Forestry Commission, UK

1. Facilities

Plant material: Two experiments have been carried out in the sixteen open top chambers (Willson, Waddell & Durrant, 1987) at Headley in the south-east of England (during the duration of the contract, and will be referred to as Headley II and Headley III. Although an elevated ozone treatment was included in both experiments, results from that treatment are not reported here.

Headley II: One year old seedlings of *Quercus petraea* (ident. 92(4008), Herefordshire: reg.), *Fraxinus excelsior* (ident. 91(20), Moray: unreg.) and *Pinus sylvestris* (ident. 89(2009), Elgin: reg.) were acclimated in elevated or ambient CO_2 in a greenhouse at the Forestry Commission Research Station, Farnham, UK from January to April 1994. They were transferred to eight open-top chambers (Willson, Waddell & Durrant, 1987) and two outside plots in April 1994, with 42 plants per species per chamber planted in the soil within plastic sleeves and exposed to their respective CO_2 and O_3 treatments for the duration of the 1994 growing season. In November 1994, the plants were replanted (sixteen plants per species per chamber) in the sixteen open-top chambers and four outside plots. Each chamber was divided into three sectors, with ash planted to the north to reduce self-shading since these were the largest trees. Two harvests were carried out: in December 1995, four plants per species per chamber were removed, with the remaining twelve plants per species per chamber harvested in January 1997.

Headley III: Seeds of *Quercus petraea*, *Quercus robur* and *Quercus rubra* were planted in seed modules in January 1996, and exposed to ambient or 700 ppm CO_2 (daylight hours only) in a greenhouse at the Forestry Commission Research Station for the duration of the 1996 growing season. They were planted in the ground in the sixteen open-top chambers and four outside plots in March 1997. The two native oak species were inter-planted, whilst the red oak were planted in a separate (north facing) sector of the chamber.

Treatments: In 1994, the plants inside the chambers were fumigated with ambient air, elevated CO_2 or O_3 and combinations thereof, resulting in four duplicated treatments. For 1995, a further treatment of drought was added to the experimental design, with treatment duplication maintained through the use of eight additional chambers

CO_2: Ambient (350 ppm) or 700 ppm (see table 1). The elevated CO_2 concentration was maintained by a PC operated positive feedback system (32 minute time-step), using an infra red gas analyser (WMA2: PP-systems, Herts., UK). Mass flow controllers (model 5850TR: Rosemount Instruments, Cheshire, UK) regulated the introduction of CO_2 to individual chambers. Airflow through the chambers was approximately two air changes per minute (0.57 m^3 s^{-1}) during the day, whereas at night, airflow was reduced to approximately half this value by louver vents regulated by a sunlight activated switch. These airflows resulted in a mean temperature differential of 2.4°C between the ambient chambers and outside plots, although the mean maximum daily temperature during the growing season was 5°C higher within the ambient chambers. No temperature difference was observed between the ambient and elevated CO_2 chambers.

H_2O: During the 1994 growing season, all chambers were irrigated by aerial sprinklers supplying water at a rate of 12 l h^{-1} for four hours overnight. In 1995 the trees were planted directly into the soil within the open-top chambers, a heavily cultivated sandy humo-ferric podzol and subjected to two water supply treatments during 1995 and 1996. Soil water potential was measured with a gypsum block (Watermark soil moisture blocks: Irrometer Co., California, USA) in one chamber and one outside plot for each water treatment at a depth of 20 cm, activating drip irrigation at 10 and 150 kPa. Activation resulted in the supply of 8 l of water through 36 drip heads per chamber (EH12; Olson Irrigation Systems, California, USA). For Headley III, the gypsum blocks were replaced by soil capacitance 'Theta' probes (Delta-T Devices, UK), providing irrigation set-points of 25% and 10% v/v water content, comparable with the water treatments from Headley II. The irrigation of the open-top chambers and outside plots were treated separately to account for the differences in intercepted rainfall and evapo-transpiration.

2. Results

2.1 Leaf level observations

Headley II: Physiological measurements were carried out throughout the three growing seasons, and these results are summarised in Table 1, with brief descriptions of the methodology outlined in the legend.

a)

parameter	A	E	g_s	WUE	A_{max}	CE	A	E	g_s	WUE	A_{max}	A_{max}	V_{max}	J_{max}	ρ_{st}
year	1994	1994	1994	1994	1994		1995	1995	1995	1995	1995	1996	1996	1996	1995
OAK															
ambient					23		6.4	2.2	113	3.2	32	13.3			672
H_2O	9.8	3.8	250	3.05	23	.071	9.3	2.7	186	3.6	30	11.1	42	131	815
CO_2					19		13.6	1.7	81	8.9	32	22.6			676
CO_2+H_2O	17.9	3.3	177	5.44	23	.064	17.7	2.3	136	8.8	29	17.9	35	100	678
ASH															
ambient															
H_2O	12.3	3.2	339	3.8											
CO_2															
CO_2+H_2O	18.5	2.8	212	6.6											

b)

