

## PLANT DEFENSE, HERBIVORY, AND CLIMATE CHANGE

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Anticipated patterns of climate change (Schneider, this volume) will have multiple direct effects on the physiology of both plants and herbivores. However, the community-level consequences cannot be predicted solely from these direct effects because climate change can also have surprisingly large effects on the interactions between plants and their herbivores. For example, a minor increase in average temperature (only 1°C) altered the interactions between mountain birch and a principal insect herbivore enough to triple the potential rate of population growth of the insect (see "Increased temperature," p. 88). Consequently, any attempt to predict how changing climates will affect plant-herbivore communities must address the complexities of such biotic interactions.

Climate change can influence interactions between plants and herbivores in several ways. For example, expected environmental changes in carbon dioxide levels, temperature, cloud cover, and water and nutrient availability will affect plant susceptibility to herbivores (Larsson et al., 1986; Waterman and Mole, 1989; Johnson and Lincoln, 1991). Climate change will also directly affect herbivore nutritional requirements (Robbins, 1983; Scriber and Slansky, 1981), development time (Taylor, 1981; Solbreck, 1991), and overwinter survival (Pease et al., 1979; Bale, 1991). In addition, herbivores will experience the indirect effects of changes in food quality (Bryant and Reichardt, 1992). Thus global change will certainly alter the nature and strength of many plant-herbivore interactions and will sometimes yield dramatic consequences at the level of populations, communities, and ecosystems.

Considerable empirical evidence attests to the impact of herbivores on

Ayres, M. P. 1993. Global change, plant defense, and herbivory. Pages 75-94 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Biotic interactions and global change*, Sinauer Associates, Sunderland, MA.

plant population dynamics (Louda, 1983; McAuliffe, 1986; Rice, 1987; Crowley, 1989; Swank and Oechel, 1991). Enclosure studies, apparently without exception, indicate that plant communities are very sensitive to vertebrate herbivory (Watt, 1960; Ross et al., 1970; Pease et al., 1979; Cargill and Jefferies, 1984). Even modest levels of herbivory can modify plant communities by altering competitive interactions (Cottam et al., 1986; Kakes, 1989) and by changing the trajectory of plant succession (Launchbaugh 1960; Brown et al., 1987; Brandner et al., 1990; De Steven, 1991). Herbivory may also affect ecosystem attributes such as nutrient flux, primary productivity, insolation, fire frequency and severity, and gas and water exchange (Miller et al., 1976; Grant et al., 1985; Bazely and Jefferies, 1986; McNaughton and Georgiadis, 1986; Dyer et al., 1991; Harrington, 1991; Hobbs et al., 1991; Veblen et al., 1991; Schimel, this volume).

There are empirical and theoretical bases for expecting global climate change to affect the physiology of plants and herbivores in ways that impact plant-herbivore interactions and ripple through ecosystems. For example, when a recent irruption of the autumnal moth (*Epirrita autumnata*, Geometridae) killed hundreds of square kilometers of birch forest in Fennoscandia (Tenow, 1972; Kallio and Lehtonen, 1975), the abrupt edge of the outbreak zone was apparently delimited by winter temperatures lethal to *Epirrita* (Tenow and Holmgren, 1987). Similarly, the population dynamics of *Epirrita* may be influenced by the effects of summer temperature (Niemelä, 1980) and nutrient availability (Tuomi et al., 1984) on birch tree resistance. Thus, changes in winter temperatures, summer temperatures, or nutrient availability could alter the probability and extent of future outbreaks in this system. Agricultural losses to the European corn borer (*Ostrinia nubilalis*, Noctuidae) are clearly related to climatic effects on the life history and population dynamics of the pest (Showers, 1981; Showers et al., 1989). In fact, temperature-driven models that relate insect phenology to stages of plant susceptibility have become a vital tool in the management of many agricultural and horticultural pests (Hatfield and Thomason, 1982; Herms, 1990; Taylor and Shields, 1990). Plant stress resulting from unusual weather patterns may underlie catastrophic herbivore outbreaks in ecosystems throughout the world (White, 1984; Mattson and Haack, 1987a; Larson 1989).

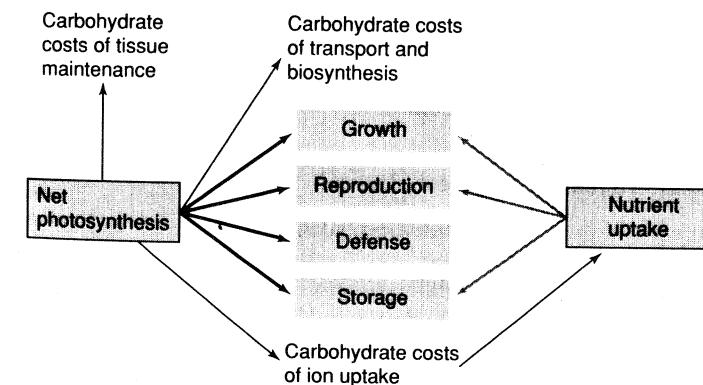
The diversity of plausible mechanisms by which global change could alter plant-herbivore interactions [Mattson and Haack (1987a) suggested dozens relevant to drought alone] indicates a need for identifying where the effects are most likely to be dramatic. In this chapter, I summarize relevant models of plant and herbivore physiology and evaluate their predictions regarding the response of plants, herbivores, and plant-herbivore interactions to expected patterns of global change. This chapter provides a framework for integrating existing data and also serves as a vehicle for directing future research towards critical or inadequately understood mechanisms.

## RESOURCE ACQUISITION AND ALLOCATION IN PLANTS

Plant growth and reproduction are dependent upon the acquisition and use of three classes of resources: carbon, mineral nutrients, and water. Plants vary tremendously in their allocation of these resources depending upon the genotype, ontogeny, and environment of the plant (Bloom et al., 1985). In general, plants may allocate photosynthates and mineral nutrients to reproduction (providing the most immediate fitness benefit), to growth (maximizing the potential for future reproduction), to defense (protecting resources already acquired), or to storage (Figure 1). In addition, plants expend substantial carbon in respiration (Ryan, 1991). The high phenotypic plasticity that characterizes plants is a joint function of environmental variation in resource availability and of phenotypic plasticity in patterns of resource acquisition and allocation. By changing resource availability and allocation, global change is likely to alter plant characteristics that are relevant to herbivores, to affect herbivore population dynamics, and to cause herbivore-mediated changes in plant communities.

## MODELS OF PHENOTYPIC RESPONSE IN PLANTS

At least three theoretical models have been proposed to explain phenotypic responses in plants: (1) the carbon/nutrient balance hypothesis, (2) the growth/differentiation balance hypothesis, and (3) the optimal allocation hypothesis. Hypotheses based on carbon/nutrient balance and growth/dif-



**FIGURE 1.** A model of resource allocation in plants. Carbohydrate products of photosynthesis that are not expended in respiration may be invested in growth, reproduction, defense, or storage. Plant growth and especially reproduction require substantial nitrogen and are therefore dependent on nutrient uptake, but many plant defenses are purely carbon based. Plant respiration includes the costs of tissue maintenance, ion uptake, and transport and biosynthesis.

ferentiation balance follow from considerations of plant form and function; they emphasize physiological constraints and predict phenotypic responses that may or may not be evolutionarily adaptive. Conversely, the principle of optimal allocation assumes that natural selection has resulted in plant responses that maximize growth (a fitness surrogate) and predicts phenotypic responses that may or may not be possible within the physiological milieu of the plant. Each of these models has well-established explanatory powers, and collectively they provide a solid foundation for predicting the effects of climate change on plant allocation patterns and resistance to herbivory. Where their domains overlap, predictions are frequently (but not always) congruent.

#### **Carbon/nutrient balance**

Plant growth requires both carbon and nutrients (see Figure 1). Nutrient limitations, which are ubiquitous among wild plants (Chapin, 1980), typically limit growth more than they do photosynthesis. Consequently, nutrient-limited plants tend to accumulate more carbohydrates than can be immediately invested in growth. If the ratio of carbon to nutrients increases, excess carbohydrates may be shunted into secondary metabolism and the production of carbon-based compounds like condensed tannins may increase (Bryant et al., 1983). Such secondary metabolites can deter herbivory and are often described as "defensive" (Rhoades and Cates, 1976; Haukioja, 1980; Mooney and Gulmon, 1982; Coley, 1986). However, under the carbon/nutrient balance hypothesis, secondary metabolites may alternatively be thought of as "storage" or "waste" products that only have incidental effects on herbivores (Tuomi et al., 1988). Predictions based on carbon/nutrient balance differ for nitrogen-based (e.g., alkaloids) versus carbon-based secondary metabolites. This chapter, as well as most of the relevant data, focuses on carbon-based metabolites.

