9

What can we learn from microcosms?

Compiled by Manfred Forstreuter

9.1 Introduction

The responses of ecosystems to elevated CO_2 have received little attention (Körner and Arnone, 1992). To make realistic predictions of ecosystem responses to a changing environment, field measurements investigating the behaviour of whole stands and ecosystems under natural environmental conditions are necessary. Present predictions of responses to elevated CO_2 are mainly based on results of short-term physiological responses, often based on short-term experiments with single plant organs or individual plants. From these results we cannot definitely conclude how ecosystems will respond to elevated CO_2. More knowledge of variation in physiological changes and interactive processes at stand or community scale is needed.

The microcosm technique (see Chapter 1) comprises investigations with elevated CO_2 on small-scale, juvenile tree stands, designed so that interactions with environmental and biotic variables can be studied. Environmental variables such as temperature, PPFD, nutrients and water, as well as community variables such as intra- and inter-specific competition, both above and below ground, can be included in this experimental approach. Results from leaf measurements can be directly integrated and compared with results from whole-canopy measurements. Models predicting CO_2 and H_2O gas exchanges at canopy and stand scale can also be parameterised and validated.

This chapter will discuss the long-term, direct effects of elevated CO_2 on woody vegetation by using the microcosm technique with model ecosystems of juvenile stands of beech.

9.2 Is canopy structure influenced by elevated CO_2 concentration?

Investigations on young beech stands grown in microcosms in ambient and elevated CO_2 were made in natural environmental conditions over a period of three years. Measurements were made at leaf scale, whole plant scale, canopy scale and stand scale, comparing ecosystem responses at two atmospheric CO_2 concentrations (TUB).

Total leaf area in the beech canopy grown in elevated CO_2 was significantly increased. No significant differences in leaf-area index (LAI) between the CO_2 treatments were seen in the first growing season. In the second season the LAI of the canopies in elevated CO_2 increased by 24% in comparison to the canopies in ambient CO_2. In the third season the stands in elevated CO_2 developed 48% more leaf area than the stands in ambient CO_2 (Figure 9.1). In both treatments the young beech stands formed a closed canopy in the second year with average values of LAI of 5.0 (ambient) and 6.2 (elevated). In the third year, the stands developed nearly the same LAI of 4.4 (ambient) and 6.2 (elevated) as in the previous year, indicating that ceiling LAI in the prevailing environmental conditions was reached.

Growth of the beech stands was significantly enhanced in elevated CO_2 (Overdieck, 1994; Overdieck and Forstreuter, 1995) and was associated with increases in tree height and, therefore, with a deeper canopy. Increased branching in elevated CO_2 also affected LAI in each stratum of the canopy. Figure 9.2 shows vertical profiles of leaf-area density of the canopies in elevated and ambient CO_2 concentration at the end of the third season.

There were no differences in mean leaf size between CO_2 treatments. In elevated CO_2 a larger number of leaves per tree resulted in an increase in leaf area density of up to 34%, especially in the lower layers of the canopy. The specific leaf area (SLA) increased significantly from the top to the bottom layer of the canopy (Figure 9.3). The SLA in a given canopy layer was directly proportional to the accumulated LAI above this layer (Figure 9.4). The SLA of shade leaves shows the influence of high and low PPFD within the canopy on leaf anatomy. At the same PPFD, leaves in elevated CO_2 had smaller SLA than leaves grown in ambient CO_2, i.e. in elevated CO_2 leaves were heavier per unit area than in ambient CO_2.

Structural and spatial changes in the above-ground structure of beech stands, such as branching, leaf anatomy, leaf-area density and total leaf area, influence the profiles of PPFD, VPD and temperature within the canopies, and may, therefore, affect net ecosystem CO_2 fluxes and evapotranspiration rates of these stands (Overdieck and Forstreuter, 1994).

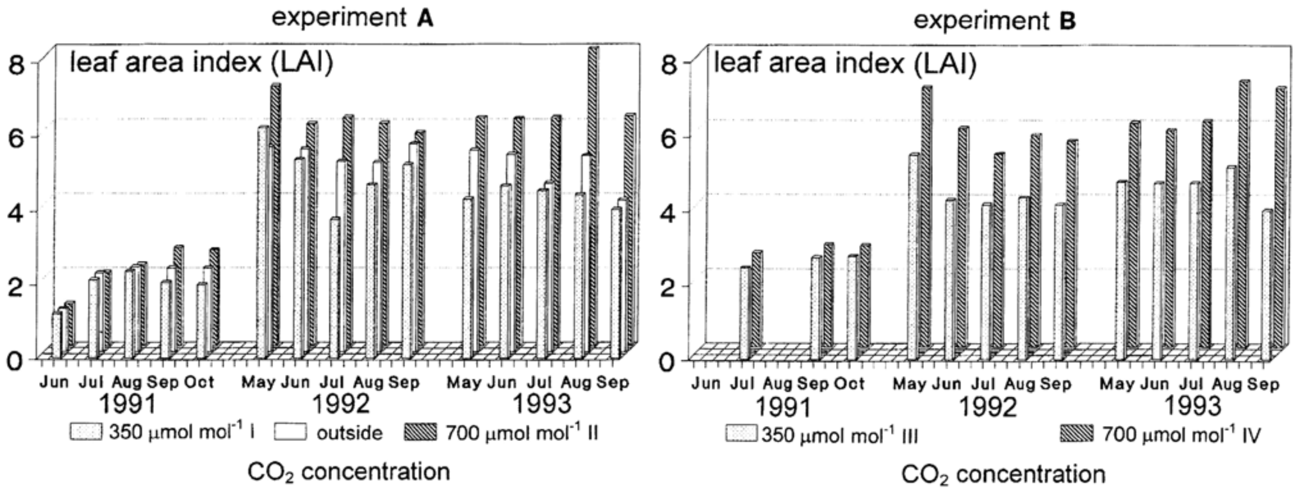

Figure 9.1 Leaf area index (LAI) of four juvenile beech stands in 350 or 700 µmol mol^{-1} CO$_2$ in two pairs of microcosms (parallel experiments A and B) and an outside plot (TUB).

