In deep shade, elevated CO_2 increases the vigor of tropical climbing plants

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Abstract

Climbing plants have profound influences on tropical forest dynamics and may take particular advantage from atmospheric CO_2 enrichment, thus potentially enhancing tree turnover. Here we test the effect of a four-step CO_2-enrichment on growth of three typical Yucatan (Mexico) climbers, across two low photon flux densities, representing typical understory situations. In pairs of two, species of *Gonolobus* (Asclepiadaceae), *Ceratophytum* (Bignoniaceae) and *Thinouia* (Sapindaceae) were grown on Yucatan forest soil in growth cabinets, which simulated the diurnal climate variation. Biomass increased non-linearly in response to CO_2 enrichment from 280 (preindustrial) to 420 ppm and 560 ppm, but then (700 ppm) leveled off. The relative effect of CO_2-enrichment between the two lower (280–420 ppm) CO_2 concentrations was 63% at low light (LL = 42 μmol m^{-2} s^{-1}), compared to 37% at high light (HL = 87 μmol m^{-2} s^{-1}). This overall response of species pairs was the combined effect of linear and non-linear responses of the individual species across CO_2 treatments. Plant biomass was 61% larger in HL compared to LL. The species-specific response depended on the neighbor, a species grew with h, irrespective of plant size. Stem length increased, but not consistently across species and light conditions. Specific stem length (SSL, length per dry mass) declined non-linearly in all three species as CO_2 concentration increased (more pronounced at LL than at HL). SLA (leaf area per unit leaf dry mass) became lower as CO_2 concentration increased (more pronounced in HL). Enhanced vigor of climbers under elevated CO_2 as documented here may accelerate tropical forest dynamics and lead to greater abundance of early succesional tree species. This could reduce forest carbon stocking in the long run.

Keywords: biomass, competition, forest dynamics, lianas, Mexico, non-linear growth responses, SLA, vines

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Introduction

According to large-scale surveys, tropical forest turnover seems to have increased worldwide (Phillips & Gentry, 1994). Although this view is not shared by all experts (e.g. Condit *et al.*, 1996; Condit, 1997), it was not disputed that there is a possibility that accelerated tree turnover could be mediated by increased vigor of climbing plants, which in itself could result from atmospheric CO_2 enrichment. Climbers are well adjusted to

explore low light environments (Putz & Holbrook, 1991) and invest a comparatively high fraction of their biomass in leaves (Putz, 1984; Castellanos, 1991; Condon *et al.*, 1992). They contribute to host tree mortality (Putz, 1984; Stevens, 1987), can slow tree growth (Perez-Salicrup & Barker, 2000) and cause distinctive injury to stems and branches of young trees (Lutz, 1943). Phillips & Gentry (1994) reported that in five out of six forests studied in palaeotropical and neotropical regions, liana and strangler density had increased since 1983. Enhanced turnover of trees would be in favor of early successional tree species, which commonly store less carbon per unit land area than late successional species (Philips, 1997).

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Forest carbon stocking depends on the mean residence time of carbon in biomass and commonly declines as tree turnover accelerates (Körner, 2000). Thus, driven by CO_2-enhanced liana growth, tropical forests could become a net source rather than a sink for carbon over longer periods.

Seedlings of climbers, like other understory plants, are growing in a very light limited environment. For theoretical reasons, deep shade should not preclude elevated CO_2 from stimulating photosynthesis. In fact, due to a reduction of the light compensation point, the relative effect should become even stronger as one approaches severe light limitations (Long & Drake, 1991). Experimental evidence obtained in controlled environments supports this prediction (e.g. Bazzaz & Miao, 1993; Winter & Virgo, 1998). Two recent *in situ* studies, one in a humid tropical forest (Würth *et al.*, 1998) and the other one in a deciduous temperate forest (Hättenschwiler & Körner, 2000), demonstrated a strong stimulation of seedlings by CO_2 enhancement in microhabitats with photon flux densities of only ca. 1% of that outside the forest. These observations are in line with the general observation that shade plants are very sensitive to CO_2-enrichment (Kerstiens, 1998).

A recurring question is, whether plants growing in the understory of a dense forest experience natural CO_2-enrichment (from respiratory sources), thus causing any additional CO_2 enrichment to become less significant. This possibility has been explored in at least 15 studies, dating back to the beginning of the century, and except for calm nights and the litter surface, this idea has been falsified (see Würth *et al.*, 1998; Hättenschwiler & Körner, 2000). During the day, CO_2 concentrations in closed stands may even become depleted.

