

Does elevated CO₂ facilitate naturalization of the non-indigenous *Prunus laurocerasus* in Swiss temperate forests?

S. HÄTTENSCHWILER† and C. KÖRNER

Institute of Botany, University of Basel, Schönbeinstrasse 6, CH-4056 Basel, Switzerland

Summary

1. An increasing abundance of the non-indigenous evergreen woody plant species *Prunus laurocerasus* has been observed in the understorey of Swiss temperate forests. We addressed the question whether rising atmospheric CO₂ concentration contributes to the success of this species in a comparative test with four co-occurring native species (*Ilex aquifolium*, *Hedera helix*, *Fraxinus excelsior*, *Carpinus betulus*).

2. We grew plants from germination to the end of the third growing season in open-top chambers exposed to either ambient or two elevated CO₂ concentrations (500 and 660 µmol mol⁻¹) in a deeply shaded forest understorey (1.2–3.2% of full sun).

3. Species differed greatly in their response to CO₂. Biomass growth in *Prunus* increased by an average of 56% at the two elevated CO₂ concentrations compared to ambient CO₂; there was no significant difference between 500 and 660 µmol mol⁻¹. In contrast the native *Ilex*, with the same functional traits, a similar life history and occurring in the same habitat, showed no significant CO₂ response.

4. A particularly large and nearly linear CO₂ effect on seedling growth was observed in the liana *Hedera* with 100% more biomass and 137% longer stems at 660 µmol CO₂ mol⁻¹ compared to ambient CO₂. Seedlings of the deciduous tree species *Fraxinus* produced 43% more biomass at elevated CO₂ (no significant difference between 500 and 660 µmol mol⁻¹), but there was no significant CO₂ effect on *Carpinus* seedlings.

5. Our results indicate that elevated CO₂ might contribute to the current spread of *Prunus* in natural forests. The strong CO₂ response in *Hedera* suggests an increasing rate of tree colonization with rising CO₂. Increasing dominance of non-indigenous understorey species and accelerated liana colonization of canopy trees could both have far-ranging consequences for forest community dynamics and composition.

Key-words: Broad-leaved evergreen species, global change, *Hedera helix*, plant species invasion, seedling biomass growth

Functional Ecology (2003) **17**, 778–785

Introduction

As a consequence of expanding global transport and commerce, introductions of non-indigenous species have increased dramatically in the past 500 years (di Castri 1989). A few non-indigenous species eventually become invasive (Mack *et al.* 2000) and threaten native plant communities and ecosystems through competition, predation or altered ecosystem processes (Vitousek & Walker 1989; D'Antonio & Vitousek 1992; Schmitz *et al.* 1997; Callaway & Aschehoug 2000). Biotic invasions are a major feature of global change (Vitousek *et al.* 1996; Mack *et al.* 2000), other elements of which, such as changes in land use, climate, nitrogen deposition

or atmospheric CO₂ concentration, may enhance the probability of persistence and naturalization of immigrating species and facilitate and/or accelerate invasion rates (Dukes & Mooney 1999).

For example, winters have become increasingly mild and summers moist in the past 30 years compared to the long-term average. These changes have been associated with a dramatic spread of non-indigenous evergreen woody plant species in the understorey of winter-deciduous temperate forests in Switzerland (Klötzli *et al.* 1996; Walther 1999). These authors observed an increasing distribution, abundance and vigour of several evergreen broad-leaved (laurophyllous) species (e.g. *Prunus laurocerasus*, *Laurus nobilis*, *Eleagnus pungens*) that had naturalized from gardens and parks, where they have been planted for centuries. Significant changes in species composition, structure and function

of winter-deciduous forests at low altitudes are to be expected if the current invasion by evergreen woody plant species continues.

Rising atmospheric CO₂ concentration may have an additional favourable effect on seedling growth in the forest understorey, and might contribute to improved establishment of non-indigenous species. In the light-limited forest understorey, the relative CO₂ effects may be particularly large because higher CO₂ concentrations reduce the photosynthetic light compensation point (Osborne *et al.* 1997) and increase sunfleck utilization efficiency (Naumburg & Ellsworth 2000) in understorey plants. Both these responses may result in a significantly improved carbon balance and growth of shaded plants. Large stimulations of biomass growth under elevated CO₂ have been observed in a variety of species in the natural understoreys of tropical (Würth, Winter & Körner 1998) and temperate forests (Hättenschwiler & Körner 2000). Seedlings of co-occurring tree species, however, showed distinct responses to elevated CO₂ (Hättenschwiler 2001) as reported in an earlier growth chamber experiment (Bazzaz & Miao 1993). Such CO₂-related interspecific differences in plant growth are common (Körner & Bazzaz 1996; Körner 2000) and likely to change community composition, with consequences for biodiversity and ecosystem processes (Körner 2000).

In the present study we asked how the widespread and increasingly abundant non-indigenous evergreen *Prunus laurocerasus* responds to elevated CO₂ in a temperate forest understorey, and if this response differs from that of native woody plant species.

