

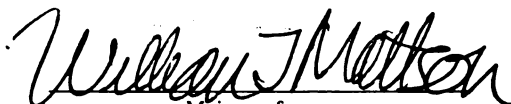


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**VARIATION IN THE RESOURCE ALLOCATION PATTERNS
OF PAPER BIRCH: EVIDENCE FOR PHYSIOLOGICAL TRADE-OFFS
AMONG GROWTH, REPRODUCTION, DEFENSE**

VOLUME I

By

Daniel Albert Herms

A DISSERTATION

**Submitted to
Michigan State University
in partial fulfillment of the requirements
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DOCTOR OF PHILOSOPHY

**Department of Entomology
and
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ABSTRACT

VARIATION IN THE RESOURCE ALLOCATION PATTERNS OF PAPER BIRCH: EVIDENCE FOR PHYSIOLOGICAL TRADE-OFFS AMONG GROWTH, REPRODUCTION, AND DEFENSE

By

Daniel Albert Herms

Allocation theory assumes that plants partition limited resources among growth, reproduction, and defense in ways that maximize fitness. Allocation plasticity may allow plants to express adaptive phenotypes in variable and stressful environments. However, phenotypic plasticity has rarely been investigated in field-grown trees.

In a field experiment, 72 half-sibling paper birch (*Betula papyrifera* Marsh.) trees (age eight) were subjected to a factorial combination of three levels each of water and nitrogen, and two levels of defoliation. Growth, gas exchange, total leaf area, leaf chemistry and morphology, nutrient use efficiency, reproduction, wound response, and resistance to bronze birch borer (*Agilus anxius* Gory) and gypsy moth (*Lymantria dispar* (L.)) were quantified. Trade-offs among growth, reproduction, and defense were detected.

Tree growth was directly correlated with net photosynthesis and total leaf area. Irrigation linearly increased growth, photosynthesis, stomatal conductance, and bronze birch borer resistance in 1988, but had no effect in 1989. Severe drought during 1988 may have enhanced the effects of low irrigation by increasing

evapotranspiration, and thus stomatal limitations on photosynthesis.

Tree growth was correlated positively with leaf nutrient and water concentrations, but inversely with phenolic concentrations and the ability of gypsy moth larvae to digest foliage. Fertilization decreased larval ability to convert digested food to biomass. Larvae compensated for both effects by increasing consumption. Hence, foliage quality had no effect on growth rate or pupal mass. Artificial defoliation (40%) in 1987 and 1988 decreased larval growth and male pupal mass in 1988; there was no delayed induced resistance in 1989.

Bronze birch borer resistance increased linearly with irrigation in 1988, and was positively correlated with tree growth, photosynthesis, and wound-callus formation both years. Drought may interact with high temperature to decrease borer resistance. Trunk-girdling experiments supported the hypothesis that bronze birch borer resistance is dependent on rapid callus formation, which is driven by current photosynthate.

Nitrogen fertilization caused male-biased sex ratios in birch. Female reproductive effort (FRE) in one year was inversely correlated with growth rate the previous year. FRE was a strong photosynthetic sink, decreasing growth, callus formation, and bronze birch borer resistance.

I dedicate this work to my brother, Thomas.

**His inner peace, moral strength,
contentment, and good nature, I can only strive for.**

All who know him are better for it.

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INTRODUCTION

Allocation theory assumes that organisms partition finite resources among competing processes of growth, reproduction, and defense in ways that maximize fitness in different environments. Inherent to this theory is the assumption that physiological trade-offs exist among growth, reproduction, and defense. Phenotypic plasticity may be adaptive, allowing the expression of the best possible phenotype in varying environments.

Human activity is resulting in environmental change on a global scale. Enhanced atmospheric CO₂ may alter patterns of precipitation, increasing the frequency and severity of drought in some regions. Agricultural and industrial pollution is increasing nitrogen deposition in forest ecosystems. These anthropomorphic changes are sparking considerable interest in how plants respond to environmental stress. Tree responses to multiple stresses are poorly understood. The effects of stress on tree resistance to insects are even less understood. This dissertation reports the results of a three-year, controlled field experiment on the effects of a factorial combination of three levels each of irrigation and nitrogen fertilization, and two levels of defoliation on paper birch (*Betula papyrifera*) growth, reproduction, and resistance to bronze birch borer (*Agrilus anxius*) and gypsy moth (*Lymantria dispar*).

Paper birch is a fast growing, early successional species native to the northern and boreal forests of North America. The bronze birch borer is the most important

insect herbivore of birch, and is thought to colonize preferentially and kill stressed trees. Outbreaks of bronze birch borer have been associated with wide-spread dieback of birch, and are thought to be triggered by drought or defoliation. Gypsy moth is the most important defoliator of deciduous trees in North America. It has become well established in Michigan within the last ten years. If not already, it will soon be the most important insect pest in the state. Paper birch is an important host of gypsy moth in Michigan, and will likely affect the population dynamics of this insect in Michigan. Bronze birch borer and gypsy moth represent two very different feeding guilds. Hence, the mechanisms of birch resistance to these insects will be different, and stress will affect these mechanisms in different ways.

The practical objective of this research was to evaluate the effects of stress on the resistance of birch to these two insects. Allocation theory and the hypothesis that physiological trade-offs occur among growth, reproduction, and defense provided the conceptual framework from which predictions were derived and tested during the course of this research, and within which the results were interpreted.

Chapter One reviews and synthesizes the literature addressing the physiological and ecological constraints on the phenotypic expression and evolution of plant defenses against herbivores. Chapter Two reports the results of experimentally-manipulated soil fertility, soil moisture and defoliation on the growth, carbon assimilation, water relations, nutrient use efficiency, and leaf morphology of paper birch. Chapter Three reports the results of these experimental manipulations on the expression of birch resistance to gypsy moth, and the response of gypsy moth to changes in its host plant. Finally, Chapter Four reports on investigations into the mechanism of birch resistance to bronze birch borer, the effects of stress on these mechanisms, and discusses the possible interaction of birch growth, reproduction, and defense in driving the population dynamics of the bronze birch borer.

CHAPTER ONE

THE DILEMMA OF PLANTS: TO GROW OR DEFEND

Physiological and Ecological Constraints on the Evolution of Plant Defense

In recent years, empirical studies of plant/herbivore interactions have increased exponentially (Scriber & Ayres 1988), however progress toward a unifying and organizing theory of plant defense has not kept pace (Courtney & Kibota 1989). Early guiding paradigms have been reconsidered and alternative ones proposed (Ehrlich & Raven 1964; Feeny 1976; Rhoades & Cates 1976; Rhoades 1979; Bryant et al. 1983,1988; Coley et al. 1985; Lorio 1988; Loehle 1988). The complexity of the subject has hindered the development of a comprehensive framework. Any substantive theory of plant defense must transcend disciplines as well as levels of biological organization.

Tilman (1990) argued that predictive ecological theory should explicitly address the confluence of environmental constraints and organismal trade-offs as the basis for understanding biotic interaction. Accordingly, this chapter considers the physiological and ecological factors affecting the costs and benefits of and the resulting consequences for the evolution of plant defense in different environments. Discussed are: (1) the physiological basis for the often observed negative correlation between growth and defense in plants, and (2) how this phenotypic trade-off interacts with the ecological forces of competition and herbivory in different environments to manifest itself as a genetic trade-off in the evolution of

plant life histories. This chapter emphasizes the integrated nature (*sensu* Schlichting 1989) of plant traits for herbivore resistance, competitive ability, and environmental tolerance and focus upon the central role of competition in shaping the evolution of plant defense.

This chapter organizes the diverse literature relevant to plant defense theory while constructing a synthetic review based upon the primary premise of allocation theory: there are inevitable fitness trade-offs associated with varying patterns of resource allocation in different environments (Cody 1966; Stearns 1976,1989a; Southwood 1988; Tilman 1990). The objective is to generate and clarify testable predictions that would otherwise remain unapparent or ambiguous.

PHYSIOLOGICAL CONSTRAINTS AT THE CELLULAR LEVEL

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 1932,1953; Luckner & Nover 1977; Salisbury & Ross 1978; Luckner 1980; Wiermann 1981; Wareing & Phillips 1981). Growth consists of cell division followed by cell enlargement (Loomis 1932; Wareing & Phillips 1981). Both processes are resource demanding with precise requirements for a complex suite of interacting factors including light, water, mineral macro- and micro-nutrients, temperature, photoassimilates, growth regulators, and the regulating effects of neighboring cells (Dale 1976,1988; Lovatt 1985; McIntyre 1987; Boyer 1988; Kirk & Loneragan 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 (Dale 1976). Hence, leaf growth after lamina unfolding is a diminishing function of cell division, but an increasing function of cell enlargement. The final stages of leaf growth result from cell expansion caused by turgor pressure resulting from vacuolization (Dale 1976). Cytoplasm and secondary cell wall synthesis, however, continue to increase the dry weight of the cell (Wareing & Phillips 1981). The course of leaf growth may range, depending on species and environmental conditions, from a few days to several weeks (McIntyre 1987; Dale 1988).

Cellular differentiation is the sum of the chemical changes that occur in maturing cells, and the resultant morphological changes leading to qualitative differences among cells and cell specialization (Loomis 1932,1953; Salisbury & Ross 1978; Wareing & Phillips 1981; Lorio 1986). Differentiation processes tend to follow cell division and enlargement, although overlap occurs. Examples of differentiation processes include the thickening of leaf cuticle and secondary cell walls, production of wax and cellular inclusions, and secondary metabolism (Loomis 1932, 1953; Luckner & Nover 1977; Böhm 1977; Luckner 1980; Wiermann 1981; Lindsey & Yeoman 1983; Lorio 1986,1988; Collin 1987). 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 (Luckner & Nover 1977; Böhm 1977; Luckner 1980; Wiermann 1981; Torsell 1983). Unlike the products of primary metabolism which are common to all plants, the presence of particular secondary metabolites often show taxonomic relationships and may be related to the evolutionary history of the plant (Torsell 1983; Gottlieb 1990; Harborne 1990).

Secondary Metabolism is Constrained During Cell Growth

In meristematic cells and tissues undergoing vigorous growth, secondary metabolism and other differentiation processes are limited (Orians & Janzen 1974; Böhm 1977; Jalal & Collin 1977; Luckner & Nover 1977; Luckner 1980; Wiermann 1981; Lindsey & Yeoman 1983; Sakuta & Komanine 1987; Collin 1987).

Limitations at the cellular level are due to: (a) lack of enzymatic machinery necessary for their synthesis, (b) lack of fully developed vacuoles, plastids, and cell walls for their compartmentation (Orians & Janzen 1974; Böhm 1977; Wiermann 1981; Lindsey & Yeoman 1983; Hrazdina & Wagner 1985), and (c) substrate competition resulting from the high demand for resources by the primary "growth" processes (Orians & Janzen 1974; Margna 1977; Phillips & Henshaw 1977; Lindsey & Yeoman 1983; Collin 1987; Margna et al. 1989).

Competition for substrate occurs because primary and secondary metabolic pathways share common intermediates and precursors. For example, acetyl CoA serves as the precursor for terpenoids and also the entry point to the Krebs's cycle (Gray 1987). Phenylalanine is the rate limiting precursor for phenylpropanoid (lignin, flavonoids, condensed tannins, etc.) synthesis 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 and growth processes compete for common substrates. If the allocation to one increases, the allocation to the other must decrease, assuming the supply of resources remains constant (Phillips & Henshaw 1977; Margna 1977; Margna et al. 1989). Alkaloid synthesis, with its amino acid precursors, also competes directly with protein synthesis, and consequently with growth (Lindsey & Yeoman 1983; Hegnauer 1988).

Inactive primordial or meristematic cells may contain small concentrations of secondary metabolites sequestered in mini-vacuoles (Rao 1988). During subsequent cell division and enlargement, primordial secondary chemicals are metabolized or diluted by increases in cell contents (Rao 1988). Only when cell growth slows and nears completion do secondary metabolites accumulate in appreciable quantities. The limited expression of secondary metabolism in dividing cells 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 & Nover 1977).

PHYSIOLOGICAL CONSTRAINTS AT THE ORGANISMAL LEVEL

Growth and Differentiation at the Organismal Level:

Resource Limitations Induce Physiological Trade-Offs

Growth and differentiation processes occur at the cellular level, but it is their effects at higher levels of organization that shape the structure and function of the plant (Wareing & Phillips 1981). An intact plant can be considered an integrated network of cellular systems. These systems are organized into specialized morphological subunits among which the distribution of limited resources is regulated through complex source/sink relationships. Growth processes (cell division and expansion) lead to an irreversible change in plant size. Cellular differentiation processes coordinated at higher levels of organization result in the development of specialized tissues and organs, including vascular tissue, resin ducts, trichomes, and spines, as well as the functional integration and organization characteristic of intact plants (Wareing & Phillips 1981).

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 (Mooney 1972; Gifford & Evans 1981; Mooney et al. 1983; Bryant et al. 1983; Willson 1983; Gifford et al. 1984; Bloom et al. 1985; Coley et al. 1985; Fitter 1986; Bazzaz et al. 1987; Loehle 1988). 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. For example, epidermal cells in leaves mature before palisade cells, and in many dicots, cells in the tips of leaves cease dividing before the base (Dale 1988; Boyer 1988). Some shoots of plants with indeterminate patterns of growth continue to elongate after other shoots have terminated growth.

Modular Construction Affects Resource Allocation Priorities

Higher plants grow by means of the reiterated production of morphological subunits, or modules (Harper & White 1974). 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 & White 1974; Harper 1977; Harper & Bell 1979; Watson & Casper 1984; J. White 1979, 1984; Gill 1986; Hardwick 1986; Halle 1986; Barlow 1989; Tuomi & Vuorisalo 1989a,b). Modules within a plant are semi-autonomous, in that the translocation of resources within and among them can be restricted (J. White 1984; Watson & Casper 1984; Watson 1986; Gill 1986; Dickson 1989; Wardlaw 1990). However, the degree of modular integration varies among species on a continuum from nearly complete autonomy to high interdependence (Watson & Casper 1984). In spite of their semi-autonomous 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 allocation among modules should be adaptive (Hardwick 1986). 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 & Vuorisalo 1989a,b).

Patterns of resource allocation within a plant are determined by within-module, as well as between module (whole plant) allocation priorities. For example, individual leaves and modules do not export assimilates until their own growth requirements have been met (Dougherty 1979; McLaughlin et al. 1979; Dickson 1989; Dickson & Isebrands 1990; Wardlaw 1990). At the level of the whole plant, patterns of resource allocation 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 & White 1974; Harper 1977; Harper & Bell 1979; J. White 1979,1984; Watson & Casper 1984; Waller 1986; Franco 1986; Halle 1986; Hardwick 1986; Dickson 1989; Haukioja et al. 1990; Wardlaw 1990). The net outcome is that leaf/canopy growth usually takes highest priority, while allocation to defense and storage receives lower priority (Chung & Barnes 1980; Waring & Pitman 1985; Dickson & Isebrands 1990; Chapin et al. 1990). Variation in the growth rates of plants is largely the result of variation in the rate and duration of growth of individual modules and in the number of functional meristems (Hardwick 1986).

Growth Rate is Governed by Allocation to Leaf Area

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 weight) (Hunt 1978; Lambers 1987; Hirose 1987,1988b):

$$\text{RGR} = \text{NAR} * \text{LAR}$$

In both wild plants and domesticated crops, differences in growth-rates and dry matter accumulation result primarily from differences in patterns of resource allocation rather than differences in NAR. Plant breeders have had little success selecting for biochemically based improvements in photosynthesis. Rather, 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 & Jones 1977; Gifford & Evans 1981; Gifford et al. 1984; Lambers 1987; Patrick 1988; Austin 1989; Poorter & Remkes 1990).

A major premise of this paper is that the allocation of resources to secondary chemistry and structural defenses decrease growth by diverting resources from the production of new vegetative structures. This trade-off has ecological consequences that affect the success or failure of particular resource allocation patterns in particular environments. Plants must grow fast enough to compete, yet also maintain the physiological adaptations (defenses) necessary for survival in the presence of micro- and macro- herbivores.

Secondary Metabolism is Limited by High Growth Demands for Assimilates

As cells mature, cellular level constraints on secondary metabolism (such as a lack of compartmentation sites) become minimal. However, constraints operating at higher levels of organization may continue to limit secondary metabolism (Orians & Janzen 1974; Luckner & Nover 1977). Growth processes demand high levels of limited plant resources. Therefore, if a large proportion of modules within a plant are undergoing growth simultaneously, other processes including secondary metabolism in otherwise "capable" tissues may be substrate limited (Gulmon & Mooney 1986). Secondary metabolism may be limited in modules that have completed growth if photoassimilates are exported from these "sources" to strong vegetative or reproductive "sinks" (i.e. modules undergoing rapid growth) (Mooney et al. 1983).

Competition for substrate between primary and secondary metabolism is well documented in cell cultures (Phillips & Henshaw 1977; Margna 1977; Lindsey & Yeoman 1983; Collin 1987) and appears to occur in whole plants as well. In fact, many intraspecific comparisons document negative phenotypic correlations between growth rate and secondary metabolism in both wild and domesticated plants (Hanover 1966a; Van den Berg & Matzinger 1970; Matzinger et al. 1972; del Moral 1972; Podstolski et al. 1981; Krischik & Denno 1983; Gershenzon 1984; Mihaliak & Lincoln 1985,1989; Mihaliak et al. 1987; Waring et al. 1985; Wink & Witte 1985; Haukioja et al. 1985a; Larsson et al. 1986a; Coley 1986; Lorio & Sommers 1986; Lightfoot & Whitford 1987,1989; Bryant 1987; Bryant et al. 1987a,b; Margna et al. 1989; Appleton & van Staden 1989; Glyphis & Puttick 1989; Hrutfiord & Gara 1989; Waterman & Mole 1989). Björkman & 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*).

Trade-offs should be expected not only because of the diversion of resources from leaf production but because the synthesis of secondary metabolites is expensive (Chung & Barnes 1977; Chew & Rodman 1979; McDermitt & Loomis 1981; Gulmon & Mooney 1986). The direct costs of a phenolic resin, cyanogenic glycoside, and alkaloid have been minimally estimated to be about 2.6, 2.8, and 5.0 g CO₂ per g metabolite, respectively (Gulmon & Mooney 1986). Furthermore, the energetic cost of maintaining these biochemical pathways may be considerable, especially for compounds with a short half-life such as certain alkaloids and terpenoids that must be continually synthesized to maintain a given concentration in the plant (Coley et al. 1985; Fagerström 1989; Kakes 1989).

The exact form of the trade-off function has yet to be established for any plant species. Current understanding predicts a non-linear relationship between growth and secondary metabolism (Mattson & Haack 1987b; Tuomi et al. 1988a; Horner 1990) (Figure 1). Photosynthesis and growth do not respond equally to gradients of resource availability. Net photosynthesis can be maintained in existing cells at resource levels below those required to support growth (Hsiao 1973; Chapin 1980; Bradford & Hsiao 1982; Sharpe et al. 1985; McDonald et al. 1986; Daie 1988; Dietz 1989). At very low resource levels, both growth and photosynthesis are highly constrained and assimilation is adequate only to support baseline maintenance. Hence, secondary metabolism is limited. Moderate increases in resource availability enhance photosynthesis more than growth, resulting in increased availability of carbon that can be allocated to secondary metabolism. In resource-rich environments, growth receives allocation priority, and the availability of carbon to support secondary metabolism is decreased.

A non-linear relationship between growth and secondary metabolism makes it difficult to use observational data to test the hypothesis that a trade-off occurs

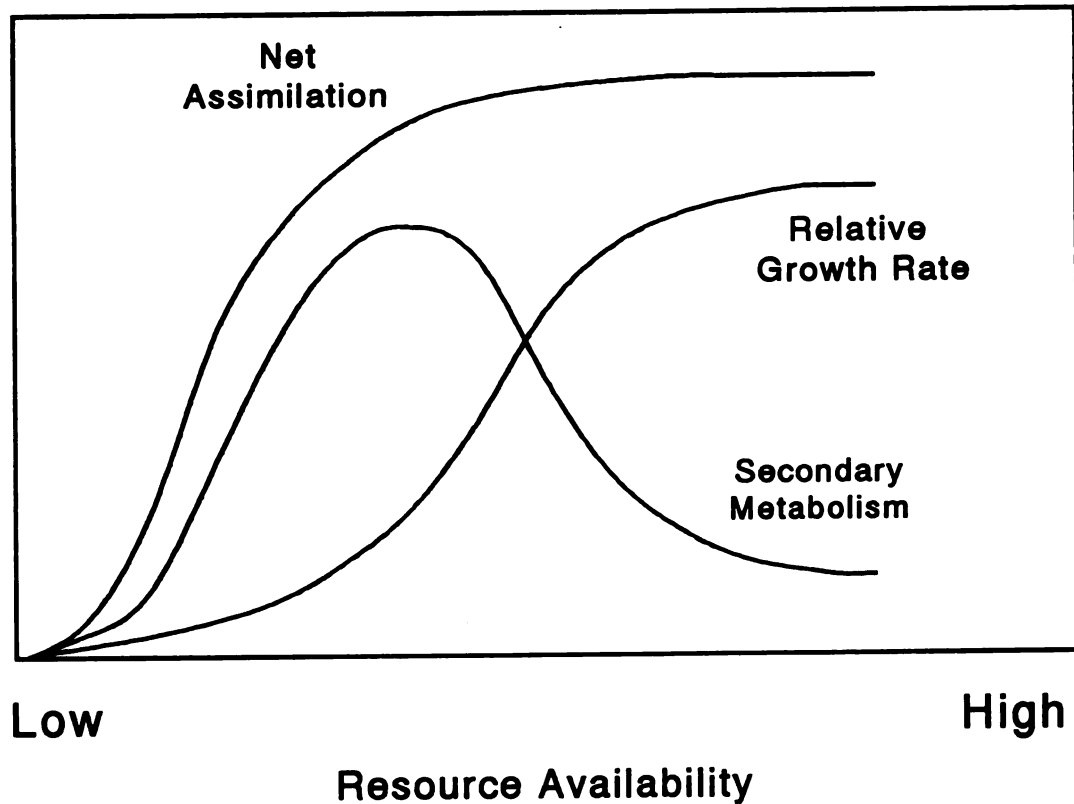


Figure 1. Norms of reaction for net assimilation rate, relative growth rate, and secondary metabolism in response to changing resource availability. Note that at low to moderate levels of resource availability (light, water, nutrients), rates of net assimilation, growth, and secondary metabolism are 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.

between them. For example, Denslow et al. (1987,1990) and Briggs & 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. However, when the variation in resource acquisition rate (i.e. photosynthesis) is large relative to the variation in resource allocation patterns, positive phenotypic correlations should occur between processes even when they share a common resource base (i.e. at low to moderate resource levels) (van Noordwijk & de Jong 1986) (Figure 1) . Bryant et al. (1983) and Tuomi et al. (1988a) predicted this pattern with respect to phenotypic plasticity in growth and secondary metabolism. The physiological trade-off (negative phenotypic correlation) becomes evident when the variation in resource acquisition rate is small relative to the variation in allocation patterns (i.e. at moderate to high resource levels) (van Noordwijk & de Jong 1986) (Figure 1). Thus, it is not possible to infer the lack of a physiological trade-off between growth and defense unless resource acquisition rates are known. To paraphrase the economic analogy of van Noordwijk & de Jong (1986), wealthy people can own a big house and a big car.

Diverse Roles of Secondary Metabolites Decrease Their Cost as Defenses

The trade-off between growth and allelochemical production creates the potential for a substantial cost to chemical defense. However, secondary metabolites may play diverse roles within plants modulating their cost as defensive compounds. Putative functions include attraction of pollinators (anthocyanins and flavonoids) (Rhoades 1979), protection from UV light (phenolic resins, flavonoids) (Rhoades 1977; Caldwell et al. 1983), structural support (lignin and tannins) (Rhodes 1985; Haslam 1988; Chalker-Scott & Krahmer 1989), temporary nutrient

storage (alkaloids, cyanogenic glycosides) (Wink & Witte 1985; Selmar et al. 1988; Poulton 1990; Harborne 1990), phytohormone regulation (flavonoids) (Rhodes 1985; Doberski 1986; Jacobs & Rubery 1988; Chalker-Scott & Krahmer 1989), drought resistance (tannins, phenolic resins) (Rhoades 1977; Pizzi & Cameron 1986; Bariska & Pizzi 1986; Meinzer et al. 1990), facilitation of nutrient uptake (phenolics) (Boyer et al. 1989), the protection of roots from acidic and reducing environments (tannins) (Kimura & Wada 1989), and modulators of plant relationships with symbiotic nitrogen-fixing bacteria (flavonoids) (Peters et al. 1986; Hartwig et al. 1990; Lynn & Chang 1990). A multi-faceted role for secondary metabolites in plants could decrease their effective cost as defense compounds. Furthermore, some secondary metabolites may be metabolized and returned to the resource pool available for primary metabolism, further attenuating their costs (Seigler & Price 1976; Wink & Witte 1985; Frischknecht et al. 1986; Selmar et al. 1988; Harborne 1990).

SECONDARY METABOLISM IS ENHANCED BY LOW GROWTH DEMAND FOR ASSIMILATES

Environmental constraints on growth further mitigate the cost of defense. Growth processes are slowed considerably by even moderate shortages of any one required resource. However, net photosynthesis is not as sensitive to resource limitation (Hsiao 1973; Chapin 1980; Bradford & Hsiao 1982; Sharpe et al. 1985; McDonald et al. 1986; Daie 1988; Dietz 1989; Horner 1990). Consequently, environments suitable for growth are only a small subset of those suitable for net carbon fixation. When growth is limited more than photosynthesis, photosynthates may be allocated to other processes with little or no trade-off with growth. In

resource-limited environments these photosynthates are often allocated to secondary metabolism which in some cases increases the plant's resistance to herbivores (Mattson 1980; Bryant et al. 1983,1985, 1987a,b; Bryant 1987; Gershenzon 1984; Wermilinger et al. 1985; Waring et al. 1985; Jonasson et al. 1986; Larsson et al. 1986a; Lorio 1986,1988; Laine & Henttonen 1987; Mattson & Haack 1987 a,b; Mihaliak & Lincoln 1985,1989; Mihaliak et al. 1987; Lightfoot & Whitford 1987,1989; Glyphis & Puttick 1989; Muller et al. 1987,1989; Horner 1990).

Resource Allocation Patterns Explained by the C/N Balance Hypothesis

The carbon/nutrient (C/N) balance hypothesis of Bryant et al. (1983) emphasizes the apparent regulatory effect of the plant's C/N ratio on its balance between primary and secondary metabolism. Nutrient deficiency limits growth more than photosynthesis and carbohydrates accumulate, increasing the C/N ratio within the plant. These carbohydrates are allocated to carbon-based secondary metabolites (such as terpene and phenolic compounds and others having only carbon, hydrogen, and oxygen as part of their structure), enhancing the plant's resistance to herbivores. The correlative and experimental evidence is substantial (Waterman & Mole 1989).

Evidence supporting the C/N balance hypothesis comes from manipulations of the C/N ratio of the plant through fertilization and shading. For example, fertilization generally increases the nutrient concentration of the plant, stimulating growth while decreasing the plant's C/N ratio, concentration of carbon-based defenses, and herbivore resistance (Mihaliak & Lincoln 1985; Mihaliak et al. 1987; Waring et al. 1985; Larsson et al. 1986a; Bryant 1987; Bryant et al. 1987a,b; Lightfoot & Whitford 1987,1989; Glyphis & Puttick 1989; Price et al. 1989).

Shading decreases the C/N ratio within the plant by decreasing carbon assimilation, often resulting in decreased concentrations of carbon-based secondary metabolites (Woodhead 1981; Waterman et al. 1984; Waring et al. 1985; Larsson et al. 1986a; Bryant 1987; Bryant et al. 1987a; Mole et al. 1988).

Sex-Biased Herbivory as Evidence

Sex-biased herbivory has been observed in dioecious plants with male plants generally experiencing greater herbivory than females (Lovett Doust & Lovett Doust 1985; Danell et al. 1985; Ågren 1987; Elmqvist et al. 1988; Alliende 1989; Boecklen et al. 1990). We extend the predictions of the C/N balance hypothesis to this pattern.

The reproductive structures of many species are photosynthetic, contributing in varying degrees to their own economy of energy and biomass (Dickmann & Kozlowski 1970; Bazzaz et al. 1979; Reekie & Bazzaz 1987a; Blanke & Lenz 1989). Furthermore, enhanced sink strength associated with rapidly developing reproductive structures may stimulate increased photosynthesis in nearby source leaves through feed-back mediated effects (Neales & Incoll 1968; Geiger 1976; Herold 1980; Watson & Casper 1984; Foyer 1987, 1988).

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 & de Wit 1975, 1976; Bazzaz et al. 1979; Thompson & 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, especially in female plants which must mature fruits and seeds (Sinclair & de Wit 1975; van Andel & Vera 1977; Lovett Doust 1980; Williams & Bell 1981; Thompson & Stewart 1981; Abrahamson & Caswell 1982; Mooney & Gulmon 1982; Bullock 1984; Bazzaz & Reekie 1985;

Reekie & Bazzaz 1987b; Sanz et al. 1987; Allen & Antos 1988). Hence, differential allocation of nutrients to reproductive structures may increase the C/N ratio in the foliage. The effect should be strongest in female plants because of their higher nutrient investment in reproduction. The predicted result is decreased growth, higher levels of secondary metabolites, and greater resistance to herbivores in female relative to male plants. In accord, male plants are generally reported to grow faster (Lloyd & Webb 1977; Wallace & Rundel 1979; Hoffmann & Alliende 1984; Bullock 1984; Clark & Clark 1988; Ramp & Stephenson 1988; Allen & Antos 1988; Snow & Whigham 1989; Krischik & Denno 1990; Jing & Coley 1990), experience greater herbivory (Lovett Doust & Lovett Doust 1985; Danell et al. 1985; Ågren 1987; Elmqvist et al. 1988; Alliende 1989; Boecklen et al. 1990; Krischik & Denno 1990; Jing & Coley 1990), and have lower concentrations of secondary metabolites or less tough foliage (Palo 1984; Price et al. 1989; Boecklen et al. 1990; Krischik & Denno 1990; Jing & Coley 1990). We predict the same pattern to occur in monoecious plants, with the C/N ratio of the foliage increasing in proportion with female reproductive effort.

Delayed Induced Resistance as Evidence

Defoliation of deciduous trees sometimes increases resistance to herbivores in subsequent years (delayed induced resistance or DIR) (Wallner & Walton 1979; Werner 1979; Haukioja 1980,1982; Schultz & Baldwin 1982; Tuomi et al. 1984; Haukioja & Neuvonen 1985a; Neuvonen et al. 1987; Bryant et al. 1991), whereas equivalent defoliation of evergreens usually does not (Niemelä et al. 1984; Bryant et al. 1988,1991; Wagner et al. 1988). The C/N balance hypothesis has been extended to explain this phenomenon (Tuomi et al. 1984,1988a,1991; Niemelä et al. 1984; Bryant et al. 1988,1991), which stems from fundamental differences in the carbon allocation patterns between deciduous and evergreen plants (Dickson 1989).

During the growing season, most of the nutrient capital of deciduous trees and coniferous evergreen species, and most of the carbon capital of the evergreen species, is contained within the foliage. Much of the carbon reserves of deciduous species, 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, thus a relative nutrient deficiency in the plant (Tuomi et al. 1984; Bryant et al. 1991). Furthermore, the nutrient deficiency may be aggravated by fine-root mortality resulting from defoliation-induced stress (Bryant et al. 1988; Tuomi et al. 1991). The result may be an increased C/N ratio, and increased allocation to carbon-based secondary metabolites in subsequent years (Tuomi et al. 1984, 1988a, 1991; Bryant et al. 1988, 1991).

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 et al. 1988a). 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. 1980b; Bryant et al. 1991), and consequently undiminished or increased foliar nutrient concentrations (Piene 1980; Piene & Percy 1984; Bryant et al. 1991), a decreased C/N balance, and thus decreased carbon-based secondary metabolite concentrations, and no DIR (Tuomi et al. 1984, 1988a; Niemelä et al. 1984; Bryant et al. 1988, 1991).

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; Haukioja & Neuvonen 1985a; Tuomi et al. 1984,1988a,b,1991; Bryant et al. 1988,1991)? Divergent predictions can be derived from the two hypotheses. The active defense hypothesis predicts that the presence of DIR should correspond with a plant's evolutionary history of herbivory; the C/N balance hypothesis predicts DIR should be independent of historical patterns of herbivory (Bryant et al. 1991). The C/N balance 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. 1985b; Tuomi et al. 1988a). Tuomi et al. (1988b,1991) argue that because of the semi-autonomous nature of plant modules (Watson & Casper 1984), the C/N balance 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 C/N balance hypothesis (Haukioja & Neuvonen 1985a; Haukioja et al. 1985b).

Tests of these hypotheses have yielded support for both. Consistent with the C/N Balance 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 et al. 1988b); 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 the opposite of 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 & Neuvonen 1985a; Haukioja et al. 1985b); 3) defoliation of mountain birch by *E. autumnata* resulted in stronger DIR than artificial defoliation (Haukioja & Neuvonen 1985a); 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 Linked Directly to the C/N Balance

Concentrations of carbon-based secondary metabolites are not always inversely correlated with the growth rate or the C/N balance of the plant, suggesting they may not be linked directly to changes in the C/N balance of the plant. For example, plants grown in enhanced CO₂ atmospheres have failed to show changes in secondary metabolite concentration despite increased carbon/nutrient ratios (Stuhlfauth et al. 1987; Lincoln & Couvet 1989; Fajer et al. 1989; Fajer 1989; Johnson & Lincoln 1990). Furthermore, secondary metabolism may often increase in response to moderate drought stress (del Moral 1972; Gershenzon 1984; Sharpe et al. 1985; Lorio 1986,1988; Mattson & Haack 1987a,b; Waterman & Mole 1989; Charles et al. 1990), even though moderate drought stress results in a decreased C/N balance in the plant because carbon acquisition is generally limited more than nutrient uptake (Hosner et al. 1965; Viets 1972; Hanson & Hitz 1982; Bloom et al. 1985; Rego 1986; Mattson & Haack 1987b).

When photosynthesis is not limiting, the total concentration of phenolic

compounds within a plant decreases in response to fertilization-induced increases in plant growth. However, this may not always be the case with total terpene concentrations. Muzika (1989), working with several populations of grand fir (*Abies grandis*), simultaneously measured changes in growth as well as total concentrations of phenolic and terpene compounds in response to changing soil nitrogen. Total phenolic concentrations had the predicted inverse relationship with soil nitrogen and growth (Muzika 1989); however, changes in terpene concentrations varied among populations, increasing in some and decreasing in others (Muzika 1989; Muzika et al. 1989). Positive correlations between growth, nitrogen content, and terpenoid production were also found in fertilized birch seedlings (*Betula pendula*) (Rousi et al. 1990) and peppermint (*Mentha piperita*) (Clark & Menary 1980).

Not all carbon-based compounds are created equally. Different metabolic precursors of phenolic and terpene biosynthesis may explain these varying effects. Phenolic biosynthesis, because of an amino acid precursor (phenylalanine), is in direct competition with protein synthesis and thus growth (Phillips & Henshaw 1977; Margna 1977; Margna et al. 1989). On the other hand, acetyl CoA, the precursor of terpene synthesis, is common to many pathways (Gray 1987). Due to substrate competition, inverse correlations between growth rate and terpene concentration are common (Hanover 1966a; Mihaliak & Lincoln 1985, 1989; Lorio 1986; Lorio & Sommers 1986; Mihaliak et al. 1987; Bryant et al. 1987a). However, if the cost of terpene production is diffused across other processes involving acetyl CoA (e.g. storage), positive correlations between growth rate and terpene concentrations are possible, even if the rate of resource acquisition remains constant.

Secondary Metabolism and Source-Sink Theory

Plants export carbon from sources (leaves and storage organs) to sinks (active meristems and sites of reserve accumulation) via phloem transport (Wareing & Patrick 1975). Sink strength (the relative ability of different sinks to attract carbon) is a product of sink size and sink activity; actively growing meristems are especially strong photosynthetic sinks (Ho 1988; Dickson & Isebrands 1990; Wardlaw 1990). 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 & Patrick 1975; Ågren 1985a,1988; McIntyre 1987; Daie 1988; Patrick 1988; Wardlaw 1990). When sink strength is decreased as a result of moderate water or nutrient limitation, photosynthates accumulated in excess of growth requirements may be allocated to other processes such as storage and secondary metabolism (Chapin 1980; Mattson 1980; Bryant et al. 1983; Sharpe et al. 1985; Lorio 1986; Chapin et al. 1990; Wardlaw 1990).

Source strength is a function of the availability of carbon for export. Sun-adapted plants growing in the shade experience decreased net assimilation and thus carbon limitation. Primary metabolic processes receive priority for the use of limited carbon, and concentrations of carbon-based secondary metabolites may generally decrease (Bryant et al. 1983; Waring & Pitman 1985). Shading has been shown to decrease plant resistance to bark beetles (Waring & Pitman 1985; Christiansen et al. 1987), browsing mammals (Bryant 1987; Bryant et al. 1987a), insect folivores (Larsson et al. 1986a), and fungal pathogens (Matson & Waring 1984; Entry et al. 1986). Increasing source strength through enhanced atmospheric CO₂ generally increases plant growth by enhancing net assimilation and resource use efficiency (Wittwer 1983; Enoch 1984; Strain 1985; Idso et al. 1988; Bazzaz 1990), but enhanced CO₂ appears to have little effect on secondary metabolite

concentrations (Stuhlfauth et al. 1987; Lincoln & Couvet 1989; Fajer et al. 1989; Fajer 1989; Johnson & Lincoln 1990).

Resource Allocation Explained by The G/D Balance Hypothesis

The growth/differentiation (G/D) balance hypothesis (Loomis 1932,1953) provides an alternative to the C/N balance hypothesis for explaining and predicting patterns of source-sink interaction, including the trade-off between growth and secondary metabolism (Loomis 1932; Lorio 1986,1988; Tuomi et al. 1991). The fundamental premise of the G/D balance hypothesis is the existence of a negative correlation between the allocation of resources to growth and those allocated to nongrowth (differentiation) processes because of cellular constraints and substrate competition resulting from source-sink interactions. Increased growth will decrease the allocation of resources to differentiation processes. Any factor that limits growth more than photosynthesis, such as moderate drought, nutrient limitation, and low temperature (Chapin 1980; Bradford & Hsiao 1982; Daie 1988; Pollock 1990; Wardlaw 1990), will increase the pool of resources available for allocation to secondary metabolism and other differentiation processes (Bryant et al. 1983; Sharpe et al. 1985; Lorio 1986; Horner 1990).

Is Phenotypic Plasticity in Secondary Metabolism Adaptive?

Allocation theory assumes that natural selection has shaped the regulation of source-sink interactions such that photoassimilates are allocated in ways that maximize fitness (Cody 1966; Dickson 1989). 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 & White 1974;

Werner 1975; Harper 1977; Solbrig 1981; Westoby 1984; Coley et al. 1985; Bloom et al. 1985; Pearcy et al. 1987; Peet & Christensen 1987; Bazzaz et al. 1987; Chapin 1988; Fagerström 1989). Hence, adaptive patterns of source-sink interaction should generally maximize growth rate within environmental constraints.

Phenotypic patterns of secondary metabolism may represent adaptive uses of limited resources (e.g. del Moral 1972; Gershenzon 1984; Zangerl & Berenbaum 1990). Increased secondary metabolism will be favored when that investment enhances plant fitness to a degree greater than would the same resource investment in an alternative process such as carbohydrate storage or growth. The potential adaptiveness of phenotypic plasticity is well recognized (Bradshaw 1965; Caswell 1983; Via & Lande 1985; Schlichting 1986; Schlichting & Levin 1986; Grime et al. 1986; West-Eberhard 1989; Stearns 1989b). Phenotypic plasticity is under genetic control and subject to natural selection. Genotype x environment interactions (non-parallel norms of reaction) represent genetic variation in phenotypic plasticity (Bradshaw 1965; Via & Lande 1985; Schlichting 1986; Stearns 1989b; van Noordwijk 1989). Variation in reaction norms have been commonly found when looked for (Schlichting 1986; Stearns 1989b). Muzika et al. (1989) provide evidence for the existence of intra-specific variation in reaction norms for terpene metabolism in response to soil fertility. Plants adapted to resource-rich environments commonly display particularly high plasticity in their growth rates, root:shoot ratios, nutrient absorption rates, and allocation to secondary metabolism (Grime 1979; Chapin 1980; Bryant et al. 1983; Grime et al. 1986). Allocation plasticity may enable plants to assume the most adaptive phenotype in a particular environment, buffering the effects of spatially and temporally varying resources (Grime et al. 1986; West-Eberhard 1989).

As environmental constraints on growth are relaxed, growth processes receive allocation priority for resources (Bazzaz et al. 1987). Enhanced secondary

metabolism in response to sink-limitation imposed by drought stress or nutrient limitation may enhance survival, especially defense, when the plant has limited ability to compensate (via growth) for herbivory (Gershenzon 1984). Improved plant performance (increased photosynthesis, relative growth rates, and resource use efficiencies) in enhanced CO₂ atmospheres indicates plants may be adapted to the higher levels of atmospheric CO₂ they have encountered in their evolutionary history (Enoch 1984). Furthermore, limited evidence suggests herbivore resistance is increased in enhanced CO₂ environments despite no increase in secondary metabolite concentrations, due to decreased foliar nutrient concentrations and possibly increased herbivore consumption of secondary metabolites per unit of nutrient (Lincoln et al. 1986; Lincoln & Couvet 1989; Fajer et al. 1989; Fajer 1989; Johnson & Lincoln 1990). Thus, it should be adaptive for plants to increase their growth-rate rather than secondary metabolism as constraints imposed by low atmospheric CO₂ concentrations are relaxed, despite an increased C/N ratio within the plant.

Before a plastic response can be assumed to be adaptive, it must be determined that the plasticity results from environmentally cued 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 demonstrated in the case of constitutive secondary metabolism. However, the experimental evidence suggests phenotypic variation in secondary metabolite concentration results from regulated changes in biosynthetic pathways in response to environmental cues rather than a passive response to an altered C/N ratio within the plant (e.g. del Moral 1972; Mole et al. 1988; Lincoln & Couvet 1989; Johnson & Lincoln 1990).

Predictions of the G/D Balance and C/N Balance Hypotheses Compared

The trade-off between resources allocated to growth and those allocated to differentiation processes (in particular secondary metabolism and leaf toughening) is the primary cause of phenotypic variation in plant resistance to herbivores.

Alteration of the C/N balance of the plant is only one factor that can affect the shape of this trade-off. 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 G/D balance hypothesis and the C/N balance hypothesis are consistent (see Table 1 for a comparison of the predictions of the two hypotheses). In other cases, their predictions diverge. Drought stress inhibits growth and enhanced CO₂ stimulates growth. The G/D balance hypothesis predicts increased secondary metabolism in response to drought-induced sink-limitation even if the C/N ratio decreases, and predicts source-limited plants will increase growth at the expense of secondary metabolism in response to enhanced CO₂, even though the C/N ratio increases.

The C/N hypothesis is powerful because nutrient availability is a major factor limiting primary production on a global scale (Ågren 1985b). The G/D balance hypothesis views source-sink interactions in light of underlying physiological processes rather than particular environmental variables, perhaps providing a more general conceptual model for predicting and explaining phenotypic patterns of secondary metabolism.

Table 1. Comparison of change in secondary metabolism in response to environmental factors as predicted by the Carbon/Nutrient (C/N) Balance Hypothesis and Growth/Differentiation (G/D) Balance hypothesis.

Environmental Condition	Physiological State of Plant	Change in C/N Balance	Change in G/D Balance	Predicted Proportional Change in Secondary Metabolism	
				<u>G/D Hypothesis</u>	<u>C/N Hypothesis</u>
nutrient limitation	sink limited	↑	↓	↑	↑
drought stress	sink limited	↓	↓	↑	↓
shade stress	source limited	↓	↓	↓	↓
enhanced CO ₂	relaxation of source limitation	↑	↑	↓	↑

Unifying Phenotypic and Genotypic Theories of plant Defense Through the Growth/Differentiation Balance Framework

Interspecific comparisons reveal that inherently slow growing plants have quantitatively higher levels of defense than inherently fast growing species, and generally experience lower levels of herbivory (Cates & Oriens 1975; Grime 1979; Chapin 1980; Mattson 1980; Bryant & Kuropat 1980; Bryant et al. 1983,1989a; Coley 1980;1983,1988; Coley et al. 1985; MacLean & Jensen 1985; Loehle 1988; Pimentel 1988). These genotypic trade-offs result from the same physiological constraints as phenotypic trade-offs between growth and defense.

The G/D balance concept, as historically applied to cellular and organismal level physiological processes (Loomis 1932,1953; Luckner & Nover 1977; Böhm 1977; Salisbury & Ross 1978; Luckner 1980; Wiermann 1981; Wareing & Phillips 1981; Lindsey & Yeoman 1983; Lorio 1986,1988; Tuomi et al. 1991), can also provide a framework for understanding genotypic, as well as phenotypic, trade-offs between growth and defense (Lorio 1988). In the rest of this paper, we relate the G/D balance concept to the evolution of the plant life-history strategies. We try to construct a hierarchical conceptual framework telescoping physiological, ecological, and evolutionary theories into a unified system of theories explaining and predicting plant allocation patterns in ecological and evolutionary time. Within this framework, phenotypic and genetic theories of plant defense can be unified.

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." 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.

Plants are 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 between 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 non-growth processes and structures required to retain and make efficient use of resources under adverse environmental conditions and/or in the presence of intense herbivory. The result is a low relative growth rate. Obviously, growth processes are dependent on and highly integrated with differentiation processes. For example, the formation of vascular tissue is a differentiation process on which growth is dependent. However, many differentiation processes, including the production of secondary metabolites and structural traits which limit herbivory, divert resources from growth.

The patterns we discuss are well recognized and underpin other theories of plant life-history evolution (Southwood 1977; Grime 1977,1979; 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 characteristic of fertile habitats common during the early stages of secondary-succession following disturbance (Grime 1979; Coley et al. 1985; Huston

& Smith 1987; Taylor et al. 1990). Differentiation-dominated species have experienced 'adversity-selection' (Greenslade 1983; Southwood 1977,1988; Sibly & Grime 1986) leading to the evolution of traits consistent with the stress tolerant strategy of Grime (1977,1979). They inhabit resource-limited environments, grow slowly, possess high levels of defenses, and often occupy late-successional resource-depleted habitats (Grime 1979; Coley et al. 1985; Huston & 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- and differentiation-dominated plants are summarized in Table 2.

The G/D continuum differs from related life-history classifications of Southwood (1977,1988), Grime (1977,1979), 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.

ECOLOGICAL CONSTRAINTS ON THE EVOLUTION OF PLANT DEFENSE

The physiological trade-off between growth and differentiation processes constrain the evolutionary responses of plants as they interact with their biotic and

Table 2. 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 turn-over 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:		
in resource-rich environments	High	Low
in resource-limited environments	Low	High

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

abiotic environments. As plants respond to selection imposed by competition, their potential evolutionary responses to herbivory also become limited. Competition occurs when two plants require the same resources which 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 x environment interactions in competitive ability (Tilman 1988,1990; Berendse & Elberse 1990). 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 & Grime 1976; Wilson & Keddy 1986a,b; Shipley & Keddy 1988; McGraw & Chapin 1989), and vice-versa (Chapin 1980; Shipley & Keddy 1988; McGraw & 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. Competitive ability and plant defense are negatively correlated in high resource environments because of a shared resource base, and positively correlated in low resource environments because of shared functional roles and correlated responses to selection. Furthermore, the greatest impact of herbivores on plant fitness may be the differential effects of herbivory on

the competitive abilities of competing species (Fox & Morrow 1986; Louda et al. 1990). We emphasize a central role for competition in shaping the evolution of plant defense.

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 & Huston 1989). However, the carrying capacity of even the richest environments is limited, and slow-growing plants risk the pre-emption of water, nutrients, light, and space by faster growing competitors. Competition limits the potential successful allocation patterns in resource-rich environments (Tilman 1988,1990; Smith & 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, allocation to leaf area, and leaf turn-over (Grime 1977,1979; Bazzaz 1979; Chapin 1980,1988; Mooney & Gulmon 1982; Wilson & Keddy 1986; Grime et al. 1986; Grime & Hodgeson 1987; Huston & Smith 1987; Chapin et al. 1987; Gaudet & Keddy 1988; Goldberg 1990; Taylor et al. 1990; Berendse & Elberse 1990). Resource allocation to processes not directly contributing to the immediate further acquisition of new resources result in departures from exponential rates of growth (Wareing & Phillips 1981; Harper 1989). These processes include secondary metabolism and the construction of structural defenses.

Adaptations Minimizing Defense Costs in Growth-Dominated Plants

The greatest potential indirect (opportunity) costs of defense, in the form of lost growth and resource acquisition, occur in growth-dominated plants inhabiting resource-rich environments (Fagerström 1989; Chapin 1989). These indirect costs of defense, 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 & Cates 1976; Rhoades 1979; Bryant et al. 1983; Coley et al. 1985; Coley 1987). However, growth-dominated plants 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 little success (Brown 1988; Simms & Rausher 1987,1989).

Inducible Resistance

Rapid inducible resistance, or secondary metabolism elicited in response to injury from insects or pathogens, may be an adaptation minimizing the cost of defense (Edwards & Wratten 1983; Harvell 1990; Haukioja 1991). Unlike constitutive resistance, 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 & Niemelä 1979; Bell 1981; Wratten et al. 1984; Braga et al. 1986; Edwards & Wratten 1987; Frischknecht et al. 1987; Baldwin 1988; Apostol et al. 1989; Karban et al. 1989; Haukioja 1991). 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 (Eilert 1987; da Cunha 1987; Threlfall & 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 still may 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 & Lawton 1985). Because of the semi-autonomous 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 & Casper 1984; Tuomi et al. 1988b; Marquis 1988). A primary effect of inducible resistance may be to disperse herbivory (Edwards & Wratten 1983,1987; Silkstone 1987; Gibberd et al. 1988; Wratten et al. 1988; Croxford et al. 1989; Raupp & Sadof 1989; but see Bergelson et al. 1986), thereby minimizing impact on any one module and on overall fitness reduction of the plant (Janzen 1979). 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 et al. 1990; Haukioja 1991). Zangerl and Berenbaum (1990) provide the first evidence for heritable variation in induced plant resistance to an insect.

Potent but Low Levels of Constitutive Defenses

The defense of growth-dominated plants adapted to fertile habitats is often based on low concentrations of highly potent, low molecular weight toxins and deterrents. Often these are nitrogen and sulfur based compounds such as alkaloids, cyanogenic glycosides, and glucosinolates (McKey 1974,1979; Levin 1976a; Feeny 1976; Grime 1977,1979; Mattson 1980; Mooney et al. 1983; Bernays 1983; Bryant et al. 1983,1985; Coley et al. 1985; Waterman & Mole 1989). These metabolites may often be metabolized and recycled through primary metabolism (Seigler & Price 1976; Wink & Witte 1985; Frischknecht et al. 1986; Selmar et al. 1988; Harborne 1990). Hence, they may confer defense even though they are not present in large amounts, and are not lost forever from the plant resource pool.

Plants may optimize a small defensive investment by allocating defenses to tissues in direct proportion to their value and vulnerability (McKey 1974,1979; Rhoades 1979). For example, Nitao and Zangerl (1987) found that wild parsnip (*Pastinaca sativa*) increased the concentration of furanocoumarins in reproductive structures 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 are resistant to the vast majority of herbivores present in their environments (Dethier 1980; Bernays & Chapman 1987). Because some deterrents are nontoxic when ingested, Bernays & Graham (1988) have questioned whether behavioral deterrents represent evolved defenses to herbivores. However, if they lead to reduced herbivory, deterrents will be favored regardless of whether or not they are toxic to organisms that avoid them.

Temporal Variation in Patterns of Growth and Defense

The opportunity cost of defense will vary depending upon when it is assessed over the course of the plant activity cycle. In many ecosystems, soil moisture and microbial-mediated nutrient availability are at peaks early in the growing season (Chapin 1980; Gutschick 1981; Lee et al. 1981). Many plants complete their growth with an intense but short flush corresponding with the temporal availability of the resources required to drive growth. The growth flush 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 & Chu 1974; McLaughlin & McConathy 1979; Dickson 1989; Chung & Barnes 1980; Chapin et al. 1990; Wardlaw 1990). These processes are then supported without a trade-off with growth. Thus, secondary metabolites may be synthesized when the opportunity costs are low and stored for future use when defense is constrained. The resin duct defense of some conifers to bark beetles may be one such example (Lorio 1986,1988). 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 (including contingency storage required to compensate for resources lost to random disturbance such as hail, frost, and fire) (Chapin et al. 1990).

The value of a leaf may be highest when it is young, because of the potential future rate of return if its photoassimilates are reinvested into vegetative structures furthering resource acquisition (Harper 1989). Expanding leaves are also most nutritious to herbivores because of high concentrations of nutrients and water, and low concentrations of structural components (Mattson 1980; Coley 1980,1983; Scriber 1984; Mattson & Scriber 1987; Ayres & MacLean 1987). Consequently, young leaves frequently experience higher levels of herbivory than mature leaves (Coley 1980; Raupp & Denno 1983; Krischik & Denno 1983; Landsberg 1988;

Ernest 1989; Núñez-Farfan & Dirzo 1989; Mitchell Aide & Lodoño 1989). Thus, it should be adaptive to defend young leaves. A paradox results because increasing the amount of resources allocated to defense during canopy expansion diverts resources from new leaf production.