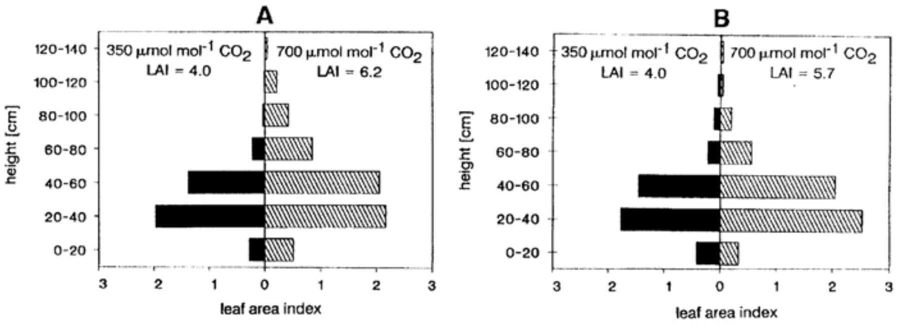

Figure 9.2 Vertical distribution of leaf area in four juvenile beech stands at 700 and 350 µmol mol^{-1} CO$_2$ in two pairs of microcosms (A, B) after three years of exposure (TUB).

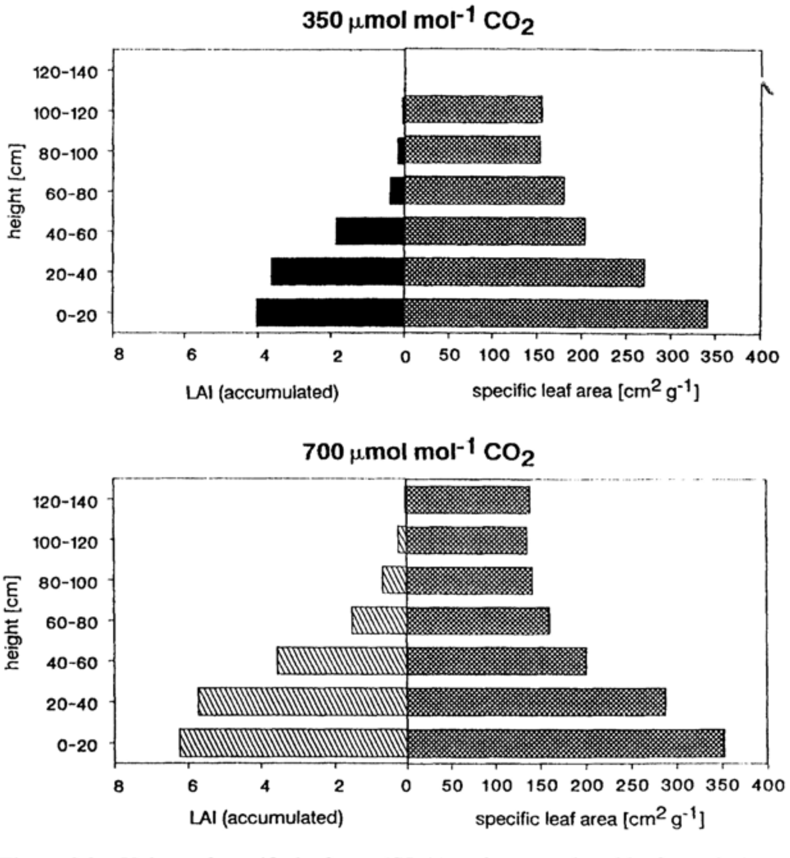

Figure 9.3 Values of specific leaf area (SLA) and accumulated leaf area index (LAI) in juvenile beech stands after three years of exposure to 350 and 700 µmol mol^{-1} CO$_2$ (TUB).

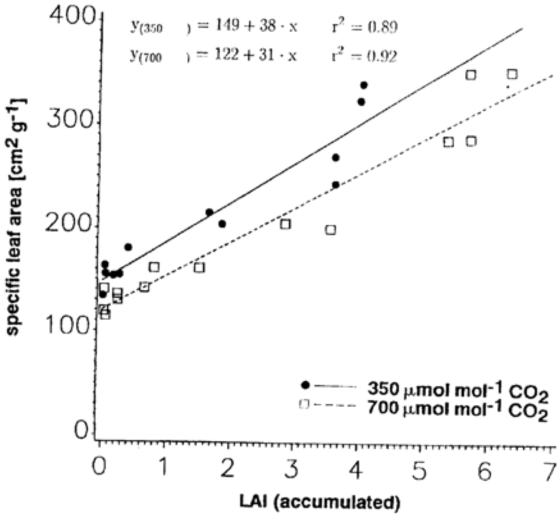

Figure 9.4 Relation between the specific leaf area (SLA) in a particular canopy layer and the leaf-area index (LAI) accumulated above, in four juvenile beech stands exposed to 350 and 700 μmol mol^{-1} CO_2 (TUB).

9.3 Are juvenile or mature beech stands sinks or sources for elevated CO_2?

Measurements of net photosynthesis (A), dark respiration (R_D) and net ecosystem CO_2 exchange were made on beech during long-term exposure to ambient or elevated CO_2 concentration at leaf, branch and stand scale (TUB). The results can be interpreted by means of mathematical models and enable scaling up of CO_2 responses to atmospheric CO_2 from leaf to stand and to larger forest ecosystems.

9.3.1 Leaf scale

Some details regarding leaf-scale responses of photosynthesis appear in Chapters 2 and 3. Single-leaf measurements showed that leaves grown and measured in elevated CO_2 had higher net photosynthetic rates than leaves grown in ambient CO_2. The mean net photosynthetic rate at light saturation (A_{sat}) was enhanced by a factor of 1.56 in elevated CO_2. Mean rates of 3.0 (1991), 4.5 (1992) and 4.9 (1993) μmol mol^{-1} s^{-1} were measured on a leaf-area basis in ambient CO_2 and of 6.5 (1991), 6.2 (1992) and 6.6 (1993) μmol CO_2 mol^{-1} s^{-1} in elevated CO_2 (Figure 9.5). In elevated CO_2 there

