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THE DILEMMA OF PLANTS: TO GROW OR DEFEND

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ABSTRACT

Physiological and ecological constraints play key roles in the evolution of plant growth patterns, especially in relation to defenses against herbivores. Phenotypic and life history theories are unified within the growth-differentiation balance (GDB) framework, forming an integrated system of theories explaining and predicting patterns of plant defense and competitive interactions in ecological and evolutionary time.

Plant activity at the cellular level can be classified as growth (cell division and enlargement) of differentiation (chemical and morphological changes leading to cell maturation and specialization). The GDB hypothesis of plant defense is premised upon a physiological trade-off between growth and differentiation processes. The trade-off between growth and defense exists because secondary metabolism and structural reinforcement are physiologically constrained in dividing and enlarging cells, and because they divert resources from the production of new leaf area. Hence the dilemma of plants: They must grow fast enough to compete, yet maintain the defenses necessary to survive in the presence of pathogens and herbivores.

The physiological trade-off between growth and differentiation processes interacts with herbivory and plant-plant competition to manifest itself as a genetic trade-off between growth and defense in the evolution of plant life history strategies. Evolutionary theories of plant defense are reviewed. We also extend a standard growth rate model by separating its ecological and evolutionary components, and formalizing the role of competition in the evolution of plant defense. We conclude with a conceptual model of the evolution of plant defense in which plant physiological trade-offs interact with the abiotic environment, competition and herbivory.

INTRODUCTION

IN RECENT YEARS, empirical studies of plant/herbivore interactions have increased exponentially (Scriber and Ayres, 1988), but progress toward a unifying and organizing theory of plant defense has not kept pace. The complexity of the subject has hindered the development of a synthetic framework, because any comprehensive treatment of plant defense theory must transcend both the disciplines and the levels of biological organiza-

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tion. We review and synthesize the literature addressing physiological and ecological constraints on the expression and evolution of plant defense against herbivores. Phenotypic and life history theories are unified within the growth-differentiation balance (GDB) framework, forming an integrated system of theories explaining and predicting patterns of plant defense in ecological and evolutionary time. The objective is to generate testable predictions that would otherwise remain unapparent or ambiguous.

Our major premise is that the allocation of resources by plants to chemical and structural defenses decreases growth by diverting resources from the production of leaf area and other vegetative structures. This trade-off has ecological consequences that affect the success or failure of particular resource partitioning and allocation patterns in particular environments. Hence the dilemma of plants: They must grow fast enough to compete, and yet maintain the physiological adaptations (defenses) necessary for survival in the presence of herbivores and pathogens.

PHYSIOLOGICAL CONSTRAINTS ON PLANT DEFENSE

Growth and Differentiation: Cellular Processes

Plant growth and development occurs at the cellular level through the processes of cell division, cell enlargement, and cell differentiation (Loomis, 1953; Wareing and Phillips, 1981). Growth consists of cell division followed by cell enlargement, and leads to an irreversible change in plant size. Both cell division and expansion are resource demanding, with precise requirements for light, water, minerals, temperature, photoassimilates, growth regulators, the regulating effects of neighboring cells, and other factors (Dale, 1976, 1988; McIntyre, 1987; Boyer, 1988; Patrick, 1988). Early stages of leaf growth, before and after budbreak, consist almost entirely of cell division with cell numbers per leaf increasing exponentially until the leaf lamina has unfolded. Thereafter, the rate of increase in cell number slows as the proportion of dividing cells declines as a negative logistic function of time. Hence, leaf growth after lamina unfolding is a diminishing function of cell division, but an increasing function of cell enlargement (Dale, 1976, 1988). The final stages of leaf growth result from cell expansion caused by turgor pressure resulting from vacuolization (Dale, 1976). Even after leaves reach full size, cytoplasm and secondary cell wall synthesis continue to increase the dry weight of the cell (Wareing and Phillips, 1981). The pattern of growth within a leaf is not uniform. For example, epidermal cells mature before palisade cells and, in many dicots, cells in the tips of leaves cease division before those in the base (Boyer, 1988; Dale, 1988). Depending on species and environmental conditions, the course of leaf growth may range from a few days to several weeks (McIntyre, 1987; Dale, 1988).

Cellular differentiation processes include the chemical changes that occur in maturing cells, and the resultant morphological changes leading to qualitative differences among cells and cell specialization. Differentiation processes tend to follow cell division and enlargement, although overlap occurs (Loomis, 1932, 1953; Wareing and Phillips, 1981). Examples of cellular differentiation processes include the thickening of leaf cuticle and secondary cell walls, production of wax and cellular inclusions, and secondary metabolism (Loomis, 1932, 1953; Böhm, 1977; Luckner and Nover, 1977; Luckner, 1980; Wiermann, 1981; Lindsey and Yeoman, 1983; Lorio, 1986, 1988). At higher levels of organization, cellular differentiation processes result in the development of vascular tissue, resin ducts, secretory glands, trichomes, spines, and other specialized tissues.

Secondary metabolism includes the biosynthesis, transport, accumulation and storage of metabolic products of the shikimic, polyketide and mevalonic pathways, as well as pathways generating alkaloids, glucosinolates and other compounds (Böhm, 1977; Luckner and Nover, 1977; Luckner, 1980; Wiermann, 1981; Torssell, 1983). Unlike the products of primary metabolism that are common to all plants, the secondary metabolic profile of different plant species varies considerably, reflecting evolutionary history and taxonomic relationships (Ehrlich and Raven, 1964; Bate-Smith, 1984; Gottlieb, 1989, 1990; Harborne, 1990).

Certain Differentiation Processes Limit Herbivory

Although primary roles for secondary metabolites have been implicated in some physiological processes (Seigler and Price, 1976; Seigler, 1977), defense is generally assumed to be their raison d'être (Fraenkel, 1959; Whittaker and Feeny, 1971; Levin, 1976a; Swain, 1977; McKey, 1979; Rhoades, 1985; Williams et al., 1989; Harborne, 1990). Indeed, secondary metabolites that deter colonization and feeding are primary reasons why plants escape the vast majority of herbivores occurring in their environment (Dethier, 1980; Bernays and Chapman, 1987). Differentiation processes that result in structural reinforcement (e.g., toughened leaves, trichomes and spines) are also critical plant traits that limit herbivory (Levin, 1973; Coley, 1983, 1987; Pollard and Briggs, 1984; Cooper and Owen-Smith, 1986; Schoener, 1988).

There are, of course, no absolute barriers to herbivory (Mattson et al., 1988). Herbivores have evolved a number of strategies for circumventing the resistance mechanisms of their hosts, including physical sabotage of structural and chemical defense systems (Carroll and Hoffman, 1980; Dillon et al., 1983; Tallamy, 1985; Compton, 1987; Dussourd and Eisner, 1987; Roy and Bergeron, 1990; Dussourd and Denno, 1991), and the enzymatic detoxification of secondary metabolites (Dowd et. al., 1983; Brattsten, 1988; Lindroth, 1991). Some herbivores sequester plant secondary metabolites for deterring their own predators (Eisner et al., 1974; Brower and Glazier, 1975; Peterson et al., 1987; Pasteels et al., 1988; Bopré, 1990; Björkman and Larsson, 1991), repelling competing herbivores (Raupp et al., 1986), or pheromone precursors (Hughes, 1974; Bopré, 1990). Some insects even use secondary metabolites as nutrients (Kato, 1978; Bernays and Woodhead, 1982; Bernays et al., 1983).

Cellular Ontogeny Constrains Secondary Metabolism

In developing tissue, secondary metabolite production can be constrained by the lack of enzymatic machinery necessary for their synthesis, and the lack of fully developed cell walls, vacuoles, idioblasts, resin ducts, laticifers, and other specialized structures required for their compartmentation (Orians and Janzen, 1974; Böhm, 1977; Jalal and Collin, 1977; Wiermann, 1981; Lindsey and Yeoman, 1983; Hrazdina and Wagner, 1985; Mersey and Cutler, 1986; Collin, 1987; Sakuta and Komanine, 1987; Aerts et al., 1991; Cotton et al., 1991; Kim and Mahlberg, 1991; Koops and Groeneveld, 1991; Lewinsohn, Gijzen, Savage, and Croteau, 1991; Wagner, 1991). In meristematic (dividing) cells, the limited expression of secondary metabolism is apparently a fundamental constraint, as this pattern is observed with few exceptions in bacteria, fungi and animals, as well as in higher plants (Luckner and Nover, 1977).

In a seeming paradox, concentrations of some secondary metabolites (particularly low-molecular-weight phenolics, terpenes and alkaloids) are highest during early stages of seedling growth and leaf expansion, and/or are synthesized only in young tissue (Dement and Mooney, 1974; Cates and Rhoades, 1977; Frischknecht et al., 1986; Potter and Kimmerer, 1986; Puttick, 1986; Mauffette and Oechel, 1989; Aerts et al., 1991; Fujimori et al., 1991; Porter et al., 1991; Singh et al., 1991). Plants may overcome ontogenetic constraints on secondary metabolism in a number of ways.

Stored Secondary Metabolites

Previously synthesized secondary metabolites may be stored for use when and where their biosynthesis is constrained (Bryant et al., 1983). Many plants secrete stored phenolic or terpenoid resins over newly expanding foliage (Curtis and Lersten, 1974; Rhoades, 1977; Dell and McComb, 1978; Shain and Miller, 1982; Williams et al., 1983; Johnson et al., 1984; Fahn, 1988; Zobel and Brown, 1990a,b). Inactive meristematic cells may store previously formed secondary metabolites in small vesicles that later fuse with the vacuole as it develops during cell growth (Rao, 1988). Several studies show concentrations of secondary metabolites to be highest in buds (or at budbreak) and then to decline as leaves expand (Crankshaw and Langenheim, 1981; Palo, 1984; Horner, 1988; Mauffette and Oechel, 1989; Hatcher, 1990). Some plants provision seeds with high concentrations of secondary metabolites, possibly to protect the seed and the rapidly growing seedling before it has developed the capability to synthesize significant quantities on its own (Janzen, 1971; McKey, 1974; Wink and Witte, 1985; Frischknecht et al., 1986; Selmar et al., 1988; Bodnaryk and Palaniswamy, 1990).

Precocious Differentiation of Compartmentation Sites

Ontogenetic constraints on secondary metabolism can vanish rapidly. Secondary metabolites are frequently concentrated in epidermal cells (Levin, 1976a; McClure, 1979; Wiermann, 1981; Neumann et al., 1991), which are among the first cells in leaves to mature (Dale, 1988). In some plants, epithelial ducts, laticifers, glandular trichomes, and other cells specialized for the synthesis and accumulation of secondary metabolites are differentiated during early stages of leaf and seedling development (Vogelmann et al., 1987; Gilliland et al., 1988; Jahnen and Hahlbrock, 1988; Williams and Ellis, 1989; Kim and Mahlberg, 1991).

Whole-Plant Resource Trade-Offs Constrain Secondary Metabolism

Constraints operating at higher levels of organization can limit secondary metabolism in ontogenetically "capable" tissues. Plants have limited resources to support their physiological processes, hence all requirements cannot be met simultaneously, and trade-offs occur among growth, maintenance, storage, reproduction and defense. 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 (Mooney, 1972; Mooney and Chu, 1974; Gifford and Evans, 1981; Bryant et al., 1983; Mooney et al., 1983; Gifford et al., 1984; Bloom et al., 1985; Coley et al., 1985; Bazzaz et al., 1987; Loehle, 1988; Loomis et al., 1990; Chapin, 1991; Körner, 1991).

Growth processes demand particularly high levels of limited plant resources (Chung and Barnes, 1980a,b; McLaughlin et al., 1980; Patrick, 1988). Therefore, during periods of intense growth, secondary metabolism may be substrate and/or energy limited (Croteau et al., 1972; Mooney and Chu, 1974; Orians and Janzen, 1974; Luckner and Nover, 1977; Margna, 1977; Mooney et al., 1983; Gulmon and Mooney, 1986; Margna et al., 1989; Chapin, 1991). Trade-offs are inevitable because the resource requirements of secondary metabolism are also substantial (Croteau et al., 1972; Chung and Barnes, 1977; Chew and Rodman, 1979; McDermitt and Loomis, 1981; Gulmon and Mooney, 1986; Williams et al., 1987; Lambers and Rychter, 1990). The cost of synthesizing a phenolic resin, a cyanogenic glycoside, and an alkaloid have been minimally estimated at about 2.6, 2.8 and 5.0 g CO_2 per g metabolite, respectively (Gulmon and Mooney, 1986).

Furthermore, primary and secondary metabolic pathways share common precursors and intermediates (Margna, 1977; McClure, 1979; Lindsey and Yeoman, 1983; Baldwin et al., 1987; Margna et al., 1989). Jensen (1985) estimated that at least 60 percent of total plant biomass is composed of molecules that transversed the shikimate pathway, which gives rise to certain amino acid precursors (tryptophan, phenylalanine and tyrosine) of protein, phenolics, alkaloids and cyanogenic glycosides. Phenylalanine is the rate-limiting precursor for phenylpropanoid synthesis (e.g., lignin, flavonoids and condensed tannins), and at the same time is an essential amino acid for protein synthesis (Margna, 1977; McClure, 1979; da Cunha, 1987; Margna et al., 1989). Plant growth is heavily dependent on protein synthesis for the manufacture of photosynthetic, biosynthetic and regulatory enzymes, as well as for structural protein. As such, phenolic synthesis competes with growth for common substrate (Margna, 1977; Phillips and Henshaw, 1977; Margna et al., 1989). Alkaloid synthesis, with its amino acid precursors, also competes directly with protein synthesis, and consequently with growth (Lindsey and Yeoman, 1983; Hegnauer, 1988). Acetyl CoA serves as the precursor for terpenoids and also the entry point to the Kreb's cycle (Gray, 1987).

Trade-offs between primary and secondary metabolism are well documented in cell cultures (Phillips and Henshaw, 1977; Lindsey and Yeoman, 1983; Collin, 1987) and at the whole plant level. Many intraspecific comparisons document physiological trade-offs between growth rate and secondary metabolism in both wild and crop species (Hanover, 1966a; del Moral, 1972; Mooney and Chu, 1974; Podstolski et al., 1981; Krischik and Denno, 1983; Mihaliak and Lincoln, 1985, 1989a; Waring et al., 1985; Coley, 1986; Larsson et al., 1986; Lorio and Sommers, 1986; Bryant, 1987; Bryant, Chapin, Reichardt, and Clausen, 1987; Bryant, Clausen, Reichardt, McCarthy, and Werner, 1987; Lightfoot and Whitford, 1987, 1989; Appleton and van Staden, 1989; Glyphis and Puttick, 1989; Hrutfiord and Gara, 1989; Margna et al., 1989). Björkman and Anderson (1990) have also documented a trade-off between growth and structural defenses (the elaboration of which diverts resources from the production of leaf area) in South American blackberry (*Rubus bogotensis*).

