daughter plants to overcome any sterility from changes in ploidy level, and the fixation of favorable heterozygous gene combinations in asexually produced plants.

At the same time, most systematists also reached the conclusion that such success is limited: asexual species represent an evolutionary blind alley with little potential for evolving new genera (Stebbins 1950; Grant 1981). Although the capacity for vegetative propagation is found in nearly all perennial plants and is undoubtedly quite ancient, asexual seed production is considered a condition recently evolved from sexual reproduction in a closely related sexual species. In fact, the formation of asexual seed in some species still requires partial fertilization by pollen. Other species are capable of forming both sexual and asexual seed in the same flower head on an individual plant (see Silander, this volume). The independent occurrence of asexual seed formation in a wide range of species suggests considerable selection favoring its local evolution. Yet no higher taxa are exclusively asexual.

To support the concept of an evolutionary blind alley, Grant (1981) has argued that groups of clonal species display four stages of evolution: the initial formation of asexual offspring; proliferation and spread of clones beyond the range of their sexual ancestors; the extinction of identifiable sexual ancestors following the success of asexual descendants; and the eventual extinction of these clonal species without taxonomic descendants. Compared with asexual seed formation, vegetative propagation appears to be of even more limited evolutionary potential. Vegetative propagules formed by runners, small bulbs, or root sprouts are considerably more restricted in their capacity for dispersal, and very old clones propagated vegetatively may accumulate viral diseases leading to clonal senescence. Thus the paradox: despite the great success and apparent ecological and genetic advantages of asexuality, implying strong selection favoring its development and maintenance within populations, it appears to represent a dead end to the evolutionary biologist and to lead ultimately to extinction. What are the immediate fitness advantages of asexual

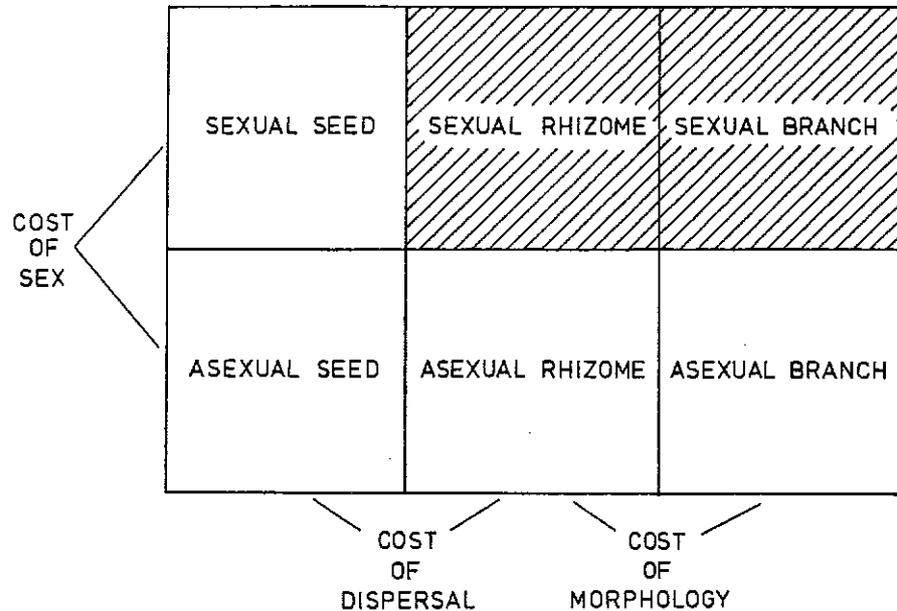
reproduction that account for its widespread occurrence in many populations, and why are these advantages so transitory in evolutionary time that no higher plant taxa are exclusively asexual?

*Antennaria parlinii*, a dioecious, facultatively asexual composite, illustrates this paradox. Bayer and Stebbins (1983) compared the distribution of populations of female plants that produce only asexual seed with the local history of glaciation in Ohio. In unglaciated areas, populations consisted mostly of male and female sexual individuals; in glaciated regions, most or all individuals in populations were asexual. Bayer and Stebbins argue that asexuality is favored in a dioecious, colonizing species because multiple colonizations by both male and female plants would not be required for successful establishment of a population. While this may be true, a correlational approach over a broad geographical area can provide little evidence for the apparent advantages of asexuality. Only studies of the fate of sexual and asexual individuals in populations growing under different habitat conditions can begin to test hypotheses concerning the costs and benefits of asexual seed formation.

The answers to such questions have become the province of evolutionary ecologists, and over the last ten years the biology of clonal growth and asexual reproduction has received an increasing amount of theoretical and field study (Maynard Smith 1978; Harper 1981). Within these efforts the scale of thought and observation has shifted from the level of the species to that of the individual organism: how does asexuality, either vegetative or seed, affect the fitness of females, and what factors determine the relative allocation of resources to sexual and asexual reproduction? Ecologists have realized that an answer to these questions for plants will require a much greater understanding of the natural history of clonal growth and reproduction in field populations. This will ultimately require an experimental evaluation of hypotheses concerning the effects of different patterns of clonal propagation on the fitness of organisms.

To understand the biology of clonal growth and reproduction in plants, one must begin with the fundamental distinction between the asexual production of seeds (agamospermy) and vegetative propagation (involving a form of growth and development by plant meristems). Biologists who examine various aspects of asexual reproduction often make comparisons between processes that confuse and confound three important distinctions in the biology of plants. Figure 8.1 illustrates these distinctions and the comparisons appropriate to particular ecological and evolutionary questions.

The first distinction occurs between asexual and sexual seed formation; it is primarily genetic. The evolutionary benefits of either form of seed formation must be interpreted in terms of the production of genetically uniform or genetically diverse offspring by female organisms. Thus the evolution of agamospermy in a sexually interbreeding population directly addresses the question of the evolution and maintenance of sexual reproduction in the face of



**Fig. 8.1.** Diagrammatic presentation of contrasts between different growth and reproductive comparisons in clonal plants. Appropriate comparisons involve sex, dispersal, or morphology. Higher plants do not form sexual rhizomes or branches (upper right boxes). See text for further explanation.

its apparent disadvantages (Maynard Smith 1978; G. Bell 1982). These disadvantages can include costs of attracting mates, fecundity costs of producing males, and the genetic cost of recombination, which can disrupt coadapted gene complexes. These potential costs are balanced against two hypothetical advantages. First, there are benefits for offspring of rare genotype when selection is frequency-dependent (Price and Waser 1982). Predators and pathogens, as well as intense competition among siblings for resources, could provide such selective environments. Second, production of genetically diverse offspring may benefit the fitness of a female when future environmental conditions are very unpredictable (Maynard-Smith 1978). There has been very little work examining the fitness advantages and disadvantages of agamospermous seed production, although the repeated evolution of agamic complexes strongly suggests that asexual seeds obtain significant ecological advantages under certain conditions.

A second distinction, here called the "cost of dispersal," occurs between seed production and the multiple branching of asexual ramets. Because this process leads to ramets that are capable of independent survival while remaining genetically identical to the mother plant (Cook 1979, 1983), it is frequently referred to as "vegetative reproduction." At the same time, however,

it is developmentally quite distinct from sexual reproduction because the new individual grows from an organized population of cells forming a meristem rather than from a single germ cell (Harper 1981, this volume). Although theoretically possible, there exists no sexual analog to multicellular ramet proliferation. The comparison between *asexual* seed production and rhizome formation contrasts the ecological distinctions between distant seed dispersal capabilities with the high probability of successful ramet establishment through the growth of rhizomes. Although comparisons of *sexual* seed production and asexual rhizome production are often made (Abrahamson 1979), these are inappropriate because they confound genetic and ecological differences.

The final distinction contrasts development of a horizontal stem or root that forms new ramets with vertical growth of a single ramet rooted at one location. This cost of morphology has no sexual analog and reflects the advantages of competitive dominance through vertical interception of light versus the benefits of lateral spread with multiple root and shoot establishments. There exists a continuum between those plants which develop as a single stem with multiple branches and those which fragment into separate individuals sharing a common genetic identity (Harper, this volume). However, in this comparison, the formation of a clone remains fundamentally a branching process.

Despite the branching nature of vegetative propagation, it does possess two distinctive features that distinguish the development of a tree such as a maple from the formation of clones in aspens and grasses (Cook 1983). First, clonal plants possess the capacity to initiate adventitious roots or shoots from stem or root tissue, thus permitting considerable ecological flexibility for the maintenance of a balance between the different functions of above- and below-ground parts. This also creates a new axis of polarity physically distant from the mother plant. Second, the proliferation of this developmental process leads to increasing occupation of horizontal space by the genet. Thus the ramets of a clone, unlike the branch modules of a tree, display a much greater capacity for spatial spreading and for establishment of independent axes of growth at locations physically distant from the site of original seedling establishment. If the lifespan of ramets is significantly shorter than that of genets, the clone will effectively move in space, sequentially occupying new habitat.

In discussing the costs and benefits of clonal growth and asexual reproduction, biologists typically focus on only one or two of these contrasts. Geneticists tend to examine genetic differences involved in the cost of sex, ecologists see clone formation in terms of the cost of dispersal and establishment, and morphologists interpret ramet development as a type of branching. Plant ecologists have focused their study of clonal plants on three primary questions:

1. How much phenotypic and genotypic variation exists in clonal plant populations?

2. What are the appropriate demographic measures of fitness in clonal plant populations?
3. How do the physiology and morphology of individual clones contribute to differential fitness?

This chapter will review selected aspects of each of these questions.

