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Original article

High plant species diversity indirectly mitigates CO_2- and N-induced effects on grasshopper growth

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ABSTRACT

We examined how elevated atmospheric [CO_2] and higher rate of nitrogen (N) input may influence grasshopper growth by changing food plant quality and how such effects may be modified by species diversity of the plant community. We reared grasshopper nymphs (*Melanoplus femurrubrum*) on *Poa pratensis* from field-grown monocultures or polycultures (16 species) that were subjected to either ambient or elevated levels of CO_2 and N. Grasshopper growth rate was higher on *P. pratensis* leaves grown in monocultures than in polycultures, higher on *P. pratensis* grown under elevated than under ambient [CO_2], and higher on *P. pratensis* grown under elevated than under ambient [N]. The higher growth rate observed on *P. pratensis* exposed to elevated [CO_2] was, however, less pronounced for polyculture- than monoculture-grown *P. pratensis*. Growth rate of the grasshoppers was positively correlated with leaf [N], [C], and concentration of soluble carbohydrates + lipids. Concentration of non-structural carbohydrates + lipids was higher in leaves grown under elevated than under ambient [CO_2], and the difference between *P. pratensis* grown under ambient and elevated [CO_2] was greater for monoculture- than polyculture-grown *P. pratensis*. In addition, leaf N concentration was higher in *P. pratensis* grown in monocultures than in polycultures, suggesting that plant species richness, indirectly, may influence insect performance by changed nutritional value of the plants. Because we found interactive effects between all factors included ([CO_2], [N], and plant species diversity), our results suggest that these parameters may influence plant–insect interactions in a complex way that is not predictable from the sum of single factor manipulations.

1. Introduction

Various human activities cause terrestrial ecosystems to experience multiple environmental changes such as reduced species diversity, increased concentration of atmospheric CO_2 ([CO_2]), and increased nitrogen (N) deposition (Vitousek et al., 1997; Sala et al., 2000). Three important anthropogenic changes, a loss in plant biodiversity, elevation of atmospheric [CO_2] and increased N deposition, are likely to occur simultaneously, so interactive effects among them seem likely. Thus, increased knowledge of their combined effects on insect performance may be necessary in order to understand and

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predict future effects of global changes on insect populations as well on plant communities.

The individual effects from elevated [CO_2] (Watt et al., 1995; Bezemer and Jones, 1998) and [N] (Mattson, 1980; White, 1993) on insect herbivores are relatively well known, but their combined effects, especially in relation to plant species diversity, are less well documented or understood. In general, plants with high N concentration, and low carbon (C) concentration are considered to be of high food quality for insects, and positive effects on insect performance, such as shorter development time, larger adult body mass, and higher reproductive output following increased [N] of food plants are well documented (Mattson, 1980; Ritchie, 2000). Hence, performance of grasshoppers can be expected to increase on plants grown under increased N input.

Plants grown under elevated [CO_2] often have lower [N] and higher [C] than plants grown under ambient conditions (Reich et al., 2001a; Yin, 2002), and insect performance can thus be expected to be poorer under elevated [CO_2]. Accordingly poor performance of insects feeding on such plant material has also been reported (Watt et al., 1995; Bezemer and Jones, 1998; Agrell et al., 2000). However, insects may to some extent compensate for lower food [N] by increasing their food intake (e.g. Bezemer and Jones, 1998) or increasing their post-ingestive assimilation efficiency of the ingested food (Barbehenn et al., 2004a) and thereby maintain their growth rate. In addition, plants grown under elevated [CO_2] may contain higher concentrations of carbohydrates (Barbehenn et al., 2004b), which may be beneficial for insects (Ayers, 1993), so even without compensatory feeding the response to elevated [CO_2] may not necessarily be negative. However, not all types of carbohydrates are easily converted into energy by insects. Structural carbohydrates, found in cell walls, such as cellulose, lignin and hemicellulose (neutral detergent fiber) are of less importance, or may even negatively influence growth rates of insects. In contrast, non-structural carbohydrates, such as starch and sugars, and lipids are energy rich and may positively influence the growth rate of insects. Thus, the growth response of insects may range from negative to positive depending on which fraction of carbohydrates is most affected by elevated [CO_2] and how food [N] is affected. The growth response will also vary depending on which of the above mentioned factors is most important for the performance of the individual insect.