Modular Construction Affects Resource Use Priorities

Growth and differentiation processes occur at the cellular level, but their functional integration at higher levels of organization shapes the structure and function of the plant (Wareing and Phillips, 1981). Higher plants can be considered an integrated network of cellular systems. These systems are organized into specialized morphological subunits (modules) among which the distribution of limited resources is regulated through complex source/sink relationships (Loomis et al., 1990). Modules are repeated multicellular units originating from single meristems, that combine to form higher levels of organization from roots and branches to entire plants (Harper and White, 1974; Harper and Bell, 1979; Watson and Casper, 1984; Halle, 1986; Barlow, 1989; Tuomi and Vuorisalo, 1989a,b). Higher plants grow by means of the reiterated production of these modules.

Modules within a plant are semiautonomous, in that the translocation of resources within and among them can be restricted (Watson and Casper, 1984; Dickson, 1989; Wardlaw, 1990). However, the degree of modular integration varies among species on a continuum from nearly complete autonomy to high interdependence (Watson and Casper, 1984). In spite of their semiautonomous nature, competition among modules for limited resources is well documented (Gill, 1986). Even though the growth and reproduction of some modules may be supported at the expense of others, the "competitive" pattern of resource partitioning among modules should be adaptive (Hardwick, 1986; Loomis et al., 1990). The survival of each module is ultimately dependent on the survival of the genet, hence there should be strong selection against "selfish" interactions among modules that decrease the inclusive fitness of their "metapopulation," the genet (J. White, 1979, 1984; Hardwick, 1986; Tuomi and Vuorisalo, 1989a,b).

Patterns of resource use within a plant are determined by within-module allocation, as well as between-module (whole plant) partitioning priorities. For example, individual leaves and modules do not export assimilates until their own growth requirements have been met (McLaughlin et al., 1979; Dickson, 1989; Wardlaw, 1990; Dickson and Isebrands, 1991). At the level of the whole plant, patterns of resource distribution reflect the power of modules to draw assimilates (i.e., their sink strength), which is a function of: (a) the number of meristems giving rise to modules, (b) the rate of module initiation per meristem, (c) the developmental fate of the module (i.e., vegetative and/or reproductive), (d) the rate and duration of the growth of each module, and (e) the nature of vascular connections among modules (Harper and White, 1974; Harper and Bell, 1979; Watson and Casper, 1984; Halle, 1986; Hardwick, 1986; Dickson, 1989; Haukioja et al., 1990; Dickson and Isebrands, 1991).

When environmental conditions are favorable, vegetative growth generally receives resource priority over secondary metabolism and storage (Mooney and Chu, 1974; Chung and Barnes, 1980a,b; Waring and Pitman, 1985; Bazzaz et al., 1987; Chapin et al., 1990; Dickson and Isebrands, 1991). Consequently, quantitative variation in the secondary metabolism of plants is a function of variation in the rate and duration of growth of individual modules, as well as the proportion of modules undergoing growth at any one time. If a large proportion of modules within a plant are undergoing growth simultaneously, secondary metabolism will be limited by lack of substrate (Mooney and Chu, 1974; Orians and Janzen, 1974; Luckner and Nover, 1977; Margna, 1977; Mooney et al., 1983; Gulmon and Mooney, 1986; Margna et al., 1989; Chapin, 1991). In plants with indeterminate patterns of growth, some modules continue to grow after others have matured (e.g., Clausen and Kozlowski, 1965; Kozlowski and Clausen, 1966). Secondary metabolism in mature modules will be limited if they export much of their photoassimilates to strong vegetative or reproductive "sinks" undergoing rapid growth.

The Opportunity Cost of Plant Defense

The relative growth rate (RGR) of a plant is equal to the product of its net assimilation rate (NAR) (net carbon accumulation per unit of time) and leaf area ratio (LAR) (ratio of total leaf area to total plant dry mass) (Hunt, 1978; Lambers, 1987):

$$\mathrm{RGR} = \mathrm{NAR} * \mathrm{LAR}.$$

In both wild plants and domesticated crops, differences in growth rates and dry matter accumulation result primarily from differences in patterns of resource partitioning rather than differences in NAR. It is the differential investment of photoassimilates into new leaf area that is largely responsible for both genotypic and phenotypic differences in growth rates (Potter and Jones, 1977; Gifford and Evans, 1981; Gifford et al., 1984; Lambers, 1987; Patrick, 1988; Poorter, 1990; Poorter and Remkes, 1990; Poorter et al., 1990; Chapin, 1991; Körner, 1991). Hence, there is a very substantial "opportunity cost" of plant defense. Secondary metabolism and the elaboration of structural defenses decreases growth by diverting resources from the production of new leaf area (Chapin, 1989; Fagerström, 1989; Baas, 1990; Körner, 1991).

Primary Roles for Secondary Metabolites Decrease Their Cost as Defenses

Defense is not the only role of secondary metabolites in plants (Seigler and Price, 1976; Seigler, 1977). Other functions include attraction of pollinators (anthocyanins and flavonoids) (Brehm and Krell, 1975; Rhoades, 1979), protection from UV light (phenolic resins, anthocyanin, flavonoids) (Rhoades, 1977; Lee and Lowry, 1980; Caldwell et al., 1983; Les and Sheridan, 1990), structural support (lignin and tannins) (Rhodes, 1985; Haslam, 1988; Chalker-Scott and Krahmer, 1989), temporary nutrient storage (alkaloids and cyanogenic glycosides) (Wink and Witte, 1985; Selmar et al., 1988; Harborne, 1990; Poulton, 1990), phytohormone regulation (flavonoids and other simple phenolics) (Rhodes, 1985; Doberski, 1986; Jacobs and Rubery, 1988; Chalker-Scott and Krahmer, 1989), drought resistance (tannins, phenolic resins) (Rhoades, 1977; Bariska and Pizzi, 1986; Pizzi and Cameron, 1986; Meinzer et al., 1990), facilitation of nutrient uptake (phenolics) (Boyer et al., 1989; Baas, 1990), protection of roots from acidic and reducing environments (tannins) (Kimura and Wada, 1989), and mediators of plant relationships with symbiotic nitrogen-fixing bacteria (flavonoids) (Peters et al., 1986; Baas, 1990; Hartwig et al., 1990; Lynn and Chang, 1990). Furthermore, some secondary metabolites may be metabolized and returned to the resource pool available for primary metabolism, further attenuating their costs (Robinson, 1974; Seigler and Price, 1976; Wink and Witte, 1985; Frischknecht et al., 1986; Selmar et al., 1988; Harborne, 1990; but see Mihaliak et al., 1991). The diverse roles of secondary metabolites in plants may decrease their opportunity costs as defensive compounds.

Resource Availability and Source/Sink Interactions

Plants export carbon from sources (leaves and storage organs) to sinks (active meristems and sites of reserve accumulation) via phloem transport (Wareing and Patrick, 1975). Sink strength (the relative ability of different sinks to attract carbon) is a product of sink size and activity; actively growing meristems are especially strong photosynthetic sinks (Ho, 1988; Dickson, 1989; Wardlaw, 1990; Dickson and Isebrands, 1991; Körner, 1991; Luxmore, 1991). Strong meristematic activity requires copious supplies of water and nutrients to drive cell division and expansion. Hence, sink strength is a function of resource availability (Wareing and Patrick, 1975; Ågren, 1985a, 1988; McIntyre, 1987; Daie, 1988; Hirose, 1988a; Patrick, 1988; Wardlaw, 1990; Chapin, 1991; Luxmore, 1991).

Photosynthesis and growth do not respond equally to gradients of water and nutrients. Growth processes are slowed considerably by even moderate shortages of nutrients or water. Net photosynthesis, however, is not as sensitive to resource limitation (Hsiao, 1973; Chapin, 1980a; Bradford and Hsiao, 1982; McDonald et al., 1986; Daie, 1988; Dietz, 1989; Körner, 1991; Luxmore, 1991). Consequently, environments suitable for growth are only a small subset of those suitable for net carbon fixation. Thus, when moderate nutrient deficiency or drought impose sink limitations upon growth, carbohydrates accumulate in excess of growth requirements (Chapin, 1980a; McDonald et al., 1986; Daie, 1988; Dietz, 1989; Chapin et al., 1990; Wardlaw, 1990). The accumulation of carbohydrates, however, may eventually inhibit photosynthesis through negative feedback mechanisms (Neales and Incoll, 1968; Watson and Casper, 1984; Foyer, 1987, 1988; Körner, 1991; Luxmore, 1991).

Source strength is a function of the availability of carbon for export (Wareing and Patrick, 1975). At very low resource levels (light, moisture and nutrients) photosynthesis (carbon assimilation) and growth are both limited. In source-limited plants, primary metabolic processes and maintenance respiration may receive priority use of limited carbon (Waring and Pitman, 1985). Increased resource availability will increase both the photosynthetic and growth rates of source-limited plants. Enhanced atmospheric CO_2 generally increases the growth of C_3 plants by enhancing net assimilation and resource use efficiency, suggesting that plants chronically experience a degree of source limitation (Strain, 1985; Idso and Kimball, 1988; Bazzaz, 1990; Farrar and Williams, 1991; Hilbert et al., 1991).

Nonlinear Effects of Resource Availability on Secondary Metabolism

The exact form of the trade-off function between growth and secondary metabolism has yet to be established for any plant species. However, source/sink theory predicts a nonlinear relationship between growth rate, secondary metabolism, and consequently plant defense (Mattson and Haack, 1987a; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988; English-Loeb, 1989, 1990; Horner, 1990) (Fig. 1). In resource-rich environments, growth processes receive allocation priority for resources (Bazzaz et al., 1987), decreasing the relative availability of carbon for the support of secondary metabolism and structural reinforcement. Hence, within a population, the fastest growing plants will be the least resistant to (but perhaps the most tolerant of) herbivores (Bryant et al., 1983; Mihaliak and Lincoln, 1985; Larsson et al., 1986; Bryant, 1987; Bryant, Chapin, Reichardt, and Clausen, 1987; Bryant, Clausen, Reichardt, McCarthy, and

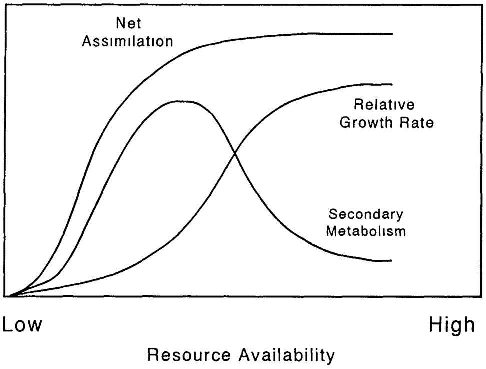

FIG. 1. NORMS OF REACTION FOR NET ASSIMILATION RATE, RELATIVE GROWTH RATE, AND SECONDARY METABOLISM IN RESPONSE TO CHANGING RESOURCE AVAILABILITY

At low to moderate levels of resource availability (light, water and nutrients), rates of net assimilation, growth and secondary metabolism are positively correlated. At moderate to high levels of resource availability, net assimilation rate is constant, relative growth rate and secondary metabolism are inversely correlated, and the physiological trade-off between growth and secondary metabolism is apparent.

Werner, 1987; Hrutfiord and Gara, 1989; Room et al., 1989; Kimberling et al., 1990). This observation lies at the heart of the "vigor hypothesis" of Price (1991).

Environmental constraints on growth can mitigate the cost of defense. Any factor that limits growth more than photosynthesis, such as moderate drought, moderate nutrient limitation, and low temperature (Chapin, 1980a; Bradford and Hsiao, 1982; Daie, 1988; Pollock, 1990; Wardlaw, 1990), will increase the carbon pool available for allocation to secondary metabolism with little or no trade-off with growth (Mattson, 1980; Bryant et al., 1983, 1985, 1988; Gershenzon, 1984; Mihaliak and Lincoln, 1985, 1989a; Waring et al., 1985; Larsson et al., 1986; Lorio, 1986, 1988; Bryant, 1987; Bryant, Chapin, Reichardt, and Clausen, 1987; Bryant, Clausen, Reichardt, McCarthy, and Werner, 1987; Lightfoot and Whitford, 1987, 1989; Mihaliak et al., 1987; Muller et al., 1987, 1989; Glyphis and Puttick, 1989; Charles et al., 1990; Horner, 1990). Hence, sink-limited plants will be more resistant to herbivores than plants experiencing no environmental limitations upon growth. They may have little capacity, however, to compensate for the herbivory they do experience.

At very low resource levels, both growth and photosynthesis are highly constrained. Essential primary metabolic processes and baseline maintenance may receive priority use of limited carbon. Because of energy and substrate limitation, carbon-based secondary metabolism and herbivore resistance generally decline (Bryant et al., 1983; Waring and Pitman, 1985). Consequently, shading generally decreases plant resistance to herbivores, including bark beetles (Waring and Pitman, 1985; Christiansen et al., 1987), browsing mammals (Bryant, 1987; Bryant, Chapin, Reichardt, and Clausen, 1987), insect folivores (Larsson et al., 1986), and fungal pathogens (Matson and Waring, 1984; Entry et al., 1986). Furthermore, carbon-limited plants will have very limited ability to tolerate herbivory (e.g., McGraw et al., 1990).

A nonlinear relationship between growth and secondary metabolism makes it difficult to use observational data to test the hypothesis that a trade-off occurs between them. For example, Denslow et al. (1987, 1990) and Briggs and Schultz (1990) questioned the existence of a trade-off between growth and secondary metabolism based on their findings of positive correlations between growth rate and concentrations of secondary metabolism. As resource availability (light, water and nutrients) increases from low to moderate, however, net photosynthesis also increases. Increased carbon assimilation creates the possibility for positive correlations between growth and secondary metabolism despite competition for a common resource base (i.e., van Noordwijk and de Jong, 1986) (Fig. 1). Bryant et al. (1983) and Tuomi, Niemelä, Chapin, Bryant, and Sirén (1988) predicted this pattern with respect to phenotypic plasticity in growth and secondary metabolism. At moderate to high resource levels, where net photosynthesis is close to maximum, the physiological trade-off becomes evident as a negative correlation between growth and secondary metabolism (Fig. 1). Thus, it is not possible to infer the lack of a physiological trade-off between growth and secondary metabolism, unless the rate of change in resource acquisition is known.

Phenotypic Variation in Secondary Metabolism: Two Hypotheses

Plant resistance to herbivores results from the interaction of a suite of genetically based chemical and structural traits. Phenotypic variation in herbivore resistance, however, results primarily from variation in plant nutrient and secondary metabolite concentrations. Two conceptually similar hypotheses have been advanced to predict environmental effects on the phenotypic expression of secondary metabolism: (1) the carbon/nutrient balance (CNB) hypothesis (Bryant et al., 1983; Tuomi et al., 1984; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988; Reichardt et al., 1991), and (2) the growth-differentiation balance (GDB) hypothesis (Loomis, 1932, 1953; Lorio, 1986, 1988).