Materials and methods

STUDY SITE AND PLANT MATERIAL

The study was conducted at the previously established Hofstetten experimental forest area, 12 km south-west of Basel (47°28' N 7°30' E) at an elevation of 550 m a.s.l. (Hättenschwiler & Körner 2000). The forest is about 120 years old and is composed of various broad-leaved deciduous and coniferous tree species, with *Fagus sylvatica* and *Quercus robur* as the dominant canopy species. The tallest trees reach a height of about 35 m with a tree canopy leaf area index of ≈5.0. Long-term mean annual precipitation is 885 mm, and long-term average daily mean temperatures are -2.0 °C in January and 18 °C in July. The topsoil has a pH of 5.8, is comparatively nutrient-poor (see Hättenschwiler & Körner 2000 for nutrient analyses), and is underlain by limestone bedrock.

Prunus laurocerasus L., the common non-indigenous evergreen woody species found in Swiss deciduous forests, was the focus of our experiment. *Prunus laurocerasus* is native to the humid Black Sea coast and South-west Asia, and occurs on relatively moist soils in forest understoreys or as a subdominant tree. It has been planted as an ornamental plant in gardens and parks all over southern and western Europe for ≈400 years,

from where it has escaped during the past 20–30 years. It is now common in the understorey of native forests at lower elevations (<750 m a.s.l.) and contributes significantly to the increasing dominance of evergreen understorey vegetation observed in Swiss forests (Walther 1999; Walther & Grundmann 2001). For comparison, four additional species native to Switzerland, representing three different functional types of woody plant, were included in the experiment. Like *P. laurocerasus*, *Ilex aquifolium* L. is a broad-leaved evergreen shrub or small tree (up to 6–10 m tall) *Hedera helix* L. is a broad-leaved evergreen liana; and *Carpinus betulus* L. and *Fraxinus excelsior* L. are broad-leaved deciduous canopy trees (study species are denoted by genus hereafter). *Ilex* occurs in the same habitat, attains about the same size, shares the same morphological type of leaves, and produces similar-sized, fleshy fruits dispersed by birds, as is *Prunus*, but occurs much further north in oceanic parts of Europe (up to 64° northern latitude). Except for *Buxus sempervirens* L., which has a more restricted occurrence in some dry forests in the south-west of Switzerland, *Ilex* is the only native broad-leaved evergreen small tree in Swiss forests. The liana *Hedera* grows up to the top of the tallest trees (>30 m), has a similar distribution to *Ilex*, and is a common and abundant species in a variety of forests. *Hedera* often covers the forest floor, where it can grow for many years until it contacts an appropriate tree to climb. The deciduous tree *Carpinus* is a common canopy species in oak-dominated forests at lower elevations (<750 m a.s.l.); *Fraxinus* commonly co-occurs with beech and oak, and is somewhat more shade tolerant than *Carpinus*. All study species occur naturally at or near our study site.

Seeds of *Carpinus* and *Fraxinus* were collected from single trees at the study site in autumn 1997 and stored at 5 °C for 8 weeks to allow the seeds to ripen completely. The seeds were then stratified in a 1 : 1 mix of sand and peat in the Botanical Garden of the University of Basel from January to March 1998. Because *Prunus* and *Ilex* seeds germinate only after two winters of stratification, they were collected from shrub-sized individuals in a garden near Basel (*Prunus*) and in the Botanical Garden of the University of Basel (*Ilex*) in late autumn 1996. After collection, the fruits were soaked in water (replaced every 3–4 days) for 2 weeks, the softened mesocarp was then rubbed off and the stones were allowed to dry, followed by stratification as described above from December 1996 to March 1998. As soon as the seeds started to germinate in early April 1998 they were inserted directly into the undisturbed forest soil within each of the 36 open-top chambers (OTC). At the same time, germinating *Hedera* seeds were collected from the forest floor at the study site and transferred to the OTCs.

Forty-eight (0.04 × 0.04 m) seed positions were defined per OTC using a grid, and species were randomly allocated to each position. A total of 15 germinating seeds of each of the two species, *Carpinus* and *Fraxinus*, and a total of six germinating seeds of the remaining three

species, were inserted into each OTC. More seeds of the deciduous tree species were used as greater initial mortality was expected because of their small seeds. Spontaneously emerging natural seedlings and forbs within the OTCs were removed, but the natural litter layer remained in place.

EXPERIMENTAL DESIGN

Although the experiment was carried out in the same forest understorey as a previous study with a similar experimental design (Hättenschwiler & Körner 2000), new and undisturbed positions were chosen for all 36 OTCs. The cylindrical OTCs had a diameter and height of 38 cm and were constructed from 2 mm thick UV-transmitting Plexiglas (gs 2458, Röhm GMBH, Germany). The relatively small chamber size had the advantage of well defined microsites in terms of light availability. Each OTC was randomly assigned to either ambient ($366 \mu\text{mol mol}^{-1}$) or two elevated CO_2 concentrations (500 and $660 \mu\text{mol mol}^{-1}$) resulting in 12 OTCs per CO_2 treatment. Three large blowers produced a steady but gentle flow of air sampled at 1 m above the forest floor. The air was distributed to the chambers by manifolds. Two blower systems received computer-controlled CO_2 additions to the airflow to achieve the target CO_2 concentrations (see Körner *et al.* 1996; Hättenschwiler & Körner 2000 for more details on CO_2 control and system performance). Carbon dioxide enrichment started on 10 April 1998 and continued during winter, except for 8–12 weeks between mid-December and end of February when snow covered the ground, and ended on 3 October 2000 with the final plant harvest. The actual CO_2 concentrations deviated little from target concentrations, with annual averages of 502, 499 and $505 \mu\text{mol mol}^{-1}$, and 661, 658 and $663 \mu\text{mol mol}^{-1}$ for the intermediate and high CO_2 concentrations, respectively, over the three consecutive years.

