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Allocating Resources to Reproduction and Defense

New assessments of the costs and benefits of allocation patterns in plants are relating ecological roles to resource use

Fakhri A. Bazzaz, Nona R. Chiariello, Phyllis D. Coley, and Louis F. Pitelka

Most species of higher plants have qualitatively similar resource requirements for growth and reproduction (Chapin et al., p. 49, this issue). They differ, however, in the way they use resources to carry out three essential functions—reproduction, defense against herbivores, and growth. Each of these functions requires a complex set of resources, including carbon, nitrogen, and phosphorus, that make up the structures (leaves, stems, fruits, roots) associated with different functions. Variation in resource allocation occurs through differences in the chemical composition of structures, the relative mass of different structures or organs, and the relative numbers of different structures a plant produces. This variation occurs within individuals through time, within and among populations, and especially among species (Figure 1).

Examinations of this variation cross many fields of ecology, including physiological studies of the relationship between structure and function in plants, biochemical studies of

Resource allocation to plant structures of different composition, size, number, and function varies within and among populations and especially among species.

coevolutionary diversification in plant defense, and theoretical studies of life history evolution. These and other areas contribute to an understanding of resource use in two ways: by elucidating specific components of variation, such as phylogenetic constraints in biochemistry, and by applying concepts of allocation at different levels of plant organization.

At an evolutionary level, allocation involves balancing fecundity against survival probability through the lifespan and the effects of this balance on fitness. At an ecological level, allocation includes the relationship between investment in one function and investment in others, such as the relationship between defense and growth. At a physiological level, allocation entails the partitioning of resources within the plant and the consequences of this partitioning for resource gain or loss. Because ecological functions clearly have a physiological basis (e.g., reproduction requires the production of flowers and seeds) allocation patterns at different levels should be correlated.

Here we examine the sources of variation in allocation to sexual reproduction, clonal growth, and defense (primarily chemical defense of leaves). Our goal is twofold: to suggest general trends in allocation and their significance, both among and within species, in relation to environment; and to identify both conceptual and procedural difficulties involved in quantifying allocation.

Resource-based perspectives

Principle of allocation. Higher plants have a life cycle in which juvenile, purely vegetative stages are followed by reproductive stages, which are eventually followed by senescence and death. For many years, explanations of this cycle have emphasized resource allocation. As early as the 1800s, studies suggested that reproduction competes with vegetative functions, depleting resources necessary for maintenance and growth. For example, flower-removal studies by Mattiolo (1899) demonstrated that preventing flowering can extend a plant's lifespan and growth. Molisch (1930) described resource depletion in reproduction as *Erschöpfungstod* (exhaustion death).

The idea that reproduction, growth, and defense interact within the individual and compete for limited resources is now considered an established principle. Because there are trade-offs between a plant's various functions, the concept of costs and benefits helps explain allocation patterns at both the physiological and evolutionary levels. For example, re-

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Structure	Function	Source or sink	% N	Level of defense	Allocation of biomass
Mature reproductive structures	Reproduction, dispersal, genetic recombination	-- to +	2-10	++	1-60%
Support structures and new inflorescences	Structural support, competition, attraction	- to +	0.2-2	+	
New leaves	CO ₂ assimilation	- → ++	1-6	+++	20-70
Mature leaves	CO ₂ assimilation	++	0.5-0.3	++	
Stem	Support and transport, competition for light	-	0.2-2	+	0-50
Clonal ramet	"Reproduction", local dispersal, horizontal growth	- → +	1-5	+	0-30
Roots	Uptake of water and minerals. Competition for same.	--		+	5-70

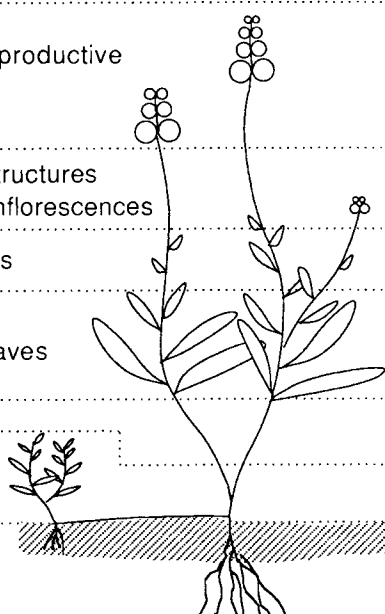


Figure 1. General relationship between structure and function in plants and allocation characteristics associated with various parts. Source or sink indicates the degree to which the structure produces (+, ++) or uses (–, --) photosynthate. Changes in source-sink status through time are indicated by symbols separated by an arrow; variability in source-sink status among species is indicated as a range (e.g., reproductive parts). Percent N indicates the general range in nitrogen content (mass of N:mass dry tissue). Level of defense allocation is a relative ranking from low (+) to high (+++). Percent of total biomass indicates the range among species in the percent of biomass allocated to each structure per year.

production has a demographic cost, which can be measured in populations where some individuals reproduce and others do not. Increased mortality following reproduction has been observed in growth forms ranging from buttercups (Sarukhán 1976) to tropical palms (Piñero et al. 1982). Reproduction in one year may reduce the probability of reproduction in the next, as observed in the grass *Poa annua* (Law 1979), mayapples (Sohn and Policansky 1977), and species of birch (Gross 1972). Reproduction also has a parallel physiological cost, requiring resources that would otherwise support vegetative growth, as evidenced by decreased width of annual tree rings (Kozlowski 1971) or a reduced number of leaves in rosettes (Antonovics 1980).