## VARIATION IN CLONAL PLANT POPULATIONS

### SIZE OF CLONES

Although there have been no systematic surveys of the occurrence and frequency of clones in natural populations, it is clear that some species are capable of forming very large and very old clones (table 8.1). Aspen stands covering many hectares have been identified as single clones of great age (Kemperman and Barnes 1976). Because bracken spores germinate in the bed of ash after fire has destroyed the existing vegetation, Oinonen (1967a, 1967b) was able to date very large clones back to the fourteenth century by correlating the diameter and position of the genet with the known history of battles in

**Table 8.1.** Some large and successful clones.

SPECIES	SIZE	AGE (YEARS)	ORIGIN	SOURCE
Ground cedar <i>Lycopodium complanatum</i>	250 m	850	Rhizome	Oinonen 1967b
Bracken <i>Pteridium aquilinum</i>	489 m	1400	Rhizome	Oinonen 1967a
Black spruce <i>Picea mariana</i>	14 m	300+	Layering	Legere and Payette 1981
Red fescue <i>Festuca rubra</i>	220 m	1000+	Tillering	Harberd 1961
Sheep fescue <i>Festuca ovina</i>	8.25 m	1000+	Tillering	Harberd 1962
Velvet grass <i>Holcus mollis</i>	880 m	1000+	Tillering	Harberd 1967
Reed grass <i>Calamagrostis epigeios</i>	50 m	400+	Rhizome	Oinonen 1969
Lily of the valley <i>Convallaria majalis</i>	83 m	670+	Rhizome	Oinonen 1969
Quaking aspen <i>Populus tremuloides</i>	81 ha	10,000+	Root buds	Kemperman and Barnes 1976
Creosote <i>Larrea tridentata</i>	7.8 m	11,000+	Basal	Vasek 1980
Huckleberry <i>Gaylussacia brachycerium</i>	1980 m	13,000	Rhizome	Wherry 1972

various Russo-Finnish wars. Wu, Bradshaw, and Thurman (1975), using electrophoretic markers to identify genets in *Agrostis stolonifera*, found only two clones in an extensive lawn population of unknown age. After 11,000 years of very small annual expansion by basal branching, a creosote bush in the Mojave Desert of California has formed a clone of independent shoots more than seven meters across (Vasek 1980). A stand of black spruce that covers 160 square meters of tundra in northern Quebec probably spread by branch layering from a single tree over 400 years ago (Legere and Payette 1981). These isolated studies of clones in nature indicate that clonal growth and reproduction may be very successful for some species.

This success is achieved by various modes of vegetative propagation: bulbils, runners, rhizomes, tillers, and root buds. It is particularly characteristic of certain habitats and floras (Abrahamson 1979). Often species growing at high latitudes and altitudes, in aquatic habitats, the temperate or boreal forest understory, in grazed grasslands, and fire-disturbed vegetation display extensive clone formation. For entire populations of these species most ramets derive from some form of vegetative propagation. Seedling recruitment appears to be a rare event. Two-thirds of the perennial species common in most regions of Great Britain grow and reproduce clonally. Many of the most pernicious weeds are serious economic pests precisely because they grow from underground roots, rhizomes, and bulbs (Leakey 1981).

There are many species in which the physiological individual is identical with the genetic individual and in which genets with multiple ramets are not formed. Most annual and biennial herbs and many tree species appear to be aclonal. More common is the considerable variation among closely related species in the degree to which vegetative propagation and clonal spread occurs. Keating, Hoch, and Raven (1982) examined the distribution of different types of perennating organs among 17 taxa of the genus *Epilobium* and revealed wide variation in the degree of vegetative spread that could potentially occur. Some species form a single stem or a dense, compact clump of stems, whereas others develop multiple ramets from extended stolons, rhizomes, or root buds. Very little correlation was found between the form or degree of clonality and any chromosomal evidence of phylogeny. The authors concluded that similar perennating organs had independently evolved several times in different taxa. They suggested that comparative studies would reveal much closer correlations between perennation mechanisms and the ecological conditions of the habitat; phylogenetic history appears to place little constraint on the evolution of clonality in plants.

Within a habitat there is considerable variation in capacity for lateral spread among species (Sobey and Barkhouse 1977). In boreal forests, some species, such as *Trillium*, *Dryopteris*, and *Smilacina*, display little horizontal growth and tend to occupy a single location for long periods of time. Other

species, such as *Maianthemum*, *Aralia*, and *Trientalis*, extend great distances across the forest floor in one growing season. These capacities for clonal spread might appropriately be scaled to the size of the individual ramet. *Osmunda* forms a series of tall fronds up to 0.5m high but has very little lateral expansion, creating a tight clonal clump. On the other hand a *Trientalis* ramet is less than 20 cm high, but it may form two or three stolons up to 80 cm long. The degree to which a clone explores new terrain is also affected by the average lifespan of ramets. Both *Trientalis* and *Medeola* shoots die at the end of the growing season in which they are formed, and the location of the genet changes each year. Ramets of *Viola blanda* survive for approximately five years, but the genet lives much longer through the production of stoloniferous daughter plants that lie up to 35 cm from the parent (Cook 1983). Aspen trees (*Populus tremuloides*) form extensive clones from root buds, and the individual ramets live more than 100 years (Barnes 1966).

#### DIVERSITY OF CLONAL POPULATIONS

There is also variation in the number of clones coexisting within populations (Sebens and Thorne this volume; Silander, this volume). Fields of certain grass species are dominated by very few genets (Harberd 1961, 1962, 1967; also see Wu, Bradshaw, and Thurman 1975). Within a field of *Holcus mollis*, for instance, Harberd could identify only four distinct genetic individuals, with one genotype spread over a half-mile of ecologically diverse terrain. With a clone displaying such ecological amplitude, there was little evidence for any local genetic adaptation. Similarly, some populations of *Festuca rubra* contained a low diversity of genets (Harberd 1961), though other populations were very diverse (Harberd and Owen 1969; Smith 1972). Populations of clover (*Trifolium repens*) are occupied by a very large number of clones in a relatively uniform habitat. In controlled trials under uniform conditions, Burdon (1980) examined 22 traits among 50 plants sampled from a small grazed pasture. Ninety-nine per cent of the 1,225 pair-wise comparisons revealed distinct genetic differences, indicating a diversity of coexisting genets which might be maintained by the selective nature of livestock foraging (Cahn and Harper 1976), the selective attack of pathogens (Burdon 1980), or competitive relations with immediate neighbors (Turkington and Harper 1979).

The most direct approach to understanding these patterns of variation is through comparative demographic studies of clonal species (Harper 1981; Harper and Bell 1979; Harper 1977). By explicitly recognizing the modular nature of plant growth, Harper noted that the population dynamics of clonal plants may be analyzed at several levels: the number of zygotes or genets in the population, the number of ramet modules within genets, and the number of

leaf/axillary bud modules within ramets. With such an analysis an understanding of growth of the genet can be obtained through the demographic processes of module birth and death. Beyond this very generalized prescription for examining clonal plant populations, there has been little explicit theoretical work examining the life-history consequences of clonal growth and reproduction until now (Hughes 1984; Caswell, this volume).

The difficulty stems from the complex nature of clonal growth. From the perspective of ramets, the appearance and loss of modules can be treated as a population process. From the perspective of the genet, however, formation of modules is a branching process, and loss may be partly controlled by internal mechanisms of senescence. Not all modules are equal, because the position of a ramet within the clone may influence its fate. In addition, ramets are not independent; their growth and senescence may be strongly affected by internal mechanisms of development mediated both by resource availability and hormonal balances. As will be discussed below, interpretation of field data on clonal plants depends on the perspective with which the dynamics of ramets are analyzed.

#### REPRODUCTIVE STRATEGIES

Traditionally, ecologists have begun with the observation that organisms must compete for a share of limited resources. An understanding of the benefits of a particular trait therefore involves a knowledge of the ways the trait facilitates acquisition of resources and is transmitted to offspring through reproduction, thereby increasing the relative fitness of the individual. The study of reproductive strategies in plants has generally been focused on the ways in which individuals distribute resources between growth, maintenance, and reproduction throughout the life cycle. How, for example, has natural selection shaped patterns of allocation in individuals of different species growing in different habitats? The results of such allocation studies have often been interpreted in terms of the theory of *r* and *K* selection (Gadgil and Solbrig 1972; Primack 1979). In the most simple terms, this theory predicts that habitats characterized by abundant resources and density-independent sources of mortality will favor a large and early allocation of resources to reproduction. Environments characterized by very limited resources and density-dependent sources of mortality, due to competition, will select for a smaller and later allocation of resources to reproduction. Allocation patterns have been typically measured by determining the proportion of total biomass contributing to the production of offspring (Thompson and Stewart 1981).

This approach was rather easily extended to clonal species, both in theory (Williams 1975) and practice (Abrahamson 1979). In keeping with the tradi-

tional botanical view that development of a clone is a form of vegetative reproduction, plant ecologists measured individual reproductive effort by determining the proportion of biomass devoted to new ramet production. Implicitly this approach treated the ramet as the evolutionarily relevant individual, and the growth of a daughter ramet as an appropriate unit of fitness. Once so defined, however, the nature of the question was changed from one of growth versus reproduction to one of sexual seed production versus asexual ramet production.

Although such studies confound genetic and ecological distinctions (fig. 8.1), four generalizations have emerged (Abrahamson 1979). First, when comparing different species, it appears that sexual and asexual reproduction "compete" for resources within the plant, and selection for greater allocation to seed production will occur at the expense of allocation to clonal expansion (Harper 1977; Abrahamson 1979); individuals "reproduce" by one or the other means, depending on the different probabilities of sexual or asexual offspring establishment. Second, the relative allocation to asexual reproduction is phenotypically conservative under a wide range of habitat conditions when compared with sexual reproductive effort (Thompson and Beattie 1981; Ogden 1974). Under harsher environmental conditions, the formation of flowers and fruits may be completely inhibited, but new ramets will continue to be produced. Third, species growing in later stages of succession allocate relatively less resources to seed production while the asexual contribution remains constant or increases (Newell and Tramer 1978; Abrahamson 1979). Finally, as density of the population of ramets increases, individuals tend to allocate greater resources to sexual seed production, thereby favoring successful establishment of individuals through dispersal (Abrahamson 1979). This finding conforms to the predictions of the strawberry-coral model of Williams (1975), but has recently been questioned (Pitelka, Stanton, and Peckenham 1980; Thompson and Beattie 1981).