The Carbon/Nutrient Balance Hypothesis

Bryant et al. (1983) originally formulated the CNB hypothesis to explain the effects of fertilization and shade on phenotypic variation in secondary metabolism. The CNB hypothesis predicts that concentrations of carbon-based secondary metabolites (e.g., terpenes, phenolics, and other compounds that have only C, H and O as part of their structure) will be positively correlated with the carbon/nutrient (C/N) ratio of the plant. Conversely, concentrations of nitrogen-based secondary metabolites (e.g., alkaloids, nonprotein amino acids, cyanogenic compounds, proteinase inhibitors, and others having N as part of their structure) are predicted to be inversely correlated with the C/N ratio of the plant (Bryant et al., 1983).

The CNB hypothesis is based upon the following premises. Moderate nutrient deficiency limits growth more than photosynthesis. Hence, nutrient-deficient plants accumulate carbohydrates, increasing the C/N ratio within the plant. Carbohydrates accumulated in excess of growth requirements are allocated to C-based secondary metabolites. In contrast, increased nutrient uptake in fertile soils decreases the C/N ratio within the plant; C-based secondary metabolism declines as growth receives allocation priority. As other factors begin to limit growth, nitrogen assimilated in excess of growth requirements may be allocated to the production of N-based secondary metabolites.

Light intensity can also affect the C/N balance within the plant, and consequently secondary metabolism. Shade decreases the C/N ratio of plants by limiting carbon assimilation more than nutrient uptake. Concentrations of C-based secondary metabolites decline as limited available carbon is allocated to growth. Nitrogen assimilated in excess of growth requirements, however, may be diverted to N-based secondary metabolic pathways. On the other hand, increased light intensity is predicted to increase net photosynthesis, thereby increasing the C/N ratio within the plant, and concentrations of C-based secondary metabolites. Concentrations of N-based secondary metabolites are predicted to decline as N is allocated to photosynthetic and growth processes.

Substantial experimental and correlative evidence supports the CNB hypothesis (Waterman and Mole, 1989). Fertilization has been shown to increase concentrations of N-based secondary metabolites (Nowacki et al., 1976; Mattson, 1980; Gershenzon, 1984) and decrease concentrations of C-based secondary metabolites (Mihaliak and Lincoln, 1985; Waring et al., 1985; Larsson et al., 1986; Bryant, 1987; Bryant, Chapin, Reichardt, and Clausen, 1987; Bryant, Clausen, Reichardt, McCarthy, and Werner, 1987; Lightfoot and Whitford, 1987, 1989; Mihaliak et al., 1987; Glyphis and Puttick, 1989; Price et al., 1989; Waterman and Mole, 1989). Shading has been shown to increase concentrations of N-based secondary metabolites (Van Horne et al., 1988), and decrease concentrations of C-based secondary metabolites (Woodhead, 1981; Waterman et al., 1984; Waring et al., 1985; Larsson et al., 1986; Bryant, 1987; Bryant, Chapin, Reichardt, and Clausen, 1987; Mole et al., 1988; Van Horne et al., 1988; Nichols-Orians, 1991).

The CNB Hypothesis Extended to Sex-Biased Herbivory

In dioecious species, male plants may generally experience greater herbivory than females (Danell et al., 1985, 1991; Lovett Doust and Lovett Doust, 1985; Ågren, 1987; Elmqvist et al., 1988; Alliende, 1989; Boecklen et al., 1990; Jing and Coley, 1990; Krischik and Denno, 1990). This pattern of sex-biased herbivory may be explained by the CNB hypothesis.

The reproductive structures of many species are photosynthetic, contributing in varying degrees to their own economy of energy and biomass (Bazzaz et al., 1979; Reekie and Bazzaz, 1987a; Cipollini and Levey, 1991). 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, 1987, 1988; Luxmore, 1991).

While reproductive structures contribute directly and indirectly to their own carbon requirements, the substantial nutrient investment required for their maturation is obtained in full from the rest of the plant (Mooney, 1972; Sinclair and de Wit, 1975; Bazzaz et al., 1979; Thompson and Stewart, 1981;

Alpert et al., 1985). As a result, the diversion of nutrients from vegetative to reproductive structures may be proportionally greater than that of carbon (Sinclair and de Wit, 1975; van Andel and Vera, 1977; Wallace and Rundel, 1979; Lovett Doust, 1980; Thompson and Stewart, 1981; Williams and Bell, 1981; Mooney and Gulmon, 1982; Bullock, 1984; Bazzaz and Reekie, 1985; Reekie and Bazzaz, 1987b; Allen and Antos, 1988). Hence, differential partitioning of nutrients to reproductive structures may increase the C/N ratio in the foliage. The effect should be strongest in female plants because the maturation of fruit and seeds requires a proportionally higher nutrient investment than does the maturation of male reproductive structures (Wallace and Rundel, 1979; Bullock, 1984; Antos and Allen, 1990; Cipollini and Stiles, 1991). Thus, female plants are predicted to grow slower, have higher concentrations of C-based secondary metabolites, and be more resistant to herbivores than conspecific males. In accord, male plants are generally reported to grow faster (Lloyd and Webb, 1977; Wallace and Rundel, 1979; Bullock, 1984; Hoffmann and Alliende, 1984; Allen and Antos, 1988; Clark and Clark, 1988; Ramp and Stephenson, 1988; Snow and Whigham, 1989; Antos and Allen, 1990; Jing and Coley, 1990; Krischik and Denno, 1990), experience greater herbivory (Danell et al., 1985, 1991; Lovett Doust and Lovett Doust, 1985; Ågren, 1987; Elmqvist et al., 1988; Alliende, 1989; Boecklen et al., 1990; Jing and Coley, 1990; Krischik and Denno, 1990), and have lower concentrations of secondary metabolites or less tough foliage (Palo, 1984; Price et al., 1989; Boecklen et al., 1990; Jing and Coley, 1990; Krischik and Denno, 1990). A similar pattern may occur in monoecious species, with the C/N ratio of the foliage, C-based secondary metabolism, and herbivore resistance increasing in proportion with female reproductive effort.

The CNB Hypothesis Extended to Delayed Induced Resistance

Defoliation of deciduous trees sometimes increases resistance to herbivores in the years following defoliation (delayed induced resistance or DIR) (Wallner and Walton, 1979; Werner, 1979; Haukioja, 1980, 1982; Schultz and Baldwin, 1982; Tuomi et al., 1984; Haukioja and Neuvonen, 1985; Neuvonen et al., 1987; Bryant et al., 1991), whereas equivalent defoliation of evergreens usually does not (Niemelä et al., 1984, 1991; Bryant et al., 1988, 1991; Wagner, 1988). The CNB hypothesis has been extended to explain this phenomenon, proposing that this pattern stems from fundamental differences in the carbon partitioning patterns of deciduous and evergreen plants (Tuomi et al., 1984, 1990; Niemelä et al., 1984, 1991; Bryant et al., 1988, 1991; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988).

During the growing season, most of the nutrient capital of deciduous trees is contained within the foliage. Substantial carbon reserves, however, remain in the roots and other woody tissues. Consequently, defoliation of deciduous species can result in the loss of proportionally more nutrients than carbon, and thus a relative nutrient deficiency in the plant (Chapin, 1980b; Tuomi et al., 1984; Chapin, Shaver, and Kedrowski, 1986; Mihaliak and Lincoln, 1989b; Bryant et al., 1991). Furthermore, defoliation-induced stress may result in fine-root mortality, decreasing nutrient uptake, and thus further aggravating the nutrient deficiency (Bryant et al., 1988; Tuomi et al., 1990). The net result may be an increased C/N ratio in years following defoliation, resulting in increased concentrations of C-based secondary metabolites (Tuomi et al., 1984, 1990; Bryant et al., 1988, 1991; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988).

Evergreens store a larger proportion of carbon in their foliage than do deciduous species. Hence, carbon and nutrient reserves are lost in similar proportions when evergreens are defoliated (Bryant et al., 1983, 1988; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988). Furthermore, coniferous evergreens and slow-growing deciduous species that have been defoliated may not replace carbon as rapidly as nutrients because of their inherently low rates of photosynthesis (Bond, 1989; Sprugel, 1989; Bryant et al., 1991). Hence, their defoliation can result in a relative carbon deficiency within the plant (Ericsson et al., 1980;

Bryant et al., 1991; Niemelä et al., 1991), and consequently undiminished or even increased foliar nutrient concentrations (Piene, 1980; Piene and Percy, 1984; Bryant et al., 1991; Niemelä et al., 1991). The predicted result is a decreased C/N balance, decreased concentrations of C-based secondary metabolites, and no DIR (Niemelä et al., 1984; Tuomi et al., 1984; Bryant et al., 1988, 1991; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988).

The Carbon/Nutrient Balance Hypothesis: Evaluating the Evidence

DIR: Incidental Effect of Defoliation or Evolved Response to Herbivory?

Is DIR an incidental consequence of defoliation-induced alterations in the C/N balance of the plant or adaptive plasticity evolved in response to herbivory (Haukioja, 1980; Tuomi et al., 1984, 1990; Haukioja and Neuvonen, 1985; Bryant et al., 1988, 1991; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988; Tuomi, Niemelä, Rousi, Sirén, and Vuorisalo, 1988)? Divergent predictions can be derived from the two hypotheses. The active defense hypothesis predicts that the presence or strength of DIR should correspond with a plant's evolutionary history of herbivory; the CNB hypothesis predicts DIR should be independent of historical patterns of herbivory (Bryant et al., 1991). The CNB hypothesis predicts DIR should be weak or nonexistent in nutrient-rich environments, where nutrients lost as a result of defoliation are more rapidly replaced; this prediction cannot be derived from the active defense hypothesis (Haukioja et al., 1985; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988). Tuomi, Niemelä, Rousi, Sirén, and Vuorisalo (1988) and Tuomi et al. (1990) argue that because of the semiautonomous nature of plant modules (Watson and Casper, 1984), the CNB hypothesis predicts the effects of defoliation should be localized within damaged modules and branches; a systemic response (detectable in modules distant from the site of injury) would be more consistent with the active defense hypothesis. If DIR is an active defense, then it may be triggered by herbivore-specific cues, and natural defoliation may result in a stronger DIR than artificial defoliation; this prediction is not derivable from the CNB hypothesis (Haukioja and Neuvonen, 1985; Haukioja et al., 1985).

Tests of these hypotheses have yielded support for both. Consistent with the CNB hypothesis: (1) the expression of DIR in mountain birch was localized, being confined to branches defoliated the previous year, and not detected in neighboring undamaged branches on the same tree (Tuomi, Niemelä, Rousi, Sirén, and Vuorisalo, 1988); (2) defoliation resulted in a relative nutrient deficiency and DIR in three fast-growing species, but increased nutrient concentrations and decreased herbivore resistance in three slow-growing species (Bryant et al., 1991); and (3) in the same study, Bryant et al. (1991) found the presence and absence of DIR to be opposite that predicted, based on historical patterns of herbivory experienced by the six species.

Consistent with the active defense hypothesis: (1) DIR in mountain birch (*Betula pubescens*) was stronger in trees from within than from outside the historical outbreak range of the autumnal moth (*Epirrita autumnata*) (Haukioja, 1980); (2) fertilization strengthened DIR and did not shorten its relaxation time in mountain birch (Haukioja and Neuvonen, 1985; Haukioja et al., 1985); (3) defoliation of mountain birch by *E. autumnata* resulted in stronger DIR than artificial defoliation (Haukioja and Neuvonen, 1985); and (4) in a comparison of four deciduous species, DIR was strongest in the two species with historical associations with outbreak herbivores, even though they were the slowest growing of the four species (Neuvonen et al., 1987).

Secondary Metabolism Is Not Consistently Linked to the C/N Balance of the Plant

Not all data are consistent with the CNB hypothesis. In some cases, fertilization increased concentrations of C-based secondary metabolites (Clark and Menary, 1980; Muzika et al., 1989; Björkman et al., 1991; Rousi et al., 1991), or had no effect (Chapin, Shaver, and Kedrowski, 1986; Rousi et al., 1987). In others studies, shading had no effect on C-based secondary metabolism (Lincoln and

Langenheim, 1978; Langenheim et al., 1981; Lincoln and Mooney, 1984). The evidence from experiments addressing the effects of drought and enhanced CO_2 on secondary metabolism also appears inconsistent with the CNB balance hypothesis. Moderate drought stress may generally decrease the C/N balance in the plant because carbon acquisition is limited more than nutrient uptake (Hosner et al., 1965; Viets, 1972; Bloom et al., 1985; Rego et al., 1986; Mattson and Haack, 1987a). Hence, the increased concentrations of N-based secondary metabolites observed in some drought-stressed plants are consistent with the CNB hypothesis (Ball and Hoveland, 1978; Briske and Camp, 1982; Frischknecht et al., 1987). The increased concentrations of C-based secondary metabolites observed in other plants, however, appear inconsistent (del Moral, 1972; Gershenzon, 1984; Lorio and Sommers, 1986; Allen et al., 1987; Ramachandra Reddy and Rama Das, 1988; Charles et al., 1990; Horner, 1990; Ross and Berisford, 1990; Rhizopoulou and Diamantoglou, 1991). Enhanced CO_2 generally increases the C/N ratio within the plant by increasing carbon assimilation and decreasing foliar nutrient concentrations (Strain, 1985; Idso and Kimball, 1988; Bazzaz, 1990). In the few existing studies, however, enhanced CO_2 had no effect on secondary metabolite concentrations (Stuhlfauth et al., 1987; Fajer, 1989; Fajer et al., 1989; Lincoln and Couvet, 1989; Johnson and Lincoln, 1990).

As Reichardt et al. (1991) point out, in many of the studies apparently inconsistent with the CNB hypothesis, concentrations of individual "dynamic" secondary metabolites (compounds that are continually catabolized and resynthesized) were quantified. They argue that measuring static concentrations of such compounds underestimates their true rate of production. The CNB hypothesis may predict most accurately environmental effects on stable "end products" with little or no metabolic turnover (e.g., condensed tannins and lignin which remain in senescent foliage, and insoluble, nonvolatile resins secreted over plant surfaces), the final concentrations of which represent cumulative production (Reichardt et al., 1991). Mihaliak et al. (1991), however, demonstrated that the previously observed rapid metabolic turnover of terpenes in peppermint (*Mentha* × *piperita*) was an experimental artifact. They suggested that other cases also be reexamined before this phenomenon is assumed to be a general occurrence.

The presence of internal metabolic tradeoffs may provide an alternative explanation to secondary metabolic turnover for interpreting some data inconsistent with the CNB hypothesis. Within a plant, changes in the concentrations of individual secondary metabolites are not always correlated with overall changes in total secondary metabolism (e.g., Gilmore, 1977; Berenbaum et al., 1986; Coassini Lokar et al., 1987; Zangerl and Berenbaum, 1987; Hegerhorst et al., 1988; Muzika et al., 1989; Reichardt et al., 1991). If two compounds originate from different branches within the same pathway, concentrations of one compound may increase at the expense of the other (Chew and Rodman, 1979; Baldwin et al., 1987; Berenbaum and Zangerl, 1988; Hegerhorst et al., 1988).