To understand how reproduction and senescence contribute to the fitness of a genotype, theoretical studies have considered the effects of genes controlling age-specific fecundity. Genes that augment the reproductive value of early life stages at the cost of later reproductive value tend to increase in frequency during evolution,

suggesting that eventual senescence should be the general rule (Hamilton 1966)—as indeed it is. Thus we can view senescence as reproductive exhaustion, or resource depletion, that has been programmed by evolutionary dynamics.

Antiherbivore chemistry. A resource-based perspective is much newer in studies of defense against herbivores. Until recently, most plants were viewed as passive prey, and secondary compounds (so called because they are not associated with primary metabolism) were considered waste products. Contrary to this perspective, secondary compounds may be effective deterrents to herbivores. Since this role was suggested (Fraenkel 1959), studies in biochemistry and ecology have identified the structure and mode of action of a vast number of chemicals in the arsenal of higher plants.

In most communities, herbivores are important selective agents, consuming 10–20% of annual plant production. Often their damage is more devastating. Many field and labora-

tory studies have found that herbivory is negatively correlated with levels of particular secondary chemicals (Coley 1983, McKey et al. 1978), providing strong support for the benefits of defense. Defense also has its costs. In the absence of herbivores, pest-resistant varieties often have lower yields than susceptible varieties, suggesting there is a trade-off between allocation to defense and growth (Pimentel 1976). Studies of wild plants indicate that the overall allocation to defense is negatively correlated with plant growth rate (Coley 1986). The cost of defense, together with the unpredictability of herbivore attack, may explain why some plants have evolved inducible defense systems.

The first comprehensive theory of plant defense strategies, the theory of plant apparency (Feeny 1976, Rhoades and Cates 1976), suggested that interspecific differences in defense have evolved in response to the risk of discovery by herbivores, the cost of defense, and the value of plant parts. Herbivore behavior played a major role in this hypothesis. Physio-

logical approaches have extended this idea to an explicit cost-benefit framework in which the effects of defense allocation on rates of herbivory can be weighed against the effects on growth (Coley et al. 1985, Mooney and Gulmon 1982).

Understanding the costs and benefits of an allocation pattern requires a means of measuring the resources committed to any function and determining the consequences of alternative patterns of resource allocation. These can be considered the direct and indirect costs of allocation, and they correspond roughly to the levels of allocation we have termed physiological and ecological. In the discussion that follows, we focus primarily on the direct costs of allocation. Increasingly, models of growth and allocation, together with studies of comparative physiology, are being used to determine alternative allocation patterns and to assess indirect costs.

Reproductive allocation

Allocation of biomass. The most widely used measure of direct allocation costs is the amount of biomass in

specific organs, or, within an organ, the amount of mass that is committed to a particular function. In studying reproductive allocation, most investigators have focused on the amount of biomass in reproductive organs (flowers, fruits, seeds) relative to vegetative biomass (leaves, stems, roots), measured at plant maturity or at the end of a growing season. This particular approach is based on two assumptions: that biomass partitioning is a reflection of the allocation of the limiting resources, and that different functions are limited by the same resources.

Several factors support these assumptions. Seeds should be provisioned with the resources necessary for eventual growth, so the resource requirements of reproduction should be similar to those of growth. Moreover, plants possess a variety of mechanisms that compensate for aboveground versus belowground resource limitation, as well as limitation by specific resources. These compensatory mechanisms reduce the variation in a plant's internal resource balance relative to its external resource balance (Chapin et al., p. 49, Pearcy et al., p. 21, this issue).

Life history and reproductive allocation. Stimulated by theoretical studies of life history evolution, empirical studies of reproductive allocation have been a major research focus in plant ecology. Theoretical studies suggest that life history and competition should have major effects on reproductive allocation. In open habitats, the fitness of colonizing plants is likely to depend on fecundity, whereas in a crowded habitat, high fecundity may compromise the competitive ability of the plant to persist (Harper 1967). For parallel reasons, plants that reproduce once in a lifetime (annuals and monocarpic perennials) should have a higher reproductive allocation than plants that reproduce multiple times (iteroparous perennials), because it pays to maximize the present reproduction if future reproduction has been sacrificed.

Some studies support these predictions. Comparing a wide variety of species, one sees a trend toward higher reproductive allocation in annuals and monocarpic perennials than in iteroparous perennials (Abrahamson 1979), consistent with the idea that perennials must forego some reproductive expenditure to retain sufficient resources for perennation. Yet there are exceptions to this pattern. Some perennials have very high reproductive allocation, such as the tropical palm *Astrocaryum mexicanum* (Sarukhán 1980), while some annuals have very low reproductive allocation (Hickman 1977). However, if we limit comparisons to congeneric species, the prediction that annuals should have higher reproductive allocation than perennials is consistently supported (Figure 2). Because reproductive characteristics are among the most conservative traits in plants, predicted trends in reproductive allocation may apply only within certain taxonomic boundaries or where morphological constraints on resource allocation are similar. Basic features of the inflorescence, such as the availability of meristems, may significantly constrain reproductive allocation, especially in morphologically very simple plants (Watson and Casper 1984).

Plant size and allocation. Within a species, total biomass often is a close correlate of reproductive allocation.