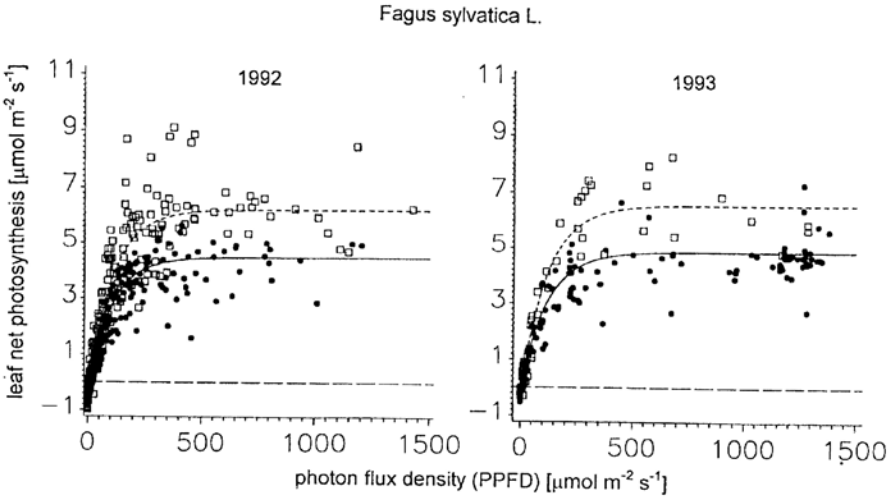

Figure 9.5 The correlation between PPFD and net photosynthetic rate of leaves of beech in various canopy layers (July 1992: LAI = 4.2 (ambient), LAI = 6.1 (elevated); August 1993: LAI = 4.0 (ambient), LAI = 6.2 (elevated)) in stands in ambient or elevated CO_2 (functions in Table 9.1). Open symbols: elevated CO_2; closed symbols: ambient CO_2 (TUB).

was larger variability in net photosynthesis between leaves within the canopy in constant environmental conditions (temperature: 20 °C, VPD: 0.8 kPa) compared with ambient CO_2. Functions of net photosynthesis versus PPFD are shown in Table 9.1 (equations 9.1 to 9.4). The initial slope of the PPFD response curve, i.e. the apparent maximum quantum yield, was higher in elevated than in ambient CO_2. However, A/C_i curves showed no significant differences in carboxylation efficiency between the two CO_2 treatments (Figure 9.6). The rate of net photosynthesis was always higher in elevated than in ambient CO_2: even after long-term exposure to elevated CO_2, no decline in net photosynthesis was evident. However, in elevated CO_2 stomatal conductance decreased significantly.

In an experiment by Wullschleger *et al.* (1992), the net photosynthetic rate on a unit leaf-area basis of saplings of *Liriodendron tulipifera* and *Quercus alba*, exposed for 24 weeks to ambient or elevated CO_2 (ambient + 300 $\mu mol\ mol^{-1}$), increased in the elevated CO_2 treatment by 60% and by 39–51%, respectively. Light-saturated net photosynthesis of the leaves of sweet chestnut saplings grown and measured at 700 $\mu mol\ mol^{-1}$ CO_2 increased from 29% to 57% relative to the ambient, 350 $\mu mol\ mol^{-1}$ treatment during the first half of the growing season (Mousseau, 1993). With time, a decline in photosynthetic rate was observed in elevated CO_2; in the

Table 9.1. *Equations to describe rates of net photosynthesis, dark respiration and gross photosynthesis by leaves and a model of penetration of incident PPFD into the canopy calculated using statistical regression procedures (SAS Institue 1988), based on data from leaf photosynthesis measurements with a mini-cuvette gas exchange system and measurements of PPFD in the canopy made with a quantum sensor*

Model/Year	Equation/Description	Equation No.
Leaf model	P_{Nleaf}: Leaf net photosynthetic rate (μmol $\mathrm{m^{-2}\,s^{-1}}$)	
	I : Photon flux density (PPFD) (μmol $\mathrm{m^{-2}\,s^{-1}}$)	
1992	$P_{\mathrm{Nleaf(350)}} = 4.48\,(1 - \mathrm{e}^{-0.0097(I-8)})$	9.1
	$P_{\mathrm{Nleaf(700)}} = 6.21\,(1 - \mathrm{e}^{-0.0093(I-10)})$	9.2
1993	$P_{\mathrm{Nleaf(350)}} = 4.86\,(1 - \mathrm{e}^{-0.0085(I-4)})$	9.3
	$P_{\mathrm{Nleaf(700)}} = 6.55\,(1 - \mathrm{e}^{-0.0097(I-6)})$	9.4
	R_{DLeaf}: Leaf dark respiration rate (μmol $\mathrm{m^{-2}\,s^{-1}}$)	
	T_{L}: Leaf temperature (°C)	
1992	$R_{\mathrm{DLeaf}} = -0.346 + 0.288\mathrm{e}^{0.046T_{\mathrm{L}}}$	9.5
1993	$R_{\mathrm{DLeaf}} = 0.024\mathrm{e}^{0.115\,T_{\mathrm{L}}}$	9.6
	P_{Gleaf} : Leaf gross photosynthetic rate (μmol $\mathrm{m^{-2}\,s^{-1}}$)	
	I : Photon flux density (PPFD) (μmol $\mathrm{m^{-2}\,s^{-1}}$)	
1992	$P_{\mathrm{Gleaf}} = P_{\mathrm{Nleaf}} + R_{\mathrm{Dleaf}}$	9.7
	$P_{\mathrm{Gleaf}} = 4.88\,(1 - \mathrm{e}^{-0.0096(I-0)})$	9.8
	$P_{\mathrm{Gleaf}} = 6.63\,(1 - \mathrm{e}^{-0.0093(I-3)})$	9.9
Light model	I_{top} : Incident photon flux density (PPFD) (μmol $\mathrm{m^{-2}\,s^{-1}}$)	
	I_{layer} : Photon flux density (PPFD) in a canopy layer (μmol $\mathrm{m^{-2}\,s^{-1}}$)	
	L_{acc} : Leaf area index (LAI) accumulated above a set canopy layer ($\mathrm{m^2\,m^{-2}}$)	
1992	$I_{\mathrm{layer(350)}} = I_{\mathrm{top}}\exp - (0.64L_{\mathrm{acc}})$	9.10
	$I_{\mathrm{layer(700)}} = I_{\mathrm{top}}\exp - (0.64L_{\mathrm{acc}})$	9.11

second half of the season, there were no significant differences in photosynthetic rate between the ambient and elevated CO_2 saplings.