This whole approach to the study of reproductive strategy has come under increasing criticism for a number of reasons (Harper 1977; Antonovics 1980; Thompson and Stewart 1981; Abrahamson and Caswell 1982). There are methodological problems. What tissues are appropriately considered reproductive, particularly when many reproductive organs are also photosynthetic? How can environmental variables be more rigorously measured and interpreted than can the simple categories "successional," "stressful," or "density-dependent"? What is the appropriate currency for measurement of reproductive effort—biomass, energy, or particular nutrients? For example, allocation patterns for nutrients are significantly different from those for biomass or energy (Abrahamson and Caswell 1982). There are also problems with the definition of appropriate comparisons and their interpretations. Are differences between early and late successional species really applicable to questions concerning the

evolution of life history simply because such environments are assumed to reflect different selective regimes? To what extent are patterns within species due to selection for ecotypic differentiation or to phenotypic variation? Finally, there are problems that apply specifically to clonal species. Should measures of reproductive effort be based on genets, the units of natural selection? Would such patterns be similar to those seen in ramets? Is ramet production properly to be considered reproduction at all, or is it more appropriately defined as growth enhancing the survival of the genet and future sexual reproduction?

All these problems have rendered suspect any simple interpretations of "reproductive effort" in clonal plants. Such studies appear too crude and variable to provide any critical evidence for the ecological or evolutionary benefits of traits, especially clonal growth and reproduction. An alternative approach involves measuring reproductive strategies in terms of the actual units of production, offspring, along with their survivorship through time. Demographic statistics are much more difficult to acquire, but they promise more precise tests of specific hypotheses.

#### CLONAL PLANT DEMOGRAPHY

An increasing number of studies of the demography of plant populations have been conducted (Harper 1977; Solbrig 1980), some of which involve clonal species (Cook 1983). Plant ecologists, faced with the distinction between ramets and genets and the difficulties of identifying the latter, have studied the demography of clonal plant populations in terms of the birth rate, death rate, and age structure of ramets (Harper and Bell 1979). The underlying identity of genets in natural populations is usually unknown. Most investigators follow a simple methodology for gathering such demographic statistics. Quadrats of variable size are established within populations and the positions of all ramets mapped. At variable intervals a new census is conducted to record the birth of any new ramets or the death of established ramets. The positions of any new seedlings are also identified. Often several different populations in contrasting habitats are compared. Sometimes perturbations, such as the application of fertilizer treatments, are applied. From the census data, standard demographic statistics are calculated. In all cases the subsequent analysis is based on the dynamics of ramets; the dynamics of genets are unknown. These studies have yielded four generalizations that present a rather consistent picture of the demography of clonal species.

1. *The dynamics of clonal plant populations are dominated by the clonal birth and death of ramets; the recruitment of new genets through seedling establishment is rare.* After censusing marked populations of *Primula veris* and *Listera* for nearly thirty years, Tamm (1972) noted that establishment of seedlings was very infrequent. Most

new plants in the population were the product of clonal branching. Similarly, the orchid *L. ovata* recruited approximately two new asexual shoots each year between 1944 and 1977 while losing only six of the original inhabitants. Successful establishment of seedlings of the sand sedge *Carex arenaria* and the herb *Hieracium pilosella* was also very infrequent (Bishop, Davy, and Jefferies 1978; Noble, Bell, and Harper 1979). Sarukhan and Harper (1979), after two years of observation of eight-square-meter plots of the buttercup *Ranunculus repens*, observed a high frequency of seedling germination, usually associated with disturbance such as the hoof prints of grazing cows (Harper 1977). However, the successful recruitment of seedlings was rare and only a few known genets were followed (Soane and Watkinson, 1979). The average seedling survived for approximately five months, whereas daughter plants initiated on epigeal stolons survived three-and-a-half times as long. Although this rate of seedling recruitment appears very low (approximately 3 percent each year), it is probably sufficient to maintain a high diversity of clones in the population (Soane and Watkinson 1979; Sebens and Thorne, this volume).

Because the production of each asexual offspring usually involves a substantially greater maternal investment of resources and a longer period of dependency, the probability of successful establishment is much higher than that of seedlings (table 8.2). In patches of the stolon-forming herb *Hieracium floribundum*, less than 1 percent of the recruitment of new plants is derived from seeds (Thomas and Dale 1975). Reader and Thomas (1977) gathered demographic statistics for this species over a range of densities and constructed a model simulating the growth of a patch. Annual rates of seedling and stolon recruitment, growth, and death were all density-dependent, resulting in a simulated equilibrium density of 33 ramets per square meter in about 25 years. About 10 percent of the population originated through recruitment of seedlings.

If recruitment of new genets is rare, then most of the flux of ramets must involve interactions between clones. A balance between rates of clonal extinction and recruitment of seedlings would result in the maintenance of high numbers of genets. Alternatively, extinction rates may exceed recruitment, and the population will come to be dominated by a few widely spread clones.

**Table 8.2.** Probability of establishment and survival for one year by new genets (seeds and seedlings) versus new, asexually derived ramets in four clonal plant species.

SPECIES	GENET		RATIO (RAMET/GENET)	SOURCE
	(SEED)	RAMET		
<i>Viola blanda</i>	.30	.82	2.7	R. Cook (pers. com.)
<i>Ranunculus repens</i>	.12	.71	5.9	Sarukhan and Harper 1973
<i>Narcissus pseudonarcissus</i>	.005	.045	9.0	Barkham 1980
<i>Hieracium floribundum</i>	.008	.27	34	Thomas and Dale 1975

Recruitment of new genets may occur only after catastrophic disturbance creates abundant safe sites favoring seedling establishment. There is scanty evidence for either alternative.

2. Rates of ramet mortality are relatively constant or increase over years, but they usually vary seasonally. In the long series of observations on *Primula veris* (Tamm 1972), turnover of the population was very low. Individual ramets survived for long periods, and the half-life of one population was approximately 50 years. The rate of mortality appeared constant, although this rate differed considerably for populations in different habitats; site history (succession, mowing) also altered this rate. More extensive data for *Ranunculus repens* (Sarukhan and Harper 1979) revealed a strong seasonal variability within the overall constant rate of loss of initially mapped ramets. Peak rates of death occur in spring, probably due to seedling mortality, and in late summer, when parent ramets begin to senesce and connections to daughter shoots disintegrate. Individual ramets survive approximately 18 months. Lovett-Doust (1981b) repeated this work for woodland and grassland populations of *R. repens*. She counted cohorts of equal-aged ramets for 18 months and found that mortality is strongly seasonal, with the highest rates in August and September (fig. 8.2), when daughter ramets are

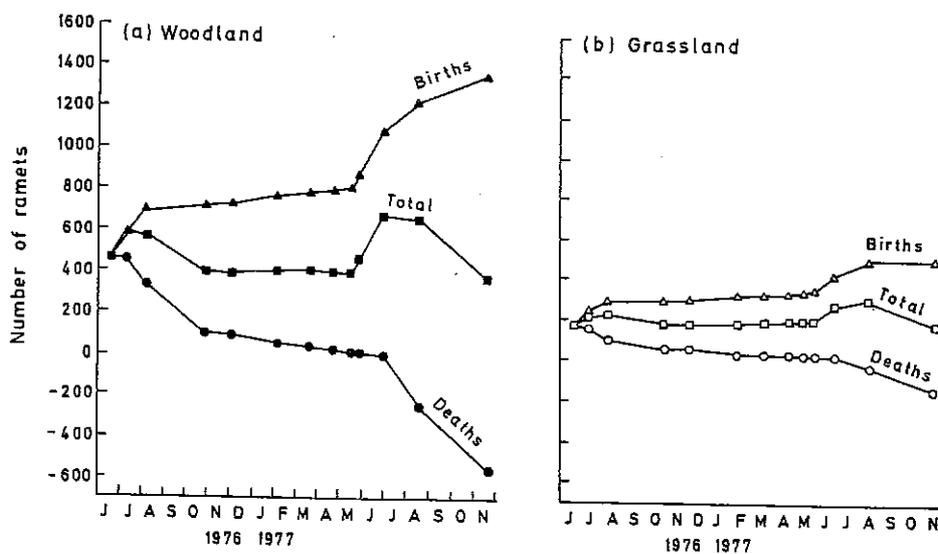


Fig. 8.2. Population densities and cumulative births and deaths among ramets of *Ranunculus repens* in ten  $0.5 \times 0.5$  m quadrats in woodland and grassland populations (redrawn from Lovett-Doust 1981b). Note the two humps in stable population numbers, which indicate that a rise in recruitment rate precedes a rise in the death rate. Highest rates of death are in late summer and fall, when newly formed daughter ramets are becoming physiologically independent. (Reprinted with permission from Dr. Brian Hopkins, Editor, *Journal of Ecology*, New England College, Tortington Park, Arundel, West Sussex BN18 0DA, United Kingdom.)

achieving independence. Unlike Sarukhan and Harper (1979), she discovered very few seedlings, and spring mortality rates were relatively low. Strongly seasonal mortality rates are also observed in ramets of *Carex arenaria* (Noble, Bell, and Harper 1979). Each shoot can live up to two years after initiation in early summer; it must survive through winter before it can develop flowers, and ramets inevitably die following seed dispersal. Thus the highest rates of death occur in late summer and fall.