The Twin Peaks Hypothesis

Concentrations of low molecular weight "qualitative defenses" are frequently highest in immature leaves and seedlings. These initial defensive investments may appear substantial when expressed as a foliar concentration. However, concentrations calculated for small immature leaves do not necessarily translate into large absolute investments based on the total pool of stored resources driving canopy expansion. As leaf maturation proceeds, concentrations of these "qualitative" defenses generally decline (possibly as their constitutive nutrients are cycled into primary metabolism), but leaves are protected by increasing concentrations of high-molecular weight polymers such as lignin and tannins ("quantitative" defenses) and structural defenses (Mooney & Chu 1974; Dement & Mooney 1974; McKey 1974,1979; Feeny 1970,1976; Rhoades & Cates 1976; Lawton 1976; Cates & Rhoades 1977; Cooper-Driver et al. 1977; Haukioja et al. 1978a; Coley 1983; Rhoades 1983; Prudhomme 1983; Mooney et al. 1983; Scriber 1984; Raupp 1985; Schroeder 1986; Potter & Kimmerer 1986; Frischknecht et al. 1986; Mattson & Scriber 1987; Bazzaz et al. 1987; Wagner et al. 1990).

The existence of twin peaks in foliar defense, with one peak in newly emerged leaves, followed by a decline and another peak as leaves mature, may be a common phenomenon. The high concentrations of secondary metabolites commonly observed in immature leaves may be generally biosynthesized the previous year and stored for the future defense of over-wintering buds and undifferentiated expanding tissue in which secondary metabolism is constrained

(Bryant et al. 1983). Many plants secrete stored phenolic or terpenoid resins over newly expanding foliage (Rhoades 1977; Dell & McComb 1978; Williams et al. 1983; Fahn 1988; Zobel & Brown 1990). 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 & Lersten 1974) and gypsy moth (*Lymantria dispar*) (Meyer & Montgomery 1987). The resistance of young cottonwood leaves to gypsy moth declines rapidly as the leaves expand (Meyer & Montgomery 1987) and the surface resin is diluted, volatilized, and/or weathered (Shain & Miller 1982). Concentrations of phenolic compounds in *Hymenaea* and *Salix* are highest in buds and decline as leaves expand (Crankshaw & Langenheim 1981; Palo 1984). An early peak in secondary metabolites concentrations, followed by a decline as leaves expand, and another peak as leaves mature, has also been observed in tobacco, Douglas-fir, bracken, *Diplacus*, and *Eucalyptus* (Sheen 1969; Radwan 1975; Tempel 1981; Mooney et al. 1981; Williams et al. 1983; Macauley & Fox 1980; Cates 1987). In some plants, secondary metabolites synthesized by the parent plant are stored in the seed and mobilized to protect the rapidly growing seedling before it has developed the capability to synthesize significant quantities on its own (McKey 1974; Wink & Witte 1985; Frischknecht et al. 1986; Selmar et al. 1988).

The rapid early-season decline in secondary metabolite concentrations may result from dilution as leaves expand and/or the cycling of low-molecular weight secondary metabolites into primary metabolism (Wink & Witte 1985; Frischknecht et al. 1986; Selmar et al. 1988; Zobel & Brown 1990). As cell differentiation proceeds and leaves attain the ability to synthesize and compartmentalize secondary metabolites, high molecular weight compounds such as tannins and lignin accumulate (Feeny 1970, 1976; Mooney & Chu 1974; McKey 1979; Rhoades & Cates 1976; Haukioja et al. 1978a; Mattson & Scriber 1987). The twin peaks pattern may

explain the observation that leaves are most vulnerable to herbivores and stress as they make the transition from photosynthetic sinks to photosynthetic sources (Coleman 1986).

Genetic Mosaics

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 which have the potential for large increases in their number of modules from one year to the next. Unlike animals which maintain a separate germ line, plants are characterized by somatic embryogenesis in which all tissues are totipotent, retaining 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 & Slobodchikoff 1981; Buss 1983; Whitham et al. 1984; Gill 1986; Tuomi & Vuorisalo 1989a,b). In fact, genetic mosaicism in plants is well documented (Hartmann & Kester 1975; Grant 1975; Whitham et al. 1984; Gill 1986). 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 & Slobodchikoff 1981; Whitham et al. 1984; Antolin & Strobeck 1985).

Qualitative variation may represent an adaptive alternative to quantitative increases in constitutive defense. 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 & Krischik 1989). Plants may increase their resistance to herbivores through minor mutations in metabolic pathways resulting in the production of a more diverse and/or toxic array of metabolites (Berenbaum 1978,1981,1983a; Bowers & Puttick

1988). A battery of secondary metabolites provides the potential for simultaneous resistance to a variety of herbivores (Bowers & Puttick 1988). Furthermore, some of the diverse secondary metabolites possessed by individual plants may be synergistic in their anti-herbivore activity (Kubo & Hanke 1985; Berenbaum 1985); synergism would enhance the cost:benefit ratio of a given defense investment (Berenbaum 1985). 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. Phylogenetic patterns in angiosperms indicate that the trend has been toward the evolution of secondary metabolites with more toxic structures (Harborne 1990; Gottlieb 1990).

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 & Collin 1977; DiCosmo & Towers 1984; Banthorpe & 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.

Mutualisms

Plant sustenance of defensive mutualisms may be a relatively inexpensive alternative to defensive chemistry (e.g. Rehr 1973), lacking the biosynthetic and maintenance costs associated with the conversion of substrate to secondary metabolites. Ants frequently serve as "pugnacious bodyguards," actively defending plants from herbivores in return for nourishing secretions from extrafloral nectaries (Janzen 1966; Bentley 1977; Beattie 1985; Schupp 1986). Extrafloral nectaries are typically associated with young, vigorously growing tissue, ceasing their secretions as

the associated organ matures (Bentley 1977; Koptur 1985). As such, they may be particularly valuable adaptations for the defense of undifferentiated tissue in which secondary metabolism is constrained.

Plants may regulate the activity and composition of secretions to optimize their cost/benefit ratio (Bentley 1977). *Piper cenocladum* fails to produce food bodies harvested by ants when ants are absent (Risch & Rickson 1981). Extrafloral nectaries of black cherry (*Prunus serotina*) 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. However, it is not known if its increased nutritional value attracts more bodyguards (Smith et al. 1990).

Some plants shelter predacious mites in domatia elaborated on maturing leaves and branches. Nearby domatia garrison mites for the rapid colonization and protection of new growth where they consume phytophagous mites and fungi (O'Dowd & Willson 1989). Domatia may be especially cheap as they require only their initial formation (O'Dowd & 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; Cheplick & Clay 1988). Endophytes may provide plants with novel chemical defenses (Carroll 1988), allowing plants to circumvent phylogenetic constraints on the evolution of new secondary metabolites (e.g. Harborne 1990).

Tolerance / Compensation

Compensatory growth may represent an alternative to chemical defense as a strategy for reducing net losses to herbivores, especially in resource-rich environments (van der Meijden et al. 1988; Chapin & McNaughton 1989).

Compensation is based on primary metabolic activity (McNaughton 1983), hence it does not incur the opportunity costs associated with chemical defense.

Furthermore, the response directly enhances competitive ability. Compensatory growth may be an especially prevalent adaptation to herbivory in high resource environments subject to intense and predictable herbivory. Such is the case in the Serengeti grasslands, subarctic salt marshes, and coral reef systems, where as much as 90% of net primary production is consumed annually by herbivores (McNaughton 1984; Westoby 1989; Hay & Fenical 1988). Plants adapted to heavy grazing have evolved compensatory mechanisms which may allow grazed plants to equal or exceed their net production in the absence of herbivores (Crawley 1983; McNaughton 1979, 1983; Ruess & McNaughton 1984; Hay & Fenical 1988; Paige & Whitham 1987; Westoby 1989). This capacity is dependent on the rapid and continual cycling of available nutrients that results from heavy grazing (Ruess & McNaughton 1984; McNaughton & Chapin 1985; Coughenour et al. 1985; McNaughton et al. 1988; Westoby 1989; Maschinski & Whitham 1989; Chapin & McNaughton 1989; Georgiadis et al. 1989; Hik & Jefferies 1990). The high degree of integration among modules which characterizes many grass species appears to contribute to compensatory ability (Watson & Casper 1984). This integration may facilitate the rapid mobilization of stored resources, as well as the exchange of resources among ramets, allowing an integrated response to herbivory at the genet level.

Resource Scarcity Favors Differentiation-Dominated Plants

Competition occurs in low resource environments (Fowler 1986; Chapin et al. 1989a; Tilman 1989; Tilman & Cowan 1989; DiTommaso & Aarssen 1989; Taylor et al. 1990). However, environmental constraints on plant growth may limit its intensity (Reader & Best 1989; Reader 1990). As opposed to resource-rich environments where competitive success is dependent on maximizing the rate of resource acquisition, success in resource-limited environments is dependent on the more conservative strategy of maximizing the retention and efficient use of scarce resources (Grime 1979; Chapin 1980,1988; Chabot & Hicks 1982; Vitousek 1982; Grime et al. 1986; Tilman 1988,1990; Goldberg 1990; Berendse & Elberse 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 resource availability (Grime 1977,1979; Chapin 1980,1988; Chapin et al. 1987; Grubb 1986; Grime et al. 1986; Huston & Smith 1987; 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 et al. 1989b).

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 which minimize 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; Bryant & Kuropat 1980; Chapin 1980; Mattson 1980; Chabot & Hicks 1982; Bryant et al. 1983; Coley et al. 1985; Southwood et al. 1986; Coley 1987; Loehle 1988; Taylor et al. 1990).

The physiological and ecological constraints on the evolution of chemical defenses in plants are minimized 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). In fact, plants adapted to resource-limited environments are characterized by a substantial investment in carbon-based allelochemicals (Janzen 1974; McKey 1978,1979; Mattson 1980; Bryant et al. 1983, 1985; Coley et al. 1985; Reichardt et al. 1990). However, 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 & Cooper 1987), possibly because their elaboration is dependent on growth processes. Although high levels of secondary metabolism may not result in decreased 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 foliar defenses may generally be weak or nonexistent in slow growing plants and tissues (Bell 1981; Braga et al. 1986; Edwards & Wratten 1987; Frischknecht et al. 1987; Wagner 1988; Apostol et al. 1989; Haukioja 1991). 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; 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. 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 RIR in differentiation-dominated plants. High constitutive levels of secondary metabolites may decrease the benefit of inducible resistance (Mattson et al. 1988). 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. Inducible defenses may be most advantageous when they occur against low background levels of other defenses.

Herbivores are Nutrient Limited

The low nutritional quality of plants growing in resource-limited environments may provide a substantial ecological (Mattson 1980) and evolutionary (Southwood 1973) barrier to herbivory. Herbivory may select for traits decreasing 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 (White 1978; Mattson & Scriber 1987; Pimentel 1988; Duchesne & Brainerd 1989; Lundberg & Åström 1990). If herbivores increase consumption to

compensate for a low quality diet, then plants will not necessarily benefit from traits that decrease their nutritive quality (Moran & Hamilton 1980). Comparisons of insect consumption rates on plants within a species varying in nutrient and secondary metabolite concentration suggest this may be a common phenomenon (Slansky & Feeny 1977; Johnson et al. 1985; Lincoln et al. 1986; M.F.J. Taylor 1989; Simpson & Simpson 1990). However, interspecific comparisons indicate that low nutritive quality, combined with high concentrations of secondary compounds and tough, sclerophyllous foliage interact to provide formidable barriers to herbivory in low resource environments (Bryant & Kuropat 1980; Mattson 1980; Bryant et al. 1983; Coley 1980,1983,1987; Mattson & Scriber 1987).

Correlated Selection for Differentiation Processes by Herbivory and Competition

In resource-limited environments, differentiation processes that limit herbivory may also contribute to the competitive success of the plant. Sclerophyllous leaves may enhance tolerance to drought stress and nutrient limitation as well as represent a major barrier to herbivory (Loveless 1962; Coley 1983; Grubb 1986; Oertli et al. 1990). High levels of 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 (Pizzi & Cameron 1986; Bariska & Pizzi 1986). Secondary metabolites may also decrease competition directly through allelopathic effects on neighboring plants (Fowler 1986).

Increased secondary metabolism may contribute directly to the maintenance of high levels of photosynthesis in resource-limited environments. Under growth-limiting conditions, end-product accumulation may result in feed-back inhibition of photosynthesis (Neales & Incoll 1968; Geiger 1976; Herold 1980; Foyer 1987,1988). When resource limitation slows vegetative and/or reproductive sink activity,

photosynthates may be shunted into secondary metabolic pathways minimizing the accumulation of photosynthetic end-products at the site of their synthesis (Hoffmann 1985; Haslam 1986; Waterman & Mole 1989). This may decrease feed-back inhibition of photosynthesis, resulting in energy overflow and the accumulation of excess carbon (Hoffmann 1985).

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 & Zeroni 1985; G.J. Taylor 1989); 2) the high concentrations of secondary metabolites required for herbivore defense and protection from abiotic stress (e.g. UV-radiation, desiccation) (del Moral 1972; Coley et al. 1985); and 3) for the removal of the otherwise toxic levels of free ammonia which 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 feed-back inhibition of photosynthesis in low resource environments (Haslam 1986).

THE EVOLUTION OF PLANT DEFENSE

A large number of studies document negative effects of herbivory on components of plant fitness including survival, growth, reproduction, and competitive ability (Kulman 1971; Rockwood 1973; Mattson & Addy 1975; Morrow & LaMarche 1978; Rausher & Feeny 1980; Parker & Root 1981; Crawley 1983, 1985, 1989a,b; Krischik & Denno 1983; Marquis 1984; Dirzo 1984; Stamp 1984;

Louda 1984; Brown 1985; Edwards 1985; Mills 1986; Cottam et al. 1986; Thomas 1986; Raffa & Berryman 1987; Paulissen 1987; Sacchi et al. 1988; Hendrix 1988; Wisdom et al. 1989; Andersen 1989; Gange et al. 1989; Louda et al. 1990). Despite the overwhelming circumstantial evidence to the contrary, it has been argued that herbivores have little effect on plant fitness (Jermy 1984). Indeed, there is little direct evidence that herbivores exert natural selection upon plants. However, the few experiments that have been designed as tests support the hypothesis that herbivores can be a force in plant evolution. Berenbaum et al. (1986) showed experimentally that insects can exert selection on plant secondary chemistry. Bryant et al. (1989b) provided strong biogeographic evidence that hares have selected for the chemical defenses of juvenile phase birch (*Betula*) and willow (*Salix*) species. Rausher and Simms (1989) demonstrated that annual morning glory (*Ipomoea pupurea*) experiences directional selection for increasing resistance to the corn earworm (*Heliothis zea*). And Simms and Rausher (1989) showed this selection to be exerted by insect herbivores, providing the first such evidence for a natural population of plants.

Secondary metabolites have been implicated in some physiological processes, however defense is generally assumed to be their *raison d'être* (Fraenkel 1959; Whittaker & Feeny 1971; Levin 1976b; Swain 1977; McKey 1979; Rhoades 1985; Williams et al. 1989; Harborne 1990). Williams et al. (1989) make a particularly strong argument that secondary metabolites evolved as defenses. The existence of genetic variation in patterns of secondary metabolism within plant species (Cope 1962; Hanover 1966b; van den Berg & Matzinger 1970; Jones 1971; Matzinger et al. 1972, 1989; McKey 1979; Juvik & Stevens 1982; Berenbaum et al. 1986; McDougal & Parks 1986; Kakes 1989; Altman et al. 1989; Mihaliak et al. 1989; Zangerl & Berenbaum 1990) creates the potential for herbivores to exert selection on those patterns.

In order to explain quantitative and qualitative patterns of plant defense, two contrasting but complementary evolutionary models have emerged. 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 defenses are costly because they divert resources from growth and that herbivory is the primary selective force shaping quantitative patterns of defense (McKey 1974; Rhoades & Cates 1976; Feeny 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 herbivory. Easily replaced, less critical tissues and organs will be less defended than hard-to-replace, indispensable ones. Furthermore, patterns of defense will reflect the frequency and severity of herbivory experienced by populations over evolutionary time (Feeny 1976; Rhoades & Cates 1976).

The Resource Availability Hypothesis

The resource availability hypothesis extends the optimal defense hypothesis, incorporating habitat quality as the primary factor determining quantitative patterns of defense (Janzen 1974; Bryant et al. 1983; Coley et al. 1985). The hypothesis predicts that the optimal level of defense will vary with the quantity of resources available in the environment to support growth. In productive habitats, competition

favours fast growing plants with low levels of defense. In unproductive habitats, limited resources constrain the ability of plants to compensate for herbivory. Thus, high levels of defense are favored.

Resource Availability: A More Restrictive View

Bryant et al. (1985,1988) and Tuomi et al. (1988a) propose that resource availability, rather than interacting with herbivory and competition to determine an optimal level of defense, is the primary determinant of quantitative levels of defense. The physiological responses of plants to resource availability determine quantitative levels of plant defense and constrain the coevolutionary relationships between plants and herbivores (Bryant et al. 1988).

The thesis (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; Tuomi et al. 1988a). The 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. 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 secondary metabolism is supported only by resources acquired in excess of primary metabolic requirements: defense bears no cost (Bryant et al. 1985; Tuomi et al. 1988a). Tuomi et al. (1988a) emphasized this point, stating that their evolutionary model based on resource availability "...differs from 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." Furthermore, Tuomi et al. (1988a)

suggest that herbivores exert no selection on levels of secondary metabolism, but they may shape the form this investment takes.

However, the existence of such a phenotypic trade-off cannot by itself support this evolutionary model. Instead, evidence is needed for genetic trade-offs (negative genetic correlation between growth and defense) (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. 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.

While the role of competition in shaping patterns of plant defense has been alluded to, and is implicit within, optimization theories of plant defense (Rhoades 1979; Bryant et al. 1983; Coley et al. 1985; Coley 1987), its central importance has not been emphasized. In many environments, competition may be a more important evolutionary force than herbivory (Tilman 1990).

The Resource Availability Hypothesis Extended

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

$$dc/dt = G * C * (1 - kD^\alpha) - (H - mD^\beta)$$

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). 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 reduced by defense (mD^β) (k and α are constants that relate an investment in defense to a reduction in growth; 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 (an important driving variable) are implicit, but subsumed in the G term.

The model can be extended by formalizing the competition component 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 optimal defense theory (Rhoades 1979) and resource availability theory (Bryant et al. 1985,1988; Tuomi et al. 1988a) regarding the cost of defense can be derived from the model.

The extended model uses the following terms:

$$\text{RGR}_{\max}, \text{RGR}_g, \text{ and } \text{RGR}_p$$

$\text{RGR}_{\max}$ is the maximum inherent relative growth rate that a plant could have evolved in a particular abiotic environment. It directly reflects 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, $\text{RGR}_{\max}$ is equal for all species of a given growth form that have evolved in a given environment.

RGR_g is the average inherent relative growth rate actually evolved by the plant population. It represents the potential growth rate obtainable under optimal environmental conditions, but also integrates the selective forces (competition (C), herbivory (H), and resource availability) acting on the growth rate of the population:

$$\text{RGR}_g = f((\text{RGR}_{\max} (\text{RGR}_{\max} - kD_i^\alpha)), C, H)$$

$$\text{where plant}_i \text{ fitness under competition} \propto w - b(\text{diff}_i)^\gamma$$

$$\text{where plant}_i \text{ fitness under herbivory} \propto z + c(\text{diff}_i)^\eta$$

This states that the average inherent growth rate evolved by a plant population (RGR_g) is a function of the difference (diff_i) in relative growth rates between the undefended ($\text{RGR}_{\max}$) and the variously defended genotypes ($\text{RGR}_{\max} - kD_i^\alpha$), and the magnitude of concomitant, often opposing selection pressures from competitors (C), and herbivores (H). Individual plant fitness under

competition will be inversely proportional to its deviation from RGR_{max} . The opposite will be true for plant fitness under herbivory. Given that growth differences between genotypes are large, then competition will favor the less defended genotypes unless there is substantial, counterbalancing pressure from herbivory. Given that the differences in growth rates between genotypes are small, then herbivory may favor better defended genotypes by significantly depressing the fitness of poorly defended ones. In resource rich environments, there would be a tendency toward evolutionary solutions to herbivory that are both efficacious and "inexpensive" (i.e. quality vs. quantity). Not so in resource poor environments, where defenses detract little if at all from RGR_{max} and competitive success is less dependent upon RGR *per se*, than on capacity to sustain photosynthesis and persist. RGR_g is equivalent to G in the model of Coley et al. 1985.

The ecological component of the model is defined using the following equation:

$$RGR_p = RGR_g * (1 - mE^e) * (1 - nC^p) * (H - pD^v)$$

where RGR_p (realized growth rate) is equal to the maximum genetic potential growth rate (RGR_g) diminished by the percent reductions caused by environmental constraints, by competition, and finally by herbivory. This equation assumes that these elements operate independently in their effects on RGR_p , which is probably untrue. But for the sake of simplicity of argument, this complication is ignored.

Comparing Resource Availability and Optimal Defense

This extended model facilitates a comparison of the assumptions and predictions of optimal defense theory and resource availability theory, and the implications for the cost of defense. Resource availability theory emphasizes environmental 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 et al. (1988a) 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 ($RGR_g = RGR_{max}$ and $kD^\alpha = 0$) (Figure 2a). Thus, under optimal environmental conditions for growth $RGR_p = RGR_g = RGR_{max}$ (Figure 2a). It should be noted that the model of Coley et al. (1985) does not make this restrictive assumption, but they do 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 ($RGR_g < RGR_{max}$ and $kD^\alpha > 0$) (Figure 2b). 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 primary assumption of optimal defense theory is met.

To summarize, resource availability theory predicts that the level of resources available in the environment is the primary determinant of growth rate and defense and that RGR_g will always be equal or close to RGR_{max} (growth is not sacrificed to support defense; defense has no cost); i.e. plants evolving under similar conditions of resource availability will evolve similar growth rates, even if subjected

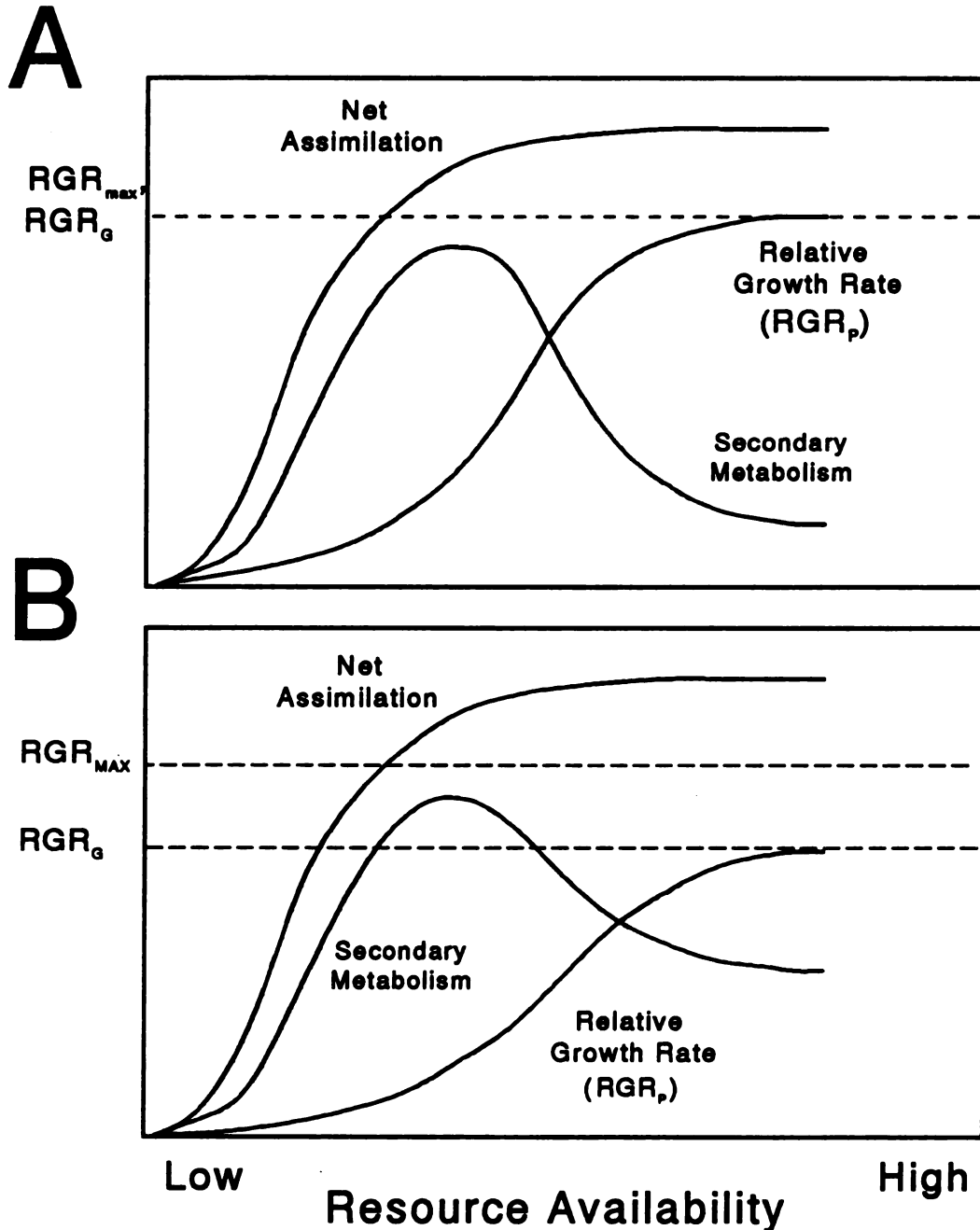


Figure 2. Comparison of reaction norms for two populations (A and B) of the same species, which evolved in equivalent abiotic environments. A evolved according to the resource availability model, with an inherent growth rate (RGR_g) equal to the maximum permitted by its abiotic environment (RGR_{max}). There is no genetic trade-off between growth and secondary metabolism ($kD^\alpha = 0$). When growing under optimal conditions, $RGR_p = RGR_g = RGR_{max}$. B evolved according to the optimal defense model. Herbivory selected for increased secondary metabolism, and consequently for an inherent growth rate (RGR_g) 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 growing under optimal conditions, $RGR_p = RGR_g < RGR_{max}$.

to different intensities of herbivory. Optimal defense theory (Rhoades 1979) predicts that herbivores can select for a RGR_g 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 anti-herbivore defense in plants have been developed and tested primarily with interspecific comparisons (Feeny 1976; Rhoades & Cates 1976; Grime 1979; Bryant et al. 1983, 1989a; Coley et al. 1985; Coley 1983, 1987, 1988; Loehle 1988). Interspecific comparisons allow the inference of process from the identification of pattern (Keddy 1989). However, evidence for the processes leading to the evolution of life-history patterns may be most directly gained by making intra-specific comparisons in resource allocation patterns, focusing on the selection pressures maintaining genetic variation within species (Stearns 1976; Futuyma & Moreno 1988; but see Stearns 1980).

Both models of plant defense predict genetically based intra-specific variation in growth rate and secondary metabolism, and postulate natural selection acting on this variation. The resource availability theory represents a physiological null model: herbivores do not select for increased defense at the expense of growth ($RGR_g = RGR_{max}$). Demonstration that herbivory can select for increased defense at the expense of growth ($RGR_g < RGR_{max}$) 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).

Intraspecific comparisons of genotypes within a population revealing a balanced polymorphism for growth and defense would also constitute evidence for optimal defense, if resources lost by the faster growing genotypes were balanced by the decreased rate of resource acquisition by the better defended genotypes.

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

Cates (1975) demonstrated genetic variation within wild ginger (*Asarum caudatum*) for growth rate and resistance to the herbivorous slug *Ariolimax columbianus*, with the faster growing genotypes being less well defended. However, the fast growing genotypes inhabited the most favorable environment while the defended genotypes were generally restricted to drier habitats (Cates 1975). Zangerl and Berenbaum (1990) found genetically based differences in induced and constitutive levels of furanocoumarins between two populations of wild parsnip (*Pastinaca sativa*). The population historically experiencing higher levels of herbivory had the highest levels of defense, but also inhabited a less favorable

abiotic environment.

A number of studies suggest that the cyanogenic morphs of *Trifolium repens* and *Lotus corniculatus* are more resistant to herbivores (Jones 1962,1966; Ellis et al. 1977a; Jones et al. 1978; Dirzo & Harper 1982; Dirzo 1984; Compton & Jones 1985) but inferior competitors (Foulds & Grime 1972; Dirzo & Harper 1982; Kakes 1989,1990) than the acyanogenic morphs. Furthermore, some evidence suggests that the distribution of the cyanogenic morph coincides with that of important herbivores (Ellis et al. 1977a,b; Compton et al. 1983). However, in these studies the cyanogenic and acyanogenic morphs were also distributed along abiotic gradients with the cyanogenic morphs more common in less favorable habitats.

The Evolution of Plant Allocation Trajectories: Competition and Herbivory Considered

We will summarize with a mechanistic conceptual model of the evolution of plant resource allocation patterns. The model is based upon the physiological and ecological constraints resulting in the trade-off between growth and defense, and incorporates the effects of natural selection from herbivores and competitors. Resource availability modulates 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. However, these values vary because of the

plant's inherent plasticity in response to abiotic factors. Therefore, each plant can be represented by a unique set of $\{X_i, Y_i\}$ paired values. Plotting these points yields a line segment showing the *allocation trajectory* for a given individual under all possible environmental conditions. An individual plant in a particular environment at any given time is represented by a discrete point on the line. This concept can be extended to the population or species level with the *allocation trajectory* representing the mean $\{X_i, Y_i\}$ values for all individuals of the population. The *allocation trajectory* for a hypothetical species with genetic variation in growth rate and allocation to secondary metabolism is presented in Figure 3.

Weldon and Slauson (1986) distinguished between the intensity and importance of 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 (H) and competition (C), respectively (Figure 4). 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 available to support growth (e.g Bryant et al. 1983; Coley 1985; Reader & Best 1989; Reader 1990). As resource availability increases, the importance of competition relative to herbivory increases. Conversely, as resource availability is reduced, the importance of competition relative to herbivory declines. However, we also assume that the importance of herbivory can vary within an environment independently of

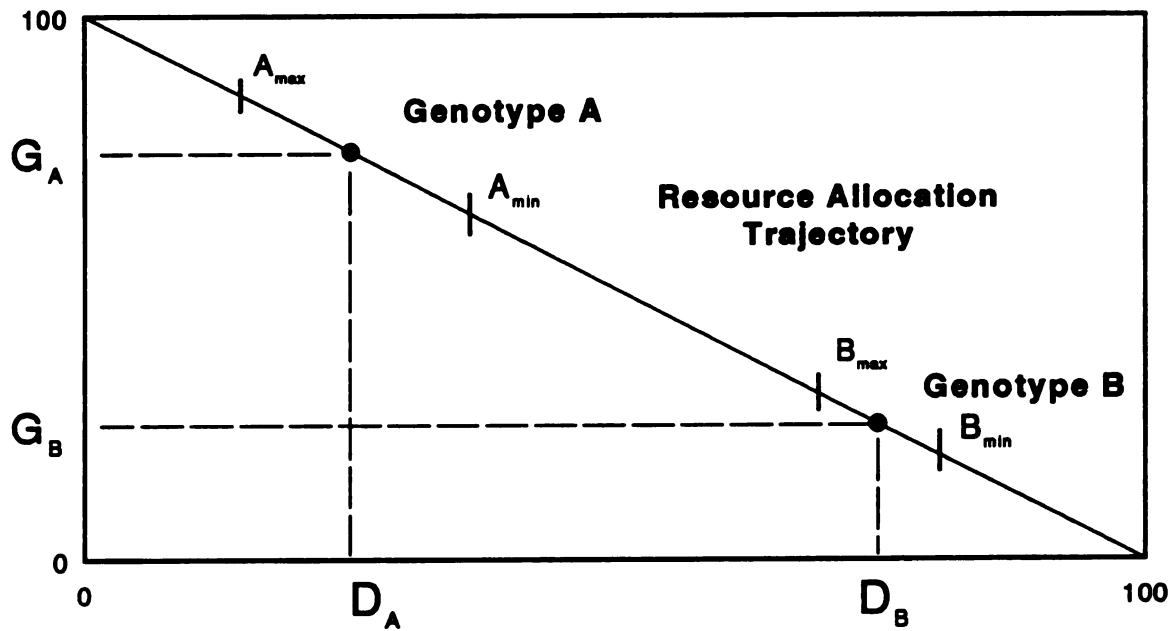


Figure 3. Conceptual model of resource allocation in a plant species with genetic variation for growth and secondary metabolism. A_{max} and A_{min} , and B_{max} and B_{min} represent limits on the range of phenotypic plasticity in the allocation patterns of genotypes A and B, respectively. Points D_A, G_A and D_B, G_B represent the actual state of genotypes A and B, respectively (or the mean states of population A and B, respectively).

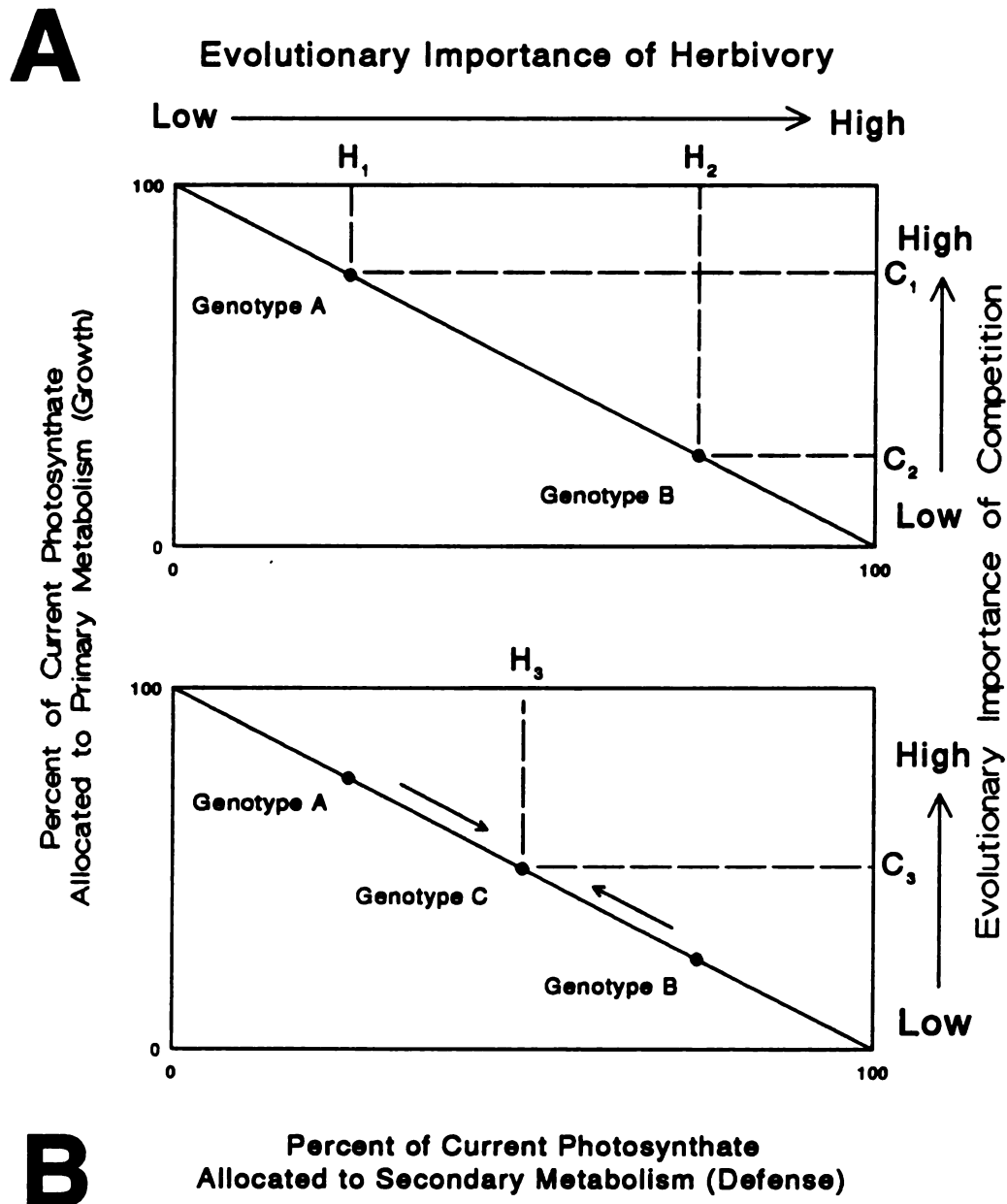


Figure 4. Conceptual model of the effects of competition (C) and herbivory (H) on the evolution of plant resource allocation patterns in varying environments. **A)** Stable polymorphism (genotypes A and B) is maintained by disruptive selection in environments in which the evolutionary importance of herbivory 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.

resource availability.

The intraspecific genetic variation represented in Figure 3 is sustained by disruptive selection exerted by contrasting environments (Figure 4a). 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) can not 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 can not 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 (Figure 4b). Genotype A is under pressure from herbivores to evolve increased defense, while genotype B, in response to competition, will evolve a faster growth rate at the expense of secondary metabolism. The two populations will converge on genotype C which will be maintained by stabilizing selection exerted by the opposing pressures of competition and herbivory.

In summary, the mix of genotypes that survive in a plant population will depend on pressures exerted by competition and herbivory, their relative importance 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 effects of selection. Species with ranges covering different habitats with selection pressures varying in importance may evolve stable polymorphisms for allocation to growth and secondary metabolism.

CHAPTER TWO

Plasticity in the Growth and Leaf Physiology of Field-Grown Paper Birch, in Response to Varying Water, Nitrogen, and Defoliation

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 & White 1974; Werner 1975; Harper 1977; Solbrig 1981; Bloom et al. 1985; Pearcy et al. 1987; Bazzaz et al. 1987; Chapin 1988; Fagerström 1989). In resource-rich environments, which are common during the early stages of secondary succession, slow-growing plants risk the pre-emption of water, nutrients, light, and space by faster growing competitors (Grime 1977,1979; Chapin 1980a; Huston & Smith 1987; Smith & Huston 1989). Rapid growth is especially critical in even-aged, monospecific stands, where stand density is inversely related to total stand biomass, and mortality is a function of the rate of whole stand biomass accumulation (Gorham 1979; Westoby 1984; Peet & Christensen 1987). Slow-growing plants are unlikely to survive the thinning stage of stand development (Peet & Christensen 1987).

Paper birch, *Betula papyrifera* Marsh., is a short-lived, early-successional tree native throughout the northern and boreal forests of North America, where it often forms even-aged stands (Preston 1976; Barnes & Wagner 1981; Perala & Alm 1990). Paper birch is intolerant of shade and requires high levels of nutrients and water

(Perala & Alm 1990). Hence, a high relative growth rate is critical to the establishment, survival, and long-term reproductive success of paper birch.

Physiological and Morphological Determinants of Relative Growth Rate

The relative growth rate (RGR) of plants is equal to the product of their net assimilation rate (NAR) (net carbon accumulation per unit leaf area per unit time) and their leaf area ratio (LAR) (ratio of total leaf area to total plant dry weight) (Hunt 1978; Lambers 1987; Hirose 1987,1988a,b; Poorter & Remkes 1990). LAR is equal to leaf weight ratio (LWR) (total leaf biomass/total plant biomass) divided by specific leaf mass (SLM) (leaf mass/leaf area). Thus, the growth rates of plants can be expressed as the following:

$$\text{RGR} = \text{NAR} * \text{LWR} / \text{SLM}$$

Variation in the relative growth rate of plants (RGR) may result from variation in any one of these components. However, differential investment of photoassimilates into increased leaf area is largely responsible for both genotypic and phenotypic differences in the growth rates of both wild plants and domesticated crops; variation in net photosynthetic rate has been found to be less important (Potter & Jones 1977; Gifford & Evans 1981; Gifford et al. 1984; Lambers 1987; Patrick 1988; Austin 1989; Poorter & Remkes 1990). Because of logistical difficulties in quantifying NAR and leaf area, few data exist for larger woody plants.

Respiration and other carbon losses (volatilization, exudation, leaching) are important components of NAR (Konings 1990; Poorter & Remkes 1990). However, net rate of photosynthesis was highly correlated with NAR ($r=0.82$) for a number of species from different studies, and thus is a good estimator of NAR (Konings 1990). Hence, the effects of environmental factors on tree growth can be analyzed via their

effects on photosynthesis, leaf area, and specific leaf mass.

Drought Effects on RGR

Water deficits may decrease photosynthesis through direct inhibition of the photosynthetic capacity of mesophyll cells and/or stomatal limitation of CO₂ uptake (reviewed in Hsiao 1973; Hsiao et al. 1976; Boyer 1976; Kozlowski 1979,1982; Berry & Downton 1982; Hanson & Hitz 1982; Farquhar & Sharkey 1982; Sharkey 1985; Schulze 1986 a,b; Turner 1986; Kriedemann 1986; Teskey & Hinckley 1986; Schulze et al. 1987; Daie 1988; Gholz et al. 1990). Water deficits may also have a negative effect on total leaf area by: 1) decreasing the total number of leaves per plant (Boyer 1976; Kozlowski 1982; Jordan 1983; Myers & Landsberg 1989), 2) decreasing the rate of leaf expansion and final leaf size (among the most sensitive physiological processes to water stress) (Hsiao 1973; Bradford & Hsiao 1982; Kozlowski 1982; Barlow 1986; McIntyre 1987; Hsiao & Jing 1987; Roden et al. 1990), and 3) increasing the proportion of resources allocated to root growth at the expense of leaf production (Teskey & Hinckley 1986; Daie 1988).

Nitrogen Effects on RGR

The relative growth rate of plants is directly correlated with their total nitrogen content (Ågren 1985a; Hirose 1988a,b; Hilbert 1990). Nitrogen availability affects the growth of plants in a number of ways. A strong, positive correlation between net rate of photosynthesis and foliar nitrogen concentration is well documented (Nátr 1975; Chapin 1980a; Linder & Rook 1984; Field & Mooney 1986;

Hirose 1988b; Walters & Reich 1989). Total leaf area also correlates with nitrogen availability, because increased nitrogen often results in: 1) increased total numbers of leaves per plant (Coyne & van Cleve 1977; Linder & Rook 1984; Walters & Reich 1989), 2) larger but less dense leaves (Radin & Boyer 1982; Linder & Rook 1984; Hirose 1986,1987,1988b; McDonald et al. 1986; McDonald 1989), and 3) an increase in the allocation of carbon to shoots relative to roots (Grime 1977,1979; Chapin 1980a,1988; Linder & Rook 1984; Hirose 1986,1987,1988a,b; Ågren & Ingestad 1987; Kachi & Rorison 1989; Walters & Reich 1989).

Defoliation Effects on RGR

Severe defoliation of trees decreases growth via the loss of existing photosynthetic tissue, and the future diminished production of leaf area (Kulman 1971; Heichel & Turner 1976,1983,1984; Verkaar 1988). Such defoliation typically decreases carbohydrate reserves and rates of wound closure, and increases susceptibility to and mortality from secondary pests such as wood borers and root rot fungi (Kulmam 1971; Wargo et al. 1972; Wargo & Houston 1974; Dunbar & Stephens 1975; Wargo 1977a,b; Ericsson et al. 1980b; Wargo 1981; Gregory & Wargo 1986; Hilton et al. 1987).

The detrimental effects of defoliation on plant growth may often be ameliorated by compensatory responses (*i.e.* McNaughton 1983). Defoliation can increase net photosynthesis in the residual leaves (Wareing et al. 1968; Bassman & Dickmann 1982, 1985; Heichel & Turner 1983; Stafford 1989; Welter 1989), improve water balance within the plant (Stephens et al. 1972), and increase allocation of carbon to leaf area at the expense of root growth and carbohydrate storage (Chapin 1980b; Bassman & Dickmann 1982,1985; Stafford 1989)

Objectives

This paper addresses the hypothesis that variation in plant growth rate will reflect the effects of treatment variables on net assimilation rate and/or total leaf area. In a 3-year, controlled field experiment, beginning with eight year-old trees, I investigated the effects of three levels of irrigation, three levels of nitrogen fertilization, two levels of defoliation, and their interactions on the growth, photosynthesis, water relation, nutrient use efficiency, and leaf area of paper birch. Subsequent chapters examine their effects on birch reproduction and herbivore resistance.

METHODS AND MATERIALS

Experimental Site

Experimental plots were constructed at the Dow Gardens in Midland, Michigan, which is located at the southern limits of the natural distribution of paper birch. The experimental plots consisted of 80 adjacent cells, each exactly 2 x 2 m, in 8 rows and 10 columns. Each cell was enclosed by a water-impermeable chlorinated polyethylene barrier (cell liner) 30 mils thick, extending 1 m vertically into the ground, and 10 cm vertically above ground level. The liner isolated the soil environment of each cell and allowed for the establishment of individual nutrient and moisture regimes for each tree.

In April 1985, 105 half-sibling (common mother) paper birch trees were obtained from a Michigan nursery and transplanted into the experimental plots. When transplanted into the plots, the trees were entering their sixth growing season.

One tree was planted in each cell; and the remaining trees in a nursery plot adjacent to the experimental plots to serve as replacements for the experimental trees, in the event of mortality. In April 1986, 16 replacement trees were transplanted into the experimental plot. Trees were allowed to become established during 1985 and 1986 before treatments were applied in 1987. During this period, trees were irrigated, weeded, and insects controlled, as necessary, to promote the establishment of the trees.

Experimental Treatments

Soil Moisture - Three Levels of Irrigation

The experimental design called for three levels of soil moisture: e.g. zero, 40, and 80 cm of irrigation. However, 32.1 cm of natural precipitation between 1 May and 1 September 1987 prevented the establishment of detectable treatment differences. Thus, it was necessary to exclude precipitation from the study site in 1988 and 1989 via beneath-canopy tents. Frames were constructed to support the tents which were made from 30 mil black PVC sheeting. The tents excluded precipitation while still exposing the canopy and most of the trunk to ambient conditions, and could be opened to allow access to the trees. The frames supported the plastic at a center height of about 40 cm above ground level, and an edge height of about 20 cm. The tents were open on all sides to allow air circulation, and air and soil temperatures under the plastic did not exceed ambient. The black plastic also prevented the establishment of weeds in the cells, thus eliminating competition as a confounding factor.

Tents were installed in mid-April during 1988 and 1989 (before bud-break) and removed in mid-September. Water applied in 5 cm increments spaced

approximately equally throughout the growing season (late April - early September), resulted in the following three treatment levels: 10, 30, and 90 cm of water in 1988, and 10, 25, and 75 cm of water in 1989. Mean precipitation for Midland County (1951-1980) for the period May 1 through Aug. 31 was 28.5 cm (Michigan Department of Agriculture), hence the three treatments represented about 1/3 normal, normal, and 3 times normal precipitation, respectively.

Soil Fertility: Three Levels of N Fertilization

Three levels of soil nitrogen were established through fertilization: zero, 175, and 350 kg N/ha/yr. Beginning in October 1986, trees were fertilized twice annually, in mid-April and mid-October, with 34-0-0 ammonium-nitrate. Half of the total annual N was applied at each treatment. At the same time trees were fertilized with N, sucrose (2000 kg/ha) was applied to the soil of the trees receiving zero N so as to further deplete naturally occurring N. Soil microbes are generally carbon limited, and sucrose provides a readily available carbon substrate. The subsequent rapid growth of microbes immobilizes much of the nitrogen in microbial biomass, decreasing the N available to the trees (Foster et al. 1980; Sparling et al. 1981; Margolis & Waring 1986).

Defoliation - Two Levels

Two levels of defoliation were established: half the trees received no defoliation and the other half received approximately 40% artificial defoliation (manually tearing every other leaf, leaving only the petiole and a basal fragment intact). Defoliation of an individual tree was initiated and completed in the same day: defoliation of all trees was completed over a four day period (26-29 May 1987; 24-27 May 1988) just after leaf expansion was complete.

To estimate the effect of defoliation on total leaf area at the time of

defoliation, 30 undamaged fully expanded leaves and 30 leaves that had been torn in two during artificial defoliation, were sampled from throughout the canopy of each tree. The cumulative leaf area of each sample was determined with a leaf area meter (LICOR, Inc., Lincoln, NE). Percent defoliation was estimated for each tree as: (cumulative area of damaged leaves/cumulative area of intact leaves)/2.

Plant Physiological Measurements

Tree Growth

From 1986-1989, annual trunk expansion was calculated from measurements of trunk diameter made before growth was initiated in the spring (early April) and after growth terminated in the fall (mid-October). Caliper readings were always made at the same location and orientation on the trunk, at a height of 70 cm above the ground. Height growth was also measured in 1988 and 1989.

Gas Exchange

Gas exchange was measured with a closed IR CO₂ analysis system (LI-6200, LICOR Inc., Lincoln, NE). Net CO₂ assimilation (A_{area}) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$), stomatal conductance (g) (cm s^{-1}), and the partial pressure of intercellular CO₂ (C_i) ($\mu\text{mol mol}^{-1}$) were calculated according to von Caemmerer & Farquhar (1981). Ambient CO₂ concentrations were measured at the beginning and end of each sampling period. Net CO₂ assimilation was also calculated on a leaf mass basis (A_{mass}) ($\mu\text{mol CO}_2 \text{ g}^{-1} \text{ sec}^{-1}$). Measurements were made on a single intact leaf per tree under light saturating (no cloud cover) conditions. Flow rate of air through the system was adjusted to maintain humidity constant within the chamber. All measurements were made between 0800 and 1000 EST. In 1988, measurements

were made on 22 July, 29 July, 12 August, and 8 September. In 1989, measurements were made on 16 June, 28 June, 11 July, 25 July, 7 August, and 30 August.

Paper birch produces two types of leaves which can display substantial dimorphism: "early leaves" which are physiologically initiated in the growing season prior to their emergence, and "late leaves" which are physiologically initiated during the same growing season in which they emerge (Clausen & Kozlowski 1965). To eliminate this dimorphism as a source of variation, measurements were always made on leaves originating from overwintering buds (i.e. early leaves). Only leaves from the south side of the tree were sampled.

Water Potential

During 1988, pre-dawn and mid-day leaf water potentials were measured using the pressure chamber method (Scholander et al. 1965; Waring & Cleary 1967). Measurements were made on 10 June, 24 June, 8 July, 22 July, and 26 August. One leaf per tree was sampled; measurements were made within 30 seconds of abscission. Pre-dawn sampling was conducted between 0300 and 0530 EST, and mid-day measurements were made between 1200 and 1430 EST. As with gas exchange, measurements were made only on fully expanded leaves, originating from overwintering buds. Mid-day measurements were only made on leaves from the south side of the tree in full sun.

Foliar Nitrogen and Phosphorus

Foliage samples were taken on 9 June, 15 July, and 24 August in 1988, and on 6 June, 5 July, and 23 August in 1989. As with water potential and gas exchange measurements, only leaves originating from overwintering buds were sampled. On each date, a sample of 15 leaves was taken per tree: leaves were selected from throughout the canopy. Leaves with obvious insect or mechanical injury were

avoided. Upon collection, samples were sealed immediately in zip-lock plastic bags and placed on dry ice in a cooler. All samples were taken between 0700 and 0830 EST to standardize for diurnal variations in leaf water content and chemical composition.

Leaves were transported immediately to the laboratory (located less than 100 m from the experimental plots) where their fresh weight and leaf area was determined followed by oven drying at 60°C for 48 hrs. The dried foliage was weighed to estimate percent leaf water content (fresh weight) (LWC). Leaves were ground to pass a 40 mesh screen in a Wiley mill, and then stored in envelopes in darkness at room temperature until chemical analysis.

Total nitrogen and phosphorus were measured using standard micro-Kjeldahl techniques. A 150 mg sample of powdered foliage was digested with 5 ml concentrated sulfuric acid and a catalyst mixture (1.5 g K₂SO₄ and 175 mg HgO) for one hour at 385 °C. Sample volume was increased to 75 ml with DI (distilled / deionized) water. Sub-samples of ca. 3 ml were stored in sealed plastic vials and then analyzed colorimetrically with a Technicon Auto-analyzer II. The accuracy of the total N and P analyses were checked using National Bureau of Standards standard reference materials; agreement was within 5% of certified values. Precision was checked by conducting two separate digestions for several samples; mean relative deviations were less than 5%. Results were calculated on both a leaf mass (N_{mass} and P_{mass}) (% dry weight) and a leaf area basis (N_{area} and P_{area}) (mg m⁻²).

Leaf Area

The mean area of individual leaves on a tree was estimated by taking 3 samples of 15 leaves each (the same samples used for N and P analysis) and measuring the cumulative area of each 15-leaf sample with a LiCor leaf area meter;

mean individual leaf area was calculated for each sample by dividing the cumulative area by 15. Mean leaf size (cm^2) for the tree was estimated as the mean of the three samples. After leaf area was determined, the three leaf samples were oven-dried at 60°C to constant weight. Specific leaf mass (SLM) (g m^{-2}) was calculated for each tree from the three samples by dividing the dry weight of each sample by its cumulative area and then taking the mean of the three samples.

The total number of leaves on each tree was determined in 1988 and 1989 by counting all leaves on each tree during August (after shoot elongation and new leaf formation had terminated, but before leaf abscission had begun). Total leaf area for each tree was then estimated by multiplying the mean individual leaf size for the tree by the total number of leaves on the tree.