#### **Growth/differentiation balance**

The principle of growth/differentiation balance (Loomis, 1932, 1953; Lorio, 1986, 1988; Herms and Mattson, 1992) asserts that tissue growth is negatively associated with tissue differentiation because both processes compete for the same pool of carbohydrates and because differentiation requires a mature intracellular architecture. Tissue differentiation in plants is defined to include processes that typically occur after cell expansion has been completed: lignification of cell walls, thickening of leaf cuticle, production of thorns and trichomes, and secondary metabolism leading to products such as tannins, terpenes, and alkaloids. Plants with a surplus of carbohydrates beyond that which can be invested in growth (because of other limitations such as water or nutrients) are said to be "sink-limited" (Wareing and

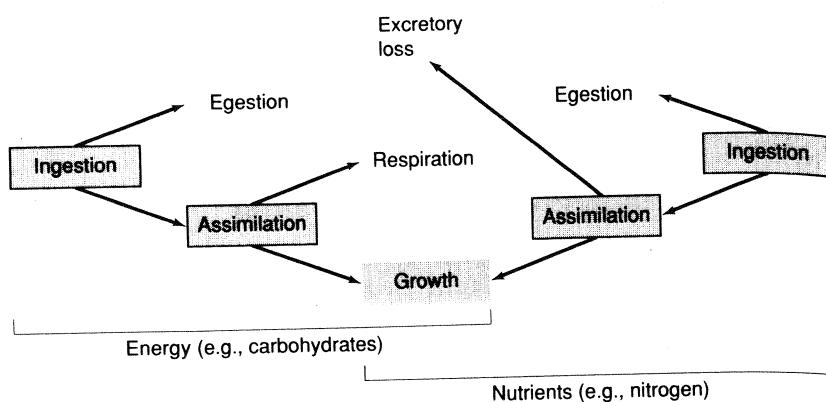
Patrick, 1975; Wardlaw, 1990; Luxmoore, 1991), and are predicted to invest proportionally more carbon in differentiation. Conversely, "source-limited" plants (whose growth is limited by carbon supply) are predicted to invest proportionally more carbon in growth. Plants with a high allocation to differentiation should have relatively low concentrations of water and protein, but relatively high concentrations of secondary metabolites (Herms and Mattson, 1992). Any kind of environmental stress that retards growth more than it does photosynthesis (e.g., nutrient stress or mild water stress) should shift allocation of carbohydrates towards differentiation, and this shift should generally be detrimental to herbivores. Predictions based on growth/differentiation balance and carbon/nutrient balance overlap broadly, but not completely (see "Changes in water balance," below). The growth/differentiation balance hypothesis is unique in specifying the importance of cellular development.

#### **Optimal allocation**

Because plants deal in so many resources and currencies, plant fitness is strongly influenced by strategies of allocation (Mooney, 1972; Bazzaz et al., 1987). Applying the tools of resource economics, Bloom et al. (1985) and Chapin et al. (1990) predicted optimal phenotypic responses of plants to various environmental scenarios. Optimally allocating plants should adjust to changes in resource availability in ways that stabilize exchange ratios (the relative amounts of two resources that can be acquired for a given expenditure of a single resource). A corollary is that plants should balance their allocation such that growth is equally limited by all three resource classes (i.e., nitrogen, carbon, and water). Empirically based models provide a powerful means of refining and testing these predictions (Hirose, 1988; Pons et al., 1989; Sinclair and Horie, 1989; Hilbert et al., 1991).

#### **HERBIVORE NUTRITION AND ENERGETICS**

The growth and reproduction of herbivores, like that of plants, depends on the acquisition of carbon (chiefly as digestible carbohydrates) and nutrients (e.g., protein nitrogen) (Figure 2). However, because animals require more nitrogen than plants do (tissue concentrations of 7–14 percent versus 0.5–4 percent), herbivore growth may commonly be limited by dietary nitrogen (Mattson, 1980; White, 1984). The upper limits of diet quality for both vertebrate and insect herbivores are thought to be a joint function of protein content and of digestible carbohydrates (Robbins, 1983; Slansky and Scriber, 1985). If either or both are low, herbivores can sustain only low productivity (growth, fattening, fecundity, and lactation). Moreover, plant secondary chemicals can constrain herbivore growth below these limits by deterring consumption (Bernays and Simpson, 1982), interfering with digestive effi-



**FIGURE 2.** A model of herbivore energetics and nutrition. Herbivore growth is dependent upon the acquisition of both energy and nutrients. Of that which is consumed, some fraction of energy and nutrients is assimilated. Some fraction of assimilated energy is expended in respiration, and some fraction of assimilated nutrients is lost as excretory waste products (e.g., urea). The remainder supports herbivore growth. Plant secondary metabolites may deter consumption, interfere with assimilation, elevate respiratory expenses, or increase excretory losses.

ciency (Robbins et al., 1987), or elevating respiratory and/or excretory losses (Thomas et al., 1988).

In this chapter, I characterize changes in plant palatability based in part on tissue concentrations of nitrogen and secondary metabolites, but I emphasize that host "quality" is also a function of the particular herbivore. Different taxa of herbivores, even when fed the same diet, can differ dramatically in growth and survival (Lederhouse et al., 1992), usually because they are differentially sensitive to secondary metabolites. Other plant attributes, such as toughness, water content, fiber content, and micronutrients, are also of demonstrable relevance to herbivores, but these typically covary with nitrogen (Coley, 1983; Scriber, 1984) and are less often measured.

## EFFECTS OF GLOBAL CHANGE ON HERBIVORY

### Increased carbon dioxide

Under the carbon/nutrient balance hypothesis, an increased supply of carbon will increase the ratio of carbon to nutrients and should therefore lead to reduced tissue concentrations of nitrogen, but to increased tissue concentrations of carbon-based secondary metabolites. As predicted, leaf nitrogen concentration consistently declines about 18 percent under CO<sub>2</sub> enhancement.

However, no study has detected significant changes in secondary metabolite concentrations (Table 1). For example, the concentration of cardenolides in *Digitalis lanata* changed by less than 1 percent (7510 versus 7450 nmol/g) when CO<sub>2</sub> was tripled, even though plant productivity was increased by 63 percent (Stuhlfauth et al., 1987). The number of studies measuring secondary metabolite concentrations under CO<sub>2</sub> manipulation is presently limited and is skewed toward herbaceous plants. Also, some of the measured compounds may be metabolic intermediates with such high turnover rates that static concentration is a poor indicator of defensive investment (Reichardt et al., 1991). Nonetheless, this stability of secondary metabolism seems counter to predictions based on carbon/nutrient balance.

The consistent depression of leaf nitrogen concentrations under elevated CO<sub>2</sub> levels (Table 1) could either be a nonadaptive perturbation or an optimizing allocation response that maximizes whole-plant carbon gain by producing more leaf area of lower nitrogen concentration. These alternatives could be tested by evaluating the joint response of photosynthesis to leaf nitrogen and atmospheric CO<sub>2</sub> concentration. Photosynthetic rate generally increases with leaf nitrogen content (Field and Mooney, 1986; Hirose, 1988), presumably because of increased concentrations of a rate-limiting enzyme (rubisco, RuBP carboxylase). Enhanced CO<sub>2</sub> immediately increases photosynthetic rates (average of 62 percent increase in 18 experiments with 9 tree species; Eamus and Jarvis, 1989; Bazzaz, 1990), although photosyn-

**TABLE 1.** Effects of enhanced CO<sub>2</sub> on plant tissue concentrations of nitrogen and secondary metabolites.

Nitrogen	Secondary metabolites <sup>b</sup>	Plant	Reference
-24*	-19	<i>Plantago</i>	Fajer et al., 1989
-17*	9	<i>Plantago</i>	Fajer, 1989
-26	—	Lima bean	Osbrink et al., 1987
-11*	—	Soybean	Lincoln et al., 1984
-7	—	Soybean	Lincoln et al., 1986
-25*	7	Peppermint	Lincoln and Cuovet, 1989
-18*	-20	Sagebrush	Johnson and Lincoln, 1990
-18*	4	Sagebrush	Johnson and Lincoln, 1991

\*Effects are expressed as percent change relative to control.

<sup>b</sup>All secondary metabolites are carbon-based (i.e., contain no N).

<sup>\*</sup>P < 0.05

thetic rates may return to near their original levels following plant acclimation (perhaps involving reallocation of nitrogen; Tissue and Oechel, 1987; Eamus and Jarvis, 1989). Whole-plant carbon gain per unit of nitrogen ( $\mu\text{mol CO}_2 \cdot \text{mol N}^{-1} \cdot \text{s}^{-1}$ ) could be maximized at a lower concentration of leaf nitrogen in an atmosphere with elevated  $\text{CO}_2$  concentration (Hilbert et al., 1991).

Depending on assumptions, the principle of optimal allocation could predict increases, decreases, or no change in concentrations of carbon-based antiherbivore defenses under enhanced  $\text{CO}_2$ . If the benefits of defense increase linearly with investment in secondary chemistry, and if the cost function declines under enhanced  $\text{CO}_2$ , then optimal allocation predicts that increased  $\text{CO}_2$  will favor increased concentrations of defensive metabolites. However, if antiherbivore defenses are maximally effective at relatively low concentrations (the "qualitative" defense scenario; Rhoades and Cates, 1976), then the optimal investment in defense would probably not change under enhanced  $\text{CO}_2$ . Clearly, these predictions are so all-encompassing as to be useless without additional information.

Increasing atmospheric  $\text{CO}_2$  should not have any direct physiological effects on herbivores (Fajer et al., 1991). However,  $\text{CO}_2$ -induced changes in host plants may sometimes be detrimental to herbivores. In 4 of 9 studies, insect herbivores raised on plants grown with enhanced  $\text{CO}_2$  had reduced survival, reduced growth rate, increased development time, or reduced pupal mass (Table 2). Insects feeding on enhanced- $\text{CO}_2$  plants appeared to compensate for low nutritive quality (low nitrogen content) by increasing food consumption (average of 48 percent higher, significant in 6 of 6 studies). In 3 of 6 cases of increased consumption, growth rates did not change, indicating successful compensation. The effects of enhanced  $\text{CO}_2$  on insect growth, survival, and pupal mass were usually less than those of some other sources of variation in host quality (e.g., long-term inducible resistance, leaf maturation, and among-tree variance; Table 2).