This downregulation of photosynthesis has generally been found to occur in experiments with trees in elevated CO_2 where the trees were grown in pots or where the trees were nutrient-limited. The reduction in photosynthetic capacity in elevated CO_2 is most pronounced when the supply of carbohydrates outstrips the sink capacity and is characteristic of plants grown in small pots, whereas plants grown in the field generally show little or no reduction (see also Arp, 1991). By contrast, no downregulation or

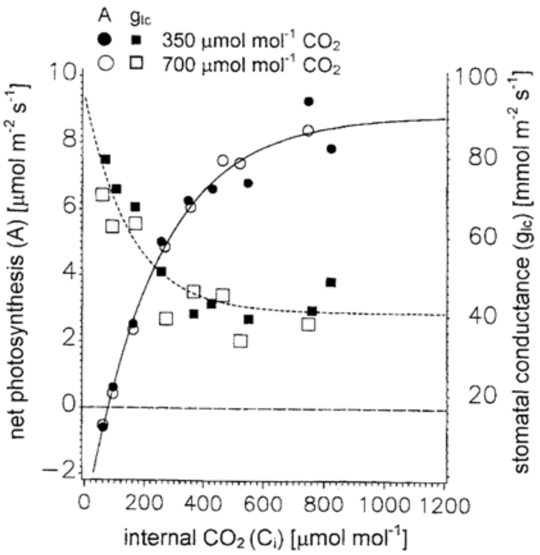

Figure 9.6 Net photosynthetic rate (*A*) and stomatal conductance (*g*) in relation to internal CO_2 concentration (C_i) for beech leaves grown in microcosms in ambient or elevated CO_2 (TUB).

acclimation of photosynthesis in leaves of beech was observed in elevated CO_2 by the end of July, suggesting that beech is likely to continue responding to increasing atmospheric CO_2 concentration.

9.3.2 Branch scale

Measurements of CO_2 exchange of branches of mature beech trees were made in branch bags (UPS) (see Chapter 1). From 1992 to 1994 branches were exposed to ambient or elevated CO_2. Elevated CO_2 had a large effect on net photosynthèsis: in the first year the PPFD-saturated net photosynthetic rate (A_{sat}) of the branches increased by 85% (Dufrêne *et al.*, 1993). The A/C_a curves indicated no downregulation of photosynthesis: the photosynthetic rate of branches exposed to ambient or elevated CO_2 concentration increased by the same amount when CO_2 concentration was increased from 350 to 700 µmol mol^{-1}. These results are similar to the results on beech saplings (Chapter 2). Nearly the same increase in A_{max} of 88% (from 9.22 µmol m^{-2} s^{-1} (ambient) to 17.3 µmol m^{-2} s^{-1} (elevated)) was measured in 1993 (Figure 9.7). In 1994 the branches in ambient CO_2 showed almost the same photosynthetic rate as in the previous years. By contrast, photosynthesis of the branches in elevated CO_2 (A_{sat}) decreased to the rate of the ambient CO_2 branches. Possible mechanisms underlining

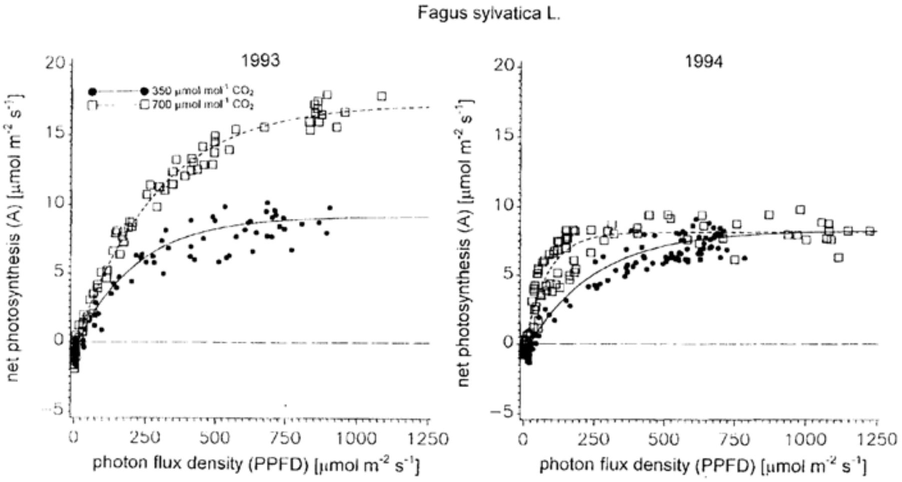

Figure 9.7 The relation between rate of net photosynthesis (*A*) and photon flux density (PPFD) of leaves of beech, measured on mature branches in branch bags (see Chapter 1) at 350 and 700 µmol mol^{-1} CO_2 in June 1993, 1994 (unpublished data of J.-Y.Pontailler 1994) (UPS).

the progressive downward trend in net photosynthetic rate are discussed further in Chapter 2.

9.3.3 Stand scale

The effects of elevated CO_2 on CO_2 and water vapour exchange of juvenile beech stands were studied in long-term experiments over three years. Model ecosystems, consisting of 48 (first year), 36 (second year), and 25 (third year) young saplings (1.5 years old at the start) were grown in 0.4 m^3 blocks of unfertilised homogenised soil (loamy sand; carbon content 2.7% dry mass; C/N 19; bulk density 1100 kg m^{-3}) in microcosms (air volume 1 m^3) climatised according to outside conditions at the two CO_2 concentrations. Soil humiditiy was kept constant at 20% of soil volume. The total CO_2 input–output of the microcosms was measured directly to calculate the net CO_2 ecosystem flux (NEF) on a ground-area basis of the enclosed model ecosystems (see Chapter 1 for further details).

In the first growing season (1991), the young stands were sources of CO_2: respiration over 24 h exceeded daytime photosynthesis in both CO_2 treatments. In elevated CO_2, nighttime respiration losses of the stand exceeded the losses in ambient CO_2 (Figure 9.8A). Both stands had LAI of 2.0. The larger dark respiration loss in elevated CO_2 was compensated by higher photosynthetic rates during daytime with the result that the daily net CO_2

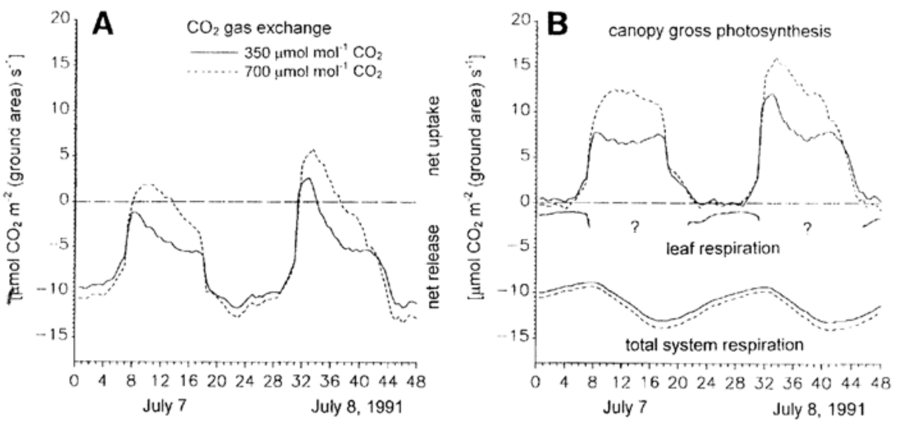

Figure 9.8 The daily course (July 7 to July 8) of components of CO_2 exchange of two beech microcosms (48 juvenile beech saplings including the upper soil) during the first growing season in ambient (350 µmol mol^{-1}) and elevated CO_2 (700 µmol mol^{-1}) (TUB).

release amounted to 0.50 mol CO_2 m^{-2} d^{-1} in elevated CO_2 and 0.59 mol CO_2 m^{-2} d^{-1} in ambient CO_2. In the afternoon there was a depression of CO_2 uptake.