Experimental Design and Statistical Analysis

The study was designed as a completely randomized factorial experiment with soil nitrogen (three levels), irrigation (three levels), and defoliation (two levels) as the main effects. There were four replications per treatment combination, giving a total of 72 trees in the experiment. Individual trees were considered the experimental unit: multiple observations per tree were analyzed using a nested design.

Treatment effects on photosynthesis, stomatal conductance, water potential, foliar N and P, individual leaf size, SLM, and LWC were tested using repeated measures analysis of variance (RMANOVA) (SAS Institute, Inc. 1985, p. 229). Univariate RMANOVA is more powerful than multivariate RMANOVA; however, valid application of univariate RMANOVA requires that differences between all pairs of measurements within subjects have homogeneous variances (i.e. the data

must exhibit sphericity) (Gurevitch & Chester 1986; Potvin et al. 1990). Since the hypothesis of sphericity was rejected (Mauchly's criterion, $P=0.10$) for the stomatal conductance and both pre-dawn and mid-day water potential data, these data were analyzed using multivariate RMANOVA. All other variables were analyzed using univariate RMANOVA. Because nitrogen and irrigation are quantitative factors, treatment level means were compared using trend analysis (Chew 1976).

Coefficients for the unequally spaced levels of the irrigation treatment were calculated according to Robson (1959). Results are reported as least square means $\pm$ standard error.

Analysis of covariance (ANCOVA) was used to analyze trunk expansion, total leaf area, and percent increase in total leaf area from 1988 to 1989. Trunk expansion in 1986 (the year following transplanting and preceding treatment initiation) was the covariate, and was highly significant in all cases ($P<0.001$).

The relationship between dependent variables was examined using linear or nonlinear correlation analysis. For variables measured repeatedly over the year, tree specific means of all measurements made during the year were analysed.

RESULTS

Growth

Entering the 1988 growing season (their ninth), the trees were on average 3.3 ± 0.1 m tall, and had an average trunk diameter of 3.6 ± 0.1 cm. The trees grew 70.7 ± 0.7 and 75.6 ± 0.7 cm taller and their trunk diameters increased 10.3 ± 0.6 and 12.6 ± 0.6 mm during 1988 and 1989, respectively (Table 3).

There was a positive logarithmic correlation between radial trunk expansion

Table 3. Comparison of growth, net photosynthesis (A), stomatal conductance (g), and ratio of intercellular to ambient CO₂ partial pressure (C_i / C_a) of paper birch (*Betula papyrifera*), between 1988 (n=72) and 1989 (n=66) (mean $\pm$ standard error).

	1988	1989
Trunk Expansion (mm)	10.33 $\pm$ 0.64	12.56 $\pm$ 0.62
Height Growth (cm)	70.72 $\pm$ 0.74	75.58 $\pm$ 0.70
A ($\mu\text{mol m}^{-2} \text{s}^{-2}$)	11.89 $\pm$ 0.48	14.79 $\pm$ 0.37
g (cm s^{-1})	0.58 $\pm$ 0.04	1.06 $\pm$ 0.04
C_i / C_a	0.64 $\pm$ 0.02	0.76 $\pm$ 0.02

and total leaf area during both 1988 ($r=0.80$) and 1989 ($r=0.74$) (Figure 5). Total leaf area was strongly related to the diameter growth of the slowest growing trees, but the effect diminished in the faster growing trees. There was also a positive exponential correlation between trunk growth and rate of photosynthesis during both 1988 ($r=0.69$) and 1989 ($r=0.66$) (Figure 6). In contrast to the effect of leaf area, increasing photosynthesis had little effect on the growth of slow growing trees with low leaf areas, but strongly enhanced the growth of trees with a high total leaf area. Trunk growth was also positively correlated with individual leaf size both years ($r=0.60$ in 1988 and 0.52 in 1989) (Table 4). In short, the fastest growing trees had the largest leaves, greatest total leaf area, and highest rates of photosynthesis.

Irrigation significantly and linearly enhanced trunk expansion in 1988 ($F=4.89$; d.f. = 1,53; $P=0.031$), but had no effect in 1989 (Figure 7). Likewise, irrigation had a significant positive linear effect on height growth in 1988 ($F=8.89$; d.f. = 1,54; $P=0.004$), but none in 1989 (Figure 8).

During 1988, fertilization had a significant quadratic effect on trunk expansion ($F=3.92$; d.f. = 1,53; $P=0.053$) (trunk expansion was greatest at the medium level of fertilization), but no effect on height growth (Table 5). Fertilization had no effect on trunk expansion or height growth in 1989 (Table 5). Foliar N_{mass} was weakly correlated with growth in 1988 ($r=0.27$) and 1989 ($r=0.29$) (Table 4). However, the correlation was not significant when nitrogen concentration was expressed on a leaf area basis. The same pattern was true of phosphorus (Table 4), but the correlation between P_{mass} and trunk expansion was much stronger in both 1988 ($r=0.50$) and 1989 ($r=0.45$) than that for nitrogen.

Artificial defoliation in 1987 and 1988 had no effect on trunk expansion in 1988 (10.9 ± 0.79 cm and 10.3 ± 0.79 cm for the defoliated and non-defoliated trees, respectively) or 1989 (13.1 ± 0.78 cm and 12.2 ± 0.82 cm, for the defoliated and non-defoliated trees, respectively).

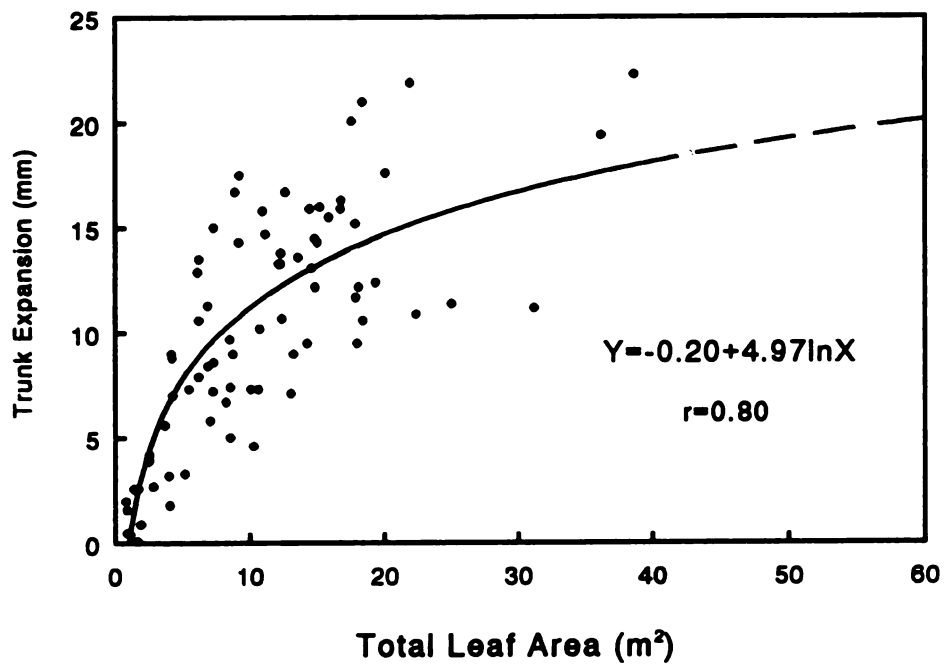
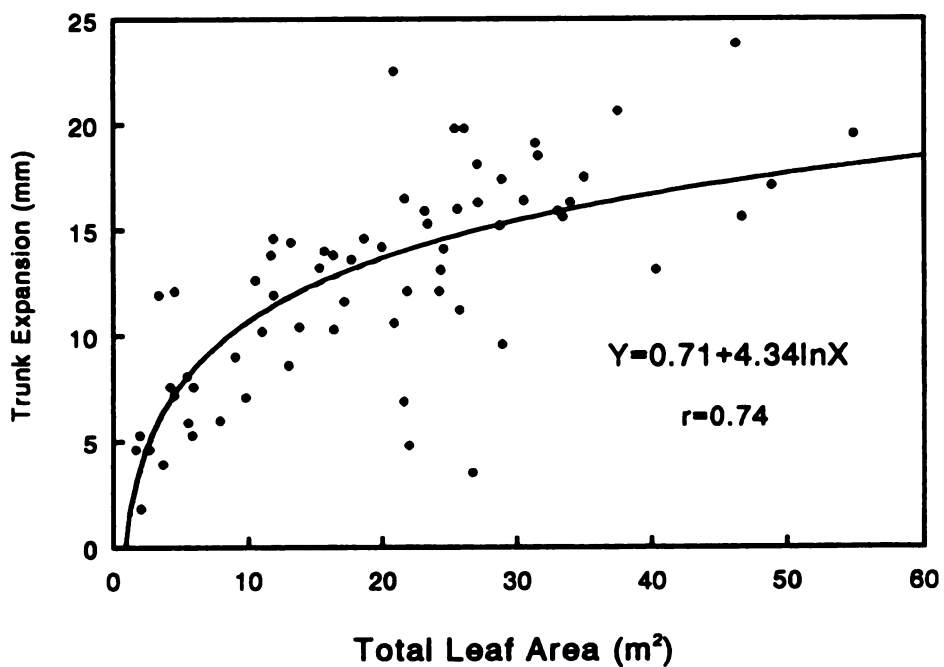
A**B**

Figure 5. Relationship between total leaf area and increase in the trunk diameter of paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B).

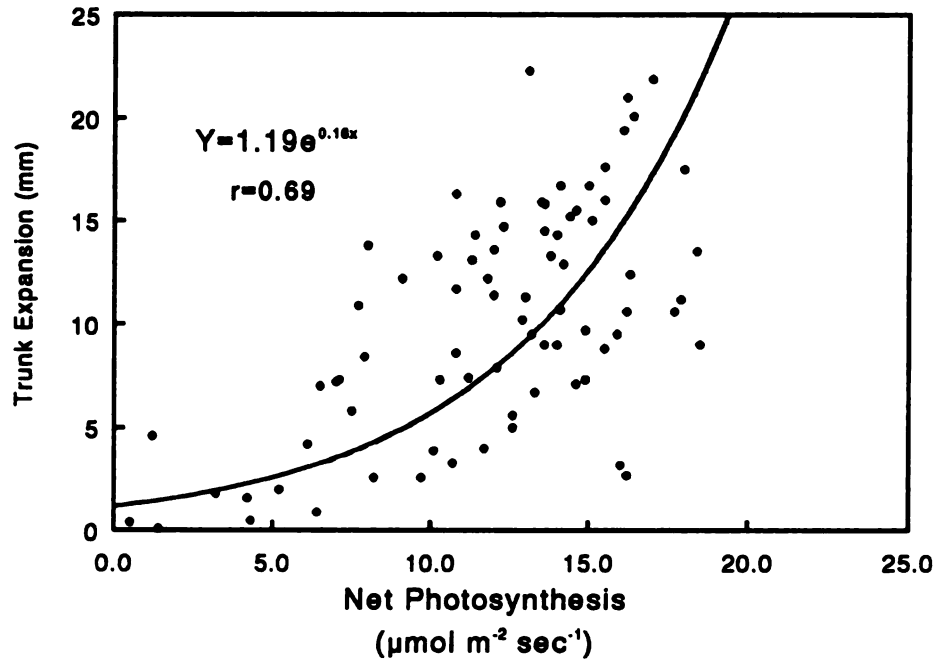
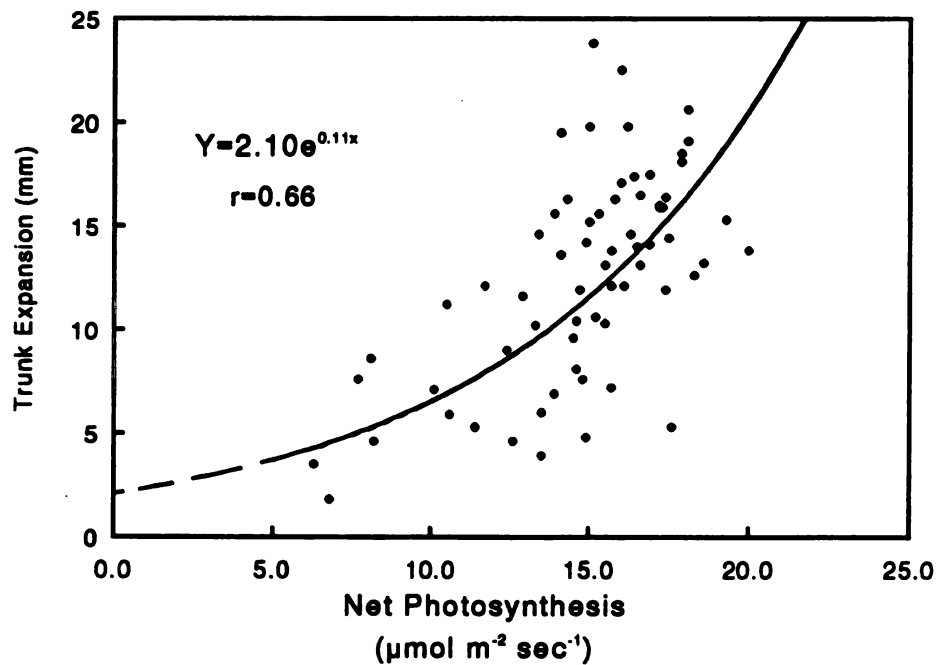
A**B**

Figure 6. Relationship between net photosynthesis (A) and the increase in trunk diameter of paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B). Photosynthesis values represent tree-specific means of all measurements made during the year.

Table 4. Pearson correlation coefficients for physiological variables influencing the growth rate of paper birch. The upper value is the coefficient for 1988 (n=72); the lower value is the coefficient for 1989 (n=66)^{1,2}.

	Growth	A _{area}	A _{mass}	TLA	LS	SLM	PNUE	PPUE
N _{area}	NS	NS	NS	NS	NS	0.57 **	-0.45 **	-0.30 *
	NS	0.29 *	-0.30 *	-0.42 **	-0.33 **	0.67 **	-0.51 **	-0.29 *
N _{mass}	0.28 *	NS	NS	NS	NS	-0.33 *	NS	NS
	0.31 *	NS	0.41 **	NS	NS	-0.39 **	NS	NS
P _{area}	NS	0.28 *	NS	NS	NS	0.40 **	NS	-0.28 *
	NS	0.32 *	NS	NS	NS	0.44 **	NS	-0.39 **
P _{mass}	0.50 **	NS	0.41 **	0.38 **	0.31 *	-0.37 **	0.34 *	NS
	0.45 **	NS	0.45 **	0.32 **	0.37 *	-0.36 *	0.41 **	NS
TLA	0.64 **	0.37 **	0.46 **	1.00	0.64 **	-0.42 **	0.45 **	0.37 *
	0.70 **	0.34 *	0.53 **	1.00	0.53 **	-0.56 **	0.52 **	0.40 **
LS	0.60 **	0.47 **	0.52 **	0.64 **	1.00	-0.31 *	0.46 **	0.39 **
	0.52 **	0.47 **	0.55 **	0.53 **	1.00	-0.43 **	0.55 **	0.35 *
SLM	-0.44 **	NS	-0.46 **	-0.42 **	-0.31 *	1.00	-0.40 **	-0.37 **
	-0.49 **	NS	-0.62 **	-0.56 **	-0.43 **	1.00	-0.52 **	-0.47 **
LWC	0.39 **	NS	0.35 *	0.33 *	0.39 **	-0.65 **	0.33 *	0.29 *
	0.30 *	NS	0.38 **	0.30 *	0.33 *	-0.66 **	0.30 *	0.29 *
PNUE	0.63 **	0.93 **	0.95 **	0.45 **	0.46 **	-0.40 **	1.00	0.91 **
	0.66 **	0.85 **	0.91 **	0.52 **	0.55 **	-0.52 **	1.00	0.77 **
PPUE	0.55 **	0.91 **	0.91 **	0.37 **	0.39 **	-0.37 **	0.91 **	1.00
	0.51 **	0.74 **	0.81 **	0.40 **	0.35 *	-0.47 **	0.77 **	1.00

¹ Abbreviations: A_{area} = net photosynthesis per unit leaf area; A_{mass} = net photosynthesis per unit leaf mass; TLA = total leaf area; LS = individual leaf size; SLM = specific leaf mass; g = stomatal conductance; Ci/Ca = ratio of leaf intercellular to ambient CO₂ partial pressure; PNUE and PPUE = photosynthetic nitrogen and phosphorus use efficiency, respectively; N_{area} and N_{mass} = nitrogen concentration per unit leaf area and per unit leaf mass, respectively; P_{area} and P_{mass} = phosphorus concentration per unit leaf area and per unit leaf mass, respectively; LWC = percent leaf water content.

² * indicates significance at 0.01 level; ** indicates significance at 0.001 level; NS = not significant.

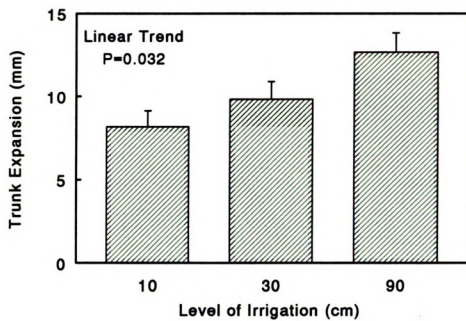
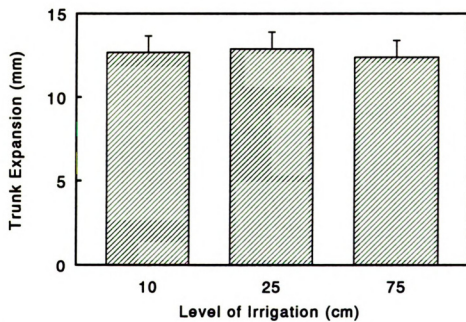
A**B**

Figure 7. The effect of irrigation on the increase in trunk diameter of paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

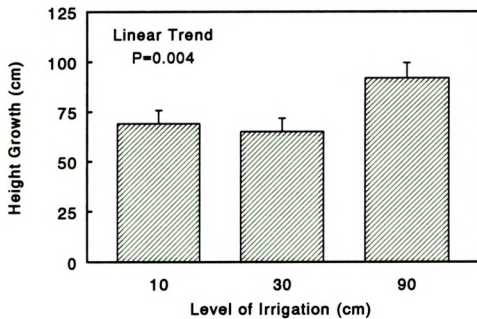
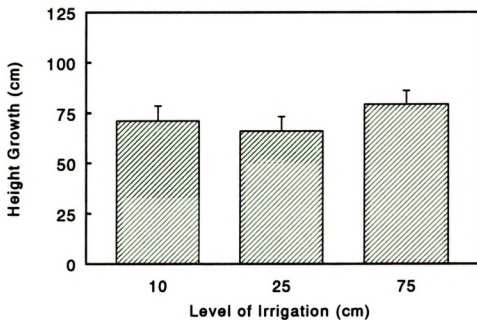
A**B**

Figure 8. The effect of irrigation on the height growth of paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

Table 5. The effect of fertilization on paper birch (*Betula papyrifera*) trunk diameter growth, height growth, and net photosynthesis (*A*) in 1988 and 1989, and percent increase in total leaf area from 1988 to 1989. Values for photosynthesis are tree specific means of all measurements made during the year. Standard errors are in parantheses. *P* is the probability at which the hypothesis of a linear trend can be rejected (quadratic trend in the case of 1988 trunk expansion).

	Level of Fertilization (kg ha ⁻¹)			
	0	175	350	<i>P</i>
Trunk Expansion (mm)				
1988	10.2 (1.0)	12.2 (1.0)	9.5 (1.1)	0.053
1989	12.1 (0.9)	13.2 (1.0)	12.6 (1.1)	0.751
Height Growth (cm)				
1988	76.7 (6.8)	80.1 (7.7)	71.0 (7.6)	0.601
1989	73.8 (7.2)	63.8 (6.6)	78.8 (7.5)	0.630
<i>A</i> (μ mol m ⁻² s ⁻²)				
1988	12.5 (0.8)	12.7 (0.8)	11.4 (1.0)	0.351
1989	13.9 (0.6)	15.3 (0.6)	15.6 (0.7)	0.075
% Increase in Leaf Area from 1988 to 1989	85.7 (14.1)	61.1 (15.3)	48.5 (16.7)	0.095

Foliar N and P

Fertilization significantly and linearly increased foliar N concentration (when expressed on a leaf mass basis) in 1988 ($F = 18.9$; d.f. = 1,54; $P < 0.001$) and 1989 ($F = 9.49$; d.f. = 1,48; $P = 0.003$) (Figure 9). The same pattern was observed for N_{area} in 1988 ($F = 12.1$; d.f. = 1,54; $P < 0.001$) and 1989 ($F = 3.14$; d.f. = 1,48; $P = 0.083$) (Figure 9). Irrigation and defoliation had no effect on foliar N or P in either year.

Gas Exchange

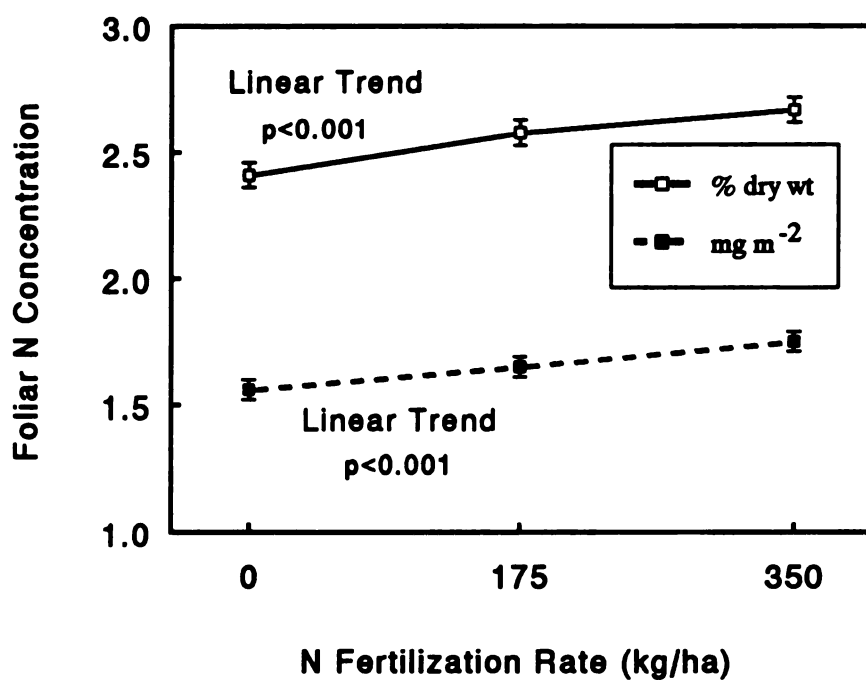
Averaged across all trees, A , g , and C_i / C_a were substantially reduced in 1988 relative to 1989 (11.9 ± 0.48 vs. $14.8 \pm 0.37 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$ for A , 0.58 ± 0.04 vs. $1.06 \pm 0.04 \text{ cm}^2 \text{ sec}^{-1}$ for g , and 0.64 ± 0.02 vs. 0.76 ± 0.01 for C_i / C_a in 1988 and 1989, respectively) (Table 3).

Irrigation significantly and linearly increased net photosynthesis (A) ($F = 6.03$; d.f. = 1,54; $P = 0.017$) and stomatal conductance (g) ($F = 16.2$; d.f. = 1,54; $P < 0.001$) in 1988, but had no effect 1989 (Table 6, Figures 10 & 11).

There was a strong positive logarithmic correlation between A and g during 1988 ($r = 0.88$) and 1989 ($r = 0.80$) (Figure 12), and between stomatal conductance and the ratio of ambient CO_2 to intercellular CO_2 (C_i / C_a) in 1988 ($r = 0.80$) and 1989 ($r = 0.69$) (Figure 13); C_i / C_a leveled off at a value of about 0.75 as g increased above 0.2 cm s^{-1} .

Fertilization had no effect on A in 1988 (Table 5), but A increased linearly with fertilization in 1989 ($F = 3.32$, d.f. = 1,48; $P = 0.075$) (Table 5). There was no relationship between A and foliar N in 1988, either when expressed on a leaf area or

A



B

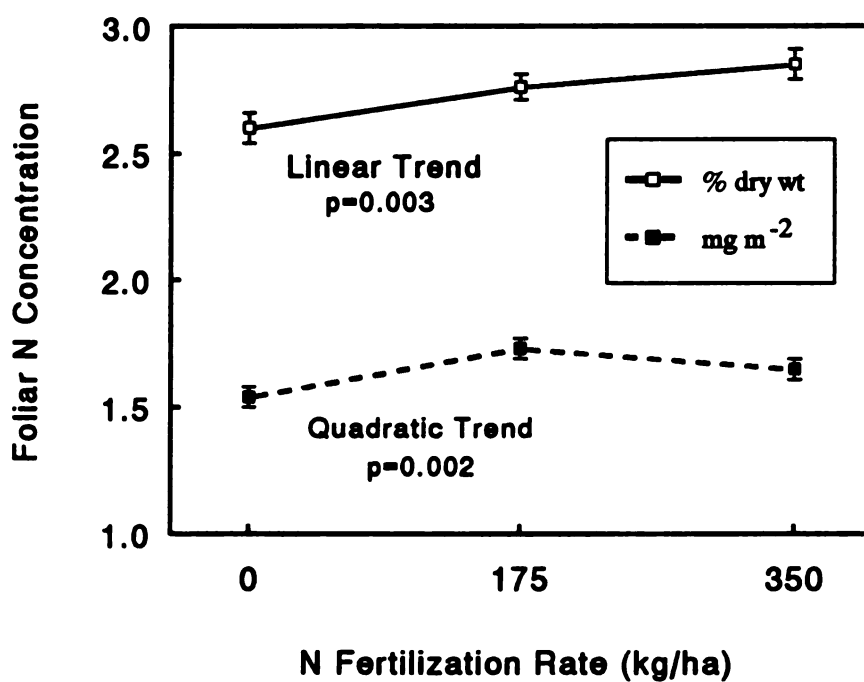


Figure 9. The effect of nitrogen fertilization on the foliar nitrogen concentration of paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

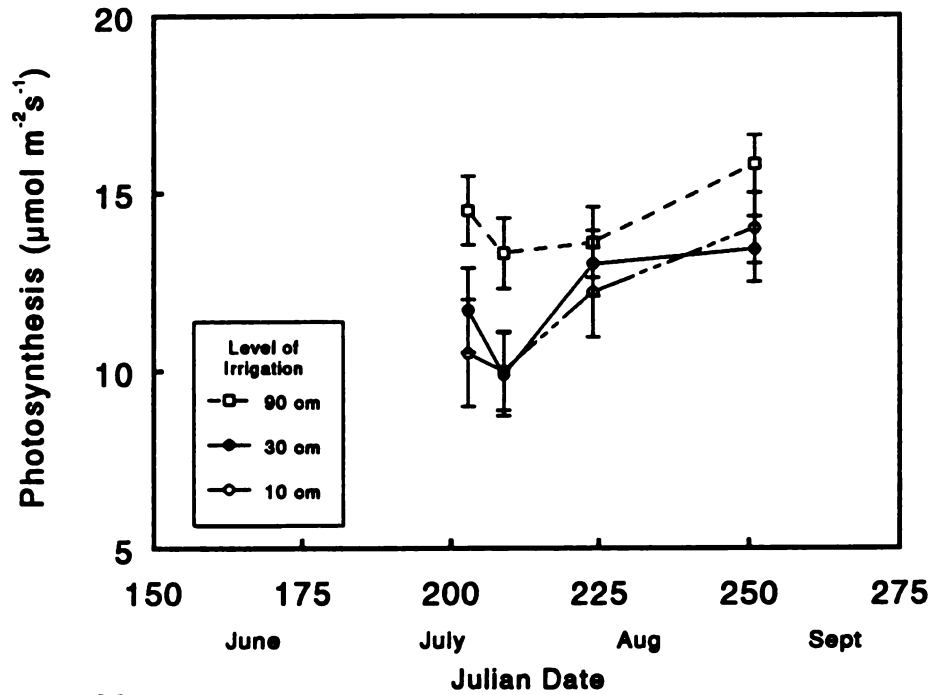
Table 6. The effect of irrigation on the net photosynthesis (A), stomatal conductance (g), pre-dawn water potential (ψ_{AM}), and mid-day water potential (ψ_{PM}), of paper birch (*Betula papyrifera*) during 1988 and 1989. Values are tree specific means (standard errors in parentheses). P is the probability at which the hypothesis of a linear trend can be rejected (repeated measures ANOVA).

	Level of Irrigation (cm) ¹			<i>P</i>
	low	medium	high	
<i>A</i> (μmol m ⁻² s ⁻²)				
1988	11.5 (0.8)	12.0 (0.9)	14.3 (0.7)	0.017
1989	14.7 (0.7)	14.6 (0.7)	15.5 (0.6)	0.323
<i>g</i> (cm s ⁻¹)				
1988	0.56 (0.05)	0.49 (0.05)	0.79 (0.05)	<0.001
1989	1.04 (0.06)	1.00 (0.08)	1.15 (0.07)	0.163
<i>ψ</i> _{AM} ² (MPa)				
1988	-0.21 (0.01)	-0.21 (0.01)	-0.18 (0.01)	0.040
<i>ψ</i> _{PM} ² (MPa)				
1988	-1.38 (0.03)	-1.34 (0.03)	-1.37 (0.03)	0.614

¹Levels of irrigation were 10, 30, and 90 cm during 1988, and 10, 25, and 75 cm during 1989, for low, medium, and high, respectively.

²Water potential was measured in 1988 only.

A



B

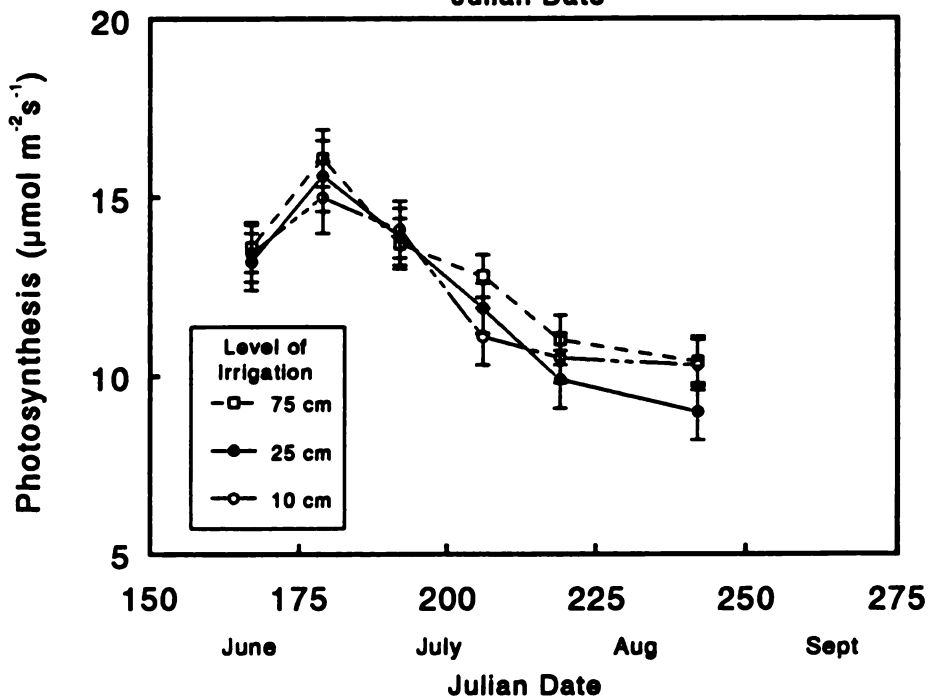
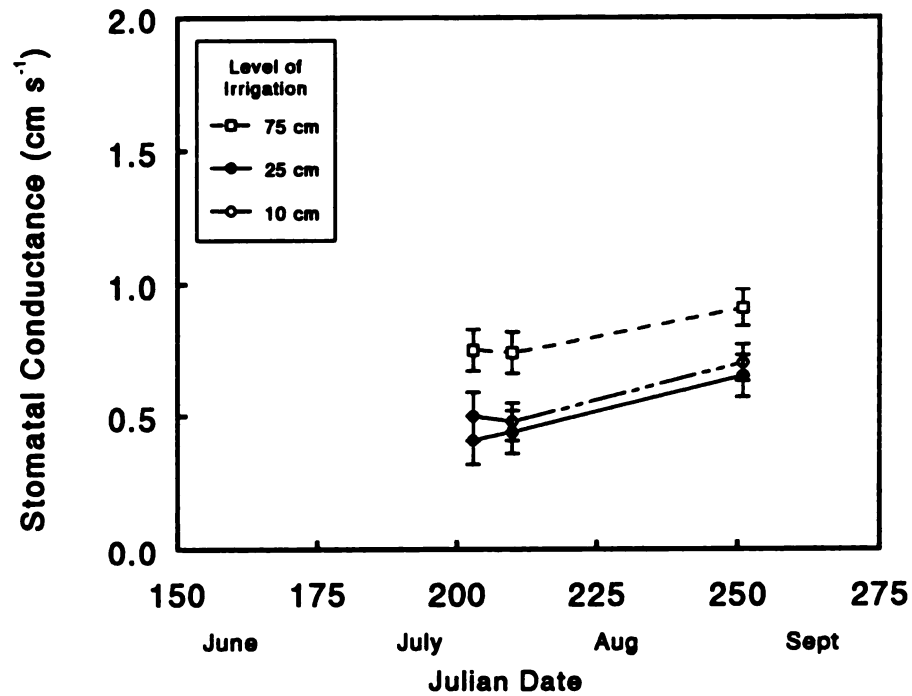


Figure 10. The effect of irrigation level on net photosynthesis (A) of paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

A



B

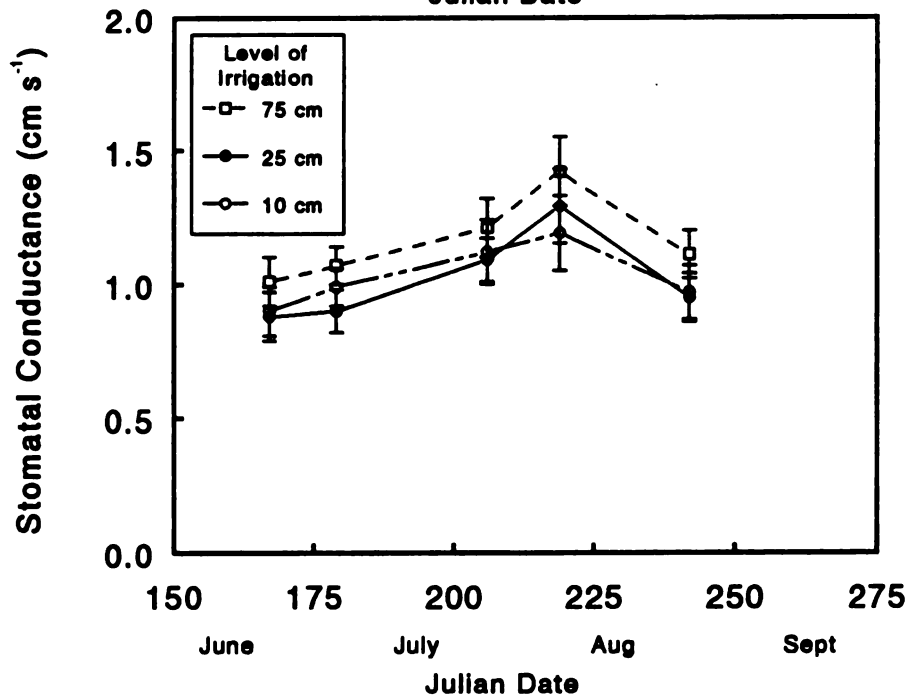


Figure 11. The effect of irrigation on the stomatal conductance (g) of paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

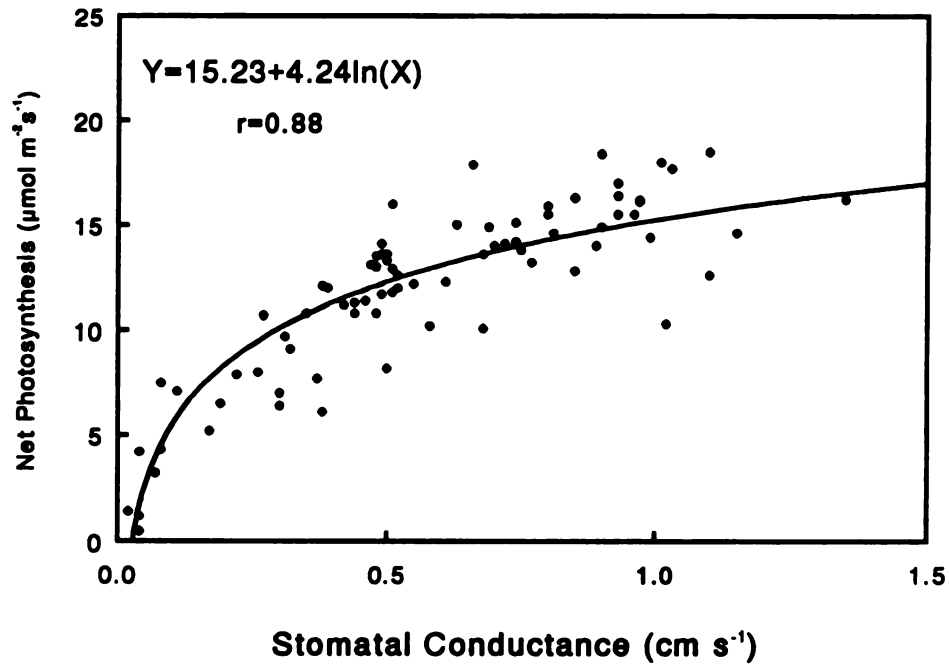
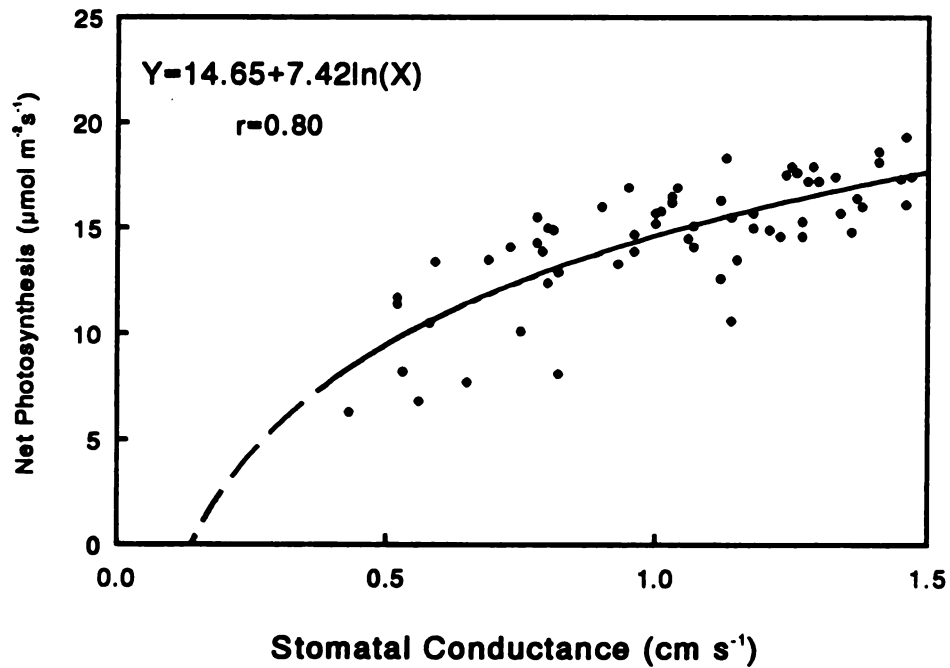
A**B**

Figure 12. Relationship between stomatal conductance (g) and net photosynthesis (A) in paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B). Values are tree-specific means of all measurements made during the year.

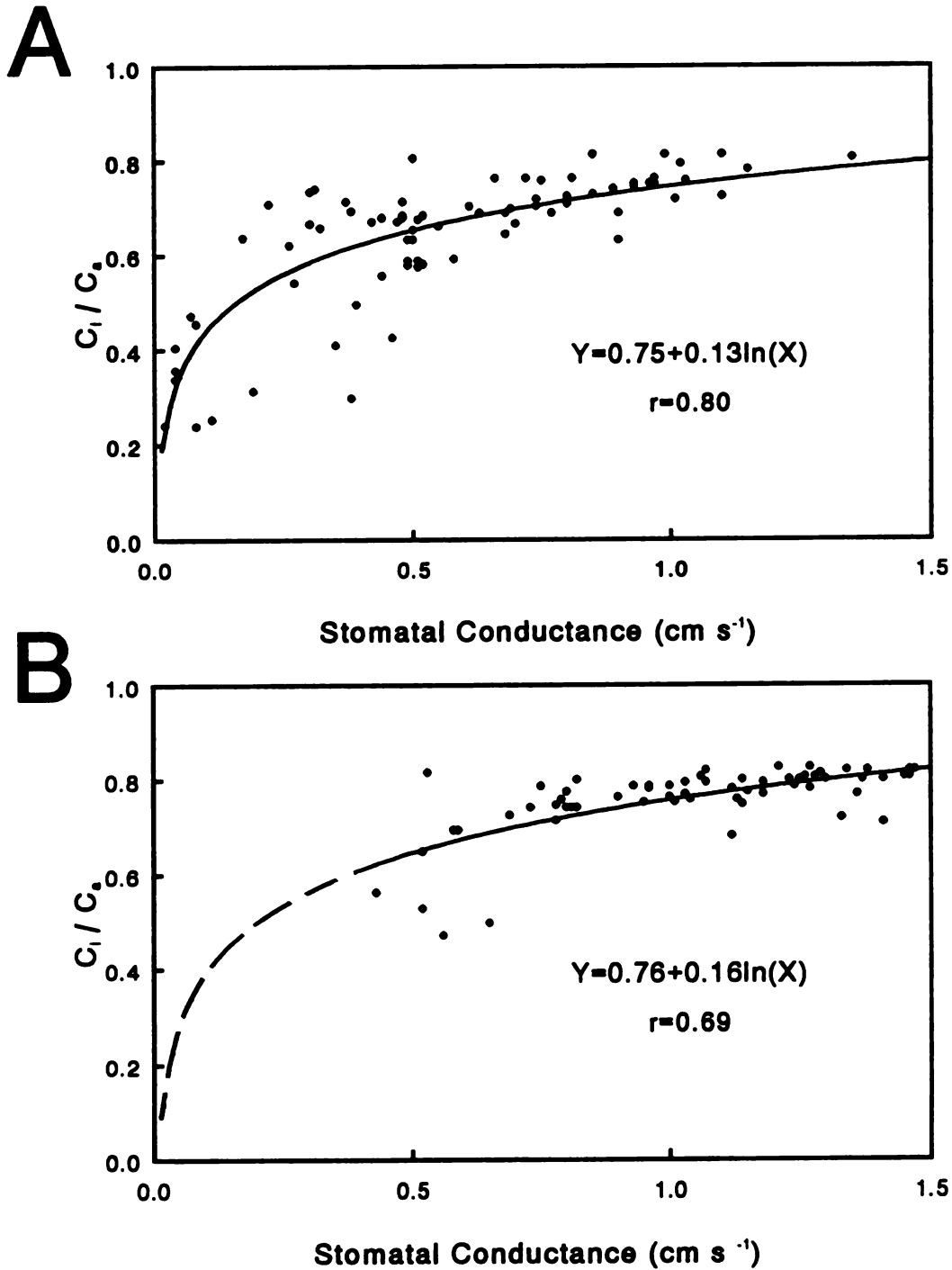


Figure 13. Relationship between stomatal conductance (g) and the ratio of intercellular to ambient CO_2 concentration (C_i / C_a) in paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B). Values are tree-specific means of all measurements made during the year.

a leaf mass basis (Table 4), but during 1989, A and N were positively correlated on both a leaf area ($r=0.29$) and leaf mass basis ($r=0.41$) (Table 4, Figure 14). A and foliar P were positively correlated on both a leaf area and leaf mass basis, during both years (Table 4, Figure 15). Defoliation had no effect on A_{area} in either 1988 or 1989.

Water Potential

During 1988, irrigation significantly and linearly increased pre-dawn water potential ($F=4.39$; d.f. = 1,53; $P=0.041$) (Table 6, Figure 16). Effects were most pronounced late in the season. There was a significant effect of time on pre-dawn water potential (Wilks' Lambda, $F=110.0$; d.f. = 4,48; $P<0.001$). Pre-dawn water potential was low on 10 June, high on 24 June, then decreased over the next two sampling dates (8 July and 24 July), and increased again on 26 August. This was a highly significant cubic pattern ($F=150.5$; d.f. = 1,51; $P<0.001$) (Figure 16).

Irrigation had no apparent effect on mid-day water potential (Table 6, Figure 16). However, mid-day water potential was inversely correlated with pre-dawn water potential ($r= -0.26$; $n=72$; $P=0.023$), photosynthesis ($r= -0.39$; $n=72$; $P<0.001$), and stomatal conductance ($r= -0.32$; $n=72$; $P<0.001$) (Table 4). This indicates that photosynthesis and stomatal conductance tended to be highest in leaves having the lowest mid-day water status. Soil nitrogen and defoliation had no effect on pre-dawn or mid-day water potential in 1988.

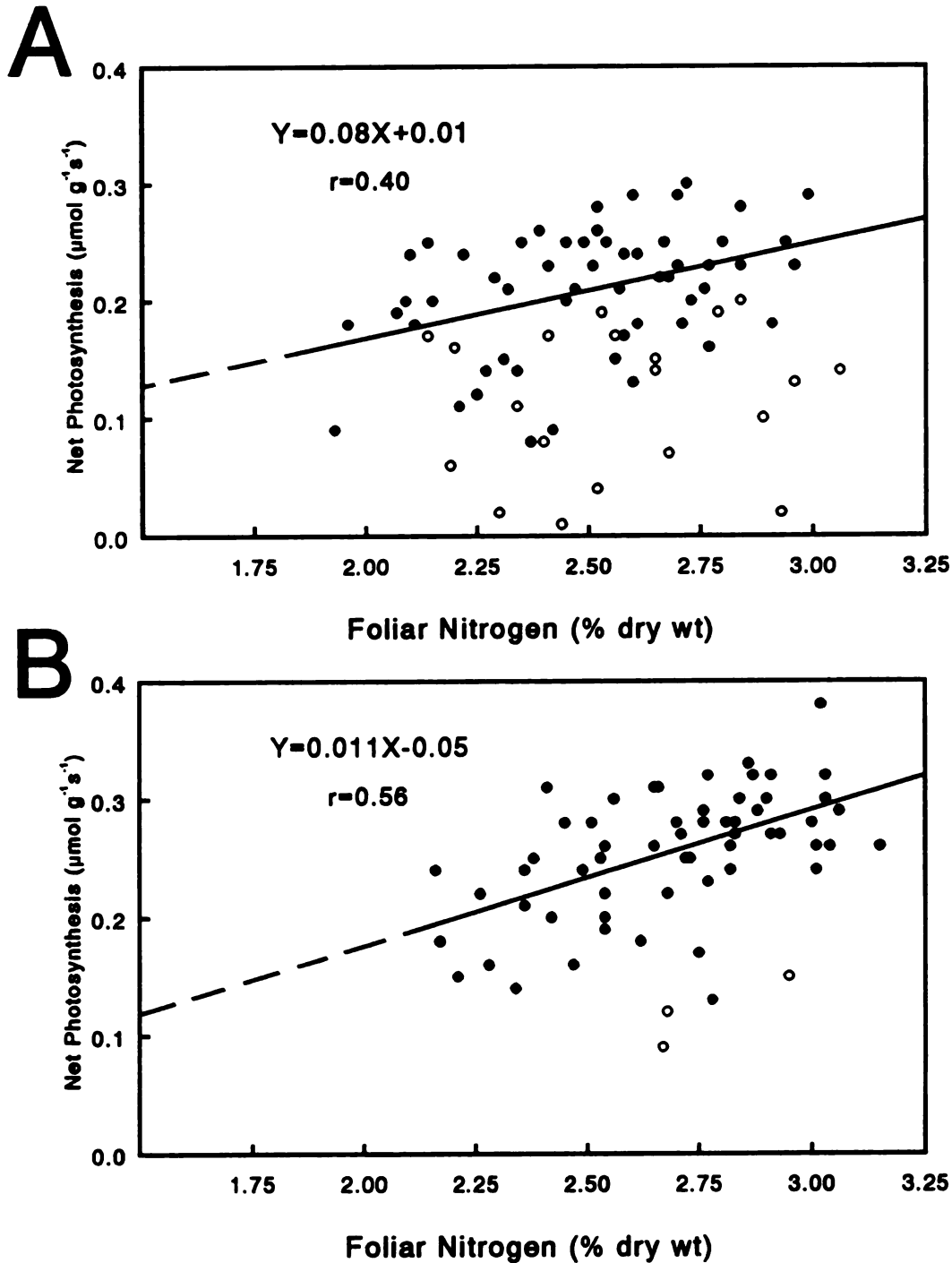


Figure 14. Relationship between foliar nitrogen (N_{mass}) and net photosynthesis (A) in paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B). Open circles represent trees having stomatal limitations to photosynthesis ($C_i/C_a < 0.6$), and are not included in the regression analysis. Values are tree-specific means of all measurements made during the year.

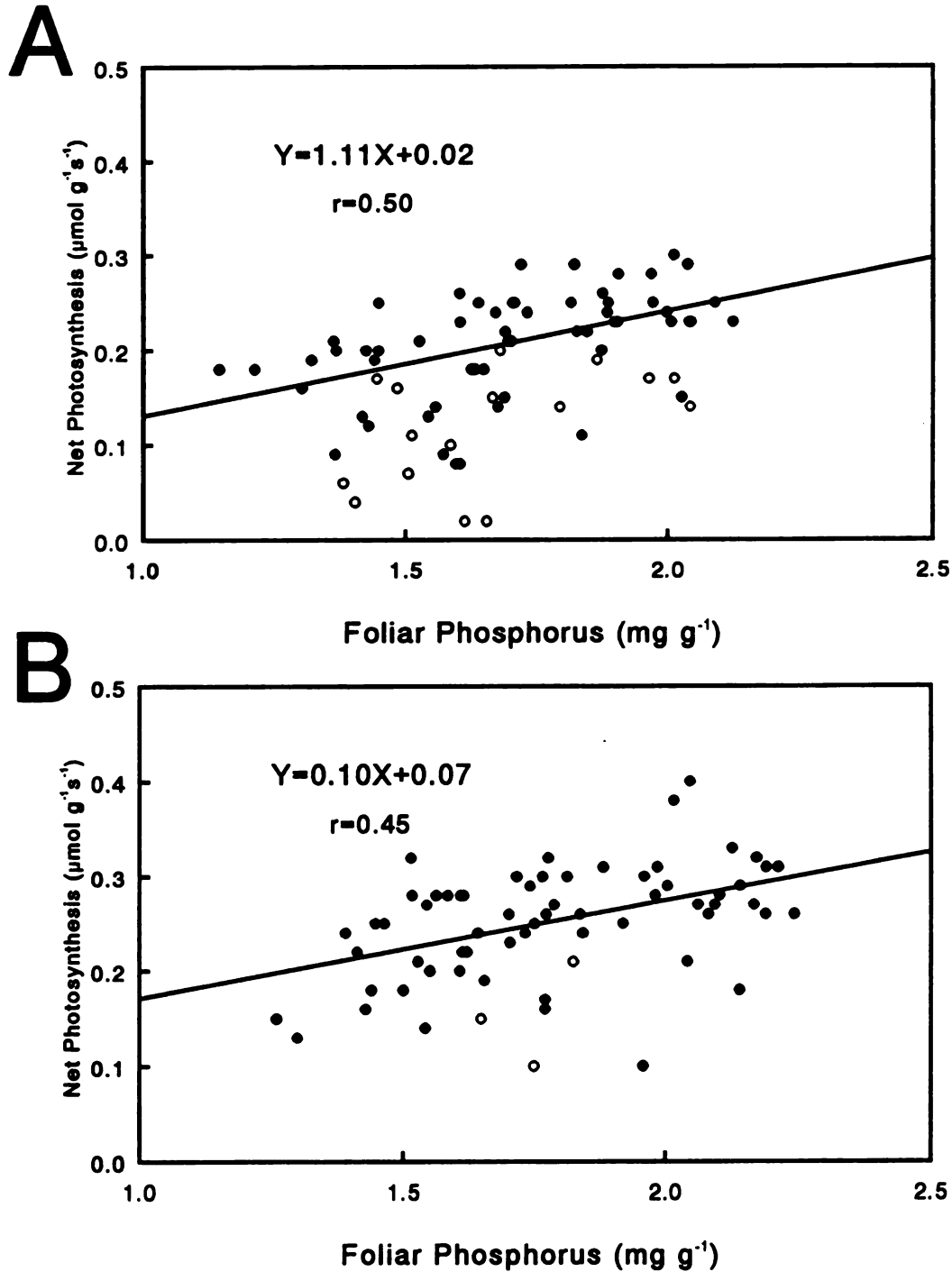


Figure 15. Relationship between foliar phosphorus (P_{mass}) and net photosynthesis (A) in paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B). Open circles represent trees having stomatal limitations to photosynthesis ($C_i/C_a < 0.6$), and are not included in the regression analysis. Values are tree-specific means of all measurements made during the year.

