Oecologia (1997) 109: 286–290

L. Hughes · F. A. Bazzaz

Effect of elevated CO_2 on interactions betwe en the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae) and the common milkweed, *Asclepias syriaca*

Received: 9 January 1996 / Accepted: 30 July 1996

Abstract We measured the effect of elevated CO_2 on populations of the western flower thrips, *Frankliniella occidentalis* and on the amount of leaf damage inflicted by the thrips to one of its host plants, the common milkweed, *Asclepias syriaca*. Plants grown at elevated CO_2 had significantly greater aboveground biomass and C:N ratios, and significantly reduced percentage nitrogen. The number of thrips per plant was not affected by CO_2 treatment, but the density of thrips (numbers per gram aboveground biomass), was significantly reduced at high CO_2. Consumption by thrips, expressed as the amount of damaged leaf area per capita, was significantly greater at high CO_2, and the amount of leaf area damaged by thrips was increased by 33%. However overall leaf area at elevated CO_2 increased by 62%, more than compensating for the increase in thrips consumption. The net outcome was that plants at elevated CO_2 had 3.6 times more undamaged leaf area available for photosynthesis than plants at ambient CO_2, even though they had only 1.6 times the overall amount of leaf area. This study highlights the need for measuring the effects of herbivory at the whole-plant level and also the importance of taking herbivory into account when predicting plant responses to elevated CO_2.

Key words *Asclepias syriaca* · Elevated CO_2 · *Frankliniella occidentalis* · Thrips · Herbivory

Introduction

The atmospheric concentration of CO_2 is expected to double during the next century (Houghton et al. 1992). Plants grown in elevated CO_2 commonly exhibit increased photosynthetic rates and carbohydrate storage (Bazzaz 1990; Ceulemans and Mousseau 1994). From the perspective of an insect herbivore, these plants are of poorer nutritional quality than those grown at current levels (Lincoln et al. 1993) due to changes in foliage water content, leaf toughness, levels of defensive chemicals and, most importantly, dilution of foliage nitrogen concentration (reviewed by Ayres 1993; Lincoln et al. 1993; Watt et al. 1995). In general, insect herbivores fed on foliage from plants grown at elevated CO_2 develop more slowly, consume more tissue, and have greater mortality (Lincoln et al. 1993; Watt et al. 1995). Most studies have measured these effects on insects kept in isolation from their host plants, and therefore the impacts of these changes on both plant performance and insect populations are not known. Furthermore, most studies have focused on leaf-chewing insects, and the response of insects from other feeding groups is poorly understood.

The impetus for this study was the occurrence of an infestation of the western flower thrips, *Frankliniella occidentalis* (Pergande), in a glasshouse in which experiments on the effects of elevated CO_2 were being conducted. This infestation gave us the opportunity to investigate the effects of elevated CO_2 on "natural" thrips populations, and on the level of damage caused by the thrips to one of its host plants, *Asclepias syriaca*, the common milkweed.

Materials and methods

Study species

The western flower thrips, *Frankliniella occidentalis*, is widespread on glasshouse and horticultural crops in North America (Broadbent

---

L. Hughes (✉)[1] · F. A. Bazzaz
Dept. of Organismic and Evolutionary Biology,
Harvard University, 16 Divinity Ave,
Cambridge, MA 02138, USA
fax: (617) 495 9300 e-mail: lhughes@oeb.harvard.edu