Continuous microclimate measurements inside and outside the OTCs showed no significant differences resulting from the use of OTCs and no differences among the CO_2 treatments (Hättenschwiler & Körner 2000), because of the buffering effect of the tree canopy. Photosynthetically active photon flux densities (PPFD) were measured with a permanent light sensor 15 cm above the ground in each OTC (GaAsP photo diodes, spectral response range 300–680 nm, G1115, Hamamtsu Photonics, Hamamtsu City, Japan). Two additional sensors were placed outside the forest as a reference. The photo diodes were sealed in a waterproof tube covered with a white diffuser cap. All sensors were calibrated with a quantum sensor (LI-189, LI-COR Inc., Lincoln, NE, USA). Readings were logged at 10 s intervals (CR 10 with relay multiplexer, Campbell Scientific Ltd, Loughborough, UK) and means of 5 min measurements were stored. Light data were continuously collected for 10–20 days of each month (March 1999–September 1999, June 2000–August 2000). The

microsite-specific light availability for the 36 OTCs is indicated as the daily PPFD measured on overcast summer days during the peak season (June–August), as in a previous study (Hättenschwiler & Körner 2000). On average, the total daily PPFD on overcast summer days ranged from 0.41 to $2.26 \text{ mol m}^{-2} \text{ day}^{-1}$ (0.9–5.0% of full sun) in the forest understorey studied. These values compare to $20.5 \pm 0.7 \text{ mol m}^{-2} \text{ day}^{-1}$ measured on the same overcast summer days, and to $44.8 \pm 0.6 \text{ mol m}^{-2} \text{ day}^{-1}$ measured on clear summer days outside the forest.

During the winter following the second growing season, intruding mice largely destroyed the seedlings in 10 OTCs. We were fortunate that the mice affected the CO_2 treatments more or less equally, reducing the final replication to eight OTCs per CO_2 treatment and covering a range in total daily PPFD from 0.53 in the darkest OTC to 1.42 mol m^{-2} (1.2–3.2% of full sun) in the brightest OTC (Fig. 1). The mean daily PPFD across the eight OTCs within each CO_2 treatment was almost identical among CO_2 treatments (Fig. 1), with an overall mean daily PPFD of $0.99 \text{ mol m}^{-2} \text{ day}^{-1}$ (2.2% of full sun) across the 24 OTCs used for the final analysis. On average, more than 80% of all 5 min means of PPFD were below $15 \mu\text{mol m}^{-2} \text{ s}^{-1}$ on a typical overcast summer day (98% in the darkest OTC and 67% in the brightest).

PLANT SAMPLING AND DATA ANALYSIS

Seedlings were checked regularly for survival during the first growing season, and to a lesser extent in the second and third seasons. To minimize shading among seedlings in OTCs, some seedlings were removed (particularly weak seedlings were removed first, then those for maximizing spatial distance among remaining seedlings) at the end of the first and second seasons, leaving three or four individuals per species and per chamber. For the final harvest (3–6 October 2000), after three growing seasons, we dug out the entire soil block covered by the OTC to a depth of 20 cm. Each individual seedling was then washed out of the soil using a hose. Seedlings were divided into roots, stems and leaves, and all plant parts were oven-dried at 80°C for 36 h and weighed. For the determination of total leaf area and specific leaf area (SLA), we took leaf discs from different leaves (avoiding the middle vein) of each seedling (five or six discs per seedling) using a cork borer of a known diameter. From the measured dry masses of all plant parts, root mass fraction (RMF: root mass/total seedling mass), stem mass fraction (SMF: stem + petiole mass/total seedling mass), leaf mass fraction (LMF: leaf mass/total seedling mass), and leaf area ratio (LAR: total leaf area/total seedling mass) were calculated.

Data of individual seedlings within each OTC were averaged for each species and used as the sample units ($n = 8$ replicates per CO_2 concentration). Analyses of covariance (ANCOVA) were performed to test differences

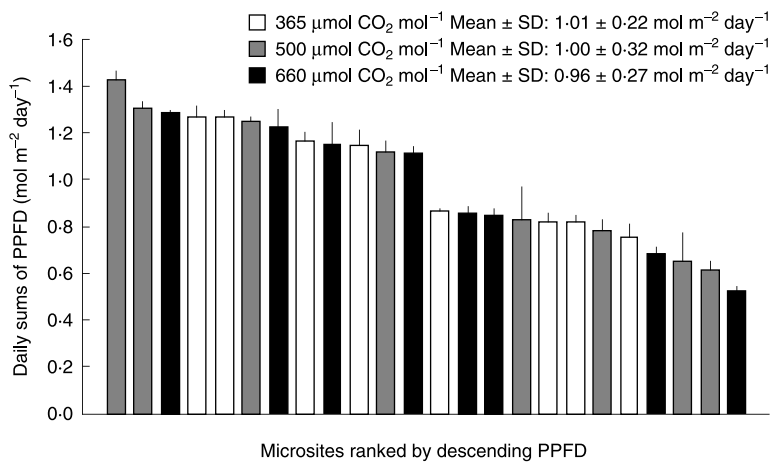


Fig. 1. Mean daily sums of photosynthetically active photon flux density (PPFD) within eight open-top chambers (OTCs) maintained at each of three different CO₂ concentrations. Data are means from three overcast days in June, July and August 1999; error bars represent standard deviations. Light was measured continuously and stored as 5 min averages. All readings above 1 μmol m⁻² s⁻¹ were considered for the calculation of daily sums (accuracy of light sensors ±1 μmol m⁻² s⁻¹).