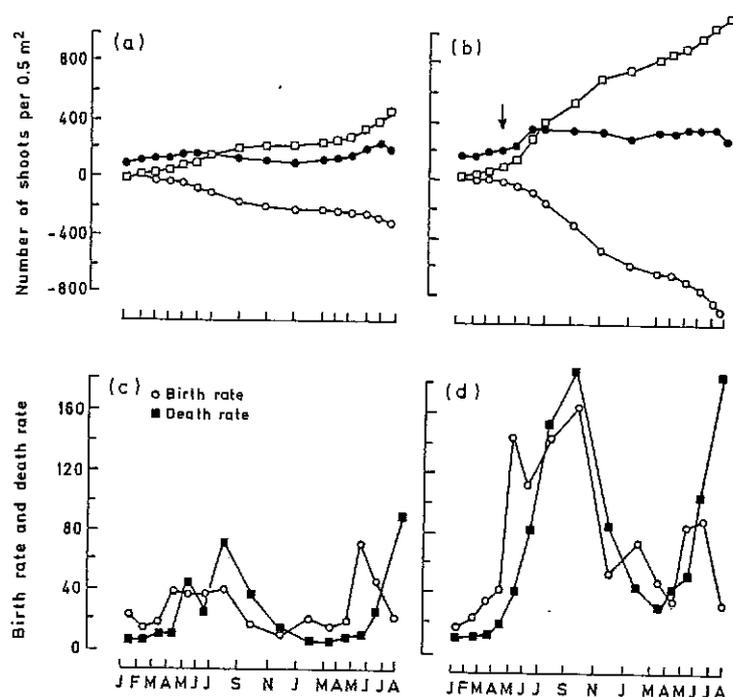
3. *Population numbers remain relatively constant despite a great flux of ramets because birth and death rates are equal and synchronous.* The most important finding of Sarukhan and Harper (1979) was the remarkable stability of buttercup populations despite high rates of birth and death (see also Hughes and Jackson 1980, n.d.; Jackson, this volume, for similar patterns in clonal animals). For instance, a plot in which 117 ramets were mapped in April 1969 experienced a modest increase to 139 by April 1971. Yet during this interval more than 244 new ramets were born and 222 ramets died. Lovett-Doust found a similar stability in ramet numbers among *R. repens* in both woodlands and grasslands (fig. 8.2). Since so few seedlings were observed in this study, the great flux of plants must involve the asexual production and death of ramets.

Relatively constant population numbers amid high turnover of ramets has also been found in *Viola blanda* (Newell, Solbrig, and Kincaid 1981), *Hieracium pilosella* (Bishop, Davy, and Jefferies 1978), *Eriophorum vaginatum* (Fetcher and Shaver 1983), and *Carex arenaria* (Noble, Bell, and Harper 1979). In each instance death rates appear to match birth rates. For example, Noble, Bell, and Harper counted 160 shoots of *C. arenaria* in a half-meter plot of high-density *Carex*. One year later shoot numbers had dropped to 149, yet during this period 355 new ramets had emerged and 366 had died (fig. 8.3). In all cases that permit accurate calculations, a rise in birth rate is followed by an increase in death rate (fig. 8.3), leading to a seasonal hump in population numbers.

The usual interpretation of synchronous birth and death rates has been density-dependent regulation of population numbers. The implied mechanism is competition between ramets for limited resources in the habitat, leading to an increase in mortality. This view has been succinctly stated by Noble, Bell, and Harper (1979:1006):

The seasonal cycles of birth and death rates of shoots were generally so closely synchronized that it is difficult to believe they are not causally related. It can be surmised that it is the birth of new shoots that generates the density stress responsible for the death of old shoots. Similarly, the high birth rate stimulated by fertilizer addition may itself cause the density stress that shortens the expectation of life of older shoots.

Although interramet competition is suggested as a mechanism for regulating



**Fig. 8.3.** Population densities, cumulative births and deaths, and rates of birth and death among ramets of *Carex arenaria* in sand dunes (redrawn from Noble, Bell, and Harper 1979). Population densities in control (a) and fertilized (b) plots. ● = net shoot populations, ○ = cumulative deaths, □ = cumulative births. Birth and mortality rates in control (c) and fertilized (d) plots. Note that mortality rates follow high birth rates and that increasing the fertility of the plot increases the flux of ramets in the population. ○ = birth rate, ■ = death rate. (Reprinted with permission from Dr. Brian Hopkins, Editor, *Journal of Ecology*, New England College, Tortington Park, Arundel, West Sussex BN18 0DA, United Kingdom.)

numbers, evidence for competition has been more difficult to find. Sarukhan and Harper (1979) could find no relationship between mortality and density in buttercups, though the probability of ramet production declined with density. Likewise, Waller (1981) and Schellner, Newell, and Solbrig (1982) found no evidence of neighborhood competition or effects of density on growth and mortality of ramets in eight populations of *V. blanda*.

4. *Increase in availability of resources increases both birth rates and death rates synchronously with modest effects on population numbers.* Evidence for this generalization is scanty and somewhat inconsistent. Application of fertilizer treatments to plots of *Carex arenaria* led to rapid initiation of growth among many dormant buds on the underground rhizomes, doubling the birth rate, followed by a similar doubling of the rate of death (Noble, Bell, and Harper 1979). The

average density of ramets increased from approximately 150 to only 200, despite the birth of more than 1,000 new ramets. Similarly, severe disturbance to the soil surface (vehicle tracks and vegetation removal) led to higher rates of tiller production and mortality in the tussock-forming cottonsedge *Eriophorum vaginatum* in the Alaskan tundra (Fetcher and Shaver 1983). Higher concentrations of foliar nitrogen and phosphorus in these plants suggests that disturbance increases the availability of resources to colonizing plants. However, application of fertilizer to another tundra site increased tillering rate but failed to stimulate mortality.

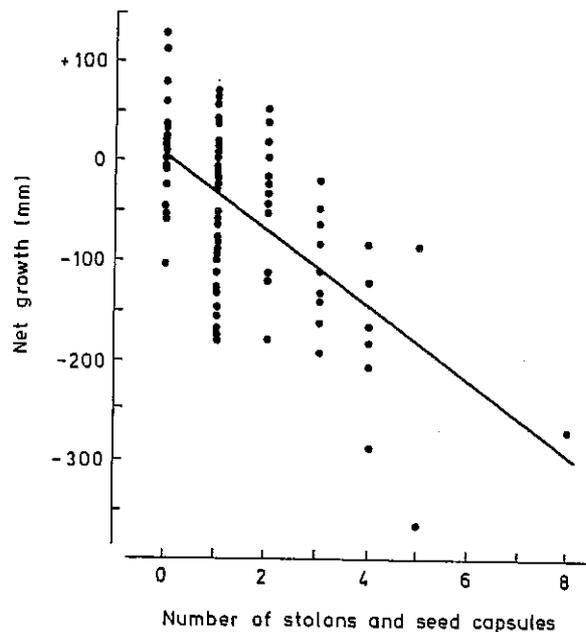
The overall picture is one of population stability amid a great flux of ramets due to high death rates following high birth rates, with density-dependent competition among ramets the primary mechanism regulating numbers of shoots. Increases in availability of resources increase rates of birth and death equally, with relatively minor effects on population numbers, and rates of recruitment of new genets are relatively low.

This interpretation of the dynamics of clonal plant populations has recently been questioned (Cook 1983) because of two limitations in the evidence. First, the genet identities of ramets are unknown. Because genets usually survive longer than their constituent ramets, demography based solely on ramets will give a very misleading picture of the flux of genetic individuals in the population (see also Hughes and Jackson 1980, n.d.; Hughes n.d.; Jackson, this volume). For instance, rates of ramet mortality in *Viola blanda* fall for three years after the germination of seedlings and then rise again in the fourth or fifth year of life. In striking contrast, rates of genet mortality continue to decline through time (Cook 1983). Because ramets have generally been studied without knowledge of their clonal identities, relations between birth and death rates have necessarily been inferred from average statistics. However, these data are insufficient to determine whether individual births and deaths are related in a causal manner.

The second limitation in the density-dependent interpretation is the assumption that the birth, performance, and death of ramets in a population are independent of their clonal identity and similar to that of a clonal plants. From this it follows that the interactions between individual shoots are mediated entirely by competition for external resources. However, ramets within a clone are rarely independent (Pitelka and Ashmun, this volume). Performance of ramets may be in part determined by shortages of resources due to the presence of neighboring plants; but it may also be greatly affected by the growth and development of other physiologically interconnected ramets within the clone too distant for direct above-ground interference.

Clones of many plant species may remain physiologically integrated well beyond the initiation and establishment of daughter ramets (Pitelka and Ashmun, this volume). Specific studies, often using labeled assimilates (Ginzo and Lovell 1973; Chapin, van Cleve, and Chapin 1979; Tietema 1980; Tietema

and van der Aa 1981; Newell 1982) have revealed extensive physiological integration in clones of *R. repens*, *E. vaginatum*, *C. arenaria*, and *V. blanda*. Both movement of new assimilates to support establishment of daughter ramets and redistribution of resources from senescence of older shoots contribute to this physiological integration. Lovett-Doust (1981a) also demonstrated parent-daughter dependence by severing stolons connecting parent shoots and developing daughter ramets of buttercups. This prevented transfer of resources between parent and daughter and led to a reallocation of growth. Daughter ramets initiated a more substantial root system, suggesting an earlier reliance on the parental root system. Parent plants increased the number of leaves, presumably with resources that would have been transported to developing stolons, and their leaves failed to senesce as did those of control plants. In *V. blanda*, careful census of clones has revealed a negative relation between the future net growth of a ramet and the number of daughter stolons it produced (Cook 1983; fig. 8.4). This probably represents the differential movement of resources supporting regrowth of parent and daughter ramets in spring. Abundant evidence exists, therefore, that ramets within clones are not indepen-



**Fig. 8.4.** Negative relationship between net growth (growth in size in year 2 minus growth in size in year 1) of *Viola blanda* plants and the number of stolons and seed capsules they produced in year 1 (Cook 1983). The correlation coefficient is  $-0.44$  and is highly significant. This relationship probably represents allocation of resources to growth of daughter plants over the parent plant, leading to eventual death of the parent and movement of the clone in space.

dent and that, for some period of time, clones function as integrated organisms at the physiological level.