The CNB hypothesis predicts that carbohydrates accumulated in excess of growth requirements will be allocated to C-based secondary metabolism, but does not predict how those carbohydrates will be distributed among the diverse pathways and compounds present within plants. Dynamic compounds (e.g., phenolic glycosides) are often present in small concentrations. Hence, changes in their concentrations will not substantially affect total secondary metabolism. They may increase as total secondary metabolism declines and vice versa. On the other hand, secondary metabolites that accumulate in high concentrations (often stable end products such as condensed tannins and surface resins) are more likely to be directly correlated with total allocation to secondary metabolism. Studies that measure concentrations of the compounds present in highest concentrations (or ideally, total output of secondary metabolic pathways) represent the best tests of the CNB hypothesis.

The Growth-Differentiation Balance Hypothesis

The GDB hypothesis (Loomis, 1932, 1953; Lorio, 1986, 1988; Tuomi et al., 1990) provides a framework for understanding phenotypic variation in secondary metabolism that is similar, but more comprehensive than that of the CNB hypothesis. As with the CNB hypothesis, the fundamental premise of the GDB hypothesis is the existence of a physiological trade-off between growth and differentiation processes, including secondary metabolism. The GDB hypothesis differs from the CNB hypothesis by explicitly addressing the very important developmental constraints on secondary metabolism, as well as all extrinsic factors affecting secondary metabolism. The GDB hypothesis subsumes the CNB hypothesis, predicting that any environmental factor that slows growth more than photosynthesis can increase the resource pool available for allocation to secondary metabolism (Loomis, 1932, 1953). Hence, the predictions of the CNB hypothesis are a subset of the predictions of the GDB hypothesis.

In the cases of source limitation imposed by shade and sink limitation imposed by nutrient deficiency (be it the result of environmental impoverishment, defoliation, or reproductive effort), the predictions of the GDB and CNB hypotheses are the same. Only the GDB hypothesis, however, predicts that sink limitation imposed by extrinsic factors such as moderate drought (Hsiao, 1973; Bradford and Hsiao, 1982; Daie, 1988; Wardlaw, 1990; Luxmore, 1991) and low temperature (Pollock, 1990; Körner, 1991) will result in the accumulation of carbohydrates, and increased concentrations of secondary metabolism. Consistent with the GDB hypothesis, several studies have shown concentrations of secondary metabolites and other products of cellular differentiation to increase in response to moderate drought (del Moral, 1972; Gershenzon, 1984; Lorio and Sommers, 1986; Allen et al., 1987; Mattson and Haack, 1987a,b; Ramachandra Reddy and Rama Das, 1988; Charles et al., 1990; Ross and Berisford, 1990; Premachandra et al., 1991) and low temperature (Lincoln and Langenheim, 1978; Firmage, 1981; Appleton and van Staden, 1989; but see Laine and Henttonen, 1987).

Extending the predictions of the GDB hypothesis to the effects of increased atmospheric CO_2 on secondary metabolism requires an understanding of how enhanced CO_2 will alter the source/sink balance within the plant. The growth rate of C_3 plants generally increases as a result of increased source strength (Strain, 1985; Idso and Kimball, 1988; Bazzaz, 1990; Farrar and Williams, 1991). The effects of enhanced CO_2 on sink activity, however, are not well understood (Farrar and Williams, 1991), but are likely to interact in complex ways with temperature, soil fertility, and water availability (Farrar and Williams, 1991; Hilbert et al., 1991). In the few experimental tests, enhanced atmospheric CO_2 has had little effect on secondary metabolism (Stuhlfauth et al., 1987; Fajer, 1989; Fajer et al., 1989; Lincoln and Couvet, 1989; Johnson and Lincoln, 1990).

The CNB hypothesis is often sufficient to explain phenotypic patterns in secondary metabolism because nutrient availability is a major factor limiting primary production on a global scale (Ågren, 1985b). The GDB hypothesis, however, addresses all environmental factors affecting source-sink interactions, thereby providing a more complete framework for understanding phenotypic patterns of secondary metabolism.

Is Phenotypic Plasticity in Secondary Metabolism Adaptive?

Life history theory assumes that natural selection has shaped resource allocation patterns so as to maximize fitness (within genetic constraints) in different environments (Cody, 1966; Stearns, 1976, 1989a; Southwood, 1988; Tilman, 1990). Plant fitness is strongly correlated with the plant's ability to acquire and retain resources. Within a population this ability is usually positively correlated with growth rate (Harper and White, 1974; Werner, 1975; Solbrig, 1981; Westoby, 1984; Bloom et al., 1985; Coley et al., 1985; Bazzaz et al., 1987; Pearcy et al., 1987; Peet and Christensen, 1987; Chapin, 1988; Fagerström, 1989). Hence, adaptive patterns of source-sink interaction should tend to maximize growth rate within environmental constraints.

The potential adaptiveness of phenotypic plasticity is well recognized (Bradshaw, 1965; Caswell, 1983; Via and Lande, 1985; Grime et al., 1986; Schlichting, 1986; Schlichting and Levin, 1986; Stearns, 1989b; West-Eberhard, 1989). Plasticity may enable plants to assume the most adaptive phenotype in a particular environment, buffering the effects of spatial and temporal variation in resource availability (Grime et al., 1986; Robinson, 1986; Crick and Grime, 1987; Szaniawski, 1987; West-Eberhard, 1989; Farrar and Williams, 1991). Plants display phenotypic plasticity in such traits as growth rate, leaf area, root:shoot ratio, nutrient absorption rate, and secondary metabolism (Chapin, 1980a; Bryant et al., 1983; Grime et al., 1986; Robinson, 1986; Ågren and Ingestad, 1987; Hirose, 1988a,b; Hilbert, 1990). Species with inherently high growth rates may be generally more plastic than those of slower growth (Grime, 1979; Chapin, 1980a; Bryant et al., 1983; Grime et al., 1986).

Phenotypic patterns of secondary metabolism may represent adaptive uses of limited resources (del Moral, 1972; Gershenzon, 1984; Zangerl and Berenbaum, 1990). Genotype × environment interactions (i.e., nonparallel norms of reaction) represent the genetic variation necessary for the evolution of adaptive patterns of phenotypic plasticity, and are commonly found when looked for (Bradshaw, 1965; Via and Lande, 1985; Schlichting, 1986; Stearns, 1989b; van Noordwijk, 1989). The presence of intraspecific variation in norms of reaction for secondary metabolism has been demonstrated in *Abies grandis* (grand fir) (Muzika et al., 1989), *Mentha* × *verticillata* (mint) hybrids (Maffei, 1990), and *Pastinaca sativa* (wild parsnip) (Zangerl and Berenbaum, 1990).

If phenotypic plasticity in secondary metabolism is adaptive, then predicting patterns of secondary metabolism in response to environmental variation requires a knowledge of the costs and benefits of the different allocation patterns in the different environments. Three extreme phenotypes are possible: (1) rapid growth coupled with low secondary metabolism, (2) slow growth coupled with high secondary metabolism, and (3) slow growth coupled with low secondary metabolism (and high carbohydrate storage). Limited resources preclude the fourth possibility of rapid growth coupled with high secondary metabolism. Increased secondary metabolism will be favored if that investment enhances plant fitness to a degree greater than would the same resource investment in an alternative process such as storage or growth. Increased secondary metabolism in response to sink-limitation imposed by drought or nutrient limitation may enhance survival by increasing stress tolerance in harsh environments (del Moral, 1972; Rhoades, 1977; Bariska and Pizzi, 1986; Pizzi and Cameron, 1986; Moreland and Novitzky, 1988; Meinzer et al., 1990), and defense when the plant has limited ability to compensate (via growth) for herbivory (Bryant et al., 1983; Gershenzon, 1984).

Before a plastic response can be assumed to be adaptive, it must be determined that the plasticity results from genetically based changes in the organism (developmental conversion) rather than a passive and incidental response to a variable environment (phenotypic modulation) (Smith-Gill, 1983). This has not been conclusively demonstrated in the case of secondary metabolism. In many cases, changes in secondary metabolism are correlated with changes in the C/N balance of the plant. Experimental evidence, however, suggests that phenotypic variation in secondary metabolism results from highly regulated changes in biosynthetic pathways in response to environmental cues rather than an incidental response to environmental variation (del Moral, 1972; Chapin, Shaver, and Kedrowski, 1986; Mole et al., 1988; Lincoln and Couvet, 1989; Johnson and Lincoln, 1990).

GROWTH-DIFFERENTIATION BALANCE AND THE EVOLUTION OF PLANT LIFE HISTORY STRATEGIES

Interspecific comparisons reveal that inherently fast-growing plants have lower levels of defense than inherently slow growing species, and also generally experience higher levels of herbivory (Cates and Orians, 1975; Bryant and Kuropat, 1980; Chapin, 1980a; Coley, 1980, 1983, 1988; Mattson, 1980; Bryant et al., 1983, 1989; Coley et al., 1985; MacLean and Jensen, 1985; Sheldon, 1987; Loehle, 1988; Pimentel, 1988; Price, 1991). This pattern results from the genotypic manifestation of the physiological trade-off between cell growth and differentiation processes.

This trade-off has ecological consequences that affect the evolution of particular resource allocation patterns in specific environments. In the rest of the paper, we relate the GDB balance concept to the evolution of plant life history patterns, focusing on these consequences. In doing so, we try to construct a hierarchical framework, linking physiological, ecological and evolutionary theories into a unified system of theories explaining and predicting patterns of plant defense in ecological and evolutionary time.

The Growth-Differentiation Life History Continuum

Stearns (1976) defined a life history tactic "as a set of coadapted traits designed by natural selection to solve particular ecological problems" (p. 4). Competition and herbivory (macro- and micro-) are the dominant biotic forces that affect the fitness of plants. In concert with abiotic factors, they shape the evolution of plant life history tactics. Selection exerted by competitors and herbivores interacts with resource availability to result in fitness trade-offs associated with different resource allocation patterns in different environments. The set of integrated physiological traits that minimizes the cost of these trade-offs in a particular environment will be favored by natural selection. We rank these sets of coadapted traits along a growth-differentiation (G-D) continuum of life history tactics.

Plant strategies can be classified according to the cumulative strength of growth relative to differentiation processes occurring within the plant, as indicated by the proportion of total available resources allocated to each of these processes. Growth-dominated plants invest a high proportion of their resources into processes and structures further enhancing resource acquisition, resulting in high relative growth rates. Differentiation-dominated plants invest a high proportion of their resources into the nongrowth processes and structures required to retain and make efficient use of resources under adverse environmental conditions and/or intense herbivory. The consequence is a low relative growth rate.

Obviously, growth processes are dependent on and highly integrated with differentiation processes, and vice versa. For example, the growth of all higher plants is dependent on the differentiation of vascular tissue (Wareing and Phillips, 1981). Conversely, the elaboration of resin ducts and other specialized tissues differentiated for the compartmentation of secondary metabolites is dependent on cell growth. Indeed, their size and number may be proportional to the growth rate of the plant during their construction phase (e.g., Björkman et al., 1991). Nonetheless, many differentiation processes, including the production of secondary metabolites and structural traits that limit herbivory, divert resources from the production of leaf area, and thus act to constrain plant growth.

The patterns we discuss are well recognized and underpin other theories of plant life history evolution (Grime, 1977, 1979; Southwood, 1977; Greenslade, 1983; Coley et al., 1985; Taylor et al., 1990). Growth-dominated plants correspond with the competitive and ruderal strategies of Grime (1977, 1979). They inhabit resource-rich environments, grow rapidly, possess low quantitative levels of chemical defenses, and are often characteristic of early stages of secondary succession (Grime, 1979; Coley et al., 1985; Huston and Smith, 1987; Taylor et al., 1990). Differentiation-dominated species have experienced "adversity-selection" (Southwood, 1977, 1988; Greenslade, 1983; Sibly and Grime, 1986) leading to the evolution of traits consistent with the stress tolerant strategy of Grime (1977, 1979). They typically inhabit resource-limited environments, grow slowly, possess high levels of defenses, and often occupy late-successional sites (Grime, 1979; Coley et al., 1985; Huston and Smith, 1987; Taylor et al., 1990).

The location of a species along the G-D continuum of life history tactics may correspond most closely to the degree of "I (Impoverishment)-selection" (sensu Taylor et al., 1990) experienced by the plant. I-selection intensifies as the mean annual magnitude of environmental carrying capacity (in the absence of disturbance) decreases (Taylor et al., 1990). We predict that the proportion of resources allocated to differentiation processes will increase as I-selection intensifies. Physiological characteristics of growth-dominated and differentiation-dominated plants are summarized in Table 1.

The G-D continuum differs from related life history classifications of Grime (1977, 1979), Southwood (1977, 1988), Greenslade (1983), Coley et al. (1985), and Taylor et al. (1990) by emphasizing the physiological processes and constraints underlying the tactics, rather than the habitats in which they evolve. Thus, we feel that the G-D continuum provides a useful framework, facilitating recognition and understanding of the physiological and ecological constraints underlying the evolution of these tactics.

TABLE 1

Summary of traits predicted to be characteristic of growth- and differentiation-dominated perennial plants

Plant trait	Growth dominated plants	Differentiation dominated plants
Relative growth rate	high	low
Resource acquisition rate	high	low
Resource use efficiency	low	high
Resource turnover rate	high	low
Allocation to leaf area	high	low
Storage reserves	low	high
Degree of sclerophylly	low	high
Secondary metabolism	low	high
Respiration rate	high	low
Proportion of respiratory energy supporting maintenance	low	high
Phenotypic plasticity	high	low
Constitutive resistance to herbivores	low	high
Induced resistance to herbivores	high	low
Competitive ability		
Resource-rich environments	high	low
Resource-limited environments	low	high

Sources: Grime, 1979; Chapin, 1980a; Coley et al., 1985; Coley, 1987; Huston and Smith, 1987; Chapin et al., 1990.

ECOLOGICAL CONSTRAINTS ON THE EVOLUTION OF PLANT DEFENSE

The physiological trade-off between growth and differentiation processes constrains the evolutionary responses of plants as they interact with their biotic and abiotic environments. As plants respond to selection imposed by competition, their potential evolutionary responses to herbivory become limited. Competition occurs when two plants require the same resources that are in short supply, resulting in the decreased performance of one or both (Grime, 1979; Tilman, 1985). Competition for several resources may occur simultaneously, and the relative ability of a plant to acquire different resources may vary (Tilman, 1985, 1986, 1988, 1990). The competitive ability of a plant is ultimately measured by its ability to reproduce relative to other species with which it competes, and is a function of the following traits: (1) the plant's rate of resource acquisition, (2) the rate at which acquired resources are lost, and (3) the efficiency of conversion of acquired resources to biomass (Goldberg, 1990).

