DOES REPRODUCTION COMPROMISE DEFENSE IN WOODY PLANTS?

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PRINCIPLES OF RESOURCE ALLOCATION

A general principle of adaptive allocation was proposed by Cody (1966) who hypothesized that 1) all living organisms have finite resources to partition among growth and competing physiological processes such as reproduction and defense; and 2) natural selection results in the evolution of unique resource allocation patterns that maximize fitness in different environments. Today, it is well established that plants have limited resources to allocate among these processes (Bazzaz et al. 1987), and theories of life-history strategy rests on the assumption that there are fitness trade-offs associated with varying patterns of resource allocation (Stearns 1976, 1989, Reznick 1985, Bazzaz et al. 1987, Lovett Doust 1989). Trade-offs occur when an increase in resources allocated to one fitness component, such as growth, reduces the allocation to another, such as reproduction. Natural selection (acting within phylogenetic, physiological, and ecological constraints) should shape patterns of resource allocation, balancing the costs and benefits associated with these trade-offs, resulting in the evolution of life-history strategies maximizing fitness. There are direct and indirect costs associated with allocation to "nongrowth" processes such as reproduction. Direct costs are energy and assimilates invested in reproductive structures. Indirect costs are unrealized growth and future reproduction as a result of this investment (Bazzaz and Reekie 1985, Bloom et al. 1985, Bazzaz et al. 1987, Reekie and Bazzaz 1987c, Ronsheim 1988, Lovett Doust 1989).

The physiological cost of reproduction in the form of reduced vegetative growth has been documented in a number of cases (Gross 1972, Harper and White 1974, Gifford and Evans 1981, Willson 1983, Luken 1987, Clark and Clark 1988, Snow and Whigham 1989, Dick et al. 1990). However, this cost may not be universal (Tuomi et al. 1982, Reekie and Bazzaz 1987c, Reznick 1985). Genetic, ecological, and physiological trade-offs between growth and defensive secondary chemistry are also well documented (Bryant et al. 1983, Krischik and Denno 1983, Coley et al. 1985, Loehle 1988, Bazzaz et al. 1987, Pimentel 1988). Resource allocation patterns are the expression of source-sink

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interactions within the plant and their control on assimilate partitioning. Complex physiological changes in patterns of assimilate partitioning are required to bring about the maturation of inflorescences, fruits, and seeds. Very likely, these changes will affect traits conferring plants with resistance to herbivores. Few studies, however, have examined the potential interactions between reproduction and defense.

In this paper we explore two hypotheses suggesting how plant reproduction may directly and indirectly affect herbivory and review the limited experimental evidence supporting each: 1) reproductive structures as carbon sinks reduce the allocation of resources to defense; 2) reproductive structures as nutrient sinks increase the carbon/nutrient ratio in nearby vegetative tissues, resulting in their increased secondary metabolism and consequent increased resistance to herbivores.

TRADE-OFFS BETWEEN REPRODUCTION AND DEFENSE

Plants have limited resources to support their physiological processes, hence all requirements can not be met simultaneously, and trade-offs occur among growth, maintenance, storage, reproduction, and defense processes. Consequently, there is sequential growth and maturation of tissues within organs and organs within plants and/or strong inverse relationships between the allocation of resources to growth and nongrowth processes, including reproduction and defense (Mooney 1972, Mooney and Chu 1974, Gifford et al. 1984, Bloom et al. 1985, Willson 1983, Krischik and Denno 1983, Coley et al. 1985, Alpert et al. 1985, Loehle 1988, McLaughlin and McConathy 1979, Bazzaz et al. 1987, Patrick 1988).

Though rarely documented, reproductive effort may come at the expense of defense, if resources are diverted from resistance mechanisms to reproductive structures. This may occur commonly in the case of nitrogen-based secondary metabolites such as alkaloids and cyanogens, the concentrations of which often decline in foliage as growth shifts from vegetative to reproductive processes (Mattson 1980, Krischik and Denno 1983, Harborne 1990).