among species and CO₂ treatments with microsite-specific light availability as the covariate (Sokal & Rohlf 1981). In these analyses, treatment effects were tested as differences in the elevation of the *Y*-intercept of linear regressions between growth variables and light availability. The effect of the covariate (light) was tested as the regression slope and whether it differed from zero, and the interactions between treatments and light were tested as the differences among slopes of the regression lines (Sokal & Rohlf 1981). Treatment effects, i.e. the differences in the *Y*-intercepts of regressions, were tested at the lower end of the light gradient (1.2% of full sun); the upper end (3.2% of full sun); and also at 2.2% of full sun as the intermediate light availability. Differences between individual levels within factors were tested using Fisher's LSD *post hoc* tests. All biomass-related variables were ln-transformed prior to statistical analyses to meet the requirement of

normal distribution. SYSTAT ver. 5.2.1 (Systat Inc., Evanston, IL, USA) was used for statistical analyses.

Results

SEEDLING SURVIVAL AND HEIGHT GROWTH

Average mortalities of 20 and 12% in deciduous and evergreen species, respectively, were observed within the first 4 weeks after seeds were transferred to the OTCs. This initial mortality occurred randomly, with no differences among CO₂ treatments and among OTCs differing in light availability. Following these initial losses, survival remained high with only little additional seedling death throughout the entire experiment and no CO₂- or light-related differences.

The final stem length after three growing seasons differed among species (Table 1; Fig. 2). *Post hoc* contrast analyses revealed significant differences between *Carpinus* as the tallest and *Ilex* ($P = 0.038$) and *Prunus* ($P = 0.043$) as the smallest species, but no other significant differences among species. Increased atmospheric CO₂ concentration had a significant positive effect on final stem length (Table 1; Fig. 2), but the species differed in their response (significant species × CO₂ interaction). Seedlings of the two broad-leaved evergreens *Ilex* and *Prunus* did not grow taller at elevated CO₂, whereas the two broad-leaved deciduous species *Fraxinus* and *Carpinus* had significantly longer stems at the intermediate CO₂ concentration of 500 μmol mol⁻¹ with no further stimulation at 660 μmol CO₂ mol⁻¹. In contrast, stem length in the evergreen liana *Hedera* showed a strong and linear response to increasing CO₂ concentration. *Hedera* stems were 1.7–2.4 times longer at 500 and 660 μmol CO₂ mol⁻¹ compared to seedlings grown at current ambient CO₂. The average (mean of the two elevated CO₂ concentrations) relative CO₂ stimulation in stem length of +103% in *Hedera* is substantially larger than that in *Fraxinus* (+17%) or in *Carpinus* (+25%).

Table 1. Analyses of covariance of seedling stem length, biomass, biomass fractions (see text) and morphological traits (LAR, SLA; see text) with species and CO₂ as fixed factors and microsite-specific light availability as covariate

Variable	Species		CO ₂		Species × CO ₂		Light		Light × species		Light × CO ₂		<i>r</i> ²
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Stem length	16	<0.001	9.9	<0.001	2.2	0.04	3.4	0.07	0.4	0.84	1.3	0.27	0.58
Total mass	41	<0.001	9.9	<0.001	0.7	0.66	6.1	0.02	0.4	0.82	0.3	0.77	0.72
Leaf mass	34	<0.001	4.5	0.014	0.6	0.81	4.6	0.03	0.3	0.91	0.4	0.69	0.64
Stem mass	41	<0.001	15	<0.001	1.0	0.45	5.9	0.02	0.6	0.64	0.8	0.45	0.73
Root mass	63	<0.001	9.5	<0.001	0.8	0.62	5.8	0.02	0.6	0.69	0.6	0.53	0.79
LMF	105	<0.001	3.2	0.05	0.9	0.56	1.1	0.30	0.5	0.75	2.4	0.10	0.85
SMF	29	<0.001	3.3	0.05	0.6	0.79	0.9	0.34	0.8	0.56	0.9	0.43	0.62
RMF	40	<0.001	0.1	0.88	0.7	0.69	0.0	0.98	1.2	0.30	3.5	0.03	0.69
LAR	16	<0.001	3.7	0.03	0.6	0.79	0.1	0.76	0.2	0.95	6.9	0.002	0.53
SLA	682	<0.001	0.6	0.53	1.4	0.20	2.8	0.10	0.5	0.71	7.0	0.002	0.97

Tests for differences among different levels of fixed factors (*Y*-intercept) were done at the intermediate light level of 2.2% of full sun (1.01 mol m⁻² day⁻¹). *F* ratios, *P* values and coefficients of determination (*r*²) are shown.