On the basis of NEF measurements during the night a temperature-dependent model of total system respiration was used to calculate the canopy gross photosynthesis of the stands during two days in July, 1991 (Figure 9.8B). Daily gross photosynthesis of the model stands was increased by 44% from 0.72 mol CO_2 m^{-2} d^{-1} in ambient CO_2 to 1.04 mol CO_2 m^{-2} d^{-1} in elevated CO_2.

In the second growing season (1992), a NEF data set for juvenile beech stands in ambient and elevated CO_2 was collected, in addition to microclimate variables, over the whole growing season. Figure 9.9 shows half-hourly average measurements for August and September. Respiration rates of both stands were still large and respiration losses during the night, as well as photosynthetic CO_2 gains during the day, were again larger in elevated than in ambient CO_2. For each month the PPFD-dependent functions of half-hourly NEF were calculated for both CO_2 concentrations (Figure 9.10) using the 'least squares method' (SAS Institute, 1988). In July, maximum NEF was 10 µmol m^{-2} s^{-1} in ambient CO_2 and 19 µmol m^{-2} s^{-1} in elevated CO_2, an increase of 90%. The variability in the data reflects the change in LAI of the stands and the influence of temperature. In September, variability in NEF was less than in July and the calculated PPFD saturation values were 12 µmol m^{-2} s^{-1} in ambient CO_2 and 19 µmol m^{-2} s^{-1} in

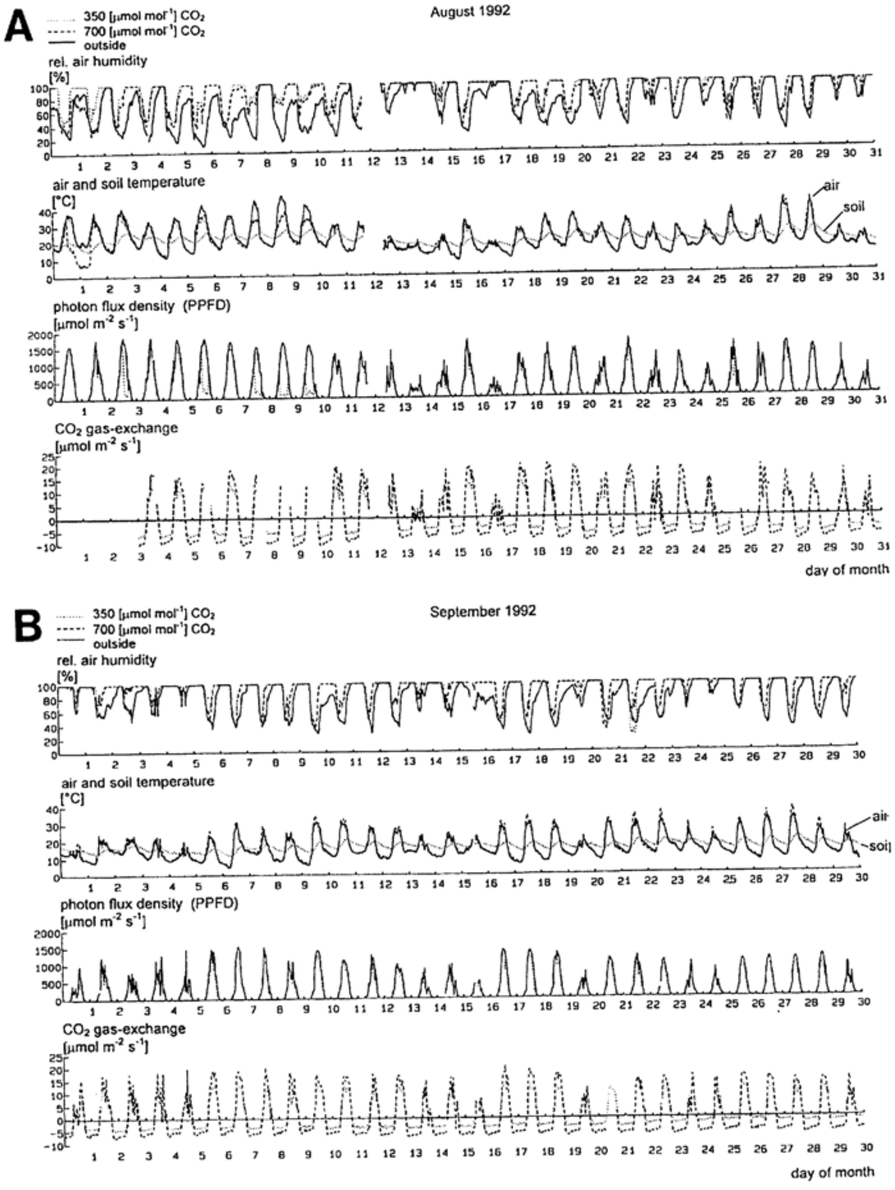

Figure 9.9 Daily courses of relative air humidity, soil (in ambient CO_2 only) and air temperatures, and PPFD, in the microcosms with ambient and elevated CO_2 concentration and outside, together with the net ecosystem fluxes (NEF), based on half-hourly mean values, of young stands of beech saplings ($n = 36$) grown for two years in elevated (dotted line) or ambient CO_2 (solid line) on natural homogenised soil (TUB).