#### Soil nutrient availability

Global climate change should alter soil moisture, soil temperature, and litter quality in ways that affect decomposition processes and thus nutrient availability for plants (Anderson, 1991). Many scenarios are possible (Pastor and Post, 1988; Mooney et al., 1991), and patterns are likely to vary regionally, but the general effect may be to reduce mineral nitrogen availability because of increased C:N ratios in the litter (Bazzaz, 1990). Nitrogen fertilization typically leads to plant tissue with higher concentrations of nitrogen and lower concentrations of secondary metabolites (Table 3; note that the one evergreen—Scots pine—was an exception in that resin acids actually increased by 20 percent). Thus, plants that become increasingly nitrogen-limited due to climate-induced changes in mineralization rates are

TABLE 2. Effects on herbivores of growing plants in an enhanced  $\text{CO}_2$  environment.<sup>a</sup>

Survival	Effect on herbivore (percent change)				Reference
	Relative growth rate	Relative consumption rate	Development time ( $T/\text{Dev}$ )	Pupal mass ( $M_{\text{Pupa}}$ )	
<b>ENHANCED <math>\text{CO}_2</math></b>					
-15*	—	—	7*	3	Fajer et al., 1989
-2	-13*	34*	—	—	Fajer, 1989
—	—	—	0	-1	Akey et al., 1988
—	—	—	-1	—	Osbrink et al., 1987
—	-12	81*	—	—	Lincoln et al., 1984
—	-5*	20*	—	—	Lincoln et al., 1986
—	10	23*	—	—	Lincoln and Cuovet, 1989
—	26	74*	—	—	Johnson and Lincoln, 1990
—	-40*	53*	—	—	Johnson and Lincoln, 1991
<b>LONG-TERM INDUCIBLE RESISTANCE</b>					
-25*	—	—	6*	-18*	Haukioja et al., 1985
—	-32*	—	—	—	Neuvonen and Haukioja, 1984
<b>LEAF MATURATION</b>					
—	-40*	-18*	—	—	Ayres and MacLean, 1987a
<b>AMONG-TREE VARIANCE</b>					
—	-32*	—	—	—	Ayres et al., 1987

<sup>a</sup>Effects (expressed as percent change relative to control) due to some other sources of intraspecific variation (long-term inducible resistance, leaf maturation, and among-tree variance) are included for comparison.

\* $P < 0.05$

likely to decline in quality for herbivores. The phenotypic response of plants to altered nutrient availability may be substantial (average of 38 percent increase in tissue nitrogen and 26 percent decrease in secondary metabolites in fertilized plants; Table 3), and the secondary effects on herbivores may also be considerable. Compared to foliage of control trees, foliage of fertilized quaking aspen had lower concentrations of condensed tannin (-83 percent), tremuloiden (-31 percent), and salicin (-50 percent), but higher concentrations of nitrogen (+100 percent). Apparently as a result, the large aspen tortrix (Lepidoptera: Geometridae), a defoliator of aspen, produced 25 percent larger pupae on fertilized trees (Bryant et al., 1987b). Snowshoe

**TABLE 3.** Effects of fertilization on plant tissue concentrations of nitrogen and secondary metabolites.

Nitrogen	Percent change in tissue concentration <sup>a</sup>	Secondary metabolites <sup>b</sup>	Tissue	Reference
56*	-24*	Leaf	Larsson et al., 1986	
100*	-55*	Leaf	Bryant et al., 1987a	
26*	-29*	Leaf	Johnson and Lincoln, 1991	
26*	20*	Needle	Bjorkman et al., 1991	
31*	-38*	Shoot	Bryant et al., 1987b	
-11	-29*	Shoot	Bryant, 1987	

<sup>a</sup>Effects are expressed as percent change relative to control.

<sup>b</sup>All secondary metabolites are carbon based.

\*P < 0.05

hares were nearly perfect at recognizing and preferentially consuming shoots from fertilized birch trees (which contained 38 percent less papyriferic acid than control trees; Bryant et al., 1987a), and moose browsed preferentially on Scots pine growing in high-nutrient sites (Danell et al., 1991).

The typical effects of nutrient availability on plant tissue composition and palatability to herbivores conform well with all three theories. Under the carbon/nutrient balance hypothesis, fertilization yields increased nitrogen, therefore reduced C:N, higher tissue nitrogen, and lower secondary metabolism. Under the growth/differentiation balance hypothesis, fertilizing a nutrient-limited plant promotes growth, and the resulting growth-dominated plant contains higher nitrogen and lower secondary metabolites. Under the principle of optimal allocation, plants in a high-nutrient environment have less difficulty replacing nutrients lost to herbivory, absorb a greater opportunity cost if they do not grow maximally, and therefore invest less in antiherbivore defense (Bryant et al., 1983).

#### Changes in cloud cover

Reduced radiation, such as that resulting from increased cloud cover, tends to depress plant carbon budgets and to lower secondary metabolism (average of 52 percent reduction in tissue concentrations of secondary metabolites; Table 4). Shading appears to have a larger effect on secondary metabolism than does either fertilization or enhanced CO<sub>2</sub>, but a lesser effect on tissue nitrogen concentration. Although studies are few, shading can clearly have

**TABLE 4.** Effects of shading on plant tissue concentrations of nitrogen and secondary metabolites.

Nitrogen	Percent change in tissue concentration <sup>a</sup>		Tissue	Reference
	Secondary metabolites <sup>b</sup>	Nitrogen		
-4	-70*	Leaf	Larsson et al., 1986	
4	-44*	Leaf	Mole et al., 1988	
0	-62*	Shoot	Bryant et al., 1987b	
7	-33*	Shoot	Bryant, 1987	

<sup>a</sup>Effects are expressed as percent change relative to control.

<sup>b</sup>All secondary metabolites are carbon based.

\*P < 0.05

enormous effects on the palatability of plants to herbivores. For example, snowshoe hares consumed nearly all the birch shoots from shaded trees while consuming virtually none of the control shoots (Bryant et al., 1987a). Similarly, leaf beetles consumed five times as much foliage from willows grown in low light compared with control willows (Larsson et al., 1986).

Carbon/nutrient balance readily explains the reduced concentrations of secondary metabolites in shaded trees (reduced carbon yields reduced C:N, yields reduced allocation of carbon to secondary metabolism). However, reduced secondary metabolism can also be interpreted as a reduced commitment to differentiation processes in response to source limitations. Both the carbon/nutrient balance and the growth/differentiation balance hypotheses appear to predict increased concentrations of tissue nitrogen, which does not occur. Reduced allocation to secondary metabolism in response to shading may be optimal if carbon stress is an early symptom of being overgrown by competitors (maximal allocation to growth under these circumstances may increase the probability of surviving to reproduction, even though defense is compromised); but if the increased risk of catastrophic herbivory outweighs the competitive benefits, then the response is maladaptive.

Changes in cloud cover will affect some poikilothermic herbivores directly by altering their operative temperature (Rawlins and Lederhouse, 1981; Grossmueller and Lederhouse, 1985; Casey et al., 1988; Kukal et al., 1988; Weiss et al., 1988; Dunham, this volume). General circulation models (GCMs) do not appear to be as explicit or accurate with regard to changes in radiation as would be desirable (Schneider, this volume) given the likely biological effects.

### Changes in water balance

Correlative and experimental evidence suggests that changes in plant water balance can alter palatability to herbivores and influence herbivore population dynamics (White, 1984). Mattson and Haack (1987a) highlighted 10 insect families in 5 orders "that historically have reached outbreak proportions following drought."

Moderate water stress tends to retard growth more than it does photosynthesis (Kozlowski, 1982; Allen et al., 1987; Wardlaw, 1990). Thus, carbohydrates accumulate, and plant allocation to differentiation processes (e.g., secondary metabolism) should increase. Under severe water stress, however, photosynthesis declines (Ehleringer and Cook, 1984; Gollan et al., 1985). Plants then become carbon-limited, and their secondary metabolite content should decline. This reasoning, which predicts a curvilinear response of secondary metabolism to water stress, has been supported by studies of tannin in Douglas fir (Horner, 1990) and of rubber in guayule (Reddy and Das, 1988). In many other studies, however, the concentration of secondary metabolites simply increases following drought stress (Table 5; 27 of 27 studies reviewed by Mattson and Haack, 1987b). Presumably plant species differ in the water deficit (MPa of leaf water potential) at which secondary metabolism is maximized. Many studies to date involve only two water treatments, which are obviously too few to describe a curvilinear function. Considerations of carbon/nutrient balance alone seem inadequate

**TABLE 5.** Effects of water stress on plant tissue concentrations of secondary metabolites.

Percent change in secondary metabolites <sup>a</sup>	Tissue	Leaf water potential (MPa)	Reference <sup>b</sup>
61*	Leaf	-0.05 to -0.6	Charles et al., 1990
-14	Leaf	-0.7 to -1.3	Stuhlfauth et al., 1987
7	Leaf	-0.35 to -0.65	Horner, 1990
-17*	Leaf	-0.65 to -1.00	Horner, 1990
71*	Stem	-0.5 to -2.5	Reddy and Das, 1988
-5	Stem	-2.5 to -3.0	Reddy and Das, 1988
163*	Stem	-1.8 to -3.0	Allen et al., 1987

<sup>a</sup>All secondary metabolites are carbon-based. Effects are expressed as percent change relative to control.

<sup>b</sup>In two studies where a nonlinear response was suggested, the regions of positive and negative slope were evaluated separately. Twenty-seven of 27 other studies reviewed by Mattson and Haack (1987b) showed an increase in secondary metabolites following drought stress.

\*P < 0.05

to predict changes in secondary metabolism based on changes in water balance. Water stress is thought to retard photosynthesis more than it does nutrient uptake (Bloom et al., 1985; Mattson and Haack, 1987a), which should reduce the C:N ratio and lead to reduced secondary metabolism. This prediction of the carbon/nutrient balance hypothesis seems inconsistent with the data.

The consequences for herbivores of drought stress in their host plants can be beneficial (bark beetles attacking white fir; Ferrell, 1978), negligible (gypsy moths feeding on birch trees; Herms, 1991), mildly detrimental (sawflies feeding on ponderosa pine; McCullough and Wagner, 1987), or extremely detrimental (six times higher neonatal mortality in shoot-galling sawfly larvae attacking willows; Preszler and Price, 1988). Water stress made 12 of 41 plant species more palatable to locusts, but 5 of 41 less palatable (Bernays and Lewis, 1986). Spider mite populations were highest on either well-watered or severely stressed bean plants, but low on moderately stressed plants (English-Loeb, 1990); this pattern is predicted if secondary metabolism rises, then falls, with increasing water stress. The overall diversity of effects is likely due to differences among plants in their response to drought stress as well as to differences among herbivores in their sensitivity to plant responses (Larsson, 1989). There is no substitute for more empirical studies with ecologically relevant plants, herbivores, and treatments.