Present address:
[1]The Biological Laboratories, Harvard University,
16 Divinity Ave, Cambridge, MA 02138, USA

et al. 1987; Steiner 1990) and Europe (zur Strassen 1986). Like other phytophagous thrips, it feeds by scraping the surface of plant cells and sucking out the cell contents (Comegys and Schmitt 1965). Destruction of the epidermal cells is accompanied by whitening and scabbing of the outer surface. Fecal material deposited near the feeding site becomes colonized with fungus, further reducing the photosynthetic capacity of the plant (Chisolm and Lewis 1984). Thrips usually concentrate on rapidly growing tissues such as young leaves, flowers and terminal buds. Species such as *F. occidentalis* can cause severe retardation of plant growth, destruction of buds and flowers, malformation of fruits, and mortality of seedlings (Lewis 1973; Ananthakrishnan 1984, 1993). *F. occidentalis* has an extremely wide range of hosts, including many weed species (Yudin et al. 1986), and commonly spreads to crops when the weeds start to senesce (Bailey 1933; Yudin et al. 1988). As this species is also a vector of tomato spotted wilt disease (Sakimura 1962) and is resistant to many pesticides (Steiner 1990; Higgins 1992), it is considered to be the most important and difficult to control pest on glasshouse crops in both Europe and the USA (van Dijken 1992).

The common milkweed, *Asclepias syriaca*, is an herbaceous perennial weed found throughout North America (Woodson 1954), particularly in disturbed areas.

Methods

A. syriaca seeds (V and J Seed Farms, Woodstock, Ill.) were germinated in flats containing ProMix and placed in each of six glasshouse modules. Adjacent modules were paired, with one module within each pair randomly assigned to either 350 (ambient) or 700 $\mu l\,l^{-1}$ (elevated) CO_2 concentrations. CO_2 was controlled with an automatic monitoring and injection system using a Licor 6251 infrared gas analyzer (IRGA, Licor, Lincoln, Neb.). Temperature was held constant at 25°C during the day (16 h) and 20°C at night (8 h). Natural illumination was supplemented by high density discharge (HID) lights, providing light levels of 1800 µE at bench level. An outbreak of *F. occidentalis* which had occurred in the glasshouse several weeks previously, and had proved unmanageable by either conventional pesticides or biological control agents, resulted in the seedlings becoming "naturally" infested when only a few days old. At 2 weeks old, the seedlings were transplanted to 1.8-l pots. Plants were watered daily but not fertilized during the experiment and were uncaged, allowing the thrips to move freely between plants within a module.

By the time the plants were 6 weeks old considerable damage to the leaves was evident and the aboveground parts of 15 plants from each module were harvested. Each plant was placed in plastic bag filled with pure CO_2 to kill the thrips. The insects were brushed off the foliage and counted under a dissecting microscope. To obtain an index of damage caused by the thrips, the 3rd pair of leaves from the apex of each plant were digitized into a computer as 1-bit images using a flatbed scanner at 30 pixels cm^{-1} (LaCie Silverscanner, LaCie, Or.). The image processing program NIH Image (W. Rasband, NIH, v1.57) with a gray scale of 256 levels and a resolution of 120 dots cm^{-1} was used to skeletonize the image until the only pixels remaining corresponded to the undamaged (darkest) portion of each leaf. The total area of each leaf and the area damaged by thrips was then estimated. The leaves were then dried with the rest of the plant at 70°C and weighed. The leaves and stems of each plant were then ground together and the carbon and nitrogen content of the homogenate analyzed using a Europa CHN Analyzer (Model ANCA-*nt*, Europa Elemental Instruments, UK).

Statistical analysis

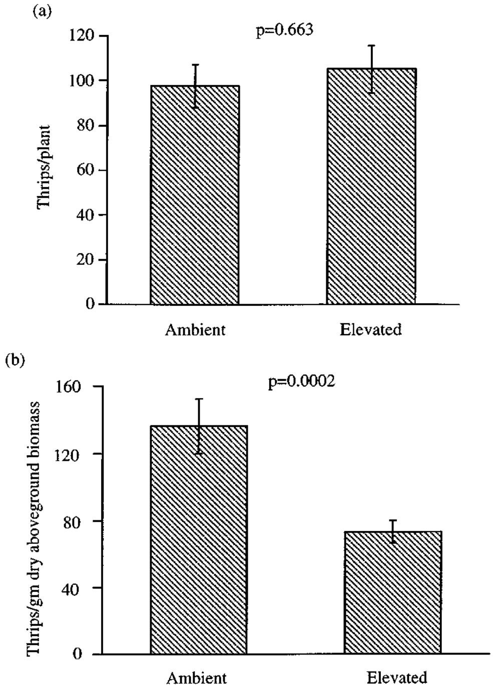
Data were analyzed using ANOVA with CO_2 level and block (pair of adjacent glasshouse modules) treated as fixed factors. Unless otherwise noted, block and block × CO_2 interactions were not significant. The amount of leaf area damaged was averaged over the pair of leaves sampled from each plant. Where appropriate, data was either square-root or log transformed to improve normality.