Resistance of conifers to bark beetles is generally correlated with their growth efficiency, i.e. stemwood production per unit foliage (Waring et al. 1980, Waring 1983, Mitchell et al. 1983, Larsson et al. 1983, Waring and Pitman 1985). Susceptible individuals with low growth efficiencies are characterized by depleted levels of the stored energy necessary to support defensive reactions (Waring and Schlesinger 1986, Christiansen et al. 1987). Because heavy pollen and cone production can reduce growth efficiency, episodes of reproduction may increase susceptibility to bark beetles. For example, cone production has been shown to depress stem-wood growth and leaf area in several species of conifers (Eis et al. 1965, Owens 1969, Tappeiner 1969, Dick et al. 1990). Carbon allocated to reproduction at the expense of energy and substrate required for resin synthesis and wound-induced hypersensitive responses may contribute to increased bark beetle and pathogen susceptibility. Reproductive effort may interact with environmental stress to suppress conifer resistance to bark beetles and contribute synergistically to outbreaks.

Birch Reproduction and Resistance to Bronze Birch Borer

The pistillate catkins of *Betula* are known to be strong photosynthetic sinks, competing with and reducing resource allocation to vegetative growth (Gross 1972, Tuomi et al. 1982, Caesar and MacDonald 1983). Frequently trees producing especially heavy seed crops subsequently exhibit severe dieback symptoms (Gross 1972, Houston 1987).

Our studies into the physiology of birch resistance to bronze birch borer suggest there may be a direct trade-off between female reproductive effort and resistance to the bronze birch borer (*Agrilus anxius*). Bronze birch borer larvae feed under the bark on the xylem-cambium-phloem interface and

are restricted to feeding upon living tissue. Feeding girdles the tree, disrupting the downward transport of photoassimilates. Dieback of roots occur as they are isolated from their energy source, thereby limiting nutrient and water uptake. As attack intensifies, dieback initiates and spreads within the canopy. Heavily infested trees are invariably killed (Anderson 1944, Barter 1957, Carlson and Knight 1969).

From 1986 to 1989, we conducted a controlled, factorial, field experiment investigating the effects of soil moisture, soil fertility, and defoliation on the expression of birch resistance to bronze birch borer. We found soil moisture to be the most important environmental variable affecting resistance. Water deficit reduced rates of photosynthesis, growth, and wound-callus formation, as well as resistance to bronze birch borer (Herms and Mattson, unpubl. data). We found that paper birch resistance to bronze birch may be based largely on generalized trunk responses to wounding, especially rapid wound-callus formation. Furthermore, we found that the strength of this response is dependent on an adequate supply of available current photosynthate (Herms and Mattson, unpubl. data). Feeding-wounds stimulate callus formation, which if rapid enough, may entirely encapsulate small larvae within suberized tissue containing high concentrations of secondary chemicals and low concentrations of nutrients. Normally xylem tissue is a poor source of nutrition (Haack and Slansky 1987); callus tissue may be even worse, preventing larvae from completing development. Larvae may also be physically crushed as they are overgrown by callus. In effect, larvae may be in a developmental race against the tree. Larvae move through the tree in essentially two-dimensional space as they feed, their rate of progress correlated with their rate of consumption. Lesion development characteristic of a hypersensitive response occurs in phloem and xylem tissue surrounding the wound. A rapid rate of callus formation, coupled with reduced rates of larval movement through the wood, may result in larval encapsulation. Implicit in this hypothesis is the prediction that the rate of callus formation necessary for resistance should be presented by a threshold value approximately equal to the maximum rate of larval movement through the plant. Our data suggest that birch trees with rates of callus formation falling below about 0.02 mm/day are highly susceptible to bronze birch borer.

Paper birch (*Betula papyrifera*) is monoecious, with pistillate (female) and staminate (male) catkins produced as separate structures. Male catkins are produced at the end of indeterminate long-shoots in mid- to late-summer following the termination of shoot elongation. They overwinter, elongating and releasing pollen as vegetative buds open in spring. Female inflorescences emerge from overwintering-buds on short shoots as buds break in spring. Female catkin maturation commences upon pollination, and continues throughout the growing season. Seeds mature in late summer and drop throughout the fall and winter.