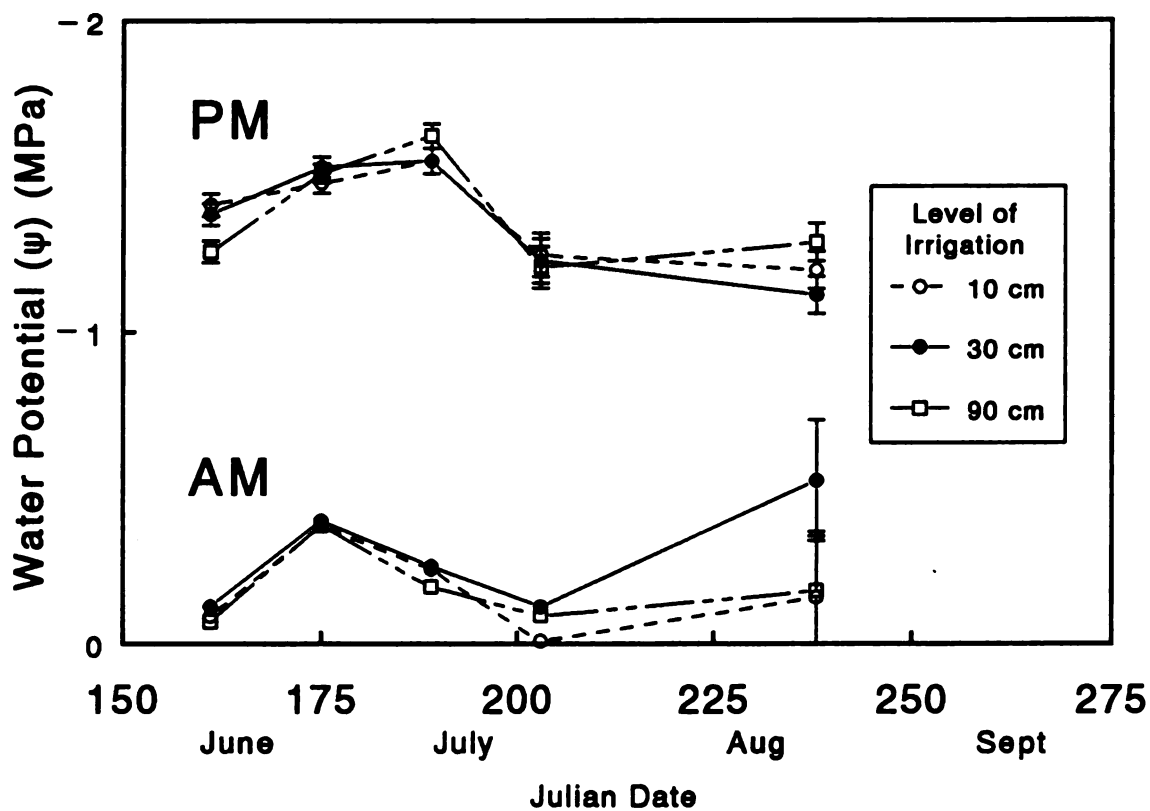


Figure 16. The effect of irrigation on pre-dawn (AM) and mid-day (PM) water potential of paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

Leaf Area

When shoot extension terminated in early August of 1988, trees averaged $4,628 \pm 299$ leaves and a total leaf area of $9.3 \pm 0.9 \text{ m}^2$ (including estimated losses to artificial defoliation). At the same time in 1989, trees averaged 8583 ± 601 leaves per tree, and total leaf area of $20.2 \pm 1.5 \text{ m}^2$.

Artificial defoliation removed $40.2 \pm 0.01\%$ total leaf area in 1988. However, defoliation in 1987 and 1988 had no effect on total leaf number in 1988 and 1989, or total leaf area in 1989. Fertilization also had no effect on total leaf number or area in 1988 or 1989. However, fertilization did have a marginally significant linear effect on percent increase in total leaf area from 1988 to 1989 ($F=2.90$; d.f. = 1,46; $P=0.096$) (Table 5). Surprisingly, the trend was for leaf area to increase as soil nitrogen decreased. Irrigation had no effect on total leaf area in 1988 or 1989, or on the percent change in total leaf area from 1988 to 1989.

As previously mentioned, there was a positive logarithmic correlation between total leaf area and growth during 1988 and 1989 (Figure 5). During 1988 and 1989, there were also significant positive correlations between total leaf area and A , g , individual leaf area, LWC, and P_{mass} (but not P_{area}) (Table 4). There was a negative correlation between N_{area} and total leaf area in 1989, but not in 1988 (Table 4).

There were no significant treatment effects on the size of individual leaves, specific leaf mass (SLM), or leaf water content (LWC). Individual leaf size, however, was directly correlated with trunk expansion, A , total leaf area, and LWC (Table 4). The size of individual leaves was negatively correlated with SLM and C_i / C_a (Table 4). SLM was negatively correlated with trunk expansion, total leaf area, SLA, LWC, and foliar N and P (on both a leaf area and leaf mass basis) (Table 4). LWC was directly correlated

with trunk expansion, total leaf area, as well as leaf nitrogen and phosphorus concentration (Table 4).

Phenological Patterns

Net photosynthesis changed significantly over both 1988 ($F=6.61$; d.f. = 3,162; $P<0.001$) and 1989 ($F=66.60$; d.f. = 1,250; $P<0.001$) (Figure 10). However, during 1988, net photosynthesis was fairly constant the first three dates measured (22 July, 29 July, and 12 August), but then increased on 8 September. On the other hand, during 1989, net photosynthesis was highest in early summer, and then declined as the season progressed.

Stomatal conductance also changed significantly over the course of the season in 1988 (Wilks' Lambda, $F=7.63$; d.f. = 2,51; $P=0.001$) and 1989 (Wilks' Lambda, $F=4.79$; d.f. = 4,47; $P=0.003$), following the same general pattern as photosynthesis (Figure 11).

During both 1988 and 1989, both foliar N and P concentrations declined over the season (Figure 17). Once leaves were fully expanded, there was no change in leaf size. However, during 1988 and 1989 SLM increased while LWC decreased (Figure 18).

DISCUSSION

Tree Growth

Growth rates of plants have been found to be highly correlated with allocation of photoassimilates to increased leaf area, and to a lesser degree with

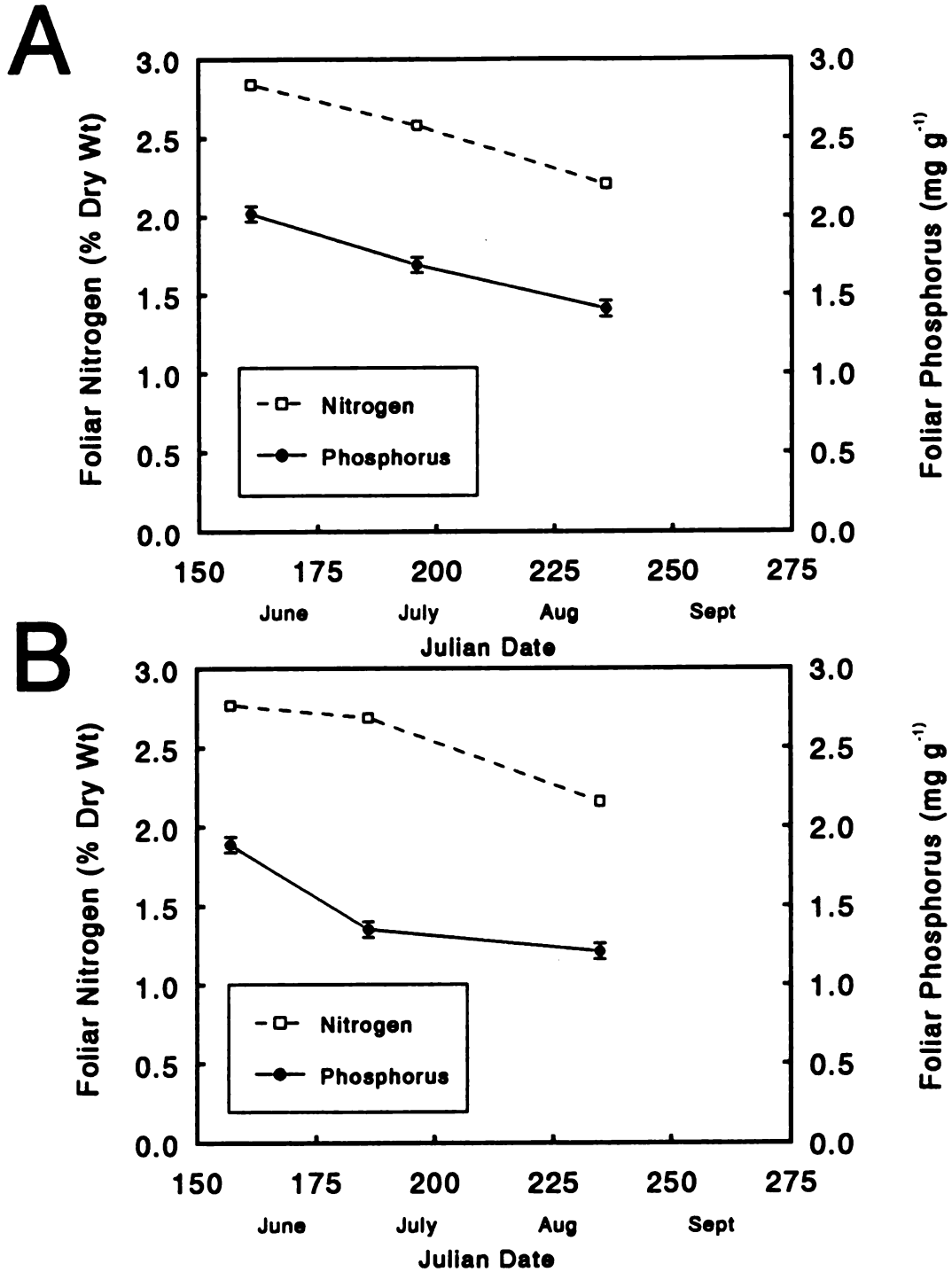


Figure 17. Phenological pattern of foliar nitrogen and phosphorus concentrations in paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

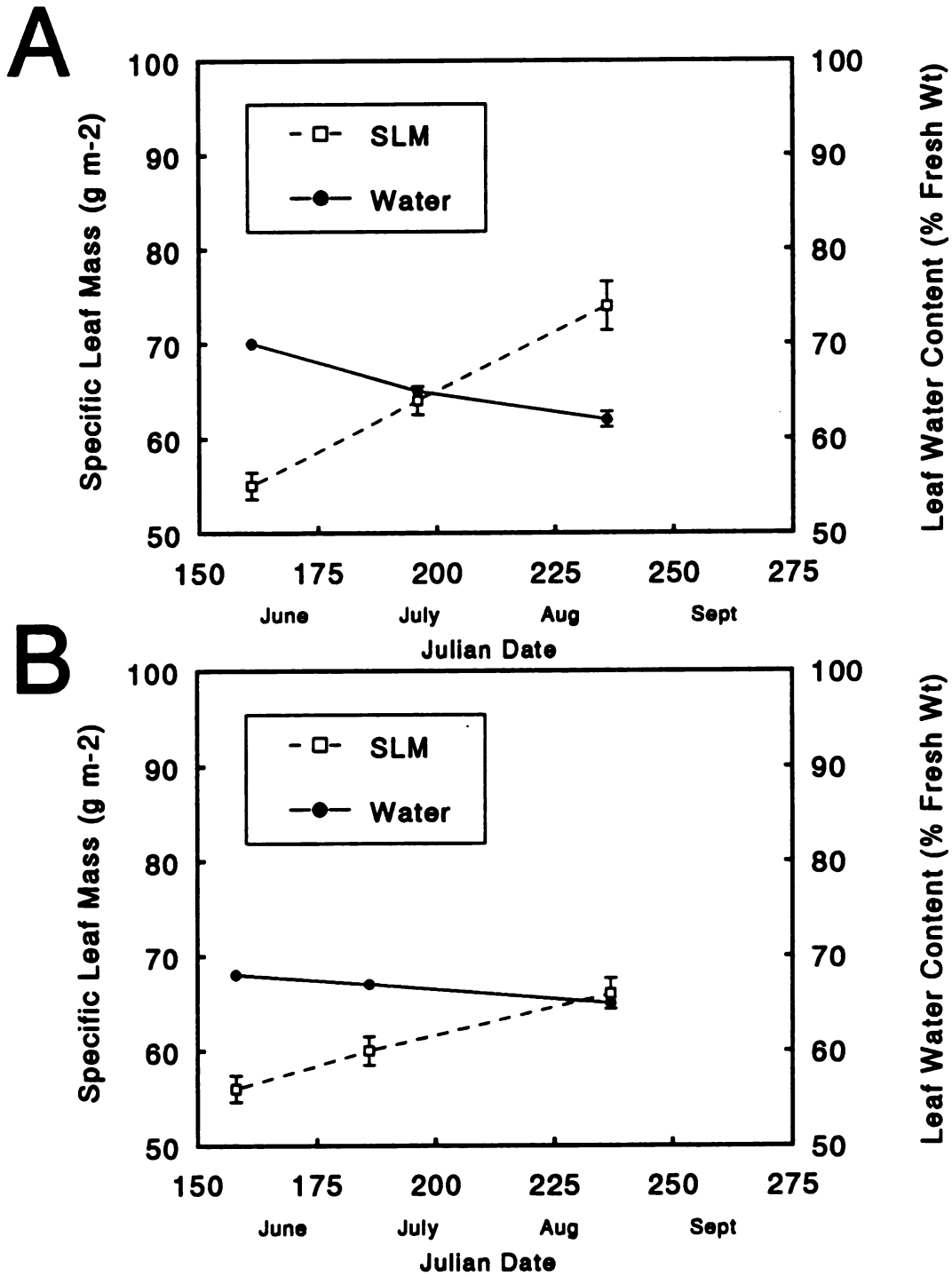


Figure 18. Phenological pattern of change in the specific leaf mass (SLM) and leaf water content (LWC) of paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

photosynthesis (Potter & Jones 1977; Gifford & Evans 1981; Gifford et al. 1984; Lambers et al. 1988; Poorter & Remkes 1990; Poorter et al. 1990) However, most evidence supporting this relationship comes from studies of wild herbaceous plants, crops, and tree seedlings; there are few data for larger field-grown trees. In this controlled field study of paper birch trees from age 8-10, growth rate was most closely associated with total leaf area for the more slowly growing trees with lower rates of photosynthesis, while growth rate was more closely associated with net photosynthesis in the faster growing trees with higher total leaf areas.

Treatments had a surprisingly small effect on growth compared with uncontrolled factors. The complete factorial statistical models (with 1986 growth as a covariate) only accounted for 42% and 48% of the total variation in trunk growth in 1988 and 1989, respectively. For example, while nitrogen fertilization had a significant curvilinear effect on growth in 1988 (with growth being greatest at the medium level of fertilization: 150 kg/ha), it had no effect on growth in 1989. Furthermore, foliar P was more highly correlated with growth, total leaf area, individual leaf size, and A than was foliar N, during both years.

Fertilization did increase A in 1989, and had a marginally significant negative linear effect on percent increase in leaf area from 1988 to 1989 ($P=0.095$). The higher percent increase in total leaf area in the nitrogen deficient plants was balanced by the lower A , with a net result was no fertilization effect on growth in 1989.

Gas Exchange and Water Relations

Positive linear and curvilinear correlations between photosynthesis and stomatal conductance have been reported for many species, including woody plants (e.g. Lakso & Seeley 1978; Wong et al. 1979; Benecke et al. 1981; Kozlowski 1982; Field & Mooney 1983; Küppers et al. 1986,1988; Davis et al. 1987; Monson & Grant 1989; Harrison et al. 1989). Historically, this relationship has been interpreted as evidence that stomatal closure, by limiting the diffusion of CO₂ to mesophyll cells, is of primary importance in limiting photosynthesis in water-stressed plants (Hsiao 1973; Bradford & Hsiao 1982; Kozlowski 1982). However, Boyer (1976) and Hanson & Hitz (1982) noted that there was little evidence to support the hypothesis that internal CO₂ concentrations limit photosynthesis as stomata close. Recent evidence suggests that nonstomatal limitations may often contribute more to the overall limitation of photosynthesis than do stomatal limitations on the diffusion of CO₂ (Wong et al. 1979,1985; Farquhar & Sharkey 1982; Hanson & Hitz 1982; Cornic et al. 1983; Ehleringer & Cook 1984; Tenhunen et al. 1984; Turner et al. 1985; Teskey et al. 1986; Pezeshki & Chambers 1986; Reich et al. 1989), although stomatal limitations to photosynthesis do occur (Ehleringer & Cook 1984; Goolan et al. 1985; Pezeshki & Chambers 1986; Reich et al. 1989).

Cowan (1977) and Cowan & Farquhar (1977) predicted a pattern of optimal stomatal behavior, in which stomata respond to environmental changes to minimize the amount of water lost for a given amount of carbon gained. Plants should respond to stresses that inhibit the intrinsic photosynthetic capacity of chloroplasts (e.g. through inhibition of photosynthetic reactions or deficiencies of photosynthetic enzymes) by closing their stomata, such that the rate of diffusion of CO₂ is limited only to the rate it can be used by the mesophyll, thus conserving water while maintaining a constant C_i / C_a . A linear relationship between A and g , as C_i / C_a

remained constant, has been reported for a number of species growing under a wide range of environmental conditions (Wong et al. 1979,1985; Field et al. 1983; Teskey et al. 1986; Küppers et al. 1986; Frederick et al. 1989). In these cases, CO₂ assimilation was limited by the photosynthetic capacity of the mesophyll rather than by stomatal limitation of CO₂ diffusion to mesophyll cells.

Recently it has been demonstrated that when stomatal closure is not uniform over the entire leaf surface, values of C_i calculated from gas exchange measurements will be erroneous, suggesting biochemical limitations to photosynthesis, when in fact, stomatal closure fully accounts for inhibition of photosynthesis (Terashima et al. 1988; Downton et al. 1988). This phenomenon has been documented in several cases (Terashima et al. 1988; Downton et al. 1988; Daley et al. 1989; Loreto & Sharkey 1990, Epron & Dreyer 1990), and Downton et al. (1988) suggest that stomatal limitation may fully account for inhibition of photosynthesis by water deficit.

A model of optimal stomatal conductance developed by Givnish (1986) predicts a linear relationship between g and A when nutrient availability affects mesophyll capacity, but a curvilinear relationship as stomata close in response to moisture deficits. The curvilinear relationship is predicted on the basis of the nonlinear relationship that exists between photosynthesis and transpiration (Cowan 1982). Stomatal resistance to the diffusion of water vapor and CO₂ limits both transpiration and A to a high degree at low values of g . As g increases, the marginal cost of transpiration decreases (Givnish 1986), and the proportionally greater increase in A relative to transpiration results in increased water use efficiency (DeLucia & Heckathorn 1989). Empirical studies have shown this curvilinear relationship to be consistent with optimal stomatal behavior (Farquhar et al. 1980; Hall & Schulze 1980; Meinzer 1982).

The curvilinear relationship observed in this study during 1988 (Figure 12)

suggests that water availability was the important factor controlling g and A . At the lowest values of g , A and C_i/C_a increased rapidly with only small increases in g . As g increased above a value of about 0.2 cm s^{-1} , the transpirational costs decreased, g increased faster than A , and C_i/C_a was maintained constant as the photosynthetic capacity of the mesophyll increased (Figure 13).

Thus, in 1988, the relative contribution of nonstomatal (biochemical) limitations to total photosynthetic limitation was greater than stomatal limitations in trees experiencing low to moderate moisture stress. However, as water stress became more severe, stomatal limitation to photosynthesis increased in relative importance. This result is consistent with the data of Federer (1980) who found that, as opposed to the drought tolerating white oak (*Quercus alba*), paper birch avoids drought through stomatal closure and leaf abscission.

Similar curvilinear relationships in response to soil drying have been reported for other species (Nagarajah & Schulze 1983; Küppers et al. 1986; DeLucia & Heckathorn 1989). However, this response contrasts somewhat with that observed by Talhouk (1988) and Reich et al. (1989) for potted *Betula papyrifera* and *Ulmus americana* seedlings, respectively. In their studies, stomatal limitation were most important at moderate water stress. However, at severe water stress biochemical limitations became more important, as evidenced by an increased C_i/C_a while g and A were both very low. The development of drought stress may be more gradual in field-grown trees than in potted seedlings, allowing the photosynthetic machinery of field-grown trees to better acclimate moisture-deficits. Assuming optimal stomatal behavior, the lack of biochemical limitations on photosynthesis in field-grown trees, suggests that they are maximizing water use efficiency at low water availability.

During 1989, a more linear relationship between A and g was observed (Figure 12), suggesting that stomatal limitations to photosynthesis were less

important. This is consistent with the lack of significant irrigation effects on growth, A , or g . The constancy of C_i / C_a at about 0.75 C_i / C_a as g declined (Figure 13) is further evidence that variations in photosynthetic rates among trees were due mostly to variations in their mesophyll capacity for carbon fixation rather than in stomatal limitations to CO_2 diffusion.

Decreased leaf water potential, resulting from decreased leaf turgor as soil moisture deficits develop, has been considered to result in the closure of stomata, and thus to decrease photosynthesis (Turner 1974; Boyer 1976; Kozlowski 1979,1982; Bradford & Hsiao 1982; Berry & Downton 1982; Barlow 1983; Kramer 1988). Recently, however, the physiological importance of leaf water potential in controlling stomatal behavior has been questioned (Turner et al. 1985; Gollan et al. 1985,1986; Schulze 1986a,b ; Turner 1986; Küppers et al. 1986; Passioura 1988; Schulze et al. 1988; Reich & Hinckley 1989; Jones 1990).

In companion laboratory studies, Turner et al. (1985) and Gollan et al. (1985) found no relationship between leaf conductance, transpiration rate, or photosynthetic rate and leaf water potential in the herbaceous mesophyte *Helianthus annuus* or the woody sclerophyll *Nerium oleander*, respectively. They concluded that for both species, declining soil water status as sensed by the roots, rather than leaf water status, controlled leaf gas exchange, and that any relationship between leaf water potential and stomatal behavior was coincidental. Furthermore, they concluded that leaf water potential was determined by the transpiration rate, rather than vice versa (Gollan et al. 1985). Several other field experiments have also failed to demonstrate a relationship between gas exchange and leaf water potential and/or have found stomatal conductance to be more closely associated with soil moisture and pre-dawn leaf water potential (when in equilibrium with soil water potential) than changes in leaf water status (Bates & Hall 1981; Gollan et al. 1986; Küppers et al. 1986,1988; Reich & Hinckley 1989). Plant growth regulators

have been proposed as the mechanism for communicating the status of soil moisture to the shoots (Turner et al. 1985; Gollan et al. 1985; Schulze 1986a,b; Turner 1986). Zhang and Davies (1989) demonstrated that abscisic acid produced in dehydrating roots and subsequently translocated to the shoots can provide a sensitive indication of soil moisture status.

The results of this study also support the hypothesis that soil moisture, rather than leaf water potential, controls leaf gas exchange. This was evidenced by the fact that pre-dawn water potential was lowest, while growth, photosynthesis, and stomatal conductance were greatest at the highest level of irrigation. Furthermore, mid-day leaf water potential was inversely correlated with A and g . There is no evidence that diurnal osmotic adjustment occurs in *Betula* (Osonubi & Davies 1978); this suggests that leaves with the greatest stomatal apertures and highest rates photosynthesis had the lowest turgor pressure, while plants that maintained high mid-day turgor pressure, achieved this by stomatal closure at a cost of reduced photosynthesis.

Several factors may account for the lack of irrigation treatment effects in 1989. Averaged across all trees, growth, A , g , and C_i / C_a , were all substantially lower in 1988 than in 1989 (Table 3). The summer of 1988 was much hotter and dryer than that of 1989 (Figure 19). Consequently, evapotranspiration may have been much greater in 1988 than 1989, resulting in more rapid and substantial depletion of soil moisture in 1988. Lower mean A , g , and C_i / C_a in 1988 relative to 1989 are consistent with the hypothesis of a higher over-all level of moisture stress in 1988, resulting in increased stomatal limitations on photosynthesis. Paper birch is adapted to cool climates (Parella & Alm 1990); maximum growth and photosynthesis occurs at about 20° C (Lawrence & Oechel 1983). The higher temperatures occurring in 1988 also may have acted directly to reduce growth and A in 1988 relative to 1989. Paper birch is considered to be intolerant of drought (Federer

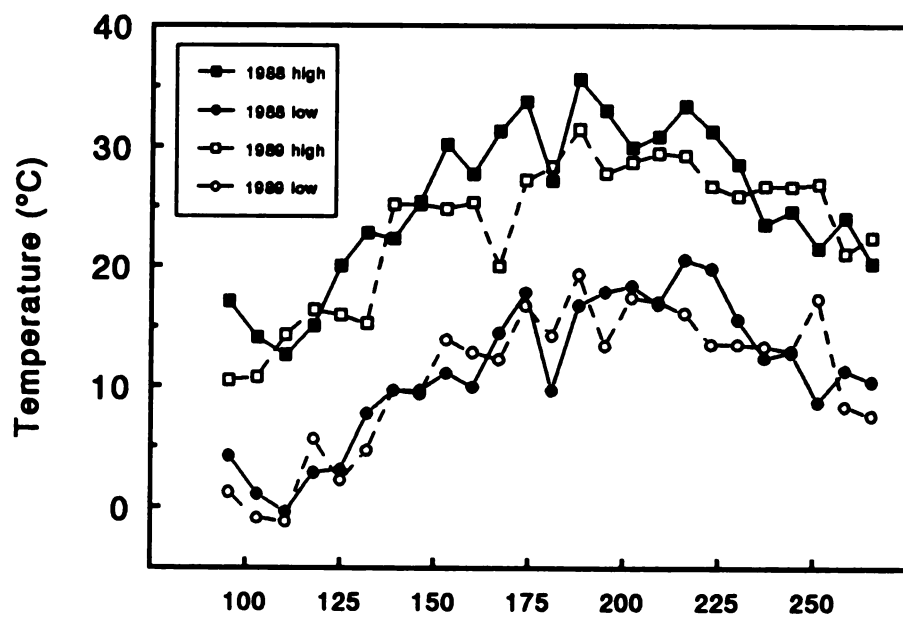
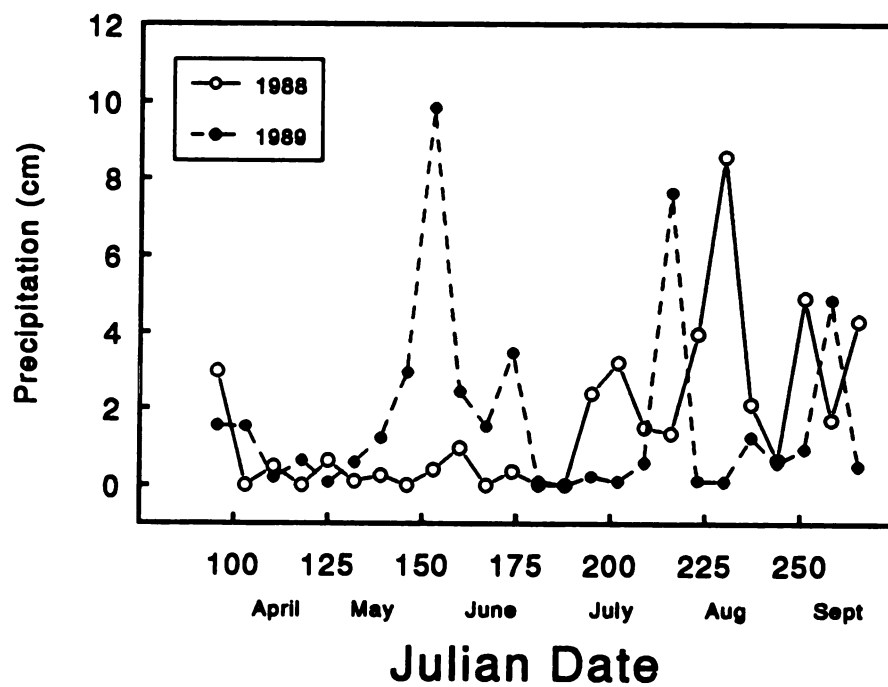
A**B**

Figure 19. Comparison of average weekly high and low temperatures, and weekly precipitation in Midland, Michigan, in 1988 and 1989.

1980; Perala & Alm 1990; Ranney et al. 1990). The results of this study suggest that the effects of drought on paper birch are much more pronounced when accompanied by high temperatures.

Other factors also may have contributed to the differences observed between 1988 and 1989 in birch response to irrigation. Of the 13 trees experiencing the most severe photosynthetic limitations in 1988 ($C_i / C_a < 0.5$), 8 died during August of 1988 from colonization by bronze birch borer (*Agrius anxius* Gory). Paper birch displays high genetic variation, even within families (Sohasky 1977). The individuals eliminated from the population during 1988 may been the most sensitive to water stress.

Plants may display physiological and/or morphological phenotypic plasticity which may enable them to adapt to environmental variability (Bradshaw 1965; Schlichting & Levin 1986; Grime et al. 1986). For example, as water deficits develop, many plants maintain cell turgor through osmotic adjustment (increasing cell solute content), thus maintaining a water potential gradient between leaves and the soil as the soil dries (Hsiao 1976; Hanson & Hitz 1982; Percy 1983; Abrams 1988). This response is generally stronger if water deficits develop gradually over time and if plants are preconditioned by previous exposure to drought (Hanson & Hitz 1982; Percy 1983; Abrams 1988). There is some evidence that paper birch has at least limited capacity for osmoregulation on a seasonal basis (Pothier & Margolis 1990). However, no diurnal osmotic adjustment occurs in the closely related European white birch (*Betula pendula*) (Osonubi & Davies 1978).

Some species subjected to moisture stress increase the proportion of carbon they allocate to root growth (Schulze 1986b, Givnish 1986; Teskey & Hinckley 1986; Mazzoleni & Dickmann 1988; Daie 1988). It is conceivable that by 1989 the root systems of the trees were substantial enough to tap subsurface water supplies, so irrigation treatments no longer resulted in treatment effects. On 26 July 1989, pre-

dawn water potential measurements were made on 4 trees from each irrigation treatment. There were no differences among the treatments, suggesting that the plants were not experiencing different soil moisture regimes.

Water stress can have a negative impact on leaf area by inhibiting leaf expansion and decreasing leaf numbers (Kriedemann 1986; Myers & Landsberg 1989; Joly & Hahn 1989). In this study, however, as a result of accumulated snow melt and spring rains, soil moisture was high as the beneath-canopy tents were installed in mid-April. Hence, plants did not experience water deficits while leaves were expanding, and the irrigation treatments had no effect on the size of individual leaves. Furthermore, drought stress experienced in 1988 had no carry-over effect on leaf number per tree or total leaf area in 1989, possibly because the most severely impacted trees died during 1988. Since irrigation had no effect on leaf area, it must be concluded that the effects of irrigation on growth in 1988 were due to stomatal limitations on photosynthesis in severely stressed trees.

Nutrient Relations

Plant nutrition can have substantial influence on growth through effects on total leaf area, specific leaf mass, and net photosynthesis (Linder & Rook 1984; Hirose 1987, 1988a,b; Walters & Reich 1989; Konings 1990; McDonald 1990). Based on a comprehensive set of inter- and intra-specific comparisons, Field & Mooney (1986) concluded that there exists a direct and general correlation between foliar N and net photosynthesis (A) that is largely independent of species and environmental conditions. The correlation is generally higher when expressed on a leaf mass basis than when it is expressed on a leaf area basis (Field & Mooney 1986). The causal relationship between foliar N and A is based on the high

correlation between foliar N and both photosynthetic enzymes and chlorophyll content (Field & Mooney 1986; Evans 1989; Sinclair & Horie 1989; Evans & Seemann 1989). Karlsson & Nordell (1988) observed a strong linear relationship between leaf N and A ($r=0.71$) in mountain birch (*Betula pubescens*).

In this study, there was no significant relationship between foliar N and A during 1988 (on either a leaf area or leaf mass basis) (Table 4). However, during 1989, there was a significant correlation on both a leaf area basis ($r=0.29$) and a leaf mass basis ($r=0.40$) (Table 4). A closer examination of the 1988 data suggests that the relationship between N_{mass} and A_{mass} was masked by stomatal limitations to A . When trees exhibiting stomatal limitations to A (C_i/C_a ratios below 0.6) are removed from the analysis, the correlation between N_{mass} and A_{mass} is significant (r increases from 0.15 to 0.40 in 1988, and from 0.40 to 0.56 in 1989) (Figure 14). Field & Mooney (1986) also noted that stomatal limitations add variation to the relationship between foliar N and A .

While phosphorus has been shown to limit the growth and photosynthesis of a number of species (e.g. DeJong 1982; Wong et al. 1985; Sharkey 1985; Sivak & Walker 1986; Brooks 1986; Robinson & Gieresch 1987; Black 1988; Israel & Rufty 1988; DeLucia et al. 1989; Lauer et al. 1989; Chapin et al. 1989; Houman et al. 1990; Kirschbaum & Tompkins 1990), the effects of N are generally considered to be more pronounced (Nátr 1975; Chapin 1980a). In this study, P_{mass} was more highly correlated with growth, A , individual leaf size, and total leaf area than was nitrogen, during both 1988 and 1989 (Table 4) (Figure 15). These data suggest that the trees were more limited by P than N. Safford (1982) and Chapin et al. (1983) also found paper birch to be limited by P, and Perala & Alm (1990) consider *Betula* species, as a group, to be generally more limited by P than N. Phosphorus was also found to limit the growth and/or photosynthesis of *Pinus radiata* (Sheriff et al. 1986) and *Pinus strobus* (Reich & Schoettle 1988) more than N.

Several factors may have contributed to the higher correlation between foliar P and A . As the growth rate of *Betula pendula* slows, its requirement for P increases proportionally more than its requirement for N (Ericsson & Ingestad 1988). The same may be true of *Betula papyrifera*. Additionally, the plants experiencing stomatal limitation to photosynthesis (C_i / C_a ratios below 0.6) generally had low foliar P concentrations (Figure 17). Removing stomatically limited trees from the analysis only increased r from 0.41 to 0.50 in 1988. A number of studies have found plant concentration and uptake of P to be correlated with soil moisture (reviewed in Viets 1972) and stomatal conductance (Terry & Ulrich 1973; Clarkson & Scattergood 1982; Sheriff et al. 1986). Both the rate of diffusion of P through the soil to the roots and P availability to the plant declines as the soil dries (Viets 1972).

Leaf Area

The significant effects of fertilization on foliar N concentrations did not translate into significant effects on growth and photosynthesis. Plants may demonstrate physiological and morphological plasticity in a number of traits, allowing them to compensate, at least in part, for growth limiting conditions (Grime et al. 1986; Hirose 1987; McDonald 1990). In particular, plants have often been observed to increase their SLM in response to nutrient deficiency (Gulmon & Chu 1981; Waring et al. 1985; McDonald et al. 1986; Jurik 1986a; Sage & Pearcy 1987; Hirose 1986, 1987; McDonald 1990). Empirically based models of Hirose (1986, 1987) show that specific leaf mass is an important variable controlling growth rate ($RGR = NAR * LWR / SLM$). Increasing SLM can have the effect of concentrating nutrients on a leaf area basis and thus increasing A_{area} (Mooney et al. 1978; Gulmon & Chu 1981; Jurik 1986a; Hirose 1987). However, there is a tradeoff

between SLM and leaf area (assuming the allocation of resources to leaf biomass remains constant) (e.g. Mooney et al. 1978; Gulmon & Chu 1981; Garnier et al. 1989). Hirose (1987) has shown that plants can minimize the effect of nutrient deficiency on RGR by increasing SLM to an optimal value.

The data of this study are consistent with the model of Hirose (1987). As N_{mass} decreased, SLM increased during both 1988 ($r = -0.33$) and 1989 ($r = -0.39$) (Table 4). Associated with increased SLM, were increased N_{area} ($r = 0.57$ and 0.67 in 1988 and 1989, respectively) and P_{area} ($r = 0.40$ and 0.44 in 1988 and 1989, respectively) (Table 4), indicating that nutrients were being concentrated on a leaf area basis. An increased N_{area} was associated with an increase in A , during 1989 ($r = 0.29$) (due to stomatal limitations on photosynthesis, this relationship was not significant in 1988). *Ulmus americana* seedlings respond to changes in soil fertility in a similar manner (Walters & Reich 1989).

There was a negative correlation between SLM and total leaf area, during both 1988 ($r = -0.42$) and 1989 ($r = -0.56$) (Table 5). This is consistent with the existence of a trade-off in the allocation of carbon between thicker leaves at the expense of increased leaf area. Growth simulation models for corn and soybean indicate that trade-offs also exist in the allocation of nitrogen (Sinclair & Horie 1989). Nitrogen can be increasingly allocated to leaf growth, resulting in the construction of large leaf area which intercepts more radiation, or N may be concentrated in a smaller leaf area, maximizing photosynthetic rates (e.g. Sage & Pearcy 1987). In the model of Sinclair & Horie 1989, for a given level of total plant N, there was an optimum leaf N concentration at which biomass accumulation was maximal.

Many species have been shown to increase their root:shoot ratios in response to decreased nutrient availability (Gulmon & Chu 1981; Waring et al. 1985; Hirose 1987; Walters & Reich 1989; Kachi & Rorison 1989; Chapin 1991), including *Betula*

pendula (McDonald et al. 1986) Furthermore, most plants increase their potential to absorb nitrogen on a per gram of root basis, when growing under nutrient limiting conditions (Lee & Rudge 1986; Rufty et al. 1990; Chapin 1991). Together, these plastic responses increase the total plant N content (Hirose 1987). The increased N could be used to increase leaf area (with decreased concentrations of photosynthetic enzymes) or to increase foliar N concentrations and thus rates of photosynthesis (at the expense of total leaf area) (e.g. Sinclair & Horie 1989).

During 1989 (after two years of fertilization treatments), in response to decreasing level of nitrogen fertilization, there was observed: 1) a decrease in foliar N_{area} , 2) a decrease in net rate of photosynthesis, and 3) a greater percent increase in leaf area from 1988 to 1989 (Table 5, Figure 9). No measurements of allocation to root production or root activity were made in this study. However, these results are consistent with plastic responses which increase the rate of nutrient uptake in response to decreased soil fertility, resulting in increased leaf area at the expense of an increased rates of photosynthesis. This may be an especially valuable plastic response for trees with initially low total leaf area. There was a logarithmic relationship between total leaf area and growth (Figure 5), but an exponential relationship between photosynthesis and growth (Figure 6). Thus, increased leaf area has a much stronger effect on the growth rate of slow growing trees than does an increased rate of photosynthesis.

Nutrient Use Efficiency

Nutrient use efficiency (NUE) has been defined as the quantity of dry matter produced per unit of nutrient acquired by the plant (Chapin 1980a), and is a function of: 1) the length of time a unit of nutrient is retained by the plant, and 2)

the instantaneous rate of carbon fixation per unit of nutrient in the plant (Berendse & Aerts 1987; Aerts 1990). There appear to exist fundamental physiological constraints between these two components, such that one can be increased only at the expense of the other (Berendse & Aerts 1987; Aerts 1990).

The overall NUE of plants generally increases as nutrient availability decreases (Chapin 1980a; Vitousek 1982; Boerner 1984; Birk & Vitousek 1986; Walters & Reich 1989). Boerner (1984) found that the four deciduous tree species, *Quercus prinus*, *Q. alba*, *Acer rubrum*, and *Fagus grandifolia* all were able to maintain constant growth rates by increasing their NUE as soil fertility decreased.

Photosynthetic nutrient use efficiency (photosynthetic rate per unit of nutrient in the foliage) is one component of NUE (Field & Mooney 1986; Chapin et al. 1987; Chapin 1988). During both 1988 and 1989, there was a strong positive correlation between net photosynthesis and both photosynthetic nitrogen use efficiency (PNUE) and photosynthetic phosphorus use efficiency (PPUE) (Table 4). This seems to be a general pattern both between and within species (Gulmon & Chu 1981; Field & Mooney 1986; Chapin et al. 1987), and may result because plants invest an increasingly greater proportion of their total nutrients into photosynthetic enzymes and other photosynthetic apparatus as their nutrient content increases (Evans 1989). Leaves with low N may have a greater proportion of their N in nonphotosynthetic components such as structural protein, regulatory and respiratory enzymes, nucleic acids (Chapin et al. 1987), and nitrogen containing compounds that generally accumulate in response to nutrient deficiency (Rabe 1990).

Many studies have reported PNUE to increase with increasing foliar N, both within and among species (Field & Mooney 1986; Hirose & Werger 1987; Sage & Pearcy 1987; Chapin 1988). However, other studies have found PNUE to be inversely correlated with nutrient availability, thus contributing to the higher level of overall NUE generally observed of plants growing in low fertility soils (Birk &

Vitousek 1986; Reich et al. 1989). In this study, PNUE was inversely correlated with N_{area} ($r = -0.45$ in 1988 and -0.51 in 1989) and SLM ($r = -0.40$ in 1988 and -0.52 in 1989) (Table 4). Thus, PNUE was the lowest when N was concentrated within dense leaves. This may result if the proportion of total leaf N invested in photosynthetic enzymes decreases as leaves become more dense (Field & Mooney 1986). Alternatively, this can result from inefficient allocation of nitrogen (Field & Mooney 1986). Nitrogen may occur in relative excess if some other rate-limiting factor such as phosphorus is deficient (Israel & Rufty 1988; Reich et al. 1989). There was a negative correlation between PNUE and foliar P_{mass} during both 1988 ($r = -0.34$) and 1989 ($r = -0.41$), suggesting that a P deficiency was limiting the efficient use of N in photosynthesis (Table 4). During 1988 and 1989, SLM was positively correlated with P_{area} but negatively correlated with P_{mass} , indicating that P was being concentrated on an area basis as P concentrations dropped (Table 4). Reich and Schoettle (1988) also observed a negative correlation between PNUE and foliar N in *Pinus strobus* as a result of P deficiency.

Reich et al. (1989) also found a negative correlation between N_{area} and PNUE for *Ulmus americana*, and suggest that optimal utilization of leaf N in photosynthesis results from the production of more leaves with lower N contents as opposed to fewer leaves with higher N contents. Their hypothesis is supported in this study by negative correlations between N_{area} and both PNUE and total leaf area in 1989 ($r = -0.42$), and positive correlations between PNUE and both total leaf area and growth (Table 4).

Phenological Patterns

Foliar concentrations of N and P decreased over the season (Figure 17). This is a widely reported pattern, resulting from dilution as leaf biomass increases, and resorption of nutrients for translocation to new foliage and for dormant season storage (Verry & Timmons 1976; Bowersox & Ward 1977; Chapin et al. 1980; Field 1983; Chapin & Tyron 1983; Chapin & Kedrowski 1983; Boerner 1984; Kost & Boerner 1985; Mattson & Scriber 1987). Specific leaf mass steadily increased and leaf water content decreased, over the course of the season, during 1988 and 1989 (Figure 18). This pattern occurs in many species (Field & Mooney 1983; Reddy et al. 1989). However, Jurik (1986a) found the SLM of paper birch and several other deciduous trees to remain relatively constant over the season. An increase in SLM results as leaves accumulate biomass, often in the form of secondary cell wall structure, starch, and secondary metabolites (Feeny 1970; Coley 1983; Mattson & Scriber 1987; Reddy et al. 1989).

During 1989, net photosynthesis declined over the course of the summer. This pattern has been observed before, and corresponds with the decline in concentrations of foliar N and photosynthetic enzymes (Field 1983; Field & Mooney 1983). However, Jurik (1986b) found photosynthesis in paper birch to remain constant over the course of the season until leaves senesced in Autumn. During 1988, photosynthesis declined from 22 July to 29 July, and then increased over the rest of the season. The pattern of photosynthesis may have been affected more by environmental than phenological patterns. July of 1988 was characterized by high temperatures and low humidity, factors that are known to have adverse effects on photosynthesis (Berry & Downton 1982; Farquhar & Sharkey 1982; Hanson & Hitz 1982; Schulze 1986). When photosynthesis was measured on 29 July, air temperature was 34°C and relative humidity was less than 50%. However,

environmental conditions were more favorable when photosynthesis was measured on 12 August and 8 September. On both dates, air temperature was less than 25°C and relative humidity was greater than 60%.

Tree Response to Defoliation

Severe defoliation decreases the radial growth of trees in proportion to the degree of defoliation received (Kozlowski 1969; Kulman 1971; Ericsson et al. 1980b). However, trees may compensate for less severe defoliation. Artificial defoliation resulting in 50% leaf area removal significantly decreased the growth of *Quercus suber* (Magnoler & Cambini 1970). However, partial artificial defoliation of *Quercus robur* (33%) (Hilton et al. 1987) and *Populus* spp. (50%) (Gao et al. 1985) had no effect on growth. Miller & Wagner (1989) also found that the growth reduction in *Pinus ponderosa* in response to defoliation by the pandora moth (*Coloradia pandora*) was not proportional to the amount of defoliation received.

In this study, artificial defoliation during 1987 and 1988 (decreasing leaf area about 40% at the time of defoliation), had no effect on growth during 1987, 1988, or 1989. Plants may ameliorate the effects of defoliation (at least in part) through compensatory responses (Mattson & Addy 1975; McNaughton 1983). In response to defoliation, the rate of photosynthesis generally increases in the remaining leaves, at least in the short term (Wareing et al. 1968; Bassman & Dickmann 1982, 1985; Heichel & Turner 1983; Stafford 1989). Increased photosynthesis in defoliated plants may result from higher levels of carboxylating enzymes (Wareing et al. 1968; Kolodny-Hirsch 1986; Welter 1989), increased stomatal conductance (Turner & Heichel 1977; Heichel & Turner 1983), improved water balance (Stephens et al. 1972; Ericsson et al. 1980a), increased light penetration within the canopy (Welter

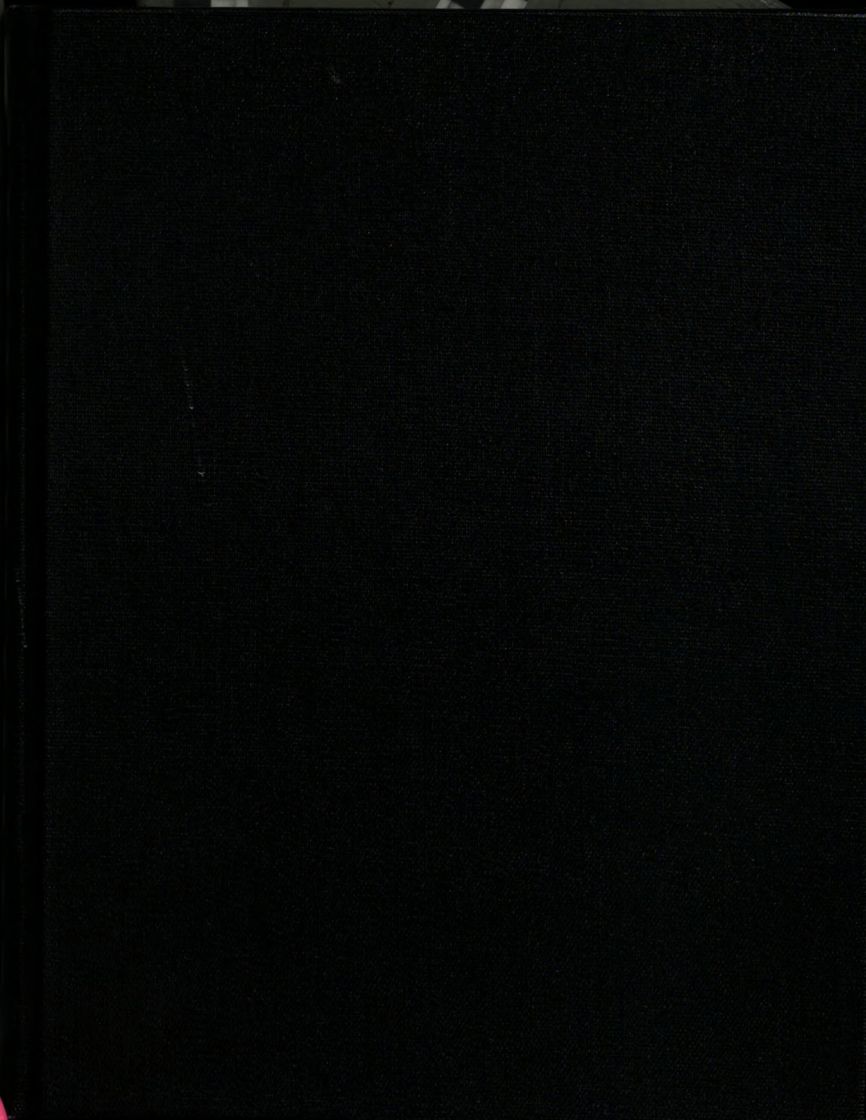
1989), and enhanced nutrient availability from defoliation-induced increases in the rate of nutrient cycling (Mattson & Addy 1975; McNaughton 1983). Photosynthesis was increased 63% in mountain birch trees (*Betula pubescens*) that had been defoliated the previous year, as compared with undamaged trees (Prudhomme 1982).

In response to defoliation, plants may also increase the proportion of resources they allocate to the production of new leaf area (Bassman & Dickmann 1982,1985; Brown & Ewel 1988; Stafford 1989). Deciduous trees often refoliate following severe early season defoliation (>50-75%) (Heichel & Turner 1976; Herms et al. 1987). Stored carbon is mobilized for use in the construction of the new canopy (Wargo et al. 1972). However, carbohydrate reserves can be replenished by the new canopy following refoilation (Parker 1981; Herms et al. 1987).

In this study, defoliation had no significant effects on photosynthesis. However, the mean rate of photosynthesis was higher in the defoliated trees during 1988 on every date measured. The difference was largest on 22 July, the first date measured (12.9 ± 0.9 vs. $11.3 \pm 0.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the defoliated and nondefoliated trees, respectively) ($P=0.13$). The difference between the means then decreased steadily with each sampling date. Bassman & Dickmann (1985) found that the defoliation-induced increases in the photosynthesis of *Populus x euramericana* were no longer detectable after five weeks. In this study it is conceivable that defoliation increased photosynthesis, and that this increase may have been detectable if photosynthesis measurements had been made earlier in the season and/or sampling had been replicated to greater degree.

Water / Nutrient Interactions

Soil fertility and soil moisture can interact significantly to affect plant growth and performance (Chapin et al. 1987). Increased soil fertility can increase water use efficiency (Linder & Rook 1984; Brix & Mitchell 1986), but also increase plant susceptibility to the effects of drought stress, by increasing leaf area and decreasing root:shoot ratios (Linder & Rook 1984; Landsberg 1986; Linder et al. 1987). Irrigation and fertilization can act synergistically to increase the growth of plants (Brix 1972; Axelsson & Axelsson 1986; Raison et al. 1990). However, in this study there was no discernable pattern of interaction between any of the main effect factors.



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**VARIATION IN THE RESOURCE ALLOCATION PATTERNS
OF PAPER BIRCH: EVIDENCE FOR PHYSIOLOGICAL TRADE-OFFS
AMONG GROWTH, REPRODUCTION, DEFENSE**

VOLUME II

By

Daniel Albert Herms

A DISSERTATION

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CHAPTER THREE

Variation in the Resource Allocation Patterns of Paper Birch: Induced and Constitutive Resistance to Gypsy Moth

Host quality plays a central role in plant resistance to herbivores, and may be an important factor associated with population outbreaks of phytophagous insects (Mattson & Addy 1975; Feeny 1976; Rhoades & Cates 1976; Bryant & Kuropat 1980; Rhoades 1983; T.C.R. White 1984; Coley et al. 1985; Mattson & Haack 1987a,b). Phytophagous insects are frequently limited by the nutritional quality of their host; nitrogen content is especially critical (T.C.R. White 1974,1978,1984; McNeill & Southwood 1978; Mattson 1980; Brodbeck & Strong 1987). Plant secondary chemistry also affects herbivore performance; the defensive role of secondary metabolites against herbivores is well documented (Levin 1976b; Swain 1977; Bryant & Kuropat 1980; Rhoades 1985; Coley et al. 1985; Williams et al. 1989; Harborne 1990). The toxic and deterrent effects of secondary metabolites may be the primary reasons why plants are resistant to the vast majority of herbivores (Bryant & Kuropat 1980; Dethier 1980; Bernays & Chapman 1987). However, other insects have adapted to their host plant's unique secondary metabolites, using them as host-finding/acceptance cues and/or sequestering them for their own defense, (Dethier 1980; Carroll & Hoffman 1980; Blum 1983; Miller & Strickler 1984; Tahvanainen et al. 1985; Metcalf 1986; Pasteels et al. 1988; Bowers 1988;

Tallamy & Krischik 1989).

Phenolic compounds are a prominent class of putative defensive compounds, especially in deciduous trees (Swain 1979). Correlative and *in vitro* studies led to the early conclusion that tannins and other high molecular weight phenolics represent generalized defenses, acting in a dosage dependent manner to form insoluble, digestion-inhibiting complexes with proteins and carbohydrates (Feeny 1969,1970,1976; Levin 1976b; Rhoades & Cates 1976; historical reviews in Schultz 1989 and Bernays et al. 1989). Limited experimental evidence supports this hypothesis in the case of ruminants (e.g. Robbins et al. 1987). However, the case for plant phenolics as non-specific, digestion-inhibiting defenses against insects in general, is no longer tenable (Bernays 1981; Martin et al. 1985,1987; Bernays et al. 1989). A number of studies found no correlation between plant phenolic concentrations and insect performance (e.g. Fox & Macauley 1977; Bernays 1978; Lowman & Box 1983; Lawson et al. 1982; Smiley & Wisdom 1985). Explanations include larval adaptations within the midgut, such as an elevated pH, and the presence of surfactants, which may inhibit tannins from forming insoluble complexes with dietary proteins or digestive enzymes (Berenbaum 1980; Martin & Martin 1983,1984; Martin et al. 1985,1987; Schultz & Lechowicz 1986). In other cases, insects can apparently utilize phenolic compounds as nutrients (Kato 1978; Bernays & Woodhead 1982; Bernays et al. 1983).

