

Do Elevated Temperature and CO₂ Generally Have Counteracting Effects on Phenolic Phytochemistry of Boreal Trees?

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Received: 11 October 2006 / Accepted: 27 November 2006 /
Published online: 10 January 2007
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Abstract Global climate change includes concomitant changes in many components of the abiotic flux necessary for plant life. In this paper, we investigate the combined effects of elevated CO₂ (720 ppm) and temperature (+2 K) on the phytochemistry of three deciduous tree species. The analysis revealed that elevated CO₂ generally stimulated increased carbon partitioning to various classes of phenolic compounds, whereas an increase in temperature had the opposite effect. The combined effects of both elevated CO₂ and temperature were additive, i.e., canceling one another's individual effects. Obviously, the effects of global climate change on leaf chemistry must simultaneously consider both temperature and CO₂. If these results are generally applicable, then the counteracting effect of the temperature is likely to play a major role in alpine, boreal, and arctic zones in determining the balance between populations of plants and herbivores.

Keywords Climate change · Secondary compounds · Metabolism · *Betula* · *Salix* · Phenolics

Introduction

Global climate change, considered as an increase in atmospheric CO₂ and temperature, can influence interactions between plants and their herbivores by changing the quality of plants as food by making them more stoichiometrically unbalanced for their herbivores (Loladze 2002; Sterner and Elser, 2002). For example, a review of the literature on CO₂ elevation by Bezemer and Jones (1998) revealed that leaf nitrogen concentration decreased on average

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by 15%, whereas carbohydrates and plant phenolics increased by 47% and 31%, respectively. Zvereva and Kozlov (2006), in their metaanalysis of the consequences of the simultaneous elevation of CO₂ and temperature on plant traits, made similar conclusions about CO₂ effects, but concluded that temperature alone typically had opposite effects, whereas temperature and CO₂ combined had negligible effects. Both reviews concluded that insects from different feeding guilds generally responded to CO₂-mediated changes in host-plant quality by compensating for decreased nitrogen levels and increased phenolic levels in the plant tissues by increasing their food consumption, but suffered lowered food conversion efficiencies, and longer larval development.

General circulation models (GCM) indicate that, especially in arctic, alpine, and boreal zones, elevated temperatures will accompany rising levels of CO₂ (Prentice et al., 1992; IPCC 1996). In these geographic zones, the effects of elevated temperature may be especially important because the growth of most plants is typically temperature-limited. Although the effects of elevated atmospheric CO₂ on plant physiological processes has long been studied, the combined effects of elevated temperature and CO₂ are only poorly known. The growth-differentiation balance model of plant development suggests elevated CO₂ may generally increase carbon partitioning to secondary metabolites like phenyl propanoids because it typically increases plant source strength (rates of photosynthate accumulation) more than sink strength (Herms and Mattson, 1992; Mattson et al., 2005). However, the effects of elevated temperature are much less predictable because it is not fully obvious how that will simultaneously influence both source and sink processes and thus the crucial source-sink carbon balance over plant development.

Temperature increases generally raise the rates of biochemical reactions, but such reactions also depend on the supplies of available substrates and enzymes to sustain them. If plant sink (growth) processes are more sensitive to ameliorative changes in temperature than is photosynthesis (Mattson and Haack, 1987a,b; Herms and Mattson, 1992), then the plant's source-sink balance may generally decline with rising temperatures because sink demands will outpace source supplies. This could lead to reduced carbon partitioning to facultative secondary metabolism. Although this reasoning is obviously elementary, as a starting point it suggests that under favorable growing conditions (i.e., adequate nutrients and water), the effects of elevated CO₂ and temperature might be counterbalancing, as was evident in the Zvereva and Kozlov (2006) metaanalysis. However, metaanalysis indicates only pattern or a trend combined from completely separate studies and tells very little about the metabolic processes lying behind the phenomena. In this study, we go a layer deeper to understand better those partitioning processes affected by elevated CO₂ and temperature treatments by using a dataset coming from one controlled experimental system (Kellomäki et al., 2000). Here, we use graphic vector analysis (GVA), which allows us to analyze if the target phytochemical response is associated with changes in total dry weight, or target chemical content, or is some combination of these two partitioning alternatives.

We argue that to predict the effects of global climate-change-mediated responses in phytochemistry and plant–herbivore relationships, the CO₂ × temperature interaction must be more fully considered.