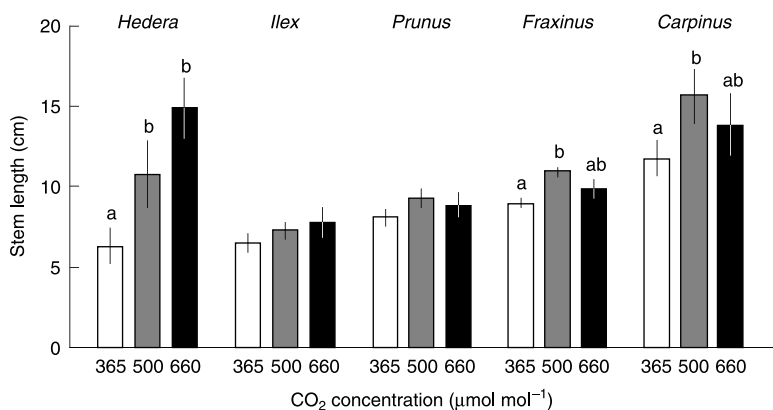


Fig. 2. Final stem length in seedlings of five different woody plant species exposed to three different CO₂ concentrations (means ± SE of eight OTCs). Seedlings grew in the deeply shaded forest understorey for a total of three growing seasons. Different letters indicate significant differences among CO₂ treatments within species.

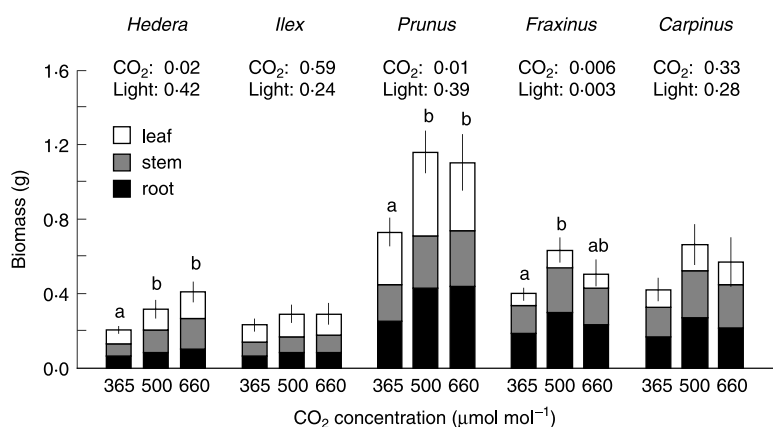


Fig. 3. Total seedling biomass of five different woody plant species exposed to three different CO₂ concentrations over three growing seasons (means ± SE of eight OTCs). Levels of significance from analyses of covariance to test for effects of CO₂ and light (covariable) within species are shown. Different letters indicate significant differences among individual treatment levels within those species exhibiting a significant CO₂ effect.

Differences in microsite light availability only marginally affected seedling height growth, and the weak positive correlation between stem length and light availability across the narrow light gradient was similar among species and CO₂ treatments (no light × species and light × CO₂ interactions; Table 1).

BIOMASS PRODUCTION AND ALLOCATION

Total seedling biomass production over the three growing seasons was significantly different among species and CO₂ concentrations (Table 1; Fig. 3). *Prunus* produced significantly more biomass than the two other evergreen species *Ilex* ($P = 0.033$, *post hoc* contrast) and *Hedera* ($P = 0.031$). No other *post hoc* pairwise comparisons between species were significant. The average relative CO₂ effect on seedling biomass across species was +51% at 500 and +48% at 660 μmol CO₂ mol⁻¹ compared to ambient CO₂, suggesting no further CO₂ stimulation beyond 500 μmol CO₂ mol⁻¹. Although the species × CO₂ interaction was not significant, there was some apparent

variation among species in their CO₂ response (Fig. 3). Tested separately within each species, a significant CO₂ effect on total biomass was found in *Hedera* (+78%, mean across both CO₂ concentrations), *Prunus* (+56%) and *Fraxinus* (+43%), but not in *Ilex* and *Carpinus* (Fig. 3). As the mean biomass in *Carpinus* even declined somewhat beyond 500 μmol CO₂ mol⁻¹, similarly to *Fraxinus*, we additionally tested the CO₂ effect between ambient CO₂ and the intermediate CO₂ concentration, and between ambient CO₂ and the pooled data across the two high CO₂ concentrations. Neither analysis yielded significant CO₂ effects ($P > 0.09$) because of the large variation in the size of *Carpinus*. Leaf, stem and root biomass differed in their relative contributions to total biomass among species, but showed essentially the same pattern of CO₂ effects as did total biomass (Table 1; Fig. 3).

Seedling biomass generally increased with increasing light availability. However, differences in microsite-specific light availability explained comparatively little variability in biomass (Table 1).