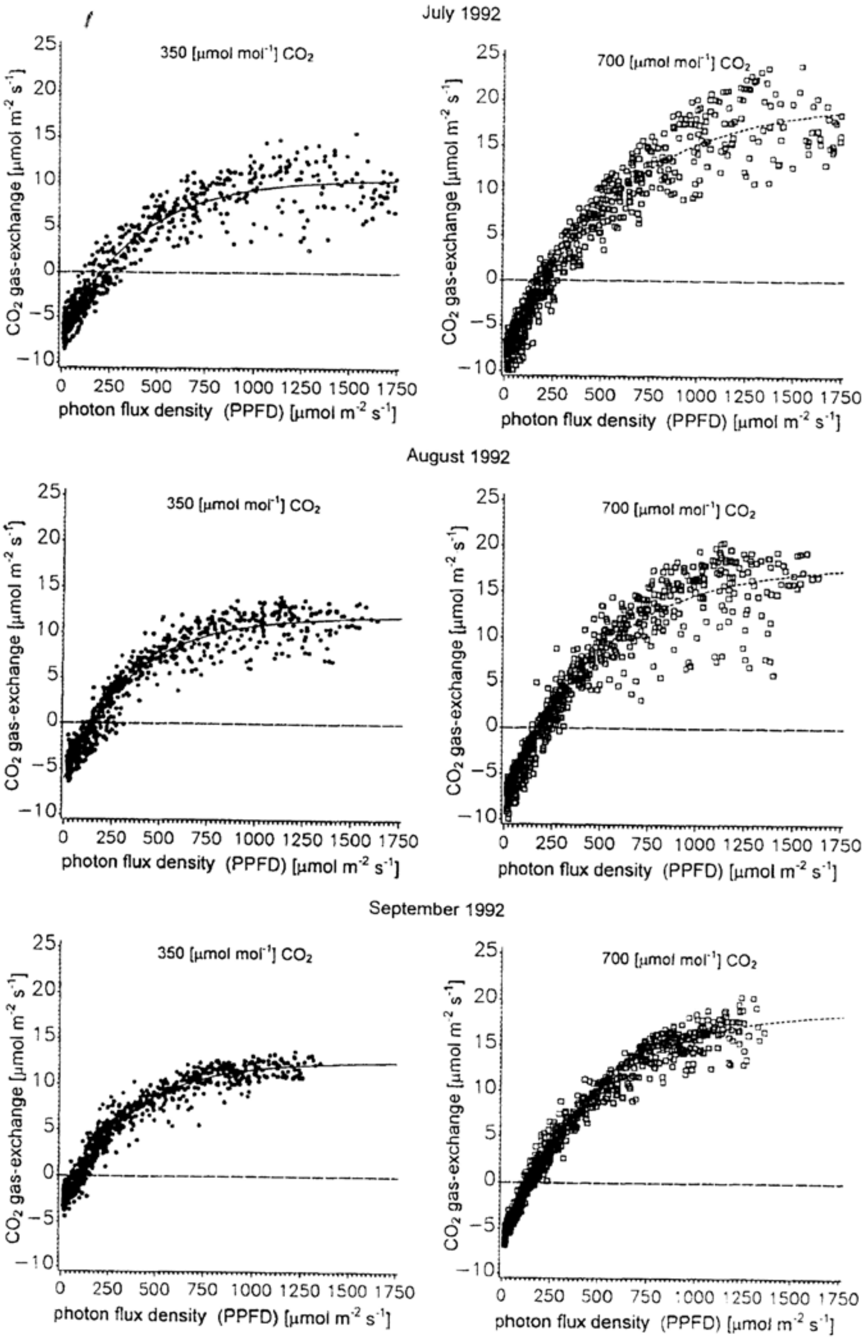

Figure 9.10 Relations between CO_2 gas exchange and PPFD in July, August and September 1992 of juvenile beech stands exposed for two growing seasons to ambient or elevated CO_2 (TUB).

elevated CO_2, a slightly smaller increase. In elevated CO_2 both PPFD saturation of NEF and the PPFD compensation point occurred at higher PPFD values than in ambient CO_2.

At the beginning of the growing season, stands in elevated CO_2 benefited from additional atmospheric CO_2 and both photosynthesis and growth were strongly increased during this stage of development. In elevated CO_2 the young trees built up a closed canopy with denser foliage, as a result of a higher rate of branching and an increase in canopy height compared with the saplings in ambient CO_2. Stem diameter and stem height were significantly increased and stems constituted a large sink for carbon. In this phase of development the young stands were sinks for CO_2. Daily NEF (half-hourly values accumulated over 24 h) was 0.13 mol CO_2 m^{-2} d^{-1} in elevated CO_2 and 0.02 mol CO_2 m^{-2} d^{-1} in ambient CO_2 at an average PPFD of 38.9 mol m^{-2} d^{-1} during July (Figure 9.11). Net CO_2 uptake over the whole day was clearly enhanced in elevated CO_2 compared with ambient CO_2. Figure 9.11 shows higher light-use efficiency of CO_2 uptake by the steeper slope of the linear regression in elevated CO_2 than in ambient CO_2.

During August and September the PPFD-dependent functions of half-hourly NEF showed, for both CO_2 treatments, that potential CO_2 uptake in the microcosms at high PPFD was slightly reduced, whereas single-leaf measurements of net photosynthesis showed that photosynthetic capacity was still high in elevated CO_2 at that time (Figure 9.5). However, incident PPFD was falling and PPFD in the lower canopy layers, especially in the stands with high LAI, fell below the PPFD compensation point. Total respiration losses (above and below ground; see Chapter 3) were clearly enhanced in the elevated-CO_2 microcosm. Falling temperature during the second half of the season may have slightly reduced the increase in respiration rates. This, and shorter daylengths, led to a strong reduction of daily CO_2 uptake in the elevated-CO_2 microcosm. In August, NEF values of the microcosms were 0.04 in elevated CO_2 and 0.08 mol CO_2 m^{-2} d^{-1} in ambient CO_2 at an average PPFD of 31.4 mol m^{-2} d^{-1}, i.e. NEF in ambient CO_2 was higher than in elevated CO_2.