Results

Plants grown at high CO_2 had, on average, an 80% greater aboveground biomass ($F_{(1,84)} = 57.6$, $P < 0.0001$), and 62% greater leaf area ($F_{(1,84)} = 27.6$, $P < 0.0001$) than those at ambient CO_2. There was a small, but significant reduction in percent nitrogen ($F_{(1,83)} = 4.33$, $P = 0.041$) and a significant increase in C:N ratio ($F_{(1,83)} = 4.61$, $P = 0.034$) in plants grown at elevated CO_2 [ambient CO_2: %N = 4.84 ± 0.11, C:N 9.18 ± 0.10; elevated CO_2: %N = 4.58 ± 0.11, C:N 9.52 ± 0.13 (means ± SE)]. The number of thrips per plant at elevated CO_2 was not significantly different from that at ambient CO_2 ($F_{(1,83)} = 0.19$, $P = 0.663$, data square-root transformed, Fig. 1a). However the density of thrips, expressed as number of thrips per gram of aboveground biomass, was significantly less on plants at elevated CO_2 ($F_{(1,83)} = 15.67$, $P = 0.0002$, data log transformed, Fig. 1b).

Thrips were observed feeding on all aboveground plant parts but were concentrated on the youngest tissues in both CO_2 treatments, preferentially feeding on the areas closest to the leaf veins. The amount of damaged leaf area (measured for the third pair of leaves) was approximately 33% greater at elevated CO_2 ($F_{(1,83)} = 12.20$, $P = 0.0008$, Fig. 2). There was also a significant CO_2 × block interaction in this analysis ($F_{(2,83)} = 5.15$, $P = 0.0079$), due to there being a much

Fig. 1 a Mean number of thrips per plant (± SE) and **b** mean number of thrips per gram of dry aboveground biomass (± SE)



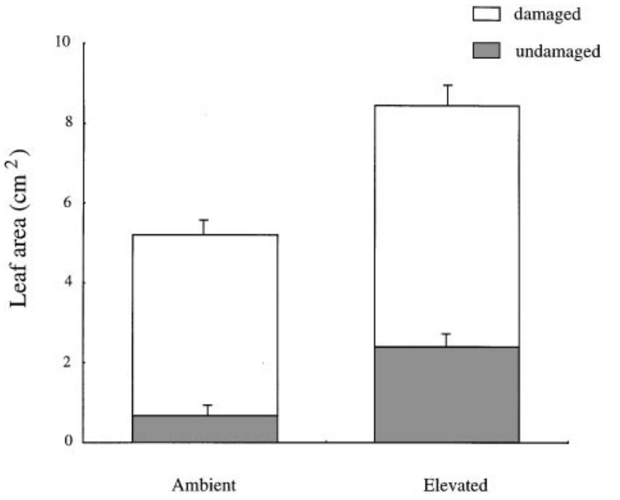


Fig. 2 Amount of damaged and undamaged leaf area, averaged for pair of leaves at the third highest node in each plant [SE for total leaf area = 0.64 (ambient), 0.92 (elevated)]