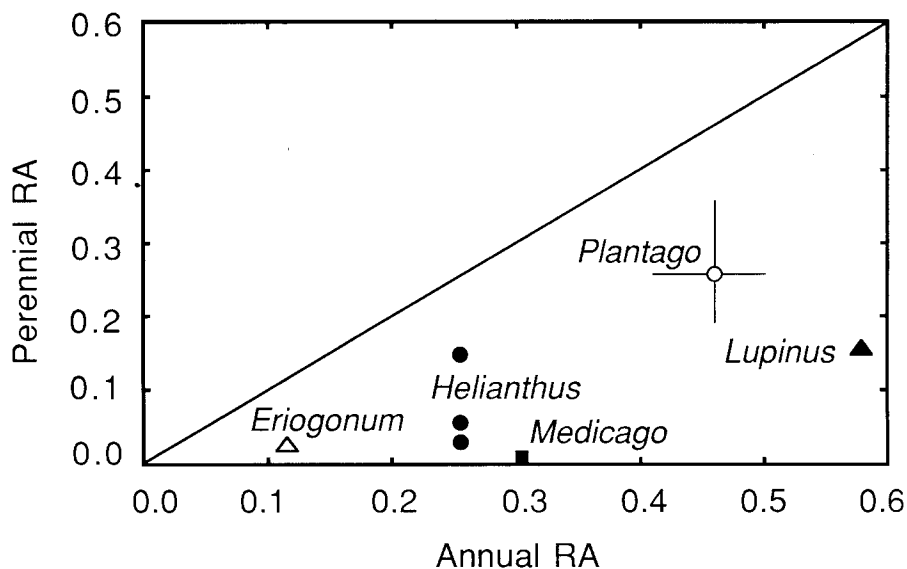


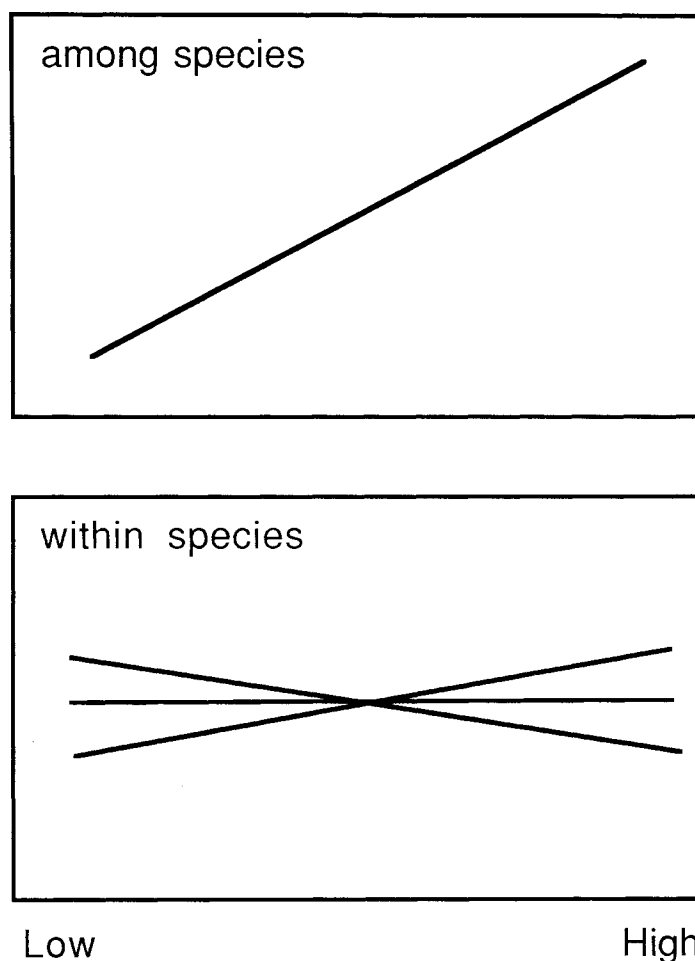
Figure 2. Relative reproductive allocation (RA) in congeneric or conspecific annuals and perennials. For *Lupinus*, *Medicago*, *Helianthus*, and *Eriogonum* the data are in units reproductive dry mass/total dry mass. For *Plantago*, the data are in units mg seeds/2 cm² leaf area. The *Lupinus* data are two-year means of naturally growing plants (one annual, one perennial species) (Pitelka 1977). The *Helianthus* data represent one annual and three perennial species (Gaines et al. 1974). The *Medicago* data represent one annual and one perennial species (Turkington and Cavers 1978). The *Plantago* data represent the mean and range of four perennial species and nine annual species (Primack 1979). The *Eriogonum* data reflect the annual and perennial subspecies of *E. inflatum*. Source: Chiariello, unpublished data.

In monocarpic and polycarpic perennials, we now have abundant evidence for the role of plant size, or relative growth rate, in determining relative allocation to sexual reproduction; in many plants, a size or biomass threshold must be reached before flowering occurs (Werner 1975). A number of studies indicate that within a population, variation in individual plant size is a function of resource availability rather than genetic differences among plants (Solbrig 1981). Thus, there will often be a fairly direct linkage between resource availability, the conversion of those resources to biomass, and ultimately, the production of sexual and vegetative propagules. Environmentally determined variation in mean plant size or size class distribution may explain much of the reported environment-related variation among populations in reproductive effort (Samson and Werk 1986). Within species, reproductive allocation can either increase or decrease with size, presumably depending on morphological characteristics. Comparing among species, reproductive allocation is generally higher in species with high relative growth rates (Figure 3).

Resource availability may also affect allocation to male versus female function. Although there are some exceptions (e.g., Wallace and Rundel 1979), male individuals of dioecious species generally are overrepresented in sites of lower water availability, whereas females tend to occur in wetter sites (Freeman et al. 1976). Even in monoecious plants, moisture availability can influence the ratio of male to female function.