Methods and Materials

Analytical Procedures We employed graphic vector analysis (GVA) for representing and interpreting the fundamental changes in the plants' growth and phytochemical components

in response to different treatments (Timmer and Stone, 1978; Haase and Rose, 1995; Koricheva, 1999). This method, although laborious, has been proposed as an alternative to simply examining phytochemical concentrations to understand environmental effects on carbon partitioning to the synthesis of the target compounds (Koricheva, 1999). If GVA is more insightful than simply evaluating changes in concentrations of target compounds, it is because GVA also requires measuring and evaluating total plant (or organ) growth that is necessary to construct the axes. GVA is, in fact, three-dimensional plotting of target compound concentration (Y axis), total plant (organ) content (X axis), and total plant (organ) size (Z axis). Instead of using raw values, the data are converted to their relative values, using the control as the standard in the following manner:

$$(\text{elevated value} - \text{control value}) \times \text{control value}^{-1}$$

Total relative dry weight growth of a plant is the inverse of the slope of the aforementioned plot of Y vs. X variables, and all such plotted plant-relative dry weights will lie on diagonal lines corresponding to the Z axis (Fig. 1). If the goal is to measure and evaluate treatment effects on plant carbon partitioning to a target phytochemical compound, there are two basic responses, either increased or decreased relative partitioning, as indicated on the Y axis by relative concentrations being greater or less than 1, respectively. If, however, one also considers how treatments affect relative plant organ size (presented here as specific leaf weight) in addition to partitioning to the target compound, there are eight possible outcomes (Fig. 1, Table 1): increased relative synthesis and a) decreased or b) increased specific leaf weight (*i.e.*, gm^{-2}); decreased synthesis and c) decreased or d) increased specific leaf weight; no change in synthesis and either e) decreased or f) increased specific leaf weight; and finally, g) increase or h) decrease in synthesis, but no change in specific leaf weight.

The use of relative values allows one to present the results of several plant species, and treatments on the same graph. Each point represents the relative mean value of each plant species for each compound in question. We did not test the data statistically, because that was already done in the studies from which these data were extracted (Lavola and

Fig. 1 Interpretation of directional shifts in chemical concentration, chemical content, and specific leaf weight. Modified from Timmer and Stone (1978), Haase and Rose (1995), and Koricheva (1999). Dotted lines represent reference lines for no change in phytochemical character in question. Dashed line indicates relative plant unit biomass, reference point (control sample) has values (1, 1, 1). Letters refer to quadrants in Table 1

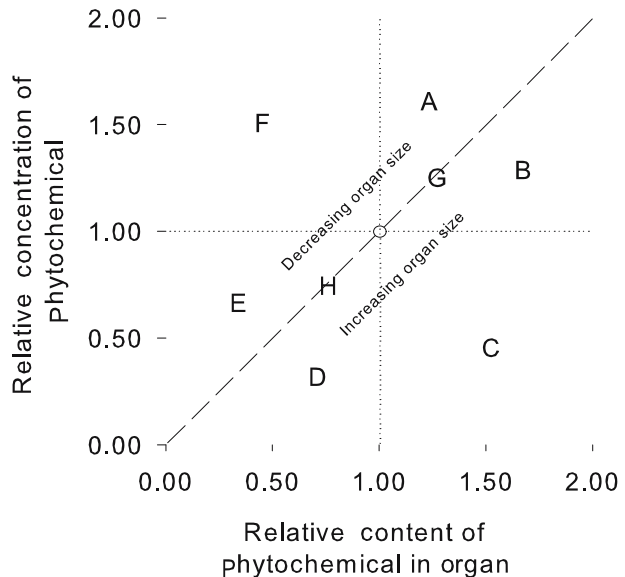


Table 1 Interpretations of quadrants in Fig. 1

Graph section	Total dry weight response	Concentration response	Chemical content response	Interpretation: phytochemical synthesis rate relative to growth rate, and overall growth response
A	–	+	+	>relative synthesis/<organ size
B	+	+	+	>relative synthesis/>organ size
C	+	–	+	<relative synthesis/>organ size
D	+	–	–	<relative synthesis/>organ size
E	–	–	–	<relative synthesis/<organ size
F	–	+	–	>relative synthesis/<organ size
G	0	+	+	>relative synthesis
H	0	–	–	<relative synthesis