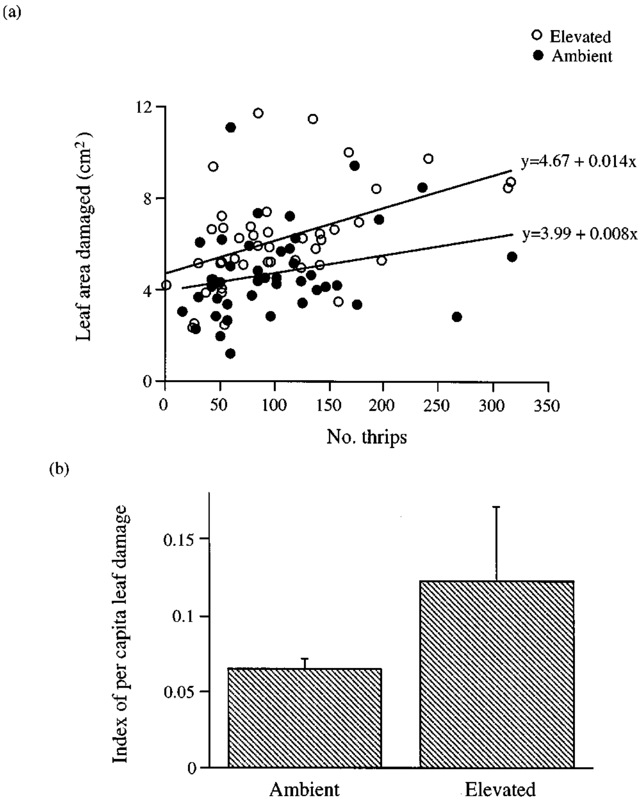


Fig. 3 a Relationship of thrips numbers (per plant) to amount of damaged leaf area (averaged for third pair of leaves) at ambient and elevated CO_2: ambient CO_2, slope = 0.008 ± 0.009 (95% c.l.), r^2 = 0.044, $F_{(1,42)}$ = 2.92, P = 0.0952; elevated CO_2, slope = 0.014 ± 0.009, r^2 = 0.21, $F_{(1,42)}$ = 11.92, P = 0.0013. **b** Index of per capita damage at ambient and elevated CO_2 (mean damaged area of third pair of leaves divided by number of thrips per plant, ± SE)

greater difference between treatments in one of the three blocks; this difference was, however, in the same direction as in the other blocks. As there was no difference in thrips populations between the two CO_2 treatments, the increase in area damaged at elevated CO_2 indicates that consumption by the thrips, on a per capita basis, was increased in this treatment. This increase in consumption is indicated by the steeper slope at elevated, compared to ambient, CO_2, of the regression relationship between numbers of thrips and area damaged (Fig 3a), although the slopes were not significantly different between CO_2 treatments due to the large scatter in the points (ambient CO_2: slope ± 95% confidence limits = 0.008 ± 0.009; elevated CO_2, 0.014 ± 0.009). When consumption is indicated by an index of per capita damage (leaf area damaged, averaged over the two leaves at the third node, divided by the number of thrips collected from the plant), the difference between CO_2 treatments is clearer, with the index of per capita damage at elevated CO_2 being nearly twice that at ambient CO_2 (Fig. 3b, $F_{(1,80)}$ = 4.673, P = 0.0336, data log-transformed).

Despite apparently higher consumption rates by thrips at elevated CO_2, the increased growth of plants in this treatment more than compensated for the increased herbivory. In fact the amount of undamaged leaf area was approximately 3.6 times higher at elevated CO_2 ($F_{(1,80)}$ = 40.74, P < 0.0001, Fig 2). As the general increase in leaf area was only 1.6 fold, the net outcome was that the proportional advantage of plants at high CO_2 was actually increased by the presence of the thrips.

Discussion

There has been much speculation as to the effect of elevated CO_2 concentrations on plant-herbivore interactions in the future. The results of this study indicate that while consumption rates by individual herbivores may increase, damage to plants may be more than compensated for by the direct effects of elevated CO_2 on plant biomass.