Given the significance of climbers for forest dynamics and that approximately 40% of the global forest biomass is bound in tropical forests (Brown & Lugo, 1982), experimental evidence for the CO_2-sensitivity of tropical climbers is highly needed. Here, we present an analysis of growth responses to CO_2-enrichment of three species of tropical climbing plants on natural substrate with a specific aim at testing the interaction between understory light availability in a four step CO_2 gradient, ranging from preindustrial (280 ppm) to future (700 ppm) CO_2 concentration. Our hypotheses are: (1) The relative stimulation of growth by elevated CO_2 is larger when light is severely limiting, (2) CO_2-effects are non-linear, with larger responses at low as compared to higher ranges of CO_2 concentration, (3) fast growing species are more responsive to CO_2-enrichment than slow growing species, and (4) neighbor species influence the CO_2 response of a target species.

Materials and methods

Plants and soil

Seeds of three climbing plant species were collected in a lowland tropical forest of the Yucatan Peninsula, Mexico in April 1998 (3 km west of the village Ejido Las Margaritas, Quintana Roo). Fruits were collected in the field directly from plants. Ten fruit samples (approximately 1000 seeds per sample/species) were taken from 10 different individuals. The species *Gonolobus* aff. *cteniophorus* (Blake) R.E. Woodson (Asclepiadaceae), *Ceratophytum tetragonolobum* (Jacq.) Sprague & Sandwith (Bignoniaceae) and *Thinouia tomocarpa* Standley (Sapindaceae) belong to the three most important families of the neotropical lowland forest (Gentry, 1991) and are frequently found growing in close proximity. They represent different morphotypes and differ in seed mass (mean $\pm$ SE; *Gonolobus* 130 ± 2 mg, *Ceratophytum* 84 ± 3 mg and *Thinouia* 41 ± 6 mg, $n = 40$ seeds/species, $P < 0.001$; ANOVA type I for species difference). *Gonolobus* is a twining, strongly branching, thin stemmed and soft leaved climber, which starts to wind very early during its growth. On the contrary, *Ceratophytum* does not branch during early growth and has a tendril system to climb. *Thinouia* is the typical example of a strong woody liana, which is self-supporting until a height of approximately 80 cm. For convenience, we address these species by genus with *Gonolobus,* the most and *Thinouia* the least vigorous species.

CO_2 responses of plants depend on nutrient availability and soil conditions in general (Körner, 2000; Oren *et al.*, 2001). To achieve as natural as possible growth conditions, we used the original Yucatan soil in our experiment. A total of 1.4 tons of soil was collected horizonwise (to a depth of 25 cm, the black fraction, and deeper, the red fraction) in the same place where the seeds were sampled. The 2 mm fraction of four mixed sub samples (red + black mixed) revealed the following characteristics: pH (in CaCl) 7.1; organic carbon $3.8 \pm 0.1\%$ (mean $\pm$ SE); in mg kg^{-1}: P_2O_5 (in citric acid solution) 10 ± 0.4; Ca 6700 ± 150, K 1215 ± 13, Mg 765 ± 9, Na 106 ± 5, Al 12 ± 2, Fe 6.1 ± 0.3, and Mn 2.7 ± 0.4 (all in NH$_4$Cl extracts). The soil was filled in bags of diffusive fabric in natural moisture (soil was sampled during the dry season when water content was very low), and was shipped to Basel, Switzerland, where it was filled layer by layer, into experimental containers, without any further treatment and within 6 weeks of collection in the field. This should ensure soil conditions with a soil microflora and mineral nutrient status as close to natural as possible (no fertilizer was added).

Growth conditions

Plants were grown in rectangular 9-l containers (27 × 16.5 × 22 cm) filled with 15 kg of soil (9 kg of deeper red soil and 6 kg of black topsoil) in four phytotron units. Each of the four chambers was divided in two sections; one called low light (LL) and the other one high light (HL). We used a white fabric to lower the light intensity in the LL half of the chamber. Photon flux density (PFD) was set at ca. 42 μmol m^{-2} s^{-1} in the LL section, and ca. 87 μmol m^{-2} s^{-1} in the HL section. Photoperiod was 12 h. Temperature was controlled in small steps to simulate a diurnal course with night temperatures of 22 °C, and midday temperatures reaching 32 °C. The relative humidity during the dark period was 95–99%, and dropped to 60% at midday. Plants were watered once a week, which was sufficient to keep the soil moist under the given growth conditions. Support for climbing was provided by four 1.7 m bamboo sticks per container.