However, negative effects of phenolics on insects are well documented; although, they generally act as deterrents or post-digestive toxins rather than as digestion inhibitors (Bernays 1978; Reese et al. 1982; Klocke & Chan 1982; Lincoln et al. 1982; Berenbaum 1983b; Manuwoto et al. 1985; Lincoln 1985; Manuwoto & Scriber 1986; Rossiter et al. 1988; Karowe 1989; reviewed in Bernays et al. 1989 and Schultz 1989). Despite the substantial caveats against the sweeping generalizations once made regarding the defensive role of phenolic compounds, it is still generally

acknowledged that phenolics represent an important class of compounds protecting plants from herbivores and pathogens (Bernays et al. 1989; Schultz 1989).

Phenotypic Variation in Defense: Constitutive Resistance

Outbreaks of folivorous insects have been correlated historically with plant stress, including drought and nutrient deficiency (Mattson & Addy 1975; Rhoades 1983; T.C.R. White 1974,1984; Waring & Pitman 1985; Mattson & Haack 1987a,b). Some have proposed that stress increases the nutritional quality and/or compromises the chemical defenses of plants (Rhoades 1983; T.C.R. White 1984; Waring & Pitman 1985; Brodbeck & Strong 1987). However, Larsson (1989), after a critical review of the literature, found little sound experimental evidence to support this hypothesis. In fact, many studies have found that concentrations of secondary metabolites often increase in response to drought or nutrient limitation (reviews in Gershenzon 1984, Mattson & Haack 1987a,b, and Waterman & Mole 1989). Several studies have also shown that plant resistance to herbivores increases in concert with environmentally-induced increases in secondary metabolite concentrations (Larsson et al. 1986a; Mihaliak et al. 1987; Bryant 1987; Bryant et al. 1987a,b; Lightfoot & Whitford 1987,1989).

However, severe and prolonged stress debilitates photosynthesis as well as growth, often resulting in low concentrations of secondary metabolites and consequently compromised defense against herbivores (Waring & Pitman 1985). Thus, variation in plant resistance to herbivores in response to stress may be nonlinear; plants under moderate stress may be most resistant, while plants at either end of the stress continuum may be less resistant (Figure 1, Chapter 1) (Mattson & Haack 1987a,b; Horner 1990).

Phenotypic Variation in Secondary Metabolism: Two Hypotheses

To explain phenotypic patterns in secondary metabolism, Bryant et al. (1983) proposed the carbon/nutrient (C/N) balance hypothesis, which predicts that the concentration of carbon-based secondary metabolites (e.g. phenolic and terpenoid compounds) is a function of the C/N balance within the plant. It is based upon the premise that plant growth processes are slowed more by nutrient deficiency than is photosynthesis (e.g. Chapin 1980a; McDonald et al. 1986; Dietz 1989). Hence, nutrient limited plants can accumulate carbohydrates in excess of growth requirements, which are subsequently allocated to the production of secondary metabolites. Thus, concentrations of carbon-based secondary metabolites should be inversely correlated with the nutrient concentration and growth rate of the plant. The correlative and experimental evidence supporting this hypothesis is substantial (Waterman & Mole 1989).

The Growth/Differentiation (G/D) balance hypothesis presents a similar but broader explanation for phenotypic patterns in secondary metabolism (Loomis 1932,1953; Lorio 1986,1988). Plant activity at the cellular level can be classified as either growth (cell division and enlargement) or differentiation (chemical and morphological changes leading to qualitative differences among cells and cell specialization) (Loomis 1932,1953; Salisbury & Ross 1978; Wareing & Phillips 1981; Lorio 1986,1988). The fundamental premise of the G/D balance hypothesis is the existence of a negative correlation between the allocation of resources to growth and those allocated to differentiation processes (including secondary metabolism), because of physiological constraints on secondary metabolism in dividing cells, and the high level of resource required to support growth (see Chapter 1 for more detailed discussion and complete citations). Increased growth will decrease the allocation of resources to differentiation processes. Any factor that limits growth

more than photosynthesis, be it nutrient limitation (Chapin 1980a; McDonald et al. 1986; Dietz 1989), or moderate drought (Bradford & Hsiao 1982; Sharpe et al. 1985; Daie 1988), will increase the supply of photosynthates available to support secondary metabolism and other differentiation processes (Loomis 1932,1953; Lorio 1986,1988).

Phenotypic variation in secondary metabolism may represent an adaptive use of limited resources. Increased allocation to secondary metabolism in response to drought or nutrient deficiency may enhance defense (or other stress survival responses) when the plant has limited ability to compensate (via growth) for herbivory (del Moral 1972; Gershenzon 1984). Increased secondary metabolism under growth limiting conditions may represent an allocation alternative to increased carbohydrate storage. Hence, there may be a trade-off between the protection of resources at present and the acquisition of resources in the future. Allocation theory predicts that increased secondary metabolism will be favored when that investment enhances plant fitness to a degree greater than would the same resource investment in an alternative process such as carbohydrate storage or growth. On the other hand, the C/N balance hypothesis assumes that phenotypic patterns of secondary metabolism represent inevitable responses to alterations in the C/N balance within the plant.

A prediction fundamental to both the G/D and C/N balance hypotheses is the existence of trade-off between growth and secondary metabolism. When growth is limited by nutrient deficiency, the predictions of the two hypotheses are identical. However, the G/D hypothesis is more general, addressing any factor that affects the G/D balance of the plant. Constitutive levels of carbon-based secondary metabolites may not generally correlate with the C/N balance of the plant when the C/N balance is affected by environmental factors other than soil fertility, such as enhanced CO₂ or drought (see Chapter 1 for citations). Water stress limits carbon

acquisition more than nutrient uptake (Viets 1972; Bloom et al. 1985; Mattson & Haack 1987a). Hence, the C/N balance of drought stressed plants should be lower than that of well-watered plants. Therefore, the C/N balance hypothesis predicts that concentrations of carbon-based secondary metabolites should also be lower in drought-stressed plants, while the G/D balance hypothesis predicts the opposite.

The generality of the two hypotheses could be tested by simultaneously manipulating soil fertility and soil moisture, and quantifying photosynthesis, growth, secondary metabolism, and nutrient concentrations. This study represents the first such test.

Phenotypic Variation in Defense: Inducible Resistance

Inducible resistance may be another form of adaptive phenotypic plasticity in plant defense (Harvell 1990). If chemical defenses against herbivores are metabolically expensive to plants, then it would be advantageous for plants to be less well defended when herbivores are absent than when plants are subject to herbivory (Haukioja 1982; Edwards & Wratten 1983; Harvell 1990). Indeed, many species of plants have been shown to increase their concentrations of foliar secondary metabolites and/or become less suitable for herbivores in response to foliar injury (reviewed in Rhoades 1985; Schultz 1988; Wagner 1988; Wratten et al. 1988; Karban & Myers 1989; Harvell 1990; Haukioja 1991).

Defoliation of mountain birch (*Betula pubescens*) induces a two-component response. Rapidly-induced resistance (RIR) is triggered within hours or days of injury but relaxes within a few weeks (Haukioja & Niemelä 1976; Haukioja 1980, 1982, 1991; Haukioja et al. 1985b; Hanhimäki 1989). Delayed induced resistance (DIR) appears in the year following defoliation, and may last three or

more years before relaxing (Haukioja 1980,1982; Haukioja & Neuvonen 1985a; Haukioja et al. 1985b; Neuvonen et al. 1987,1988). Both components are usually sublethal, resulting in reduced growth rates, higher probability of mortality, lower pupal masses, and reduced fecundity of insects feeding on the foliage (Haukioja & Niemelä 1976,1979; Haukioja 1980,1982; Haukioja et al. 1985b). These effects were correlated with increased concentrations of foliar phenolic compounds (Niemelä et al. 1979; Tuomi et al. 1984; Haukioja & Hanhimäki 1985). Rapid damage-induced decrease in host quality and/or increases in secondary metabolism have also been demonstrated in paper birch (*Betula papyrifera*) (Talhouk et al. 1990) and European white birch (*B. pendula*) (Wratten et al. 1984; Bergelson et al. 1986; Hartley & Lawton 1987; Silkstone 1987; Hartley 1988; Hartley & Firn 1989).

Delayed Inducible Resistance and Insect Outbreaks

DIR and its subsequent relaxation may be a density dependent factor capable of regulating the population cycles of some outbreak folivores (Haukioja & Hakala 1975; Haukioja 1980,1982; Schultz & Baldwin 1982; Haukioja et al. 1983,1985b; Rhoades 1985; Haukioja & Neuvonen 1987; Edelstein-Keshet & Rausher 1989; Haukioja 1991). This hypothesis is based on the following logic. As the herbivore population increases and the level of defoliation experienced by the tree increases, the strength of DIR also increases. The adverse effects of DIR on insect performance cause the insect population to decline. Foliage quality eventually improves as defoliation subsides, and DIR relaxes, releasing the insect from constraints upon population growth imposed by poor host quality.

Mattson et al. (1988) predicted that DIR is especially likely to evolve in species that form mono- or oligo-specific communities in resource-rich

environments; paper birch commonly does so following fire, and thus may be predicted to evolve DIR. Deciduous trees with adequate carbon and nutrient reserves can often tolerate even severe defoliation with relatively minimal impact (Kulman 1971; Chapin 1980b; Herms et al. 1987). Hence, compensatory responses may be especially strong in fast growing species inhabiting resource-rich sites (Mattson et al. 1988; van der Meijden et al. 1988; Chapin & McNaughton 1989). However, compensation is generally not complete (Mattson et al. 1988; Veerkar 1988), and moderate to severe defoliation generally decreases growth (Kulman 1971).

Defoliation may affect plant fitness most profoundly by decreasing competitive ability (Harper 1977; Fox & Morrow 1986; Louda et al. 1990). In diverse plant communities, the population fluctuations of the various specialist herbivores associated with each plant species are likely to be asynchronous. Consequently, herbivory will be distributed unequally among species (Mattson et al. 1988). The competitive status of species receiving high levels of herbivory will decline relative to those receiving low levels. However, in mono- and oligo-specific plant communities, competition will be largely intra-specific. Furthermore, since all individuals share the same suite of herbivores, defoliation is more likely to be distributed equally among individuals, and is not as likely to affect the relative competitive status of individuals; the effect of defoliation-induced competitive superiority on the differential reproduction of different genotypes will not be a factor.

In resource-rich environments, high constitutive levels of defense will not be favored (even if intra-specific genetic variation exists), because the concomitant trade-off with growth will decrease the competitive ability of defended genotypes (Coley et al. 1985; Mattson et al. 1988). As an alternative strategy, Mattson et al. (1988) hypothesized that defoliation will select for compensatory traits coupled with

DIR. The delayed density dependent effects of DIR will cause outbreak populations to decline before sustained defoliation seriously debilitates the plant. Furthermore, DIR will have no negative effects on plant fitness in the absence of herbivores. Consistent with this hypothesis, the existence of DIR has been demonstrated experimentally in paper birch (*Betula papyrifera*) (Werner 1979), grey birch (*B. populifolia*) (Wallner & Walton 1979), and mountain birch (*B. pubescens*) (Haukioja 1982; Haukioja & Neuvonen 1985a; Haukioja et al. 1985b; Neuvonen et al. 1987).

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

Is DIR an evolutionary response to herbivory or an incidental consequence of defoliation-induced alterations in the physiology of the plant (Haukioja & Niemelä 1976,1979; Rhoades 1979; Haukioja 1980,1991; Tuomi et al. 1984,1988a,b,1991; Haukioja & Neuvonen 1985a; Bryant et al. 1988,1991; Schultz 1988)? Tuomi et al. (1984,1988a,b,1991) and Bryant et al. (1988,1991) postulated that DIR may be an incidental response of defoliation-induced alterations in the C/N balance of the plant ("incidental effect" hypothesis), rather than an evolved defense against outbreak insects ("evolved defense" hypothesis). For example, during the growing season, most of the nutrient capital of deciduous trees is contained within the foliage. Much of the carbon reserves, however, remain in the roots and other woody tissues. Consequently, defoliation of deciduous trees can result in the loss of proportionally more nutrients than carbon, and thus a relative nutrient deficiency in the plant (Tuomi et al. 1984; Bryant et al. 1991). The result may be an increased C/N ratio, and increased allocation to carbon-based secondary metabolites in subsequent years (Bryant et al. 1988, 1991; Tuomi et al. 1984,1988a,1991).

Divergent predictions can be derived from the two hypotheses. The active

defense hypothesis predicts that the presence of DIR should correspond with a plant's evolutionary history of herbivory; the C/N balance hypothesis predicts DIR should be independent of historical patterns of herbivory (Bryant et al. 1991). The C/N balance 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. 1985b; Tuomi et al. 1988a). Tuomi et al. (1988b, 1991) argue that because of the semi-autonomous nature of plant modules (Watson & Casper 1984), the C/N balance 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 C/N balance hypothesis (Haukioja & Neuvonen 1985a; Haukioja et al. 1985b).

Tests of these hypotheses have yielded support for both. Consistent with the C/N Balance 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 et al. 1988b); 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 the opposite of 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 & Neuvonen 1985a; Haukioja et al. 1985b); 3) defoliation of mountain birch by *E. autumnata* resulted in stronger DIR than artificial defoliation (Haukioja & Neuvonen 1985a); 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).

Gypsy Moth as an Outbreak Species

Since its introduction from France sometime in the late 1860's, the gypsy moth (*Lymantria dispar* (L.)) has become the most important defoliator of deciduous trees in North America (Leonard 1974; Montgomery & Wallner 1988; Elkinton & Liebhold 1990). Gypsy moth populations in New England fluctuate between endemic and epidemic phases (Campbell & Sloan 1977a,b;1978). Factors thought to regulate gypsy moth populations include parasites, predators, pathogens, the availability of pupation sites, host condition, and climate (Campbell & Sloan 1977a,b;1978; Elkinton & Liebhold 1990).

Foliage quality and DIR may also play a role in regulating gypsy moth populations (Schultz & Baldwin 1982; Montgomery & Wallner 1988; Elkinton & Liebhold 1990). Defoliation of gypsy moth hosts can result in increased concentrations of phenolic compounds (Schultz & Baldwin 1982; Rossiter et al. 1988) and decreased levels of nutrients (Valentine et al. 1983). These two responses may be responsible for the observed decline in gypsy moth larval performance (growth rate, pupal mass) when feeding on foliage of trees defoliated the same season (Rossiter et al. 1988), and during the previous year (Wallner & Walton 1979;

Valentine et al. 1983).

Gypsy moth was first detected in Michigan in 1954 and existed at low levels until recently (Hanna 1982). It is now well established throughout the Lower Peninsula, causing widespread annual defoliation (*personal observation*). Paper birch has been classified as a preferred host of gypsy moth in New England (Houston 1979; Montgomery & Wallner 1988), and is also an important host in Michigan (*personal observation*). Gypsy moth has not been established in Michigan long enough to determine how populations may cycle or what the important population-regulating factors are likely to be.

Objectives

This study was undertaken to evaluate phenotypic variation in both the constitutive and inducible resistance (RIR and DIR) of paper birch to gypsy moth, in response to three levels of nitrogen fertilization and irrigation, and two levels of defoliation. To test for a trade-off between growth and defense, gypsy moth performance was examined relative to tree growth, and foliar nutrient and total phenolic concentrations.

METHODS AND MATERIALS

Experimental Design and Treatments

The experimental site, trees, treatments, design, and plant physiological measurements were described in Chapter 2. Additional methods are reported below.

Phytochemistry

General foliage sampling procedures followed Chapter 2. The dates of sampling coincided with gypsy moth feeding experiments: during 1988, samples were taken 9 June (to coincide with the fourth instar feeding trial), and 15 July (as insects were beginning to pupate in the field) to be representative of foliage consumed by late instars in the field study; during 1989, samples were taken 26 May (to coincide with the second instar laboratory experiment and the beginning of the field experiment), 6 June (to coincide with the fourth instar laboratory experiment), and 5 July (to coincide with the beginning of pupation in the field experiment). Foliage was also sampled on 24 August 1988 and 23 August 1989.

Methods for quantifying foliar water, nitrogen, and phosphorus followed Chapter 2. Total phenolic concentrations were analyzed colorimetrically using the Folin-Denis procedure with a tannic acid standard. Analysis of total sugars (glucose + sucrose + fructose) was performed simultaneously with phenolic analysis on the same extracts. Colorimetric analyses were performed on a Technicon Auto-Analyzer II using *D*-glucose as the standard. The analysis followed extraction of a 0.125 g sample of powdered foliage in 50% methanol.

Tree Phenology

Dates of first and full budbreak were recorded for all trees each year. Date of first budbreak was defined as the date that the first bud on the tree opened, exposing at least 50% of the length of the leaf lamina. Full budbreak was defined as the date on which about 95% of the buds on the tree had opened, exposing 50% of the length of the leaf lamina (i.e. about 1 out of 20 buds remained closed).

Insect Bioassay Experiments

1988 and 1989 Field Experiments

Gypsy moth larvae used in all experiments were obtained from the USDA Forest Service Gypsy Moth Rearing Laboratory in Hamden, Ct. Field experiments conducted during 1988 and 1989 were initiated with larvae obtained as newly molted second instars. Larvae were received on 1 June 1988 and 24 May 1989, and deployed in the field on the next day. During 1988, two larvae were contained on each of four branches per tree (eight larvae per tree) within a nylon mesh bag measuring 100 cm long by 115 cm in circumference. During 1989, three larvae were placed in each bag. When the rest of the tree received the artificially defoliation treatment, foliage on the four bagged branches was not damaged. Thus, larvae were initially exposed only to undamaged leaves.

Larvae were allowed to feed undisturbed within the bags until pupation. Bags were inspected daily, and pupae were removed as discovered, dried and weighed. Larval longevity (number of days until pupation) and pupal mass were recorded.

When measured on cloudless days, light intensity within bags was decreased

by about 30%, relative to ambient conditions. Decreased light intensity can have the effect of decreasing foliar phenolic concentrations (Mole & Waterman 1988; Mole et al. 1988). Rossiter et al. (1988) found that bagging did not affect phenolic concentrations in oak foliage when they rotated the bags to new branches on a weekly basis. Because of time and labor required to shift the large number of bags used in this study, bags were left in place for the duration of the experiment. The long-term effect of bagging on phenolic chemistry was tested during 1989. On 26 May (the day the field experiment was initiated), one branch was bagged on 10 of the extra trees that were not part of the experiment. No larvae were placed in these bags. On 12 July (as the larvae were pupating), 15 leaves were collected from within each bag. An additional 15 control leaves of the same age were sampled from throughout the rest of the canopy of each tree. The foliage samples were processed and analyzed for total phenolics as described previously.

1988 Laboratory Experiments

Newly molted fourth instars were received on 14 June 1988 for use in a laboratory feeding experiment. Larvae were individually confined to petri dishes (15 cm in diam., 5 cm tall) into which a plaster base had been poured. Water added to the plaster base provided a high humidity environment which maintained the turgor of detached leaves fed to larvae. Subsequent measurements showed that the fresh weight of leaves in these dishes did not change even after 72 hours. Larvae were reared in a growth chamber at 25°C, under a 18:6 light:dark cycle.

Upon receipt, three larvae were randomly assigned to each tree. Larvae were offered leaves from their assigned trees and allowed to feed for 24 hrs before the growth trials began. Larvae assigned to defoliated trees were always fed undamaged leaves. To standardize for the diurnal and phenological variation in phytochemistry that may occur in birch foliage (e.g Haukioja et al. 1978a,b; Raupp

& Denno 1983; Ayres & McLean 1987), leaves used in this and all subsequent laboratory experiments were always collected between 0700 and 0830 EST, and only leaves originating from overwintering buds were used.

After being allowed to feed for 48 hours, larvae were weighed again. Following termination of the 48 hr feeding trial, larvae were reared to pupation; foliage was changed at least every other day. Larval relative growths (RGR) ($\text{mg mg}^{-1} \text{ d}^{-1}$) were calculated both for the fourth instar feeding trial (RGR_4), and for the entire experimental period (beginning of fourth instar through pupation) (RGR_t) (see Table 7 for the formula used to calculate relative growth rate).

Larvae were inspected daily for pupation. Larval fresh weights were converted to dry weights by multiplying them by 0.17, a conversion factor determined from the fresh and dry weights of 50 sacrificial larvae. Upon hardening, pupae were oven-dried to constant mass, then weighed. Dry pupal mass (mg) and larval duration from beginning of fourth instar until pupation (days) were recorded.

1989 Laboratory Experiments

During 1989, the laboratory assay began with newly molted second instars, which were received from the USDA on 24 May. As in 1988, three larvae were assigned randomly to each tree. Rearing conditions were the same as described for 1988.

Upon receipt, larvae were allowed to feed for 24 hours before the second instar growth trial was initiated. Following this acclimatization period, all larvae were weighed. After feeding for 72 hours, larvae were weighed again, and relative growth rates for the second instar (RGR_2) were calculated. The experiment continued following the second instar feeding trial, and larvae were given fresh foliage at least every 48 hours. To maintain adequate replication, any larvae that died as second or third instars, were replaced in the experiment with larvae of the

Table 7. Summary of nutritional indices quantified in laboratory experiments. Calculations follow Ayres & McLean (1987), and incorporate minor modifications to those of Waldbauer (1968) and Slansky & Scriber (1982). All values are based on dry mass. Units are in parentheses.

$$\text{Relative Growth Rate (RGR)} = [\ln(\text{final mass}) - \ln(\text{initial mass})] / \text{time}$$

$$(\text{mg mg}^{-1} \text{ d}^{-1})$$

$$\text{Relative Consumption Rate (RCR)} = \text{consumption} / (\text{mean larval mass} * \text{time})$$

$$(\text{mg mg}^{-1} \text{ d}^{-1})$$

$$\text{Relative Frass Production (RFP)} = \text{frass} / (\text{mean larval mass} * \text{time})$$

$$(\text{mg mg}^{-1} \text{ d}^{-1})$$

$$\text{Relative Assimilation Rate (RAR)} = \text{RCR} - \text{RFP}$$

$$(\text{mg mg}^{-1} \text{ d}^{-1})$$

$$\text{Efficiency of Conversion of Ingested Matter (ECI)} = \text{growth} / \text{consumption}$$

$$(\text{mg/mg})$$

$$\text{Approximate Digestibility (AD)} = \text{assimilation} / \text{consumption}$$

$$(\text{mg/mg})$$

$$\text{Efficiency of Conversion of Digested Matter (ECI)} = \text{growth} / \text{assimilation}$$

$$(\text{mg/mg})$$

same cohort. Until they were introduced into the experiment, all replacement larvae were fed foliage from a common birch tree (one that was not part of the experiment), and were reared under the same conditions as the experimental larvae.

Larvae were weighed 24 hours after they molted the third time, marking the beginning of the fourth instar feeding trial. Larvae were then offered three freshly collected leaves. The combined area of the three leaves was determined with a leaf area meter (LiCor) before they were fed to larvae. After being allowed to feed for 48 hours, larvae were weighed again. Frass was collected, dried and weighed. The portions of the leaves not consumed were collected, and their cumulative area and dry mass determined. Initial dry mass was then calculated as:

$$\text{initial dry mass} = (\text{initial leaf area} * \text{final dry mass}) / \text{final leaf area}$$

Consumption was estimated gravimetrically by subtracting final dry mass from initial dry mass (see Table 7 for the calculation of nutritional indices). Following completion of the fourth-instar feeding trial, larvae were reared to pupation, and pupal mass and larval longevity were recorded.

Statistical Analysis

The results of the insect bioassays were analyzed with ANOVA, as described in Chapter 2. Individual trees were considered the experimental unit, with multiple observations (insects) per tree analyzed using a nested model. Relationships between dependent variables were examined with correlation analysis as described in Chapter 2. Unless explicitly stated, the tree-specific means of dependent variables measured repeatedly (e.g. foliar N and phenolics) were always used in

correlation analyses.

Gypsy moth display sexual dimorphism in size and instar number. Thus, treatment effects on male and female pupal mass and larval duration were analyzed separately for the field and laboratory experiments. However, sex-standardized values for pupal mass and larval duration were used in the correlation analyses to increase sample size and eliminate redundancy in data analyses. Male pupal mass was converted to the expected female equivalent by regressing the tree specific means of male pupal mass (X variable) against female pupal mass (Y variable). The regression equation generated from the analysis was used to calculate the predicted female equivalent from the known male pupal mass. Male larval duration was converted to the expected female equivalents in the same manner. Conversion equations were generated for each experiment separately.

RESULTS

Treatment, Growth, and Phenological Effects on Phytochemistry

Fertilization was the only treatment to substantially effect foliar nitrogen (Figure 9, Chapter 2). Irrigation had a marginally significant effect on total foliar phenolic concentrations during 1988 ($F=2.49$, d.f. = 2,54; $P<0.092$). Phenolic concentrations were highest in the most severely drought stressed trees (Figure 20). None of the treatments, including irrigation, had any effect on phenolics during 1989. The placement of mesh bags over branches also had no effect on foliar phenolic levels (phenolic concentrations were 12.6 ± 0.1 and 12.7 ± 1.1 %TAE in the bagged and unbagged foliage, respectively). None of the treatments had any effects on leaf water, phosphorus, or sugar content.

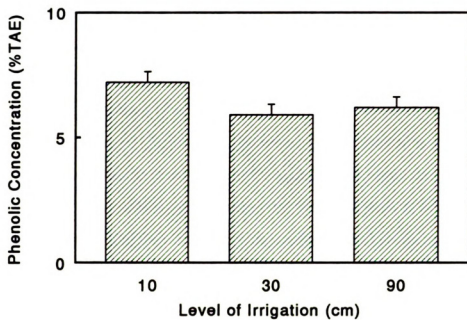
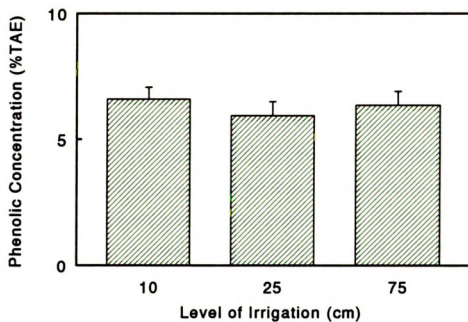
A**B**

Figure 20. Effect of irrigation on total foliar phenolic concentrations of paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

During both years, total phenolic concentrations were inversely correlated with tree growth (Figure 21), total leaf area (Figure 22), and foliar nitrogen concentrations (Figure 23). Total foliar phenolic concentrations changed significantly over the course of season during both 1988 and 1989. During 1988 there was a significant linear increase ($F = 16.3$, d.f. = 1,54; $P < 0.001$) in phenolic concentrations as leaves aged (Figure 24a). However, during 1989, when an additional sample was taken as leaves were still expanding (26 May), the pattern was different (Figure 24b). Phenolic concentrations were at a peak as leaf expansion was occurring, and then decreased into early July, before increasing into late summer. This cubic trend was significant ($F = 6.23$; d.f. = 1,47; $P = 0.016$).

Gypsy Moth Field Experiments

During both years, the survival of larvae within bags was poor (26% and 37% in 1988 and 1989, respectively). Stink bug (Pentatomidae) predation was the dominant source of mortality, obscuring treatment effects. During 1988, there was a significant effect of defoliation on male (but not female) pupal mass ($F = 6.19$; d.f. = 1,28; $P = 0.019$). The pupal mass of insects feeding on the defoliated trees was an average of 16.5% lower than that of insects feeding on control trees (Table 8). Defoliation had no effect on male or female pupal mass during 1989 (Table 8). Neither did any of the other treatments or interactions. Likewise, there were no significant correlations between pupal mass and any of the phytochemical variables in either year.

During 1988 and 1989, there were no significant treatment effects on duration of gypsy moth larval period. However, during 1988, there was a significant but weak negative correlation ($r = -0.28$, $P = 0.040$, $n = 52$) between foliar nitrogen

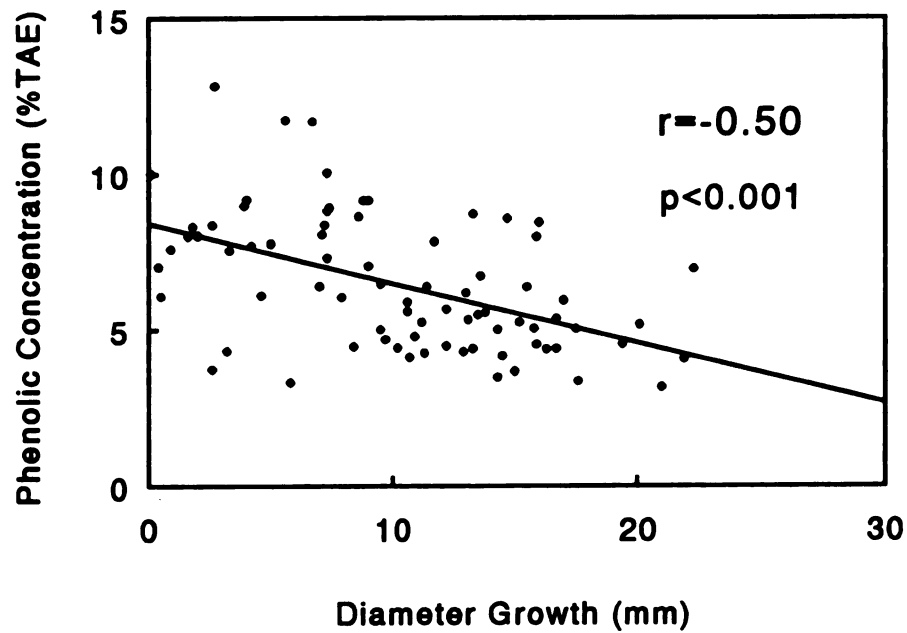
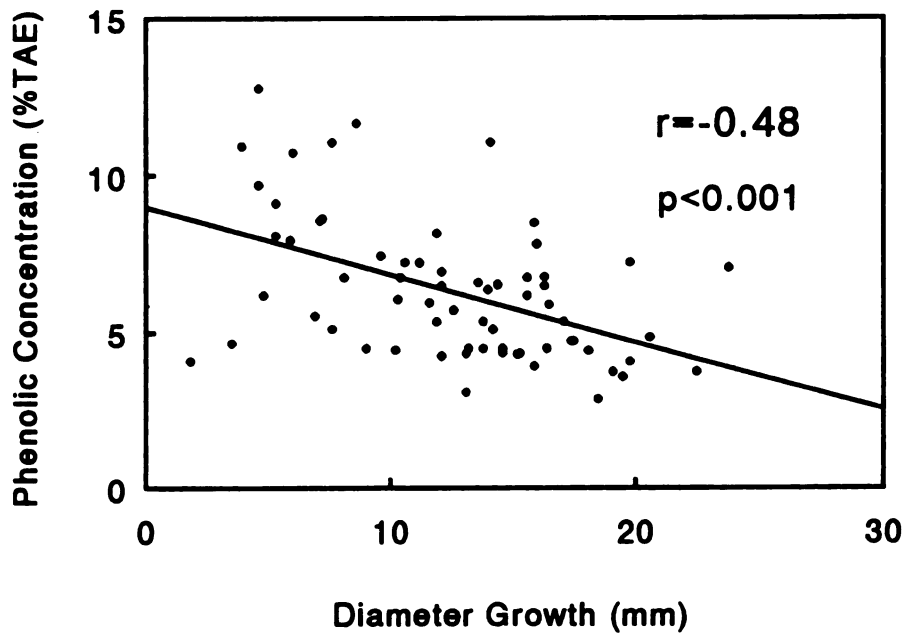
A**B**

Figure 21. Relationship between increase in trunk diameter and concentrations of total foliar phenolics in paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B). Phenolic values are tree-specific means of all measurements made during the year.

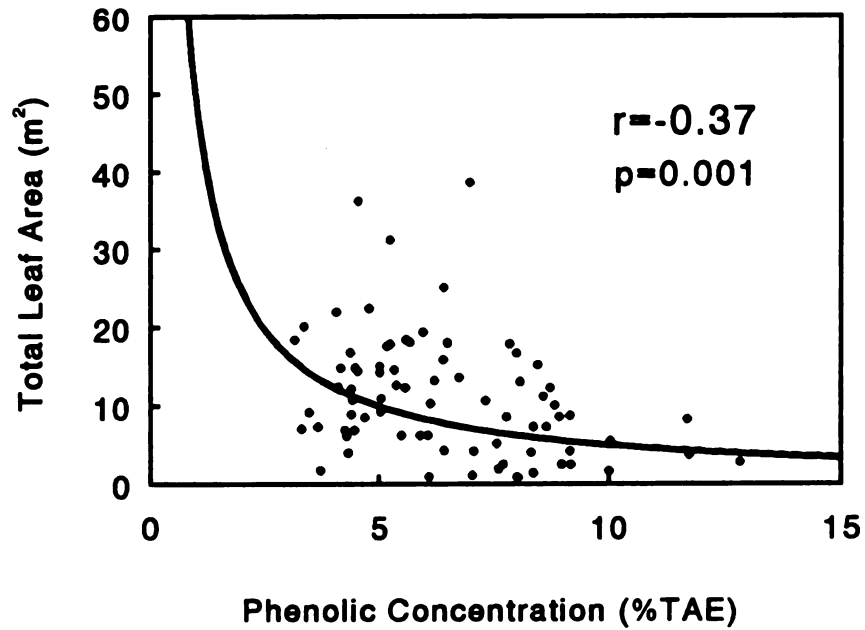
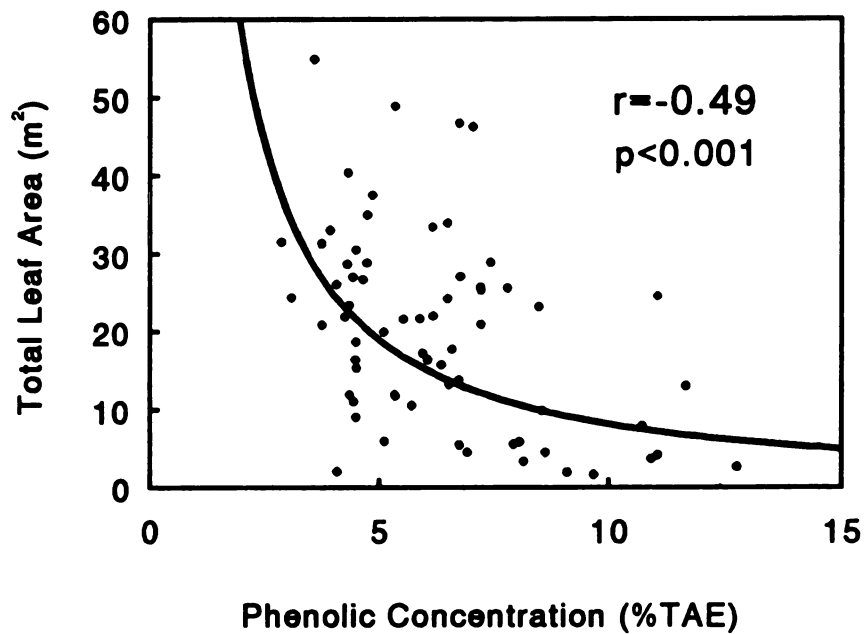
A**B**

Figure 22. The relationship between total leaf area and the concentration of total foliar phenolics in paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B). Phenolic values are tree-specific means of all measurements made during the year.

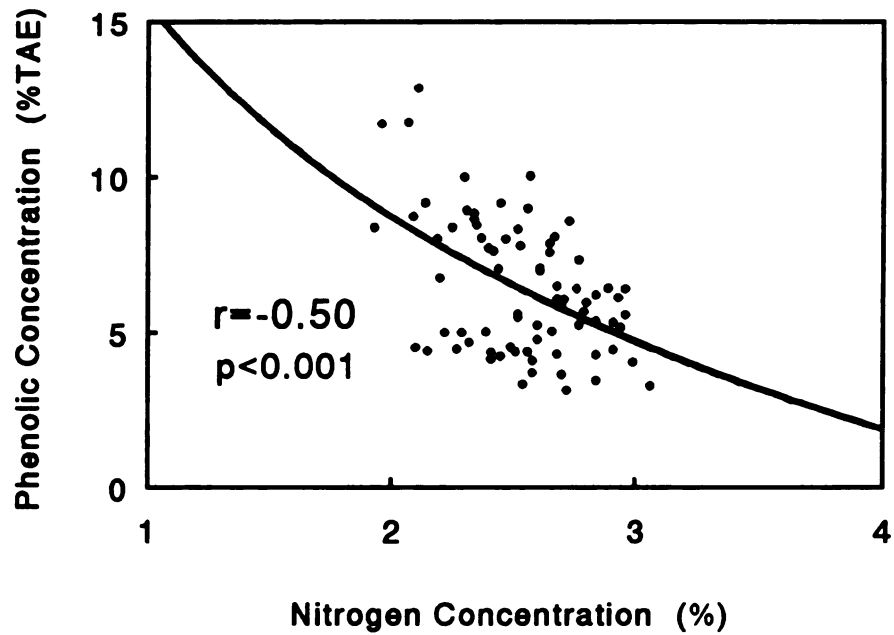
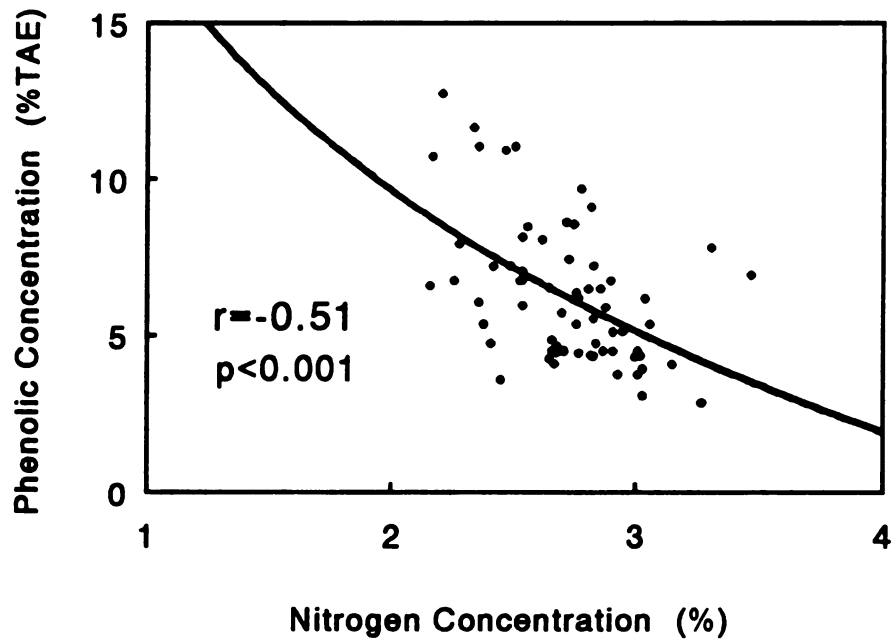
A**B**

Figure 23. The relationship between total foliar nitrogen and phenolic concentrations in paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B). Values for nitrogen and phenolics are tree-specific means of all measurements made during the year.

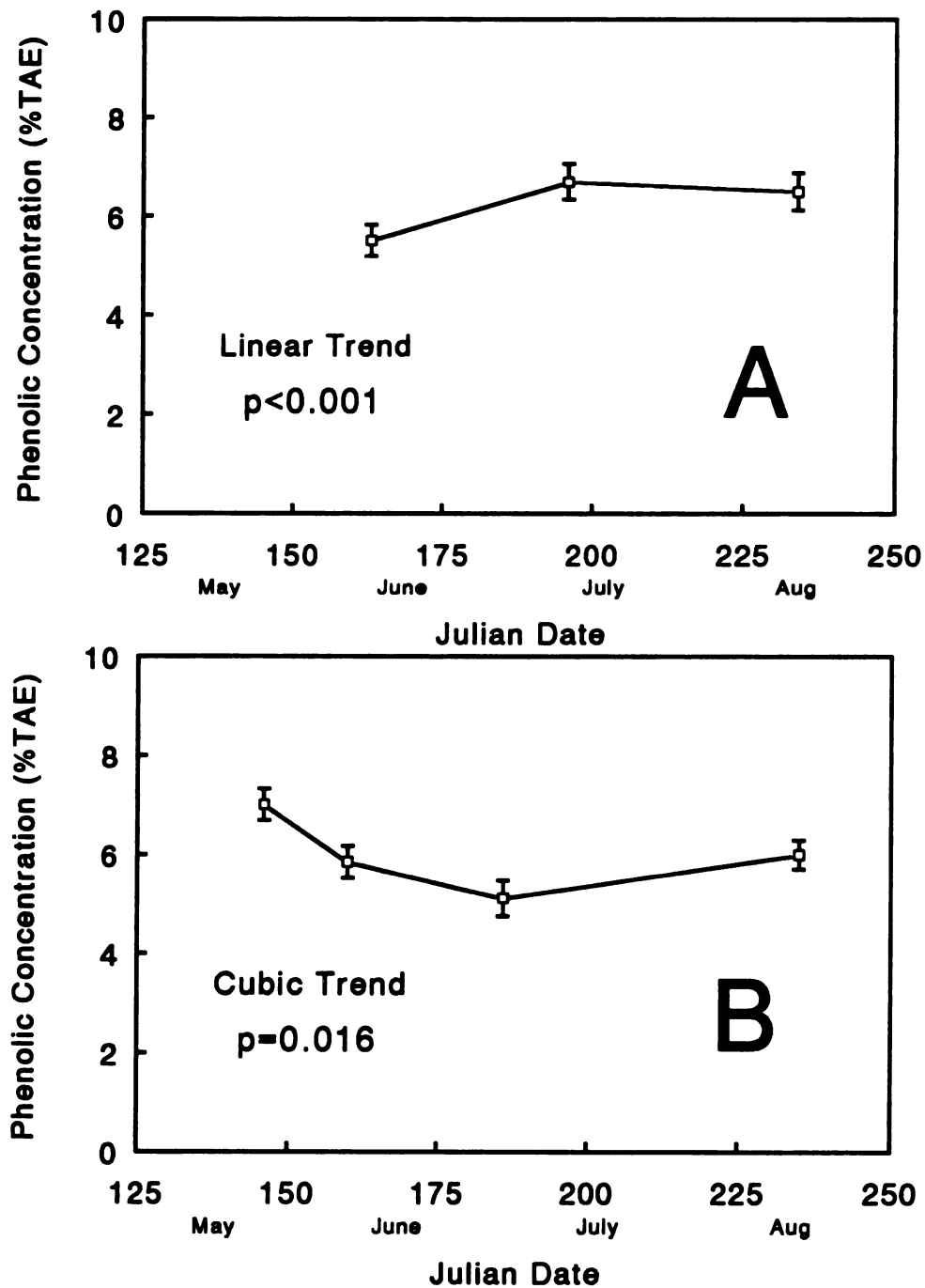


Figure 24. Phenological pattern of change in the concentrations of total foliar phenolics in paper birch, *Betula papyrifera*, during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

Table 8. The effect of 40% artificial defoliation of paper birch (*Betula papyrifera*) during 1987 and 1988, on gypsy moth larval performance during 1988 (mean $\pm$ standard error).

	Level of Defoliation (%)		
	0	40	<i>P</i>
<u>Field Experiment</u>			
Pupal Mass (mg)			
male	83 $\pm$ 4	71 $\pm$ 4	0.034
female	243 $\pm$ 20	236 $\pm$ 19	0.598
<u>Laboratory Experiment</u>			
Pupal Mass (mg)			
male	100 $\pm$ 3	92 $\pm$ 3	0.044
female	327 $\pm$ 11	305 $\pm$ 11	0.165
Relative Growth Rate (mg mg ⁻¹ day ⁻¹)			
4th instar	0.468 $\pm$ 0.009	0.445 $\pm$ 0.009	0.068
4th instar- pupa	0.132 $\pm$ 0.002	0.125 $\pm$ 0.002	0.013

(sampled 5 July, as larvae were just beginning to pupate) and duration of larval period. There was also a significant but weak positive correlation ($r=0.27$, $P=0.054$, $n=51$) between total foliar phenolic concentrations (sampled 5 July) and duration of larval period. Thus, larvae pupated fastest when feeding on foliage high in nitrogen and low in phenolics. Larval duration was not correlated with foliar phosphorus, sugar, or water content.

During 1989, there were no significant correlations between duration of larval period and any of the phytochemical variables. Duration of larval period was negatively correlated with pupal mass ($r=-0.41$, $P<0.001$, $n=61$), indicating that the insects that achieved the greatest pupal masses also grew the fastest. There was no correlation between these variables during 1988.

1988 Gypsy Moth Laboratory Experiment

Defoliation had a marginally significant negative effect on gypsy moth relative growth rate during the fourth instar feeding trial (RGR_4) ($F=3.46$; d.f. = 1,54; $P=0.068$). RGR_4 was, on average, 4.8% lower for insects feeding on defoliated trees than for those feeding on controls (Table 8). Defoliation had a slightly greater effect on relative growth rate measured from the beginning of the fourth instar through pupation (RGR_t) ($F=6.58$; d.f. = 1,54; $P=0.013$). RGR_t was, on average, 5.9% lower for insects feeding on defoliated trees than for those feeding on controls (Table 8). None of the other treatments or their interactions had significant effects on RGR_4 or RGR_t .

Defoliation had a significant effect on male pupal mass ($F=4.32$; d.f. = 1,54; $P=0.044$), just as in the 1988 field experiment. Insects feeding on defoliated trees were, on average, 7.5% smaller than those feeding on controls (Table 8). However,

defoliation had no effect on female pupal mass. None of the other treatments or their interactions had significant effects on male or female pupal mass.

There was a significant negative correlation between pupal mass (sex corrected) and foliar phenolic concentration and ($r = -0.28$, $P = 0.020$, $n = 72$) (Figure 25), and a significant positive correlation between pupal mass and foliar nitrogen concentration ($r = 0.26$, $P = 0.023$, $n = 72$) (Table 9). There were no significant relationships between either RGR_4 , RGR_t , or larval duration and foliar N or phenolics. Pupal mass and RGR_4 were both positively correlated with, whereas larval duration was negatively correlated with, leaf water content (Table 9). Both RGR_4 and RGR_t were directly correlated with foliar phosphorus content; however there was no relationship between foliar P and pupal mass or larval duration (Table 9). None of the insect performance variables were correlated with leaf sugar content (Table 9).

1989 Gypsy Moth Laboratory Experiment

Second Instar Growth Trial

None of the treatments or their interactions had any effect on relative growth measured during the second instar (RGR_2). However, there was significant variation in RGR_2 due to differences between trees within a treatment ($F = 3.74$; d.f. = 48,196; $P < 0.001$). Host phenological differences may have contributed to some of this variation. For example, date of full budbreak (date at which 95% of the leaves had at least 50% of their lamina exposed from their buds) was negatively correlated with RGR_2 ($r = -0.42$, $P < 0.001$, $n = 66$) (Figure 26). The older the leaves, the higher the growth rate of the insect. There were no relationships between RGR_2 and any of the phytochemical variables.

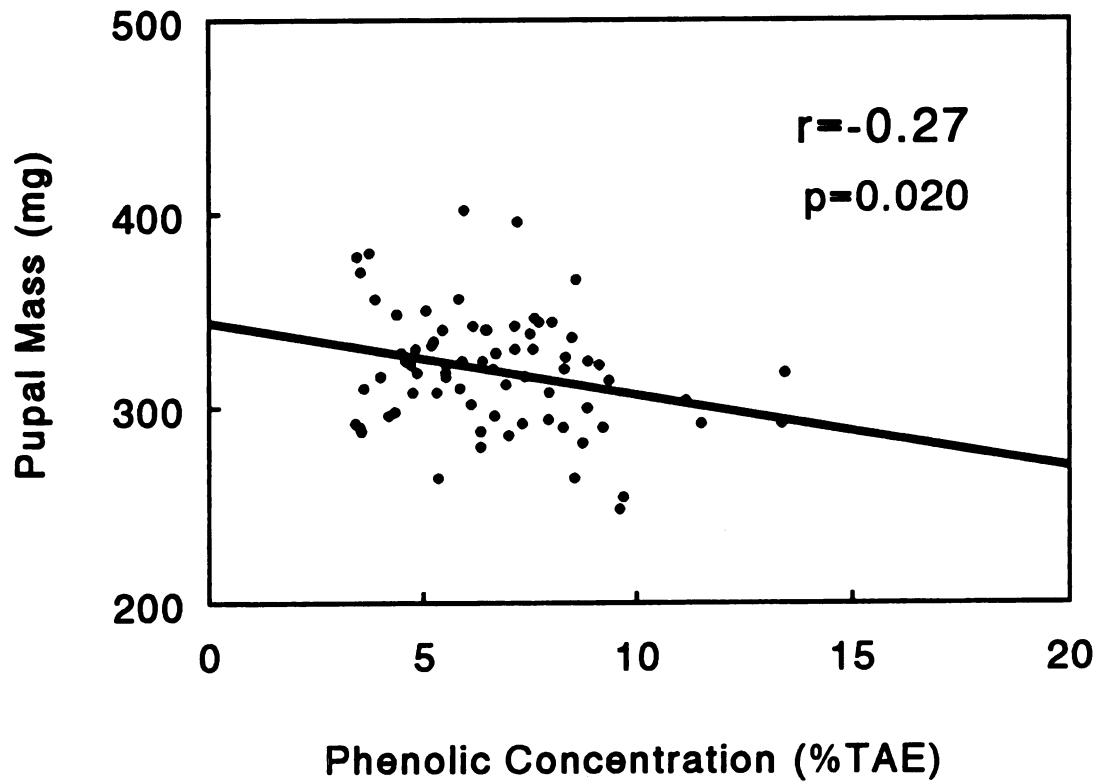


Figure 25. The relationship between total foliar phenolic concentrations of paper birch (*Betula papyrifera*) (sampled 15 July), and gypsy moth (*Lymantria dispar*) pupal mass in 1988.

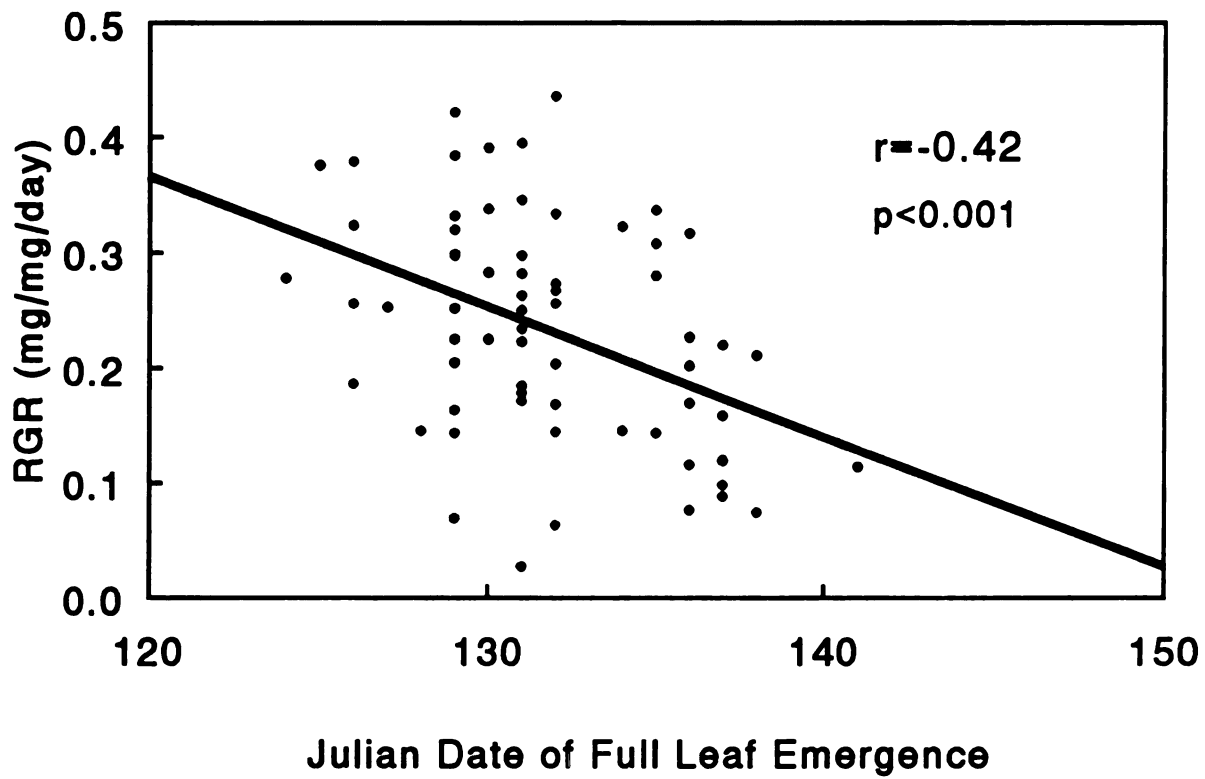


Figure 26. The relationship between the phenology of spring leaf emergence of paper birch, *Betula papyrifera*, and the relative growth rate of second instar gypsy moth, *Lymantria dispar*, during 1989.