Julkunen-Tiitto, 1994; Lavola et al., 1998; Kuokkanen et al., 2001, 2003; Veteli et al., 2002; Veteli 2003; Veteli, unpublished). The direction and magnitude of the vectors from reference or control (1, 1, 1) are used to interpret the effects of the treatments (Fig. 1, Table 1). There are four quadrants in a vector diagram with the diagonal (Z axis = 1) bisecting the upper right and lower left. All vector points to the left of the dashed diagonal are cases where the treatment plants are smaller than control, and all vector points to right of the diagonal are cases where treatment plants are larger. All changes in phytochemical concentrations (Y axis) are the result of shifts in the relative rates of synthesis of both phytochemical content and plant biomass. We avoid the GVA parlance of “diluting” and “concentrating,” etc. with respect to the target compound(s) because we believe that it is misleading and inappropriate. Growing plants are continuously adjusting their carbon partitioning based on their unfolding developmental programs, source-sink balances, environmental conditions, and stochastic events. This implies that a target compound is simply being diluted or concentrated in response to treatments and environments, and it is misleading because it suggests a passive process. Instead, carbon partitioning alternatives are of physiological and ecological import to the plant. Having a substantial capacity for changing carbon partitioning at a given time and circumstance is crucial to plant fitness.

Treatments and Studies Included The treatment conditions used in these studies were: (i) control CO_2 and temperature, (ii) elevated CO_2 and control temperature, (iii) control CO_2 and elevated temperature, and (iv) elevated CO_2 and temperature. The mean control and elevated CO_2 concentrations were 360 and 720 ppm, respectively. The elevated temperature was obtained by raising the ambient air temperature by 2 K, on average, from that of the control chambers to correspond to the climate warming scenarios predicted after a doubling of the atmospheric CO_2 concentrations (IPCC 1996). Treatments were done at the Mekrijärvi Research Station, University of Joensuu (62°47'N, 30°58'E, and 145 m a.s.l.), eastern Finland. Sixteen closed-top climate chambers were divided in four CO_2 and temperature treatments (as above), with four replicates in each (Kellomäki and Wang, 1998). Outdoor climate chamber studies (Kuokkanen et al., 2001, 2003; Veteli et al., 2002; Veteli 2003; Veteli, unpublished) and results from indoor chamber studies in which the CO_2 levels were as above (Lavola and Julkunen-Tiitto, 1994; Lavola et al., 1998) were included in the vector analysis.

The tree species used in these experiments (*Betula pubescens*, *B. pendula*, and *Salix myrsinifolia*) are species that are widely distributed and common in boreal zone. Their responses to various environmental factors have been extensively studied and, therefore,

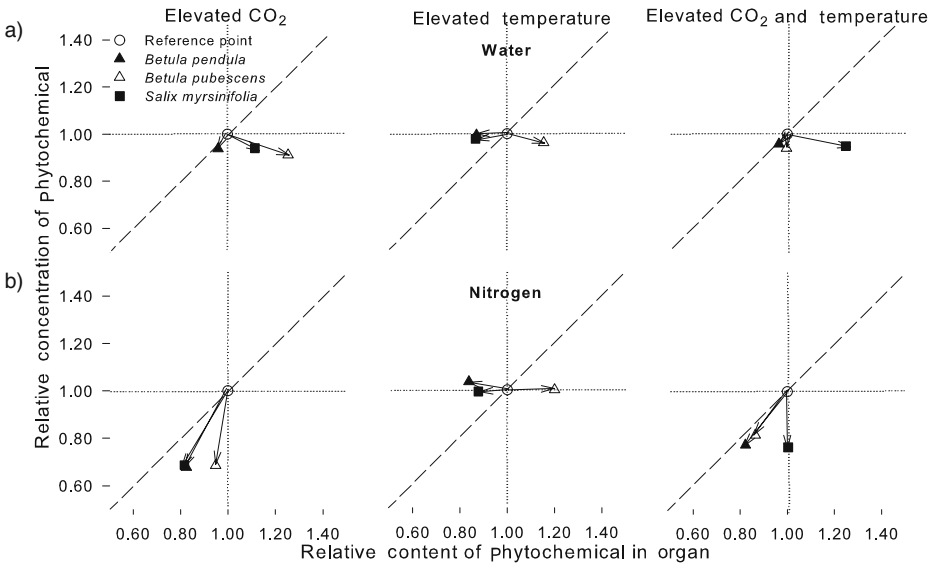


Fig. 2 Directional shifts in A) water and B) nitrogen in relation to climate change factors. The first figure in the column indicates the effect of elevated CO₂, second the elevated temperature, and the third their interaction

provide a fruitful basis for this study. Sampling and chemical analysis are described in detail by Lavola and Julkunen-Tiitto (1994); Lavola et al. (1998); Kuokkanen et al. (2001), (2003); Veteli et al. (2002); and Veteli (2003).