Trade-offs may occur among traits maximizing competitive ability in different environments resulting in genotype × environment interactions in competitive ability (Shipley and Keddy, 1988; Tilman, 1988, 1990; Berendse and Elberse, 1990a,b). Plants adapted to resource-rich environments may have a competitive advantage over plants adapted to resource-limited environments when they are grown together under high resource conditions (Mahmoud and Grime, 1976; Wilson and Keddy, 1986a,b; Shipley and Keddy, 1988; McGraw and Chapin, 1989), and vice versa (Chapin, 1980a; Shipley and Keddy, 1988; McGraw and Chapin, 1989).

Traits conferring herbivore resistance and competitive ability exhibit high phenotypic and genetic integration (sensu Schlichting, 1989), hence the trade-offs between competitive ability in different environments have important implications for the evolution of plant defense. Trade-offs among traits conferring competitive ability and herbivore resistance occur in high resource environments because of competition for a shared resource base. No such trade-offs occur in low resource environments because secondary metabolism may enhance stress tolerance and competitive ability, as well as herbivore resistance.

Resource-Rich Environments Favor Growth-Dominated Plants

In resource-rich environments abiotic constraints on plant strategies are minimal, and a variety of allocation strategies with different growth rates are theoretically possible (Tilman, 1988, 1990; Smith and Huston, 1989). The carrying capacity of even the richest environments is limited, however, and slow-growing plants risk the preemption of water, nutrients, light and space by faster-growing competitors. Competition limits the potential successful allocation patterns in resource-rich environments (Mooney and Dunn, 1970; Tilman, 1988, 1990; Smith and Huston, 1989).

Competitive success in resource-rich environments requires rapid acquisition of resources, and thus is dependent upon maximal allocation of resources to the vegetative structures (stems, foliage and roots) used to acquire those resources (Grime, 1977, 1979; Tilman, 1988, 1990). Associated traits include high intrinsic rates of growth, nutrient uptake, photosynthesis, respiration, transpiration and allocation to leaf area (Grime, 1977, 1979; Bazzaz, 1979; Chapin, 1980a, 1988; Mooney and Gulmon, 1982; Grime et al., 1986; Chapin et al., 1987; Huston and Smith, 1987; Gaudet and Keddy, 1988; Goldberg, 1990; Taylor et al., 1990; Berendse and Elberse, 1990a,b).

Optimal Defense in Growth-Dominated Plants

Lost growth and resource acquisition is the greatest cost of defense in resource-rich environments (Chapin, 1989; Fagerström, 1989). These indirect costs, coupled with the direct costs of energy and biomass invested in their construction and maintenance, constrain the evolution of high levels of defense in resource-rich environments (Feeny, 1976; Rhoades and Cates, 1976; Rhoades, 1979; Bryant et al., 1983; Coley et al., 1985; Coley, 1987). Growth-dominated plants, however, possess adaptations that optimize the benefits of minimal defensive investments, thus their realized cost of defense may be small. In fact, efforts to detect and measure this cost in plants with rapid inherent growth rates have met with little success (Simms and Rausher, 1987, 1989; Brown, 1988).

Inducible Resistance

Rapid inducible resistance (rapid accumulation of secondary metabolites in response to injury from insects or pathogens) may be an adaptation minimizing the cost of defense (Edwards and Wratten, 1983; Haukioja, 1990). Unlike constitutive resistance (resistance mechanisms present prior to injury), the cost of rapid inducible resistance is incurred only when needed. This cost, however, may be substantial if the response is intense and sustained (Baldwin et al., 1990).

The expression of induced resistance may be limited to rapidly growing plants and tissues, being weak or nonexistent in slow growing plants and tissues (Haukioja and Niemelä, 1979; Wratten et al., 1984; Braga et al., 1986, 1991; Edwards and Wratten, 1987; Frischknecht et al., 1987; Baldwin, 1988; Apostol et al., 1989). In cell cultures, induction is strongest in growing cells, but growth is temporarily interrupted upon induction as resources are diverted from primary to secondary metabolic pathways (da Cunha, 1987; Eilert, 1987; Threlfall and Whitehead, 1988). Detoxification enzymes may protect immature cells from autotoxicity during wound-induced secondary metabolite accumulation (McKey, 1974; Hendry, 1986). Constitutive levels of detoxification enzymes decline as cells mature, however, their synthesis may continue to be induced by the same elicitors that induce secondary metabolism (Hendry, 1986).

The biological significance of induced resistance has been questioned because of the lack of studies demonstrating dramatic effects on herbivore fitness parameters (Fowler and Lawton, 1985). Because of the semiautonomous nature of plant modules coupled with the ability of plants to compensate (to varying degrees) for herbivory, the impact of a given amount of herbivory on plant growth and reproduction is less when it is dispersed among many modules rather than concentrated on a few (Stephenson, 1980; Watson and Casper, 1984; Marquis, 1988, 1992; Tuomi, Niemelä, Rousi, Sirén, and Vuorisalo, 1988). A primary effect of inducible resistance may be to disperse the consumption of free-feeding herbivores such as Lepidoptera larvae (Edwards and Wratten, 1983, 1987; Silkstone, 1987; Gibberd et al., 1988; Wratten et al., 1988; Croxford et al., 1989; Raupp and Sadof, 1989; but see Bergelson et al., 1986 and Bergelson and Lawton, 1988), thereby minimizing impact on any one module and on overall fitness reduction of the plant (Janzen, 1979). Dispersal may also increase the exposure of herbivores to natural enemies, potentially providing plants with an indirect benefit of induced secondary metabolism (Schultz, 1983a,b; but see Bergelson and Lawton, 1988). The dispersion of feeding is due presumably to the local accumulation of secondary metabolites with deterrent properties. Inducible resistance may be favored by natural selection if it decreases the negative impact of herbivory on whole plant fitness, even without decreasing herbivore fitness or the total tissue loss sustained by the plant (Janzen, 1979; Haukioja, 1990; Haukioja et al., 1990). Zangerl and Berenbaum (1990) provide the first evidence for heritable variation in induced plant resistance to an insect.

Rapidly induced resistance (hypersensitivity) may have more direct and profound effects on less mobile and imbedded insects such as bark beetles, leafminers, galling insects, and adelgids (Fernandes, 1990). These insects generally have a more intimate and specific ecological and evolutionary relationship with their hosts than do free-feeding folivores, creating the opportunity for the evolution of more specific host defenses (Mattson et al., 1988; Fernandes, 1990).

Potent but Low Levels of Constitutive Defenses

The defenses of growth-dominated plants adapted to resource-rich habitats are often based on low concentrations of highly potent, low-molecular-weight toxins and deterrents. Often these are highly oxygenated carbon-based compounds, such as polyketides and terpenoids (Gottlieb, 1989), or nitrogen-based and sulfur-based compounds such as alkaloids, cyanogenic glycosides and glucosinolates (McKey, 1974, 1979; Feeny, 1976; Levin, 1976a,b; Rhoades and Cates, 1976; Mattson, 1980; Mooney et al., 1983; Coley et al., 1985). The reliance on nitrogen-based and/or sulfur-based toxins may be especially prevalent in plants evolving in fertile environments where these nutrients are unlikely to limit growth (Levin, 1976b; Mattson, 1980; Bernays, 1983; Bryant et al., 1983). These metabolites may often be metabolized and recycled through primary metabolism (Robinson, 1974; Seigler and Price, 1976; Wink and Witte, 1985; Frischknecht et al., 1986; Selmar et al., 1988; Harborne, 1990). Hence, these "qualitative" secondary metabolites (sensu Feeny, 1976) may be cost effective for two reasons: they are effective at low concentrations, and they are removed only temporarily from the plant's primary metabolic resource pool (but see Mihaliak et al., 1991).

Plants may further optimize a small defensive investment by allocating secondary metabolites in direct proportion to tissue value and vulnerability (McKey, 1974, 1979; Feeny, 1976; Rhoades and Cates, 1976; Rhoades, 1979). For example, Nitao and Zangerl (1987) found that furanocoumarin concentrations increased in the reproductive structures of *Pastinaca sativa* (wild parsnip) during the developmental stages at which their loss to herbivores would have the greatest negative impact on fitness.

Metabolites that result in little or no feeding when present in small concentrations have an especially favorable cost:benefit ratio for the plant. In fact, behavioral deterrents may be the primary reason why plants escape the vast majority of herbivores present in their environments (Dethier, 1980; Bernays and Chapman, 1987). Because some deterrents are nontoxic when ingested, it has been questioned whether behavioral deterrents represent evolved defenses to herbivores (Bernays and Graham, 1988; Wrubel and Bernays, 1990). If herbivory decreases plant fitness, however, the evolution of secondary metabolites that decrease herbivory should be favored, regardless of whether they are toxic to organisms that avoid them.

Circumventing the Opportunity Cost of Secondary Metabolism

Immature leaves are most nutritious to herbivores because of their high concentrations of nutrients and water, and low concentrations of structural components (Coley, 1980, 1983; Mattson, 1980; Ayres and MacLean, 1987; Mattson and Scriber, 1987; Kursar and

Coley, 1991). Consequently, young leaves frequently experience higher levels of herbivory than mature leaves (Coley, 1980; Krischik and Denno, 1983; Raupp and Denno, 1983; Ernest, 1989; Mitchell Aide and Lodoño, 1989; Núñez-Farfán and Dirzo, 1989). Yet, at least in indeterminate plants, the value of a leaf is highest when it is young, because the future return on photoassimilates reinvested into vegetative structures declines as the leaf ages (Harper, 1989). Thus it should be adaptive to defend young leaves. A dilemma results because increased defense during canopy expansion diverts resources from more leaf production.

The opportunity cost of defense will vary, however, depending upon when it is assessed over the course of the plant activity cycle. In many ecosystems, soil moisture and microbial-mediated nutrient availability peak early in the growing season (Chapin, 1980a; Gutschick, 1981; Lee et al., 1981). Accordingly, many plants complete their growth phase with an intense but short flush corresponding with the temporal availability of the resources required to drive growth. This is followed by a longer period of differentiation and continued photoassimilation. As growth slows, allocation to other processes such as defense and storage often increases (Mooney and Chu, 1974; McLaughlin and McConathy, 1979; Chung and Barnes, 1980a; Dickson, 1989; Chapin et al., 1990; Wardlaw, 1990). These processes are then supported without a tradeoff with growth (i.e., Tuomi et al., 1983). Thus, secondary metabolites may be synthesized when the opportunity costs are low, and stored for future use when defense is constrained.

Secondary metabolites may often be biosynthesized late in the season and used for the defense of overwintering buds and expanding tissue (Bryant et al., 1983). For example, the surface resins providing birch (*Betula* spp.) twigs with browsing resistance (Reichardt et al., 1984; Rousi et al., 1991) are biosynthesized before and after periods of intensive growth (Lapinjoki et al., 1991), and the resin duct system protecting some conifers from bark beetles is constructed after the period of intense growth (Lorio, 1986, 1988).

Many plants secrete stored phenolic or terpenoid resins over newly expanding foliage (Rhoades, 1977; Dell and McComb, 1978; Williams et al., 1983; Johnson et al., 1984; Fahn, 1988; Zobel and Brown, 1990a,b). Cottonwood (*Populus deltoides*) buds accumulate resin in late summer and secrete it over emerging leaves the following spring, thus enhancing their resistance to a leaf beetle (Curtis and Lersten, 1974) and gypsy moth (*Lymantria dispar*) (Meyer and Montgomery, 1987). The resistance of young cottonwood leaves to gypsy moth declines rapidly as the leaves expand (Meyer and Montgomery, 1987) and the surface resin is diluted, volatilized and/or weathered (Shain and Miller, 1982). While late-season secondary metabolism may not decrease the current year's growth, it may divert resources from the storage reserves needed to support maximal growth the following season (Chapin et al., 1990).

Bimodality in Phenological Patterns of Leaf Defense

Concentrations of low-molecular-weight secondary metabolites are frequently highest in buds and immature leaves, and decline as leaves expand (McKey, 1974; Rhoades and Cates, 1976; Cates and Rhoades, 1977; Palo, 1984; Frischknecht et al., 1986; Aerts et al., 1991; Porter et al., 1991). These initial defensive investments may appear substantial when expressed as a foliar concentration. Concentrations calculated for small immature leaves, however, do not necessarily translate into large absolute investments based on the total pool of resources driving canopy expansion (McKey, 1974; Aerts et al., 1991). As leaf maturation proceeds, concentrations of these qualitative defenses generally decline as a result of dilution as leaves expand and/or the cycling of low-molecular-weight secondary metabolites into primary metabolism (Wink and Witte, 1985; Frischknecht et al., 1986; Selmar et al., 1988; Bodnaryk and Palaniswamy, 1990; Zobel and Brown, 1990a,b). Low-molecular-weight phenolics may be converted to lignin or tannin polymers (Dawra et al., 1988). As leaf maturation proceeds, leaves are protected by increasing concentrations of high-molecular-weight polymers such as lignin and tannins ("quantitative" defenses) and structural defenses (Dement and Mooney, 1974; Mooney and Chu, 1974; Feeny, 1976; Rhoades and Cates, 1976; Cates and Rhoades, 1977; McKey, 1979; Coley, 1983; Potter and Kimmerer, 1986; Cates, 1987; Mattson and Scriber, 1987; Hatcher, 1990). Bimodality in phenological patterns of leaf defense appears to be a general phenomenon, and may explain the observation of Coleman (1986) that leaves are most vulnerable to herbivores and stress as they make the transition from photosynthetic sinks to photosynthetic sources.

Genetic Mosaics and Qualitative Variation

The modular construction of plants may have important evolutionary implications for plant defense (although there is little supporting empirical evidence). This may be especially true of fast-growing plants that have the potential for large increases in their number of modules from one year to the next. Unlike animals that maintain a separate germ line, plants are characterized by somatic embryogenesis in which all tissues retain the potential for reproductive differentiation. Consequently, somatic mutations within a tissue may be transmitted to all progenal modules, incorporated into their gametes, and passed to future generations (Whitham and Slobodchikoff, 1981; Mattson et al., 1982; Buss, 1983; Whitham et al., 1984; Jerling, 1985; Tuomi and Vuorisalo, 1989a,b). In fact, genetic mosaicism in plants is well documented (Whitham et al., 1984). A mosaic of variable defensive traits could be adaptive, allowing long-lived and clonally reproducing plants to negate the apparent evolutionary advantage of short-lived, rapidly evolving herbivores (Whitham and Slobodchikoff, 1981; Whitham et al., 1984; Antolin and Strobeck, 1985).