Biomass fractions differed among species (Tables 1 and 2), essentially due to the significantly larger leaf mass fractions in evergreen compared to deciduous species and concomitant differences in stem and root mass fractions. Elevated CO₂ significantly affected leaf mass fraction (lower LMF with increasing CO₂ across all species), while root mass fraction did not change (Table 1). The significant light × CO₂ interaction on RMF, however, indicates that regression lines of RMF as a function of microsite light availability differed in their slope among CO₂ concentrations. Averaged across all species RMF at ambient CO₂ was 0.34 in the OTCs of <1 mol photons m⁻² day⁻¹ and 0.38 in those of >1 mol photons m⁻² day⁻¹, as the intermediate level across the light gradient. At the two elevated CO₂ concentrations (no difference between 500 and 660 μmol CO₂ mol⁻¹), RMF was 0.39 (PPFD <1 mol m⁻² day⁻¹) and 0.35 (PPFD >1 mol m⁻² day⁻¹). The light × CO₂ interaction on RMF was significant only across all species, but not when tested within each species separately.

Specific leaf area differed considerably among species (Tables 1 and 2), driven mainly by smaller SLAs in evergreen compared to deciduous species. Because large SLA correlated well with small LMF at the species level, the leaf area ratio (LAR) as the product of SLA and LMF was similar among species (no significant differences in *post hoc* contrast analyses). While there was no significant effect on SLA, LAR decreased with increasing CO₂ except in *Ilex* (Table 2). However, SLA and LAR had significant light × CO₂ interactions. Similarly to LMF, SLA and LAR decreased slightly with light availability at ambient CO₂, but increased with increasing light availability at elevated CO₂. Again, this pattern was significant only across species, but not when tested within each species separately.

With the exception of a marginally significant reduction of SLA, microsite-specific light availability *per se* did not influence seedling biomass allocation or morphology.

Table 2. Biomass fractions (see text), leaf area ratio (LAR) and specific leaf area (SLA) in 3-year-old seedlings grown at different CO₂ concentrations of 365, 500 or 660 µmol mol⁻¹ in the forest understorey (means with SE in parentheses)

Parameter	Species				
	<i>Hedera</i>	<i>Ilex</i>	<i>Prunus</i>	<i>Fraxinus</i>	<i>Carpinus</i>
RMF (g g ⁻¹)					
365	0.31 (0.02)	0.30 (0.01)	0.34 (0.02)	0.47 (0.02)	0.38 (0.02)
500	0.29 (0.03)	0.29 (0.01)	0.37 (0.02)	0.47 (0.02)	0.39 (0.01)
660	0.26 (0.01)	0.28 (0.02)	0.40 (0.04)	0.47 (0.02)	0.37 (0.02)
SMF (g g ⁻¹)					
365	0.34 (0.02)	0.32 (0.02)	0.27 (0.02)	0.38 (0.01)	0.40 (0.02)
500	0.37 (0.01)	0.31 (0.01)	0.26 (0.01)	0.39 (0.01)	0.41 (0.01)
660	0.40 (0.01)	0.32 (0.02)	0.28 (0.02)	0.39 (0.01)	0.44 (0.03)
LMF (g g ⁻¹)					
365	0.35 (0.01)	0.38 (0.03)	0.38 (0.01)	0.15 (0.01)	0.23 (0.01)
500	0.34 (0.02)	0.40 (0.02)	0.38 (0.02)	0.14 (0.01)	0.20 (0.01)
660	0.35 (0.01)	0.41 (0.01)	0.32 (0.04)	0.15 (0.01)	0.19 (0.01)
LAR (cm ² g ⁻¹)					
365	70.0 (2.6)	61.9 (4.7)	48.2 (2.3)	62.0 (6.9)	78.7 (5.7)
500	64.9 (3.3)	67.4 (3.5)	46.4 (2.4)	60.1 (4.2)	73.8 (3.0)
660	64.4 (2.2)	67.8 (1.0)	41.1 (5.4)	58.1 (2.8)	61.4 (4.3)
SLA (cm ² g ⁻¹)					
365	200 (7)	163 (6)	126 (3)	412 (18)	350 (15)
500	192 (3)	169 (5)	122 (2)	422 (11)	364 (12)
660	186 (6)	166 (2)	129 (4)	404 (17)	331 (14)

Discussion

Seedlings of the non-indigenous evergreen *P. laurocerasus* growing in the forest understorey produced considerably more biomass at elevated atmospheric CO₂ concentration than at ambient CO₂. The initial phase of growth after germination and early establishment of seedlings is a critical part in a tree's life history, one that largely determines regeneration success (Clark & Clark 1992; Kobe *et al.* 1995). Our results suggest that rising atmospheric CO₂ facilitates seedling establishment of *Prunus* in the natural forest understorey, perhaps contributing to the observed increasing abundance of this species in Swiss forests (Walther 1999; Walther & Grundmann 2001), but cannot assess the relative importance of elevated CO₂ compared to other factors, such as warmer winters, moister summers or changes in forest management, for the apparent spread of *Prunus* in different native forests. Interactions among different elements of global change, rather than a single cause, are probably common determinants of the success of non-indigenous plant species (Dukes & Mooney 1999), but separating the effects of these elements is complex and difficult (Huenneke 1997).