Bark beetles, which have great potential for altering ecosystems (Rykiel et al., 1988; Veblen et al., 1991), may be a critical agent of change in forests subjected to drought stress (Balch and Prebble, 1940; Christiansen et al., 1987; Lorio, 1986). Seasonal changes in the resistance of pine to southern pine beetles may be explained in terms of water deficits affecting plant allocation to growth versus differentiation processes (Lorio et al., 1990). During early summer, tree growth is rapid, and the production of oleoresin defenses in attacked trees is relatively low (Lorio and Sommers, 1986). This is the time of greatest population growth in the bark beetles. With the onset of moderate water deficits in midsummer, tree growth declines, oleoresin production increases, and resistance to bark beetles also increases. This change corresponds to the ontogenetic transition from the production of earlywood to the production of latewood (Lorio, 1988). [Latewood is characterized by highly differentiated cells (forming vertical resin ducts) that function in the production and transport of oleoresin.] Under this scenario, reduced precipitation would shorten the seasonal period of rapid tree growth when vulnerability to bark beetles is greatest. However, extreme water stress, which limits photosynthesis as well as growth, should reverse the effect by limiting oleoresin production and increasing vulnerability to beetle attack. Within a region, reduced precipitation could thus lead to increased beetle damage in dry sites, but reduced beetle damage in mesic sites.

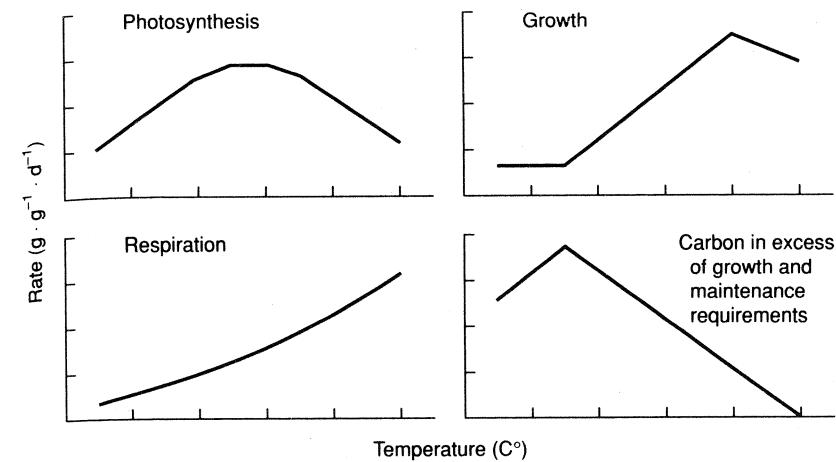
High commitments of drought-stressed trees to reproduction may ex-

acerbate their vulnerability to wood-boring beetles. Birch trees defend themselves against the bronze birch borer (Coleoptera: Buprestidae) by rapidly growing a callus around beetle larvae feeding in the cambium (Herms, 1991). The larvae die if encapsulated by the callus, but the tree dies if more than a few larvae escape their callus. Growth of the birch callus is driven by carbohydrates transported from the leaf canopy. The photosynthetic rate of ten-year-old birch trees was reduced under a low irrigation treatment; consequently, these drought-stressed trees exhibited slower callus growth and sustained higher mortality due to birch borers (Herms, 1991). This effect was accentuated because the slow-growing trees invested heavily in female reproduction, which must have reduced the carbon available to support callus growth.

### Increased temperature

General circulation models consistently predict increases of about 2–4°C in average air temperatures, with larger increases at high latitudes (Mitchell et al., 1989; Schneider, this volume). However, surprisingly little is known about the effects of such temperature changes on plant allocation patterns or resistance to herbivory. In warm years compared with cold years in Fennoscandia (thermal sums above a 5°C base = 540 to 300 degree-days from 1979 to 1984), mature foliage of *Vaccinium myrtillus* tended to have lower leaf nitrogen (1.4 percent versus 2.4 percent dry mass) and higher Folin-Denis phenolics (20 percent versus 10 percent) (Laine and Henttonen, 1987). Greenhouses that elevated average daily summer temperatures by about 3°C produced a comparable effect (13 percent reduction in leaf nitrogen compared with control plots, and a 38 percent increase in phenolics). Figure 3 suggests a preliminary model to explain these patterns in terms of temperature effects on net photosynthesis, maintenance respiration, and growth rate. The model assumes that the summer climate in Finnish Lapland includes low temperatures at which *Vaccinium* can photosynthesize but not grow. The model predicts that populations of the same plant in different regions could respond differently to the same temperature elevation, with southern populations becoming carbon-stressed but with northern populations accruing a carbon surplus. Based on results from other carbon/nutrient manipulations, I would expect increased herbivory and improved herbivore performance on plants with a temperature-induced carbon deficiency.

Many herbivores have evolved life histories in which their maximum nutritional demand coincides with the season when developing (as opposed to mature) plant tissue is maximally available. These herbivores include ungulates (Klein, 1965; Cooper et al., 1988), primates (Milton, 1979), rodents (Batzli et al., 1980), geese (Sedinger and Raveling, 1986), gypsy moths (Hough and Pimentel, 1978; Raupp et al., 1988), spruce budworm (Law-

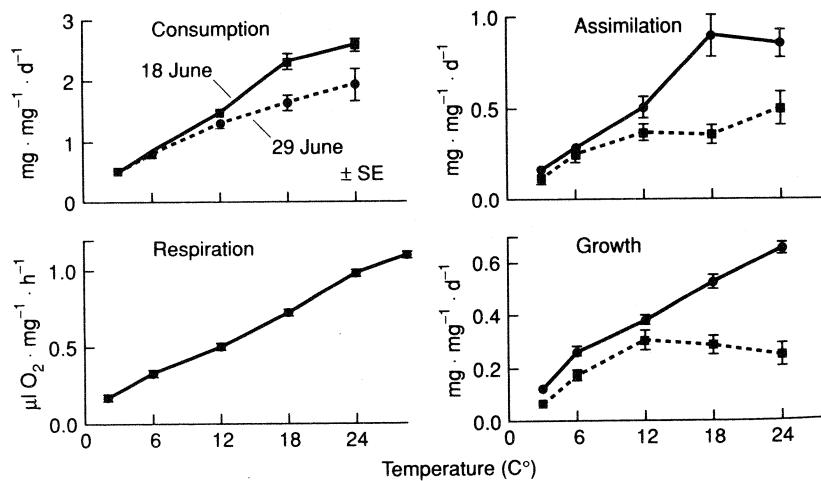


**FIGURE 3.** Generalized response of plant carbon balance to temperature. Photosynthesis tends to have a broad temperature optimum, while respiration rate increases across the full range of temperatures (Berry and Bjorkman, 1980; Sveinbjornsson, 1983; Patterson and Graham, 1987). There exists a range of low temperatures at which photosynthesis proceeds but growth does not (Pollack et al., 1983; Pollack, 1990). Beyond this lower threshold, plant growth rate tends to increase with temperature (Scott, 1970; Watts, 1974; Parsons and Robson, 1980). Consequently, carbon available for secondary metabolism (i.e., carbon in excess of growth and maintenance requirements) is predicted to increase, then decrease, with increasing temperature.

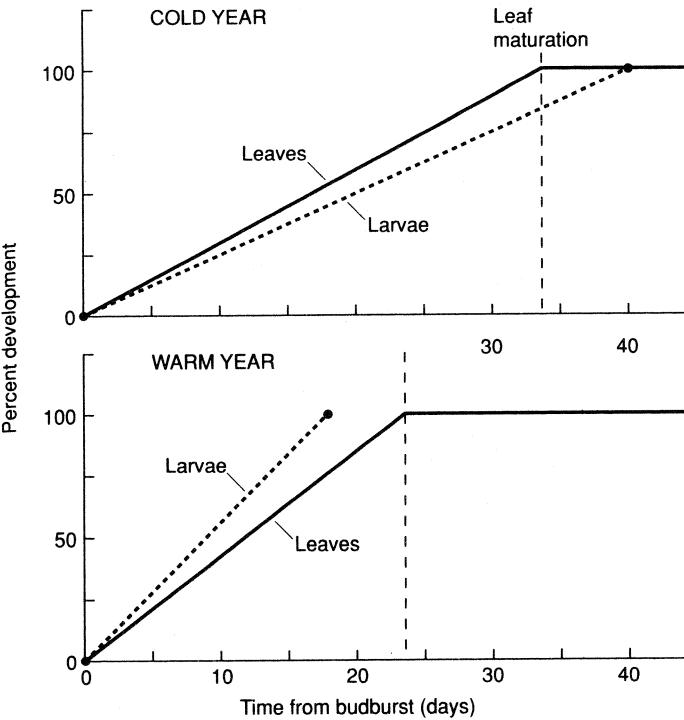
rence, 1990), and leafhoppers (Townsend, 1989). About half of forest insect pest species (27 of 54 in Martineau, 1984) appear to be early-season specialists on immature plant tissue. Developing plant tissue is typically low in fiber (thus highly digestible), high in nitrogen, and low in secondary metabolites (Mattson, 1980; Coley, 1983). Maturation of this plant tissue imposes phenological barriers to herbivores (Feeny, 1970; Schweitzer, 1979; Schroeder, 1986; Turgeon, 1986); hence herbivores of immature tissue engage in a developmental race with their host plants (MacLean, 1983). Larvae of *Epippia autumnata* (Lepidoptera: Geometridae) grew very quickly (doubling their mass every 1 to 2 days) on young birch leaves, but insect growth rate declined dramatically (−32 percent) over a period of just 3 to 6 days following the completion of leaf expansion (Ayres and MacLean, 1987a). Global warming should reduce the time during which high-quality immature foliage is available because leaf development rate increases with temperature (Scott, 1970; Ong and Baker, 1985; Watts, 1974; Pollack et al., 1983; Graves et al., 1989; Pollack 1990). This seems unavoidably detrimental to homeothermic herbivores, and may result, for example, in chronically lower

breeding success in geese and caribou (Sedinger and Flint, 1991; Kuropat and Bryant, 1979). However, insect herbivores, like the plants on which they feed, tend to grow faster at higher temperatures (Figure 4; Taylor, 1981; Scriber and Lederhouse, 1983; Ayres and MacLean, 1987b), so predictions are less clear.