The absence of any root crowding and the generally very small root systems, which did not explore the whole soil volume by the time of harvest (possibly reflecting the low light and high moisture regime) suggest that the experiment was terminated long before any pot binding could become effective.

Experimental design and statistical analysis

A completely balanced randomized factorial design was used. Factors manipulated were (1) light with two levels (LL and HL), (2) CO$_2$ with four levels (280, 420, 560 and 700 ppm CO$_2$) using a constant increment of 140 ppm CO$_2$ concentration between steps, and (3) neighbor identity. The three different species compositions were: *Gonolobus + Ceratophytum*, *Gonolobus + Thinouia* and *Ceratophytum + Thinouia*. Each treatment combination was replicated four times, hence a total of 96 containers were used. Container positions were randomized within each chamber and light treatment twice a week. Randomization between the chambers was made four times during the total 7-months experiment duration. Data were analyzed with analysis of variance (ANOVA type III) including the treatment factors CO$_2$, light and neighbor identity (Table 1). To test for the linearity of responses across all four CO$_2$ concentrations, we split the factor CO$_2$ into a test for linearity (CO$_2$ lin.) and a test for the deviation from linearity (CO$_2$ dev.lin. ;

Table 1 Analysis of variance of CO$_2$ × light × species and/or neighbor identity effects

Source	DF	Total biomass	Gonolobus				Ceratophytum				Thinouia			
			B	SSL	LA	SLA	B	SSL	LA	SLA	B	SSL	LA	SLA
CO$_2$	3													
CO$_2$ (lin.)	1	***	**	n.s.	**	***	***	***	***	**	***	***	*	*
CO$_2$ (dev. lin.)	2	***	***	***	***	***	n.s.	***	n.s.	**	n.s.	**	***	***
Light	1	***	***	***	**	***	***	***	***	n.s.	***	***	***	***
Neighbor identity (NI)	2	***	***	**	**	***	***	n.s.	***	n.s.	*	n.s.	***	*
CO$_2$ × light	3													
CO$_2$ (lin.) × light	1	**	n.s.	n.s.	**	*	***	***	n.s.	n.s.	***	*	n.s.	*
CO$_2$ (dev. lin.) × light	2	n.s.	n.s.	n.s.	*	n.s.	*	n.s.	n.s.	**	***	***	n.s.	n.s.
CO$_2$ × NI	6													
CO$_2$ (lin.) × NI	1	**	*	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
CO$_2$ (dev. lin.) × NI	5	***	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Light × NI	2	n.s.	**	n.s.	n.s.	*	***	n.s.	***	n.s.	n.s.	n.s.	*	n.s.
CO$_2$ × light × NI	6													
CO$_2$ (lin.) × light × NI	1	***	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
CO$_2$ (dev. lin.) × light × NI	5	***	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	**
Residual	12													
Total	11													

***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; n.s. = not significant. Note: The CO$_2$-effect was additionally split into a test for a linear response (lin.) and deviation from linearity (dev. lin.). Only when both, the linear model and the model which accounts for deviation from linearity show a non-significant response, there is no effect. B, total plant mass; SSL, specific stem length; LA, area of individual leaf; SLA, specific leaf area.

Neter & Wasserman, 1974). Statistical analysis was conducted using JMP 3.2.2.

Experimental procedure and laboratory analysis

Seeds were randomly selected from the mixed pool of 10 fruits per 10 individuals per species (i.e. from a total of $\approx 10\,000$ seeds, collected in the field). Seeds were germinated in the original soil in a common greenhouse and seedlings were randomly assigned to each treatment within a week of germination. Given the space in the phytotrons and the fact that none of these species will ever grow in isolation in nature, we decided to study individuals only which face interaction with others. Species were paired in such a way that any possible interspecific grouping was testable. We planted two species and two individuals per species (hence four individuals altogether) per container, yielding a total of 128 test plants per species (384 plants all together). The 212 days experiment ended when *Gonolobus* become so large that the separation and randomization of containers became too difficult. At harvest we measured, the total stem length, total number and area of leaves per plant. Specific stem length (SSL) was calculated by dividing the total accumulative stem length per individual by total stem mass. Specific leaf area (SLA) was calculated dividing the total leaf area of an individual by total leaf mass. Given the low rooting density, individuals could easily be separated with almost no root losses. Roots were washed free from substrate on a sieve. Stems, leaves and roots were separated and dried at 80 °C for >48 h and weighed.