A general feature of dioecious plants is that females allocate more biomass and nutrients to reproduction than do males (Wallace and Rundel 1979). In Jack-in-the-pulpit, allocation to female function is apparently too costly for small plants, so only large plants are female (Bierzychudek 1984). In *Ambrosia trifida*, a monoecious species, individuals that produce only female flowers have higher reproductive allocation than plants producing both sexes. However, pure female production occurs only in the smallest plants. Thus, species differ in the effect of resource availability on allocation to male versus female function (Bazzaz 1984).

Allocation to reproduction (RA)



Resource availability or relative growth rate

Figure 3. General trend in reproductive allocation (RA) among and within species as a function of resource availability, which we assume is related to plant relative growth rate. Among species, reproductive allocation increases with resource availability, partly because of the relationship between life history and habitat. Within species, reproductive allocation can increase or decrease with relative growth rate.

Timing of reproductive allocation.

Most studies have focused on the relative allocation to reproduction at the end of an entire season or year, but it is clear that the timing of reproductive allocation within the season is equally important in determining fecundity and reproductive costs and benefits. Because allocation to vegetative structures has compounding interest for plant growth, plant life cycles begin with pure vegetative growth, and in annuals, the lifespan terminates with pure reproductive allocation. Cohen's (1971) pioneering model of reproductive timing demonstrated that for an annual plant, vegetative allocation should switch completely to reproductive allocation at a

precise time (Figure 4). This "bang-bang" strategy maximizes seed set for an annual with a constant relative growth rate and a growing season of fixed length.

Extensions of these studies have shown that the optimal switch for maximizing seed set would be earlier under several conditions—the relative growth rate decreases with plant size, the probability of mortality increases with time, or the reproductive structures are photosynthetic (Cohen 1976). The optimal switch would be delayed if size confers an increasing advantage in reproduction, either through interplant competition for light (Schaffer 1977) or access to pollinators (Cohen 1976), or if flowering

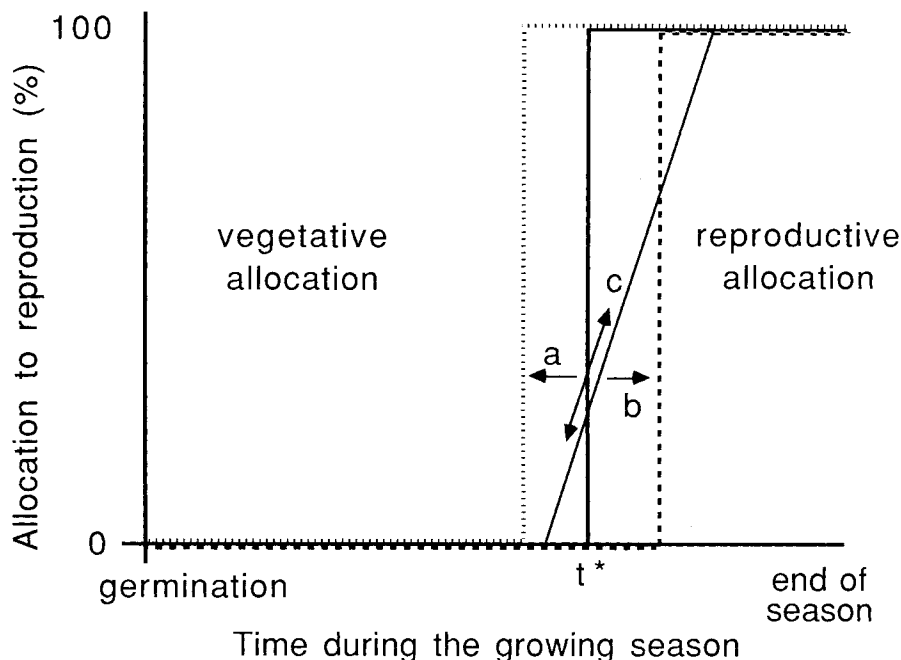


Figure 4. The optimal timing of allocation of photosynthate to reproduction, according to simple models of allocation and growth. For an isolated plant, t^* represents the optimal time for the switch from vegetative to reproductive allocation. Under altered assumptions, the switch can be shifted earlier (a) or later (b) or can be gradual (c) rather than abrupt.

uses reserves stored during the vegetative phase (Chiariello and Roughgarden 1984). The switch should be gradual rather than “bang-bang” if the season length varies (King and Roughgarden 1982) or if growth and reproduction are morphologically coupled (Cohen 1971).

Limited testing of these models suggests that species vary in the duration of a mixed allocation phase, but it is not known whether this correlates with environmental predictability. Because reproductive timing affects final vegetative biomass as well as fecundity, differences in reproductive timing may also account for measured variation in reproductive allocation.

Reproduction and photosynthesis. One of the major difficulties in measuring the direct costs of reproduction is separating the plant’s different functions. Empirical studies have assumed that by measuring the mass represented by reproductive structures, one could partition a plant’s investment between growth and reproduction. But, this measure is only as strong as the correspondence between function and structure. If reproductive structures have a partly

vegetative function, then their mass overestimates the plant’s direct investment in reproduction. Conversely, assessments of standing biomass tend to omit certain costs of reproduction, such as the production of ancillary and support structures, which may be transient and/or costly (Bazzaz and Reekie 1985). Nectar contains a number of complex chemicals in sugary solution and may be produced in large quantities, as in *Asclepias*, which during reproduction allocates up to 37% of daily photosynthate to nectar (Southwick 1984).