The total carbon budget over the whole 1992 growing season (June–September) was almost the same for both systems (Figure 9.12) and both microcosms were sinks for CO_2. In elevated CO_2, the stand strongly benefited from the higher atmospheric CO_2 concentration in the early stages of growth. This high influx of CO_2 into the ecosystem was compensated for by larger respiration losses in mid-season and with time the NEF in elevated CO_2 dropped below the NEF in ambient CO_2. The ecosystem in ambient CO_2 reached maximum net CO_2 uptake in the second half of the season and

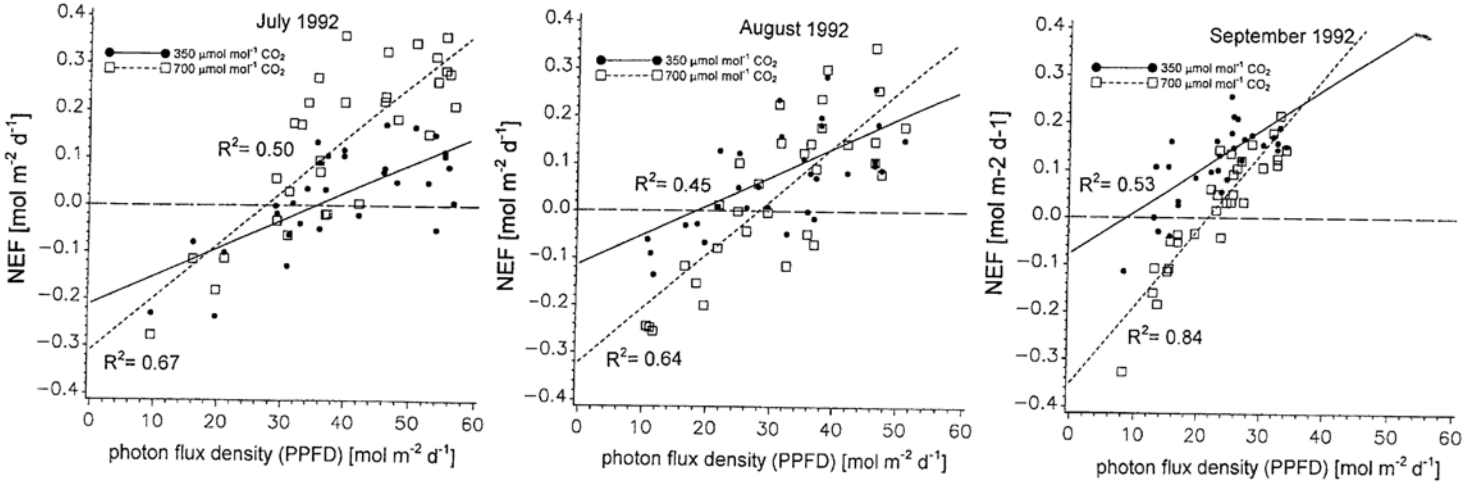

Figure 9.11 Relations between daily net ecosystem flux (NEF) (mol CO_2 m^{-2} d^{-1}) and daily PPFD (mol m^{-2} d^{-1}) (half-hourly values accumulated over 24 hours) of juvenile beech stands in ambient and elevated CO_2.

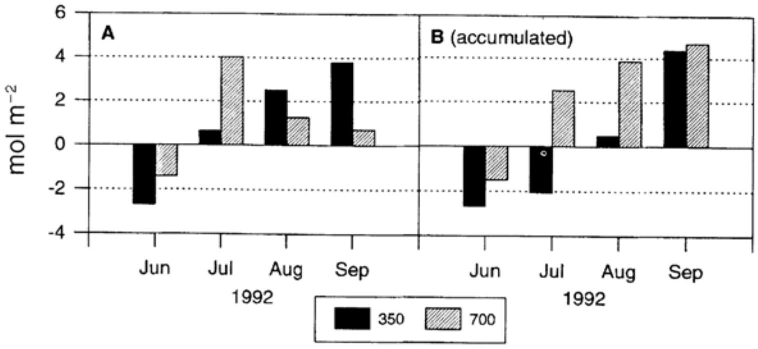

Figure 9.12 Monthly NEF of CO_2 (A) and accumulated CO_2 uptake (B) of small beech stands in ambient and elevated CO_2 on a ground area basis over the whole season in 1992.

showed a continual increase in CO_2 uptake throughout the whole season. At the end of the season the accumulated net CO_2 uptake of the two stands differed only slightly.

9.3.4 Scaling up CO_2 responses from leaf to stand scale: how important are CO_2-induced changes at the canopy scale?

Single-leaf measurements were combined with whole-stand measurements using a mathematical model (see Tables 9.1 and 9.2) for the period 14–18th August 1992. The night-time NEF of the beech stands was used to obtain a correlation between soil temperature and total system respiration (R_{Dsystem}) in ambient or elevated CO_2. Two functions were developed to calculate gross photosynthesis of the canopies (P_{Gcanopy}, Table 9.2, equations 9.12 and 9.16). After separating respiration from photosynthesis by using these functions, canopy gross photosynthetic rates were plotted against PPFD (Table 9.2, equations 9.14 and 9.15). At PPFDs higher than 400 μmol m^{-2} s^{-1}, gross photosynthesis in elevated CO_2 was higher than in ambient CO_2: in the range of PPFD between 1200 and 1800 μmol m^{-2} s^{-1}, canopy gross photosynthesis in elevated CO_2 was enhanced by 56% compared with that in ambient CO_2.

Single-leaf measurements of net photosynthetic rate ($P_{\mathrm{N,leaf}}$) and dark respiration ($R_{\mathrm{D,leaf}}$) were combined, using the temperature response of dark respiration, to calculate leaf gross photosynthetic rates (P_{Gleaf}, Table 9.1, equations 9.1–9.9). In a first approach (Table 9.2, equations 9.16 and 9.17), gross photosynthesis of the canopy was estimated using the functions describing single leaf measurements (Table 9.1) and the known LAI of 4.2 in

Table 9.2. *Equations to describe rates of dark respiration and gross photosynthesis by the canopies calculated from CO_2 gas exchange measurements over five days (August 14–18, 1992) at 350 and 700 μmol mol^{-1} CO_2 and canopy NEF in September 1992 at 350 and 700 μmol mol^{-1} CO_2 using statistical regression procedures (SAS Institute, 1988)*
Base units: * leaf area, ** ground area.