Results

Overall growth response

Total plant biomass per container across all species combinations and light regimes increased strongly with CO_2-concentration, but the response leveled off at 560 ppm (Fig. 1a, Table 1). The stimulation of biomass between 280 and 420 ppm was +48%, but only +23% from 420 to 560 ppm. Although biomass per container on average was 61% larger in HL compared to LL (Fig. 1b), the relative effect of CO_2-enrichment between the two lower CO_2 concentrations (280–420 ppm) was nearly twice as large in LL than in HL (+63% vs. +37%). The responsiveness to CO_2-enrichment with increasing CO_2 concentration declined far more rapidly at LL, with the 560–700 ppm effect even turning negative at LL.

The three species mixtures tested, responded differently to CO_2-enrichment, depending on whether *Gonolobus* was present or not (Fig. 1c). Mixtures with *Gonolobus* were stimulated up to 560 ppm and then
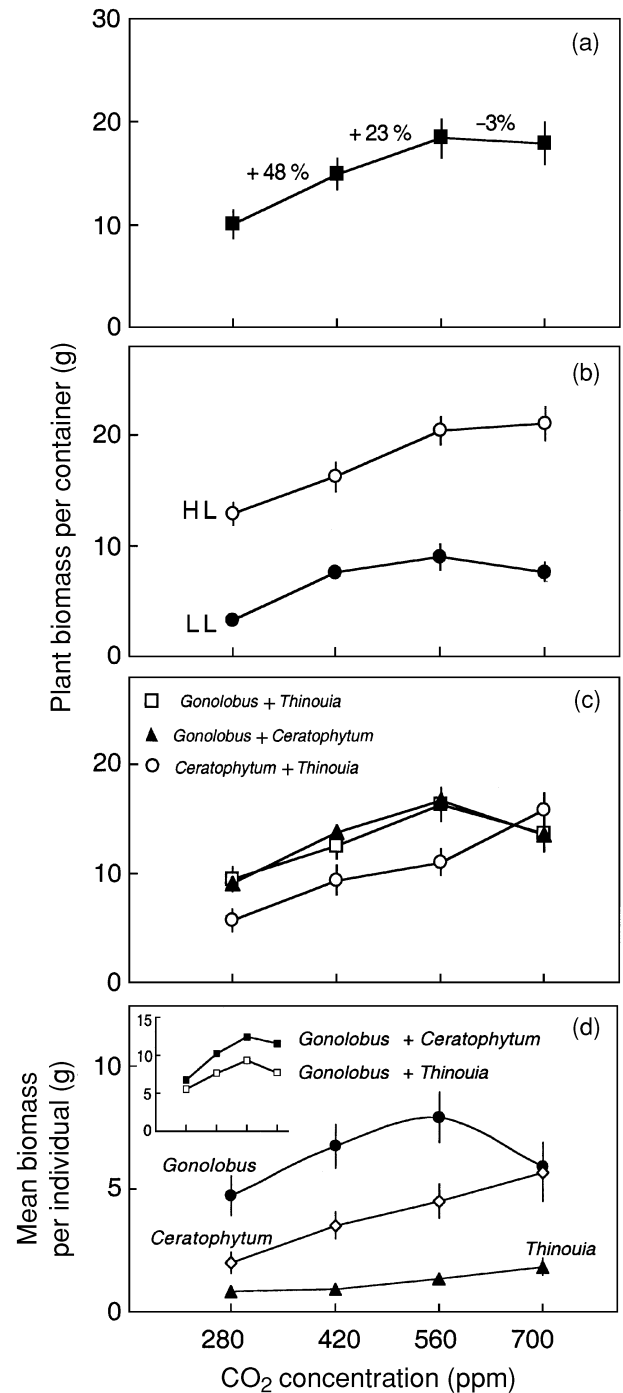
Fig. 1 Plant biomass responses to CO_2-enrichment (mean ± SE). (a) Plant biomass per container across all species combinations and light regimes (the sum of four individuals, two per species and container); (b) across species combinations but separated by light regimes; (c) across light regimes but separated by species mixes; (d) overall-means per species (insert: data for *Gonolobus* separated by type of species mix).