There is relatively little unambiguous evidence for CO₂ stimulation of invasive plant species in natural ecosystems (Dukes & Mooney 1999) because appropriate field experiments are lacking. In line with our findings, although for a completely different ecosystem, Smith *et al.* (2000) reported a higher above-ground biomass production and seed rain of the invasive annual grass *Bromus madritensis* ssp. *rubens* compared to native

annuals in response to CO₂ enrichment in the Mojave Desert. They concluded that this shift in species composition might accelerate the fire cycle, reduce biodiversity and alter ecosystem function in North American deserts. In another experiment with microcosms exposed to elevated CO₂ in OTCs, Dukes (2002) observed substantial CO₂ stimulation of biomass growth in the invasive annual forb *Centaurea solstitialis* growing in monocultures, and similar but non-significant stimulation when *Centaurea* grew in an artificially assembled community of Californian serpentine grassland species. The greater CO₂ responsiveness in *Centaurea* than in native species indicates that the effects of rising atmospheric CO₂ may be involved in the success of this problematic species invading grassland ecosystems of western North and South America (Dukes 2002). Comparisons with native species and their responses to the same environmental change are important when assessing if a non-indigenous species benefits more from the change than do native species of similar life histories or ecological niches. The native *Ilex* has the same functional traits as *Prunus*, has a similar life history and occurs in the same habitat. However, *Ilex* did not grow more under elevated CO₂ concentrations, contrasting with *Prunus*. This indicates a selective growth stimulation of a non-indigenous plant species by increasing atmospheric CO₂ compared to a native species occupying the same ecological niche. Consequently, elevated CO₂ might enhance the long-term recruitment success of the non-indigenous *Prunus*, potentially increasing its relative dominance compared to the native *Ilex*.

Other native species of contrasting functional types, however, showed a similar or even a stronger response to elevated CO₂ compared to *Prunus*. The CO₂-induced growth stimulation in the liana *Hedera* was particularly large, with 100% more biomass and 137% longer stems at 660 µmol CO₂ mol⁻¹ compared to ambient CO₂. Direct competition between *Hedera* and *Prunus* in the forest understorey is supposedly very limited. Improved establishment and faster growth of *Hedera* seedlings, however, increases the probability of tree host contact, resulting in more *Hedera* individuals climbing on trees. This may have important implications for forest community structure and ecosystem processes, because lianas influence forest regeneration and canopy composition by their impact on tree growth and mortality (Putz 1984; Schnitzer & Bongers 2002). The CO₂ response of *Hedera* as the most important and common liana species of European oceanic temperate forests agrees with an earlier study of tropical lianas exposed to elevated CO₂ in growth chambers (Granados & Körner 2002). They concluded that enhanced vigour of lianas at elevated CO₂ could accelerate tropical forest dynamics, leading to greater abundance of early successional tree species and to reduced carbon sequestration in the long term.

Biomass production of the two deciduous tree species increased less at elevated CO₂ than in *Prunus* and *Hedera*. However, we observed no common CO₂ responsiveness within the functional groups of evergreen broad-leaved species and deciduous tree species. It might be argued that the number of species was not sufficiently large to generalize about functional group responses to elevated CO₂. In accordance with our study, Hättenschwiler & Körner (2000) previously found highly different growth responses to elevated CO₂ among three deciduous tree species (*F. sylvatica*, *Acer pseudoplatanus*, *Q. robur*) and three conifer species (*Taxus baccata*, *Abies alba*, *Pinus sylvestris*). Likewise, several deciduous tree species from the north-eastern USA grown under controlled laboratory conditions responded distinctly to elevated CO₂ (Bazzaz, Coleman & Morse 1990; Bazzaz & Miao 1993). Taken together, these findings provide little evidence for a common CO₂ response within functional groups of co-occurring tree species. Moreover, species' ranking according to their CO₂ responsiveness at low light (average 1.3% of full sun) was reversed at higher light availability (average 3.4% of full sun) (Hättenschwiler & Körner 2000; Hättenschwiler 2001). The CO₂ response of the same species changes with a relatively subtle shift in understorey light availability. This does not support predictable species-specific CO₂ responses based on relative shade tolerance of co-occurring tree species, as suggested elsewhere (Kubiske & Pregitzer 1996; Kerstiens 1998). Unfortunately, the light gradient in our study was too narrow to detect distinct growth responses to elevated CO₂ with increasing light availability. The significant light × CO₂ interactions in RMF and in the morphological traits LAR and SLA,

however, hint at the possibility of such light-dependent growth responses to elevated CO₂. While the range of microsite-specific light availability between 1.2 and 3.2% of full sun covered in this study is representative for understorey conditions of most old-growth, closed-canopy forests, the species-specific CO₂ responses reported here may differ in more open forests (Hättenschwiler & Körner 2000).

In conclusion, we have demonstrated that elevated atmospheric CO₂ concentrations stimulate seedling growth of the non-indigenous *Prunus* in the natural understorey of a native forest. Moreover, *Prunus* is more responsive to CO₂ than is *Ilex*, the potential native evergreen competitor occupying the same niche; *Prunus* may thus increase in dominance in the future. Facilitation of the establishment of *Prunus* by elevated CO₂ is an example of how an element of global change may interact with the success of an invasive species, leading to shifts in community composition. The reported increasing vigour of *Hedera* in response to elevated CO₂ may have even greater consequences for community composition and ecosystem structure by changing forest dynamics.

Acknowledgements

We thank S. Pelaez-Riedl for help with seedling harvest, and L. Zimmermann for the development and maintenance of technical field installations and collection of microclimatic and CO₂ data.