Increasing global temperatures can affect the developmental race between poikilothermic herbivores and their host tissue if the temperature sensitivity of the herbivore differs from that of the host (MacLean, 1983). We tested this in the *Epirrita*–mountain birch system by building greenhouses around in situ trees (S. F. MacLean and M. P. Ayres, in preparation). Leaf maturation, and a concomitant decline in food quality for *Epirrita*, occurred more rapidly in greenhouse than in control trees (25 percent lower larval growth rates 3 weeks after budburst). However, *Epirrita* also increased development rates in response to the temperature elevation; larvae grown on greenhouse trees pupated 3–6 days earlier than did those on control trees (8–15 percent shorter development time). Furthermore, greenhouse larvae had better survival rates and produced larger pupae



**FIGURE 4.** The interacting effects of temperature and host quality on the growth of a birch herbivore, *Epirrita autumnata*. On young expanding leaves (18 June), larval consumption rate, assimilation rate, respiration rate, and growth rate all increased with increasing temperature from 3°C to 24°C. Following the completion of leaf expansion (29 June), assimilation rate declined due to reduced digestive efficiency and reduced consumption rate. Consequently, herbivore growth rate declined markedly, especially at high temperatures. On mature leaves, respiration rate increased as much as assimilation rate over the range from 12°C to 24°C, and the difference between them, growth rate, did not change (S. F. MacLean and M. P. Ayres, unpublished data).



**FIGURE 5.** Model showing hypothesized effect of temperature on the developmental race between maturing leaves and insect herbivores that consume them. Both leaf maturation and larval development are temperature-sensitive processes, but larval development is accelerated relatively more in a warm year. Leaf quality for the herbivores declines dramatically at leaf maturation, so warm years favor the insects by allowing them to complete development before the leaves do.

(yielding more fecund adults) than control larvae did. As a result, the rate of population increase of moths in the greenhouse treatment increased up to 2.9 times, suggesting that temperature increases in this system will favor the insect. Remarkably, these effects were the result of only a 1°C increase in daily mean temperature inside the greenhouses. If insects are generally more temperature-sensitive than their host plants, global warming of 2–4°C may lead (through the mechanism suggested in Figure 5) to outbreaks of many insect herbivores.

## SUMMARY

Climate change could affect plant–herbivore interactions in many ways. The challenge is to identify the mechanisms that will most directly transduce

climate change into ecological impacts. This process is expedited by physiological models of plant allocation and herbivore nutrition, but the most appropriate theoretical framework seems to vary depending upon the herbivore guild and the specific environmental change (Larsson 1989). I find it useful to distinguish among herbivores of mature plant tissue, herbivores of developing plant tissue, and bark beetles.

Changes in atmospheric CO<sub>2</sub> concentration, soil nutrients, cloud cover, water availability, and temperature all affect the composition and palatability of mature plant tissue (Table 6). Increased CO<sub>2</sub>, reductions in soil nitrogen, and sometimes increased temperature, tend to reduce tissue nitrogen; these changes should be detrimental to herbivores. Reductions in soil nitrogen, reductions in cloud cover, and sometimes increases in temperature and drought stress tend to increase concentrations of plant secondary metabolites; these changes should also be detrimental to herbivores. However, we cannot generalize that global change will be detrimental to herbivores of mature plant tissue. Such predictions require that we forecast changes in photosynthetically active radiation, plant water balance, and soil nutrient availability. Yet changes in each will presumably vary in direction and magnitude from region to region. Both temperature and CO<sub>2</sub> are likely to increase on a global scale (Schneider, this volume), but the consequences for plant-herbivore interactions of doubling CO<sub>2</sub> could easily be reversed

TABLE 6. Effects on plant tissue composition of five environmental factors associated with global change.

Environmental change ( $\approx$ amount)	Percent change in concentration <sup>a</sup>		
	Nitrogen	Secondary metabolites	Tissue
+ CO <sub>2</sub> (2 $\times$ )	-18*	-4	Leaf
+ Soil nitrogen (50 g/m <sup>2</sup> )	61*	-36*	Leaf
	26*	20*	Needle
	10	-34*	Shoot
+ Shade (50%)	0	-57*	Leaf
	3	-48*	Shoot
- Water potential (1 MPa)	—	9*	Leaf
	—	76*	Stem
+ Temperature (3°C)	-13*	38*	Leaf

<sup>a</sup>Values for CO<sub>2</sub>, soil nitrogen, shade, and water potential indicate average percent change from Tables 1, 3, 4, and 5, respectively; temperature effect is from Laine and Henttonen (1987). Effects are expressed as percent change relative to control.

\*Average includes at least one significant effect ( $P < 0.05$ ).

by changes in one or more other factors (the effects of CO<sub>2</sub> on host plant quality may be the least among five aspects of global change; Table 6). We expect nonlinear effects of temperature and water potential on plant defense. Thus, meaningful predictions require that we know the initial state of the plant, the direction and magnitude of the environmental change, and the precise form of the plant's physiological responses. This knowledge is lacking for virtually all plants. Moreover, we need a better understanding of the ways by which various environmental perturbations interact. Can the effect of simultaneously increasing temperature and reducing precipitation be predicted from the additive effects of each?

Bark beetles deserve special recognition because of their extraordinary economic and ecological impact, and because their outbreaks have been so often linked to climatic anomalies. Lorio et al. (1990) are accumulating support for a model of tree defense that relies on water balance to predict the timing of an ontogenetic switch from poorly defended earlywood to well-defended latewood.

Numerous herbivores, including perhaps half of the economically important outbreak insects, specialize on developing plant tissue that is of high quality but only ephemerally available. For these herbivores, a phenological mismatch of a few days, perhaps caused by differential effects of temperature on plants and herbivores, can halve fecundity (Ayres and MacLean, 1987a; Keesee and Wood, 1991) and thus result in huge impacts on plant-herbivore communities. Plants can reduce damage through slight phenological displacement from the herbivore (Eidt and Little, 1970; Aide, 1988; Crawley and Akhteruzzaman, 1988; Townsend, 1989; Tuomi et al., 1989). The availability of high-quality food (or, from the plant's perspective, the period of high vulnerability) is strongly temperature sensitive. Warmer temperatures will reduce the temporal availability of food, but will also increase the rate of consumption and development in poikilothermic herbivores. Unless the temperature sensitivity of plant development and insect development are identical, changes in temperature will favor either the plant or the insect (see Figure 5). Virtually nothing is known about the relative temperature sensitivity of insects and their host plants, but greenhouse experiments (above) in Finnish Lapland indicate that an increase of 1°C can potentially triple population growth of the herbivore.

Physiological models of plant allocation and herbivore nutrition already allow general predictions regarding the effects of climate change. The theory of carbon/nutrient balance provides a parsimonious explanation for many phenotypic responses to alterations of CO<sub>2</sub>, light, and nutrient availability. Its failures suggest the role of natural selection in adapting plant responses to the ecological challenges of particular environments (optimal allocation hypothesis). The theory of growth/differentiation balance explains the general importance of immature plant tissue for herbivore nutrition and provides a robust framework for evaluating the effects of water balance on plant

resistance. I anticipate that changes in temperature and water availability will have the largest impact on plant-herbivore interactions. These are the same areas where our theoretical and empirical understanding seems weakest. Nonlinear responses to temperature and moisture imply that changes in climatic variability (even without a change in the mean) can alter plant-herbivore interactions. Assessing the ecological and economic risks that accompany global change demands experiment-based research that builds on existing physiological models to predict responses of populations, communities, and ecosystems. Progress will be expedited through the selection of experimental systems that involve naturally interacting plants and herbivores.

#### ACKNOWLEDGMENTS

I thank B. D. Ayres, J. P. Bryant, F. S. Chapin, C. Field, M. A. Geber, D. A. Herms, K. S. Johnson, R. C. Lederhouse, P. L. Lorio, S. F. MacLean, W. J. Mattson, P. Niemelä, and J. M. Scriber for helpful discussions and comments on the manuscript. D. A. Herms generously shared his literature collection. Financial support was provided by USDA Grant 90-37153-5263, NSF Grant BSR 88-01184, and a Fulbright research fellowship.