leveled off; mixtures without *Gonolobus* continued to respond up to 700 ppm.
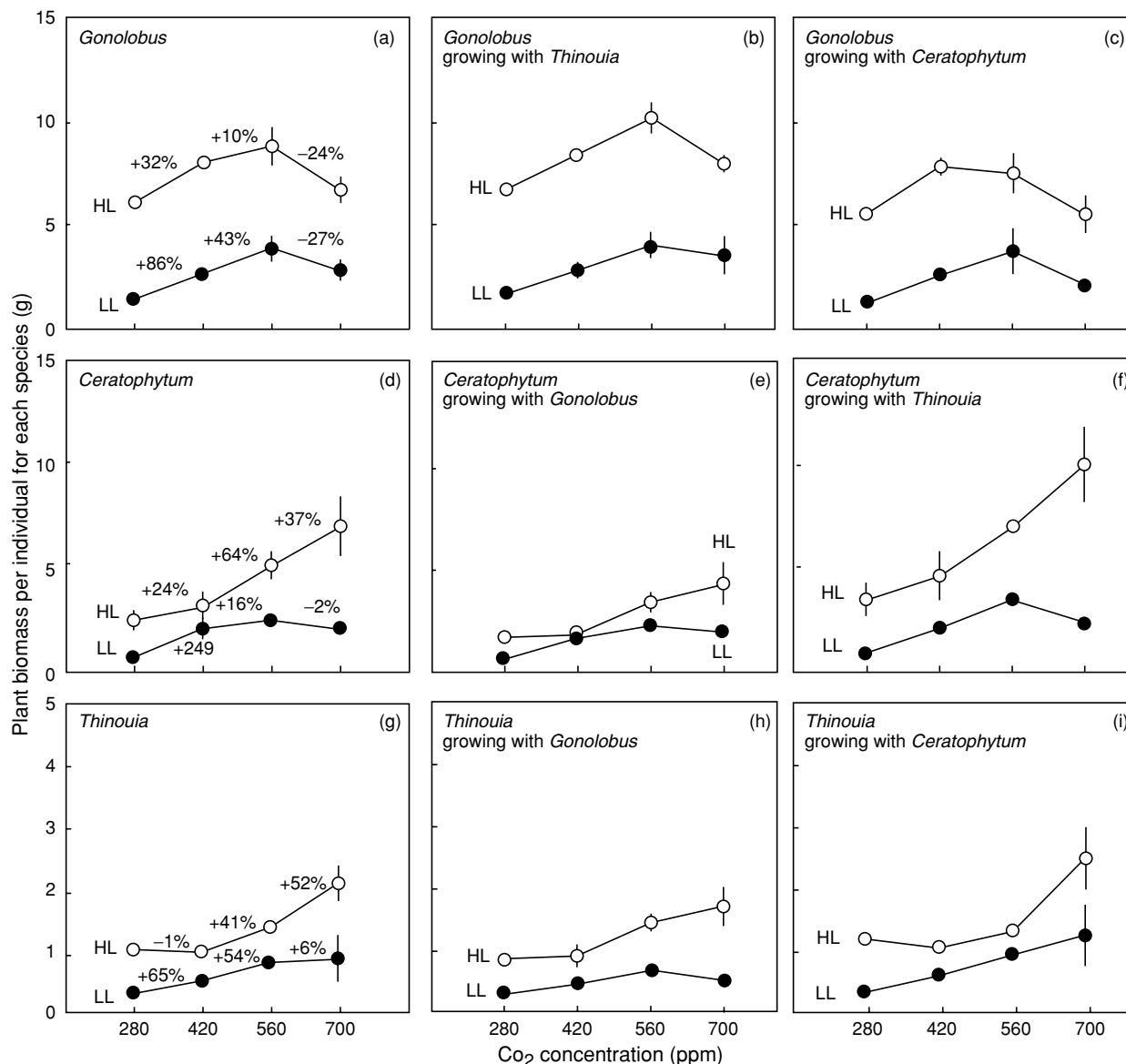
Fig. 2 The interactive effects of CO$_2$ concentration and light on species-specific biomass in each of the three species combination (mean ± SE). HL, high light; LL, low light. (a), (d), (g) data pooled across species combinations. (b), (c), (e), (f), (h), (i), across light regimes. Note the larger scale in Thinouia.

Species-specific growth responses

Mean species-specific biomass per individual across species combinations and light regimes revealed two kinds of responses (Fig. 1d, Table 1). *Gonolobus* showed a non-linear biomass response that reached its maximum at 560 ppm CO$_2$, whereas *Ceratophytum* and *Thinouia* showed no significant deviation from linearity and continued to be stimulated up to 700 ppm CO$_2$. Remarkably, the CO$_2$ saturation seen in *Gonolobus* occurred irrespective of whether *Gonolobus*, the largest species, grew together with *Ceratophytum*, the middle size neighbor or with *Thinouia*, a very small sized neighbor (insert in

Fig. 1d). *Gonolobus* also had developed a very small root system under these humid, low light conditions, far from any root crowding within the relatively large containers. Hence, space limitation or competition with a neighbor cannot explain this non-linear behavior in *Gonolobus*.