The net outcome of herbivore-plant interactions at high CO_2 will be the product of three main factors. Firstly, elevated CO_2 may directly affect insect populations via changes in the nutritional quality of plant tissue. Laboratory feeding trials have indicated that insects have longer development times and higher mortality on foliage grown at high CO_2 (e.g., Fajer et al. 1989; Roth and Lindroth 1994; Lindroth et al. 1995; Traw and Bazzaz, in press), suggesting that insect populations in the future may be reduced. Some studies in which insect populations on whole plants have been compared between different CO_2 levels have indeed shown a decrease [Butler et al. 1986 (3 of 6 species); Tripp et al. 1992; Thompson and Drake 1994], while others have found no differences [Butler 1985; Butler et al. 1986 (3 of 6 species)]. In this study, elevated CO_2 had no effect on populations of *F. occidentalis* on *A. syriaca*, measured on a per plant basis. This result is consistent with that of Butler (1985), who found that field populations of *Frankliniella* (probably also *occidentalis*) on cotton plants were not significantly different between open-topped chambers containing 500 and 650 $\mu l\,l^{-1}$ CO_2 and an adjacent crop at ambient CO_2.

Secondly, insects may alter both feeding preferences and/or consumption rates in response to changes in the composition of plant tissue at elevated CO_2. Unfortunately there are few data available on the effect of CO_2 on feeding preferences. Traw and Bazzaz (in press) found that gypsy moth larvae preferred ambient-grown leaves of yellow birch to those grown at elevated CO_2, but did not detect a preference when larvae were offered gray birch. There are, however, considerable data on the effects of foliage grown in enriched CO_2 on consumption rates. Laboratory feeding trials on leaf-chewing insects have consistently found increased consumption rates on foliage grown at elevated CO_2 (Lincoln et al. 1984, 1986; Osbrink et al. 1987; Fajer 1989; Fajer et al. 1989; Lincoln and Couvet 1989; Johnson and Lincoln 1990, 1991; Lindroth et al. 1993, 1995; Williams et al. 1994). These increases in consumption, which are on average about 40%, and may be up to 80%, are generally considered an attempt to compensate for lower nitrogen concentrations at high CO_2, nitrogen being the single most limiting resource for insect herbivores (McNeill and Southwood 1978; Mattson 1980; Scriber and Slansky 1981). These results have led some authors to speculate that herbivore damage may be greater in an enriched CO_2 environment (e.g., Lincoln et al. 1984; Fajer et al. 1989). In this study, the amount of leaf area damaged by *F. occidentalis*, on a per capita basis, was greater at elevated CO_2, indicating that these insects also increased consumption rate on foliage that had proportionally less nitrogen.

The third factor that will affect the interaction between plants and herbivores will be the direct effects of elevated CO_2 on plant growth rates and therefore plant biomass available for insects. In this study increases in plant biomass more than compensated for increases in consumption rates. This result is consistent with the few other studies in which insects have been grown on whole plants at elevated CO_2 (Osbrink et al. 1987; Caulfield and Bunce 1994). We should note however that, like most studies performed in controlled environments, the plants in this study were grown under highly favorable conditions of light and moisture, thus enhancing the CO_2 "fertilization" effect compared with what might be expected under field conditions.

The most interesting, and unexpected, result of the study, was that the presence of the herbivores actually increased the proportional advantage of plants at elevated CO_2 because although leaf area was increased by 62%, the amount of undamaged leaf area available for photosynthesis was 260% greater. This result highlights the need for further experiments that consider changes in insect consumption rates together with direct effects of CO_2 on plant biomass, and emphasizes the importance of taking herbivory into account when predicting plant responses to elevated CO_2.

Acknowledgements We are grateful to J. Kawaf for help in the glasshouse, R. Stomberg for general horticultural advice, G. Berntson for assistance with computer scanning and S. Nakahara for identifying the thrips. We also thank M. Ayres, P. Wayne and M. Jasienski for their comments on the manuscript. This research was funded by an American Association of University Women International Fellowship (to L.H.) and a grant from the US Department of Energy (to F.A.B.).