The results of our experiments confirm previous reports showing a trade-off between vegetative growth and female catkin production (Gross 1972, Tuomi et al. 1982, Caesar and MacDonald 1983). Plants capable of altering the balance of resources allocated between male and female organs generally allocate proportionally more resources to female functions in high resource environments (Freeman et al. 1980). This occurs, presumably, because successful female reproduction requires, in general, a greater commitment of resources than does male reproduction. In our experiment, however, increased female reproductive output in 1 year was associated with resource-limited growth during the previous year. Slow growth may stimulate the initiation of female flowers. Female reproduction itself then further reduces vegetative growth through resource competition. A positive feedback loop may result. Female reproductive effort stimulated by slow growth further reduces growth, which further stimulates female reproduction. Because of reduced rates of callus formation associated with increased female reproductive effort, this positive feedback loop may result in ever-increasing susceptibility to bronze birch borer and eventual tree death. In fact, stress-triggered seed production may be an adaptation which maximizes the life-time reproduction of suppressed trees that are competitively doomed and are likely to be soon killed by bronze birch borer.

Another Look at Birch Dieback: Bronze Birch Borer is Central

Some students of forest decline in North America have been reluctant to assign the bronze birch borer a central role in the occurrence of widespread birch dieback (Anderson 1944, Hawboldt 1947, Carlson and Knight 1969, Houston 1987). At best, the bronze birch borer has been credited with a minor effect on over-all patterns of tree mortality, primarily killing trees already predisposed to death by other factors, such as disease. We argue that patterns of bronze birch borer outbreaks are in some ways analogous to those of the mountain pine beetle, *Dendroctonus ponderosae*, and are sufficient in themselves to contribute significantly to historical patterns of birch dieback in North America: 1) outbreaks of the bronze birch borer, like those of the mountain pine beetle, can be classified as "eruptive" (Berryman and Stark 1985), or more specifically "pulse eruptive" (Berryman 1987); 2) much like the mountain pine beetle (Raffa and Berryman 1983, 1987, Berryman and Stark 1985), we argue that bronze birch borer populations are usually regulated largely by the availability of host plants suitable for larval development and survival (e.g. Carlson and Knight 1969). Outbreaks occur at irregular intervals when biotic and/or abiotic stress factors increase the availability of suitable host trees. 3) Once populations reach epidemic proportions, the outbreak spreads to adjacent stands as large numbers of larvae are able to overwhelm the defenses of vigorous, normally resistant trees.

Paper birch frequently forms even-aged, monospecific stands throughout the boreal forest of North America. Under conditions favoring rapid tree growth, populations of bronze birch borer are constrained to endemic levels by lack of susceptible host material. In this situation, birch borer reproduction is primarily restricted to suppressed trees succumbing to density-dependent competition during the thinning phase of stand establishment. Intolerant of shade, suppressed trees are characterized by low net assimilation rates and lack the resources necessary to support a strong wound response.

Episodes of birch dieback, and associated out-breaks of bronze birch borer, have corresponded with periods of above-average temperatures and below-average precipitation (Hawboldt and Skolko 1948, Redmond 1955, Clark and Barter 1958). Combinations of severe stresses such as drought and defoliation may simultaneously weaken trees over wide geographic areas, resulting in rapid and substantial increases in host material suitable for the bronze birch borer, thereby releasing them from this constraint on population growth (Carlson and Knight 1969).

Female reproduction in birch may play a key role in sustaining bronze birch borer outbreaks. If stress-induced reductions in growth stimulates female reproduction, and female reproductive effort further compromises resistance to bronze birch borer, the result may be a positive feedback loop which rapidly increases the number of susceptible hosts, intensifying and sustaining an outbreak.

Under conditions of extremely high attack density, the defense mechanisms of otherwise resistant trees may be overwhelmed by simultaneous colonization by many larvae. Under these circumstances, larval-feeding behavior may act to subvert host defense mechanisms, facilitating the success of their own colonization as well as colonization by other larvae. When feeding in vigorous hosts, larvae display a zig-zag pattern of gallery formation as they continually double-back against the grain of the wood (Carlson and Knight 1969). This pattern of feeding may partially girdle the tree, causing localized reductions in the strength of wound-induced resistance mechanisms. On the other hand, in severely stressed host trees, galleries show no consistent pattern, as larvae apparently feed on the freshest phloem they encounter (Carlson and Knight 1969).