## Literature Cited

- Aide, T. M. 1988. Herbivory as a selective agent on the timing of leaf production in a tropical understory community. *Nature* 336: 574-575.
- Akey, D. H., B. A. Kimball, and J. R. Mauney. 1988. Growth and development of the pink bollworm, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae), on bolls of cotton grown in enriched carbon dioxide atmospheres. *Environ. Ent.* 17: 452-455.
- Allen, S. G., F. S. Nakayama, D. A. Dierig, and B. A. Rasnick. 1987. Plant water relations, photosynthesis, and rubber content of young guayule plants during water stress. *Agron. J.* 79: 1030-1035.
- Anderson, J. M. 1991. The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecol. Appl.* 1: 326-347.
- Ayres, M. P. and S. F. MacLean, Jr. 1987a. Development of birch leaves and the growth energetics of *Epiprita autumnata* (Geometridae). *Ecology* 68: 558-568.
- Ayres, M. P. and S. F. MacLean, Jr. 1987b. Molt as a component of insect development: *Galerucella sagittariae* (Chrysomelidae) and *Epiprita autumnata* (Geometridae). *Oikos* 48: 273-279.
- Ayres, M. P., J. Suomela, and S. F. MacLean, Jr. 1987. Growth performance of *Epiprita autumnata* (Lepidoptera: Geometridae) on mountain birch: trees, broods, and tree x brood interactions. *Oecologia* 74: 450-457.
- Balch, R. E., and J. S. Prebble. 1940. The bronze birch borer and its relation to the dying of birch in New Brunswick forests. *Forestry Chronicle* 16: 179-201.
- Bale, J. S. 1991. Implications of cold hardiness for pest management. In *Insects at Low Temperature*, R. E. Lee, Jr., and D. L. Denlinger (eds.). Chapman and Hall, New York, NY. pp. 461-498.
- Batzli, G. O., H. G. Jung, and G. Gunten. 1980. Nutritional ecology of microtine rodents: linear foraging rates for brown lemmings. *Oikos* 37: 112-116.
- Bazely, D. R., and R. L. Jefferies. 1986. Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. *J. Ecol.* 74: 693-706.
- Bazzaz, F. A. 1990. The response of natural ecosystems to the rising global CO<sub>2</sub> levels. *Ann. Rev. Ecol. Syst.* 21: 167-196.
- Bazzaz, F. A., N. R. Chiarello, P. D. Coley, and L. F. Pitelka. 1987. Allocating resources to reproduction and defense. *Bioscience* 37: 58-68.
- Bernays, E. A., and A. C. Lewis. 1986. The effect of wilting on palatability of plants to *Schistocerca gregaria*, the desert locust. *Oecologia* 70: 132-135.
- Bernays, E. A., and S. J. Simpson. 1982. Control of food intake. *Adv. Insect Physiol.* 16: 59-118.
- Berry, J., and O. Bjorkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Ann. Rev. Plant Physiol.* 31: 491-543.
- Bjorkman, C., S. Larsson, and R. Gref. 1991. Effects of nitrogen fertilization on pine needle chemistry and sawfly performance. *Oecologia* 86: 202-209.
- Bloom, A. J., F. S. Chapin, III, and H. A. Mooney. 1985. Resource limitation in plants - an economic analogy. *Ann. Rev. Ecol. Syst.* 16: 363-392.
- Brandner, T. A., R. O. Peterson, and K. L. Risenhoover. 1990. Balsam fir on Isle Royale: effects of moose herbivory and population density. *Ecology* 71: 155-164.
- Brown, V. K., A. C. Gange, I. M. Evans, and A. L. Storr. 1987. The effect of insect herbivory on the growth and reproduction of two annual *Vicia* species at different stages in plant succession. *J. Ecol.* 75: 1173-1189.
- Bryant, J. P. 1987. Feltleaf willow - snowshoe hare interactions: plant carbon/nutrient balance and implications for floodplain succession. *Ecology* 68: 1319-1327.
- Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357-368.
- Bryant, J. P., T. P. Clausen, P. B. Reichardt, M. C. McCarthy, and R. A. Werner. 1987a. Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen, *Populus tremuloides* Michx. , leaves for the large aspen tortrix, *Choristoneura conflictana* Walker. *Oecologia* 73: 513-517.
- Bryant, J. P., F. S. Chapin III, P. B. Reichardt, and T. P. Clausen. 1987b. Response of winter chemical defense in Alaska paper birch and green alder to manipulation of plant carbon/nutrient balance. *Oecologia* 72: 510-514.
- Bryant, J. P., and P. B. Reichardt. 1992. Controls over secondary metabolite production by arctic woody plants. In *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*, F. S. Chapin, III, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda (eds.). Academic Press, Orlando, FL. pp. 377-390.
- Cargill, S. M., and R. L. Jefferies. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *J. Appl. Ecol.* 21: 669-686.
- Casey, T. M., B. Joos, T. D. Fitzgerald, M. E. Yurling, and P. A. Young. 1988. Synchronized group foraging, thermoregulation, and growth of eastern tent caterpillars in relation to microclimate. *Phys. Zool.* 61: 372-377.
- Chapin, F. S., III. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11: 233-260.
- Chapin, F. S., III, E. D. Shulze, and H. A. Mooney. 1990. The ecology and economics of storage in plants. *Ann. Rev. Ecol. Syst.* 21: 423-447.
- Charles, D. J., R. J. Joly, and J. E. Simon. 1990. Effects of osmotic stress on the essential oil content and composition of peppermint. *Phytochemistry* 29: 2837-2840.
- Christiansen, E., R. H. Waring, and A. A. Berryman. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *Forest Ecology and Management* 22: 89-106.
- Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in lowland tropical forest. *Ecol. Mon.* 53: 209-233.
- Coley, P. D. 1986. Costs and benefits of defense by tannins in a neotropical tree. *Oecologia* 70: 238-241.
- Cooper, S. M., N. Owen-Smith, and J. P. Bryant. 1988. Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a South African savanna. *Oecologia* 75: 336-342.

- Cottam, D. A., J. B. Whittaker, and A. J. C. Malloch. 1986. The effects of chrysomelid beetle grazing and plant competition on the growth of *Rumex obtusifolius*. *Oecologia* 70: 452-456.
- Crawley, M. J. 1989. The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. In *Insect-Plant Interactions*, Vol. 1, E. A. Bernays (ed.). CRC Press, Boca Raton, FL. pp. 45-71.
- Crawley, M. J., and M. Akteruzzaman. 1988. Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Funct. Ecol.* 2: 409-415.
- Danell, K., P. Niemelä, T. Vuorisalo, and T. Varvikko. 1991. Moose browsing on Scots pine along a gradient of plant productivity. *Ecology* 72: 1624-1633.
- De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology* 72: 1076-1088.
- Dyer, M. I., C. L. Turner, and T. R. Seastedt. 1991. Mowing and fertilization effects on productivity and spectral reflectance in *Bromus inermis* plots. *Ecol. Applic.* 1: 443-452.
- Eamus, D., and P. G. Jarvis. 1989. The direct effects of increase in the global atmospheric CO<sub>2</sub> concentration on natural and commercial temperate trees and forests. *Adv. Ecol. Res.* 19: 1-44.
- Ehleringer, J. R., and C. S. Cook. 1984. Photosynthesis in *Encelia farinosa* Gray in response to decreasing water potential. *Plant Physiol.* 75: 688-693.
- Eidt, D. C., and C. H. A. Little. 1970. Insect control through induced host-insect asynchrony: a progress report. *J. Econ. Entomol.* 63: 1966-1968.
- English-Loeb, G. M. 1990. Plant drought stress and outbreaks of spider mites: a field test. *Ecology* 71: 1401-1411.
- Fajer, E. D. 1989. The effects of enriched CO<sub>2</sub> atmospheres on plant-insect herbivore interactions: growth responses of larvae of the specialist butterfly, *Junonia coenia* (Lepidoptera: Nymphalidae). *Oecologia* 81: 514-520.
- Fajer, E. D., M. D. Bowers, and F. A. Bazzaz. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. *Science* 243: 1198-1200.
- Fajer, E. D., M. D. Bowers, and F. A. Bazzaz. 1991. The effects of enriched CO<sub>2</sub> atmospheres on the buckeye butterfly, *Junonia coenia*. *Ecology* 72: 751-754.
- Feeny, P. P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565-581.
- Farrell, G. T. 1978. Moisture stress threshold of susceptibility to fir engraver beetles in pole-size white firs. *Forest Science* 24: 85-92.
- Field, C., and H. A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. In *On the Economy of Plant Form and Function*, T. J. Givnish (ed.). Cambridge University Press, New York. pp. 25-55.
- Gollan, T., N. C. Turner, and E. D. Schulze. 1985. The responses of stomata and leaf gas exchange to vapor pressure deficits and soil water content. III. in the sclerophyllous species *Nerium oleander*. *Oecologia* 65: 356-362.
- Grant, S. A., G. R. Bolton, and L. Torvell. 1985. The responses of blanket bog vegetation to controlled grazing by hill sheep. *J. Appl. Ecol.* 22: 739-751.
- Graves, W. R., M. N. Dana, and R. J. Joly. 1989. Influence of root zone temperature on growth of *Ailanthus altissima* (Mill.) Swingle. *J. Environ. Hort.* 7: 79-82.
- Grossmueller, D. W. and R. C. Lederhouse. 1985. Oviposition site selection: an aid to rapid growth and development in the tiger swallowtail butterfly, *Papilio glaucus*. *Oecologia* 66: 68-73.
- Harrington, G. N. 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology* 72: 1138-1149.
- Hatfield, J. L., and I. J. Thomason. 1982. *Biometeorology in integrated pest management*. Academic Press, New York.
- Haukioja, E. 1980. On the role of plant defences in the fluctuation of herbivore populations. *Oikos* 35: 202-213.
- Haukioja, E., J. Suomela, and S. Neuvonen. 1985. Long-term inducible resistance in birch foliage: triggering cues and efficacy on a defoliator. *Oecologia* 65: 363-369.
- Herms, D. A. 1990. Biological clocks: using plant phenology to predict insect activity. *Amer. Nurseryman* 172(8): 56-63.
- Herms, D. A. 1991. Variation in the resource allocation patterns of paper birch: evidence for physiological tradeoffs among growth, reproduction, and defense. Dissertation. Michigan State University, East Lansing, MI.
- Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67: 283-335.
- Hilbert, D. W., A. Larigauderie, and J. F. Reynolds. 1991. The influence of carbon dioxide and daily photon-flux density on optimal leaf nitrogen concentration and root:shoot ratio. *Ann. Bot.* 68: 365-376.
- Hirose, T. 1988. Modeling the relative growth rate as a function of plant nitrogen concentration. *Physiologia Plantarum* 72: 185-189.
- Hobbs, N. T., D. S. Schimel, C. E. Owensby, and D. S. Ojima. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* 72: 1374-1382.
- Horner, J. D. 1990. Nonlinear effects of water deficits on foliar tannin concentration. *Biochem. Syst. Ecol.* 18: 211-213.
- Hough, J. A., and D. Pimentel. 1978. Influence of host foliage on development, survival, and fecundity of the gypsy moth. *Environ. Entomol.* 7: 97-102.
- Johnson, R. H., and D. E. Lincoln. 1990. Sagebrush and grasshopper responses to atmospheric carbon dioxide concentration. *Oecologia* 84: 103-110.
- Johnson, R. H., and D. E. Lincoln. 1991. Sagebrush carbon allocation patterns and grasshopper nutrition: the influence of CO<sub>2</sub> enrichment and soil mineral nutrition. *Oecologia* 87: 127-134.
- Kakes, P. 1989. An analysis of the costs and benefits of the cyanogenic system in *Trifolium repens* L. *Theor. Appl. Genet.* 77: 111-118.
- Kallio, P., and J. Lehtonen. 1975. On the ecocatastrophe of birch forests caused by *Oporinia autumnata* (Bkh.) and the problem of reforestation. In *Fennoscandian Tundra Ecosystems Part 2: Animals and Systems Analysis*, F. E. Wielgolaski (ed.). Springer-Verlag, Berlin, Germany. pp. 174-180.
- Keese, M. C., and T. K. Wood. 1991. Host-plant mediated geographic variation in the life history of *Platycotis vittata* (Homoptera: Membracidae). *Ecol. Ent.* 16: 63-72.
- Klein, D. R. 1965. Ecology of deer range in Alaska. *Ecol. Mon.* 35: 259-284.
- Kozlowski, T. T. 1982. Water supply and tree growth: Part I. Water deficits. *Forestry abstracts* 43: 57-95.
- Kukal, O., B. Heinrich, and J. G. Duman. 1988. Behavioral thermoregulation in the freeze-tolerant arctic caterpillar, *Gynaephora groenlandica*. *J. Exper. Biol.* 138: 181-193.