Results

Graphic vector analysis (GVA) shows that specific leaf mass responded rather consistently to treatments. CO₂ enrichment by itself resulted in heavier leaves per area unit on all three tree species (Figs. 2, 3, 4, and 5, first figure in a row). In contrast, elevated temperature by

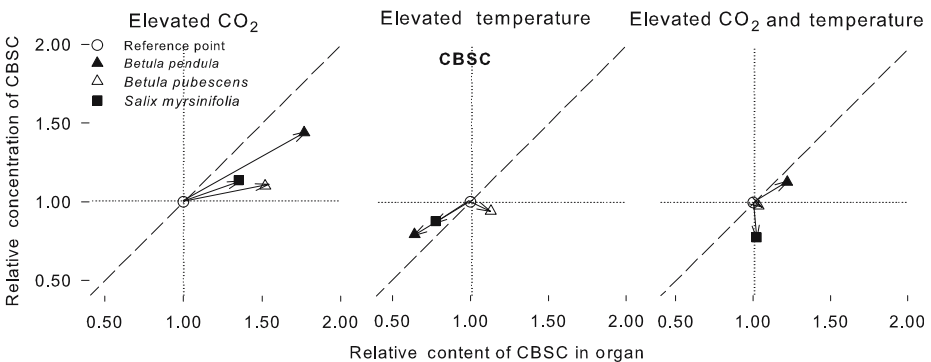


Fig. 3 Directional shifts in detected carbon-based secondary compounds in relation to climate change factors. The first figure in a column indicates the effect of elevated CO₂, second the elevated temperature, and the third their interaction

itself reduced specific leaf weights on two species, but increased that of *Betula pubescens* (Figs. 2, 3, 4, and 5, second figure in a row) The combination of elevated CO₂ and temperature resulted in no net change in specific leaf weight, except for *Salix* where it increased, as if CO₂ overwhelmed the temperature effect (Figs. 2, 3, 4, and 5, third figure in a row).

With respect to foliar chemicals, all graphs generally suggest that there is a counteracting effect between elevated CO₂ and temperature, although the effect is weakest for water and N (Figs. 2, 3, 4, and 5). In the case of water, elevated CO₂ generally increased specific leaf weights but not water uptake, and water concentrations fell. Elevated temperature had negligible effect on water concentrations, whereas the combined effect of CO₂ and temperature caused all plants to have slight decreases in water concentrations, although no declines or even increases in total leaf water content (Fig. 2a). In the case of N, elevated CO₂ generally reduced assumed N uptake and N concentration in all three species (Fig. 2b). Elevated temperature, however, had no effect on foliar N concentrations, although total N content both increased and decreased (Fig. 2b). On the other hand, the combination of CO₂ and temperature caused reduced N uptake and concentrations (Fig. 2b).

With respect to phenolic secondary metabolites, elevated CO₂ generally elicited increased synthesis of detected total carbon-based secondary compounds (CBSC) and thus increased concentrations (Fig. 3). The pattern was the same for most of the component synthetic groups such as phenolic acids, salicylates, flavonoids, and condensed tannins (Figs. 4 and 5). On the other hand, elevated temperature generally elicited diminished synthesis and concentration of total CBSC, and most of the component molecular groups. Tannins were an exception because they were diminished in only *B. pendula*. The combined treatments of CO₂ and temperature elicited steady states or small change in concentrations