References

Ananthakrishnan TN (1984) Bioecology of thrips. Indira, Michigan

Ananthakrishnan TN (1993) Bionomics of thrips. Annu. Rev Entomol 38: 71–92

Ayres MP (1993) Plant defense, herbivory and climate change. In: Kareiva PM, Kingsolver JG, Huey RB (eds) Biotic interactions and global change. Sinauer, Sunderland, pp 75–94

Bailey SF (1933) A contribution to the knowledge of the western flower thrips, *Frankliniella californica* (Moulton). J Econ Entomol 26: 836–840

Bazzaz FA (1990) The response of natural ecosystems to the rising global CO_2 levels. Annu Rev Ecol Syst 21: 167–196

Broadbent AB, Allen WR, Foottit RG (1987) The association of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) with greenhouse crops and the tomato spotted wilt virus in Ontario. Can Entomol 119: 501–503

Butler GD (1985) Populations of several insects on cotton in open-top carbon dioxide enrichment chambers. Southwest Entomol 10: 264–267

Butler GD, Kimball BA, Mauney JR (1986) Populations of *Bemisia tabaci* (Homoptera: Aleyrodidae) on cotton grown in open-top field chambers enriched with CO_2. Environ Entomol 15: 61–63

Caulfield F, Bunce JA (1994) Elevated atmospheric carbon dioxide concentration affects interactions between *Spodoptera exigua* (Lepidoptera: Noctuidae) larvae and two host plant species outdoors. Environ Entomol 23: 999–1005

Ceulemans R, Mousseau M (1994) Tansley review no. 71: effects of elevated atmospheric CO_2 on woody plants. New Phytol 127: 425–446

Chisolm IF, Lewis T (1984) A new look at thrips (Thysanoptera) mouthparts, their action and effects. Bull Entomol Res 74: 663–675

Comegys GR, Schmitt JB (1965) A list of the Thysanoptera or thrips of New Jersey. J NY Entomol Soc 73: 195–222

Dijken FR van, Dik MTA, Gebala B, Jong J de, Mollema C (1994) Western flower thrips (Thysanoptera: Thripidae) effects on crysanthemum cultivars: plant growth and leaf scarring in nonflowering plants. J Econ Entomol 87: 1312–1317

Fajer ED (1989) The effects of enriched CO_2 atmospheres on plant-insect herbivore interactions: growth responses of larvae of the specialist butterfly, *Junonia coenia* (Lepidoptera: Nymphalidae). Oecologia 81: 514–520

Fajer ED, Bowers MD, Bazzaz FA (1989) The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. Science 243: 1198–1200

Higgins CJ (1992) Western flower thrips (Thysanoptera: Thripidae) in greenhouses: population dynamics, distribution on plants, and associations with predators. J Econ Entomol 85: 1891–1903

Houghton JT, Callander BA, Varney SK (1992) Climate change 1992: the supplementary report to the IPCC Scientific Assessment. Cambridge University Press, Cambridge

Johnson RH, Lincoln DE (1990) Sagebrush and grasshopper responses to atmospheric carbon dioxide concentration. Oecologia 84: 103–110

Johnson RH, Lincoln DE (1991) Sagebrush carbon allocation patterns and grasshopper nutrition: the influence of CO_2 enrichment and soil mineral limitation. Oecologia 87: 127–134

Lewis T (1973) Thrips: their biology, ecology and economic importance. Academic Press, London and New York

Lincoln DE, Couvet D (1989) The effect of carbon supply on allocation to allelochemicals and caterpillar consumption of peppermint. Oecologia 78: 112–114

Lincoln DE, Sionit N, Strain BR (1984) Growth and feeding response of *Pseudoplusia includens* (Lepidoptera: Noctuidae) to host plants grown in controlled carbon dioxide atmospheres. Environ Entomol 13: 1527–1530