Table 9. Pearson correlation coefficients between indices of gypsy moth (*Lymantria dispar*) larval performance and foliage quality variables of paper birch (*Betula papyrifera*) for 1988 (n=72) and 1989 (n=66) laboratory experiments¹. Pupal mass and larval duration are standardized for sex.

Insect Performance Variable ²	Foliage Variable ^{2,3}				
	Phenolics	N	H ₂ O	P	CHO
1988³					
RGR ₄	NS	NS	0.41 ***	0.25 *	NS
RGR _t	NS	NS	NS	0.27 *	NS
Larval Duration	0.26 *	NS	-0.24 *	NS	NS
Pupal Mass	-0.28 *	0.26 *	0.30 **	0.28 *	NS
1989³					
RGR ₂	NS	NS	NS	NS	NS
RGR ₄	NS	NS	NS	NS	NS
RGR _t	NS	NS	NS	NS	NS
RCR	0.36 **	-0.37 **	NS	-0.28 *	NS
AD	-0.35 **	NS	0.45 ***	NS	NS
ECD	NS	NS	NS	NS	NS
Pupal Mass	NS	NS	NS	NS	NS
Larval Duration	NS	NS	NS	NS	NS

¹NS = not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

²Abbreviations and units: phenolics = total foliar phenolic concentrations (% dry weight - tannic acid equivalents); N = foliar nitrogen (% dry weight); H₂O = leaf water content (% fresh weight); P = foliar phosphorus (% dry weight); CHO = total foliar sugars (glucose + fructose + sucrose) (% dry weight). RGR₂, RGR₄, and RGR_t = relative growth rate in the 2nd and 4th instars, and over the duration of the experiment, respectively; RCR = relative consumption rate; AD = approximate digestibility; ECD = efficiency of conversion of digested food. See Table 7 for units associated with insect performance indices.

³During 1988, RGR₄ was compared to foliage sampled on 9 June. Other insect performance variables were compared with foliage sampled 15 July. During 1989, RGR₂ was compared with foliage sampled 26 May. RGR_t, pupal mass, and larval duration were compared against foliage sampled 5 July. Other insect performance variables were compared with foliage sampled 6 June.

Fourth Instar Growth Trial

All larvae survived the 72 hr second instar feeding trial, however 31% died later as second instar or third instars; replacement larvae were introduced into the experiment in the place of dead insects. Three of the replacement larvae subsequently died as third instars and were replaced again. Thus, the fourth instar feeding trial was fully replicated, but only 69% of the insects had experienced their assigned host for two full instars prior to the feeding trial. After reaching the fourth instar, only two larvae died prior to pupation, both in accidents. These insects were not replaced.

Fertilization had a significant positive linear effect on the efficiency of conversion of ingested food into larval biomass (ECI) ($F=8.71$; d.f. = 1,48; $P=0.005$). However, this was not due to fertilization effects on the approximate digestibility of the food, since fertilization had no effect on AD ($F=0.56$; d.f. = 2,48; $P=0.576$). Hence, the differences in ECI due to fertilization must have been the result of post-digestive effects. In fact, fertilization had a significant positive linear effect on the efficiency at which larvae converted digested food into biomass (ECD) ($F=6.50$; d.f. = 1,48; $P=0.014$) (Figure 27). However, the effect of fertilization on ECD was not related to the effect of fertilization on total foliar N; the correlation between ECD and foliar N was not significant ($r=0.01$).

Fertilization also had a significant negative effect on the rate at which larvae consumed foliage (RCR) ($F=3.07$; d.f. = 2,48; $P=0.056$) (Figure 27). A significant inverse correlation between foliar N and RCR ($r=-0.37$, $P=0.003$, $n=66$) (Table 9) suggests a possible connection between fertilization, foliar N, and RCR. Fertilization had no effect on RGR_4 , RGR_p , larval duration, or pupal mass (Figures 27 & 28).

During the fourth instar feeding trial, there was a negative correlation

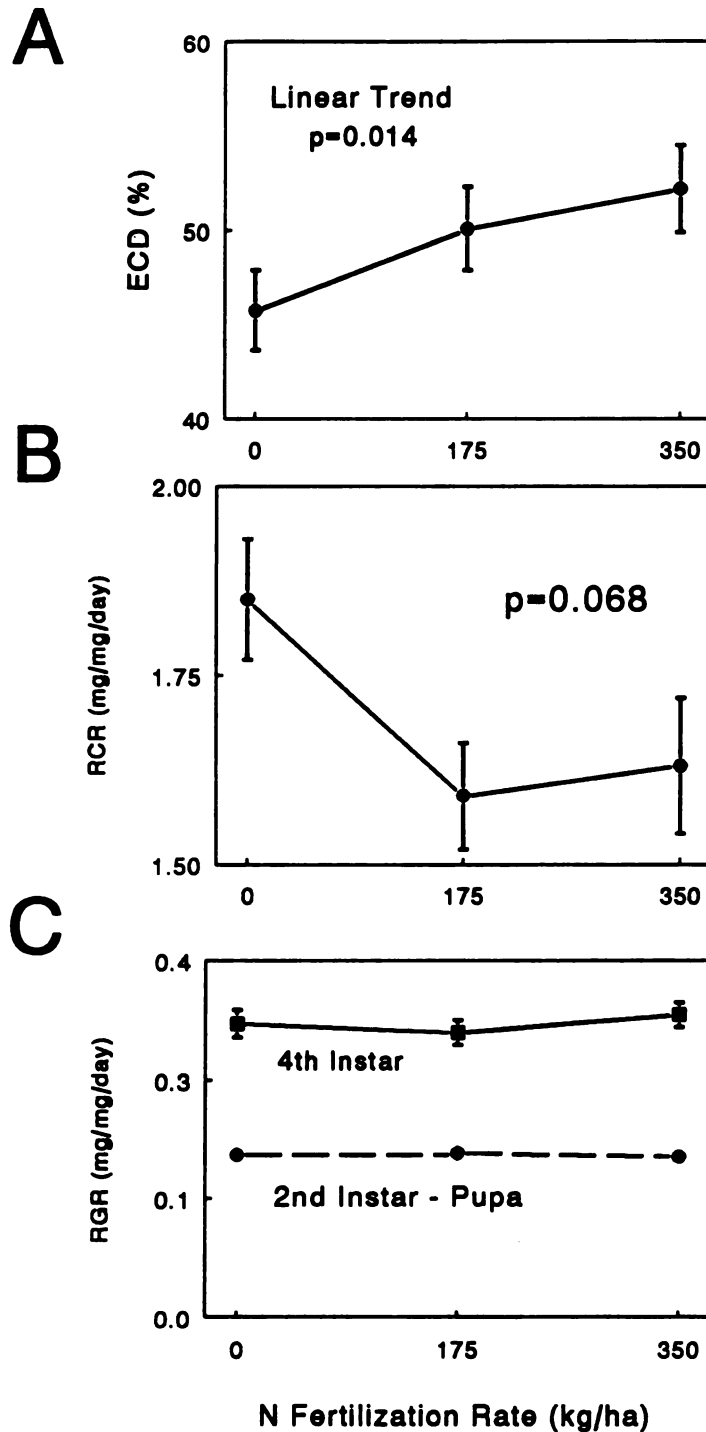


Figure 27. The effect of fertilizing paper birch (*Betula papyrifera*) with nitrogen, on the feeding energetics of gypsy moth larvae (*Lymantria dispar*), in 1989: (A) the ability of fourth instars to convert digested food to biomass (ECD), (B) relative consumption rate (RCR), and (C) relative growth rates (RGR) in the fourth instar, and from the second instar through pupation (mean $\pm$ standard error).

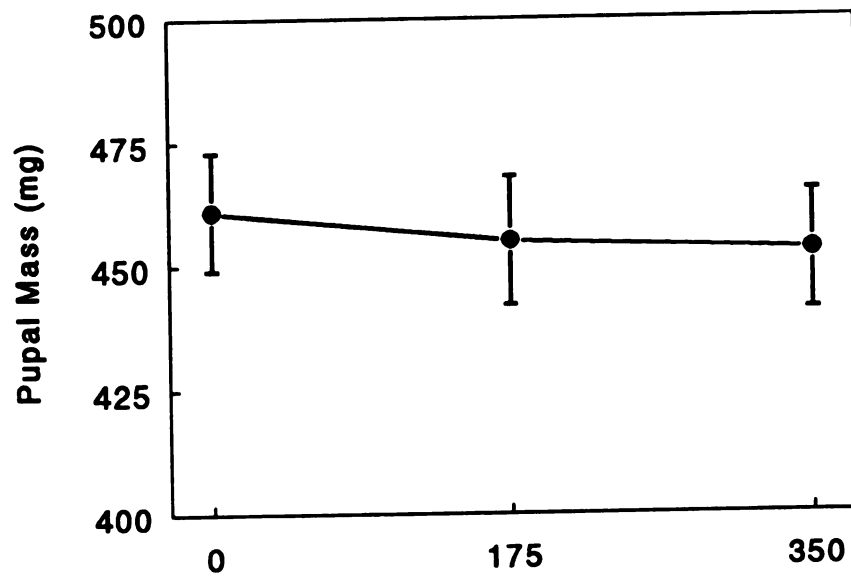
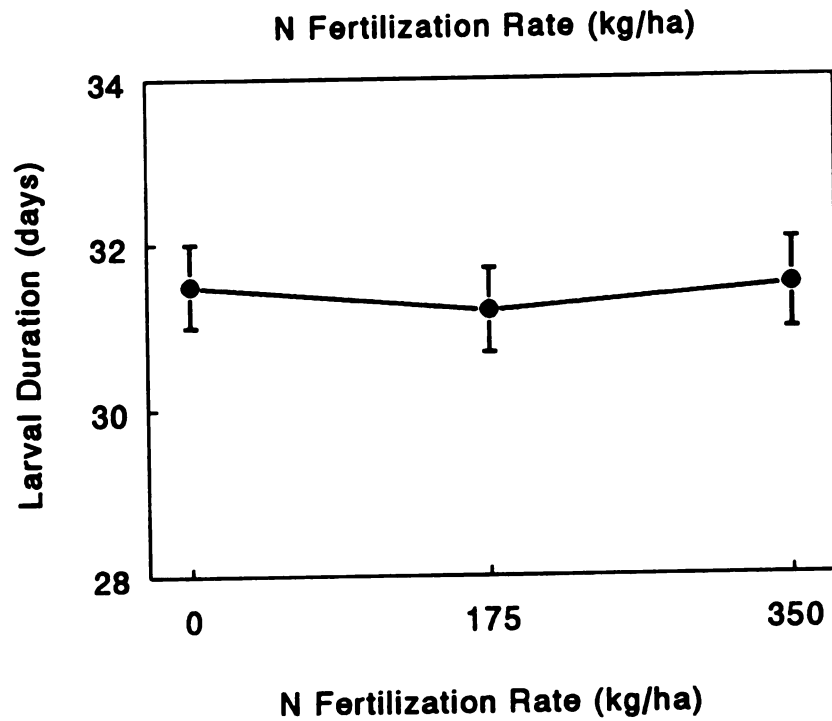
A**B**

Figure 28. The effect of fertilizing paper birch (*Betula papyrifera*) with nitrogen, on gypsy moth (*Lymantria dispar*) pupal mass and duration of larval period, in 1989 (mean $\pm$ standard error).

between foliar phenolic concentrations and ECI ($r=-0.31$, $P=0.011$, $n=66$). However, there was no correlation between phenolics and ECD ($r=0.03$). Hence, the effects of phenolic concentrations on ECI must have been through their effects on reducing the digestibility of the foliage. In fact, there was a negative logarithmic correlation between phenolic levels and AD ($r=-0.41$, $P<0.001$, $n=66$) (Figure 29). There was positive logarithmic correlation between relative consumption rate and foliar phenolic concentrations ($r=0.40$, $P<0.001$, $n=66$) (Figure 29). However, there was no relationship between foliar phenolic concentrations and RGR_4 , larval duration, or pupal mass (Figures 29 & 30).

Interestingly, RGR_4 was not correlated with either RGR_t ($r=0.03$), pupal mass, or larval duration ($r=0.13$) (Figures 31-33). However, RGR_2 was strongly, positively correlated with each of RGR_t ($r=0.64$, $P<0.001$, $n=66$), pupal mass ($r=0.53$, $P<0.001$, $n=66$), and larval duration ($r=-0.60$, $P<0.001$, $n=66$) (Figures 31-33).

Delayed Induced Resistance

Forty percent artificial defoliation in 1987 and 1988, had no effect on leaf chemistry, larval growth rate, pupal mass, or duration of larval period in 1989 (Figure 34). The C/N balance hypothesis predicts a defoliation x nitrogen interaction (Haukioja & Neuvonen 1985a; Tuomi et al. 1988a). Defoliation is predicted to increase concentrations of carbon-based secondary metabolites when growth-limiting nutrients lost to defoliation are slowly replaced, but have little or no effect in fertile soils, where nutrients lost to defoliation are rapidly replaced. There were no significant defoliation x fertilization interactions for any leaf chemistry or insect performance variables.

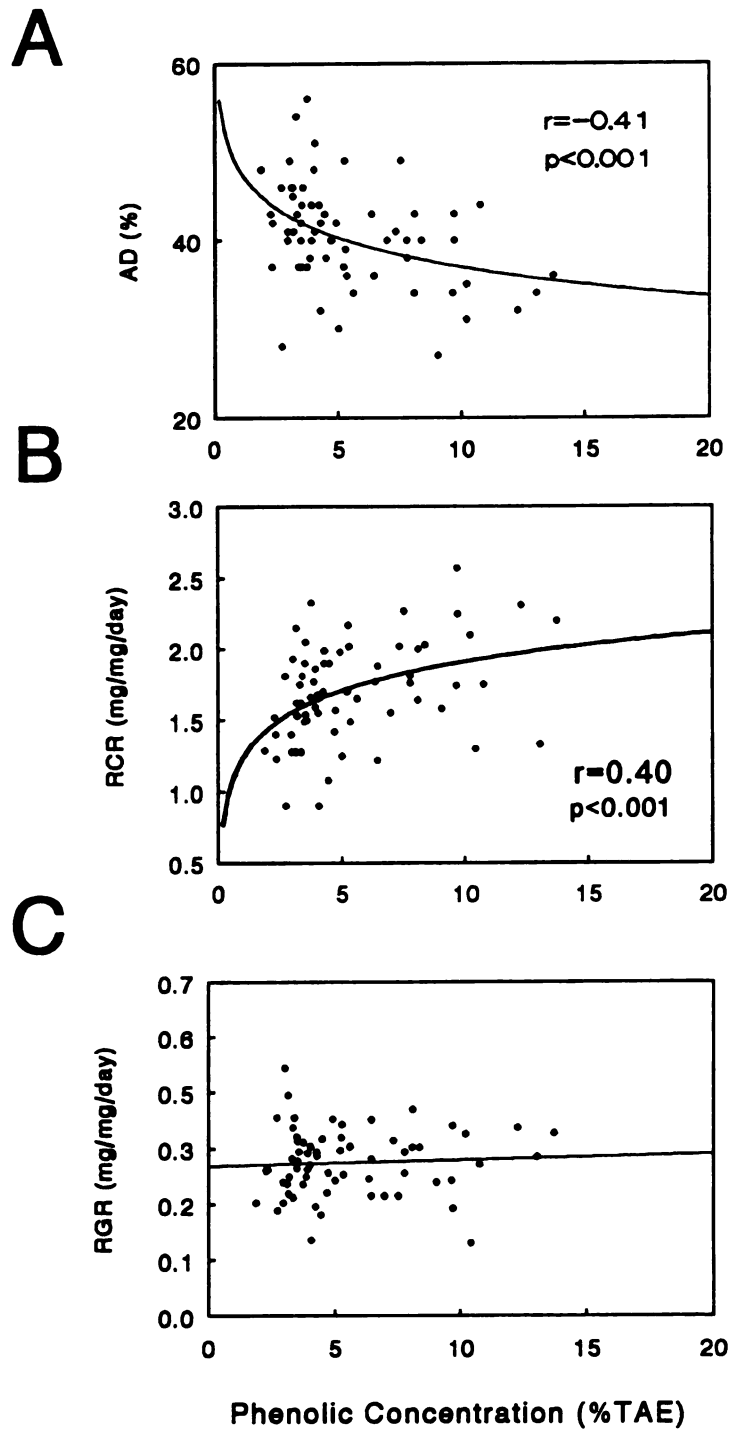


Figure 29. The relationship between the concentration of total foliar phenolics (sampled 6 June) of paper birch (*Betula papyrifera*) and gypsy moth (*Lymantria dispar*) feeding energetics, in 1989: (A) the ability of fourth instars to digest food (AD), (B) relative consumption rate of fourth instars (RCR), and (C) relative growth rates (RGR) during the fourth instar.

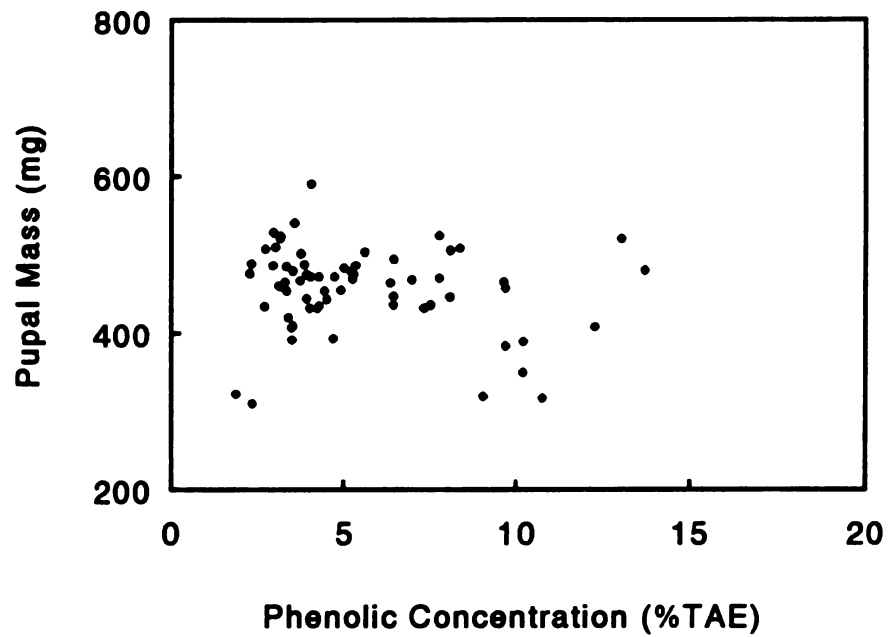
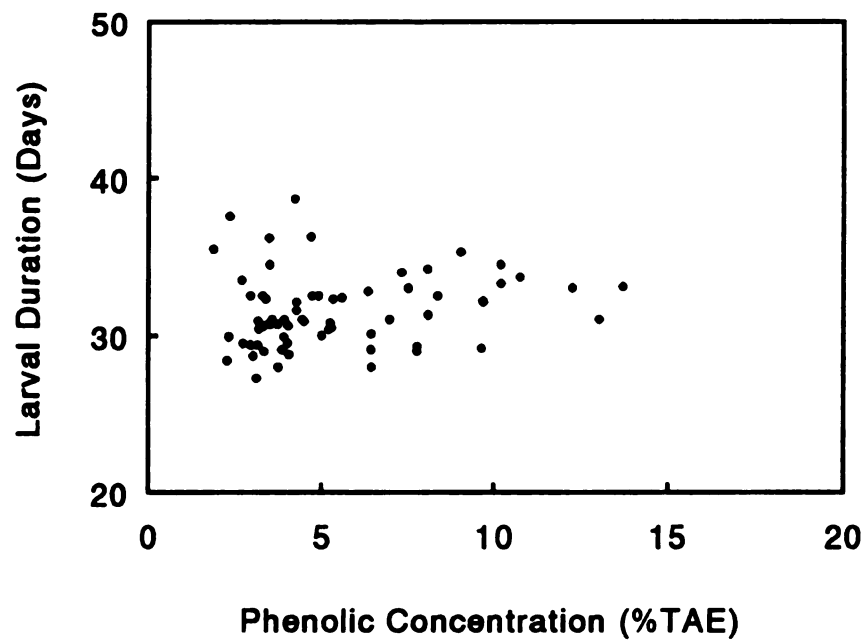
A**B**

Figure 30. The relationship between the concentration of total foliar phenolics of paper birch (*Betula papyrifera*) (sampled 5 July) and both (A) pupal mass, and (B) duration of larval period of gypsy moth (*Lymantria dispar*), in 1989.

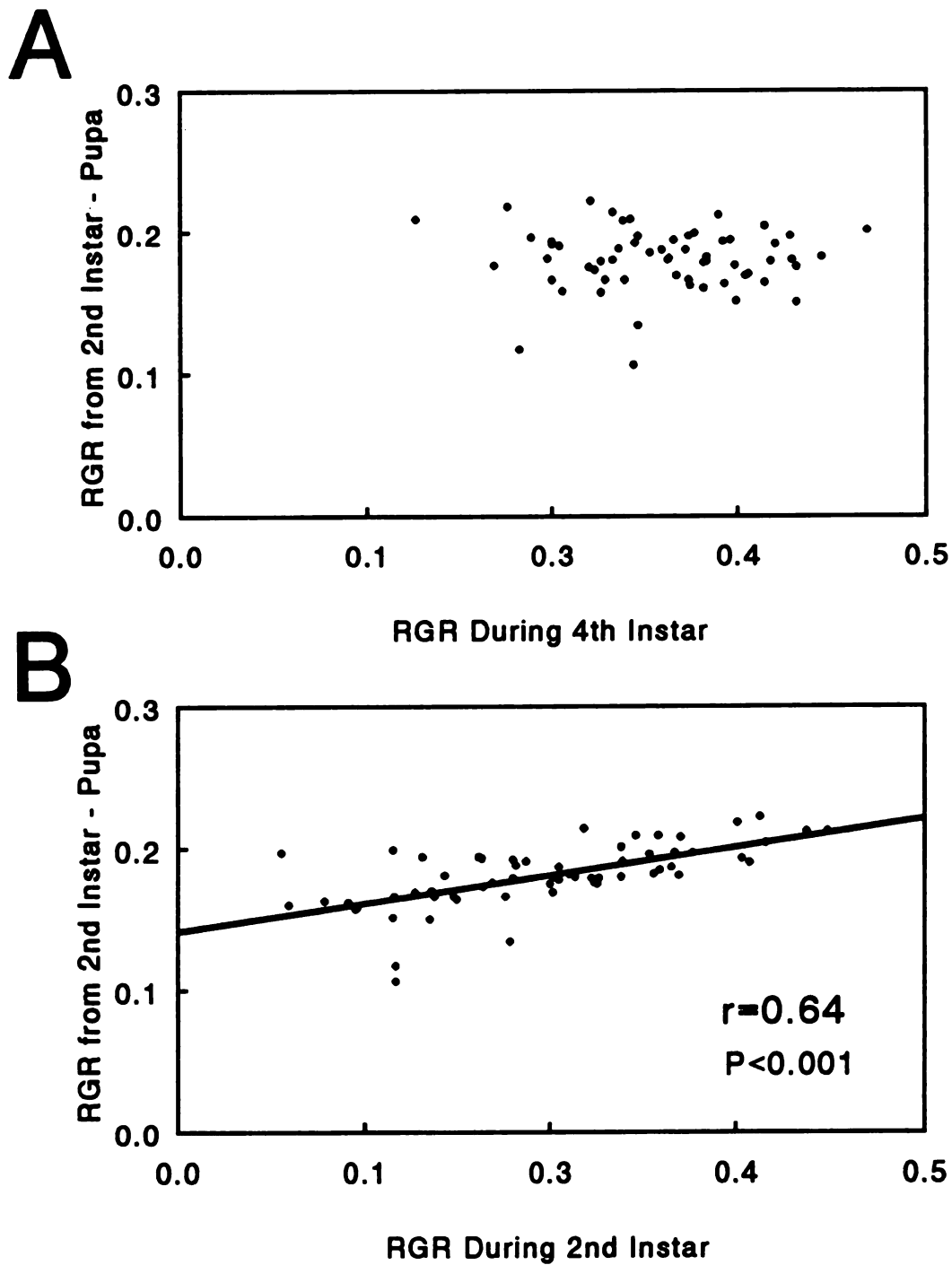


Figure 31. The relationship between relative growth rate (RGR) of gypsy moth (*Lymantria dispar*) from the second instar through pupation, and both RGR during the fourth (A) and second (B) instars, in 1989.

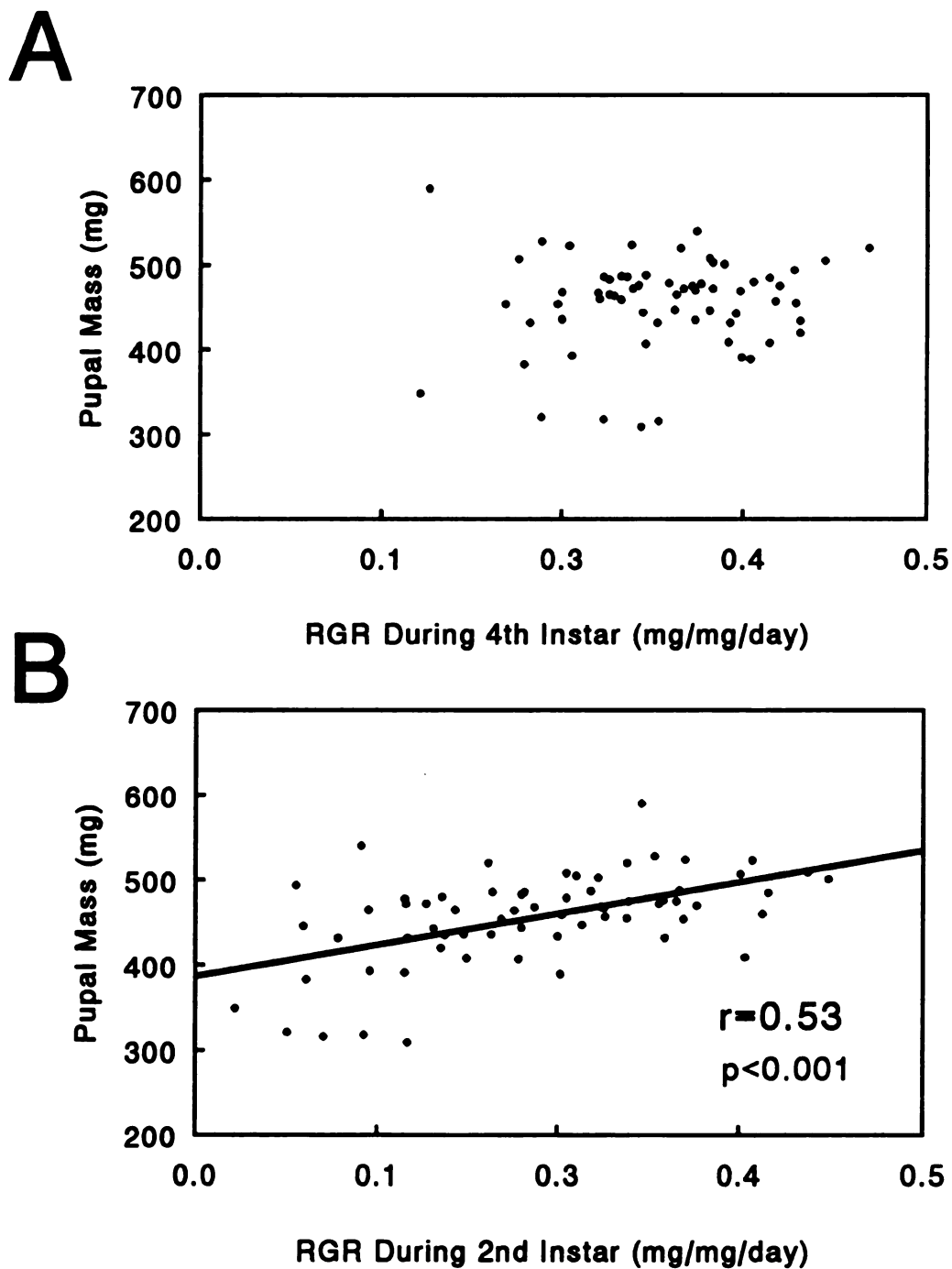


Figure 32. The relationship between pupal mass of gypsy moth (*Lymantria dispar*), and relative growth rate in the fourth (A) and second (B) instars, during 1989.

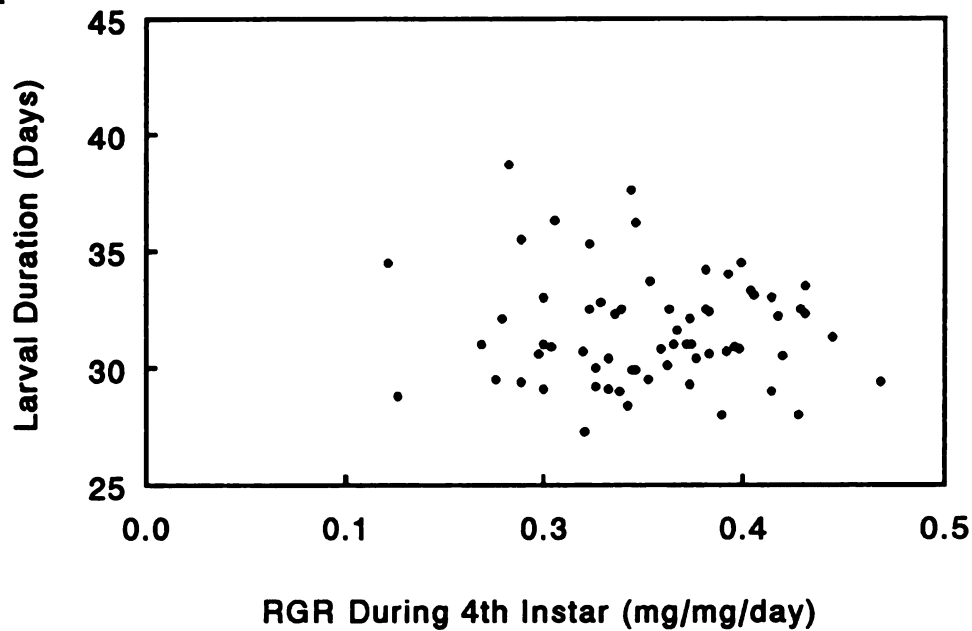
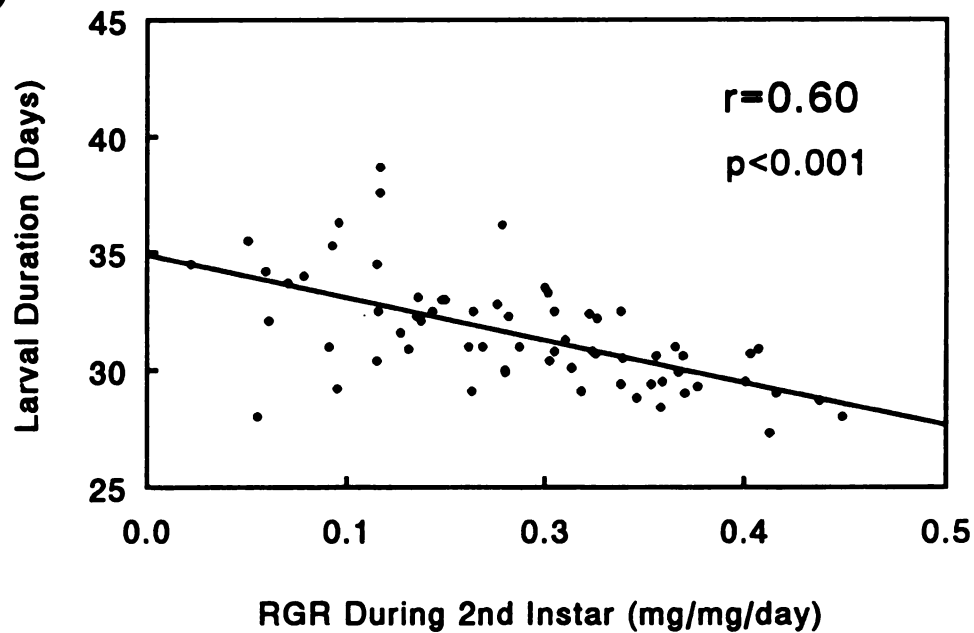
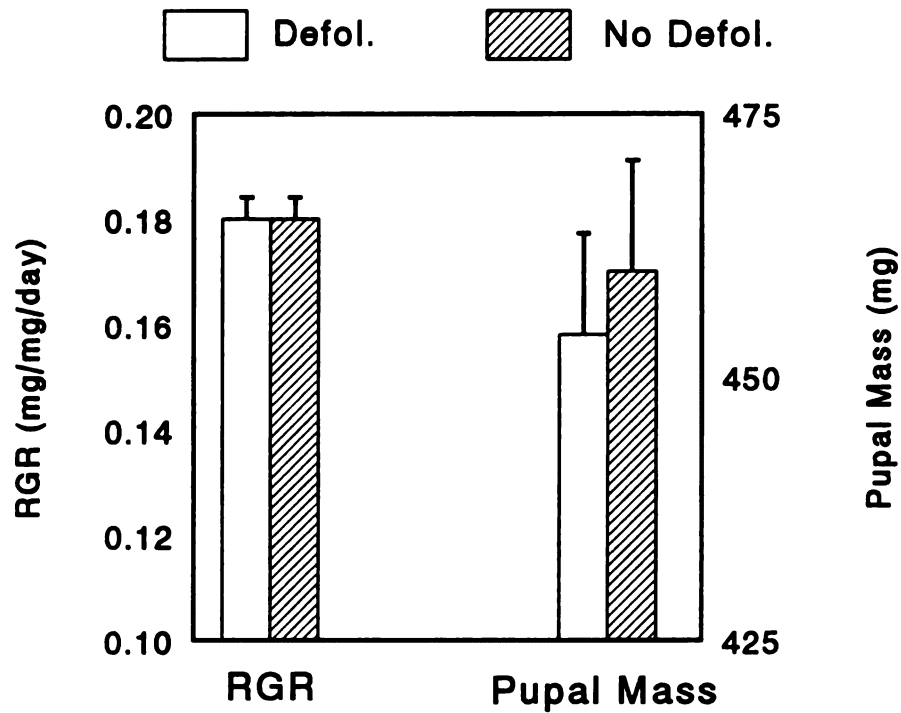
A**B**

Figure 33. The relationship between duration of larval period of gypsy moth (*Lymantria dispar*), and both relative growth rate during the fourth (A) and second (B) instars, in 1989.

A



B

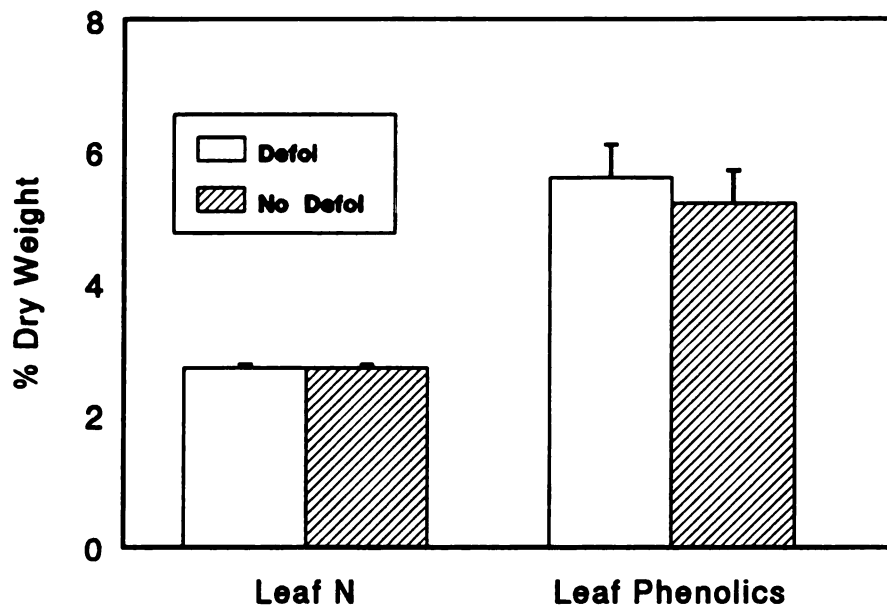


Figure 34. The effect of artificial defoliation (40%) of paper birch (*Betula papyrifera*) during 1987 and 1988, on (A) the relative growth rate (RGR) of gypsy moth (*Lymantria dispar*) from the second instar through pupation, and pupal mass, and (B) total foliar concentrations of nitrogen and phenolics, in 1989. Nitrogen and phenolic values are tree-specific means of all measurements made during the year (mean $\pm$ standard error).

Tree Growth and Insect Performance

During 1988 and 1989, there was a consistent, negative correlation between total foliar phenolics and tree growth (Figure 21). During 1988, there was a negative correlation between total phenolics and both pupal mass and duration of larval period (Table 9). However, there was no relationship between tree growth and either pupal mass, larval duration, or RGR_t (Table 9) (Figure 35). During 1989, there was a marginal, positive correlation between RGR_t and tree growth ($r=0.24$, $P<0.056$, $n=66$), but no relationship between pupal mass or duration of larval and period tree growth (Figure 36).

Correlation Between Laboratory and Field Studies

In 1988, the time to reach pupation on a particular tree in the laboratory was positively correlated with the amount of time to reach pupation on the same tree in the field ($r=0.30$, $P=0.035$, $n=52$). However, there was no correlation between laboratory and field pupal masses on the same tree ($r=0.01$, $P=0.972$, $n=52$).

In 1989, the results of the field and laboratory experiments were better correlated: $r=0.58$ for larval duration ($P<0.001$, $n=61$), and $r=0.29$ for pupal mass ($P=0.021$, $n=61$).

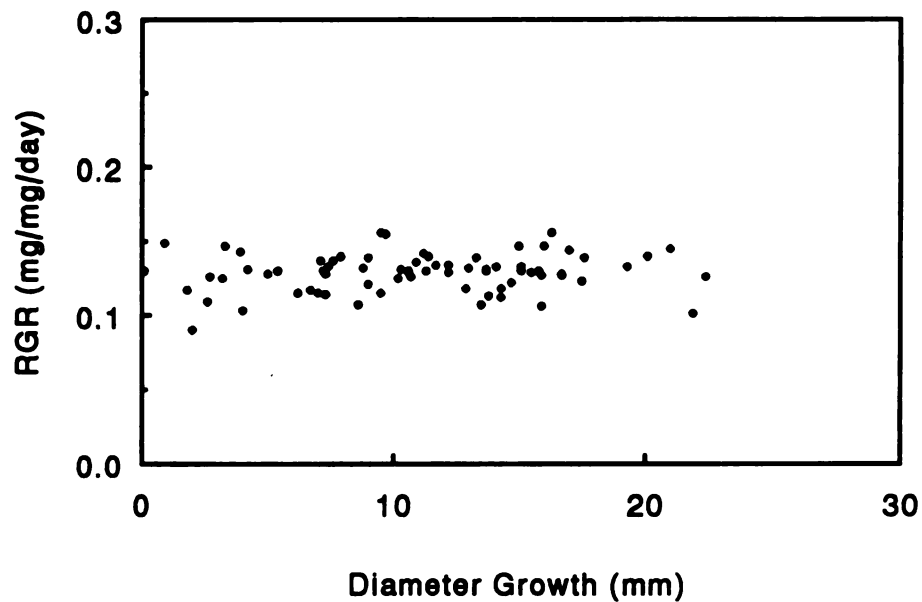
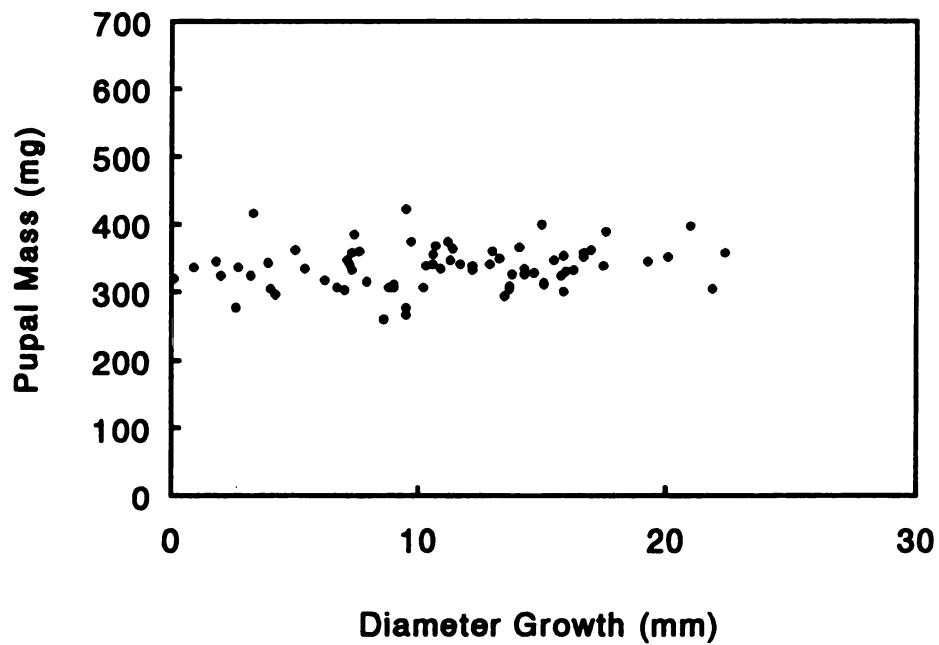
A**B**

Figure 35. The relationship between the increase in trunk diameter of paper birch (*Betula papyrifera*), and both the relative growth rate (RGR) from fourth instar through pupation (A), and pupal mass (B) of gypsy moth (*Lymantria dispar*), in 1988.

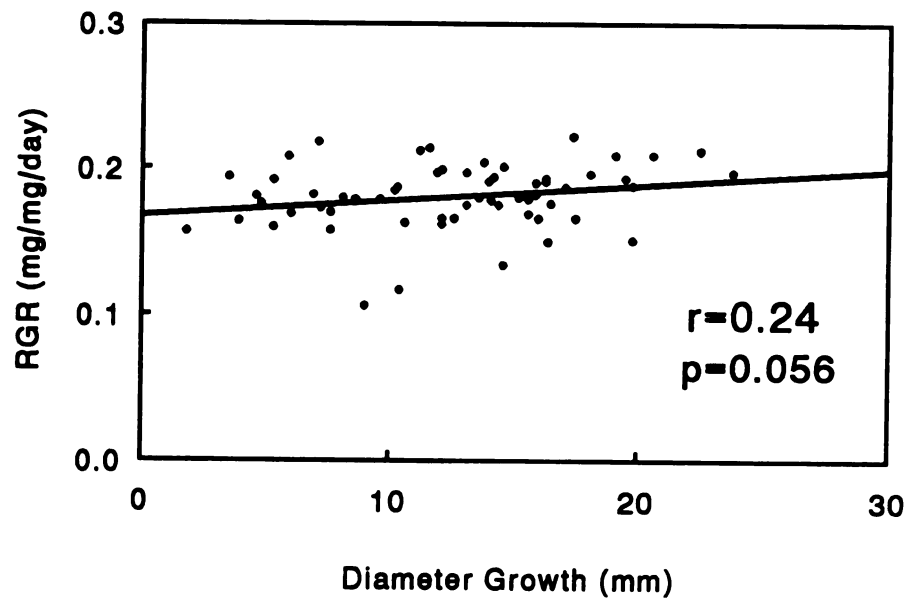
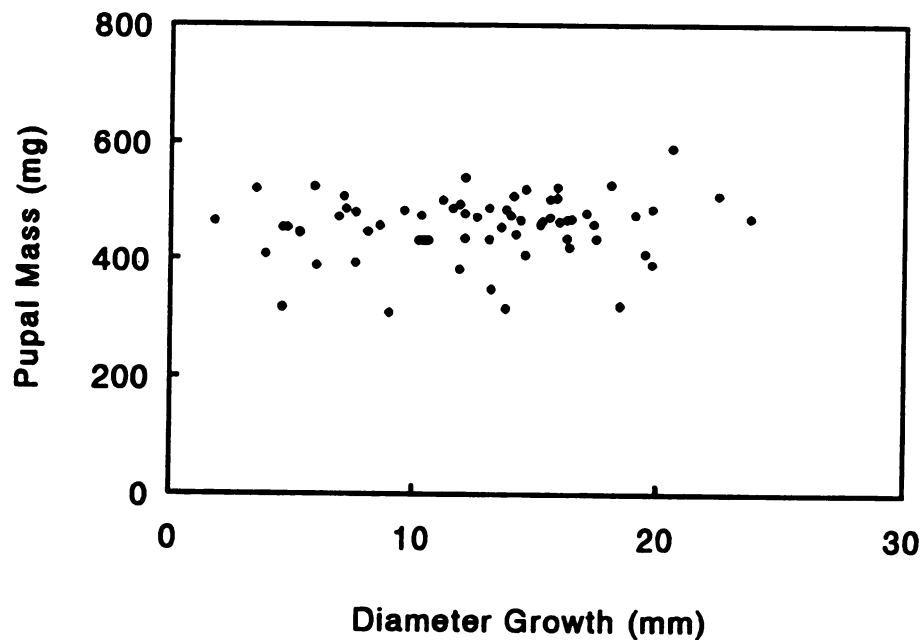
A**B**

Figure 36. The relationship between the increase in trunk diameter of paper birch (*Betula papyrifera*), and both the relative growth rate (RGR) from fourth instar through pupation (A), and pupal mass (B) of gypsy moth (*Lymantria dispar*), in 1989.

DISCUSSION

Growth versus Defense

Growth vs. Secondary Chemistry

Both the Carbon/Nutrient Balance and Growth/ Differentiation Balance hypotheses predict a negative correlation between the total resources allocated to growth and those allocated to secondary metabolism. The measurement of total phenolics is particularly appropriate for a study of the trade-off between growth and secondary metabolism, because it estimates the secondary metabolic output of a major pathway, the shikimate pathway. Up to 60% of total plant biomass is composed of molecules transversing this pathway (Jensen 1985). There is no equivalent assay that estimates the total output of the other major secondary metabolic pathways which generate terpenoids, alkaloids, and polyketide compounds. Furthermore, phenolic biosynthesis, because of its aromatic amino acid precursors, is in direct competition with protein synthesis, and thus growth (Phillips & Henshaw 1977; Margna 1977; McLure 1979; Margna et al. 1989).

The negative correlation between growth and total phenolic concentrations observed in this study during both 1988 and 1989 (Figure 21) is consistent with these hypotheses. There were also significant negative correlations between foliar N and total phenolic concentrations, consistent with the C/N balance hypotheses (Figure 23). These patterns have also been observed in other studies (Waring et al. 1985; Haukioja et al. 1985a; Larsson et al. 1986a; Bryant 1987; Bryant et al. 1987a,b; Mattson & Palmer 1988; Margna et al. 1989).

During 1988, plants receiving the least water had the highest concentrations of total phenolic concentrations (Figure 20) and grew the slowest (Figures 7 and 8,

Chapter 2). Furthermore, there was no significant effect of fertilization on foliar phenolic concentrations. These results are more consistent with the predictions of the G/D balance hypothesis than those of the C/N balance hypothesis. The lack of fertilization effect on secondary metabolism is contrary to results reported by a number of other studies (e.g. Waring et al. 1985; Larsson et al. 1986a; Mihaliak & Lincoln 1985; Mihaliak et al. 1987; Bryant 1987; Bryant et al. 1987a,b; Price et al. 1989; Glyphis & Puttick 1989). However, fertilization in this study did not have the substantial effect on plant growth reported in the other studies (even though it did have highly significant effects on foliar nitrogen concentration). During 1989, neither irrigation nor fertilization had any effect on total phenolic concentrations or tree growth.

The negative correlation between total leaf area and foliar phenolic concentration (Figure 22) is consistent with the hypothesis that the allocation of resources to secondary metabolism decreases growth by diverting resources from the production of new leaf area (a major premise of Chapter 1). However, this trade-off will have little cost in ecological time, if carbon is diverted to secondary metabolism only when growth is limited by factors such as nutrient limitation or drought (Mattson 1980; Bryant et al. 1985; Tuomi et al. 1988a).

Growth vs. Insect Resistance

The measurement of total phenolics as an indication of environmental effects on herbivore resistance has less value. Although many studies report negative correlations between total phenolics and insect performance, a cause/effect relationship cannot be assumed. The effects of phenolic compounds on herbivores are likely to be structure-specific (Zucker 1983; Clausen et al. 1990). In fact, different phenolic compounds occurring within a plant can have very different and independent effects on a particular herbivore (e.g. Berenbaum 1981; Lindroth et al.

1988; Berenbaum et al. 1989). Furthermore, concentrations of individual compounds do not always change in concert in response to environmental variation (e.g. Zangerl & Berenbaum 1987; Coassini Lokar et al. 1987; Muzika et al. 1989). Increased secondary metabolism as growth slows cannot in itself be considered evidence that the slower growing trees are always better defended.

The gypsy moth bioassay experiments offer little evidence that the slower growing trees were better defended by their higher levels of phenolics. In 1988, as phenolic concentrations increased, pupal mass decreased and larvae required more time to reach pupation (Table 9, Figure 25). However, the correlations were weak ($r = -0.27$ and 0.26 for pupal mass and larval duration, respectively) (Table 9). There was no relation between tree growth and insect performance (Figure 35). Phenolics had no effect on pupal mass, relative growth rate, or larval duration, during 1989 (Table 9). However, there was a positive correlation between tree growth and the relative growth rate of gypsy moth larvae from the beginning of the second instar through pupation (RGR_i) (Figure 36), suggesting that the slower growing trees were better defended. However, the slope was not steep, and the relationship was weak ($r = 0.24$).

These results challenge the hypothesis that increasing secondary metabolism as growth slows is an adaptive response in birch, enhancing herbivore resistance when environmental conditions limit the potential for compensatory growth. However, gypsy moth may not be a good assay organism for a test of this hypothesis. The status of paper birch as a preferred host for gypsy moth in North America, coupled with the strong correlation in gypsy moth larvae between host preference and performance on that host (Montgomery 1988), indicate that gypsy moth was pre-adapted to birch allelochemicals. Thus, it is not surprising that the growth of gypsy moth is not affected substantially by variation in paper birch chemistry. Gypsy moth also performs well on grey birch (*Betula populifolia*) (Barbosa & Greenblatt

1979), which is also native to North America. Gypsy moth and North American birches have no evolutionary history. Tests of adaptive defensive hypotheses may be more appropriately conducted with organisms that have interacted in evolutionary time. The chemical defenses of paper birch may be directed towards herbivores such as the forest tent caterpillar (*Malacosoma disstria*) with which it has evolved.

In the laboratory experiments, phenolics had negative (albeit small) effects on pupal mass and larval duration in 1988, but none in 1989. However, there was 31% mortality among second and third instars in 1989. The effects of phenolics on pupal mass and larval duration in 1989, only reflect the performance of larvae able to complete development.

The feeding history of larvae used in the experiments may also explain the differential effects of phenolics observed in the two years. Larvae fed artificial diet for before being switched to foliage as fourth instars (1988 experiment), may not have tolerated foliar phenolics as well as larvae switched to foliage after one instar (1989 experiment). Gypsy moth larvae are well adapted for switching diets (Montgomery 1988). However, optimal performance may require prior induction of specific detoxification and digestive enzymes. A number of studies demonstrate that diet quality experienced by early instars can have profound effects on host preferences, growth rate, feeding efficiency, pupal mass, and fecundity of insects subsequently switched to new diets (Scriber 1979a, 1981, 1982; Taylor 1984; Barbosa et al. 1979, 1986; Larsson et al. 1986b). Mid-gut allometry may be important (Ahmad 1986). As larvae grow, mid-gut surface area does not increase in proportion to insect biomass. Hence, older larvae require higher levels of enzyme activity, if they are to detoxify allelochemicals with the same efficiency of younger insects (Ahmad 1986). Detoxification-enzyme levels of gypsy moth larvae fed oak foliage increased 4.5 times from the mid-second to mid-fifth instar, while enzymes of larvae fed artificial diets only increased 1.8 fold (Ahmad 1986).

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Induced Resistance

There were several indications that defoliation during 1987 and 1988 induced resistance to gypsy moth in 1988. In both the laboratory and field experiments, males (but not females) had lower pupal masses when they fed on previously defoliated trees (Table 8). Gross et al. (1990) also observed differential effects of host quality on male and female pupal mass. The pupal mass of gypsy moth females is well correlated with fecundity (Rossiter et al. 1988). However, little is known about the relationship between male pupal mass and adult male fertility. Haukioja & Neuvonen (1985b) found that small *Epirrita autumnata* males were frequently sterile, and that only the largest males were able to mate successfully more than once. Mattson et al. (1983) found that female spruce budworm (*Choristoneura fumiferana*) pupal mass increased with foliar nitrogen. However, male pupal mass was not related to foliar nitrogen, above of a threshold value of 1.5%. Males may lack the direct correlation between pupal mass and reproductive success commonly observed in females (e.g. Mattson et al. 1983; Slansky & Scriber 1985; but see Leather 1988). Hence, once they reach a threshold mass, males may experience greater selection for early pupation, than for continued growth to a higher body mass (i.e. Slansky 1982; Slansky & Scriber 1985). Early pupation by males may decrease larval mortality from natural enemies (Schultz 1983; Feeny et al. 1985; Leather 1985; Wisdom 1985; but see Clancy & Price 1987), and/or enhance access to mates (Slansky & Scriber 1985).