Qualitative variation may represent an adaptive alternative to quantitative increases in constitutive defense (Bowers and Puttick, 1988; Pearson, 1989; Jones and Firn, 1991). Indeed, plants may have evolved specific adaptations for maintaining phytochemical diversity (Jones and Firn, 1991). If an herbivore is capable of detoxifying a particular secondary metabolite, then incremental increases in secondary metabolism will not necessarily equate to incremental increases in defense (Tallamy and Krischik, 1989). Plants may increase their resistance to herbivores through minor mutations in metabolic pathways, however, resulting in the production of a more diverse and/or toxic array of metabolites (Berenbaum, 1978, 1981, 1983; Bowers and Puttick, 1988; Berenbaum et al., 1989, 1991; Jones and Firn, 1991). A battery of secondary metabolites provides the potential for simultaneous resistance to a variety of herbivores (Levin, 1976a; McKey, 1979; Bowers and Puttick, 1988; Pearson, 1989; Jones and Firn, 1991). Furthermore, some of the diverse secondary metabolites possessed by individual plants may be synergistic in their antiherbivore activity, enhancing the benefit: cost ratio of a given defense investment (McKey, 1979; Berenbaum, 1985; Kubo and Hanke, 1985; Berenbaum et al., 1991). Qualitative changes in secondary metabolism that do not alter the balance of resources between growth and secondary metabolism will have no cost to the plant in the form of reduced competitive ability.

Rapid evolution of variation in plant chemistry could result from changes in the expression and repression of already existing metabolic pathways, rather than their de novo generation. Novel secondary metabolites not detected in the intact plant are sometimes biosynthesized in cell culture (Jalal and Collin, 1977; DiCosmo and Towers, 1984; Banthorpe and Brown, 1989). This phenomenon suggests the existence of repressed pathways. Somatic mutation in regulatory genes may result in qualitative variation in the expression of secondary metabolism, permitting a rapid evolutionary response to herbivory (Bowers and Puttick, 1988; Jones and Firn, 1991).

Defensive Mutualisms

Plants may co-opt the third trophic level as part of their own defense (Price et al., 1980; Barbosa and Saunders, 1985; Wisdom, 1985). Defensive mutualisms may be a relatively inexpensive alternative to defensive chemistry, lacking the biosynthetic and maintenance costs of secondary metabolism (Rehr et al., 1973). Ants frequently serve as "pugnacious bodyguards," actively defending plants from herbivores in return for shelter and/or nourishing secretions from extrafloral nectaries (Janzen, 1966; Bentley, 1977; Beattie, 1985).

The activity of pugnacious bodyguards is often primarily associated with young, vigorously growing tissue (Janzen, 1972; Downhower, 1975; Bentley, 1977; Letourneau, 1983; McKey, 1984; Koptur, 1985). As such, they may be valuable adaptations for the defense of undifferentiated tissue in which chemical and structural defense is physiologically constrained (McKey, 1984).

Plants may regulate the activity and composition of secretions, optimizing their cost: benefit ratio (Bentley, 1977). *Piper cenocladum* fails to produce food bodies harvested by ants when ants are absent (Risch and Rickson, 1981). Extrafloral nectaries of *Prunus serotina* (black cherry) are most active during the narrow phenological window in which its major defoliator, *Malacosoma americanum*, is most susceptible to ant predation (which also coincides with leaf expansion) (Tilman, 1978). Finally, artificial defoliation of *Impatiens sultani* induces a short-term increase in the amino acid concentration of its secretion, increasing the cost of the secretion, and potentially the benefit. It is not known, however, if its increased nutritional value attracts more bodyguards (Smith et al., 1990).

Some plants may actively recruit the natural enemies of their herbivores. In response to herbivore damage, some plants release volatile chemicals that attract predators and parasites of the herbivore (Dicke and Sabelis, 1990; Dicke et al., 1990; Whitman and Eller, 1990; Turlings et al., 1990). Recruiting bodyguards by releasing low concentrations of volatiles only when herbivores are present and feeding may be an especially cost-effective defense strategy (Dicke and Sabelis, 1990).

Many plants shelter predacious mites in domatia elaborated on maturing leaves and branches (O'Dowd and Willson, 1989, 1991; Willson, 1991). Nearby domatia garrison mites for the rapid colonization and protection of new growth where they consume phytophagous mites and fungi (O'Dowd and Willson, 1989, 1991). Domatia may be especially cheap as they require only their initial formation (O'Dowd and Willson, 1989).

Endophytic fungi systemically infect and form nonpathogenic mutualisms with plants, deriving energy from their host while protecting it from herbivores and pathogens through the synthesis of secondary metabolites (Carroll, 1988; Clay, 1988, 1990). Endophytes may provide plants with novel chemical defenses (Carroll, 1988), allowing plants to circumvent phylogenetic constraints on the evolution of new secondary metabolites (i.e., Harborne, 1990).

Compensatory Responses to Herbivory

Compensatory growth may represent an evolved alternative to chemical defense as a strategy for reducing net losses to herbivores, especially in resource-rich environments subject to intense and predictable herbivory (Mattson and Addy, 1975; McNaughton, 1983; Mattson et al., 1988, 1991; van der Meijden et al., 1988; Chapin and McNaughton, 1989; Westoby, 1989). Such is the case in the Serengeti grasslands, subarctic salt marshes, and coral reef systems, where as much as 90 percent of net primary production is consumed annually by herbivores (McNaughton, 1984; Hay and Fenical, 1988; Westoby, 1989). Compensation is based on primary metabolic activity, hence it does not incur the opportunity costs associated with chemical defense (Mattson et al., 1988, 1991). Furthermore, the response directly enhances competitive ability.

Plants adapted to heavy grazing have evolved compensatory mechanisms that may allow grazed plants to approach or even exceed their net production in the absence of herbivores (McNaughton, 1983; Paige and Whitham, 1987; Hay and Fenical, 1988; Westoby, 1989). Compensatory growth may result from altered allocation patterns that increase the proportion of plant biomass allocated to foliage production, and/or increased rates of photosynthesis in remaining foliage (Wareing et al., 1968; Verkaar et al., 1986; Brown and Ewel, 1988; Oesterheld and McNaughton, 1988, 1991; Prins et al., 1989; Stafford, 1989; Welter, 1989). Higher net photosynthesis in defoliated plants may result from increased allocation of nitrogen to photosynthetic enzymes (Wareing et al., 1968; Kolodny-Hirsch et al., 1986), improved water balance (Turner and Heichel, 1977; Heichel and Turner, 1983), increased light penetration within the canopy (Welter, 1989), and/or enhanced nutrient availability resulting from defoliation-induced increases in the rate of nutrient cycling (Mattson and Addy, 1975; Chapin, Vitousek, and Van Cleve, 1986; McNaughton et al., 1988; Westoby, 1989). Little or no compensation occurs in nutrient-stressed or water-stressed plants (Coughenour et al., 1985; McNaughton and Chapin, 1985; Verkaar et al., 1986; Chapin and McNaughton, 1989; Georgiadis et al., 1989; Maschinski and Whitham, 1989; Stafford, 1989).

The high degree of integration among modules characteristic of grasses and some other species (Watson and Casper, 1984) may contribute to compensatory ability. This integration may facilitate the rapid mobilization of stored resources. The exchange of resources among ramets of clonal plants may allow an integrated response to herbivory at the genet level (Marshall and Sagar, 1965; Ashmun et al., 1982; Welker et al., 1985, 1987; Schmid et al., 1990).

Resource Scarcity Favors Differentiation-Dominated Plants

Although competition occurs in low resource environments (Fowler, 1986; Chapin, McGraw, and Shaver, 1989; DiTommaso and Aarssen, 1989; Tilman, 1989; Tilman and Cowan, 1989; Taylor et al., 1990), environmental constraints on plant growth may limit its intensity (Reader and Best, 1989; Kadmon and Shmida, 1990; Reader, 1990). In contrast to resource-rich environments where competitive success is dependent on maximizing the rate of resource acquisition, success in resource-limited environments (light, nutrients, and water) is dependent on the more conservative strategy of maximizing the retention and efficient use of scarce resources (Grime, 1979; Chapin, 1980a, 1988; Chabot and Hicks, 1982; Vitousek, 1982; Grime et al., 1986; Tilman, 1988, 1990; Berendse and Elberse, 1990a,b; Goldberg, 1990; Taylor et al., 1990). Correlated traits include low metabolic rates, sclerophyllous long-lived leaves, high rates of nutrient retranslocation prior to tissue abscission, high root:shoot ratios, and growth rate insensitivity coupled with luxury consumption in response to pulses of increased resources (Grime, 1977, 1979; Chapin, 1980a, 1988; Grubb, 1986; Grime et al., 1986; Chapin et al., 1987; Huston and Smith, 1987; Berendse and Elberse, 1990a,b; Goldberg, 1990). Stress-tolerant plants also allocate an especially high proportion of available energy to maintenance respiration (G. J. Taylor, 1989). An inherently low rate of growth may be an inevitable consequence of these traits (Chapin, Groves, and Evans, 1989; Poorter, 1990). Growth rate has been shown to be inversely correlated with tolerance to nutrient (Shipley and Keddy, 1988) and water limitation (Premachandra et al., 1991).

Low Resources Favor Substantive Constitutive Chemical Defense

In resource-limited environments, several factors interact to favor the selection of high levels of secondary metabolism. These include intense selection pressure from herbivores, low opportunity cost of carbon-based secondary metabolism, and the direct contribution of secondary metabolism to competitive ability. Traits minimizing herbivory in resource-limited environments are important because of the low potential of plants in these environments to compensate for herbivory through growth, coupled with the lengthy exposure of long-lived foliage to herbivores (Janzen, 1974; McKey et al., 1978; Bryant and Kuropat, 1980; Chapin, 1980a; Gartlan et al., 1980; Mattson, 1980; Chabot and Hicks, 1982; Bryant et al., 1983, 1988; Coley et al., 1985; Southwood et al., 1986; Coley, 1987; Oksanen, 1990; D. R. Taylor et al., 1990).

The physiological and ecological constraints on the evolution of chemical defenses in plants are diminished in resource-limited environments. When shortages of nutrients and/or water limit growth, the opportunity cost (in the form of sacrificed growth) of secondary metabolism is low (Coley et al., 1985; Chapin, 1989; Fagerström, 1989; Oksanen, 1990). In fact, plants adapted to resource-limited environments are characterized by a substantial investment in carbon-based allelochemicals (Janzen, 1974; McKey et al., 1978; Gartlan et al., 1980; Mattson, 1980; Bryant et al., 1983, 1985; Coley et al., 1985; Reichardt et al., 1990). Structural defenses in the form of thorns and spines may be less common in resource-limited than in resource-rich environments (Campbell, 1986; Owen-Smith and Cooper, 1987), possibly because their elaboration is dependent on growth processes. Although high levels of secondary metabolism may not divert resources from growth in resource-limited environments, trade-offs may occur between secondary metabolism and the accumulation of storage carbohydrates and/or the high level of maintenance respiration necessary to tolerate adverse environmental conditions.

Inducible Defenses Are Limited

Rapid inducible resistance may generally be weak or nonexistent in the leaves of slow-growing plants and modules (Braga et al., 1986, 1991; Edwards and Wratten, 1987; Frischknecht et al., 1987; Apostol et al., 1989; Haukioja, 1990). This may result from inherent physiological constraints. The biosynthesis of phytoalexins requires rapid de novo synthesis of proteins (Dixon, 1986; Ebel, 1986). Thus, their production may be limited to tissue with high metabolic activity containing high levels of water, nitrogen and other nutrients (Braga et al., 1986, 1991; Eilert, 1987; Apostol et al., 1989). This may impose a major constraint on phytoalexin synthesis in differentiation-dominated plants. Furthermore, the speed of the induction process largely governs its efficacy, because defenses must build faster than the growth and spread of the colonizing organisms. Differentiation-dominated plants may be poorly adapted to utilize such defenses because of hydraulic constraints on the translocation of hormonal signals, nutrients, and/or metabolites to and from sites of herbivore injury (e.g., Braga et al., 1991). Foliar-induced resistance is not common in conifers (Wagner, 1988), the leaves of which are poorly vascularized and have lower rates of solute transport compared to those of angiosperms (Bond, 1989).

Ecological constraints may also limit the adaptive value of rapid induced resistance in differentiation-dominated plants. High constitutive levels of secondary metabolites may decrease the benefit of inducible resistance because incremental increases in secondary metabolism are unlikely to be effective against colonizing organisms with detoxification systems adapted to the already high constitutive concentrations of secondary metabolites (Mattson et al., 1988). Inducible defenses may be most advantageous when they occur against low background levels of other defenses. In agreement, Lewinsohn, Gijzen, and Croteau (1991) found the wound-induced accumulation of monoterpenes in the stems of conifer saplings to be inversely correlated with their constitutive secondary metabolite levels.

Nutritional Barriers to Herbivory

The low nutritional quality of plants growing in resource-limited environments may provide a substantial ecological (T. C. R. White, 1978, 1984; Mattson, 1980) and evolutionary (Southwood, 1973) barrier to herbivory. Herbivory may, in fact, select for traits that further lower the nutritional quality of their hosts, including the dilution of essential nutrients and the evolution of indigestible structural components such as cellulose, hemicellulose and lignin (T. C. R. White, 1978; Neuvonen and Haukioja, 1984; Mattson and Scriber, 1987; Pimentel, 1988; Duchesne and Brainerd, 1989; Lundberg and Åström, 1990; Abe, 1991; Haukioja et al., 1991). Nutrient dilution, however, can be a double-edged sword if herbivores increase their consumption to compensate for a low-quality diet (Moran and Hamilton, 1980; Price et al., 1980; Clancy and Price, 1987). Among insects, compensatory consumption may be a common phenomenon (Slansky and Feeny, 1977; Johnson et al., 1985; Slansky and Scriber, 1985; Lincoln et al., 1986; M. F. J. Taylor, 1989; Simpson and Simpson, 1990; Slansky, in press). The plant can nevertheless benefit if herbivore mortality rates increase concomitantly with consumption through increased exposure to parasites, predators and pathogens, or heightened deleterious effects of ingested allelochemicals (Lawton and McNeill, 1979; Schultz, 1983a,b; Wisdom, 1985; Loader and Damman, 1991; Slansky, in press). Moreover, compensatory feeding is seldom perfect so that reproductive capacities are usually diminished, resulting in a lower potential rate of population increase (Neuvonen and Haukioja, 1984; Slansky and Scriber, 1985; Slansky, in press).

The balance of evidence suggests that low nutritive quality, high concentrations of secondary metabolism, and tough, sclerophyllous foliage interact to provide formidable barriers to herbivory in low resource environments (Bryant and Kuropat, 1980; Coley, 1980, 1983, 1987; Mattson, 1980; Bryant et al., 1983; Mattson and Scriber, 1987; Slansky, in press).

Correlated Selection for Differentiation Processes by Herbivory, Competition, and the Abiotic Environment

In resource-limited environments, differentiation processes that limit herbivory may also contribute to the competitive success of the plant. For example, sclerophyllous leaves may enhance tolerance to drought stress and nutrient limitation as well as represent a significant barrier to herbivory (Loveless, 1962; Coley, 1983; Grubb, 1986; Oertli et al., 1990). Foliar surface resins may protect plants from desiccation in arid environments (Rhoades, 1977; Meinzer et al., 1990), and tannins may contribute to drought tolerance by increasing the elastic resilience of cell walls (Bariska and Pizzi, 1986; Pizzi and Cameron, 1986). Secondary metabolites may also directly increase competitive ability through allelopathic effects on neighboring plants (Fowler, 1986).