Like all aboveground organs, reproductive structures have direct access to two resources, carbon and light. Floral structures vary in the degree to which they are partly vegetative and so have direct access to CO_2 . In cultivated species, photosynthesis by reproductive structures is often sufficient to meet respiratory demand and sometimes exceed it, especially in grain crops. These crops have been selected for large and/or numerous fruits (a high harvest yield) under conditions of high light intensity, and wild species in natural habitats may be expected to differ. However, several studies have reported significant reproductive photosynthe-

sis in wild species (Bazzaz and Carlson 1979, Bazzaz et al. 1979). The most leaflike parts of reproductive structures, such as the calyx, are likely to have the highest photosynthetic capacity, but other parts, such as developing ovaries, may also contribute (Williams et al. 1985). In some fruits, the locular chamber provides a reservoir of respired CO_2 , some of which is repeatedly recycled.

Assessing the effect of reproductive photosynthesis on reproductive allocation includes both the degree of carbon autonomy in reproductive structures and the indirect costs to vegetative parts. The carbon supplied through reproductive photosynthesis is not cost-free because the photosynthetic capacity of reproductive structures requires nutrient investments that possibly could provide greater photosynthetic returns if they were allocated to leaves; this represents an indirect cost.

While indirect costs, or trade-offs in allocation, are fundamental to understanding variation in allocation pattern, measuring them is difficult. Much of the evidence for indirect costs is based on negative correlations between fecundity and later growth, survival, or reproduction. These correlations could result from other factors within the plant as well. For example, stress generally delays or prevents flowering in perennials, but extreme stress may promote flowering, as though a low probability of survival triggers a perennial into one final burst of reproduction. In this case, death may be due to stress, not reproduction, but there would be a correlation between reproduction and increased mortality. For this reason, it may be most useful to study trade-offs induced by experimental manipulations (e.g., Antonovics 1980). Experimental studies of allocation physiology, however, may be difficult to interpret in an ecological context.

One challenge to the concept of trade-offs is the finding that assimilation rates of sources (leaves and other tissues that photosynthesize) can be enhanced by increasing the number and size of sinks (sites that use or store the products of photosynthesis). Reproductive sinks produce a local stimulation of photosynthesis in a number of crop species, though the pattern is not universal. Little is

known of the extent to which this occurs in wild plants. Conversely, resources necessary for photosynthesis may be reallocated to reproductive structures, reducing rather than enhancing photosynthetic capacity of leaves during reproductive development. Accounting for the many interactions between reproduction and photosynthesis may significantly alter the measure of reproductive allocation (Figure 5).

Biomass versus other currencies. The magnitude of indirect costs may also depend on the currency of allocation. Although patterns of biomass and energy allocation in plants are roughly equivalent (Hickman and Pitelka 1975), elemental analyses of vegetative and reproductive structures may differ (Sinclair and Dewit 1976). This leads to different patterns of allocation for such currencies as biomass and mineral nutrients (Abrahamson and Caswell 1982), and these patterns are likely to diverge through the season or life cycle as the limiting resources vary (Mooney and Chiarllo 1984). In some cases, carbon and biomass allocation also differ (Jurik 1983). These and other findings imply different degrees of trade-offs for different resources and have prompted the search for a better allocation currency than biomass.

Vegetative reproduction

Clonal growth (or vegetative reproduction) is found in large numbers of plants and represents an important alternative means by which plants can propagate themselves. A unique feature of clonal growth is that rooting at nodes of individual shoots may create physiologically distinct plants with independent fates. This developmental feature has important physiological and ecological implications because it affects how the plant functions as a single physiological unit and interacts with its environment.

Whether a species possesses the capacity to grow clonally, and the specific mechanism it employs (e.g., bulbs, rhizomes, stolons, fragmentation), presumably reflects phylogenetic inertia as well as adaptation to particular types of environments. Clonal growth is obviously advantageous where horizontal spread is fa-

vored over vertical growth. Beyond that, it appears to have been favored in environments where seed and seedling mortality are high and where fires are frequent, as well as in other stressful environments (Abrahamson 1980).

Clonal growth is a sink for resources, and so allocation to it must be under ecological controls similar to those that govern sexual reproductive allocation. The effects of specific

types of stress seem to vary widely, but clonal growth does appear to be tied to resource availability (Ashmun and Pitelka 1984) and plant size (Grace and Wetzel 1981).

Trade-offs between asexual and sexual reproduction. There has been considerable interest in whether clonal growth and sexual reproduction compete directly for resources within a plant and, consequently, whether