Lincoln DE, Couvet D, Sionit N (1986) Response of an insect herbivore to host plants grown in carbon dioxide enriched atmospheres. Oecologia 69: 556–560

Lincoln DE, Fajer ED, Johnson RH (1993) Plant-insect herbivore interactions in elevated CO_2 environments. Trends Ecol Evol 8: 64–68

Lindroth RL, Kinney KK, Platz CL (1993) Responses of deciduous trees to elevated atmospheric CO_2: productivity, phytochemistry, and insect performance. Ecology 74: 763–777

Lindroth RL, Arteel GE, Kinney KK (1995) Responses of three saturniid species to Paper Birch grown under enriched CO_2 atmospheres. Funct Ecol 9: 306–311

Mattson WJ (1980) Herbivory in relation to plant nitrogen content. Annu Rev Ecol Syst 11: 119–161

McNeill S, Southwood TRE (1978) The role of nitrogen in the development of insect/plant relationships. In: Harborne JB (ed) Biochemical aspects of plant and animal co-evolution. Academic Press, London, pp 77–98

Osbrink WLA, Trumble JT, Wagner RE (1987) Host suitability of *Phaseolus lunata* for *Trichoplusia ni* (Lepidoptera: Noctuidae) in controlled carbon dioxide atmospheres. Environ Entomol 16: 639–644

Roth SK, Lindroth RL (1994) Effects of CO_2-mediated changes in paper birch and white pine chemistry on gypsy moth performance. Oecologia 98: 133–138

Sakimura K (1962) The present status of thrips-borne viruses. In: Maramorosch, K (ed) Biological transmission of disease agents. Academic Press, New York, pp 33–40

Scriber JM, Slansky F (1981) The nutritional ecology of immature insects. Annu Rev Entomol 26: 183–211

Steiner MY (1990) Determining population characteristics and sampling procedures for the western flower thrips (Thysanoptera: Thripidae) and the predatory mite *Amblyseius cucumeris* (Acari: Phytoseiidae) on greenhouse cucumber. Environ Entomol 19: 1605–1613

Strassen R zur (1986) *Frankliniella occidentalis* (Pergande 1895), a North American thrips (Thysanoptera) as a new inhabitant of European glasshouses. Nachrichtenbl Dtsch Pflanzenschutzdienst Berlin 38: 86–88

Thompson GB, Drake BG (1994) Insects and fungi on a C3 sedge and a C4 grass exposed to elevated atmospheric CO_2 concentrations in open-top chambers in a field. Plant Cell Environ 17: 1161–1167

Traw MB, Bazzaz FA (in press) The effects of an enriched CO_2 atmosphere on two birch species and the gypsy moth: consequences for host plant selection. Oecologia

Tripp KE, Kroen WK, Peet MM, Willits DH (1992) Fewer whiteflies found on CO_2-enriched greenhouse tomatoes with high C:N ratios. Hortscience 27: 1079–1080

Watt AD, Whittaker JB, Docherty M, Brooks G, Lindsay E, Salt DT (1995) The impact of elevated atmospheric CO_2 on insect herbivores. In: Harrington N, Stork NE (eds) Insects in a changing environment. Academic Press, London, pp 198–217

Williams RS, Lincoln DE, Thomas RB (1994) Loblolly pine grown under elevated CO_2 affects early instar pine sawfly performance. Oecologia 98: 64–71

Woodson RE (1954) The North American species of *Asclepias* L. Ann Mo Bot Gard 41: 1–211

Yudin LS, Cho JJ, Mitchell WC (1986) Host range of western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), with special reference to *Leucaena glauca*. Environ Entomol 15: 1292–1295

Yudin LS, Tabashnik BE, Cho JJ, Mitchell WC (1988) Colonization of weeds and lettuce by thrips (Thysanoptera: Thripidae). Environ Entomol 17: 522–526