The three species differed greatly in vigor. *Gonolobus*, with its thin multistem growth habit during the young stage, was the fastest growing species, but did not benefit more from CO$_2$-enrichment in relative terms, than the other two species (Fig. 2a, b, c, Table 1). Both, the light regime (Fig. 2a) and neighbor identity significantly influenced the biomass response to CO$_2$ in all three species.
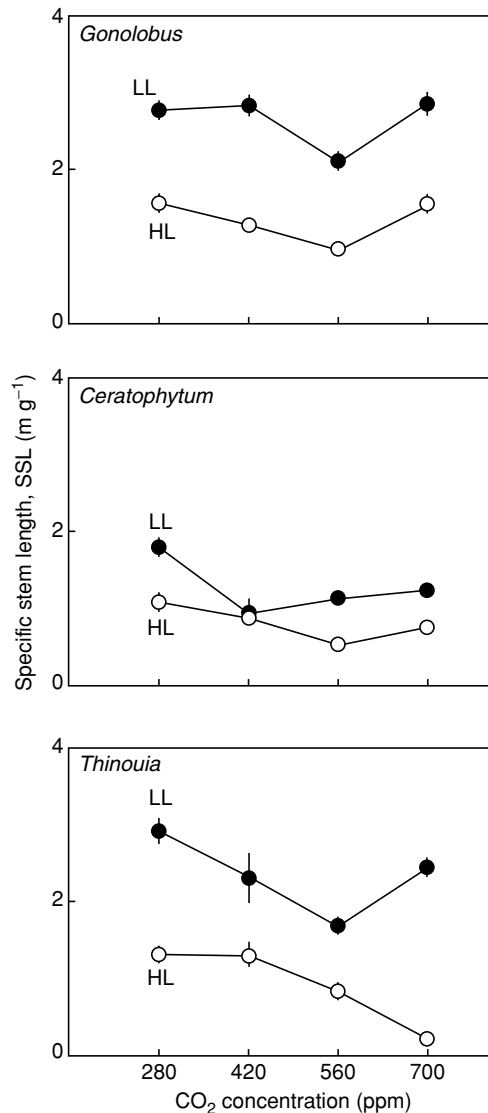
Fig. 3 Specific stem length (SSL) in response to elevated CO_2 (mean $\pm$ SE). HL, high light; LL, low light. Data pooled across species neighbor types.

It is remarkable that the slow growing *Thinouia* is the only of the three species that showed no CO_2-effect between 280 and 420 ppm when exposed to HL, irrespectively of neighbor. Hence, this slow growing species is the most sensitive one in terms of $CO_2 \times$ light interaction, responding to the current atmospheric CO_2 enrichment in deepest shade only.

Biometric responses

Stem length and specific stem length (SSL) Total stem length responded very different in every taxon and light

regime (data not shown). *Gonolobus* showed a significant ($P < 0.001$) increment length between 280 and 420 ppm in LL only. *Ceratophytum* responded with longer shoots only in the interval 560–700 ppm, but at both light regimes ($P < 0.001$). *Thinouia*, in turn, responded with larger shoots only when growing at HL and in the interval 560–700 ppm ($P < 0.001$). Hence, stem length responses were not consistent.

In contrast, elevated CO_2 significantly reduced SSL in all three species (Fig. 3, Table 1), but the response was non-linear, i.e. became smaller or even reversed as CO_2 concentration increased. SSL was twice as large in LL as compared to HL (greater length for equal mass $P < 0.001$). The shape of the CO_2 response remains largely unaffected by light. Except for *Thinouia* in HL (continuous declined of SSL with CO_2), the largest reduction of SSL occurred below 560 ppm with either no or a reversal of the response at 700 ppm The overall response pattern is a U-shaped one in LL, i.e. a reduction of SSL from low to medium CO_2-concentrations and an increase from medium to highest CO_2-concentrations. This trend is moderated at HL (no or a little reversal of the trend at high CO_2-concentration).

Together, these data suggest increasing C-investments per unit stem length as CO_2 increased from preindustrial CO_2 concentration to twice preindustrial (more 'robust' stems), but a return to 'preindustrial' investments as CO_2 becomes further increased up to 700 ppm.

