GROWTH OF JUVENILE ARIANTA ARBUSTORUM (LINNAEUS, 1758) FED ON WHITE CLOVER (TRIFOLIUM REPENS L.) GROWN UNDER AMBIENT OR ELEVATED ATMOSPHERIC CO2

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ABSTRACT: In many terrestrial ecosystems elevated atmospheric carbon dioxide (CO2) may reduce plant quality and change plant-herbivore interactions. The objective of this study was to evaluate the effects of elevated CO2 (600 ppm vs. 350 ppm) on white clover (Trifolium repens L.) and to examine the feeding response and growth of juveniles of the helicid land snail Arianta arbustorum (L.). Leaves of T. repens grown at elevated atmospheric CO2 had a lower nitrogen concentration and a lower specific leaf area than leaves grown under ambient CO2 conditions. However, elevated CO2 had no effect on leaf carbon concentration. Juveniles snails fed on either diet consumed about the same amount of leaf biomass. The lower leaf nitrogen concentration at elevated CO2 resulted in a reduced nitrogen uptake. As a consequence, juvenile Arianta arbustorum, fed on T. repens grown under elevated CO2, tended to grow more slowly than snails fed on T. repens leaves produced under ambient CO2. This indicates that rising atmospheric CO2 can indirectly affect the life cycle of terrestrial gastropods.

KEY WORDS: Arianta arbustorum, Pulmonata, Gastropoda, Helicidae, elevated carbon dioxide, herbivory

INTRODUCTION

Natural and agricultural ecosystems are being exposed to a rapid increase in atmospheric CO2 concentration. Furthermore, the accumulation of greenhouse gases is predicted to cause global temperature to rise from about 1 to 4°C over the next decades if emissions continue to increase as expected (IPCC 1996). The experimental and theoretical literature addressing the effects of rising atmospheric CO2 on plant growth and community structure is growing rapidly (for reviews see BAZZAZ 1990, KAREIVA et al. 1993, POORTER 1993, KÖRNER 1995, KÖRNER & BAZZAZ 1996). Minor changes in nutrient content, plant chemistry, leaf toughness, or moisture could alter the interactions between plants and herbivores, either through feeding intensity or food preferences. An increased supply of carbon resulting from increased photosynthesis at elevated CO2 has most often been found to increase the ratio of carbon to nitrogen in plant tissues, but increased tissue concentrations of carbon-based secondary metabolites have also been found (AYRES 1993). There is increasing evidence that plant response to elevated atmospheric CO2 is species-specific (HUNT et al. 1993, LEADLEY & KÖRNER 1996, LEADLEY & STOCKLIN 1996). While economically important crops, forest trees, and representative C3 and C4 species as model systems have been repeatedly studied (see KÖRNER & BAZZAZ 1996), less attention has been focused on the potential changes in plant-herbivore interactions. Snail breeders are aware that snail growth might be affected by an increase in atmospheric CO2 concentration, but detailed studies on the response of snails to food plants raised at elevated CO2 are so far lacking. An exception is the study of LEDERGERBER et al. (1998) which showed changes in the feeding behaviour of juvenile Helix pomatia L. kept in model plant
communities grown either at ambient or elevated CO₂ concentrations.

In the present study we examine the feeding behaviour and growth of juveniles of the land snail *Arianta arbustorum* (L.) fed on white clover (*Trifolium repens* L.) raised under ambient or elevated CO₂ conditions. *A. arbustorum* is a simultaneously hermaphroditic land pulmonate snail (family Helicidae) common in moist habitats of north-western and central Europe (KERNEY & CAMERON 1979). Its shell growth is completed after 2–5 hibernations with the formation of a lip at the edge of the aperture, which also indicates sexual maturity (BAUR & RABOUD 1988). The snails live on average 3–4 years as adults, but lifespans of up to 14 years have been recorded (BAUR & RABOUD 1988). Adult snails measure 16–22 mm in shell breadth. In the field, *A. arbustorum* deposits 1–4 clutches, each containing 20–80 eggs, per reproductive season. The eggs are laid in small holes in the soil or in decaying grass or moss (BAUR 1988). The nearly spherical eggs are approximately 3 mm in diameter (BAUR 1984). Hatching takes place 2–4 weeks after oviposition, depending on temperature.

**MATERIALS AND METHODS**

Eggs were obtained from *A. arbustorum* collected in the embankment of a track 7 km SE of Basel (47°30’N, 7°38’E; altitude 380 m a.s.l.). The adult snails were kept singly in transparent plastic containers (14 x 10 x 5 cm) lined with moist soil. The containers were kept in an environmental chamber at 19±1°C and a light/dark cycle of 18:6 h for 1 month. Fresh lettuce was provided ad libitum as food. The containers were checked twice per week for eggs. The eggs were collected, cleaned and incubated in plastic dishes lined with moist paper towelling at 19°C. Newly-hatched snails were separated daily from remaining unhatched eggs to prevent egg cannibalism (BAUR 1992). The hatchlings were kept in families in transparent plastic containers (14 x 10 x 5 cm) lined with moist soil and powdered limestone, and fed on fresh lettuce. During the first two weeks the young snails were kept outdoors at a shaded place and thereafter at room temperature (20–22°C) and natural daylight.

Plants of *T. repens* were raised in climate controlled chambers with natural daylight and a 18/10°C temperature regime at 350 ppm (ambient) and 600 ppm (elevated) CO₂ atmosphere. Plants were obtained by clonal replication. They grew in a mixture of marl and calcareous grassland soil and were regularly watered to field capacity.