In mountain birch, Tuomi et al. (1988b) found that defoliation-induced increases in phenolic concentrations was a localized response; defoliation had no effect on phenolic levels in adjacent, undamaged branches. They argued that the

localized response is consistent with the "incidental effect" hypothesis: an increase in phenolic concentrations is an incidental effect of defoliation-induced alterations in the carbon/nutrient balance of the branch. They argue that a systemic response would be consistent with the "evolved defense" hypothesis (Tuomi et al. 1988b, 1991).

In the experiment reported here, the branches on which insects were confined were left undamaged when the rest of the tree was defoliated as part of the defoliation treatment. Hence, the effect of defoliation on male pupal mass observed in this study is evidence that the induced-response in paper birch is systemic, and supports the hypothesis that the response is an active, evolved defense against herbivores (Tuomi et al. 1988b, 1991).

The results of the laboratory experiment provide more evidence for induced resistance. Larvae feeding on defoliated trees had lower relative growth rates during the fourth instar feeding trial, and over the duration of the experiment (from the beginning of the fourth instar until pupation) (Table 8).

The effects of defoliation were not large. However, demonstrating inducible-resistance is problematic (Neuvonen & Haukioja 1985; Haukioja & Neuvonen 1987). This experiment was a conservative test of induced-resistance, and any detectable effect can be confidently considered real for the following reasons: 1) The trees were artificially defoliated. Several of studies with different *Betula* species have shown natural insect defoliation results in a stronger induced response than artificial defoliation (Haukioja & Neuvonen 1985a; Neuvonen et al. 1987; Hartley & Lawton 1987; Hartley 1988; Hartley & Firn 1989). 2) Larvae were not fed damaged leaves, but were fed intact leaves adjacent to damaged leaves. The significant effect suggests a systemic response to defoliation. Haukioja & Hanhimäki (1985) also found a systemic response in *Betula pubescens*; phenolic concentrations increased in intact leaves adjacent to manually torn leaves. However, the torn leaves were of

lower quality to the geometrid *Epirrita autumnata* than the adjacent intact leaves. Furthermore, Hartley & Firn (1989) found that artificial damage increased phenylalanine ammonia lyase (PAL) activity in the damaged leaves of *Betula pendula*, but had no effect on PAL activity in the intact adjacent leaves (insect damage did increase PAL activity in the adjacent undamaged leaves). This may also explain why defoliation in this study had no detectable effect on phenolic concentrations (only intact leaves were analyzed).

3) Foliage sampling (i.e. for chemical analysis, pressure chamber measurements, insect rearing) may have "induced" the control trees, decreasing the resistance differential between them and the defoliated trees (Neuvonen & Haukioja 1985; Haukioja & Neuvonen 1987).

4) The existence of "communication" between the defoliated trees and the adjacent control trees (*sensu* Baldwin & Schultz 1983) may have induced higher levels of resistance in the control trees. Haukioja et al. (1985b) reported statistically valid evidence that "communication" occurs in *Betula pubescens* between defoliated and nondefoliated plants, resulting in higher levels of resistance in the nondefoliated trees. In this study, all control trees were within 4 m of a defoliated tree, creating the possibility that inter-tree "communication" may have obscured treatment effects.

5) Quantitative variation in phytochemistry within and between trees can be extensive (Schultz et al. 1982; Baldwin et al. 1987), reducing the probability of detecting treatment effects (Haukioja 1991). Replication in this study may have been inadequate to detect differences in phenolic concentrations between the defoliated and control trees. The coefficient of variation for the phenolic analysis was 33.8% and 36.7% in 1988 and 1989, respectively (as compared to 10.1% and 12.5 % for nitrogen in 1988 and 1989, respectively).

Short-Term or Long-term Induction?

Since trees were also defoliated during 1987, it is not possible to determine if

the negative effects of defoliation on insect performance observed in 1988 were due to rapid-inducible resistance (RIR) and/or long-term inducible resistance (DIR). To provide a test of DIR, trees defoliated during 1987 and 1988, were not defoliated during 1989. However, there were no differences between the defoliated trees and the control trees in insect performance or leaf chemistry in 1989 (Figure 36). Werner (1979) found the DIR of paper birch to intensify with each successive year of defoliation. If DIR was not detectable in 1989, following two consecutive years of defoliation, then it probably did not contribute to the response observed in 1988, after only one year of defoliation. Hence, the effects observed during 1988 should be attributed to RIR. However, it is possible that the effects observed in 1988 resulted from a synergistic interaction between RIR and DIR.

Several reasons may account for the lack of detectable DIR. DIR may not occur in the trees studied. Other tests of DIR have also failed to detect significant effects (Williams & Myers 1984; Roland & Myers 1987; Myers & Williams 1987). The 40% defoliation treatment may have been insufficient to induce long-term resistance. Werner (1979) found that DIR of paper birch intensified as the level of defoliation increased. In this study, defoliation had no effect on phenolic or nutrient concentrations. The lack of increased concentrations of foliar phenolics in the absence of a defoliation-induced nutrient deficiency is consistent with the C/N balance hypothesis ("incidental effect hypothesis") of DIR (Tuomi et al. 1984, 1988a,b, 1991; Bryant et al. 1988).

Tests of DIR are prone to Type II errors (Haukioja 1991). Some of the same factors possibly decreasing the sensitivity of the RIR test could have prevented the detection of DIR. Specifically, artificial instead of real defoliation, "communication" between control and treatment trees, induction of control trees as a result of foliage sampling and insect feeding during the field experiments of 1988 and 1989, and a high level of variation in phenolic chemistry between and within trees may have

decreased the probability of detecting a treatment effect.

Phenological Patterns of Defense

Secondary metabolism is limited in expanding leaves which are still undergoing cell division because of cellular level constraints on biosynthesis, compartmentation, and substrate demands for primary metabolism (Böhm 1977; Luckner & Nover 1977; Luckner 1980; Lindsey & Yeoman 1983) (see Chapter 1 for more detailed discussion). As a consequence, young leaves often suffer greater levels of herbivory than mature leaves (Raupp & Denno 1983; Krischik & Denno 1983; Coley 1983; Landsberg 1988; Mitchell Aide & Londoño 1989; Ernest 1989; Núñez-Farfán & Dirzo 1989). However, the "twin-peaks" hypothesis (presented in Chapter 1) proposes that some plants have evolved adaptations to protect young leaves with secondary metabolites.

Highly toxic, low molecular weight "qualitative defenses" are at peak concentrations (but still present in minute quantities) in the young foliage of many plants (McKey 1974,1979; Dement & Mooney 1974; Cates & Rhoades 1977; Potter & Kimmerer 1986). These compounds may be synthesized during the previous year and stored in the bud where their concentration is highest (e.g. Palo 1984). As the leaf expands, their concentration declines as they are diluted by biomass accumulation and/or cycled into primary metabolism. As the leaf matures, increased concentrations of high-molecular weight polymers (such as tannins and lignin) and enhanced leaf toughness result in a second, late season peak in leaf defense (Feeny 1970; Dement & Mooney 1974; Haukioja et al. 1978a; Hough & Pimentel 1978; Coley 1983; Potter & Kimmerer 1986; Mattson & Scriber 1987).

As an alternative to internal concentrations of "quantitative defenses" for the

protection of immature leaves, plants may secrete pre-formed resins over the surface of expanding leaves (Rhoades 1977; Fahn 1988). Cottonwood (*Populus deltoides*) buds accumulate resin in late summer and secrete it over emerging leaves the following spring, thus enhancing the resistance of young leaves to a leaf feeding beetle (Curtis & Lersten 1974). Concentrations of the resin decline rapidly after budbreak, possibly as a result of dilution as the leaf expands (Shain & Miller 1982). Gypsy moth performs best on the youngest leaves of some of its hosts (Raupp et al. 1988; Hough & Pimentel 1978). However, gypsy moth suffers high mortality when feeding on the young leaves of cottonwood; larval performance improves as the leaves age (Meyer & Montgomery 1987). Expanding leaves have the highest concentrations of total phenolics, presumably because of the phenolic resin coating their surface (Meyer & Montgomery 1987).

During 1988, total phenolic concentrations increased as leaves aged (Figure 24a). This pattern is common (Feeny 1970; Haukioja et al. 1978a; Krischik & Denno 1983; Coley 1983; Raupp & Denno 1983; Mattson & Scriber 1987). However, the pattern was different in 1989, when an additional foliage sample was taken as leaves were expanding. Concentrations of total phenolics were highest in the expanding leaves of birch, and then declined into mid-summer before increasing again (Figure 24b). The expanding leaves were covered with a shiny, sticky resin that disappeared within two weeks of leaf emergence (*personal observation*). The composition of this resin is unknown, but the phenological pattern of total phenolic concentration is consistent with the hypothesis that the resin contains phenolic compounds, the concentration of which declines as it is weathered and/or diluted by leaf expansion. Reichardt et al. (1984) found winter dormant buds of Alaskan paper birch (*Betula resinifera*) to contain large quantities of an uncharacterized resin that deterred hare and moose browsing. It is possible that dormant buds of *Betula papyrifera* also contain resin which is secreted over the expanding leaves in the

spring.

Correlative evidence suggests that this phenological pattern of defense may increase the resistance of young birch leaves to gypsy moth in manner similar to that observed in cottonwood by Meyer & Montgomery (1987). The relative growth rate of second instars was inversely correlated with the age of the leaves on which they fed (Figure 26). This pattern may result because the youngest leaves have the highest concentrations of the external leaf resin.

Soil Moisture and Larval Performance

Outbreaks of defoliating insects have been associated with drought (Mattson & Haack 1987a,b). However, the few experiments conducted with woody plants have generally found drought stress to have little or no effect on their resistance to defoliators (e.g. Miles et al. 1982; Young & Hall 1986; Wagner 1986; McCullough & Wagner 1987; Wagner & Frantz 1990). Talhouk et al. (1990) did find gypsy moth performance to improve on one paper birch clone experiencing drought stress. However, they found no difference in another clone.

During 1988, measurements of plant growth, photosynthesis, stomatal conductance, and pre-dawn water potential all indicated that the low soil moisture treatment resulted in the imposition of drought stress (Chapter 2). Concentrations of total phenolics were also highest in the trees receiving the least water (Figure 20). However, the irrigation treatment had no affect on the performance of gypsy moth larvae in the laboratory or in the field.

Dry weather has been implicated as a factor in gypsy moth outbreaks (Leonard 1974; Campbell & Sloan 1977b; Elkinton & Liebold 1990). However, the results of this study would seem to indicate that if drought does favor gypsy moth

outbreaks, the effect is not mediated through host quality of one of its preferred hosts, paper birch.

Soil Fertility and Larval Performance

The performance of leaf-feeding insects is generally enhanced by host fertilization, which commonly decreases the concentrations of carbon-based allelochemicals while increasing the nutrient content of the plant (e.g. Shaw et al. 1978; Lincoln 1985; Brewer et al. 1985; Larsson et al. 1986a; Mihaliak et al. 1987; Bryant et al. 1987b; Lightfoot & Whitford 1987,1989). In this study, however, fertilization-induced changes in host quality had no effect on gypsy moth relative growth rates, pupal mass, or larval duration.

Compensation For Low Host Quality

Slansky (1982) and Slansky & Scriber (1985) predicted that insects should experience selection for plastic consumption rates and food utilization efficiencies in order to maintain optimal growth rates and achieve optimal final weights. Moran & Hamilton (1980) argued that if the low nutritive quality of plants results in increased consumption by herbivores, then plants do not necessarily benefit from increased concentrations of digestibility-inhibiting secondary compounds or low levels of nutrients. Contrary to these predictions, Neuvenon & Haukioja (1984) found that *Epirrita autumnata* did not respond to defoliation-induced reductions in the host quality of mountain birch by increasing consumption to compensate for defoliation and phenologically induced reductions in host quality, respectively. However, the geometrid *Apocheima pilosaria* did increase its consumption in response to leaf damage of mountain birch (Fowler & MacGarvin 1986).

In fact, many studies have found insects to increase their consumption rate to compensate for low levels of foliar nitrogen (e.g. Slansky & Feeny 1977; Lawson et al. 1982; Slansky & Scriber 1985; Karowe & Martin 1989; M.F.J. Taylor 1989; Simpson et al. 1990; Raubenheimer & Simpson 1990; reviewed in McNeill & Southwood 1978, Mattson 1980, Scriber & Slansky 1981, Slansky 1982; Simpson & Simpson 1990). Fewer studies have reported increased consumption in response to increased levels of putative digestive-inhibiting secondary metabolites (e.g. Johnson et al. 1986; Larsson et al. 1986b).

Scriber & Slansky (1981) predicted compensatory feeding to be more common trait of generalist than specialist feeders because of the great variation in the quality of their diverse hosts. Based on this hypothesis, gypsy moth should show pronounced compensatory abilities. Indeed, Sheppard & Friedman (1990) found that older gypsy moth larvae were able to compensate for their poor ability to assimilate pine foliage by increasing consumption.

In this study, substantial evidence suggests that compensatory feeding is responsible for the lack of treatment effects on gypsy moth growth rates and pupal mass. As the level of fertilization decreased, the ability of fourth instars to convert digested food into biomass (ECD) decreased (1989 laboratory experiment) (Figure 27). Larvae compensated for the inverse relationship between ECD and fertilization by increasing their rate of consumption (Figure 27). Compensation was complete, as the rate of fertilization had no effect on growth rate, larval duration, or pupal mass (Figure 28).

A reduction in ECD results from an increased rate of respiration. Increased respiration may have resulted from increased activity associated with the increased rate of feeding, or by metabolic costs associated with detoxification of an unknown toxin. The ECD of fourth instars was not correlated with foliar nitrogen levels or any of the other foliage parameters quantified, so the effect was due to another

factor affected by fertilization. The effect of terpenes is one possibility. Terpene concentrations are often inversely correlated with plant growth and nitrogen, and often decrease in fertilized plants (Mihaliak & Lincoln 1985; Mihaliak et al. 1987; Bryant et al. 1987a), and *Betula* is known to have a well developed terpenoid chemistry (Reichardt 1981; Palo 1984; Bryant et al. 1987a; Pokhilo et al. 1990). Furthermore, certain terpenoids are known to have deterrent and/or toxic effects on gypsy moth (Barbosa & Krischik 1987; Bowers & Puttick 1989). Nitrogen-based toxins such as alkaloids usually increase in fertilized plants (Mattson 1980). Alkaloids, which are generally toxic to gypsy moth larvae (Miller & Feeny 1983; Barbosa & Krischik 1987), have been detected in *Betula nana* (Prudhomme 1983), but are not known to occur in paper birch (Barbosa & Krischik 1987).

During the 1989 laboratory experiment, the ability of fourth instars to digest foliage (AD) was negatively correlated with foliar phenolic concentrations and positively correlated with foliar water content (Table 9) (Figure 29). This is consistent with the hypothesized role of phenolic compounds as digestibility-reducers (Feeny 1976; Rhoades & Cates 1976). Tremulacin, a phenolic glycoside from quaking aspen (*Populus tremuloides*) foliage, has also been found to reduce the AD of gypsy moth (Lindroth & Hemming 1990). Alternatively, decreased AD may have resulted from decreased mid-gut retention time as consumption rates increased (Slansky & Scriber 1985). Likewise, other studies have also found leaf water content to affect host quality (Scriber 1977, 1979b; Horton 1989; Van't Hof & Martin 1989a,b). Fourth instar gypsy moths were able to compensate for decreased AD by increasing their consumption rates (Figure 29). Compensation was complete; phenolic concentrations, therefore, had no effect on growth rate, pupal mass, or larval duration (Figure 30). Hence, fourth instars demonstrated the ability to compensate for both pre- (lower ECD) and post-digestive (lower AD) effects of reduced foliage quality. However, there may be costs associated with increasing

consumption, in the form of increased exposure to predators, parasites, and disease (Schultz 1983; Slansky & Scriber 1985).

There was no relationship between leaf sugar concentration and any measure of larval performance in either year. This contrasts with other studies that found gypsy moth larval performance and host preference to be correlated with foliar carbohydrate concentrations, and sugar:tannin ratios, respectively (Lechowicz 1983; Valentine et al. 1983).

Pupal mass, larval duration, and overall growth rates of larvae were not correlated with fourth instar relative growth rate (Figures 31-33). They were, however, highly correlated with relative growth rate during the second instar (Figures 31-33). This suggests that the quality of food consumed by young insects is much more critical for the overall performance of the insect than is the quality of food consumed by older larvae (T.C.R. White 1974,1978,1984). Young gypsy moth larvae have higher nitrogen requirements than older larvae (Montgomery 1982) and may be more sensitive to the protein-binding affects of tannins (Schultz & Lechowicz 1986).

For logistical reasons, insect nutritional indices studies are usually conducted using only penultimate or final instars. The conclusions of such studies may have limited ecological or agricultural relevance. The results of this study also suggest that valid conclusions regarding gypsy moth-host interactions may be obtained economically with short-term feeding experiments using second instars.

Comparison of Field and Laboratory Studies

There are advantages and disadvantages associated with both field and laboratory insect feeding assays. Laboratory experiments offer the advantage of a

highly controlled environment. However, detached foliage may differ chemically from that experienced by larvae feeding in the field (Miller 1987; Wolfson 1988). Natural conditions are also difficult to simulate in field experiments. Larvae must be confined to the experimental plant. However, bagging may also alter host chemistry. Furthermore, predation on experimental insects may reduce the power of experiments. Predation was severe during both years of this study. The best solution may be to conduct field and laboratory experiments simultaneously, and to compare their results.

The results of the field and laboratory experiments were much better correlated during 1989 than they were during 1988 ($r=0.58$ and 0.30 for larval duration, and 0.30 and 0.01 for pupal mass during 1989 and 1988, respectively). This was probably because the 1989 field and laboratory experiments were initiated on the same day with the same cohort of second instars. During 1988, the field experiment was initiated in late May with second instars, while the field experiment was initiated in mid-June with fourth instars from a different cohort.

The correlation between the 1989 field and laboratory experiments indicates that confidence can be placed in the conclusions reached from the more highly controlled, but more artificial, laboratory experiment.

CHAPTER FOUR

Variation in the Resource Allocation Patterns of Paper Birch: Implications for Resistance to Bronze Birch Borer

Mattson et al. (1988) predicted that the level of resistance evolved by a plant against an herbivore will vary inversely with the ability of the plant to compensate for injury caused by the herbivore's feeding. The ability of woody plants to compensate for the loss of vascular and cambial tissue is limited. Hence, trees are predicted to be well defended against insects that feed within the phloem (Mattson et al. 1988).

Conifers resist bark beetles by means of wound-induced hypersensitive responses which result in the accumulation of secondary metabolites toxic to the beetles, and a constitutive terpenoid resin system which may repel colonizing beetles (Berryman 1972; Raffa & Berryman 1982; Cook & Hain 1986; Christiansen et al. 1987; Lorio 1988). Bark beetles can successfully colonize vigorous conifers only when they overwhelm the defenses of the tree by mass attack (Raffa & Berryman 1983, 1987; Mulock & Christiansen 1986).

Much less is known about the defenses of deciduous trees against phloem-feeding wood-borers. There are few phloem-feeding scolytids associated with deciduous trees (Ohmart 1989). Beetles in the family Buprestidae are among the most important phloem colonizers of living deciduous trees. In North

American forests, the bronze birch borer (*Agilus anxius* Gory) is especially prominent. The bronze birch borer is endemic to North America, occurring throughout the vast range of its important native hosts: *Betula papyrifera*, *B. alleghaniensis* (= *B. lutea*), and *B. populifolia* (Fisher 1928). Its range has been extended due to ornamental plantings of native and introduced hosts (largely *Betula pendula*).

The biology of the bronze birch borer has been described in some detail (Anderson 1944; Barter & Brown 1949; Barter 1957; Carlson & Knight 1969; Loerch & Cameron 1983, 1984; Akers & Nielsen 1984, 1990a,b). Larvae feed under the bark on the phloem and cambium, scarring the xylem. They pupate within the tree in one to two years, depending on host condition and climate. Adults emerge in late-May through August; 90% of adult emergence occurs in June in central Michigan (Herms *unpublished data*). Females oviposit on the bark; first instars bore directly into the tree upon eclosure.

Tree Stress and Resistance to Wood Borers

Circumstantial evidence indicates that stressed trees are most susceptible to colonization by buprestids (Nielsen 1981). Decreased resistance of *Quercus* spp. to twolined chestnut borer (*Agilus bilineatus*), *Populus* spp. to *A. liragus*, and *Betula* spp. to *A. anxius* has been associated with drought, defoliation, disease, and low levels of stored carbohydrates (Balch & Prebble 1940; Anderson 1944; Hawboldt 1947; Hawboldt & Skolko 1948; Nash et al. 1951; Clark & Barter 1958; Staley 1965; Barter 1957, 1965; Nichols 1968; Carlson & Knight 1969; Dunbar & Stephens 1975, 1976; Wargo 1977b; Haack & Benjamin 1982; Côté & Allen 1982; Houston 1987; Dunn et al. 1987, 1990a). The scolytid *Phloeotribus liminaris* was reported to

kill black cherry (*Prunus serotina*) weakened by defoliation (Schultz & Allen 1977). *Agilus* spp. preferentially colonize trees that have been experimentally girdled (Anderson 1944; Dunn et al. 1986,1987). However, direct evidence that natural forms of stress predispose trees to colonization by buprestids is nonexistent (Nielsen 1981).

It has been proposed that stress may decrease plant resistance to herbivores by enhancing the nutritional quality (T.C.R. White 1978,1984), or compromising the chemical defenses, of plants (Rhoades 1983). The low nutritive quality of phloem and xylem tissue is responsible for the low feeding efficiency and protracted development of wood-borers (Haack & Slansky 1987). However, little is known about the resistance mechanisms of deciduous trees to phloem-feeding insects, much less how they may be affected by stress.

Wound Responses of Phloem and Resistance to Wood Borers

Phloem responses to insect-feeding injury (and other wounds) consist of two phases: 1) the immediate synthesis of specific, low molecular weight, secondary metabolites (phytoalexins), which may slow the growth of invading organisms; and 2) subsequent formation of wound periderms, which isolate the wound, further inhibit colonizing organisms, and reestablish phellogen and cambium integrity (Mullick & Jensen 1972; Mullick 1975,1977; Biggs et al. 1984; Kemp & Burden 1986; Bostock & Stermer 1989).

The responses of phloem to wounding were similar in a number of conifer and angiosperm trees, including paper birch (Mullick 1975,1977; Biggs et al. 1984; Biggs 1985). Within hours of wounding, adjacent cells form a zone of water impervious tissue immediately internal to the wound (Mullick 1975,1977; Biggs et al.

1984; Biggs 1985; Bostock & Stermer 1989). The heavily lignified and suberized impervious zone prevents apoplastic and symplastic transport of fluid, isolating the wound from neighboring, undamaged cells (Biggs 1985). Within a few days, adjacent cells begin dividing, forming necrophylactic periderm (which compartmentalizes the wound from healthy tissue), and exphylactic periderm (which closes the wound to the external environment) (Mullick & Jensen 1972; Mullick 1977; Wilson & Grange 1984; Biggs et al. 1984; Biggs 1985).

Wound periderms ("callus" tissue), consist of the phellogen (a zone of meristematic cells), phelloderm (parenchyma cells formed inwardly from the phellogen), and phellem (cork-like tissue formed outwardly from the phellogen) (Biggs et al. 1984; Biggs 1985, 1986; Bostock & Stermer 1989). As periderm cells differentiate into xylem, phloem, and cork, only the meristematic cells of the cambium and phellogen continue dividing (Wilson & Grange 1984). Phellem cells accumulate large quantities of suberin (a heteropolymer composed of aliphatic components attached to a phenolic matrix), lignin, and other phenolic compounds, and subsequently die (Biggs 1985, 1986; Bostock & Stermer 1989). As the phelloderm gives rise to new phellem, layers of dead phellem are compressed to form the corky periderm surface (Biggs 1986; Bostock & Stermer 1989).

Although phloem responses to biotic and abiotic wounding are qualitatively similar, wounding by insects and pathogens may enhance specific components, and/or elicit *de novo* synthesis of specific secondary metabolites (phytoalexins) (Vance et al. 1980; Biggs 1984; Kemp & Burden 1986; Bostock & Middleton 1987; Fernandes 1990). Mattson et al. (1988) predict that because of the intimacy of interaction between trees and wood borers, coupled with the debilitating effects of phloem destruction, trees will evolve specifically targeted, potent defenses against phloem colonizers. Evolutionary responses of plants to various pathogens and herbivores may be responsible for the diversity in structure of their phytoalexins

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(Kemp & Burden 1986; Bostock & Stermer 1989; Fernandes 1990).

In tandem with phytoalexin synthesis, the generalized wound response may be an important resistance mechanism of deciduous trees to buprestids (Dunn et al. 1990b). Lignin decreased the growth, survival, and fecundity of the bark beetle *Dendroctonus micans*, in a dosage-dependent manner (Wainhouse et al. 1990). In many cases, disease resistance of plants is associated with rapid lignification in response to infection (Vance et al. 1980; Bostock & Stermer 1989).

Heering (1956) proposed callus formation to be the most important resistance mechanism of beech (*Fagus sylvatica*) against *Agrilus viridis*. Callus tissue impregnated with lignin and other secondary metabolites, may crush and/or intoxicate young larvae. Consistent with this hypothesis, Anderson (1944) discovered that girdled paper birch and aspen (the portion of the trunk below the girdle) were substantially more susceptible to successful buprestid colonization. Anderson (1944) concluded that high cambial activity was a prerequisite for resistance. Barter (1957) also found high levels of resistance to be associated with vigorous cambial activity. Dunn et al. (1987) also proposed that callus formation was an important resistance mechanism of oak to twolined chestnut borer. They found that oaks successfully colonized by twolined chestnut borer produced significantly less callus than did nonattacked trees (Dunn et al. 1990b). However, Carlson & Knight (1969) discounted this hypothesis and instead speculated that suffocation of larvae by the exudation of phloem sap under pressure is responsible for the resistance of deciduous trees to buprestids.

Tree Stress Slows Wound Responses

The chemical resistance of conifers to bark beetles requires a large expenditure of energy (Wright et al. 1979; Miller & Berryman 1985; Lorio 1986,1988; Waring & Pitman 1985; Christiansen et al. 1987). Bark beetle resistance is generally compromised when carbon assimilation is limited by factors such as drought, competition, or defoliation (Ferrell 1978; Wright et al. 1979,1984; Larsson et al. 1983; Waring & Pitman 1983,1985; Hard 1985; Christiansen et al. 1987; Waring 1987). The same may be true of deciduous tree resistance to wood borers (Dunn et al. 1987). Their rate of wound response is directly correlated with growth (Neely 1970,1983; Solomon & Blum 1977), and is slowed by drought (Puritch & Mullick 1975; Biggs & Cline 1986) and defoliation (Wargo 1977a).

Dunn et al. (1986) and found that oak trees with low levels of stored starch during winter were preferentially colonized by twolined chestnut borer the following summer. However, subsequent wounding experiments failed to show any relationship between levels of either winter or summer stored carbohydrates and callus formation or constitutive and induced levels of phenolic compounds in the phloem (Dunn et al. 1990b). There was also no correlation between stored carbohydrates and the strength of wound-repsonse in Norway spruce (*Picea abies*) (Christiansen & Ericsson 1986) .

The flux of currently available carbon within the tree may be more important than levels of stored reserves in supporting defensive reactions (Christiansen & Ericsson 1986; Christiansen et al. 1987; Dunn et al. 1990b). Cambial activity leading to wood production is directly dependent on the supply of current photosynthate (Glerum 1980), and the rate of callus growth is largely regulated by the flow of carbohydrates and growth regulators from the canopy (Neely 1979). The observation by Anderson (1944) that girdled trees retain resistance above the girdle,

while becoming highly susceptible below, supports this hypothesis. Girdling the phloem disrupts the downward transport of photosynthate, but has little effect on upward transport of water, nutrients, and solutes in the xylem (Noel 1970). Girdling isolates the portion of the trunk below the girdle from current photosynthate originating in the canopy. However, the entire length of the trunk retains access to carbohydrates stored in the roots. Girdling as an experimental technique provides the opportunity to study potential resistance mechanisms in the absence of confounding environmental and genetic factors.

Plant Reproduction and Wood-Borer Resistance

If resistance to wood-borers is heavily dependent on the flux of current photosynthate, then the presence of other strong photosynthetic sinks competing for a limited supply of photosynthate may compromise defense. For example, reproduction comes at a high physiological cost, obvious in the form of reduced vegetative growth (Harper & White 1974; Callow 1979; Bell 1980; Willson 1983; Luken 1987; Clark & Clark 1988; Snow & Whigham 1989; Dick et al. 1990). However, this cost may not be universal (Tuomi et al. 1983; Reekie & Bazzaz 1987c; Reznick 1985). Physiological trade-offs between growth and defensive secondary chemistry are also well documented (Bryant et al. 1983; Krischik & Denno 1983; Coley et al. 1985; Loehle 1988; Bazzaz et al. 1987; Pimentel 1988). Resource allocation patterns are the expression of source-sink interactions within the plant and their control on assimilate partitioning. Complex changes in patterns of assimilate partitioning are required to bring about the maturation of inflorescences, fruits, and seeds. These changes may affect traits conferring plants with resistance to herbivores. Few studies, however, have examined the potential interactions

between reproduction and defense.

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

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

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

wound-induced hypersensitive responses may contribute to increased bark beetle and pathogen susceptibility. Reproductive effort may interact synergistically with environmental stress to suppress conifer resistance to bark beetles and contribute to outbreaks.

Birch Reproduction and Resistance to Bronze Birch Borer

Paper birch is monoecious, with pistillate (female) and staminate (male) catkins produced as separate structures (MacDonald & Mothersill 1983). Male catkins are produced at the end of indeterminate long-shoots in mid- to late-summer, following the termination of shoot elongation. They overwinter, elongating and releasing pollen as vegetative buds open in spring. Female inflorescences emerge from overwintering-buds on short shoots as buds break in spring. Female catkin maturation commences upon pollination, and continues throughout the growing season, with seed filling in late summer.

The pistillate catkins of *Betula* are strong photosynthetic sinks, competing with and decreasing resource allocation to vegetative growth (Kessler 1969; Gross 1972; Tuomi et al. 1982b; Ceasar & MacDonald 1983). Individual and stand-level dieback has been associated with especially heavy seed crops (Gross 1972; Houston 1987). This may be a cause and effect relationship, if increased female reproductive effort diverts photosynthate from the support of defensive reactions.

Objectives

The resistance of paper birch to BBB may be dependent on rapid callus formation, the strength of which may be dependent on the supply of current photosynthate. From this hypothesis can be derived several testable predictions: 1) the resistance of birch to bronze birch borer will be correlated with rate of callus formation; 2) rate of callus formation will be correlated with the rate of net photosynthesis; 3) environmental stresses which affect net photosynthesis will also affect bronze birch borer resistance; 4) increased female catkin production decreases the supply of photosynthate available to support callus formation and thus will be inversely correlated with bronze birch borer resistance; 5) callus formation and bronze birch borer resistance will be decreased below the girdle of girdled trees.

These predictions were tested in two experiments: (1) in a controlled field experiment, paper birch was subjected to a factorial combination of three levels of soil moisture and nitrogen, and two levels of defoliation. Treatment effects on paper birch growth, photosynthesis, reproductive effort, rate of callus formation, and colonization by bronze birch borer were quantified; (2) a girdling experiment, conducted in a native stand of paper birch, the effects of trunk girdling on colonization by bronze birch borer and rate of callus formation were quantified.

METHODS AND MATERIALS

Controlled Field Experiment

The experimental site, trees, design, and plant physiological measurements were described in Chapter 2. Additional methods are reported below.

Estimation of Bronze Birch Borer Colonization

The population density of bronze birch borer was enhanced at the study site each year by felling a number of large, heavily infested trees and placing the bolts throughout the study site before adults began emerging in June. Bronze birch borer colonization was estimated by measuring the length of the portion of the trunk exhibiting external symptoms of infestation, including adult and parasite emergence holes, wood-pecker feeding holes, and bark ridges resulting from callus formation over larval galleries. The infested length was divided by the total height of the tree to obtain the percent of total length of the trunk infested (% of trunk infested).

Colonization was quantified during the spring following larval establishment and then again during the summer. This allowed adequate time for symptoms to manifest themselves. Several trees died during the study. Upon death, trees were felled, their bark removed, and length of the portion of the infested portion of the trunk measured directly. In addition, a number of local native and landscape birches were felled and debarked. Inspection of the debarked trees indicated that estimations of colonization based on external signs and symptoms provided accurate relative measures of degree of colonization. When estimations were made during

the spring following larval establishment, the major source of error was in distinguishing trees with very slight infestation from trees with no infestation.

Wounding Studies

On 13 April 1988, two small branches were pruned from the south side of each tree at their point of attachment to the trunk. At the time of pruning, the horizontal diameter (width) of each wound (mm) was measured, and ranged from 5.3 to 14.9 mm. The width was measured because callus develops from around the margin at the sides of the wound toward the center (Neely 1979). The width of each wound was measured again on 10 August 1988, and the amount of callus formation (mm) was determined by subtraction. The rate of callus formation (mm/day) was calculated by dividing this value by the number of days between measurements.

During 1989, only one pruning wound was made per tree. The wound was made on 11 April 1989 following the same procedures used during 1988. The initial width of wounds ranged from 4.9 to 10.6 mm. The rate of callus formation between 15 June - 31 August was determined as in 1988. This should be the critical time for the manifestation of resistance, since larvae are establishing within the tree then.

Reproductive Effort

The total number of male and female catkins was counted on all trees during 1988 and 1989. Sex ratios were determined for each tree as:

$$\text{sex ratio} = \text{total male catkins} / (\text{total male} + \text{female catkins})$$

Reproductive effort (RE) has been defined as the proportion of the total energy budget of an organism devoted to reproductive processes (Hirshfield & Tinkle 1975). Male and female RE of paper birch were estimated as follows: to determine mean individual male and female catkin biomass for each tree, 15 male and 15 female catkins were sampled from each tree, oven dried to constant weight, and weighed. Total male and female catkin biomass was estimated separately for each tree, as the product of the mean catkin biomass for the tree and the total number of catkins on the tree. Total foliage biomass was estimated as the product of specific leaf mass and total number of leaves per tree (see Chapter 2 for details). For each tree, reproductive effort was calculated separately for each sex as:

$$\text{reproductive effort} = \text{sex specific catkin biomass} / (\text{leaf biomass} + \text{total catkin biomass})$$

Girdling Experiment

On 11 May 1988, in a mono-specific, natural stand of paper birch colonizing an old field in Midland, Michigan, 12 trees were girdled and 12 trees were selected as paired controls. Pairings were made based on similarity in trunk diameter, canopy condition, and proximity of location within the stand. The trunk diameter of the trees at a point 1.5 m from the ground ranged from 4.0 to 10.3 cm, and the trees ranged from 7.3 to 10.4 m in height.

Trees were girdled completely by removing a 10 cm wide band of phloem from the entire circumference of the trunk. The midpoint of the girdle was 1.5 m from the ground. Care was taken to avoid damaging the xylem during the girdling process. The trunk sections on the undamaged trees corresponding to sections

above and below the girdle on the wounded trees served as controls. Hence, the experiment consisted of four treatments: above and below the girdle, and the corresponding locations on the control trees.

The effects of girdling on the rate of callus formation were determined by artificially wounding all trees on 21 June, coinciding with the establishment of newly hatching bronze birch borer larvae. Trees were wounded by removing a phloem disc 27.5 mm in diameter with an increment hammer. Four wounds were made on each tree, two 25 cm above and two 25 cm below the girdle, one on the north and one on the south side of each tree. The width of the wounds was measured on 6 September 1988, and the rate of callus formation quantified, as before.

Trees were felled on 7 September 1988, and completely debarked from 1 m below the girdle to 1 m above the girdle. Bronze birch borer colonization was quantified by counting by measuring the length of each gallery with a planimeter.

Statistical Analysis

Results of the controlled field study were analyzed as described in Chapters 2 and 3. Both bronze birch borer colonization and birch reproductive effort data were transformed to their arcsin equivalents before ANOVA (Little & Hills 1978). The girdling experiment was a randomized complete block design, with each pair of trees serving as a block. The data were analyzed by ANOVA.

RESULTS

Controlled Field Experiment

Increasing irrigation linearly increased birch resistance to bronze birch borer in 1988 ($F=4.16$; d.f. = 1,54; $P=0.046$) (Figure 37). However, soil moisture had no significant effect on bronze birch borer resistance during 1989. Irrigation also had significant positive effects on photosynthesis, stomatal conductance, and trunk expansion in 1988 (Figures 7,10, & 11, Chapter 2). None of the other main treatment effects or their interactions had significant effects on bronze birch borer resistance in 1988 or 1989.

Rate of callus formation increased exponentially with increasing photosynthesis in 1988 ($r=0.68$, $P<0.001$, $n=72$) (Figure 38). However, there was no significant relationship between rate of callus formation and photosynthesis in 1989. Callus formation also increased exponentially with trunk expansion during both 1988 ($r=0.70$, $P<0.001$, $n=72$) and 1989 ($r=0.57$, $P<0.001$, $n=66$) (Figure 39).

Resistance to bronze birch borer in 1988 and 1989 showed significant negative curvilinear relationships with photosynthesis ($r=-0.67$ and $r=-0.55$, respectively), trunk expansion ($r=-0.67$ and $r=-0.55$, respectively), and rate of callus formation ($r=-0.72$ and $r=-0.63$, respectively) (Figures 40,41, and 42).

N fertilization had a significant effect on the sex expression of birch during both 1988 ($F=3.74$; d.f. = 2,40; $P=0.044$) and 1989 ($F=3.52$; d.f. = 1,38; $P=0.040$) (Figure 43). Trees receiving no nitrogen had predominantly female expression, while trees receiving medium and high levels of nitrogen had predominantly male expression (Figure 43). The effects of nitrogen on reproductive effort were similar (Figure 44). Trees receiving no nitrogen partitioned a much higher proportion of their total reproductive biomass into female reproductive effort during both 1988

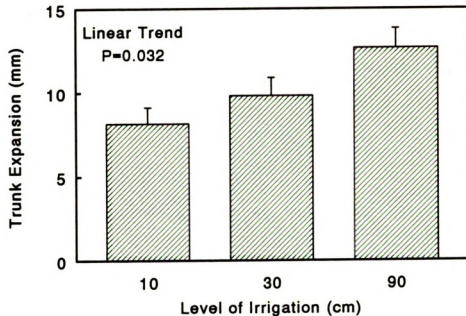
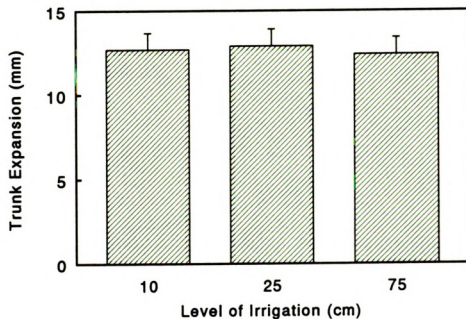
A**B**

Figure 37. The effects of irrigation on the resistance of paper birch (*Betula papyrifera*), to the bronze birch borer, (*Agrilus anxius*) during 1988 (A) and 1989 (B) (mean $\pm$ standard error).

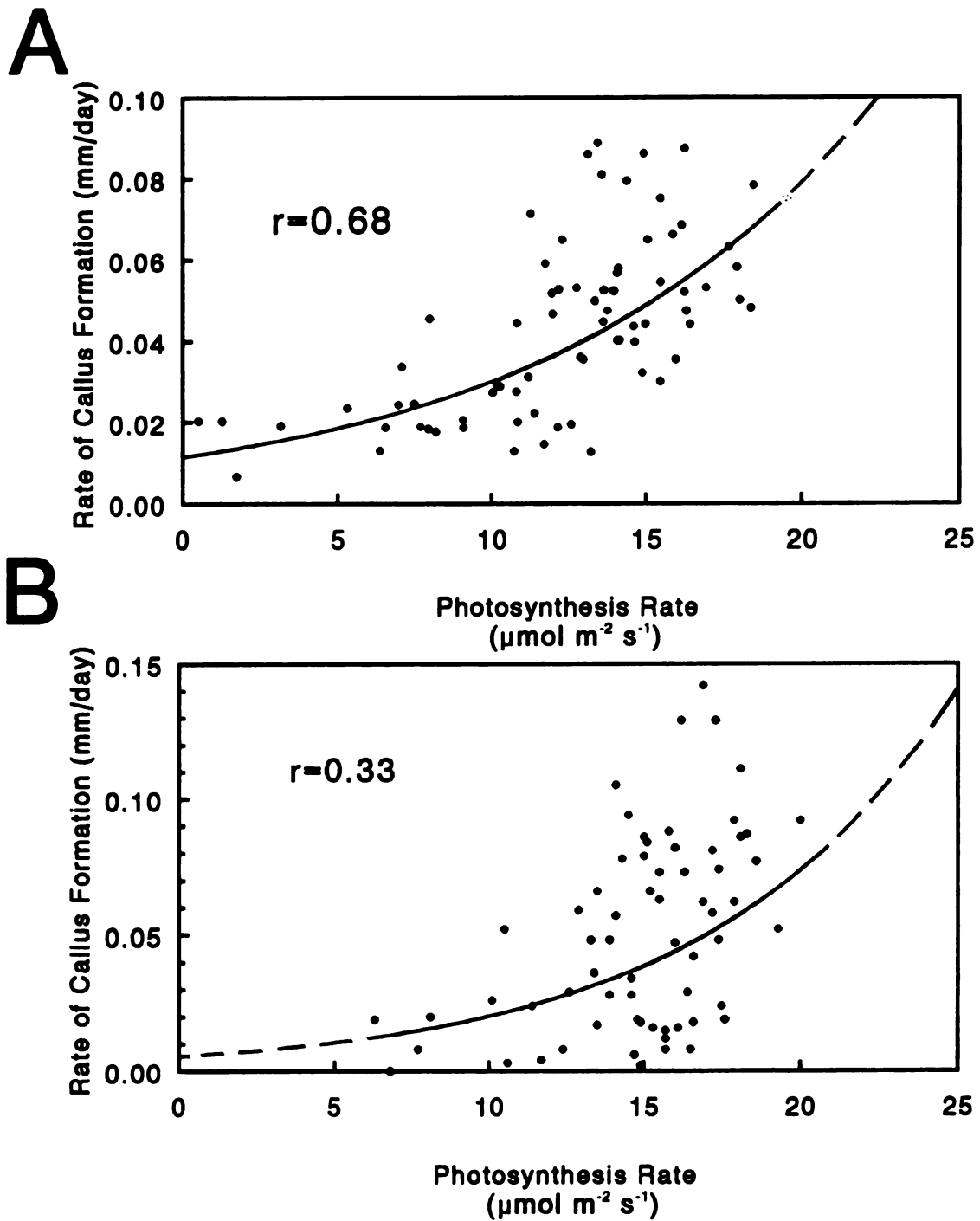


Figure 38. The relationship between net photosynthesis and rate of callus formation in paper birch (*Betula papyrifera*), during 1988 (A) and 1989 (B). Photosynthesis values are tree-specific means of all measurements made during the year.

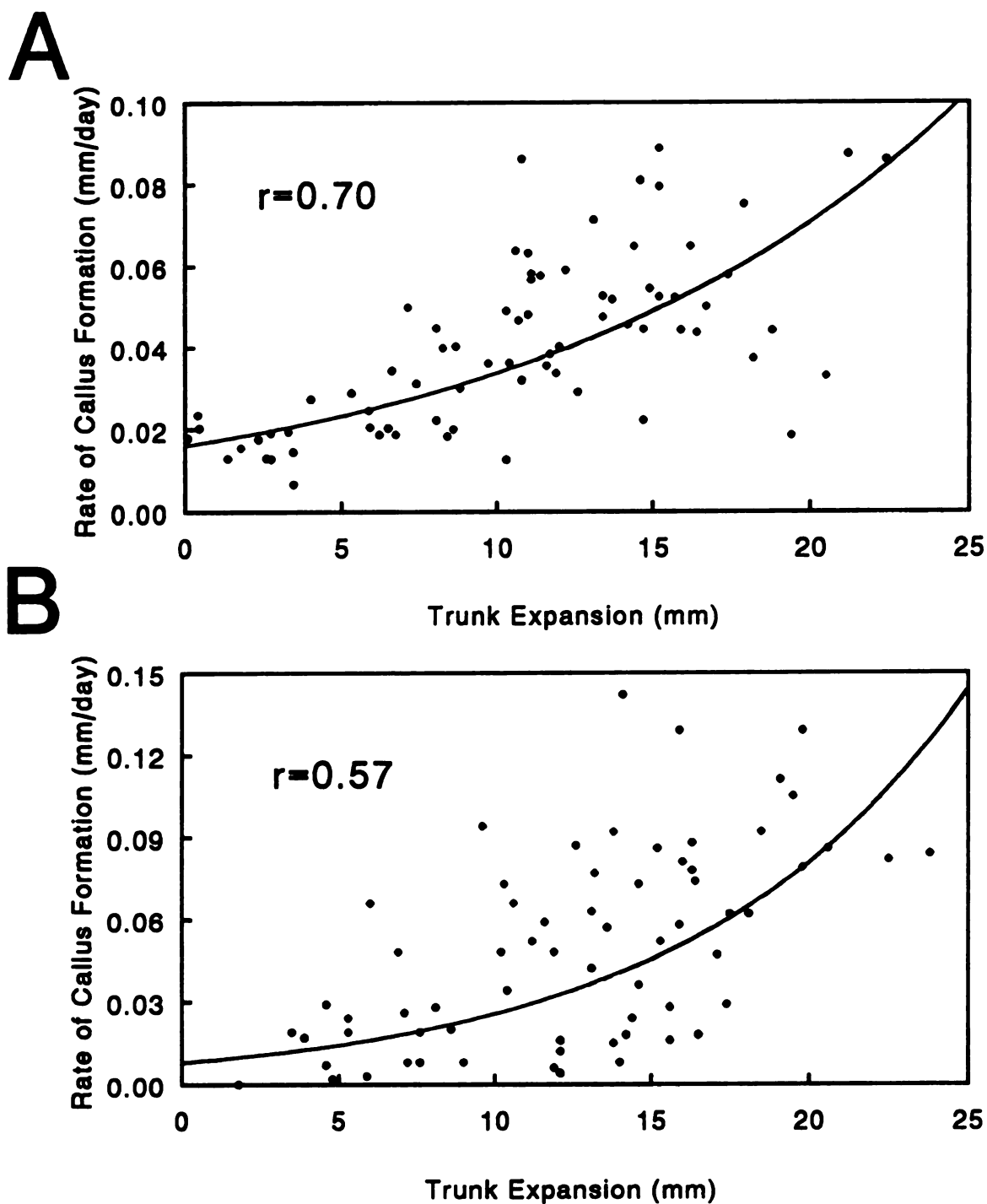


Figure 39. The relationship between increase in trunk diameter and rate of callus formation, in paper birch (*Betula papyrifera*), in 1988 (A) and 1989 (B).

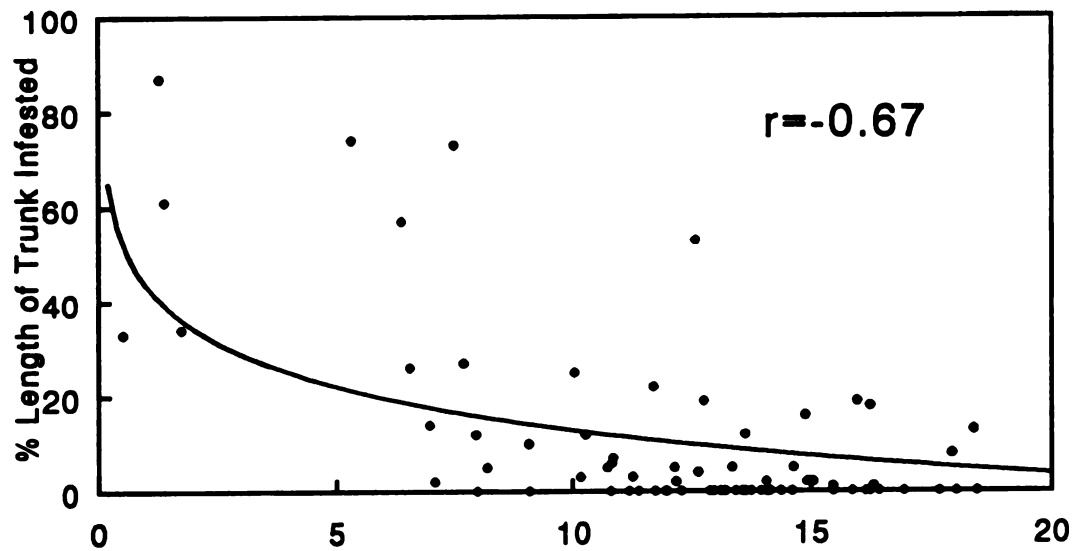
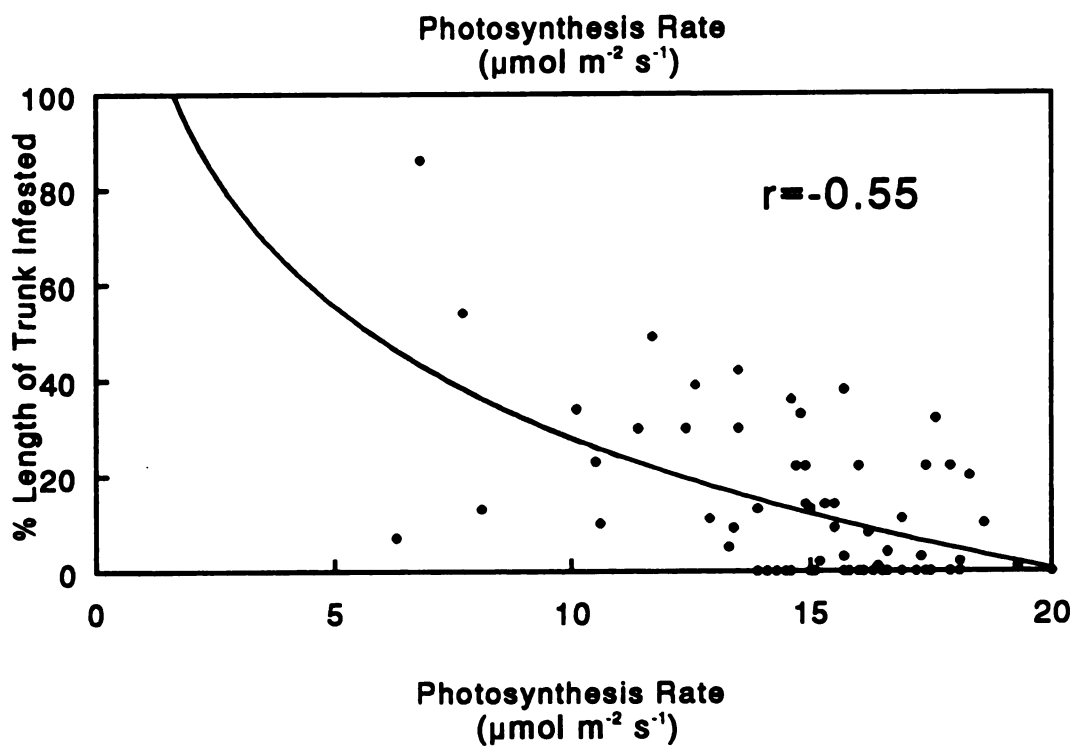
A**B**

Figure 40. The relationship between net photosynthesis and the resistance of paper birch (*Betula papyrifera*) to bronze birch borer (*Agrilus anxius*), in 1988 (A) and 1989 (B). Photosynthesis values are tree-specific means of all measurements made during the year

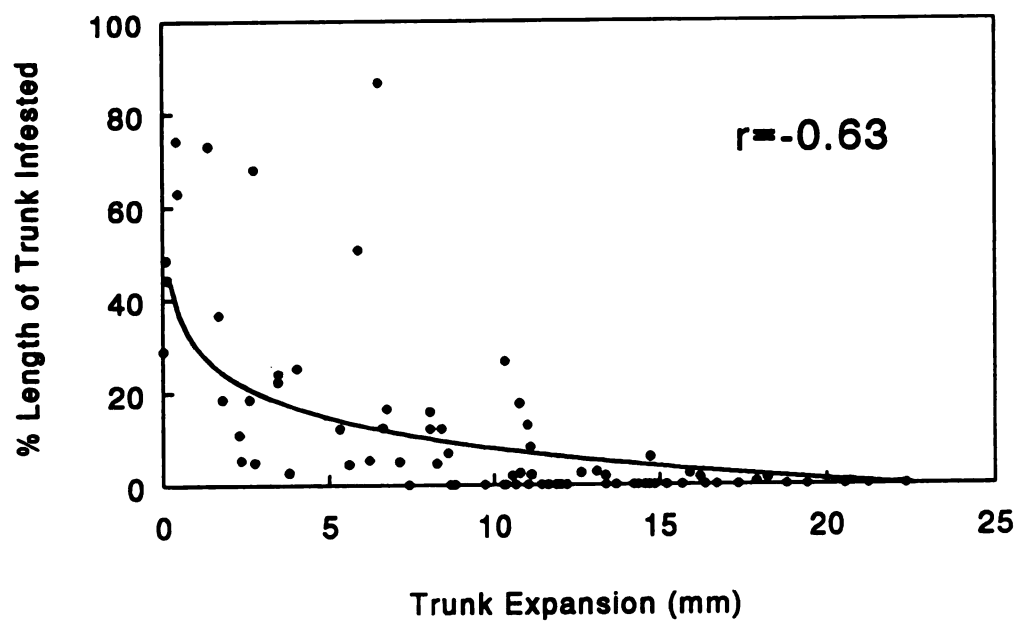
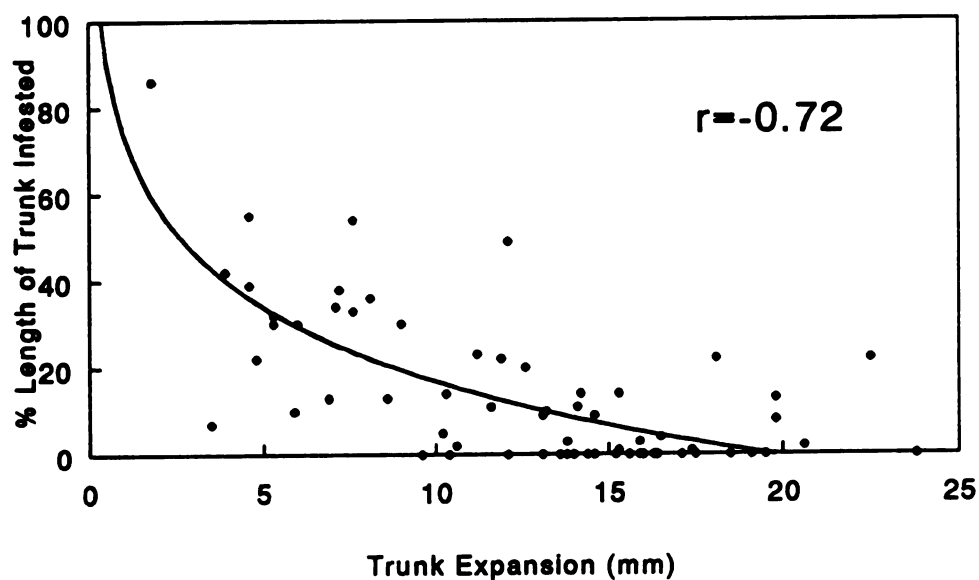
A**B**

Figure 41. The relationship between increase in trunk diameter and the resistance of paper birch (*Betula papyrifera*) to bronze birch borer (*Agilus anxius*), in 1988 (A) and 1989 (B).