- Kuropat, P., and J. P. Bryant. 1979. Foraging behavior of cow caribou on the Utukuk calving ground in northwestern Alaska. In *Second International Reindeer/Caribou Symposium*, E. Reimers, E. Gaare, and S. Skenneberg (eds.). Direktoratet for Vilt og Ferskvannsfisk, Trondheim, Norway. pp. 64-71
- Laine, K., and H. Henttonen. 1987. Phenolic/nitrogen ratios in the blueberry *Vaccinium myrtillus* in relation to temperature and microtine density in Finnish Lapland. *Oikos* 50: 389-395.
- Larsson, S. 1989. Stressful times for the plant stress-insect performance hypothesis. *Oikos* 56: 277-283.
- Larsson, S., A. Wiren, L. Lundgren, and T. Ericsson. 1986. Effects of light and nutrient stress on leaf phenolic chemistry in *Salix dasyclados* and susceptibility to *Galerucella lineola* (Coleoptera). *Oikos* 47: 205-210.
- Launchbaugh, J. L. 1960. Vegetational changes in the San Antonia prairie associated with grazing, retirement from grazing, and abandonment from cultivation. *Ecol. Mon.* 25: 39-57.
- Lawrence, R. K. 1990. Phenological variation in the susceptibility of white spruce to the spruce budworm. Dissertation. Michigan State University, East Lansing, MI.
- Lederhouse, R. C., M. P. Ayres, J. K. Nitao, and J. M. Scriber. In press. Differential use of lauraceous hosts by swallowtail butterflies, *Papilio troilus* and *P. palamedes* (Papilionidae). *Oikos*.
- Lincoln, D. E. and D. Couvet. 1989. The effect of carbon supply on allocation to allelochemicals and caterpillar consumption of peppermint. *Oecologia* 78: 112-114.
- Lincoln, D. E., D. Couvet, and N. Sionit. 1986. Response of an insect herbivore to host plants grown in carbon dioxide enriched atmospheres. *Oecologia* 69: 556-560.
- Lincoln, D. E., N. Sionit, and B. R. Strain. 1984. Growth and feeding response of *Pseudoplusia includens* (Lepidoptera: Noctuidae) to host plants grown in controlled carbon dioxide atmospheres. *Environ. Entomol.* 13: 1527-1530.
- Loomis, W. E. 1932. Growth-differentiation balance vs. carbohydrate-nitrogen ratio. *Proc. Amer. Soc. Hort. Sci.* 29: 240-245.
- Loomis, W. E. 1953. Growth and differentiation - an introduction and summary. In *Growth and Differentiation in Plants*, W. E. Loomis (ed.). Iowa State College Press, Ames, Iowa. pp. 1-17.
- Lorio, P. L., Jr. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. *Forest Ecology and Management* 14: 259-273.
- Lorio, P. L., Jr. 1988. Growth-differentiation balance relationships in pines affect their resistance to bark beetles (Coleoptera: Scolytidae). In *Mechanisms of Woody Plant Defenses Against Insects*, W. J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.). Springer-Verlag, pp. 73-92.
- Lorio, P. L., Jr., and R. A. Sommers. 1986. Evidence of competition for photosynthates between growth processes and oleoresin synthesis in *Pinus taeda* L. *Tree Physiology* 2: 301-306.
- Lorio, P. L., Jr., R. A. Sommers, C. A. Blanche, J. d. Hodges, and T. E. Nebeker. 1990. Modeling pine resistance to bark beetles based on growth and differentiation balance principles. In *Process Modeling of Forest Growth Responses to Environmental Stress*, R. K. Dixon, R. S. Meldahl, G. A. Ruark, and W. G. Warren (eds.). Timber Press, Portland, OR. pp. 402-409.
- Louda, S. M. 1983. Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. *Ecology* 64: 511-521.
- Luxmoore, R. L. 1991. A source-sink framework for coupling water, carbon, and nutrient dynamics of vegetation. *Tree Physiology* 9: 267-280.
- MacLean, S. F., Jr. 1983. Life cycles and the distribution of psyllids (Homoptera) in arctic and subarctic Alaska. *Oikos* 40: 445-451.
- Martineau, R. 1984. *Insects Harmful to Forest Trees*. Canadian Forestry Service, Canadian Gov. Publ. Centre.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Oecologia* 81: 186-191.
- Mattson, W. J., and R. A. Haack. 1987a. The role of drought in outbreaks of plant-eating insects. *Bioscience* 37: 110-118.
- Mattson, W. J., and R. A. Haack. 1987b. The role of drought stress in provoking outbreaks of phytophagous insects. In *Insect Outbreaks*, P. Barbosa and J. C. Schultz (eds.). Academic Press, New York, NY. pp. 365-407.
- McAuliffe, J. R. 1986. Herbivore-limited establishment of Sonoran desert tree, *Cercidium microphyllum*. *Ecology* 67: 276-280.
- McCullough, D. G., and M. R. Wagner. 1987. Influence of watering and trenching ponderosa pine on a pine sawfly. *Oecologia* 71: 382-387.
- McNaughton, S. J., and N. J. Georgiadis. 1986. Ecology of African grazing and browsing animals. *Ann. Rev. Ecol. Syst.* 17: 39-65.
- Miller, P. C., W. A. Stoner, and L. L. Tieszen. 1976. A model of stand photosynthesis for the wet meadow tundra at Barrow, Alaska. *Ecology* 57: 411-430.
- Milton, K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food choice by generalist herbivores. *Am. Nat.* 114: 362-378.
- Mitchell, J. F. B., C. A. Senior, and W. J. Ingram. 1989. CO<sub>2</sub>: a missing feedback? *Nature* 341: 132-134.
- Mole, S., J. A. M. Ross, and P. G. Waterman. 1988. Light-induced variation in phenolic levels in foliage of rain-forest plants. I. Chemical changes. *J. Chem. Ecol.* 14: 1-21.
- Mooney, H. A. 1972. The carbon balance of plants. *Ann. Rev. Ecol. Syst.* 3: 315-346.
- Mooney, H. A., B. G. Drake, R. J. Luxmoore, W. C. Oechel, and L. F. Pitelka. 1991. Predicting ecosystem responses to elevated CO<sub>2</sub> concentrations. *Bioscience* 41: 96-104.
- Mooney, H. A., and S. L. Gulmon. 1982. Constraints on leaf structure and function in reference to herbivory. *Bioscience* 32: 198-206.
- Neuvonen, S. and E. Haukioja. 1984. Low nutritive quality as defence against herbivores: induced responses in birch. *Oecologia* 63: 71-74.
- Niemelä, P. 1980. Dependence of *Oporinia autumnata* (Lep., Geometridae) outbreaks on summer temperature. *Rep. Kev. Subarctic Res. Stat.* 16: 27-30.
- Ong, C. K., and C. K. Baker. 1985. Temperature and leaf growth. In *Control of Leaf Growth*, N. R. Baker, W. J. Davies, and C. K. Ong (eds.). Cambridge University Press, Cambridge. pp. 175-200.
- Osbrink, W. L. A., J. T. Trumble, and R. E. Wagner. 1987. Host suitability of *Phaseolus lunatus* for *Trichoplusia ni* (Lepidoptera: Noctuidae) in controlled carbon dioxide atmospheres. *Environ. Entomol.* 16: 639-644.