Recognition of the integrated nature of clonal growth and reproduction permits an alternative interpretation of the demography of ramets of clonal species (table 8.3). The appearance of new ramets at the soil surface (birth) followed by the disappearance of an old ramet (death) may simply represent the growth of an integrated clone. Development of an axillary bud and the emergence of a young, actively growing shoot creates a sink for assimilates and for resources recovered from senescing tissue. The death of a ramet follows the developmentally programmed senescence of older shoots within the clone. Breakdown products of metabolism are transported within the clone to actively growing sinks much as mineral resources in the older leaves of a shoot are transported to younger leaves of the apical meristem following leaf senescence (Chapin 1980). Much of the "death" in a population may simply be the monocarpic flowering of ramets independent of local density. If, on average, growth of a single daughter shoot leads to senescence of a single older shoot, the number of ramets at the surface would remain constant. Birth rates would usually precede death rates, and the population of ramets at the surface would remain stable despite a great flux of shoots. Application of fertilizer, or release of resources following disturbance, probably stimulates growth of daughter buds due to loss of apical dominance (Phillips 1975). Creation of actively growing sinks for assimilates accelerates rates of tissue senescence in other parts of the clone, possibly by stimulating flowering, thus leading to ramet death at the surface. Similarly, integrated patterns of modular growth and mortality have been proposed for clonal animals (Palumbi and Jackson 1983).

This developmental interpretation can explain certain critical aspects of the

**Table 8.3.** A demographic versus developmental interpretation of clonal plant population dynamics.

DEMOGRAPHIC INTERPRETATION	DEVELOPMENTAL INTERPRETATION
1. Population change represents a demographic process of ramet birth and death.	1. "Population" change represents a developmental process of ramet initiation and senescence within clones.
2. Population regulation is mediated through density-dependent competition.	2. "Population regulation" represents the reallocation of resources from old to new tissue and the movement of the clone in horizontal space.
3. Recruitment of ramets is determined by competition between neighbors for external resources.	3. Recruitment of ramets is partly determined by a developmental program as well as the complex configuration of surrounding genets.
4. Mortality represents a potential decline in the fitness of the population.	4. "Mortality" represents a potential increase in genet fitness through a more efficient acquisition of patchy resources.

demography of the clonal species reviewed earlier. First, the mortality of older ramets of *Carex* appears to *follow* the birth of new shoots. This might represent density-dependent regulation, but it is not clear why small, developing ramets are competitively superior to larger, established ramets when the reverse might have been expected. In addition, peak mortality rates of *Ranunculus* occur in late summer and fall. This is a time when daughter ramets initiated earlier in summer are achieving independence through senescence of stolon connections. As noted by Sarukhan and Harper (1979), most parent ramets die, suggesting that this mortality is related to establishment of daughter ramets. The severing experiment of Lovett-Doust supports this interpretation. Ramets of both *Carex* and *Hieracium* are monocarpic, and the timing of flowering may be seasonally controlled by such factors as vernalization and photoperiod. Development of the inflorescence in *Hieracium* initiates stolon formation from the axillary buds of basal rosette leaves; subsequently the parent shoot dies after establishment of the daughter plant (Yeung and Peterson 1972). Second, the failure to find evidence of external competition in *Viola blanda* (Waller 1981; Schellner, Newell, and Solbrig 1982) could be due to the complex nature of genet interactions: the performance of an individual ramet will depend not only on the constellation of neighboring shoots (external competition), but also on the number and performance of other ramets remaining physiologically connected within the clone (internal integration).

It is important that future studies of clonal plant demography recognize the consequences of physiological integration; effects of developmental events within a clone should be distinguished from demographic events between ramets. Two pieces of information are essential. First, the number and identity of genets within populations must be known (Silander, this volume). Demography conducted on ramets of unknown genetic identity will continue to give misleading information concerning the dynamics of the population, particularly the dynamics of the units of selection (genets). Second, understanding of the extent and duration of physiological relations within clones must be increased. Part of this involves the developmental ecology of daughter-ramet production, including factors that determine the timing and control of ramet initiation, and the degree of resource support provided by the parent plant. It will also involve the extent to which ramets that retain physical connections are able to regulate physiological interactions in relation to habitat factors external to the clone.

## MORPHOLOGY AND PHYSIOLOGY OF CLONAL PLANTS

### DEVELOPMENTAL REGULATION OF CLONAL GROWTH

Mechanisms controlling ramet development and clonal integration are fundamental attributes of the population biology of clonal plants. Two aspects

of plant metabolism are involved. First, assimilation and transport of resources, such as carbon, water, and mineral nutrients, throughout the clone will control the capacity for new ramet growth and development (Pitelka and Ashmun, this volume). Most studies have concentrated on movement of carbon compounds between ramets, which appears to be controlled by the location of developmental sinks (sites of vigorous growth and metabolism) within the clone relative to sources of carbon in older ramets. A second aspect of plant metabolism concerns the role of internal growth hormones and the effects of external environmental factors (temperature, photoperiod, light, moisture, and nutrients) on the growth and development of ramets. Very little research has been done here, and nearly all of it involves economically important species such as aspen (*Populus*), assorted weeds (*Hieracium*, *Agropyron*), and the potato with its wild relative (*Solanum*). Various ecologically important aspects of the hormonal control of growth and development in ramets are reviewed below; root buds and axillary branches (rhizomes, stolons, bulbils) are considered separately.

*Root buds.* Ramets of many clonal species grow from buds that are regularly initiated within the tissues of the major roots of the parent plant (Peterson 1975). Root buds are often associated with lateral roots; in many woody species, they may remain dormant for variable periods, possibly due to inhibition by local soil conditions or influence of the parent plant or other surrounding shoots. No work has been conducted on the population biology of such root-derived ramets.

The parent plant exerts a dominant influence over the development of root buds into shoots. Conditions that inhibit vigorous vegetative growth of the parent lead to initiation of daughter ramets. Thus surgical removal of part or all of a shoot, or girdling the primary stem or proximal section of a root, will stimulate bud growth. Natural factors, such as the approach of winter dormancy or the period of full bloom, give a seasonality to the formation of new ramets. These effects probably involve inhibition of bud growth by concentrations of auxin produced in the parent; formation of buds on excised segments of roots in culture is stimulated by lowering the concentration of auxin in the medium.

In a similar way cytokinins stimulate root bud initiation and shoot formation in cultured roots (Peterson 1975). Application of cytokinins to local sites on root segments leads to callus formation, root initiation, and subsequent shoot development. However, there is little direct evidence that cytokinins are involved in formation of ramets in the field. Gibberellic acid (GA) inhibits bud initiation when applied to whole plants, but this may reflect an indirect effect following stimulation of parental shoot growth. GA has different effects on root segments, depending on the stage of bud ontogeny: bud initiation is inhibited, but the elongation of growing buds is stimulated.

Application of nitrogen compounds greatly promotes root bud initiation in

some cases (Peterson and Thomas 1971; Peterson 1975), but the concomitant release of axillary buds on the parent shoot can lead to subsequent root bud inhibition (McIntyre 1972). Excision of these parental axillary branches is followed by root bud elongation. Nitrogen increases both the number of buds and their rate of growth, whereas light has little effect on early bud development. Short photoperiods stimulate bud formation, but this may reflect indirect effects on growth of the parent plant.

In summary, bud initiation is probably controlled by local concentrations of auxin and cytokinin, and the former is determined by the vigor of the parent. Moreover, nutrients such as nitrogen stimulate bud formation, possibly through local proliferation of roots that may affect the auxin-cytokinin ratio.

*Axillary buds.* Both hormones and environmental factors also regulate the development of rhizomes and stolons. Quack grass (*Agropyron repens*) and potato (*Solanum tuberosum* and *S. andegina*, the wild progenitor) form daughter ramets through initiation of horizontal growing stems from the lowest axillary buds on the parent shoot. These stems grow as stolons or rhizomes on or below the soil surface and initiate tubers or shoots some distance from the parent plant. Each developmental stage—initiation, lateral growth, shoot formation—is controlled by a complex interaction between the hormonal and nutritional status of the parent and the local growing conditions of the daughter plant.

In quack grass seedlings, the buds in the axils of the coleoptile and the first two leaves can potentially form either a rhizome, which grows laterally, or an erect tiller with green leaves. Low levels of nitrogen or growth at low temperatures favors rhizome initiation, whereas the reverse conditions lead to tiller formation (McIntyre 1967). Supplying a higher level of nitrogen after rhizomes have begun growth causes the tip to turn up and develop into an erect shoot. Light intensity, per se, has no effect on the development of these buds, but decreasing the photoperiod from 18 to 9 hours inhibits rhizome formation and stimulates tiller development. The rhizome itself possesses a series of dormant buds that are axillary to scale leaves formed along its length (McIntyre 1970, 1972). At low nitrogen levels, growth of these buds is normally inhibited by dominance of the rhizome apex. Severing the apex causes the nearest bud to begin growth and form an erect shoot. The next several buds on the rhizome also initiate lateral growth as new rhizomes while those buds closest to the parent plant remain dormant. Increasing temperature or decreasing light intensity favors formation of tillers rather than rhizomes in lower buds. Moreover, when nitrogen is fed to the cut end of the rhizome, or applied to the rooting medium of the parent plant, more tillers are formed. Under field growing conditions, increasing the moisture level surrounding a rhizome causes adventitious roots to proliferate from axillary nodes; these lateral buds are released from apical inhibition to form additional rhizome branches (McIntyre 1976).

The relative concentration of plant hormones also regulates development of stolons and daughter ramets in *S. tuberosum* and *S. andegina* (Cutter 1978). Two developmental stages are involved: initiation and growth of stolons from the lowest axillary buds on the parent shoot and subsequent formation of a tuberous storage organ at the end of the growing stolon. The first stage is strongly promoted by longer photoperiods, and tuberization is stimulated by shorter photoperiods. All the axillary buds on the parental shoot can potentially form stolons. However, growth of the upper axillary buds is normally inhibited, whereas the fate of lower axillary buds—whether they remain inhibited, grow as horizontal stolons with scale leaves, elongated internodes, and an apical hook, or develop an erect, leafy branch—is partly determined by local conditions surrounding the basal nodes. Moisture and darkness, for instance, stimulate the growth of stolons.