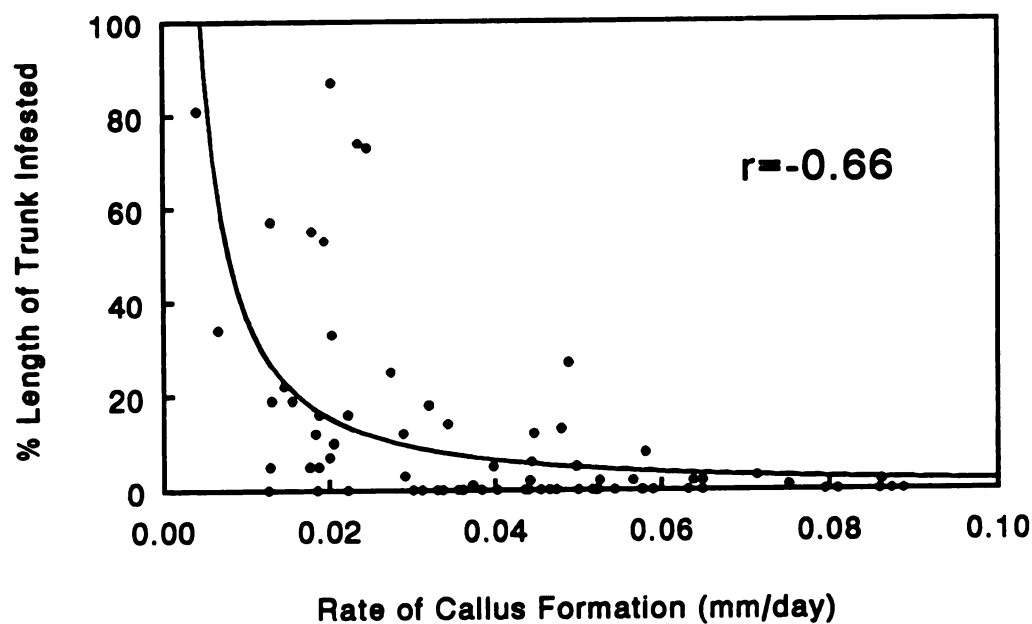
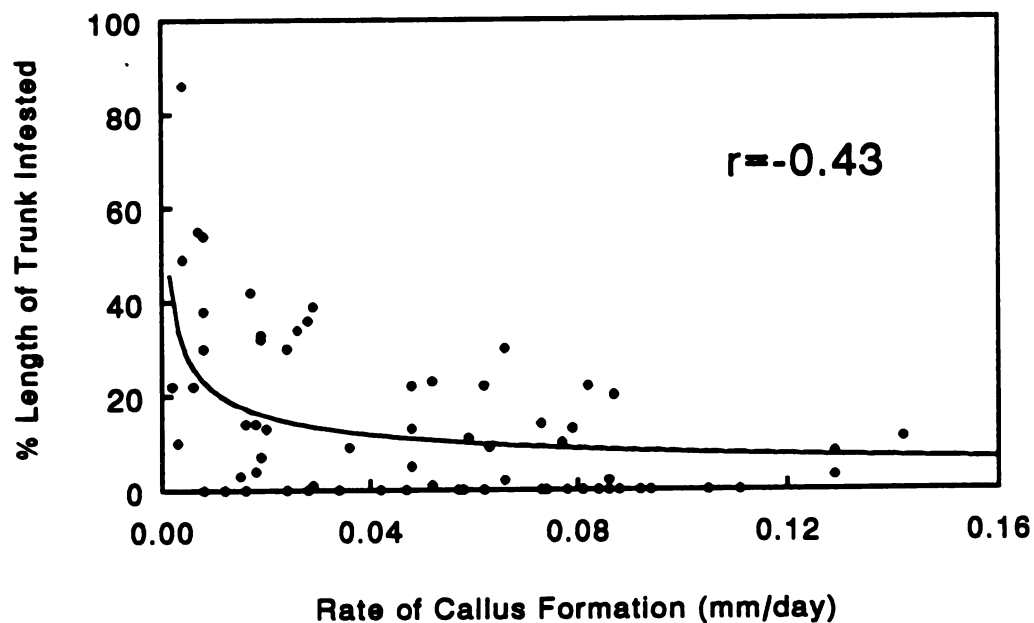
A**B**

Figure 42. The relationship between rate of callus formation and the resistance of paper birch (*Betula papyrifera*) to bronze birch borer (*Agrilus anxius*), in 1988 (A) and 1989 (B).

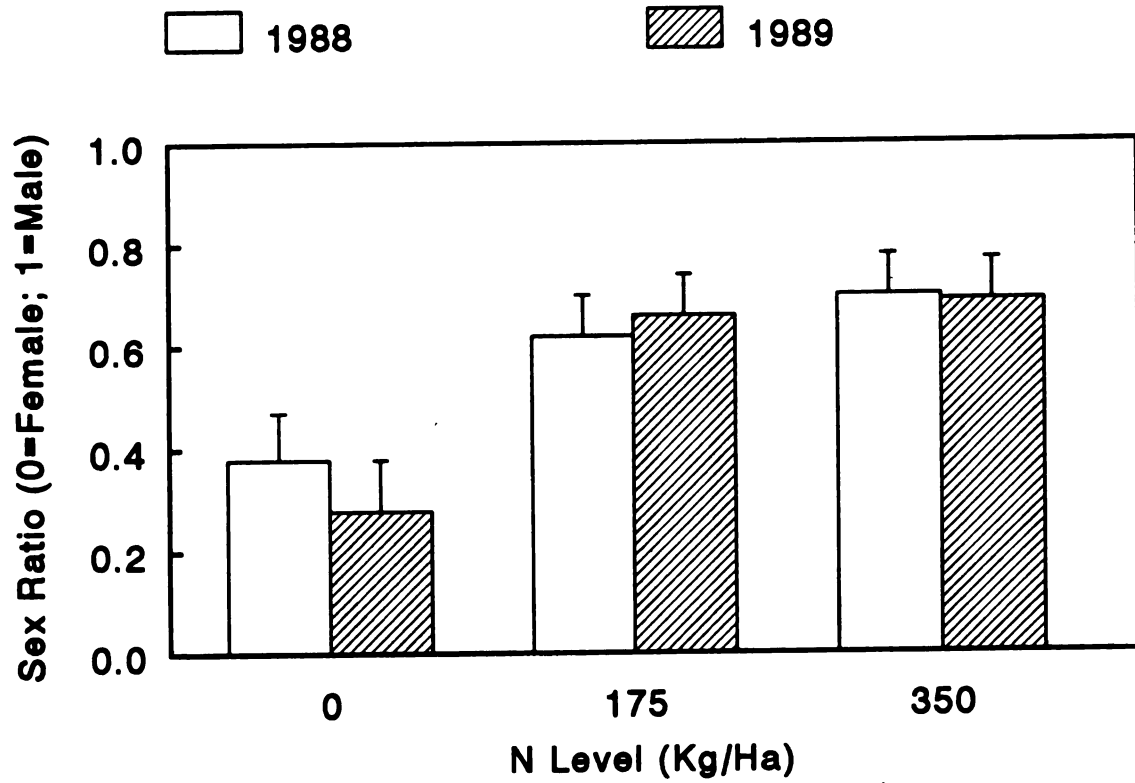


Figure 43. The effect of nitrogen fertilization on the sex expression of paper birch (*Betula papyrifera*), in 1988 (A) and 1989 (B) (mean $\pm$ standard error).

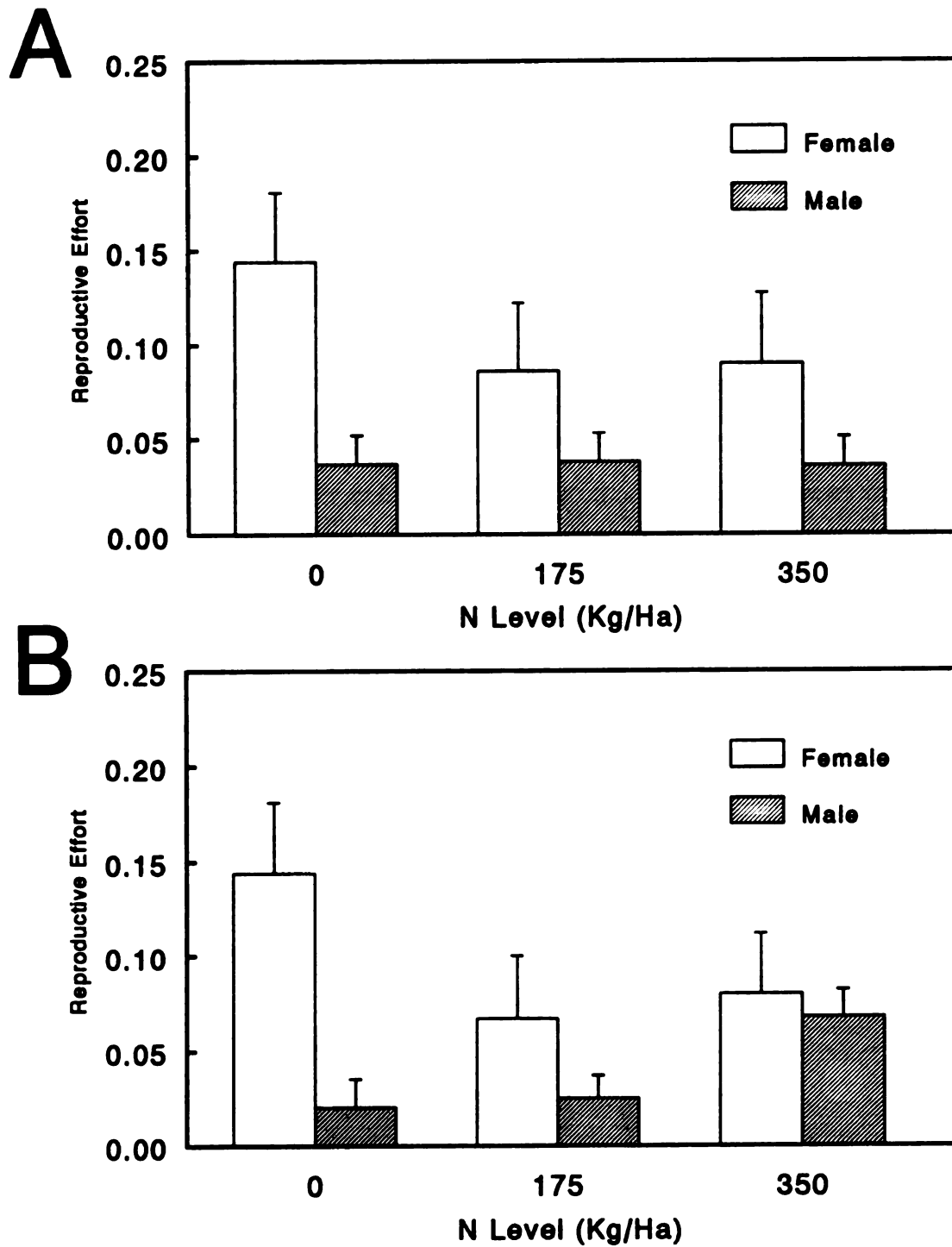


Figure 44. The effect of fertilization on the male and female reproductive effort of (*Betula papyrifera*), in 1988 (A) and 1989 (B) (mean $\pm$ standard error).

44). During 1989, male reproductive effort significantly increased as the level of nitrogen increased ($F=6.65$; d.f. = 1,48; $P=0.013$) (Figure 44).

Tree growth in one year had a significant effect on sex expression the next (Figure 45). Slower growing trees in one year had a higher proportion of female catkins the next.

Increased female reproductive effort in one year resulted in decreased growth the same year (Figure 46). There was no relationship between male reproductive effort and growth the same year in 1988 and 1989 (Figure 47). Male catkins are not produced until late summer, so the trade-off between male reproductive effort and growth may be delayed until the following growing season. However, there was also no relationship between male reproductive effort in 1988 and growth during 1989 (Figure 47).

Female reproductive effort and rate of callus formation were negatively correlated (log scale) in 1988 ($r=-0.62$), however but showed no relationship in 1989 (Figure 48). Bronze birch borer infestation was well correlated with female reproductive effort during 1988 ($r=0.76$) (Figure 49). However, the relationship was not significant during 1989.

Girdling Experiment

Girdling had a highly significant effect on the rate of callus formation ($F=98.2$; d.f. = 3,64; $P<0.001$). Rate of callus formation was less than 0.02 mm/day below the girdle, and greater than 0.08 mm/day above the girdle (Figure 50). Rate of callus formation above the girdle was also significantly higher than that of the control trees (Figure 50).

Girdling also had a significant effect on bronze birch borer resistance ($F=23.6$; d.f. = 3,64; $P<0.001$). Galleries below the girdle were on average, more

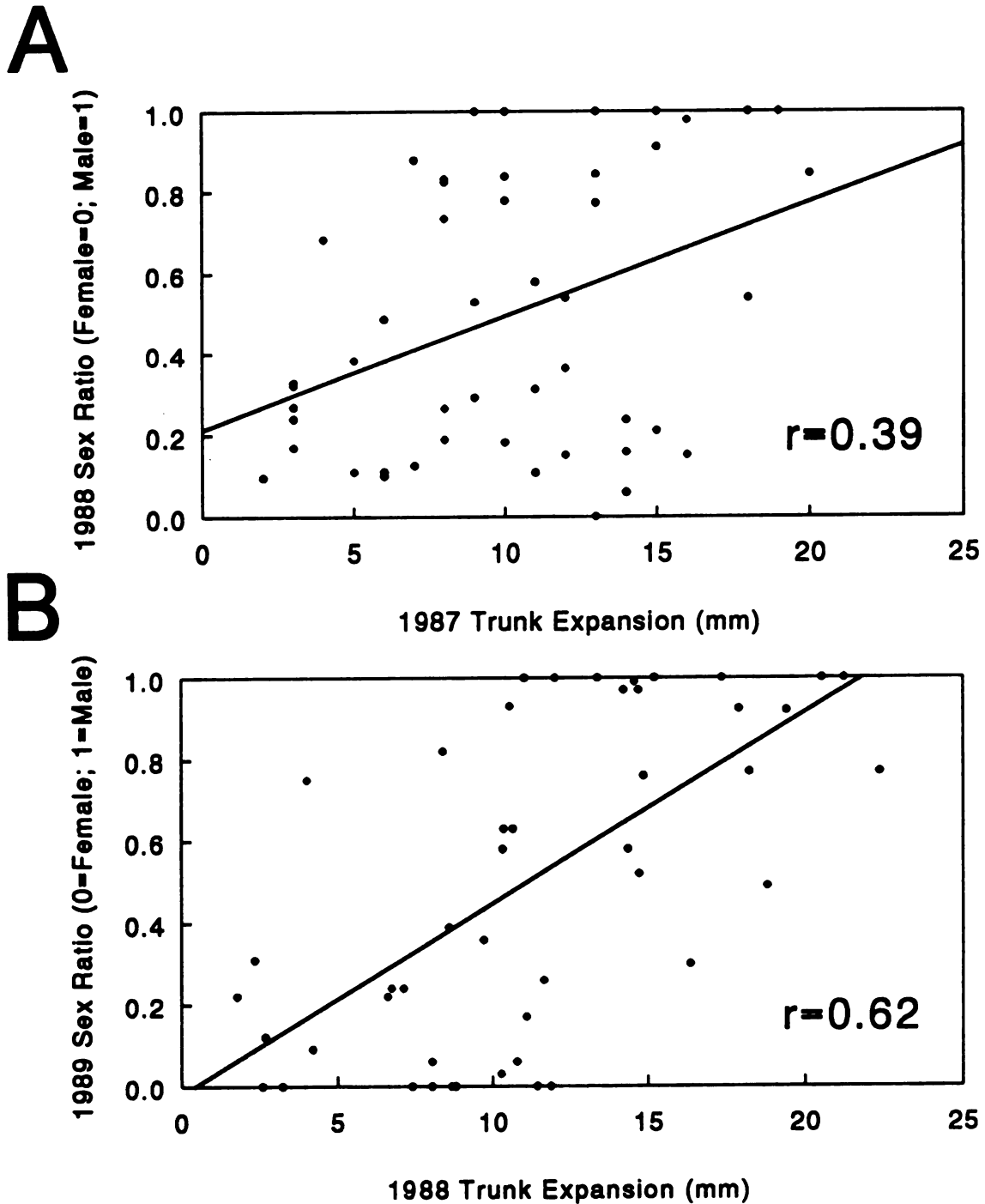


Figure 45. The relationship between the increase in trunk diameter of paper birch (*Betula papyrifera*) in 1987 and 1988, and sex expression in 1988 (A) and 1989 (B), respectively.

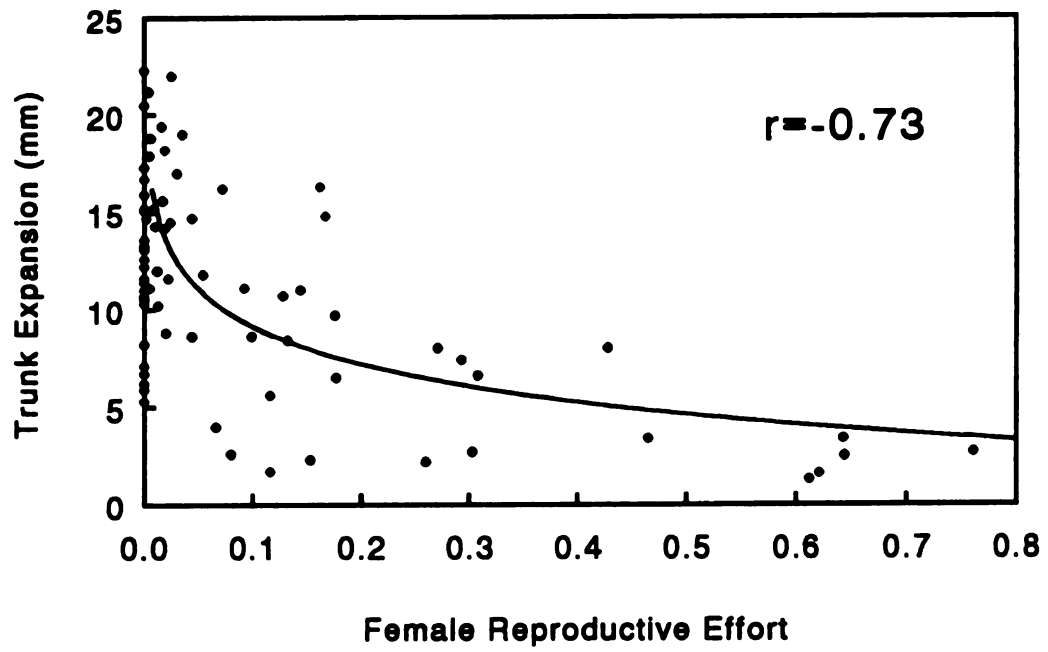
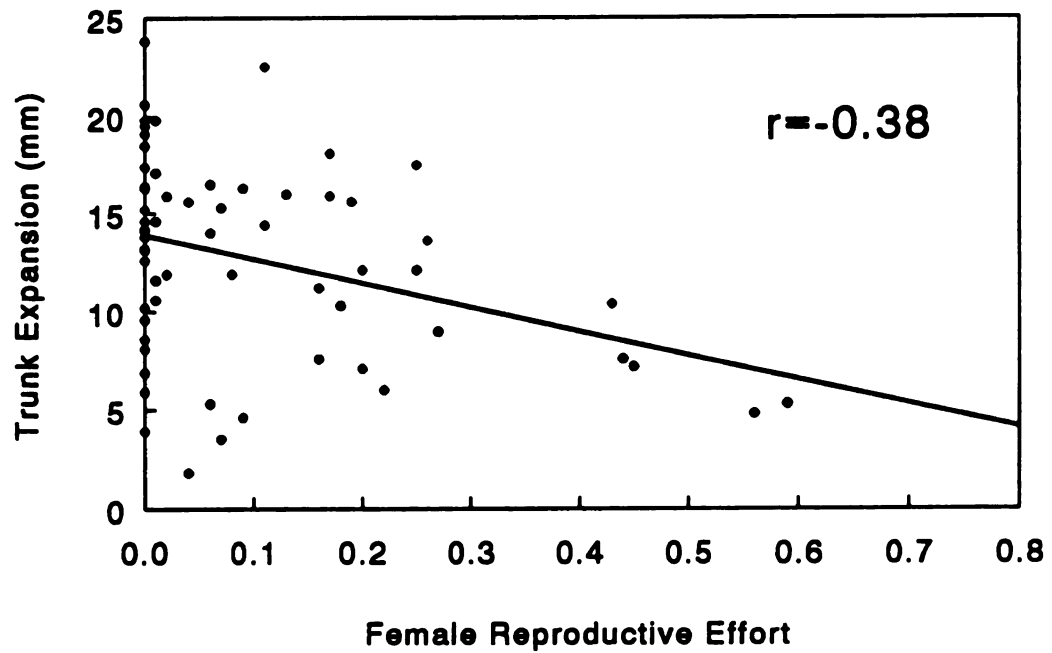
A**B**

Figure 46. The relationship between female reproductive effort of paper birch (*Betula papyrifera*) and increase in trunk expansion, in 1988 (A) and 1989 (B).

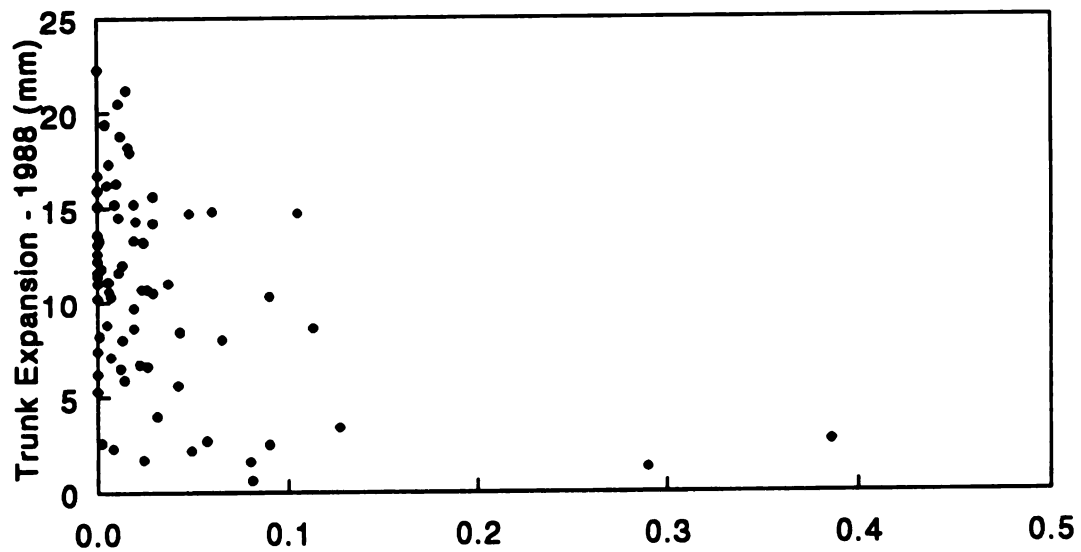
A**B**

Figure 47. The relationship between the male reproductive effort of paper birch (*Betula papyrifera*) in 1988, and increase in trunk diameter in 1988 (A) and 1989 (B).

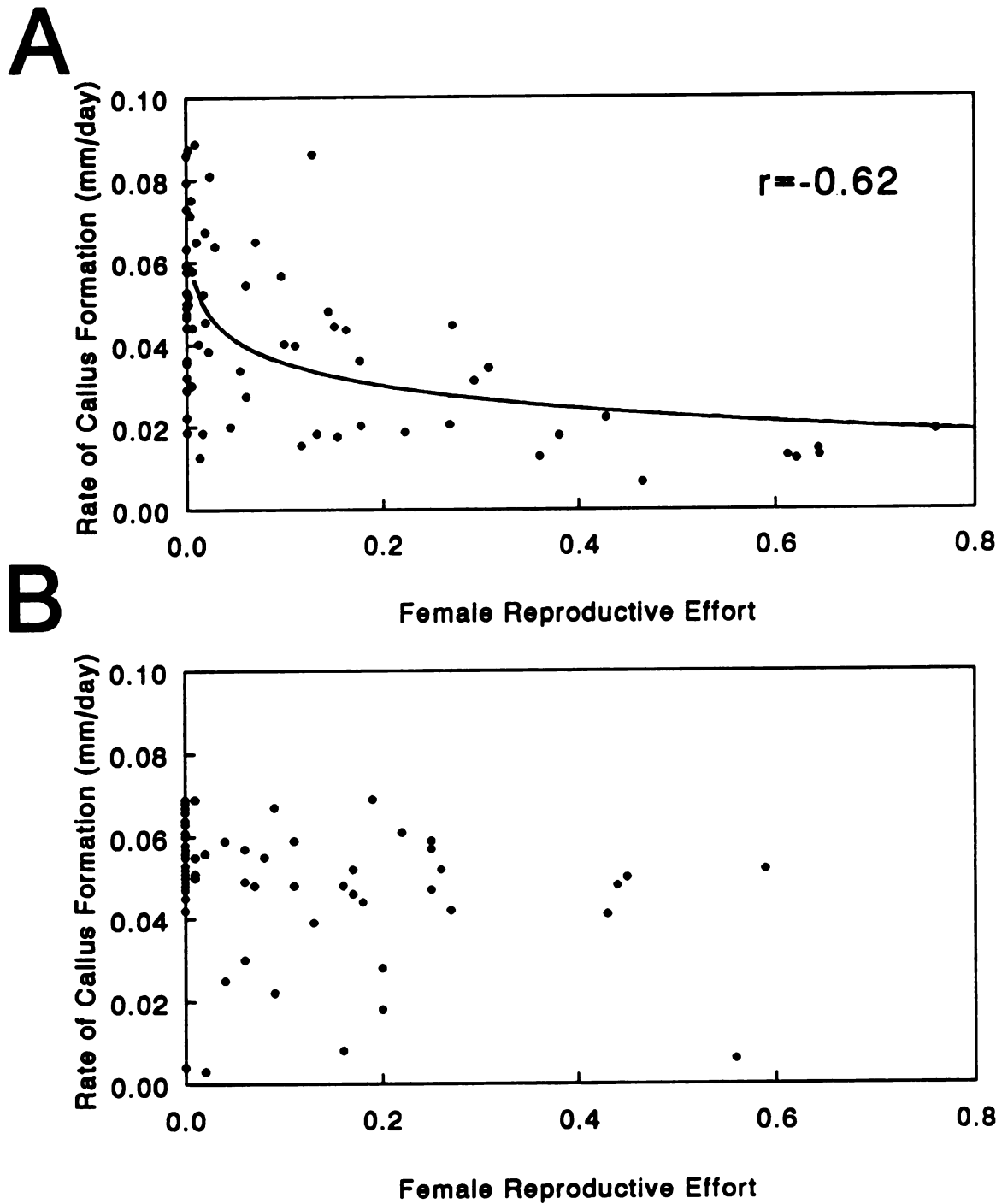


Figure 48. The relationship between the female reproductive effort of paper birch (*Betula papyrifera*), and rate of callus formation, in 1988 (A) and 1989 (B).

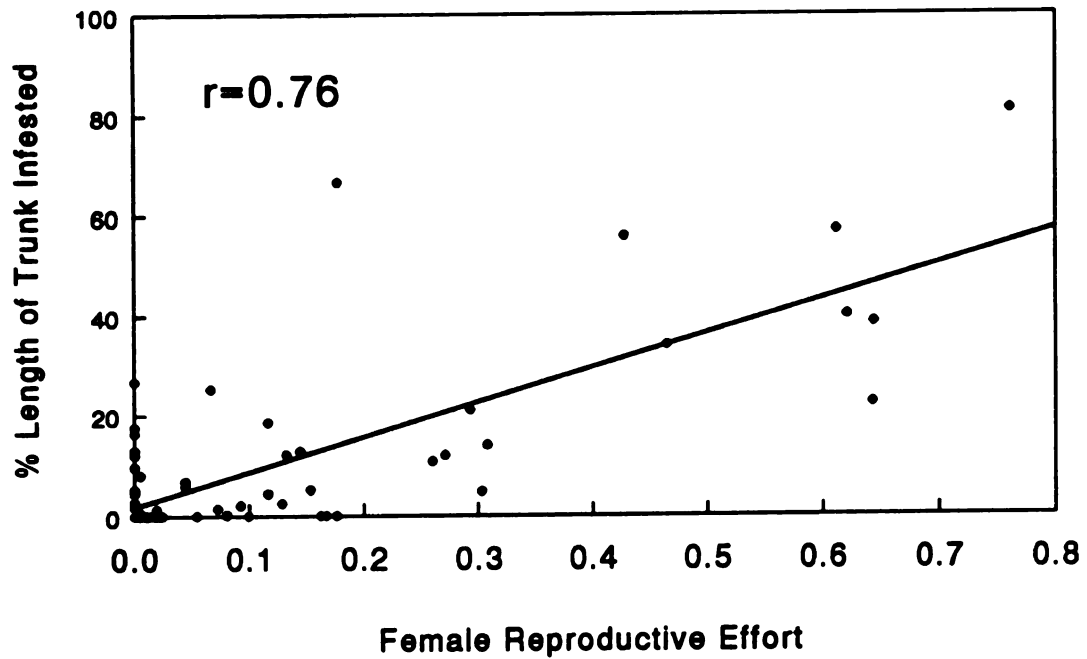
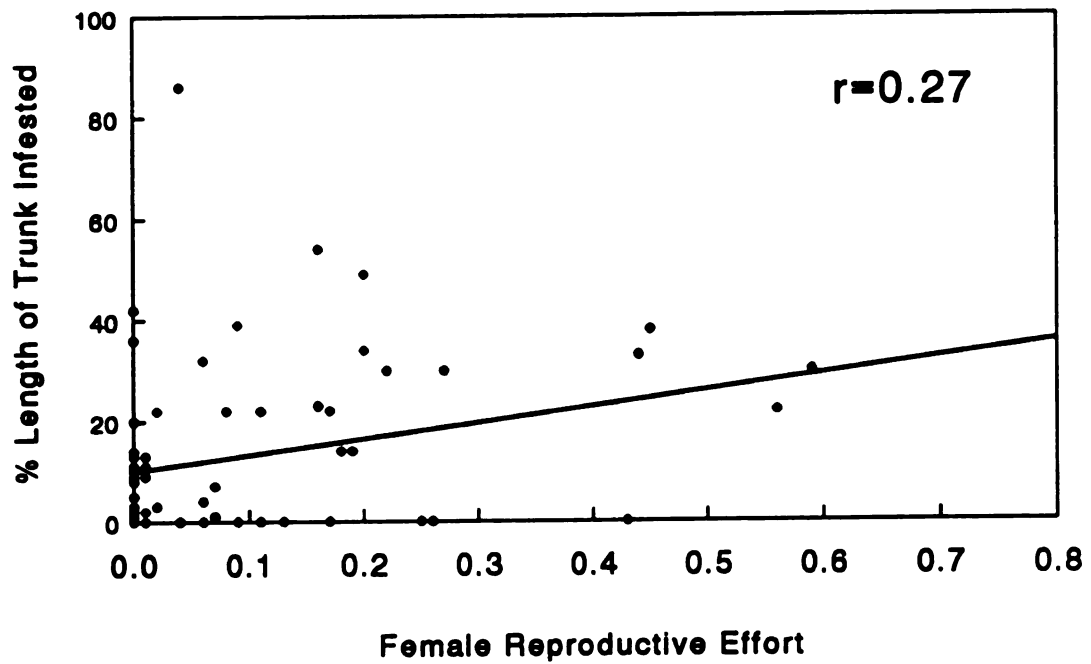
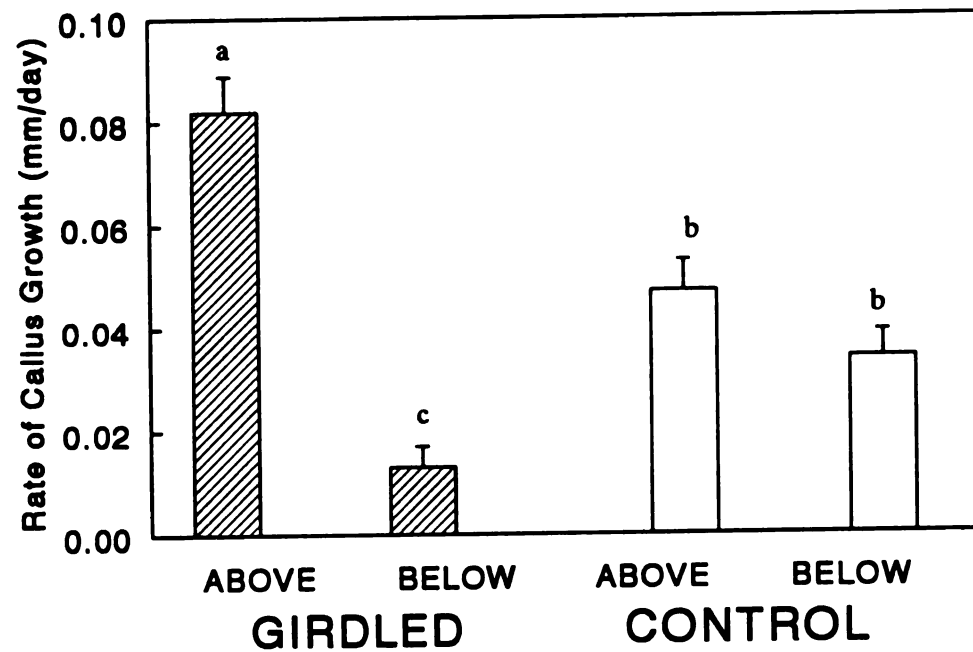
A**B**

Figure 49. The relationship between the female reproductive effort of paper birch (*Betula papyrifera*), and resistance to bronze birch borer (*Agilus anxius*), in 1988 (A) and 1989 (B).

A



B

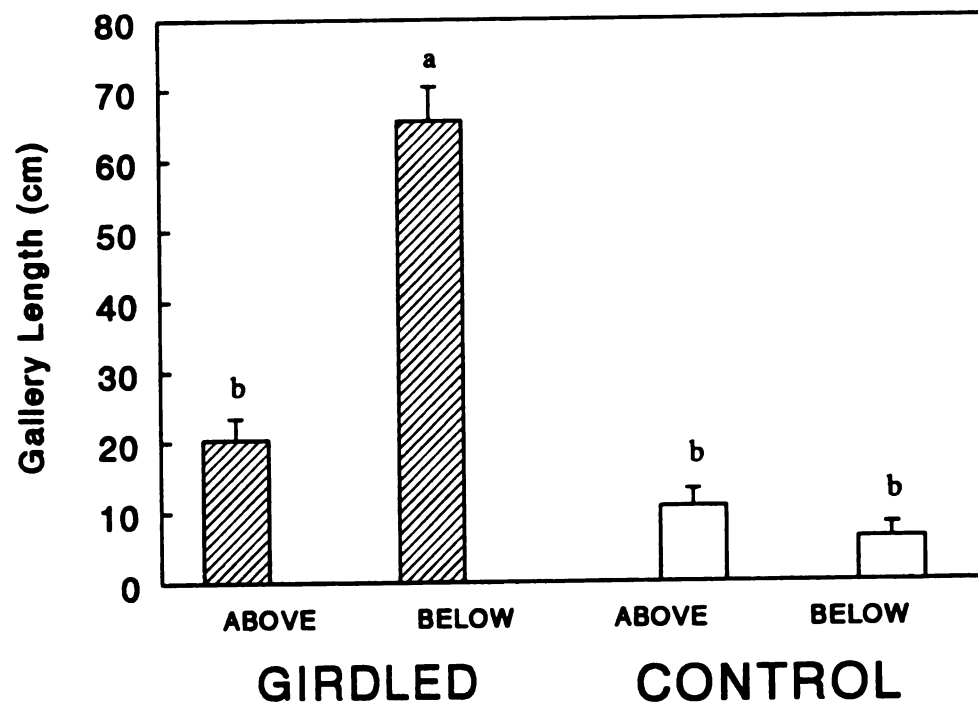


Figure 50. The effect of trunk-girdling on paper birch (*Betula papyrifera*) rate of callus formation (A), and resistance to bronze birch borer (*Agrilus anxius*) (B), in 1988 (mean $\pm$ standard error).

than three times longer than galleries above the girdle, or galleries from either location of the control trees (Figure 50).

DISCUSSION

Drought Stress and Bronze Birch Borer Resistance

Bronze birch borer resistance increased linearly with irrigation in 1988, providing the first experimental confirmation of the widely held hypothesis that drought predisposes birch to colonization by the bronze birch borer. However, irrigation had no effect on bronze birch borer resistance in 1989. Climatic differences between the years may explain these results. Averaged across all treatments, photosynthesis, stomatal conductance, and internal cellular CO₂ concentrations were greater in 1989 than 1988 (Table 3, Chapter 2). High temperatures during the drought of 1988 (Figure 19, Chapter 2) may have increased evapotranspiration, imposing stomatal limitations on photosynthesis that did not exist in 1989. Furthermore, eight trees died in August 1988 (all were heavily infested with bronze birch borer); none died in 1989 (although, four trees failed to survive the winter). Past episodes of birch dieback have been associated with above average temperatures and below average rainfall (Hawboldt & Skolko 1948; Redmond 1955; Clark & Barter 1958; Pomerleau & Lortie 1962). The results and observations of this study are consistent with the hypothesis of Clark & Barter (1958), that high temperature interacts with drought to predispose birch to bronze birch borer colonization.

Rate of Callus Formation and Bronze Birch Borer Resistance

In 1988 and 1989, there were: (A) positive correlations between photosynthesis and both trunk expansion and rate of callus formation, (B) positive correlations between trunk expansion and callus formation, and (C) negative correlations between bronze birch resistance and each of photosynthesis, growth, and callus formation. Collectively, these observations are consistent with the hypothesis that trunk expansion and callus formation are driven by current photosynthate, and that bronze birch borer resistance is related to rapid callus formation.

Girdling, which disrupts the downward translocation of photosynthate, substantially reduced the rate of callus formation below the girdle. Bronze birch borer resistance declined in proportion. Callus formation actually increased above the girdle, possibly as a result of increased availability of photosynthate. These results are also consistent with the hypothesis that resistance is based on rapid callus formation driven by the current supply of photosynthate.

Wounds created by feeding larvae may stimulate callus formation which may enclose larval galleries. Rapid callus formation may crush and/or encapsulate small larvae within water-impervious, suberized tissue, high in secondary metabolite concentration and low in nutritive quality, entombing larvae in tissue unfavorable for survival.

In effect, larvae may be in a developmental race against the tree. Larvae move through the phloem as they feed, their rate of progress correlated with their rate of consumption. Wound-induced secondary metabolite accumulation, coupled with the low nutritive quality of phloem tissue, may slow larval development. A rapid rate of callus formation, may crush larvae and/or isolate them within tissue unsuitable for survival.

Implicit in this hypothesis, is the prediction that the rate of callus formation necessary for resistance is a threshold value approximately equal to the maximum rate of larval movement through the plant. Consistent with this hypothesis, a negative power function best described the relationship between bronze birch borer colonization and callus formation during both 1988 and 1989 (Figure 42). Resistance declined rapidly as the rate of callus formation dropped below about 0.02 mm/day. In the tree-girdling experiment, rate of callus formation in the portion of the trunk below the girdle, was also below 0.02 mm/day.

A defense mechanism based on a growth process (cambial activity) is consistent with the ecological role of birch as a pioneer species in secondary succession. Intolerant of shade, birch is dependent on rapid growth to achieve dominance of a site. There is no trade-off between growth and callus-based resistance to bronze birch borer, as would be the case if resistance were based on constitutive secondary metabolites, such a resin duct system.

Bronze Birch Borer Resistance and Female Reproductive Effort

The results of our experiments confirm previous reports showing a trade-off between vegetative growth and female reproductive effort in birch (FRE) (Gross 1972; Tuomi et al. 1982; Ceasar & MacDonald 1983). There was a negative correlation between FRE and both rate of callus formation and bronze birch borer resistance in 1988. These correlations are consistent with the hypothesis that reproduction and callus formation compete for the same pool of current photosynthate, and the trade-off between them compromises defense. Hence, there is a two-fold cost of female reproductive effort in birch: decreased growth and decreased defense.

In 1989, however, there was a weaker correlation between FRE and callus formation, and none between FRE and bronze birch borer colonization. Photosynthesis was lower in 1988 (averaged across all trees) than 1989, however FRE tended to be higher (0.11 ± 0.02 and 0.09 ± 0.02 , in 1988 and 1989, respectively). Hence, the trade-off between reproduction and bronze birch borer resistance was evident during the drought year, when trees experienced decreased availability of current photosynthate, but not in 1989, when growing conditions favored a higher net photosynthesis. These data suggest that FRE takes allocation priority over callus formation and growth, when photosynthates are limiting.

When male and female fitness are affected differentially by environmental conditions, labile sex determination may be favored by natural selection (Charnov & Bull 1977). Plants with labile sex determination generally allocate proportionally more resources to female function when growing in high resource environments, presumably because successful female reproduction requires a greater commitment of resources than male reproduction (Freeman et al. 1980, 1981; Barker 1982; Devlin 1988). However, in this experiment, the proportion of resources allocated to female reproduction decreased as soil nitrogen increased. Furthermore, increased female-reproductive in one year was associated with slow growth during the previous year. Slow growth may stimulate the initiation of female flowers. Female reproduction itself then further reduces vegetative growth through resource competition. A positive-feedback loop may result. Female reproductive effort stimulated by slow growth, further reduces growth, which further stimulates female reproduction. Because of reduced rates of callus formation associated with increased female reproductive effort, this feedback loop may result in ever-increasing susceptibility to bronze birch borer and eventual tree death. Increased seed production in slow-

growing adolescent birches may be an adaptation, maximizing the life-time reproduction of drought stressed trees likely to be soon killed by bronze birch borer or fire.

Another Look at Birch Dieback: Bronze Birch Borer is Central

Some students of forest decline in North America have been reluctant to assign the bronze birch borer a central role in the occurrence of widespread birch dieback (Anderson 1944; Hawboldt 1947; Carlson & Knight 1969; Houston 1987). At best, the bronze birch borer has been credited with a minor effect on over-all patterns of tree mortality, primarily killing trees already predisposed to death by other factors, such as disease. Others have labeled the insect a primary killer of healthy trees (Balch & Prebble 1940; Nash et al. 1951). The point of view taken by an author correlates with whether epidemic (primary tree killer) or endemic (secondary mortality agent) populations were observed (Barter 1957).

I hypothesize that patterns of bronze birch borer outbreaks are, in important ways, consistent with those of the mountain pine beetle (*Dendroctonus ponderosae*), and are sufficient in themselves to contribute significantly to historical patterns of birch dieback in North America. Outbreaks of the bronze birch borer, like those of the mountain pine beetle, can be classified as "eruptive" (Berryman & Stark 1985), or more specifically "pulse eruptive" (Berryman 1987). Much like the mountain pine beetle (Raffa & Berryman 1983, 1987; Berryman & Stark 1985), we argue that bronze birch borer populations are usually regulated largely by the availability of host material suitable for larval development and survival (e.g. Carlson & Knight 1969). Outbreaks are initiated at irregular intervals when biotic and/or abiotic stress factors increase the availability of suitable host trees. Once populations reach

epidemic proportions, the outbreak spreads to adjacent stands as large numbers of larvae are able to overwhelm the defenses of vigorous, normally resistant tree.

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

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

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

Under conditions of extremely high attack density, the defense mechanisms of otherwise resistant trees may be overwhelmed by simultaneous colonization by many larvae. Under these circumstances, larval-feeding behavior may act to subvert host defense mechanisms, facilitating the success of their own colonization as well as colonization by other larvae. When feeding in vigorous hosts, larvae display a zigzag

pattern of gallery formation as they continually double-back against the grain of the wood (Anderson 1944; Barter 1957; Carlson & Knight 1969). This pattern of feeding may partially girdle the tree, causing localized reductions in the strength of wound-induced resistance mechanisms (Barter 1957; Carlson & Knight 1969). On the other hand, in severely stressed host trees, galleries show no consistent configuration, as larvae apparently feed on the freshest phloem they encounter (Barter 1957; Carlson & Knight 1969).

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

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

SUMMARY AND CONCLUSIONS

Allocation theory assumes that organisms partition finite resources among growth, reproduction, and defense in ways that maximize fitness in different environments. Inherent to this theory is the assumption that physiological trade-offs occur among growth, reproduction, and defense. Phenotypic plasticity may allow plants to express adaptive phenotypes in variable and stressful environments. However, phenotypic plasticity in field-grown trees has rarely been investigated.

Insect outbreaks are often associated with drought and nutrient poor sites, leading to the hypothesis that insect resistance is compromised in stressed plants. Changes in host secondary metabolism and nutritional factors are largely responsible for phenotypic patterns in plant resistance to herbivores. There is evidence that stressed trees are most susceptible to wood borers. However, fastest growing trees may be the least resistant to folivores, because of trade-offs between growth and defense mechanisms.

Paper birch (*Betula papyrifera* Marsh.) is a fast growing, early successional tree native to the northern and boreal forests of North America. The bronze birch borer (*Agrius anxius* Gory) is a native wood-boring specialist of *Betula*. Larvae feed under the bark, on the phloem, often girdling and eventually killing trees. Bronze birch borer is the most important insect herbivore of birch. The gypsy moth (*Lymantria dispar* (L.)) is the most important defoliator of deciduous forests in North America. It was introduced from Europe in the late 1860's, but has only caused extensive defoliation in Michigan over the last seven years.

In a three-year field-study, paper birch was subjected to a factorial combination of three levels each of water and nitrogen, and two levels of defoliation. Growth, photosynthesis, water relations, total leaf area, leaf chemistry and morphology, nutrient use efficiency, reproduction, wound response, and resistance to bronze birch borer and gypsy moth (*Lymantria dispar*), were quantified. Trade-offs among growth, reproduction, and defense were detected.

Tree growth was directly correlated with net photosynthesis, total leaf area, and leaf nutrient concentrations. Irrigation linearly increased growth, photosynthesis, stomatal conductance, and bronze birch borer resistance in 1988, but had no effect in 1989. Averaged across all treatments, growth, photosynthesis, stomatal conductance, and internal cellular CO₂ concentrations were lower in 1988. The severe drought of 1988 may have enhanced the effect of low irrigation by increasing evapotranspiration, thus increasing stomatal limitations on photosynthesis. Variation in birch stomatal conductance, nutrient use efficiency, and leaf morphology in response to varying nutrient and water supply were consistent with patterns predicted for optimization of limiting resources.

There was a trade-off (negative phenotypic correlation) between paper birch growth rate and secondary metabolism (total foliar phenolic concentrations). However, increased secondary metabolism did not translate into increased resistance to gypsy moth. Larvae compensated for decreased foliage quality by increasing consumption. Hence, foliage quality had no effect on growth rate, duration of larval period, or pupal mass.

Inducible resistance may be a form of adaptive phenotypic plasticity in plant defense. If chemical defenses are metabolically expensive to plants, then it would be advantageous for plants to be less well defended when herbivores are absent than when plants are subject to herbivory. Artificial defoliation (40%) in 1987 and 1988

decreased larval growth and male pupal mass in 1988, providing evidence for induced resistance in paper birch. However, there was no evidence of delayed induced resistance in 1989, when trees were not defoliated.

Resistance to bronze birch borer declined with decreasing irrigation in 1988, providing the first experimental evidence supporting the hypothesis that bronze birch borer resistance declines in stressed trees. High temperatures during the drought of 1988 may have interacted with low irrigation to decrease bronze birch borer resistance. Irrigation during the cooler summer of 1989, had no effect on bronze borer resistance. Bronze birch borer resistance was positively correlated with tree growth, net photosynthesis, and rate of wound-callus formation both years. Trunk-girdling experiments supported the hypothesis that bronze birch borer resistance is dependent on rapid callus formation, which is driven by current photosynthate.

There was a two-fold physiological cost of female reproductive effort: decreased growth and decreased resistance to the bronze birch borer. There was no detectable cost of male reproductive effort. Low soil fertility promoted female sex expression. Furthermore, slow growth in one year was associated with increased female reproductive effort the next. These results are contrary to predictions that female reproductive effort, because of its high cost, should increase in favorable environments. This pattern of reproductive plasticity may be adaptive in birch, maximizing the life-time reproduction in stressed trees unable to resist bronze birch borer.

SIGNIFICANT CONCLUSIONS

- 1) Irrigation linearly increased growth, photosynthesis, stomatal conductance, and bronze birch borer resistance, but had no effect in 1989.
- 2) Averaged across all treatments, growth, photosynthesis, stomatal conductance, and internal cellular CO₂ concentration were higher in 1989 than 1988.
- 3) Conclusions 1 and 2 suggest that high temperatures during the drought of 1988 enhanced the effects of low irrigation, by increasing evapotranspiration, causing stomatal limitations to photosynthesis.
- 4) Decreased growth in response to moisture stress was primarily the result of stomatal, rather than nonstomatal, limitations to photosynthesis.
- 5) Growth was highly correlated with net photosynthesis and total leaf area; rate of photosynthesis was more highly correlated with faster growing trees; total leaf area was more highly correlated with slower growing trees.
- 6) Total foliar phenolic concentrations were negatively correlated with tree growth and foliar nutrient concentrations.
- 7) Gypsy moth larvae compensated for decreased foliage quality by increasing their consumption rate; hence, there were no effects of measured foliage quality parameters on growth rate, duration of larval period, or pupal mass.
- 8) Gypsy moth pupal mass, duration of larval period, and overall growth rate of larvae were highly correlated with second instar growth rate, but were not correlated with fourth instar growth rate.
- 9) 40% defoliation in 1987 and 1988 decreased gypsy moth growth rate and male pupal mass in 1988, but there was no apparent delayed resistance to gypsy moth in 1989.
- 10) The fastest growing trees were most resistant to bronze birch borer.
- 11) Bronze birch borer resistance was dependent on rapid wound callus formation; resistance dropped rapidly as the rate of callus formation dropped below 0.02 mm/day.
- 12) Nitrogen fertilization promoted male sex expression in birch.
- 13) The degree of female sex expression in one year was negatively correlated with growth rate during the previous year.
- 14) Female reproductive effort was a strong photosynthetic sink, decreasing growth, rate of callus formation, and thus bronze birch borer resistance.

APPENDIX

APPENDIX 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1990-04

Title of thesis or dissertation (or other research projects):

Variation in the Resource Allocation Patterns of Paper Birch:
Evidence for Physiological Trade-Offs Among Growth, Reproduction,
and Defense

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name (s) (typed)
Daniel A. Herms

Date 28 January 1991

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Included as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX 1.1

Voucher Specimen Data

Page 1 of 1 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:							
		Eggs	Larvae	Nymphs	Pupae	Adults +♂	Adults ♀	Other	Museum where deposited
<u>Agrilus anxius</u> Gory	The Dow Gardens Midland, MI 6 June 1989					10	10		MSU
<u>Agrilus anxius</u> Gory	The Dow Gardens Midland, MI 10 September and 16 September 1988		20						MSU
<u>Lynantria dispar</u> (L.)	USDA Lab Culture Hamden, CT Strain NJ-F33 Larvae received: 24 May 1989		10			10	10		MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Daniel A. Herms

Date 28 January 1991

Voucher No. 1990 - 04

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Kelvin W. Foster 1/29/91
Curator Date

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