- Parsons, A. J., and M. J. Robson. 1980. Seasonal changes in the physiology of S24 perennial ryegrass (*Lolium perenne* L.). I. Response of leaf extension to temperature during the transition from vegetative to reproductive growth. *Ann. Bot.* 46: 435-444.
- Pastor, J., and W. M. Post. 1988. Response of northern forests to CO<sub>2</sub>-induced climate change. *Nature* 334: 55-58.
- Patterson, B. D., and D. Graham. 1987. Temperature and metabolism. In *Biochemistry of Plants* 12: 153-199.
- Pease, J. L., R. H. Vowles, and L. B. Keith. 1979. Interaction of snowshoe hares and woody vegetation. *J. Wildl. Manage.* 43: 43-60.
- Pollack, C. J. 1990. The response of plants to temperature. *J. Ag. Sci.*, Cambridge 115: 1-5.
- Pollack, C. J., E. J. Lloyd, J. L. Stoddart, and H. Thomas. 1983. Growth, photosynthesis, and assimilate partitioning in *Lolium temulentum* exposed to chilling temperatures. *Physiol. Plant.* 59: 257-262.
- Pons, T. L., F. Schieving, T. Hirose, and M. J. A. Werger. 1989. Optimization of leaf nitrogen allocation for canopy photosynthesis in *Lysimachia vulgaris*. In *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants*, H. Lambers, M. L. Cambridge, H. Konings, and T. L. Pons (eds.). SPB Academic Publishing, The Hague, The Netherlands.
- Preszler, R. W., and P. W. Price. 1988. Host quality and sawfly populations: a new approach to life table analysis. *Ecology* 69: 2012-2020.
- Raupp, M. J., J. H. Werren, and C. S. Sadof. 1988. Effects of short-term phenological changes in leaf suitability on the survivorship, growth, and development of gypsy moth (Lepidoptera: Lymantriidae) larvae. *Environ. Entomol.* 17: 316-319.
- Rawlins, J. E., and R. C. Lederhouse. 1981. Developmental influences of thermal behavior on monarch caterpillars (*Danaus plexippus*): an adaptation for migration (Lepidoptera: Nymphalidae: Danainae). *J. Kans. Entomol. Soc.* 54: 387-408.
- Reddy, A. R., and V. S. R. Das. 1988. Enhanced rubber accumulation and rubber transferase activity in guayule under water stress. *J. Plant Physiol.* 133: 152-155.
- Reichardt, P. B., F. S. Chapin, III, J. P. Bryant, B. R. Mattes, and T. P. Clausen. In press. Carbon/nutrient balance as a predictor of plant defense in Alaskan balsam poplar: potential importance of metabolite turnover. *Oecologia*.
- Rhoades, D.F., and R.G. Cates. 1976. Toward a general theory of plant antiherbivore chemistry. *Rec. Adv. Phytochem.* 10: 168-213.
- Rice, K. J. 1987. Interaction of disturbance patch size and herbivory in *Erodium* colonization. *Ecology* 68: 1113-1115.
- Robbins, C. T. 1983. *Wildlife Feeding and Nutrition*. Academic Press, New York.
- Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D.L. Baker, C.C. Schwartz, and W.W. Mautz. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68: 98-107.
- Ross, B. A., J. R. Bray, and W. H. Marshall. 1970. Effects of long-term deer exclusion on a *Pinus resinosa* forest in north-central Minnesota. *Ecology* 51: 1088-1093.
- Ryan, M. G. 1991. Effects of climate change on plant respiration. *Ecol. Applic.* 1: 157-167.
- Rykiel, E. J., R. N. Coulson, P. J. H. Sharpe, T. F. H. Allen, and R. O. Flamm. 1988. Disturbance propagation by bark beetles as an episodic landscape phenomenon. *Landscape Ecology* 1: 129-139.
- Schroeder, L. A. 1986. Changes in tree leaf quality and growth performance of Lepidopteran larvae. *Ecology* 67: 1628-1636.
- Schweitzer, D. F. 1979. Effects of foliage age on body weight and survival in larvae of the tribe Lithophanini (Lepidoptera: Noctuidae). *Oikos* 32: 403-408.
- Scott, D. 1970. Relative growth rates under controlled temperatures of some New Zealand indigenous and introduced grasses. *New Zeal. J. Bot.* 8: 76-81.
- Scriber, J. M. 1984. Host-plant suitability. In *Chemical Ecology of Insects*, W. J. Bell and R. T. Carde (eds.). Chapman and Hall, London. pp. 159-202.
- Scriber, J. M., and R. C. Lederhouse. 1983. Temperature as a factor in the development and feeding ecology of tiger swallowtail caterpillars, *Papilio glaucus* (Lepidoptera). *Oikos* 40: 95-102.
- Scriber, J. M. and F. Slansky Jr. 1981. The nutritional ecology of immature insects. *Ann. Rev. Entomol.* 26: 183-211.
- Sedinger, J. S., and P. L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. *Ecology* 72: 496-502.
- Sedinger, J. S., and D. G. Raveling. 1986. Timing of nesting by canada geese in relation to the phenology and availability of their food plants. *J. Anim. Ecol.* 55: 1083-1102.
- Showers, W. B. 1981. Geographic variation of the diapause response in the European corn borer. In *Insect Life History Patterns: Habitat and Geographic Variation*, R. F. Denno and H. Dingle (eds.). Springer-Verlag, New York. pp. 97-111.
- Showers, W. B., J. F. Witkowski, C. E. Mason, D. D. Calvin, R. A. Higgins, and G. P. Dively. 1989. *European Corn Borer: Development and Management*. North Central Regional Extension Publication No. 327. Iowa State University, Ames, IA.
- Sinclair, T. R., and T. Horie. 1989. Leaf nitrogen, photosynthesis, and crop radiation use efficiency: a review. *Crop Science* 29: 90-98.
- Slansky, F., Jr., and J. M. Scriber. 1985. Food consumption and utilization. In *Comprehensive Insect Physiology, Biochemistry, and Pharmacology*, G. A. Kerkut and L. I. Gilbert (eds.). Pergamon, Oxford. pp. 87-163.
- Solbreck, C. 1991. Unusual weather and insect population dynamics: *Lygaeus equestris* during an extinction and recovery period. *Oikos* 60: 343-350.
- Stuhlfauth, T., K. Klug, and H. P. Fock. 1987. The production of secondary metabolites by *Digitalis lanata* during CO<sub>2</sub> enrichment and water stress. *Phytochemistry* 26: 2735-2739.
- Sveinbjornsson, B. 1983. Bioclimate and its effect on the carbon dioxide flux of mountain birch (*Betula pubescens* Ehrh.) at its altitudinal tree-line in the Tornetrask area, northern Sweden. *Nordicana* 47: 111-122.
- Swank, S. E., and W. C. Oechel. 1991. Interactions among the effects of herbivory, competition, and resource limitation on chaparral herbs. *Ecology* 72: 104-115.
- Taylor, F. 1981. Ecology and evolution of physiological time in insects. *Amer. Natur.* 117: 1-23.
- Taylor, P. S., and E. J. Shields. 1990. Development of the armyworm (Lepidoptera: Noctuidae) under fluctuating temperature regimes. *Environ. Entomol.* 19: 1422-1431.

- Tenow, O. 1972. The outbreaks of *Oporinia autumnata* Bkh. and *Operophtera* spp. (Lep., Geometridae) in the Scandinavian mountain chain and northern Finland 1862-1968. Zool. Bidr. Uppsala, Suppl. 2: 1-107.
- Tenow, O., and B. Holmgren. 1987. Low winter temperatures and an outbreak of *Epiprilia autumnata* along a valley of Finnmarksvidda, the "cold pole" of northern Fennoscandia. In *Climatological Extremes in the Mountains, Physical Background, Geomorphological and Ecological Consequences*, H. Alexandersson and B. Holmgren (eds.). Uppsala Universitet Naturgeografiska Institutionen, Uppsala, Sweden. pp. 203-216.
- Thomas, D. W., C. Samson, and J-M. Bergeron. 1988. Metabolic costs associated with the ingestion of plant phenolics by *Microtus pennsylvanicus*. J. Mamm. 69: 512-515.
- Tissue, D. T., and W. C. Oechel. 1987. Response of *Eriophorum vaginatum* to elevated CO<sub>2</sub> and temperature in the Alaskan tussock tundra. Ecology 68: 401-410.
- Townsend, A. M. 1989. Evaluation of potato leafhopper injury among *Acer rubrum* progenies. J. Environ. Hort. 7: 50-52.
- Tuomi, J., P. Niemelä, E. Haukioja, S. Siren, and S. Neuvonen. 1984. Nutrient stress: an explanation for ant-herbivore responses to defoliation. Oecologia 61: 208-210.
- Tuomi, J., P. Niemelä, F. S. Chapin, III, J. P. Bryant, and S. Siren. 1988. Defensive responses of trees in relation to their carbon/nutrient balance. In *Mechanisms of Woody Plant Defenses Against Insects: Search For Pattern*, W. J. Mattson, J. LeVieux, and C. Bernard-Dagenm (eds.). Springer-Verlag, New York. pp. 57-72.
- Tuomi, J., P. Niemelä, I. Jussila, T. Vuorisalo, and V. Jormalainen. 1989. Delayed budbreak: a defensive response of mountain birch to early-season defoliation? Oikos 54: 87-91.
- Turgeon, J. J. 1986. The phenological relationship between the larval development of the spruce budmoth, *Zeiraphera canadensis* (Lepidoptera: Olethreutidae), and white spruce in northern New Brunswick. Can. Ent. 118: 345-350.
- Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology 72: 213-231.
- Wardlaw, I. F. 1990. Tansley Review No. 27: The control of carbon partitioning in plants. New Phytol. 116: 341-381.
- Wareing, P. F., and J. Patrick. 1975. Source-sink relations and the partition of assimilates in the plant. In *Photosynthesis and Productivity in Different Environments*, J. P. Cooper (ed.). Cambridge University Press, Cambridge. pp. 481-499.
- Waterman, P. G., and S. Mole. 1989. Extrinsic factors influencing production of secondary metabolites in plants. In *Insect-Plant Interactions, Vol. 1*, E. A. Bernays (ed.). CRC Press, Boca Raton, FL. pp. 107-134.
- Watt, A. S. 1960. The effect of excluding rabbits from acidophilous grassland in Breckland. J. Ecol. 48: 601-604.
- Watts, W. R. 1974. Leaf extension in *Zea mays*. III. Field measurements of leaf extension in response to temperature and leaf water potential. Journal of Experimental Botany 25: 1085-1096.
- Weiss, S. B., D. D. Murphy, and R. R. White. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69: 1486-1496.
- White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed foods. Oecologia 63: 90-105.