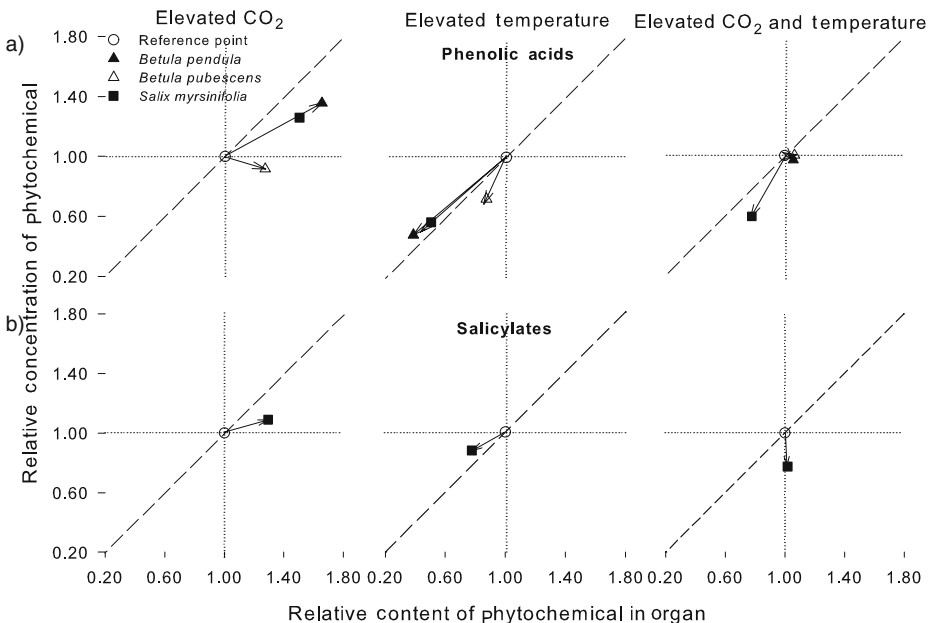


Fig. 4 Directional shifts in A) phenolic acids and B) salicylates in relation to climate change factors. The first figure in a column indicates the effect of elevated CO₂, second the elevated temperature, and the third their interaction

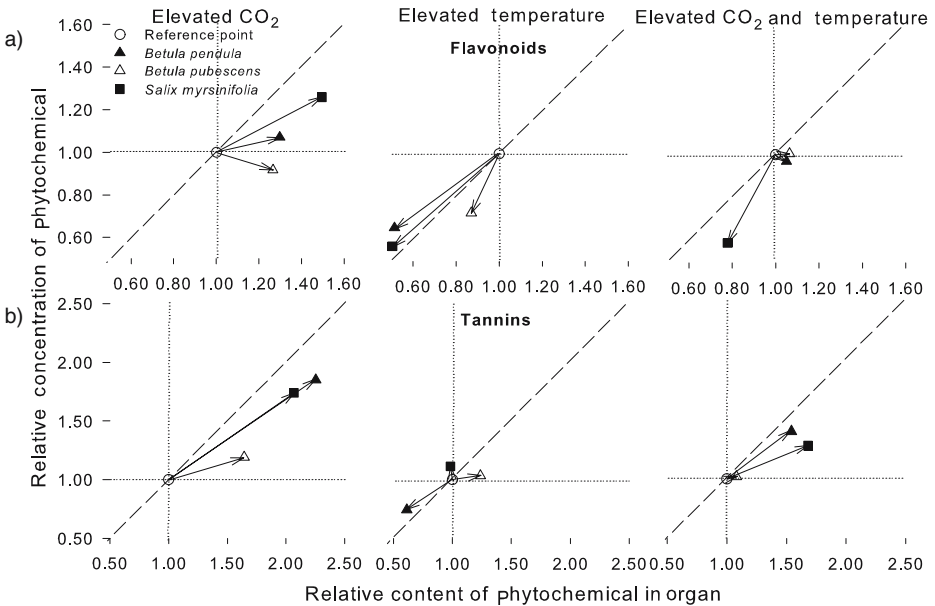


Fig. 5 Directional shifts in A) flavonoids and B) tannins in relation to climate change factors. Notify different scaling in figures A) and B). The first figure in a column indicates the effect of elevated CO₂, second the elevated temperature, and the third their interaction

of secondary compounds in most instances for the two *Betula* species. However, *S. myrsinifolia* was much more responsive. Elevated CO₂ and temperature generally caused substantially reduced concentrations of most phenolics (Figs. 3, 4, and 5a), except for tannins which increased, as was also true for *B. pendula* (Fig. 5b). The data suggest that heightened temperatures generally reduced the magnitudes of the changes that were elicited by elevated CO₂ (Fig. 5b).