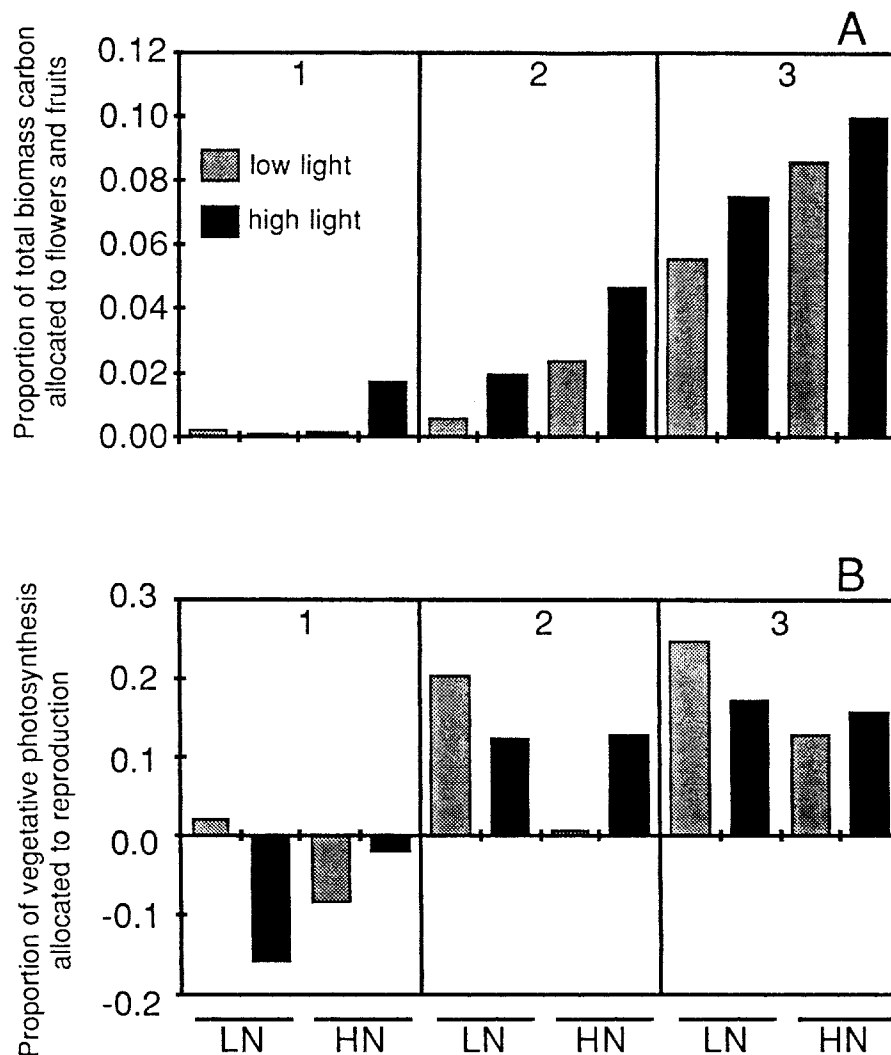


Figure 5. Reproduction allocation in three genotypes (1,2,3) of the perennial *Agropyron repens* (quack grass) grown at either low (LL) or high (HL) light levels and at either low (LN) or high (HN) nitrogen levels. Reproductive allocation is calculated as (A) proportion of total biomass carbon allocated to flowers and fruits, and (B) proportion of vegetative photosynthesis allocated to reproductive structures. Measure B includes allocation to reproductive support structures, respiratory losses of both vegetative and reproductive parts over the life of the plants, and reproductive photosynthesis (including both photosynthesis by reproductive structures and enhancement of leaf photosynthesis.) Measures of reproductive allocation in A and B are poorly correlated, primarily because of treatment effects on reproductive photosynthesis. At high nitrogen and high light, plants are better able to compensate for the cost of reproduction through reproductive photosynthesis, although genotypes differ in degree of reproductive photosynthesis. Source: Reekie and Bazzaz, unpublished data.

there should be a trade-off between the resources allocated to one versus the other. Such a trade-off appears to occur in dewberries (Abrahamson 1975), but in asters, sexual reproduction and clonal growth are similarly affected by resource availability (Ashmun et al. 1985).

Clonal species vary considerably in the extent to which potentially independent offspring remain connected to parents or siblings through such structures as rhizomes and stolons. Connections may senesce rapidly or persist for many years (Cook 1983, Pitelka and Ashmun 1986). The functional connections are significant because they determine the level of plant organization at which resource allocation to different functions and costs of allocation should be measured. The presence of functional connections can affect competitive ability (Cook 1983, Lovett Doust 1981), integrate local patchiness in resource availability (Hartnett and Bazzaz 1985), or determine the ability of individual shoots or modules to survive stress or injury (Kays and Harper 1974). When individual shoots are physiologically integrated, it may be impossible to demonstrate costs of reproductive allocation within the individual shoot.

Despite the widespread occurrence of this physiological integration in clonal plants, our understanding of the ecological and evolutionary costs and benefits is still minimal. Debate continues over whether clonal growth represents reproduction or only vegetative growth. Although genetic recombination does not occur in the production of new ramets, new variants arise from somatic mutations in meristems, and clonal growth does serve many of the same functions as sexual reproduction, such as dispersal and providing offspring. Offspring may be dispersed only locally, but given enough time clones can extend a considerable distance. Until vascular connections to new ramets senesce, vegetative offspring are provisioned during adverse conditions.

Allocation to defense

Variation among species. Species vary greatly in the type and levels of chemical defense against herbivores. Chemical defenses draw from an

enormous variety of compounds, which can differ in both concentration and distribution. Condensed tannins in leaves frequently constitute 5–20% of the dry mass, and phenolic resin concentrations can reach 40% or more (Lincoln 1980, McKey et al. 1978). Alkaloids typically represent less than one percent of dry leaf mass, and cardiac glycosides and terpenes less than five percent (Rhoades and Cates 1976). Lignin, fibers, and structural carbohydrates also contribute to defense by making the leaf tough (Coley 1983).

Comparisons among species suggest that high levels of defensive compounds are associated with resource-limited environments (Bryant et al. 1983), late successional habitats (Feeny 1976, Rhoades and Cates 1976), slow growth rates (Coley et al. 1985), woodiness (Bryant et al. 1983), and evergreens (Coley 1983, Janzen 1974, Mooney and Gulmon 1982).