Model/year	Equation/description	Equation No.
Canopy model	R_{Dsystem} : Total system respiration rate (μmol $\mathrm{m}^{-2**}\,\mathrm{s}^{-1}$)	
	T_{S} : Soil temperature (°C)	
1992	$R_{\mathrm{Dsystem(350)}} = 0.514 + 1.14\mathrm{e}^{0.065(\mathrm{TS})}$	9.12
	$R_{\mathrm{Dsystem(700)}} = 0.514 + 2.28\mathrm{e}^{0.055(\mathrm{TS})}$	9.13
1992	P_{Gcanopy} : Canopy gross photosynthetic rate (μmol $\mathrm{m}^{-2**}\,\mathrm{s}^{-1}$)	
	I : Photon flux density (PPFD) (μmol $\mathrm{m}^{-2**}\,\mathrm{s}^{-1}$)	
1992	$P_{\mathrm{Gcanopy(350)}} = 19.3(1 - \mathrm{e}^{-0.00187(I-6)})$	9.14
	$P_{\mathrm{Gcanopy(700)}} = 31.3(1 - \mathrm{e}^{-0.00131(I+1)})$	9.15
	F_{system} : Net CO_2 ecosystem flux (NEF) (μmol $\mathrm{m}^{-2**}\,\mathrm{s}^{-1}$)	
	P_{Gcanopy} : Canopy gross photosynthetic rate (μmol $\mathrm{m}^{-2**}\,\mathrm{s}^{-1}$)	
	P_{Nleaf} : Leaf net photosynthetic rate (μmol $\mathrm{m}^{-2*}\,\mathrm{s}^{-1}$)	
	R_{Dleaf} : Leaf dark respiration (μmol $\mathrm{m}^{-2*}\,\mathrm{s}^{-1}$)	
	L : Leaf area index (LAI) ($\mathrm{m}^{2*}\,\mathrm{m}^{-2**}$)	
	k : Light penetration coefficient	
A	$P_{\mathrm{Gcanopy}} = F_{\mathrm{system}} + R_{\mathrm{Dsystem}}$	9.16
	$P_{\mathrm{Gcanopy}} = (P_{\mathrm{Nleaf}} + R_{\mathrm{Dleaf}})Lk$	9.17
B	$\mathrm{P}_{\mathrm{Gcanopy}} = \sum_{\mathrm{layer}=1}^{7} P_{\mathrm{Glayer}}$	9.18
	$P_{\mathrm{Glayer(350)}} = 4.88(1 - \mathrm{e}^{-0.0096(\mathrm{Ilayer})})L_{\mathrm{layer}}$	9.19
	$P_{\mathrm{Glayer(700)}} = 6.63(1 - \mathrm{e}^{-0.0093(\mathrm{Ilayer})})L_{\mathrm{layer}}$	9.20

ambient and of 6.1 in elevated CO_2. In this approach the light penetration coefficient (k) was not taken into account and k was set to 1.

As expected, large differences between estimates of P_G by the canopy-based model and the leaf-based model were found, especially at low incident PPFD (Figure 9.13A). At near-PPFD saturation, the estimates differed by 6% in ambient CO_2 and by 30% in elevated CO_2 because the PPFD incident at the top of the canopy was reduced by absorption and reflection during transmission through the leaf layers. The canopy response to PPFD was weaker than the single-leaf response, indicating that canopy structure

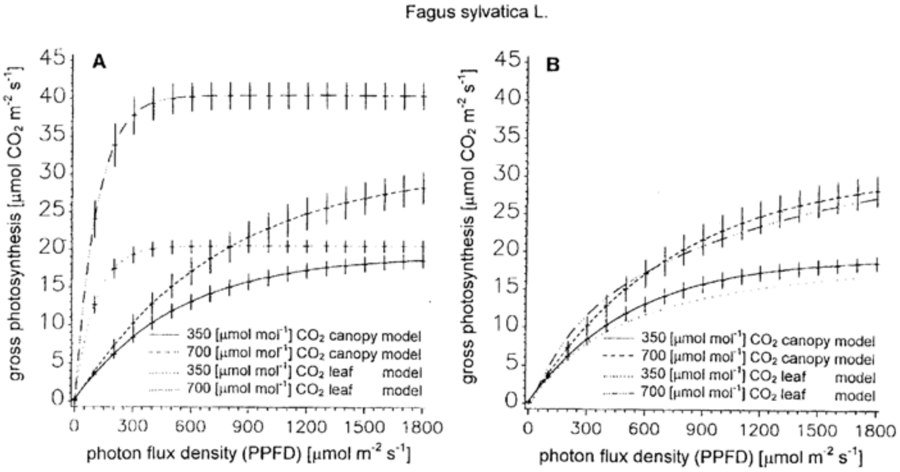

Figure 9.13 PPFD-response curves of canopy gross photosynthesis calculated from stand measurements (canopy model) and from single-leaf measurements (leaf model) of net CO_2 gas exchange and respiration rate (Tables 9.1 and 9.2) at 350 and 700 μmol mol^{-1} CO_2 in canopies of juvenile beech stands. Vertical lines represent the 95% confidence limit of the nonlinear model (least squares procedure, SAS Institute 1988). (A) Canopy gross photosynthesis was calculated from leaf measurements (leaf model) using LAI of the stands in July 1992 (LAI of 4.2 and 6.1 in ambient and elevated CO_2, respectively). (B) Canopy gross photosynthesis was calculated from leaf measurements (leaf model) using the vertical distribution of LAI and PPFD (light model, Table 9.1).

had a large influence on canopy photosynthesis. Photosynthesis (per unit leaf area) in elevated CO_2 was 39% higher than in ambient CO_2 (single-leaf measurements), whereas the canopy measurements showed an increase in photosynthesis of only 12% (per unit leaf area). This difference demonstrates the effect of different stand structures in the two CO_2 treatments on average leaf photosynthesis.

In a second approach (Table 9.2, equations 9.18–9.20) canopy structure was taken into account by using a separate PPFD penetration model (Table 9.1, equation 9.10) for each canopy in ambient and elevated CO_2. The incident PPFD reaching different levels in the canopy was measured with a quantum sensor and related to the LAI accumulated above each level assuming Beer's law, i.e. $I = I_0 e^{-kL}$, where I_0 and I are the incident PPFD above the canopy and at each level in the canopy, respectively (Monsi and Saeki, 1953). For both canopies a value of $k = 0.64$ was assumed. The measured PPFD at the soil surface was 3% of the incident PPFD in the ambient CO_2 stand and 1.8% in the elevated CO_2 stand.

Figure 9.13B shows the PPFD-response curve for canopy gross photosynthesis (P_{Gcanopy}), based on single-leaf measurements and the vertical distribution of LAI with respect to penetration of PPFD. Gross photosynthesis of each layer (P_{Glayer}) was summed to give the canopy gross photosynthesis. In this approach, estimates of P_{G} scaled up from single leaves agreed well with estimates based on the stand-scale measurements in both stands. The estimates from the single-leaf equations were within the 95% confidence interval for estimates from the stand-scale measurements. In elevated CO_2 the influence of canopy structure on canopy photosynthesis was larger than in ambient CO_2.

9.4 Conclusion

Microcosms can be used to evaluate the relative magnitudes of canopy photosynthesis and soil CO_2 efflux and can tell us when soil or vegetation will be sources or sinks for CO_2. With the help of simple models of stand processes, measurements of leaf processes can be scaled up to predict larger scale, ecosystem responses to elevated CO_2.

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