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Decline in gypsy moth (Lymantria dispar) performance in an elevated CO₂ atmosphere depends upon host plant species

Abstract  Plant species differ broadly in their responses to an elevated CO₂ atmosphere, particularly in the extent of nitrogen dilution of leaf tissue. Insect herbivores are often limited by the availability of nutrients, such as nitrogen, in their host plant tissue and may therefore respond differentially on different plant species grown in CO₂-enriched environments. We reared gypsy moth larvae (Lymantria dispar) in situ on seedlings of yellow birch (Betula allegheniensis) and gray birch (B. populifolia) grown in an ambient (350 ppm) or elevated (700 ppm) CO₂ atmosphere to test whether larval responses in the elevated CO₂ atmosphere were species-dependent. We report that female gypsy moths (Lymantria dispar) reared on gray birch (Betula populifolia) achieved similar pupal masses on plants grown at an ambient or an elevated CO₂ concentration. However, on yellow birch (B. allegheniensis), female pupal mass was 38% smaller on plants in the elevated CO₂ atmosphere. Larval mortality was significantly higher on yellow birch than gray birch, but did not differ between the CO₂ treatments. Relative growth rate declined more in the elevated CO₂ atmosphere for larvae on yellow birch than for those on gray birch. In preference tests, larvae preferred ambient over elevated CO₂-grown leaves of yellow birch, but showed no preference between gray birch leaves from the two CO₂ atmospheres. This differential response of gypsy moths to their host species corresponded to a greater decline in leaf nutritional quality in the elevated CO₂ atmosphere in yellow birch than in gray birch. Leaf nitrogen content of yellow birch dropped from 2.68% to 1.99% while that of gray birch leaves only declined from 3.23% to 2.63%. Meanwhile, leaf condensed tannin concentration increased from 8.92% to 11.45% in yellow birch leaves while gray birch leaves only increased from 10.72% to 12.34%. Thus the declines in larval performance in a future atmosphere may be substantial and host-species-specific.

Key words  Lymantria dispar · Betulaceae · Elevation CO₂ · Tannin · Nitrogen

Introduction

Atmospheric CO₂ levels are expected to double by the end of the 21st century (Houghton 1990). Within temperate forests, an increase of this magnitude has been shown to directly impact plants through changes in physiological processes (Eamus and Jarvis 1989; Bazzaz 1990; Bazzaz and Fajer 1992). Plants grown in an elevated CO₂ atmosphere commonly exhibit increased photosynthetic rates and carbohydrate storage, leading to higher ratios of carbon to nitrogen in leaves (Fig. 1), the “nitrogen dilution effect” (Wong 1979; Lincoln et al. 1993). Tree species differ in their leaf nitrogen dilution in an elevated CO₂ atmosphere (Oberbauer et al. 1986; Rochefort and Bazzaz 1990; Lindroth et al. 1993) with observed declines ranging from 4.8% in Ledum palustre (Oberbauer et al. 1986) to 46.2% in Alnus glutinosa (Norby 1987).

Insect herbivores, which are often limited by dietary nitrogen (Mattson 1980), have experienced lower growth rates (Lincoln et al. 1986; Fajer 1989; Johnson and Lincoln 1990; Lindroth et al. 1993; Roth and Lindroth 1994) and higher larval consumption rates (Lincoln et al. 1986; Lincoln and Couvet 1989; Johnson and Lincoln 1990, 1991; Lindroth et al. 1993; Lindroth 1996) on plants grown in an elevated CO₂ atmosphere. The observed correspondence between declines in insect performance and
leaf nitrogen dilution in the host plants has led to widespread speculation that leaf nitrogen dilution has an important role in the response of insects to an elevated CO$_2$ atmosphere (Lincoln et al. 1986; Fajer 1989; Johnson and Lincoln 1990; Lindroth et al. 1993; Roth and Lindroth 1994).