As borers kill susceptible trees, thereby removing them from the pool of suitable hosts, and as environmental conditions change favoring increased tree growth and stronger wound responses, the epidemic subsides. The borer population declines to an endemic level as the supply of suitable hosts dwindles.

Birch trees experiencing traumatic trunk and canopy death frequently maintain sufficient stored reserves to resprout from the roots. Substantial resprouting often follows above-ground mortality resulting from fire or snowshoe hare browsing. Higher levels of terpenoid surface resins of the bark of juvenile growth originating from root-sprouts are toxic to snowshoe hares and may contribute to the decline of hare population outbreaks (Bryant 1981, Fox and Bryant 1984). Trees killed by bronze birch borer can resprout, as well, and sprouts may be too small to permit bronze birch borer colonization for several years. Sprouting following trunk death is obviously an adaptation to catastrophic disturbances such as fire and herbivore outbreaks, contributing to the continued dominance by birch of seral sites.

Sexual Variation in Resistance and the Carbon/Nutrient Balance

Dioecious plants frequently exhibit sexual dimorphism in resources allocated to reproductive effort, with female effort generally greatest because of resources required for seed and fruit maturation (Lloyd and Webb 1977, Wallace and Rundel 1979, Hoffmann and Alliende 1984, Bullock 1984, Clark and Clark 1988, Snow and Whigham 1989, Allen and Antos 1988). Several studies have documented intraspecific sexual variation in the degree of herbivory experienced by dioecious plants (Dannell et al. 1985, Lovett Doust and Lovett Doust 1985, Ågren 1987, Elmqvist et al. 1988, Alliende 1989, Boecklen et al. 1990). The resource-competition hypothesis predicts increased herbivory on female plants because their typically greater reproductive effort competes for resources with defense mechanisms. However, data from the few existing studies suggest that the opposite is true. Male plants generally experience greater herbivory (Bawa and Opler 1978, Dannell et al. 1985, Ågren 1987, Alliende 1989, Boecklen et al. 1990).

Male and female plants may often segregate along environmental gradients (Putwain and Harper 1972, Freeman et al. 1976, Bawa 1980, Cox 1981, Bierzychudek and Eckart 1988). Differential levels of herbivory, possibly resulting in skewed sex-ratios, may arise from 1) differential frequency of herbivore encounters in their respective environments, or 2) differential defensive allocations among male and female plants.

The nutrient capital required for the growth, maintenance, and maturation of flowers, fruits, and seeds can be substantial and is obtained in full from the rest of the plant (Bazzaz et al. 1979, Thompson and Stewart 1981). Limiting nutrients may be mobilized in relatively high proportions from vegetative tissue to reproductive sinks, thereby contributing to the reductions in vegetative growth associated with reproduction (Mooney 1972, Sinclair and de Wit 1975, 1976, Thompson and Stewart 1981, Bloom et al. 1985, Alpert et al. 1985). The high quantities of nutrients required for fruit and seed maturation may contribute to nutrient deficiencies and ensuing growth reductions in female relative to male plants (Bullock 1984, Allen and Antos 1988).

The reproductive structures of many species are photosynthetic, contributing in varying degrees to their own economy of energy and biomass (Dickmann and Kozlowski 1970, Bazzaz et al. 1979, Reekie and Bazzaz 1987a). Furthermore, enhanced sink strength associated with rapidly developing reproductive structures may stimulate increased photosynthesis in nearby source leaves, through feedback mediated effects (Neales and Incoll 1968, Watson and Casper 1984, Foyer 1988, Dick et al. 1990). As a result, the diversion of carbon from vegetative to reproductive structures may be proportionally less than that of nutrients, especially in female plants (Sinclair and de Wit 1975, 1976, van Andel and Vera 1977, Lovett Doust 1980, Williams and Bell 1981, Abrahamson and Caswell 1982, Mooney and Gulmon 1982, Bullock 1984, Allen and Antos 1988, Reekie and Bazzaz 1987b, Esler et al. 1989). Biomass alone may not always be a suitable measure of reproductive effort (Thompson and Stewart 1981, Abrahamson and Caswell 1982, Bazzaz and Reekie 1985, Reekie and Bazzaz 1987b).