References

- Bazzaz, F.A. & Miao, S.L. (1993) Successional status, seed size, and responses of tree seedlings to CO₂, light, and nutrients. *Ecology* **74**, 104–112.
- Bazzaz, F.A., Coleman, J.S. & Morse, S.R. (1990) Growth responses of seven major co-occurring tree species of the northeastern United States to elevated CO₂. *Canadian Journal of Forest Research* **20**, 1479–1484.
- Callaway, R.M. & Aschehoug, E.T. (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* **290**, 521–523.
- di Castri, F. (1989) History of biological invasions with emphasis on the Old World. *Biological Invasions: A Global Perspective* (eds J. Drake, F. di Castri, R. Groves *et al.*), pp. 1–30. Wiley, New York.
- Clark, D.A. & Clark, D.B. (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs* **62**, 315–344.
- D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics* **23**, 63–87.
- Dukes, J.S. (2002) Comparison of the effect of elevated CO₂ on an invasive species (*Centaurea solstitialis*) in monoculture and community settings. *Plant Ecology* **160**, 225–234.
- Dukes, J.S. & Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* **14**, 135–139.
- Granados, J. & Körner, C. (2002) In deep shade, elevated CO₂ increases the vigor of tropical climbing plants. *Global Change Biology* **8**, 1109–1117.
- Hättenschwiler, S. (2001) Tree seedling growth in natural

- deep shade: functional traits related to interspecific variation in response to elevated CO₂. *Oecologia* **129**, 31–42.
- Hättenschwiler, S. & Körner, C. (2000) Tree seedling responses to *in situ* CO₂-enrichment differ among species and depend on understorey light availability. *Global Change Biology* **6**, 215–228.
- Hueneke, L.F. (1997) Outlook for plant invasions: interactions with other agents of global change. *Assessment and Management of Plant Invasions* (eds J.O. Luken & J.W. Thieret), pp. 95–103. Springer Verlag, New York/Heidelberg/Berlin.
- Kerstiens, G. (1998) Shade-tolerance as a predictor of responses to elevated CO₂ in trees. *Physiologia Plantarum* **102**, 472–480.
- Klötzli, F., Walther, G.-R., Carraro, G. & Grundmann, A. (1996) Anlaufender Biomwandel in Insubrien. *Verhandlungen der Gesellschaft für Ökologie* **26**, 537–550.
- Kobe, R.K., Pacala, S.W., Silander, J.A. & Canham, C.D. (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* **5**, 517–532.
- Körner, C. (2000) Biosphere responses to CO₂ enrichment. *Ecological Applications* **10**, 1590–1619.
- Körner, C. & Bazzaz, F.A. (1996) *Carbon Dioxide, Populations, and Communities*. Academic Press, San Diego, CA.
- Körner, C., Diemer, M., Schächli, B. & Zimmermann, L. (1996) Response of alpine vegetation to elevated CO₂. *Terrestrial Ecosystem Response to Elevated CO₂*, *Physiological Ecology Series* (eds G.W. Koch & H.A. Mooney), pp. 177–196. Academic Press, San Diego, CA.
- Kubiske, M.E. & Pregitzer, K.S. (1996) Effects of elevated CO₂ and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology* **16**, 351–358.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**, 689–710.
- Naumburg, E. & Ellsworth, D.S. (2000) Photosynthetic sunfleck utilization potential of understory saplings growing under elevated CO₂ in FACE. *Oecologia* **122**, 163–174.
- Osborne, C.P., Drake, B.G., LaRoche, J. & Long, S.P. (1997) Does long-term elevation of CO₂ concentration increase photosynthesis in forest floor vegetation? *Plant Physiology* **114**, 337–344.
- Putz, F.E. (1984) The natural history of lianas on Barro Colorado Island, Panama. *Ecology* **65**, 1713–1724.
- Schmitz, D.C., Simberloff, D., Hofstetter, R.H., Haller, W. & Sutton, D. (1997) The ecological impact of nonindigenous plants. *Strangers in Paradise* (eds D. Simberloff, D.C. Schmitz & T.C. Brown), pp. 39–61. Island Press, Washington, DC.
- Schnitzer, S.A. & Bongers, F. (2002) The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* **17**, 223–230.
- Smith, S.D., Huxman, T.E., Zitzer, S.F. *et al.* (2000) Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature* **408**, 79–82.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*, 2nd edn. W.H. Freeman, New York.
- Vitousek, P.M. & Walker, L.R. (1989) Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* **59**, 247–265.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L. & Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist* **84**, 468–478.
- Walther, G.-R. (1999) Distribution and limits of evergreen broad-leaved (laurophyllous) species in Switzerland. *Botanica Helvetica* **109**, 153–167.
- Walther, G.-R. & Grundmann, A. (2001) Trends of vegetation change in colline and submontane climax forests in Switzerland. *Bulletin of the Geobotanical Institute ETH* **67**, 3–12.
- Würth, M.K.R., Winter, K. & Körner, C. (1998) *In situ* responses to elevated CO₂ in tropical forest understorey plants. *Functional Ecology* **12**, 886–895.

Received 3 April 2003; revised 3 July 2003; accepted 7 July 2003