Development of these basal buds is also influenced by the presence of actively growing roots and a vigorous shoot on the parent plant. If this shoot is decapitated under long-day conditions, the upper axillary buds will grow out as leafy branches and the basal buds will form stolons. If the upper buds or branches are all removed, the lower buds and stolons will transform into erect shoots. However, if both the upper buds and the roots are removed from decapitated plants, stolons rather than leafy branches will be formed. Thus the presence of roots promotes shoot formation, but this effect is overridden and stolons are formed if the bud is subject to apical dominance (Kumar and Wareing 1972).

These morphological effects are mediated by at least three plant growth hormones interacting with environmental factors (Wooley and Wareing 1972a, 1972b; Kumar and Wareing 1972). Under the influence of apical dominance mediated by auxin, the growth of upper axillary buds is inhibited while basal buds are permitted to develop, particularly those in the moist, dark conditions of the soil. The form of the growth, stolon or shoot, is controlled by the relative concentrations of shoot-produced gibberellins, which favor stolons, and root-produced cytokinins, which favor shoots. Removing apical dominance, decreasing light, or increasing mineral nutrition all favor transforming stolons into shoots through changes in concentrations of endogenous hormones. These specific effects are set into a seasonal context by changing photoperiod.

In *S. andegina*, the parent plant controls tuber formation (Cutter 1978). The tuber represents the enlarged, starch-filled end of the stolon with numerous lateral axillary buds (eyes) and an apical bud. It will not develop unless the parent experiences a sequence of short photoperiods and/or low night temperatures. The appropriate stimulus is formed in the leaves, moves to the lowest axillary buds and through the stolons to the tip. Extension growth then ceases, cell division increases, and sugars are transformed into starch. Eventually the tuber acquires dormancy. Although the nature of the stimulus initiating tuber

development is unknown, growth hormones are clearly involved (Kumar and Wareing 1974; Cutter 1978). Short photoperiods, for instance, cause a striking decrease in the concentrations of endogenous gibberellic acids followed by the reallocation of most photosynthates to the growing tuber. The application of exogenous gibberellins can reverse these effects by inhibiting tuber growth and transforming starch to sugars.

The ecological significance of the above regulatory processes controlling ramet development may be summarized as follows:

1. The physiological integrity of an independent ramet depends on a balance between shoot growth and root growth.
2. Growth of a clone involves a balance between lateral growth of the daughter ramet and vertical growth of the parent shoot/root system.
3. Vigorous shoot growth of the parent promotes lateral growth of the daughter ramet; vigorous root growth of the parent promotes vertical shoot growth of the daughter.
4. The relative influence of the parent decreases with distance from the daughter ramet; the relative influence of local conditions of the habitat surrounding the daughter ramet increases with distance.
5. In a seasonal environment, changing photoperiod shifts the balance of daughter growth from lateral to vertical (stolon to shoot/root), possibly by shifting the relative balance of parental growth from shoot to root.

Examination of these generalizations will require field studies to determine effects of season (photoperiod, temperature) and habitat heterogeneity (moisture, soil nutrients) on the developmental ecology of daughter ramets. Future research should also focus on the physiology of roots and their role in affecting clonal form. This may involve either the roots of parent plants or the adventitious roots formed on developing daughter ramets. Heterogeneity in the distribution of soil nutrients and water, and its effect on the induction of root growth, may prove to be the most important selective force shaping the morphology of a clone and its underlying mechanisms of regulation.

#### IDEAL AND REAL CLONE MORPHOLOGY

Despite the considerable body of work done by plant physiologists on the growth and development of some clonal species, plant morphologists typically have not been concerned with the proximal mechanisms controlling clone form. Rather, they have taken an architectural approach and stressed how the modular construction of individual plants may be achieved through a process of branching (Harper 1981, this volume; Waller and Steingraeber, this volume). The module is loosely defined as a multicellular structure or unit of construction that is iterated during growth. For the individual shoot, the leaf with its associated axillary bud is considered a convenient module; for a clone, each

ramet may be taken as a module. Modular construction clearly lends a tremendous plasticity to plant development, and the growing individual resembles a population of modules, with characteristic rates of birth (branching) and death (senescence) determining the size of the shoot (White 1979). Thus growth itself becomes a demographic process (Harper 1980).

Because plants are fixed in space and lack neurological behavior, the form or architecture of the rooted shoot is a critical mechanism adapting an individual to life in one location. Recognizing the importance of modular growth, plant morphologists have developed a classification scheme that relies on the existence of architectural models to describe plant form (Halle, Oldeman, and Tomlinson 1978). The utility of this approach depends on the existence of "genetic blueprints" specifying the timing and development of modular branches. The architectural concept of plant form can also be applied to the pattern of ramet proliferation in clonal species. Form results from repeated branching of ramet modules, and successful classification of species should hinge on the precision with which the branching process repeats itself.

Because the spread of a clone involves the branching of modules in a plane, the rules determining form are potentially very simple (see Waller and Steingraeber, this volume, for a discussion of branching models). In the simplest mode, these "rules of growth" consist of the angle of divergence from the direction of parental growth, the length of the internode, and the fate of the daughter module (or bud, meristem). A meristem may either remain dormant, die, or grow itself and produce branches. An analysis of natural clones should permit the specification of these rules of growth and the presumed underlying genetic blueprint governing clonal form. Once a set of rules has been identified, a computer model can be created to simulate clonal growth and predict the form of the genet after a specified number of generations. By varying the parameters with which the model is initially constructed, the plant ecologist may be able to determine which rules create an optimal distribution of ramets in the plane. Clearly, however, the utility of such a simulation hinges on the relationship between the constructional basis of the model and that of real clones in nature.

Examination of rhizome architecture in several species has led to the suggestion (A.D. Bell 1974, 1979; A.D. Bell and Tomlinson 1979; Harper and Bell 1979) that rather precise rules of growth govern clonal form. This has permitted construction of computer simulations that display the theoretical form of the genet through time (A.D. Bell 1976). The precision of the rules of growth led Bell and Tomlinson (1979) to conclude that genet architecture is adaptive and that selection has favored precise organization to maximize the opportunity for economic exploration and exploitation of the resources in a plane (Smith and Palmer 1976; A.D. Bell and Tomlinson 1979). In particular, angles of divergence approximating  $60^\circ$  lead to the formation of a hexagonal

grid of ramets that uniformly sample or tessellate the horizontal space of the habitat, thereby minimizing the structural material needed to support a closed canopy of leaves. Maladaptive overlap of ramets, which would result from a perfect hexagonal arrangement, is avoided by small asymmetries and variations in growth parameters (A.D. Bell 1979).

Although models of clonal plant architecture clearly have value (Waller and Steingraeber, this volume), this approach to the morphology of plant clones rests on several untested assumptions. First, it is assumed that divergence angles, internode lengths, and the fate of meristems are primarily or entirely determined by genetically based rules of growth, although no genetic analyses have been performed. Second, it is assumed that these "rules" are precise enough to achieve the full and efficient occupation of space by ramets. Finally, it is assumed that selection will favor full occupation of space to maximize the acquisition of resources with minimal structural costs, although the distribution of resources in space has not been determined.

These assumptions have remained untested, in part, because the architectural approach to plant morphology has tended to focus on the ideal design of organisms rather than on the actual form such organisms display in nature. Rules of growth are derived from the mean of field measurements, and the natural variation due to environmental influences or the variability of internal growth is obscured or ignored in computer simulations. These models are primarily deterministic rather than stochastic (see Waller and Steingraeber, this volume), and the resulting geometrical patterns of ramet distribution bear little resemblance to the real distribution of ramets in the field. Consequently, adaptive interpretations of the rules of growth must be invoked very cautiously; selection will operate on the actual distribution of ramets under field conditions (phenotypic expression), not the underlying model (presumed genotypic blueprint).

A frequently cited example of geometric architecture of rhizomes is the pattern of clonal growth in *Medeola virginiana*, a herbaceous perennial of the forests of eastern North America (A.D. Bell 1974; Harper and Bell 1979; Harper 1981). A single stem with one or two whorls of leaves develops from an overwintering tuber. Bell (1974) examined clonal growth in this species by excavating plants and describing the apparent regularity of its "rules of growth." Upon these he based a simulation model that projected the growth of a clone into the future (fig. 8.5). According to Bell, each underground tuber forms only two daughter tubers during the summer: (1) the distal daughter tuber is formed from an axillary bud at the base of the parent plant, which continues the linear growth direction of the parent axis; (2) the proximal daughter tuber, which grows half as long as the distal tuber, originates from an adventitious bud at the base of the parent tuber and diverges at an angle of 45°. Three other rules govern the behavior of clonal growth: (3) the adventitious bud