Altered plant species diversity is known to influence the growth and feeding pattern of insects (Di Giulio and Edwards, 2003; Scherber et al., 2006). Most studies addressing the effects of plant species diversity for insect performance have focused on the importance of direct effects of altered species diversity, involving the quantity of preferred food plants and the importance of multiple food plant species for maintaining high performance. In addition to such direct effects, diversity may also potentially influence insect performance indirectly by changing the nutritional quality of the food plants. In N limited environments, plants growing in more productive polycultures may have lower [N] than plants growing in less productive monocultures (Reich et al., 2001b). This response appears to be largely due to enhanced resource competition for e.g. N among plants (Reich et al., 2001b, and unpublished data), which may result in lower concentration of nutrients in plant tissue. Hence, it may be hypothesized that increased plant diversity may reduce food quality and thereby the growth rates of insects feeding on plants from diverse plant communities. This raises the question how representative results from manipulation experiments using monoculture systems are for natural, more species rich systems? This question is relevant, given that many studies examining insect performance in relation to increased N input and, especially, elevated [CO_2] have used plants grown in monocultures (e.g. Johnson and Lincoln, 1991; Goverde et al., 1999; Agrell et al., 2000; Barbehenn et al., 2004a).

The combined effects from altered plant species diversity, elevated [CO_2], and increased N input on food quality and corresponding effects on insect performance may be complicated to predict, as interactive effects between factors may offset the individual effects. For example, increased N input may offset the potential lowered [N] in plants grown in species diverse plant communities or at elevated [CO_2].

To examine how growth of grasshoppers differs between diets of different chemical composition that correspond to those imposed by elevated [CO_2] and [N], and level of plant species diversity, we provided grasshopper nymphs with leaves of the grass *Poa pratensis* L. grown in monocultures or polycultures that were exposed to ambient or elevated [CO_2] or [N] in a free-air CO_2 enrichment (FACE) experiment in Minnesota, USA. We measured differences in leaf total [C], [N], concentration of neutral detergent fiber and concentration of non-structural carbohydrates + lipids on the grass provided to the grasshoppers to determine if differences in grasshopper growth were associated with differences in food plant quality.

2. Materials and methods

2.1. *Experimental design*

To examine how growth of grasshoppers differed between diets with different chemical composition we provided *Melanoplus femurrubrum* (De Geer) nymphs (4th instar) with *P. pratensis* grown in monocultures or in polycultures that were exposed to ambient or elevated CO_2 and N conditions. We used plant material from the BioCON experiment (Biodiversity, Carbon dioxide, and Nitrogen effects on ecosystem functioning, http://www.lter.umn.edu/biocon/) located at Cedar Creek Natural History Area in east-central Minnesota, USA (45°N, 93°W). The experiment consists of six circular areas (rings) each containing 61 2 by 2 m plots that were planted with seeds of 1, 4, 9 or 16 species (total of 12 g seed m^{-2}) in 1997. Since 1998, three of the six rings have been exposed to elevated [CO_2] (560 μmol mol^{-1}) using a free-air CO_2 enrichment system (FACE) and the three remaining rings represent ambient [CO_2] (370 μmol mol^{-1}). Within each ring, half of the plots are fertilized with NH_4NO_3 corresponding to N addition of 4 g m^{-2} $year^{-1}$, applied over three dates each growing season (for a more detailed description of the experiment see Reich et al. (2001b) or the above mentioned web page). In the present study we used fully expanded leaves of *P. pratensis* from monoculture plots and from 16 species plots (polycultures) that had been exposed to all combinations of ambient and elevated [CO_2] and [N]. By this we obtained eight different