Rapidly growing tissues are invariably strong photosynthetic sinks (Wareing and Patrick 1975, Patrick 1988). However, nutrient limitation slows their growth (Ågren 1988, Patrick 1988).

Photosynthesis, however, can be maintained in existing cells, at nutrient concentrations below those limiting to growth (Chapin 1980, Dietz 1989). Under sink-limiting conditions the carbon/nutrient ratio of the plant increases. Photosynthate assimilated in excess of growth requirements is frequently allocated to secondary metabolism, frequently increasing the plant's resistance to herbivores (Mattson 1980, Bryant et al. 1983, 1987a, 1987b, Mihaliak et al. 1985, 1987). Since "excess" photosynthates could be stored and contribute to future growth rather than be used in defense, enhanced secondary metabolism in response to sink limitation may represent a selected, adaptive use of resources minimizing herbivory (micro and macro) when the plant has limited ability to compensate (via growth) for it.

A nutrient deficiency in vegetative parts female plants relative to male plants resulting from a disproportionate allocation of nutrients from vegetative sources to reproductive sinks may limit vegetative growth (Allen and Antos 1988). Photosynthetic stimulation of source leaves by feedback control exerted by strong reproductive sinks, coupled with direct photosynthetic activity of reproductive tissues, may contribute to a favorable carbon economy within the plant. Together, these factors may interact to increase carbon/nutrient ratio in the foliage of female plants relative to males.

Female plants, because of reduced growth due to their greater reproductive effort, may have limited ability to compensate for herbivory relative to male plants (Ågren 1987, Elmqvist et al. 1987, 1988). Limited compensatory ability coupled with the need by female plants to protect their reproductive investment, may result in females being under stronger selection than males for powerful defense (Putwain and Harper 1972, Ågren 1987, Boecklen et al. 1990). Consequently, patterns of defense observed in female relative to male individuals of a species may mirror the phenotypic patterns of defense predicted by Bryant et al. (1983) in nutrient-deficient relative to nutrient-rich plants. Female plants, like nutrient-deficient plants, should display reduced growth, increased carbon/nutrient balance in vegetative structures, and higher concentrations of secondary metabolites. Very limited evidence supports this pattern. Male plants do seem to receive higher levels of herbivory (Putwain and Harper 1972, Dannell et al. 1985, Ågren 1987, Elmqvist et al. 1988, Alliende 1989, Boecklen et al. 1990, Krischik and Denno 1990, Jing and Coley 1990) and contain lower concentrations of secondary metabolites or have less tough foliage (Palo 1984, Boecklen et al. 1990).

Reproductive Effort in Monoecious Plants May Enhance Their Resistance to Folivores

The principles discussed above should also apply to monoecious plants if they translocate proportionally more nutrients than carbon from vegetative sources to reproductive sinks. This hypothesis predicts that the carbon/nutrient ratio of vegetative tissues will increase with increasing reproductive effort, resulting in increased concentrations of carbon-based secondary metabolites, and possibly enhanced resistance to folivores.

SUMMARY

The process of plant reproduction has pervasive effects on virtually all aspects of plant physiology and should have important effects on plant resistance to herbivores. We hypothesize that increased susceptibility to stem-invading herbivores could result as a consequence of the substantial cost of reproductive effort as resources are diverted from defensive structures and reactions to reproduction. On the other hand, we hypothesize that reproduction can increase plant resistance to folivores. Reproductive effort may result in an increased carbon/nutrient ratio in foliage, as nutrients are translocated to developing flowers, fruits, and seeds. Associated with this increased carbon/nutrient balance may be enhanced allocation to secondary metabolic pathways and increased resistance to some herbivores. Few data are available with which to test these hypotheses. The potential interactions between plant reproduction and herbivory are ripe for investigation.

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