Leaf size

Leaf size changes were inconsistent across species (Fig. 4, Table 1). However, in most treatment combinations, leaf size increased between 280 and 420 ppm. In *Gonolobus*, leaf size decreased at more than 420 ppm, but continued to increase up to 700 ppm in *Ceratophytum* and plateau or declined in *Thinouia* at > 560 ppm.
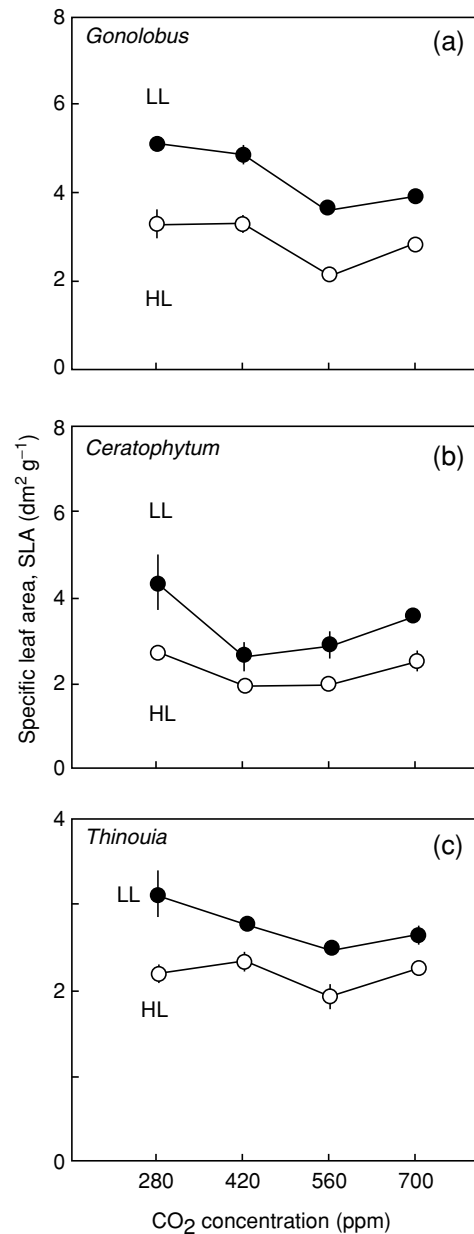
Leaf quality

Specific leaf area (SLA) Responses of SLA appear to contrast those in leaf size. Atmospheric CO_2-enrichment significantly reduced SLA in all three species (with minor exceptions) from 280 to 420/560 ppm, a trend surprisingly reversed between 560 and 700 ppm (Fig. 5 a, b, c, Table 1). Effects vary with neighbor type and seem to be slightly more pronounced at LL than at HL. Irrespective of CO_2-concentration, on average SLA was always larger at LL than at HL (*Gonolobus* + 34%, *Ceratophytum* + 32% and *Thinouia* + 21%). Once more, species specificity is high, but the contrasting trends between low and high CO_2-concentration (U-shaped CO_2-response) emerged in all three species.
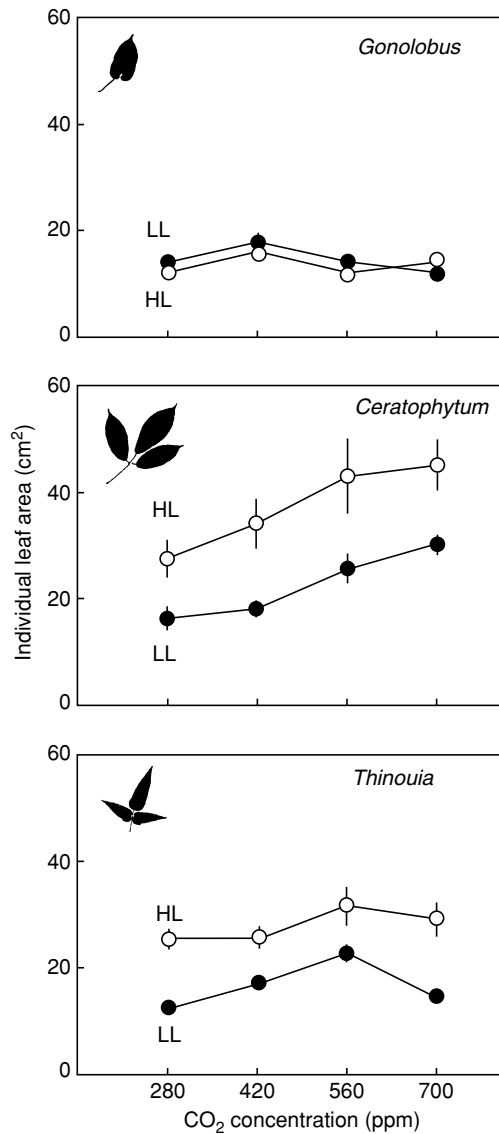
Fig. 4 Individual leaf size responses to elevated CO$_2$ (mean ± SE). HL, high light; LL, low light. Data pooled across species neighbor types.