While ecological parameters are fairly good predictors of defense levels, the biochemistry of defense compounds is constrained by phylogeny. Major biosynthetic pathways are held in common within phylogenetic groupings, so selection at the species level is constrained to chemical variations of basic pathways (Ehrlich and Raven 1964). Because classes of defensive chemicals vary significantly in carbon:nitrogen ratio and mode of action, it is most meaningful to quantify allocation to defense in terms of specific classes of chemicals.

The degree of chemical and elemental variation in defenses poses significant problems for comparatively assessing defense allocation. Investigators must calculate the total energy and nutrient costs of constructing and maintaining compounds committed to defense. Construction costs, which include the energy and nutrients contained in specific compounds as well as those required for synthetic processes, can differ significantly among defensive compounds. Synthesis of alkaloids or terpenes is almost twice as costly per gram as that of tannins or lignins (McDermitt and Loomis 1981, Mooney and Gulmon 1982). Alkaloids and terpenes, having short half-lives, also have higher maintenance costs than tannins and lignins, which turn over slowly (Coley et al.

1985). These considerations apply to reproductive allocation as well but have not been included in most estimates. For example, seeds contain high levels of carbohydrates and proteins. While these compounds are similar in energy content, proteins may cost twice as much to synthesize.

Variation within species. Although the degree of variation in defense within species does not rival that among species, it is substantial and can have significant ecological consequences. Within-species variation may be due to genetic differences, as suggested by studies under uniform or controlled environments (Langenheim et al. 1978). But much of defense variation within species is due to spatial and temporal variation in resource availability. The effects of resource availability appear as correlations between allocation pattern and such factors as habitat, internal resource balance, and plant size or age.

Within-species trends in defense suggest that allocation of resources to growth has highest priority, whereas allocation to defense increases at resource levels above normal. When there is an imbalance of resources needed for growth, plants divert the excess resources to production of defense compounds (Bryant et al. 1983). For example, if plants are shaded and therefore carbon limited, additional nitrogen can lead to increases in nitrogen-based defensive chemicals. Individuals in high light generally have higher concentrations of carbon-based defenses, such as terpenes or phenolic compounds, than do conspecifics in the shade. Both types of defense decline if the plant receives additional nitrogen and high light, which together support increased growth. Imbalances in resource availability may explain much of the intra-specific variation in defenses, although the details are not well understood.

These trends within species are sometimes opposite the general trends among species (Figure 6). Species adapted to low-nutrient availability or low-light environments (which support low potential growth rates), generally have higher defense allocations than species of resource-rich habitats. However, in species with

carbon-based defenses, shaded individuals have lower levels of defense than conspecifics in the sun, while in species with nitrogen-containing defenses, lowered nutrient availability reduces defense allocation. These relationships between growth and defense allocation, both within and among species, are quite different from the relationship between growth and reproduction (Figure 3 versus Figure 6).

Defense allocation also varies temporally in plants experiencing large seasonal changes in resource availability. If a flush of nitrogen becomes available, plants may acquire it, store it in a defensive form such as alkaloids, and later remobilize it (Mooney et al. 1983). The dynamic nature of some defensive compounds incurs high costs associated with turnover, but also allows the plant flexibility in changing defense levels. Other types of secondary compounds, such as condensed tannins and lignins, are not as labile and therefore do not allow this type of flexibility.

Interaction of functions. Just as reproductive structures may have partially nonreproductive functions (e.g., photosynthesis), defensive chemicals may have multiple functions. Phenolic compounds may defend against herbivores and also filter ultraviolet radiation (Lee and Lowry 1980). External resin coatings have similar effects, but in addition, they conserve water by reducing nonstomatal transpiration (Rhoades 1977). Lignin and other structural carbohydrates provide the supporting skeleton of the leaf in addition to reducing leaf digestibility.

In addition to chemicals, defense can include a variety of mechanical, morphological, or phenological characteristics, which are also multifunctional. Phenological events, such as seedling germination, fruiting, and emergence of leaves may coincide with times of minimum herbivore intensity. Phenologies that coincide with troughs in herbivore population size may also be synchronized with the timing of nutrient flushes (Lieberman and Lieberman 1984). Thus, the timing of defense allocation has costs and benefits relating to both herbivore pressure and the temporal availability of resources.