When generalist herbivores have been reared on several host plant species grown in an ambient or elevated CO$_2$ atmosphere, the effect of the CO$_2$ treatment on insect performance has depended upon the host plant species (Lindroth et al. 1993; Roth and Lindroth 1994). Insect herbivores commonly exhibit feeding preferences for plant tissues that provide the highest level of performance (Kimmerer and Potter 1987; Minkenberg and Ottenheim 1990; Basset 1991; but see Reavey 1991). Differential plant response to an elevated CO$_2$ atmosphere may therefore affect insect herbivore behavior. In an elevated CO$_2$ atmosphere, relative host plant preferences of a generalist herbivore may shift in favor of those host species that experience the least dilution of leaf nitrogen.

In studies of insect performance on plants in enriched CO$_2$ atmospheres, researchers have primarily considered one insect species on a single host plant species and few studies have reported information on insect behavior. Insects are also rarely reared directly on the host plants, nor are they measured over their entire developmental period.

This study addressed the in situ performance and host plant preferences of gypsy moths reared from egg to pupa on yellow and gray birch in an ambient or elevated CO$_2$ environment. Specifically, we asked the following questions:

1. Does the performance of gypsy moth larvae decrease when the larvae are reared on plants grown in an enriched CO$_2$ atmosphere?
2. Is there a correspondence between the larval response on a given species and that species’ leaf nitrogen dilution in an elevated CO$_2$ environment?
3. Does the order of larval preference for gray and yellow birch shift when the plants are grown in an enriched CO$_2$ atmosphere?

Materials and methods

Study species

Gray birch (*Betula populifolia* Marsh.) and yellow birch (*B. allegheniensis* Brit.) are ecologically important temperate tree species and host plants of the gypsy moth (*Lymanchia dispar* Linnaeus). These sympatric tree species are abundant in temperate forests throughout New England and Canada, especially in treefall gaps and along forest margins. Gray birch is a pioneer tree that colonizes recently disturbed forest, requires open sunlight, and grows well on nutritionally poor soil. Yellow birch is a mid-successional species, surviving in the understory, living longer, and requiring higher soil fertility than gray birch (Burns and Honkala 1990). Both species produce new leaves throughout the growing season.

In the field, gypsy moth larvae have been observed to prefer gray birch to yellow birch (Maurffette et al. 1983). However, the difference in observed preference was not large (yellow birch was ranked 15 and gray birch 13 out of 29 species). The gypsy moth is an abundant, introduced pest of New England’s temperate forests. Gypsy moths are univoltine and overwinter as eggs, which hatch in early spring. Larvae feed from April until they pupate in June. In 1992, gypsy moth larvae defoliated over 15 million hectares in the United States alone, an area the size of Maine, Massachusetts, New Hampshire, and Vermont combined (Liebhold et al. 1993). Female moths are flightless and lay eggs next to the pupal case. Host plant selection is performed primarily by larvae (Barbosa et al. 1979).

Plant growth

In late May 1992 gray and yellow birch seeds from the Harvard Forest in Petersham, Massachusetts, were germinated in one thousand 5.7-cm peat pots containing a mixture of sand, unsterilized soil, surface, and peat in a 2:2:2:1 ratio. Seedlings were thinned to one per pot, watered daily, and fertilized with 10 ml of quarter-strength Peter’s 20:20:20 NPK fertilizer per pot once every 2.5 weeks for 8 weeks. This fertilization rate resulted in very slow growth of the seedlings and was adjusted during the 8th week to 10 ml of half-strength Peter’s 20:20:20 NPK fertilizer per pot applied twice per week. During the 10th week, we transplanted seedlings and the soil around their roots into 10.2-cm pots. After the transplant, plants were fertilized with 135 ml of quarter-strength Peter’s 20:20:20 NPK fertilizer per pot once every 9 days on average through the remainder of the experiment. Plants continuously produced new leaves throughout the duration of the experiment.