Discussion

We showed that the interactions between elevated CO₂ and temperature are typically additive and generally cancel one another. Generally, elevated CO₂ increased the accumulation of total CBSC and specific carbon-based secondary compounds as has been proven in previous studies (Lincoln et al., 1993; Bezemer and Jones, 1998; Hunter, 2001; Zvereva and Kozlov, 2006). However, the climate changes predicted also include rising temperatures, and in this study, changes of only 2 K eliminated the effect of elevated CO₂ on analyzed carbon-based secondary compounds within the leaves. It could be assumed that CO₂ enhancement either increased the synthesis or decreased the turnover rate, and that temperature elevation caused the opposite. For almost all of the plant species previously studied, the carbohydrate concentrations of leaves have been reported to rise by an average of 47% in response to elevated CO₂ (Bezemer and Jones, 1998). In the present study, the carbohydrate concentrations were not measured, but specific leaf weights increased under enriched CO₂, which may be a result of starch accumulating in the leaves. The effect was present also in the combination of the treatments, although not so intense. Starch may or

may not enhance the herbivore's ability to digest leaves, whereas structural carbohydrates (cellulose, hemicellulose), as well as lignin, will very likely interfere with feeding and digestion, especially that of small larvae (Lincoln et al., 1993; Reavey, 1993).

The accumulation of nonstructural carbohydrates under elevated CO₂ in leaves has been reported in many studies (e.g., Johnson and Lincoln, 1991; Lindroth et al., 1993; Hall et al., 2005), but this alone does not explain the reduction in nitrogen concentration observed in this study because total leaf N content also declined. The higher C/N ratio implies perhaps a surfeit of C during leaf ontogeny, thereby allowing more partitioning to facultative synthesis of secondary metabolites. Likewise, both N concentrations and total leaf N were lower in the foliage from the combined treatments, although leaf size was unaffected for the two *Betula* species, but larger for *S. myrsinifolia*. Their C/N ratios were lower than in the CO₂ treatment but higher than in the elevated temperature treatments that were the same as control. Because insect herbivores tend to be nitrogen-limited (Mattson, 1980), possible reductions in nitrogen concentration may substantially reduce insect performance. Thus, it could be expected that the consequences of reduced nitrogen will also prevail in the boreal zone after modest temperature elevation, possibly having a reducing effect on herbivory (see, e.g., Hall et al., 2005). In total, however, the positive effect of temperature may have an ameliorating or even enhancing effect on the growth rates of insects (e.g., Lindroth et al., 1997; Holopainen and Kainulainen, 2004).

Our results here and earlier suggest that elevated CO₂ and temperature can enhance the growth of plants (Kuokkanen et al., 2001, 2004; Veteli et al., 2002; Veteli 2003) while lowering the levels of nitrogen and water in leaf tissue. The effects of elevated CO₂ on levels of CBSC are quite variable depending on the species and compound in question (see, e.g., Agrell et al., 2004; Hall et al., 2005), whereas temperature elevation tends to lower CBSC levels in these species, which is also shown as a general trend in Zvereva and Kozlov's (2006) study. These differing reactions are probably caused by different source–sink interactions: if enhanced plant growth demand is not more than matched by enhanced photosynthesis, there may be a subsequent diminution in available carbon for facultative secondary metabolism. The effect of rising temperature may be similar to the nonlinear effect of fertilization on CBSCs (Herms and Mattson, 1992; Herms, 2002). Some insect species feeding on these plants have increased consumption and reduced growth (e.g., Bezemer and Jones, 1998; Veteli et al., 2002; Zvereva and Kozlov, 2006), and, therefore, may be subjected to natural enemies for a longer time under elevated CO₂. Higher temperatures, on the other hand, may directly compensate for some of the negative effects of increased CO₂; increasing temperatures affect the distribution of some species by shifting ranges poleward and altitudinally upward (e.g., Parmesan et al., 1999; Battisti et al., 2005). The reason for these observed species range shifts can be a result of reducing extreme winter temperatures, increasing thermal sum, or subsequent changes in properties of the host plants.

Hence, we argue that in alpine, boreal, and arctic areas the effect of the rising temperature in addition to levels of atmospheric CO₂ should be taken into account in making any predictions about the effects of climate change on phytochemistry and plant–herbivore–natural enemy interactions (Mattson and Haack 1987a,b). The GCM predicts that in these areas the most important factor of climate change is temperature elevation. We conclude that when studying the effects of climate change we must consider both the effects of enriched CO₂ and elevated temperature. This is especially true in alpine, boreal, and arctic environments where temperature is often the most important factor limiting growth.

Acknowledgments We thank Dr. Marja-Leena Laitinen for valuable hints. We are also grateful to Dr. John Derome for checking the language of this article. This study was supported by the Academy of Finland (Finnish Centre of Excellence Program for Forest Ecology and Management 2000–2005, project no. 64308 and 51997).

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