Functionally different plant tissues

Allocation to defense

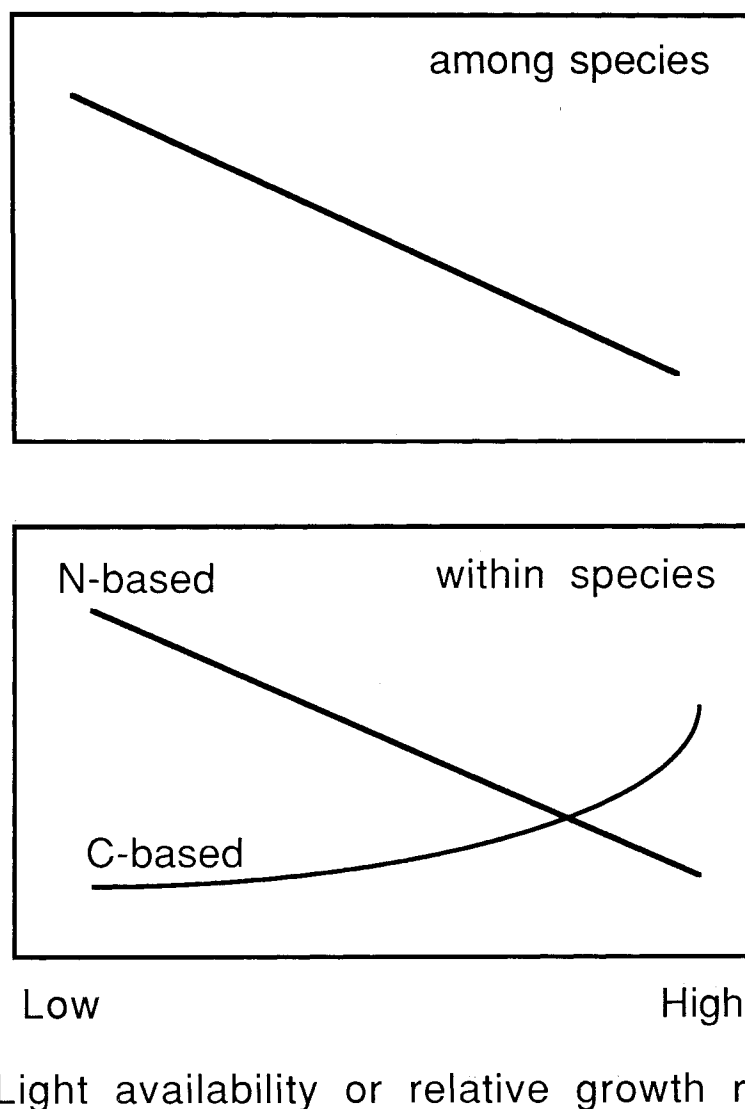


Figure 6. General trends in defense allocation among and within species as a function of relative growth rate or availability of a limiting resource, e.g., light (assuming high levels of other resources).

vary in their susceptibility to herbivores and in their contribution to plant fitness. Seeds, containing potential offspring and also high nutrient concentrations, are generally well protected chemically. Most species' young leaves are high in protein and low in fiber and lignin, making them attractive to herbivores. This may be partially offset by the accumulation of high concentrations of secondary compounds early in leaf development. With some exceptions, younger leaves have higher concentrations of defensive compounds, including relatively labile alkaloids and cardiac glycosides, as well as metabolically inactive compounds such as condensed tannins. Leaf position on a plant can also

influence the allocation of defense. Although there is still much to learn about the aboveground patterns of defense allocation, the defensive chemistry of roots and their interactions with soil herbivores is even less well studied.

Conclusions

With biologists' increasing appreciation of the complexity of plant form and function, views of allocation have evolved from very simple models of partitioning of limited resources among competing, idealized functions to increasingly complex models that consider constraints related to growth form, multiplicity of function, inter-

actions among resources, meristem availability, and ultimately, phylogeny and genetic diversity. Future research should focus on developing techniques that can investigate multiple constraints and the relationship between proximate and ultimate controls on allocation. By comparing different genotypes or closely related species, it may be possible to evaluate developmental constraints on resource allocation in an evolutionary context.

The complexity of form and function is likely to be a focus of future studies of reproductive allocation. Demonstrating significant photosynthetic contributions by reproductive structures has reshaped our thinking of resource limitation. Resource limitation varies not only with habitat, but also with time. The transition to reproduction may coincide with a shift in the critical currency of allocation. Certainly an intriguing ecological question is why and how structures are multifunctional. For example, why and when are nutrients exported from leaves to photosynthetically less efficient reproductive structures?

Resource-based approaches have emphasized the cost of defense vis-à-vis growth and have elucidated the ecological correlates of defense, many of which have received considerable study. A next step will be unraveling multiple correlations. One correlate of high defense levels, for example, is the evergreen characteristic, which can be favored as a means of nutrient conservation or a means of responding to pulses of resources. Although simple models have been very useful in explaining resource allocation patterns (Orians and Solbrig 1977), including allocation to defense (Coley et al. 1985, Gulmon and Mooney 1986), specific ecological circumstances are very likely to require more complex assessments of cost and benefit.

Diverse studies of allocation have converged on the theme of cost and benefit. This concept has proven robust from physiological to evolutionary levels, but many links between these levels are still missing, and debate continues on the ideal currency of allocation. Establishing these links requires a currency that allows a complete accounting of direct costs, and

permits calculation of indirect costs. Carbon appears to be the most useful candidate at present, because of its fundamental importance as a building block for all plant structures; the ease with which its assimilation, translocation, and allocation can be analyzed; and the evidence of assimilate limitation in plants. Also, many of the unanswered questions relating to physiological costs involve carbon. For example, are source-sink controls on photosynthesis, such as reproductive enhancement of leaf photosynthesis, consistent with a cost-benefit framework? Undoubtedly there are situations where plants are limited by resources other than carbon, such as nitrogen or phosphorus. Carbon, however, represents a currency that can integrate the costs of activities, including foraging and uptake of limiting nutrients. Thus, nitrogen limitation can be expressed as the cost of acquiring nitrogen measured in units of carbon (Bloom et al. 1985). If exchange rates between resources are determined, any resource can be used as the currency.

The allocation pattern of a plant defines its ecological roles and is therefore an important factor in understanding plant distribution and adaptation. Resource allocation is also very important in agricultural species. Furthermore, selection for increased yield in crops has succeeded more through changes in reproductive allocation than through increases in photosynthetic rates per unit leaf area (Gifford and Evans 1981). Thus an understanding of the controls on reproductive allocation in wild species has implications for crop improvement. Allocation of resources to defense may also affect the success of crops. In crop varieties with increased natural defenses that have been derived from crosses with wild relatives, losses to herbivores are substantially reduced (Pimentel 1976). Continued improvement of agronomic species is likely to draw from insights obtained through ecological studies of allocation in wild species, some of which have now been studied in as much detail as agronomic species.

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