After weighing to the nearest 0.1 mg, 6-week-old *A. arbustorum* (shell breadth: 4–6 mm) were placed singly in petri dishes (6.5 cm in diameter) lined with moist soil. Each snail was fed either ambient-CO₂ (350)-produced leaves ad libitum, or elevated-CO₂ (600)-produced leaves. Two snails of similar weight (difference < 10%) of the same clutch (family) were randomly assigned to either of the two CO₂ treatments (15 juveniles per treatment). In this way genetic differences of snails between the treatments could be minimised. The experiment was run for 40 days. The food was replaced every 2–3 days. At the same time the leaf area eaten was recorded. For this purpose we photocopied each leaf before and after

Fig. 1. Five leaves of *T. repens* before (upper row) and after (lower row) grazing by juvenile *A. arbustorum*. Scale bar 1 cm
grazing and calculated the difference between the two leaf areas using a computer scanning program (Fig. 1).

For both treatments we used regression equations between leaf area and leaf dry weight to estimate the biomass consumed by snails. At the beginning of the experiment, specific leaf area (SLA = leaf area [in cm²] per dry weight of leaf biomass [in g]; N = 12 leaves), and the concentrations of carbon and nitrogen (N = 5 leaves) were determined for single leaves of T. repens from both treatments. At the end of the experiment, the snails were placed in containers with saturated air moisture for one night, after which they were re-weighed. This treatment was necessary to allow the snails to reach the same level of water saturation as they had at the beginning of the experiment.

RESULTS

Single leaves of T. repens grown at elevated CO₂ did not differ in size from those grown at ambient CO₂ (elevated CO₂: 0.91±0.05 cm² [mean ± S.E.]; ambient CO₂: 1.01 ± 0.05 cm²; t = 1.56, df = 168, P = 0.12). However, the nitrogen concentration in the leaves was 16.6% lower at elevated CO₂ than in the leaves raised at ambient CO₂ (Table 1). In contrast, the leaf carbon concentration did not differ between the two treatments (Table 1). Specific leaf area (SLA) of T. repens raised at elevated CO₂ was 16.4% lower than in T. repens grown under ambient CO₂ (Table 1).

Juveniles of A. arbustorum fed on leaves produced at elevated CO₂ grazed a smaller leaf area than those fed on plants raised at ambient CO₂ (Table 1). However, the amount of biomass consumed was similar in both groups. Due to the reduction in leaf nitrogen concentration at elevated CO₂, the snails feeding on that diet received less nitrogen than the snails feeding on leaves produced at ambient CO₂. As a consequence, the snails fed on leaves produced at elevated CO₂ tended to grow more slowly than those fed on leaves produced at ambient CO₂. In both groups, the weight increase of individual snails was positively correlated with the amount of plant material consumed (ambient CO₂: r = 0.89, N = 15, P < 0.0001; elevated CO₂: r = 0.75, N = 15, P = 0.0009).

DISCUSSION

The present study showed that a reduction in leaf nitrogen concentration at high CO₂ can lead to a slower growth, thus confirming results of studies on insects (for reviews see LINCOLN et al. 1993, WATT et al. 1995). Measurements of juvenile growth should provide reliable estimates of net food quality. Faster growth rates are likely to reflect more favourable cost-benefit ratios of different food types to an animal. Plant tissue quality, particularly nitrogen concentration and digestibility, are the main factors influencing gastropod growth and reproduction (ROLLO & HAWRYLUK 1988, ROLLO & SHIBATA 1991).
pods commonly supplement their nitrogen-poor diets with faeces, carrion and (rarely) living animals (FRÖMMING 1954). Leaves of plants grown at elevated CO$_2$ concentrations often have lower nitrogen concentrations than plants grown at ambient CO$_2$ (BAZZAZ 1990, KÖRNER & MIGLIETTA 1994). Our data seem to confirm this general pattern. The decrease in plant nitrogen concentration may also result in consumption of greater amounts of plant material grown under elevated CO$_2$ conditions (LEDERGERBER et al. 1998, LINCOLN et al. 1993, WATT et al. 1995). In the present study, however, juvenile snails consumed smaller areas of _T. repens_ leaves grown under elevated CO$_2$ conditions. Due to the lower specific leaf area of _T. repens_ at elevated CO$_2$, the snails from both groups consumed a similar amount of biomass. It is possible that the amount of food that can pass through the digestive tract is limited in juvenile _A. arbustorum_. This hypothesis needs testing.

_T. repens_ and other legume species produce cyanogenic glucosides as a deterrent to herbivory (JONES 1973). However, there is substantial variability in the quantity of cyanogenic glucosides produced by _T. repens_ and in the tolerance of gastropods to these compounds (SOUTH 1992). In the present study juvenile _A. arbustorum_ appeared to be quite tolerant to this plant defence compound.

In the long term, plant species may respond to environmental changes such as elevated atmospheric CO$_2$ by altering the structure and composition of tissue, shifting in abundance and distribution, by going extinct, or by evolving. Predicting the kind of response is difficult. There are almost no species for which we know enough relevant ecology, physiology and genetics to predict their evolutionary response to environmental changes. There is even more uncertainty with respect to possible changes in plant-herbivore interactions and in the responses of herbivores to environmental change. Our results indicate a negative effect of rising atmospheric CO$_2$ on snail growth which could change the life cycle.

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REFERENCES


Feeding behaviour of A. arbustorum

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