Fig. 5 Responses of specific leaf area (SLA) to elevated CO$_2$ and light (mean ± SE). HL, high light; LL, low light. (a), (b), (c), data pooled across neighbor types. Note the different scale for *Thinouia*.

Discussion

Our results show that growth responses of three very different tropical climbers to a step-wise increase of CO$_2$ concentration from 280 to 700 ppm are: (1) species-specific, (2) are more pronounced at low light, (3) are linear in two and non-linear in one species, and (4) depend on the neighbor present. Most of the growth parameter tests revealed more pronounced responses in the lowest range of our CO$_2$-gradient (280–420 ppm). From this we conclude that current atmospheric changes should have profound effects on such tropical climbers. Most responses became smaller as CO$_2$ increased; some

became even reversed, when CO$_2$ concentration was increased from 560 to 700 ppm. The most striking result is that – in relative terms – the growth response to CO$_2$ is more pronounced at very low light conditions, which is in line with our first hypothesis. These results are in support of Phillips & Gentry's (1994) idea that tropical climbers might be sensitive to ongoing atmospheric CO$_2$-enrichment. It is plausible to assume that the chances for a climber to reach the top of a forest canopy will indeed increase with elevated CO$_2$, given that extremely low

light becomes less of a constraint (Phillips *et al.* unpublished results).

The distinction between relative and absolute responses to CO_2-enrichment has substantial ecological implications (Körner, 2002). As light becomes more limiting, the relative advantage of CO_2-enrichment increased. In a patchy, deep shade natural setting such stimulation will permit vines to explore microenvironments in which they would not normally achieve a positive C-balance (Hättenschwiler & Körner, 1996). Whether absolute or relative gains become more important in the real world will strongly depend on the competitive situation. The essential questions are: whether and how fast climbers manage to escape the deep shape in the sub-canopy. Once in the sun, CO_2 may become a factor of secondary significance compared to other resources.

Atmospheric CO_2-enrichment and light availability are jointly explaining the growth trends that we found. However, the different species tests responded in different ways, and the overall response per container depended on the species mix. Though growing far more vigorously than the other two species, *Gonolobus* did not exhibit a more pronounced relative stimulation by CO_2-enrichment. Hence, our third hypothesis found no support. The CO_2 responses of the three species are not in line with Poorter's (1993) and Poorter & Van Der Werf's (1998) suggestion that fast-growing species should be more responsive to CO_2-enrichment than slow-growing species. Our data and several cases reported by Thomas *et al.* (1999) do not reveal such a distinction. The basic pattern of the species-specific CO_2 responsiveness did not change when species grew with different neighbors, although the total biomass accumulated per species was neighbor dependent.

Of the two components that warrant success of climbers, namely space exploration (stem length) and shoot rigidity, only the latter was consistently increased by CO_2-enrichment. As indicated by the SSL data, the biomass gain due to elevated CO_2 was largely the result of more massive stems. In some instances, stem length was increased as well. From this we need to conclude that CO_2-enrichment is likely to increase climbers' success and the likelihood of shoot survival. Similarly, Sasek & Strain (1988) concluded that the CO_2 driven stimulation of vigor in *Pueraria lobata*, which they found would cause this weedy, subtropical climber to become more aggressive in the future. Our leaf data can be interpreted in a similar way as the stem data. Leaves became heavier, perhaps thicker and stronger, but neither did total leaf area per unit of stem increase (data not presented here) nor was there a consistent pattern of individual leaf area change.

The species and light specific response to CO_2 preclude generalizations across species and sites, but it seems safe to assume that climbers will become more competitive, and according to the response seen for the 280–420 ppm increment, are likely to take advantage already today. CO_2-effects seem to be more pronounced in deep shade, and thus are likely to improve starting conditions in the understory. Liana seedlings represent about one fifth of all woody seedlings in tropical forest understories (Rollet, 1969; Putz, 1984) and their vigor is in favor of fast growing tree species, once a gap has formed (Schnitzer *et al.*, 2000). Our study thus confirms earlier *in situ* findings of high CO_2 responsiveness of C3-species in deep shade, both in the tropics (e.g. Würth *et al.*, 1998) and the temperate zone (e.g. Hättenschwiler & Körner, 2000). It substantiates earlier suggestions of enhanced tropical forest dynamics in response to atmospheric CO_2-enrichment. Provided no counteracting responses to CO_2 enrichment will occur (e.g. trees becoming more robust against liana impact), enhanced tropical forest turnover seems like a realistic possibility, which would reduce the probability of enhanced carbon sequestration by tropical forest.

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