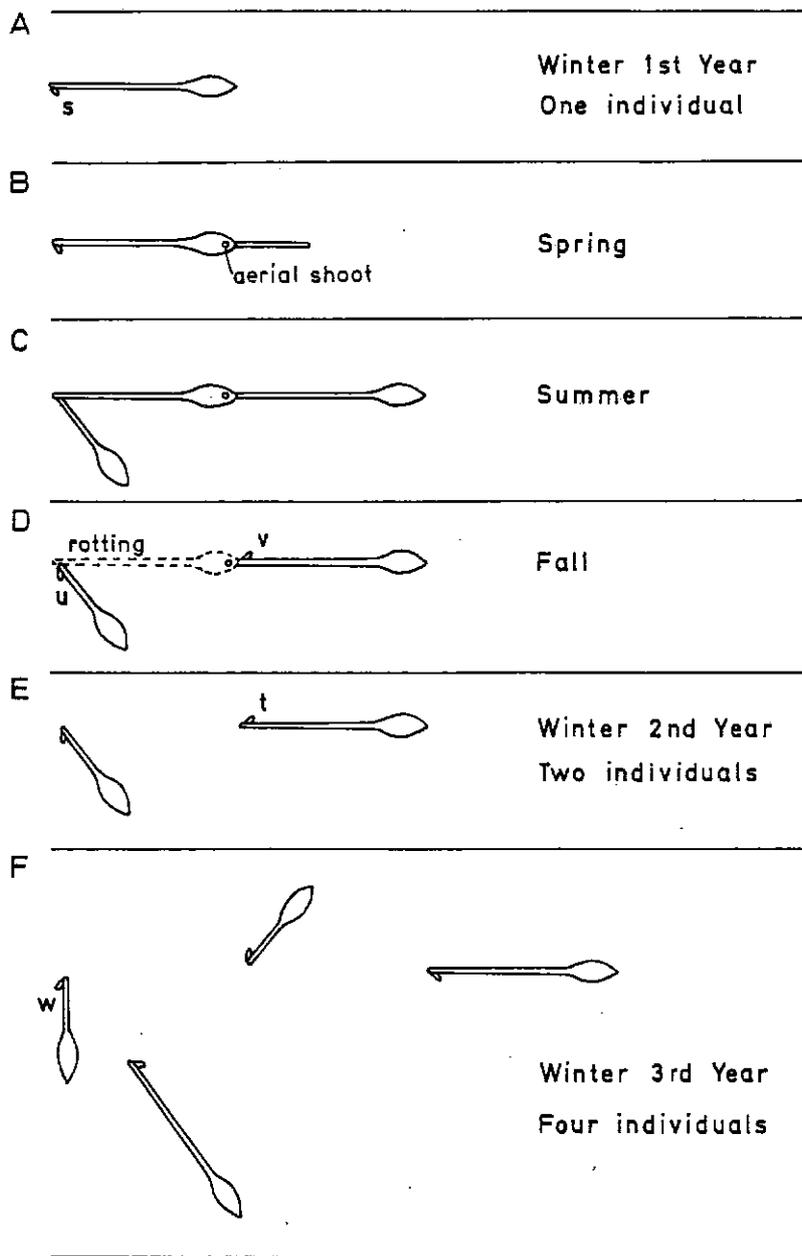
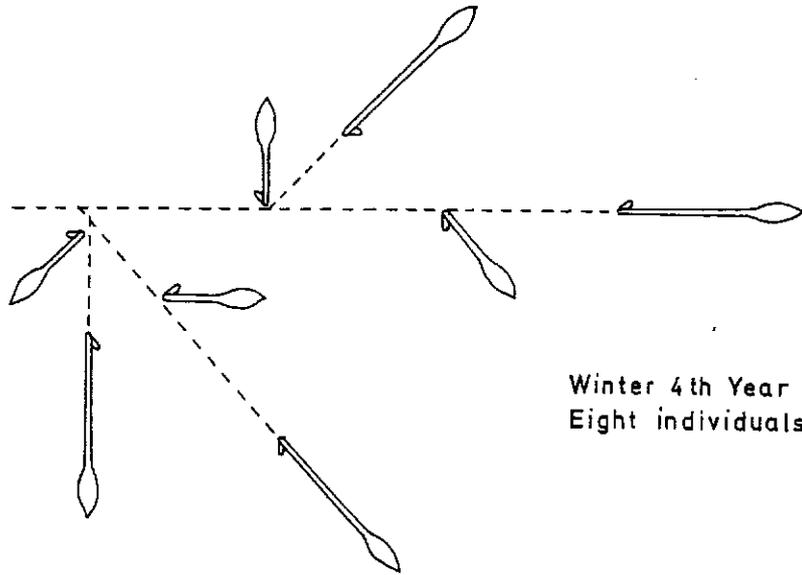


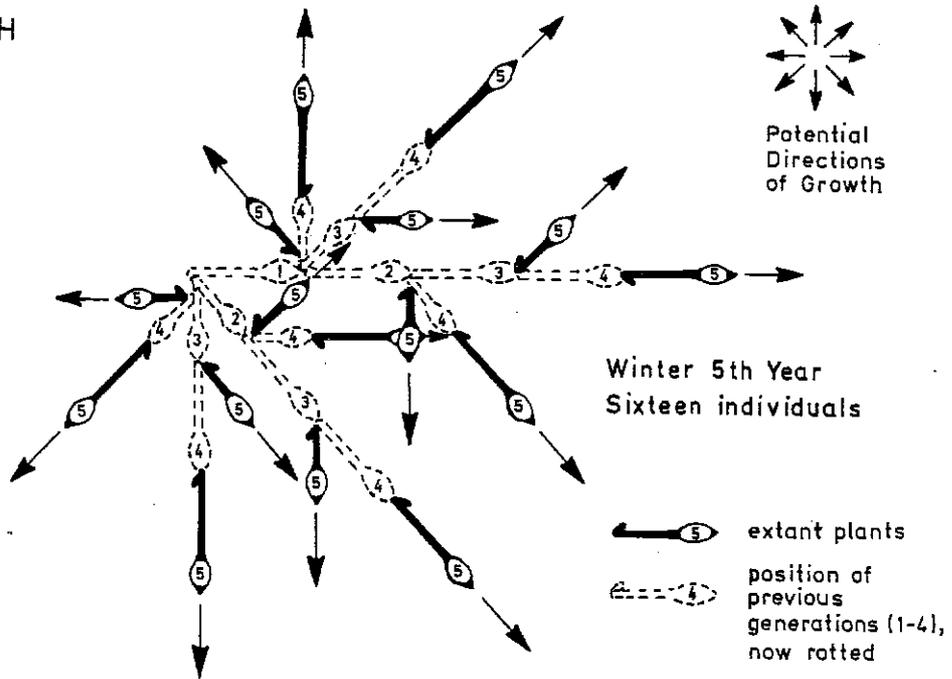
Fig. 8.5. The ideal pattern of clonal growth in *Medeola virginiana* (redrawn from Bell 1974). (Original published in the *Journal of the Arnold Arboretum*, vol. 55, 1974.)

G



Winter 4th Year  
Eight individuals

H



Winter 5th Year  
Sixteen individuals

that forms on the distal daughter tuber is located on opposite sides each generation; (4) the adventitious bud that forms on the proximal daughter tuber is located on the same side each generation; (5) the parent shoot and its associated tuber live only one year. Growth according to these rules leads to the octagonal occupation of space, thus achieving a predictable and efficient pattern of clonal expansion.

This predictability of growth has recently been questioned (Cook n.d.). Twelve square meters within a population of *M. virginiana* were excavated and mapped at the end of the growing season in a young white pine forest in Concord, Massachusetts. From the position of grandparents, parents, and daughter plants, the length of internodes and the angles of divergence were measured for all clonal extensions. This permitted the precise and statistical description of growth to be constructed on the basis of 213 parent shoots.

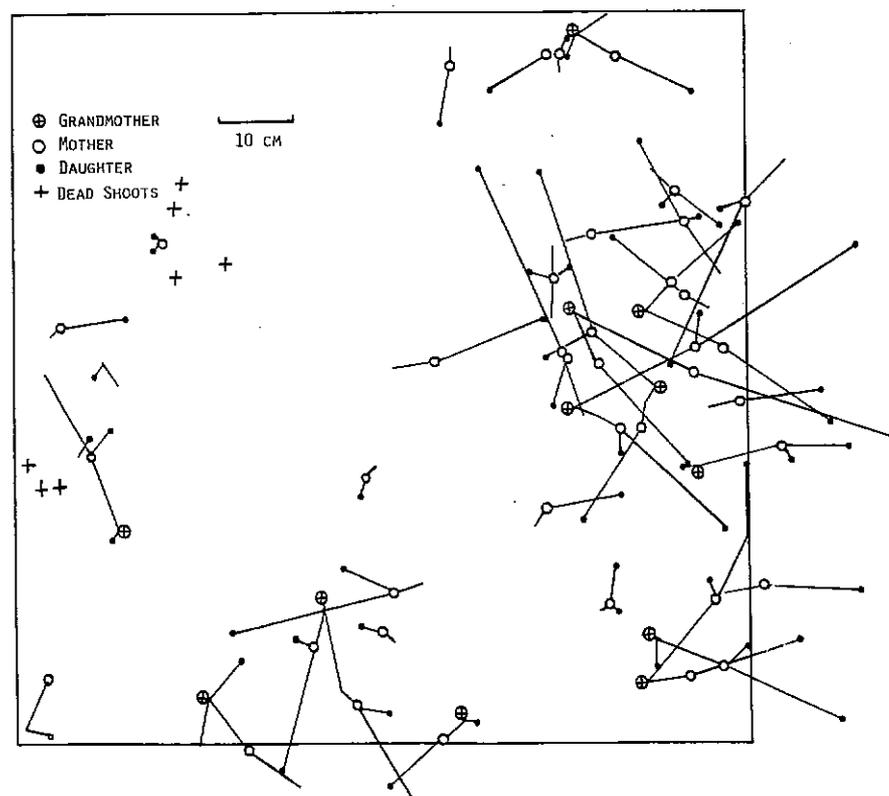


Fig. 8.6. Mapped clones within one square meter of a real population of *Medeola virginiana*. Shown are three generations of plants: grandmother shoots, whose position is indicated only by the traces of the proximal ends of stolons; mother shoots, whose position is indicated by extant plants; and daughter plants, whose position is indicated by extant tubers revealed by excavation. Crosses indicate dead shoots whose underground tubers had been eaten by small mammals.

The general conclusions from this study have important implications for all attempts to create deterministic models of clonal growth and for any adaptive interpretations of the geometric patterns of ramet location.

First, growth in *Medeola* is much more complicated than Bell's "rules of growth" might indicate (fig. 8.6). One, two, or three daughter plants are formed with probabilities of 0.40, 0.46, 0.14, respectively. Most of this proliferative production of daughter ramets occurs through growth of the second distal axillary bud at the base of the parent plant, rather than the proximal bud at the base of the stolon. Growth of the first distal bud is not linear in the direction of the parent growth axis, but diverges approximately  $15^\circ$  to the left or right with equal probability. The angle of divergence of secondary distal daughters from the axis of parental growth averages  $63^\circ$ , that of the proximal daughters,  $93^\circ$ .