Increased secondary metabolism may contribute to the maintenance of high levels of photosynthesis. Under growth-limiting conditions, end-product accumulation can result in feedback inhibition of photosynthesis (Neales and Incoll, 1968; Foyer, 1987, 1988; Körner, 1991; Luxmore, 1991). Photosynthates, however, may be shunted into secondary metabolic pathways minimizing the accumulation of photosynthetic end products at their site of synthesis, possibly resulting in increased carbon accumulation (overflow metabolism) (Hoffmann, 1985; Haslam, 1986; Mole et al., 1988; Waterman and Mole, 1989).

We propose three adaptive hypotheses for the existence of overflow metabolism sustained by secondary metabolite synthesis in low resource environments. Overflow metabolism may provide: (1) the photosynthates needed to support the high level of maintenance respiration required to tolerate adverse environmental conditions (Gale and Zeroni, 1985; G. J. Taylor, 1989); (2) the high concentrations of secondary metabolites required for herbivore defense (Coley et al., 1985) and protection from abiotic stress (e.g., UV radiation, photooxidation, desiccation) (del Moral, 1972; Moreland and Novitzky, 1988; Meinzer et al., 1990); and (3) for the removal of the otherwise toxic levels of free ammonia that generally accumulate in response to stress (Rabe, 1990), by cycling the ammonia through the shikimic acid pathway resulting in phenolic accumulation as phenylalanine is continually synthesized and subsequently deaminated. All of the preceding may interact to select for a role of secondary metabolism in decreasing feedback inhibition of photosynthesis in low resource environments (Haslam, 1986).

THE EVOLUTION OF PLANT DEFENSE

It has been argued that herbivores have little effect on plant fitness (Jermy, 1984). A large number of studies, however, document negative effects of herbivory on components of plant fitness including survival, growth, reproduction and competitive ability (Janzen, 1971; Rockwood, 1973; Wargo, 1977; Morrow and LaMarche, 1978; Bentley and Whittaker, 1979; Rausher and Feeny, 1980; Krischik and Denno, 1983; Louda, 1984; Marquis, 1984, 1992; Wright et al., 1984; Crawley, 1985, 1989a,b; Belsky, 1986; Cottam et al., 1986; Elmqvist et al., 1987; Paulissen, 1987; Hendrix 1988; Sacchi et al., 1988; Myster and McCarthy, 1989; Wisdom et al., 1989; Louda et al., 1990; Prins and Nell, 1990b; Wong et al., 1990; Strauss, 1991).

Direct evidence that herbivores can select for enhanced plant defense is accumulating (Simms and Fritz, 1990; Marquis, 1991). Different genotypes within a population must be impacted differentially by herbivores if herbivory is to select for increased resistance. Such variation has been shown to exist in *Piper arieianum* (Marquis, 1984, 1990). Genetic variation also exists within *Salix lasiolepis* (arroyo willow) for resistance to a gall-forming sawfly (Fritz and Price, 1988; Fritz, 1990), which can have negative effects on reproduction (Sacchi et al., 1988). Maddox and Root (1987) demonstrated heritable variation in *Solidago altissima* (goldenrod) resistance to a number of insects. *Ipomoea pupurea* (annual morning glory) was shown to experience directional selection from insect herbivores for increased resistance to the *Heliothis zea* (corn earworm)

(Rausher and Simms, 1989; Simms and Rausher, 1989).

The existence of genetic variation in patterns of secondary metabolism within plant species (Hanover, 1966b; McKey, 1979; Juvik and Stevens, 1982; Berenbaum et al., 1986; McDougal and Parks, 1986; Sanlaville et al., 1988; Altman et al., 1989; Kakes, 1989; Matzinger et al., 1989; Mihaliak et al., 1989; Zangerl and Berenbaum, 1990) creates the potential for herbivores to exert selection on those patterns. Berenbaum et al. (1986) demonstrated experimentally that insects can exert selection on plant secondary chemistry. In fact, phylogenetic patterns in angiosperms indicate that the trend has been toward the evolution of more toxic secondary metabolites (Gottlieb, 1989, 1990; Harborne, 1990).

Evolutionary Models of Plant Defense

Three contrasting yet complementary evolutionary models have emerged to explain quantitative and qualitative patterns of plant defense. They are the optimal defense hypothesis (e.g., McKey, 1974; Feeny, 1976; Rhoades and Cates, 1976; Rhoades, 1979), and two variants of the resource availability hypothesis: the growth rate hypothesis (Coley et al., 1985; Coley, 1987), and the environmental constraint hypothesis (Bryant et al., 1985, 1988; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988). They differ in their assumptions regarding the selective forces shaping the quantitative patterns of defense and the cost of the trade-off between growth and defense.

The Optimal Defense Hypothesis

The optimal defense hypothesis assumes that defenses are costly because they divert resources from growth, and that herbivory is the primary selective force shaping quantitative patterns of secondary metabolism (McKey, 1974; Feeny, 1976; Rhoades and Cates, 1976; Rhoades, 1979; Fagerström et al., 1987). The hypothesis predicts that because defenses are costly, resources are allocated to defense in ways that optimize that investment. Plants will defend tissues in direct proportion to the cost of their loss. Easily replaced, less critical tissues and organs will be less defended than hard-to-replace, indispensable ones (Mattson et al., 1988). Furthermore, patterns of defensive investment will reflect the frequency and severity of herbivory experienced by populations over evolutionary time (Feeny, 1976; Rhoades and Cates, 1976; Chew and Courtney, 1991).

Resource Availability:
The Growth Rate Hypothesis

The resource availability hypothesis extends the optimal defense hypothesis, predicting that the optimal level of defense will vary with the growth rate of the plant (Coley et al., 1985; Coley, 1987; Jing and Coley, 1990). The quantity of resources (water, nutrients and light) available in the environment to support growth interacts with herbivory to determine quantitative patterns of defense (Janzen, 1974; Bryant et al., 1983; Coley et al., 1985; Coley, 1987). As the potential growth rate of the plant decreases, the optimal level of defense increases (Coley et al., 1985). In resource-rich habitats, competition favors fast-growing plants with low levels of defense that detract minimally from growth. In unproductive habitats, limited resources constrain the ability of plants to compensate for herbivory. Furthermore, the opportunity cost of defense is low because of environmental constraints on growth. Hence, high levels of defense are favored.

Resource Availability:
The Environmental Constraint Hypothesis

Bryant et al. (1985, 1988) and Tuomi, Niemelä, Chapin, Bryant, and Sirén (1988) propose a more restrictive view of the resource availability hypothesis. Unlike the growth rate hypothesis, the environmental constraint hypothesis does not require that quantitative patterns of defense represent optimal responses to selection. Instead, the physiological responses of plants to resource availability govern quantitative levels of plant defense and constrain the coevolutionary relationships between plants and herbivores (Bryant et al., 1988).

The thesis that habitat quality constrains genetically based quantitative patterns of secondary metabolism is based in part on the assumption that there is little or no cost associated with the production of carbon-based secondary metabolites (Bryant et al., 1985). This thesis stems from observed phenotypic patterns of secondary metabolism in response to changes in resource availability: plants in resource-limited environments divert carbon reserves accumulated beyond growth requirements to secondary metabolism without a trade-off with growth (Bryant et al., 1985; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988). On the other hand, the same plants in resource-rich environments grow faster, but with a decreased allocation to secondary metabolism. Thus the interpretation is that insofar as a secondary metabolism is supported only by resources acquired in excess of primary metabolic requirements: defense bears no cost (Bryant et al., 1985; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988). Tuomi, Niemelä, Chapin, Bryant, and Sirén (1988) emphasized this point, stating that their allocation model based on resource availability ". . . differs from the optimal defense theory of Rhoades (1979) in that it implies no reduction in growth to support carbon-based resistance; instead allocation to secondary metabolite production occurs only when growth demands for carbon have been met" (p. 59). Tuomi, Niemelä, Chapin, Bryant, and Sirén (1988) concluded that this allocation model alone does not allow herbivores to exert selection on quantitative levels of secondary metabolism, but they may shape the form this investment takes.

The crucial point of this specific model is the extent to which secondary metabolism is supported by excess resources. Even if the model may account for some aspects of phenotypic plasticity, there may still be a background level of secondary metabolism determined by selection, depending on the costs and benefits of secondary metabolism. This requires evidence for genetic trade-offs (negative genetic correlation between growth and defense, see, Reznick, 1985; Reznick et al., 1986). This point will be developed in more detail as it relates to the evolution of plant defense.

Competition Is the Optimizer in Optimal Defense

Interspecific patterns of plant defense correlate well with patterns of resource availability because the nature of selection imposed by herbivores and competitors also correlates well with resource availability. Resource availability per se poses no inherent physiological constraints on the evolution of plant defense or on coevolutionary interactions between herbivores and plants. The evolution of high levels of defense is possible in any environment if herbivory is important enough.

Competition is the major force that constrains the evolution of plant defense. In many environments, competition may be a more important evolutionary force than herbivory (Tilman, 1990; Mattson et al., 1991). Indeed, the greatest impact of herbivores on plant fitness may be the effects that herbivores have on the ability of plants to compete (Louda et al., 1990; Prins and Nell, 1990a). Furthermore, environmental factors affect the nature of selection pressure from competition, hence resource availability plays a modulating role in the evolution of plant defense. In resource-rich environments, increased defense compromises competitive ability. Genetically based trade-offs between traits conferring competitive ability and those conferring herbivore resistance constrain the evolution of increased defense. In resource-limited environments, on the other hand, herbivore resistance is often compatible with (and in some cases conferred directly by) traits conferring competitive ability. There are few inviolate constraints on the evolution of high levels of defense.

The role of competition in shaping the resource allocation patterns of plants is implicit within optimization theories of plant defense (McKey, 1974; Feeny, 1976; Rhoades and Cates, 1976; Rhoades, 1979; Bryant et al., 1983; Coley et al., 1985; Coley, 1987). In the following discussion, we extend the growth rate model of Coley et al. (1985) to emphasize the central role of competition in the evolution of plant defense.

The Growth Rate Model Extended

Coley et al. (1985) formalized their evolutionary theory of plant defense with the following equation:

$$dC/dt = \mathrm{G} * \mathrm{C} * (1 - kD^{\alpha}) - (H - mD^{\beta}).$$

Realized growth (dC/dt) is equal to the maximum inherent growth rate of the plant permitted by the abiotic environment (G, in

$g\ g^{-1}\ d^{-1}$) multiplied by the initial biomass of the plant (C, in g), multiplied by the proportional reduction in potential growth rate as a result of resources invested in defense ($1 - kD^{\alpha}$, in $g\ g^{-1}$), minus the reduction in realized growth due to herbivory ($H - mD^{\beta}$, in $g\ d^{-1}$). The reduction in growth due to herbivory is equal to the potential herbivore pressure in the habitat assuming no defense (H), minus the degree that herbivory is decreased by defense (mD^{β}) (parameters k and α are defined as constants that relate an investment in defense to a reduction in growth; parameters m and β are constants that determine the shape of the defense effectiveness curve) (Coley et al., 1985). This model combines evolutionary (evolved defense) and ecological terms (herbivory), to calculate realized growth (in ecological time). The evolutionary and ecological effects of competition and the abiotic environment are implicit, but subsumed in the G variable.

The model can be extended by formalizing the competition and environmental components in evolutionary and ecological time. Furthermore, by separating the evolutionary and ecological components, assumptions regarding the evolutionary cost of defense can be clarified. Testable alternative predictions of the growth rate (Coley et al., 1985; Coley, 1987) and environmental constraint hypotheses (Bryant et al., 1985, 1988; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988) regarding the cost of defense can be derived from the model.

The extended model uses the following terms:

$$\mathrm{RGR}_{\mathrm{max}},\ \mathrm{RGR}_{\mathrm{p}},\ \text{and}\ \mathrm{RGR}_{\mathrm{r}}.$$

$\mathrm{RGR}_{\mathrm{max}}$ = the maximum inherent relative growth rate that a plant could have evolved in a particular abiotic environment. It directly reflects historical environmental variables, integrating the mean level of resource availability that a plant population has experienced over evolutionary time. It is independent of the effects of competitors and herbivores. Hence, $\mathrm{RGR}_{\mathrm{max}}$ is equal for all species of a given growth form that have evolved in a given environment.

$\mathrm{RGR}_{\mathrm{p}}$ = the potential inherent relative growth rate actually evolved by the plant population (= $\mathbf{R}_{\mathrm{max}}$ of Grime and Hunt, 1975). It represents the potential growth rate obtainable under optimal conditions, and integrates the selective forces [competition (C), herbivory (H), and the abiotic environment (E)] acting on the growth rate of the population:

$$\mathrm{RGR}_{\mathrm{p}} = f\left((\mathrm{RGR}_{\mathrm{max}} - (\mathrm{RGR}_{\mathrm{max}} - kD^{\alpha})),\ \mathrm{C},\ \mathrm{H},\ \mathrm{E}\right).$$

This states that the potential inherent growth rate evolved by a plant population ($\mathrm{RGR}_{\mathrm{p}}$) is a function of the magnitude of difference in relative growth rates between the undefended ($\mathrm{RGR}_{\mathrm{max}}$) and the variously defended genotypes ($\mathrm{RGR}_{\mathrm{max}} - kD^{\alpha}$), and the relative magnitude of the evolutionary importance (sensu Welden and Slauson, 1986) of the concomitant, often interacting selection pressures from C, H, and E. This model assumes no cost of traits maximizing competitive ability in the absence of competitors (an assumption that may not hold for the production of allelopathic secondary metabolites).

We define the ecological component of the model using the following equation:

$$\mathrm{RGR}_{\mathrm{r}} = \mathrm{RGR}_{\mathrm{p}}(1 - m\mathrm{c}^{\epsilon} - p\mathrm{e}^{\nu} - n\mathrm{h}^{\rho})$$

where $\mathrm{RGR}_{\mathrm{r}}$ (realized relative growth rate) is equal to the potential growth rate ($\mathrm{RGR}_{\mathrm{p}}$) diminished by the percent reductions (ecological intensity sensu Welden and Slauson, 1986) caused by competition (c), by the abiotic environment (e), and finally by herbivory (h) (parameters m and ϵ, p and ν, and n and ρ relate the effectiveness of adaptations for buffering the negative effects of competition, the abiotic environment, and herbivory, respectively, to their effect on the growth rate of the plant).

The ecological intensity of herbivory can be further defined where:

$$1 - (n\mathrm{h}^{\rho}) = 1 - (v\mathrm{r}^{\eta} - u\mathrm{d}^{\gamma}),$$

with d equal to the decrease in growth rate caused by plant tissue destroyed by herbivores and r equal to the increase in growth rate due to regrowth (compensatory growth) following herbivory (parameters u and γ, and v and η relate the effectiveness of defensive and compensatory adaptations, respectively, for limiting the negative effects of herbivory on growth rate). Hence, the ecological component of the model becomes:

$$RGR_r = RGR_p(1 - mc^{\epsilon} - pe^{\nu} - ud^{\gamma} + vr^{\eta}).$$

Hence, $RGR_p(1 - mc^{\epsilon} - pe^{\nu} - ud^{\gamma} + vr^{\eta})$ is equivalent to G in the model of Coley et al., 1985. This equation assumes that the ecological effects of competition (c), the abiotic environment (e), and herbivory (h) operate independently in their effects on RGR_r. Clipping and competition were found to have additive effects on the growth and reproduction of *Aristolochia reticulata* (Fowler and Rausher, 1985), providing some justification for this assumption.

Comparing the Optimal Defense and Environmental Constraint Models

This extended model facilitates comparison of the assumptions and predictions of optimal defense (Rhoades, 1979) and environmental constraint (Bryant et al., 1985, 1988; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988) hypotheses, and their implications for the cost of defense. The environmental constraint hypothesis emphasizes abiotic constraints on the evolution of constitutive defense and assumes that plants evolve growth rates close or equal to the maximum potential permitted by the abiotic environment. Implicitly, there is little reduction in growth resulting from the evolved level of defense. Bryant et al. (1985, 1988) and Tuomi, Niemelä, Chapin, Bryant, and Sirén (1988) emphasize that only photosynthates accumulated in excess of growth requirements are allocated to secondary metabolism, thus there is no phenotypic or genetic trade-off associated with defense ($RGR_p = RGR_{max}$ and $kD^{\alpha} = 0$) [Fig. 2(a)]. Thus, under optimal environmental conditions for growth, $RGR_r = RGR_p = RGR_{max}$ [Fig. 2(a)]. It should be noted that the growth rate model (Coley et al., 1985) does not make this restrictive assumption, but does emphasize that quantitative levels of defense are primarily determined by resource availability.

Alternatively, herbivory may select for increased defense, reducing the inherent growth rate of the plant below its evolutionary potential given its abiotic environment ($RGR_p < RGR_{max}$ and $kD^{\alpha} > 0$) [Fig. 2(b)]. This results in a negative genetic correlation between growth rate and defense that is independent of resource availability in evolutionary time. In this case, there is a cost to defense, and a

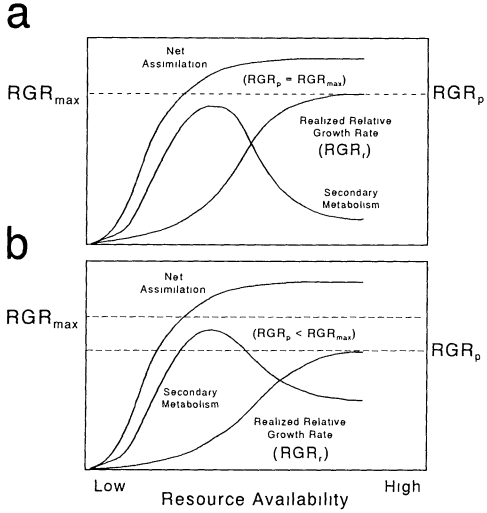

FIG. 2. COMPARISON OF MEAN NORMS OF REACTION FOR NET ASSIMILATION RATE, RELATIVE GROWTH RATE, AND SECONDARY METABOLISM, FOR TWO POPULATIONS (A AND B) OF THE SAME SPECIES, WHICH EVOLVED IN EQUIVALENT ABIOTIC ENVIRONMENTS

Population A evolved according to the environmental constraint model (Bryant et al., 1985, 1988; Tuomi, Niemelä, Chapin, Bryant, and Sirén, 1988) with an inherent growth rate (RGR_p) equal to the maximum permitted by its abiotic environment (RGR_{max}). Only photosynthates accumulated in excess of growth requirements are allocated to secondary metabolism, hence there is no phenotypic or genotypic trade-off between growth and secondary metabolism ($kD^{\alpha} = 0$). When individuals of population A are grown under optimal environmental conditions, $RGR_r = RGR_p = RGR_{max}$. Population B evolved according to the optimal defense model (McKey, 1974; Rhoades, 1979; Coley et al., 1985). Herbivory has selected for increased secondary metabolism, and consequently for an inherent growth rate (RGR_p) less than the maximum permitted by its abiotic environment (RGR_{max}). Hence, there is a genetic trade-off between growth rate and secondary metabolism ($kD^{\alpha} > 0$). When individuals of population B are grown under optimal environmental conditions, $RGR_r = RGR_p < RGR_{max}$.

primary assumption of optimal defense theory is met.

To summarize, environmental constraint theory predicts that resource availability is the primary determinant of evolved level of defense, and that RGR_p will always be equal or close to RGR_{max} (growth is not sacrificed to support defense and defense has no cost), i.e., plants evolving under similar conditions of resource availability will evolve similar growth rates, even if subjected to different intensities of herbivory. Optimal defense theory predicts that herbivores can select for a RGR_p that is less than RGR_{max} (growth is sacrificed to support defense; defense is costly). Plants evolving under similar conditions of resource availability can evolve different growth rates if they experience different intensities of herbivory.

Testing the Hypotheses

Variation between species is vast relative to the variation within species (Southwood, 1988). Thus, the existence of life history tactics has been more apparent at higher taxonomic levels (Stearns, 1980), and it is not surprising that hypotheses addressing the evolution of defense in plants have been developed and tested primarily with interspecific comparisons (Feeny, 1976; Rhoades and Cates, 1976; Grime, 1979; Bryant et al., 1983, 1989; Coley, 1983, 1987, 1988; Coley et al., 1985; Loehle, 1988). Interspecific comparisons allow the inference of process from the identification of pattern (Keddy, 1989). Evidence for the microevolutionary processes leading to the evolution of life history patterns, however, may best be discovered by making intraspecific comparisons in resource allocation patterns, focusing on the selection pressures maintaining genetic variation within species (Stearns, 1976; Futuyma and Moreno, 1988; but see Stearns, 1980).

Both the environmental constraint and optimal defense models of plant defense predict genetically based, intraspecific variation in growth rate and secondary metabolism. The environmental constraint hypothesis represents a physiological null model: herbivores do not select for increased defense at the expense of growth (i.e., $RGR_p = RGR_{max}$). On the other hand, demonstration that herbivory can select for increased defense at the expense of growth ($RGR_p < RGR_{max}$) supports the alternative of optimal defense.

The evolutionary impact of herbivory on plant defense can be tested by making intraspecific comparisons across a series of habitats with similar levels of resources but differing in herbivore pressure. Higher concentrations of secondary metabolites and lower growth rates associated with more intense herbivory would support the assumptions of the optimal defense theory of Rhoades (1979). If resources lost by the faster growing genotypes were balanced by the decreased rate of resource acquisition by the better defended genotypes, intraspecific comparisons of genotypes within a population revealing a balanced polymorphism for growth and defense would also constitute evidence for optimal defense. Models of Augner et al. (1991), which incorporate competition and herbivory, suggest that moderate levels of herbivory can maintain genetic variation for growth rate and secondary metabolism within plant populations and communities. Low and high levels of herbivory, however, will result in directional selection for rapid growth and strong defense, respectively (Augner et al., 1991).

There is limited experimental evidence from intraspecific studies demonstrating genetically based trade-offs between growth rate and/or reproductive fitness and secondary metabolism (Hanover, 1966a; Cates, 1975; Dirzo and Harper, 1982; Dirzo, 1984; Berenbaum et al., 1986; Coley, 1986; Kakes, 1989). Studies implicating herbivores as the force selecting for higher levels of secondary metabolism, however, are confounded by differences in abiotic environments, with the more resistant genotypes generally inhabiting the less favorable habitat. In these cases, the environmental constraint hypothesis cannot be eliminated.

Cates (1975) demonstrated genetic variation within *Asarum caudatum* (wild ginger) for growth rate and resistance to the herbivorous slug *Ariolimax columbianus*, with the faster-growing genotypes being less well defended. The fast-growing genotypes, however, inhabited the most favorable environment, while the defended genotypes were generally restricted to drier habitats (Cates, 1975). Similarly, genetically based differences in secondary chemistry were found in different populations of *Pastinaca sativa* (wild parsnip) (Zangerl and Berenbaum, 1990) and *Satureja douglasii* (Lincoln and Langenheim, 1979). The populations experiencing the highest levels of herbivory had the highest levels of secondary metabolism, but they also inhabited less favorable abiotic environments.

A number of studies suggest that the cyanogenic morphs of *Trifolium repens* and *Lotus corniculatus* are more resistant to herbivores (Ellis et al., 1977a; Jones et al., 1978; Dirzo and Harper, 1982; Dirzo, 1984; Compton and Jones, 1985; Burgess and Ennos, 1987), but they are inferior competitors compared to the acyanogenic morphs (Foulds and Grime, 1972; Dirzo and Harper, 1982; Burgess and Ennos, 1987; Kakes, 1989, 1990; Noitsakis and Jacquard, 1992). Furthermore, some evidence suggests that the distribution of the cyanogenic morphs coincides with that of their important herbivores (Ellis et al., 1977a,b; Compton et al., 1983). These patterns of distribution, however, also coincide with abiotic gradients, thereby again confounding the interpretation (Hughes, 1991).

The Evolution of Plant Allocation Trajectories: Competition and Herbivory Considered

We will conclude and summarize with a mechanistic conceptual model of the evolution of plant resource allocation patterns (Fig. 3). The model is based upon the plant's physiological and ecological constraints resulting in the trade-off between growth and differentiation, and incorporates the effects of natural selection from herbivores and competitors. Resource availability mediates the evolutionary outcome.

Plants allocate their photoassimilates to current use or storage. Current photosynthate is further allocated to primary (growth and maintenance) or secondary metabolic processes (defense). Stored photoassimilates can be considered future allocation to primary and/or secondary metabolism. For any given plant, the percentage of currently available photosynthate allocated to primary metabolism (Y) and the percentage allocated to secondary metabolism (X) can be (at least theoretically) determined. Because of the physiological trade-off between growth and differentiation processes, if primary metabolism (Y) increases, then secondary metabolism (X) must decrease (and vice versa). Therefore, given the plant has a specified level of resources available for allocation, each possible allocation pattern can be represented by a unique set of $\{X_i, Y_i\}$ paired values (Fig. 3). Plotting these points yields a line segment showing the *allocation trajectory* (norm of reaction) for that plant. An individual plant in a particular environment at any given time is represented by a discrete point on the line. By plotting the mean value for all individuals, an entire population is represented by a discrete point.

Welden and Slauson (1986) distinguished between the intensity and importance of

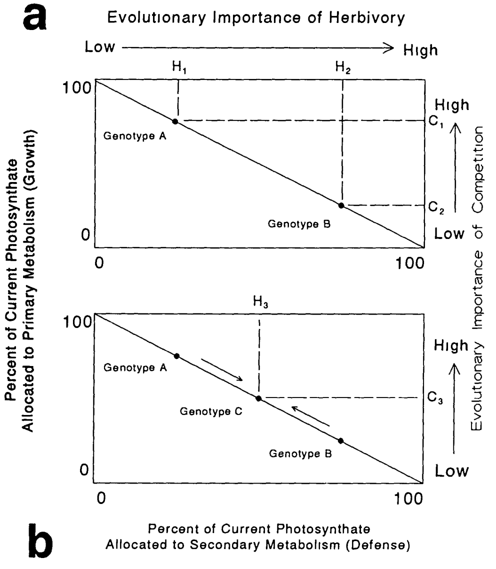

FIG. 3. CONCEPTUAL MODEL OF THE EFFECTS OF COMPETITION (*C*) AND HERBIVORY (*H*) ON THE EVOLUTION OF PLANT RESOURCE ALLOCATION PATTERNS IN VARYING ENVIRONMENTS

(a) Stable polymorphism (genotypes A and B) is maintained by disruptive selection in environments in which the evolutionary importance of herbivory relative to competition is low and high, respectively. (b) Directional selection exerted on populations A and B in an environment in which herbivory and competition are of equal importance results in the evolution of genotype C. See text for additional details.

forces of natural selection. Intensity is the amount of change in growth rate, fecundity, size, or fitness of an individual caused by one selective force independent of changes caused by others. Importance is the degree to which a selective force contributes to the overall change in fitness relative to other selective factors. If we assume competition and herbivory to be the dominant biotic forces exerting selection upon plant allocation patterns, then as the evolutionary importance of one increases, the importance of the other must decrease.

Extending the scale of the model from physiological to ecological-evolutionary, we impose upon the X and Y axes the evolutionary importance of herbivory and competition, respectively (Fig. 3). We assume that their evolutionary importance as selection pressures affecting the relative growth rates of plants are inversely correlated and are determined by the level of resources in the environment available to support growth (e.g., Bryant et al., 1983; Coley, 1985; Reader and Best, 1989; Oksanen, 1990; Reader, 1990). As resource availability increases, the importance of competition relative to herbivory increases. Conversely, as resource availability decreases, the importance of competition relative to herbivory declines. We also assume, however, that the importance of herbivory can vary within an environment independently of resource availability.

In Figure 3(a), intraspecific genetic variation is sustained by disruptive selection exerted by contrasting environments. Genotype A has evolved in an environment in which the importance of competition (C_1) is greater than the importance of herbivory (H_1). Genotype A is favored in this environment over genotype B because of faster growth rate. Genotype B, although well defended (but consequently, slower growing) cannot compete successfully in the absence of herbivores. Genotype B has evolved in an environment in which competition (C_2) is less important relative to herbivory (H_2), due either to resource limitation or more intense herbivory. Genotype B, by virtue of its slower growth rate and higher allocation to defense, is favored. In this environment, herbivores and/or resource limitation depress the realized growth rate of genotype A well below its genetic potential, and genotype A cannot compete successfully.

In an environment in which the importance of competition (C_3) and herbivory (H_3) are equal, both genotypes A and B face directional selection [Fig. 3(b)]. The population of genotype A is under pressure from herbivores to evolve increased defense, while the population of genotype B is under pressure from competition to evolve a faster growth rate at the expense of secondary metabolism. The two populations may converge on genotype C, which will be maintained by stabilizing selection exerted by the opposing pressures of competition and herbivory.

In summary, physiological constraints result in a trade-off between the high rate of growth needed to compete and the differentiation processes that limit herbivory. The mix of genotypes that survive in a plant population will depend on pressures exerted by competition and herbivory, their relative importance being determined by the environment in which the interaction is played out. Competition and herbivory will favor a certain subset of carbon allocation patterns $\{X_i, Y_i\}$ for each given environment. As selection from competition and herbivory varies over time, one or the other may become more important in directing the evolution of the plant population. Phenotypic plasticity in response to environmental variation will buffer these opposing effects of selection. Plant species with broad distributions covering many different habitats having selection pressures varying in importance may evolve stable polymorphisms for allocation to growth and differentiation.

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