Second, in nature all internode lengths and angles of divergence are highly variable (fig. 8.7 and table 8.4). Coefficients of variation approximate 40 percent, with the highest variation in the angle of divergence of the primary distal daughter tuber. Part of this variation seems to be due to interaction of the tip of the growing stolon with the physical medium of the soil. Additional variation may result from ability of the stolon to respond to environmental

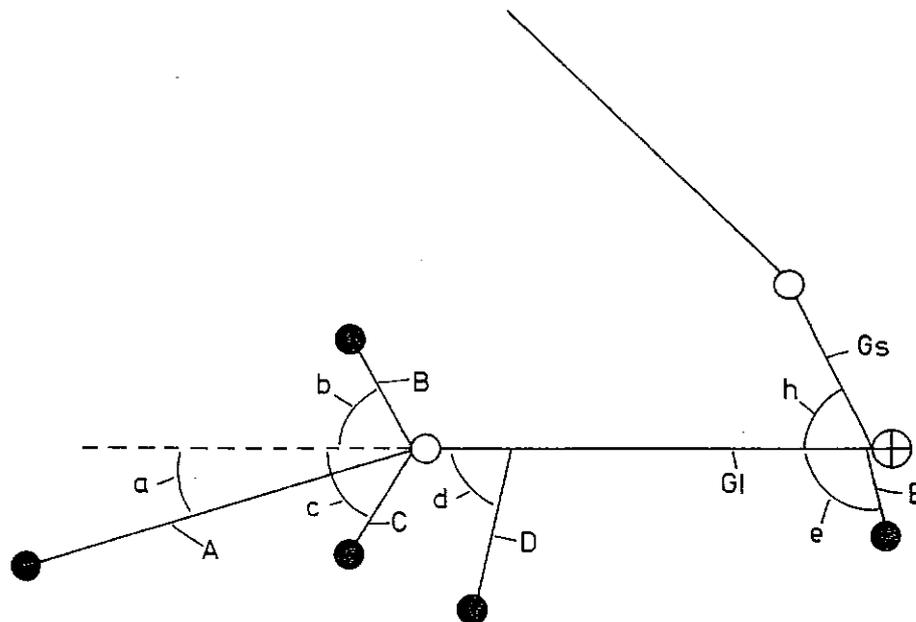


Fig. 8.7. Measured growth parameters of mapped clones of *Medeola virginiana*. Above is shown a hypothetical plant with three generations. Letters indicate respective internode lengths and angles of divergence. In table 8.4 the means and coefficients of variation are presented. Sample size ( $n$ ) gives some indication of the frequency of each growth parameter out of the total of 213 individuals measured. Fewer internodes than angles indicates loss of some tubers to herbivory.

**Table 8.4.** Average values of growth parameters for clones of *Medeola virginiana* in Concord, Massachusetts.

INTERNODE LENGTH	MEAN $\pm$ STANDARD ERROR (CM)	COEFFICIENT OF VARIATION	n	ANGLE OF DIVERGENCE	MEAN $\pm$ STANDARD ERROR (DEGREES)	COEFFICIENT OF VARIATION	n
A	14.9 $\pm$ .5	45%	198	a	15.5 $\pm$ 1.0	92%	213
B	4.6 $\pm$ .2	44%	110	b	63.1 $\pm$ 2.2	37%	110
C	4.1 $\pm$ .4	38%	16	c	65.1 $\pm$ 11.1	42%	17
D	6.5 $\pm$ .6	30%	12	d	82.3 $\pm$ 4.3	17%	17
E	3.7 $\pm$ .3	61%	50	e	93.1 $\pm$ 5.2	39%	51
G <sub>1</sub>	15.7 $\pm$ .6	26%	43	h	61.2 $\pm$ 3.2	35%	46
G <sub>2</sub>	6.5 $\pm$ .3	35%	43				

Note: See fig. 8.8 for diagram.

variables such as light, soil depth, and gradients of resources (Cook 1983). In either case this natural variation quickly reduces the predictability of daughter ramet location based on a knowledge of the parent. Species probably differ in the degree of variation expressed by growth patterns. The coefficient of variation for rhizome angle in *Solidago canadensis* is 52 percent (Smith and Palmer 1976), while the similar coefficient for rhizome internode length in *Alpinia speciosa* is 13 percent (A.D. Bell 1979).

Finally, the distribution of ramets in a natural population is not particularly regular or geometrical (fig. 8.7). Large areas remain unoccupied while ramets are clumped in other locations. Given the complex and statistical nature of daughter formation and the natural variation of growth parameters, a heterogeneous distribution of plants is not unexpected. An additional source of variation in the *Medeola* population was the death of ramets from the destruction of tubers by small mammals.

Thus the "rules of growth" in *Medeola* are not sufficiently precise to generate an optimal distribution of ramets. Adaptive interpretations of growth patterns—based on such hypothetical distributions, which are optimal—are not appropriate for an understanding of selection for particular branching angles and internode lengths. Fisher and Hibbs (1982) have also concluded that the actual distribution of branches in trees may bear little relationship to the ideal architectural model that describes an inherent "plan" of growth. The opportunistic and plastic nature of most plant development, combined with the natural heterogeneity of the environment, renders the actual form of shoots and clones highly probabilistic and unpredictable. It is this plasticity itself which may be most adaptive (Tomlinson 1982). It is unlikely that a purely architectural approach to the ideal form of clones will bring new insight to the adaptive nature of clonal species unless it is combined with field studies of clonal development in nature. The real growth of plants is far too heterogeneous and opportunistic to permit accurate simulations of form. Future research involving the construction of models must also incorporate the statistics of real growth. However, any significant evolutionary interpretation of clonal form must first experimentally assess the importance of proximal mechanisms of control, their natural variation in populations, and the adaptive benefits they bring to clonal growth.

#### ADAPTIVE BENEFITS OF CLONALITY

Throughout this review two aspects of clonality have been contrasted: growth through branching of daughter ramets, and reproduction through proliferation of physiologically independent plants that are genetically identical. The evolution of clonality has depended upon multiple adaptive benefits

that combine aspects of both growth and reproduction. Branching may be interpreted as a form of foraging confined to the plane of the earth (Janzen 1977; Harper 1977, this volume; Buss 1979; Jackson 1979). If resources such as water or soil nutrients are distributed in discrete patches, the establishment of a ramet in a new location is analogous to the growth of a branch into an opening in the canopy. At the scale of a ramet, resources within a patch of favorable habitat may be fleetingly available and rapidly dissipated by its own growth and growth of surrounding neighbors. Natural selection will match the life expectancy of a ramet to the average duration of a favorable patch. From the perspective of the genet, new patches of favorable habitat must continually be discovered and the resources harvested, leading to the variable and changing form of the clone. Presumably, these resources can be shared and redistributed among the ramets of the genet, although little is known about this aspect of ramet integration. As in any branching plant, the clone also benefits from multiplication of meristems, which permits rapid establishment of a canopy of leaves following seasonal dormancy.

A large, expanding clone can also be a formidable competitive entity capable of invading and dominating other clones and the populations of other species (Ovington 1953; Buell and Buell 1959; Tappeiner 1971; Thomas and Dale 1975). For genets that remain physiologically integrated, ramets at the interface with a competing population are able to draw resources from the metabolic reserves of interior ramets to overcome the initial competitive superiority of neighbors. The occupation of a large area by a clone may also prevent the establishment of any new genets without extensive disturbance of the existing vegetation (Harberd 1961, 1967; Kemperman and Barnes 1976; Sebens and Thorne, this volume).

Finally, multiplication of ramets may also benefit the clone, because the risk of genet extinction is spread among a number of ramets, each capable of suffering independent mortality (Jackson 1977, 1979; Buss 1979; Cook 1979; Charlesworth 1980). If risks of ramet mortality are independent, then the probability of genet extinction is the product of these separate chances of death and it will decline with the multiplication of ramets. The relative advantage of clonal reproduction is proportional to the average risk of ramet death. Independent probability of ramet mortality implies that two ramets must be physiologically independent, although precise quantitative data on this are just beginning to be accumulated (Pitelka and Ashmun, this volume). Sources of mortality that are intense but local in space would favor clonal reproduction. The effects of herbivores and pathogens colonizing spatially dispersed ramets might operate in this way. Once a shoot has been reached, rapid growth and reproduction of the herbivore may greatly increase the probability of ramet death locally, but leave the risk of genet extinction low because additional colonizing events are required. Although there is considerable information on

herbivore damage to individual shoots in many species, the associated probabilities of colonization within a clone have yet to be calculated.

These three categories of benefits are not mutually exclusive. Clearly, the ability of a ramet to discover and exploit a patch of locally high resources also enhances its ability to grow large and competitively dominate neighboring plants. In turn, this vigor confers a resistance to the effects of locally adverse and intense sources of mortality. Two types of evidence may be valuable in distinguishing these benefits in natural populations. First, the three benefits predict different relations between patterns of ramet growth and establishment, and the patchy structure of the habitat. The growth benefits of clone formation suggest that ramets will grow in locations with higher concentrations of resources. The competitive benefits will accrue to the genet when ramets are able to invade patches of lower resource availability due to the presence of competitors. The risk-spreading benefits predict a distance between ramets in relation to the intensity and nature of mortality sources, regardless of resources and neighbors. A second source of evidence may come from the developmental ecology of daughter ramets and the pattern of resource sharing among ramets in a clone. The growth benefits of clone formation suggest that resources acquired by ramets would be shared equally among the physiologically integrated members of a clone. Competitive expansion suggests that internal resources of the clone will be selectively allocated to those ramets which are competitively invading other clones or species. Finally, risk-spreading suggests that ramets will achieve physiological independence from the clone early in ontogeny, and survival will depend entirely on the ramets' ability to grow and resist pathogens and consumption.

At present far too little is known to test these predictions, and only further field studies of natural clones will provide the appropriate data. It is clear, however, that knowledge of the developmental ecology and clonal structure of such populations is essential to any evolutionary interpretation of plant ecology.

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