parameter	ψ_{pd}	ψ_{md}	[N]	[N]	[N]	[*chl*]	[CHO]	[CHO_n]	SLA	RMRT	BMRT	LMRT
year	1995	1995	1994	1995	1996	1995	1995	1995	1995			
OAK												
ambient	3.5	18.6		2.78	2.00	2.39	5.8	2.4	167			
H_2O	1.8	18.2	2.72	2.80	1.80	2.28	6.6	4.2	158	6.05	0.50	9.65
CO_2	5.3	16.9		2.34	1.62	2.25			150			
CO_2+H_2O	2.4	18.7	2.47	2.23	1.28	1.70			143	5.33	0.56	8.45
ASH												
ambient	7.7	18.8		2.28								
H_2O	6.1	15.3	1.7	2.26						6.07	0.37	4.94
CO_2	7.5	15.6		1.72								
CO_2+H_2O	6.6	14.3	1.69	1.74						5.19	0.38	5.11
PINE												
ambient				1.98	1.80	1.03						
H_2O				1.84	1.85	0.99				6.62	0.73	
CO_2				1.87	1.54	0.92						
CO_2+H_2O				1.78	1.57	1.07				5.70	0.68	

Table 1 a) Photosynthetic responses to elevated CO_2 from the Headley II experiment, 1994-1996. Photosynthesis, transpiration stomatal conductance and instantaneous water use efficiency (A, E, g_s and WUE: μmol m^{-2} s^{-1}, mmol m^{-2} s^{-1}, mmol m^{-2} s^{-1}, mmol mol^{-1})) were assessed by conventional gas exchange analysis using an LCA-3 gas exchange analysis system; light (1200 μmol m^{-2} s^{-1}) and CO_2 (1700 ppm) saturated photosynthesis (A_{max}: μmol m-2 s-1) was measured using the same equipment at a single value of C_a; ccarboxylation efficiency (*CE:*μmol mol-1)), expressed as the initial slope of the light and CO_2 response curves, was calculated from two measurements made within the linear portion of the responses; J_{max} and V_{max} were derived from the CO_2 and light response of photosynthesis with data fitted to the model of Farquhar, following the method of De Pury. b) Other physiological responses to elevated CO_2 from the Headley II experiment. Pre-dawn and mid-day water potentials (ψ_{pd} and ψ_{md}: bar) were measured from 0400-0600 h and 1200-1400 h in August 1995, respectively, using a pressure chamber (Soilmoisture Equipment Corp., USA); specific leaf area (SLA: area per unit weight - cm^2 g^{-1}) was determined on the leaves used for ψ determination; stomatal density (ρ_n: mm^{-2} was assessed by light microscopy; foliar chlorophyll ([*chl*]: mg g^{-1}) content was assessed using the method of Vernon (1965); soluble sugar and starch content ([CHO], [CHO_n]: % dry weight) was determined following the methods of Farrar (1980) using the phenol-sulphuric acid method of Dubois *et al.* (1956); total nitrogen ([N]: % dry weight) was analysed using the standard Kjeldahl method (Avery and Bascomb, 1974); root, branch and leaf total respiration (RMRT, BMRT, LMRT: nmol m^{-2} s^{-1}) were measured on excised tissue in late summer 1996 as described in Crookshanks *et al.* (1998).

A small reduction in carboxylation efficiency, expressed as the initial slope of the CO_2 response curve was observed in response to elevated CO_2 in 1994, although no reduction of light- and CO_2-saturated photosynthetic rate was observed in 1994 or 1995 (A_{max}). However, in the final year of the experiment, a significant reduction in both J_{max} and V_{max} was apparent (Fig. 2), indicating the onset of down-regulation of the photosynthetic apparatus, probably in response to the nitrogen deficiency that had developed (Table 1). The resultant CO_2 fertilisation of photosynthesis, in combination with the large reduction in stomatal conductance led to a twofold increase in instantaneous water use efficiency. However, this did not result in a change in water relations on a whole tree basis, as evidenced by pre-dawn and mid-day water potentials, which were unaffected by CO_2 treatment. The reduction in water use on a leaf area basis may be counterbalanced by increased water use on a tree basis as a result of the larger leaf area for the elevated CO_2 treatments (Fig. 1). In addition to the effect of CO_2 and irrigation treatment on stomatal conductance, there was also an indication that irrigation led to an increase in stomatal density, an effect that appeared to be negated by elevated CO_2, when the experiment (including O_3 treatments: data not shown) was treated as a

whole. With all limitations to photosynthetic CO_2 assimilation taken into account, the net effect of elevated CO_2 concentration was a marked increase in both soluble sugar and starch concentration during the middle of the day, indicative of carbon gain. This difference in non-structural, carbohydrate levels also resulted in a lower apparent specific leaf area (Table 1b) in the elevated CO_2 treatments, thereby affecting the concentrations of other foliar constituents when expressed on a leaf area basis. However, the nitrogen deficiency observed in 1996 could not be explained solely by dilution, and therefore represents a true deficiency. This was confirmed by soil nutrient analysis with a significant reduction in the irrigated, elevated CO_2 treatments (data not shown).

Headley III:

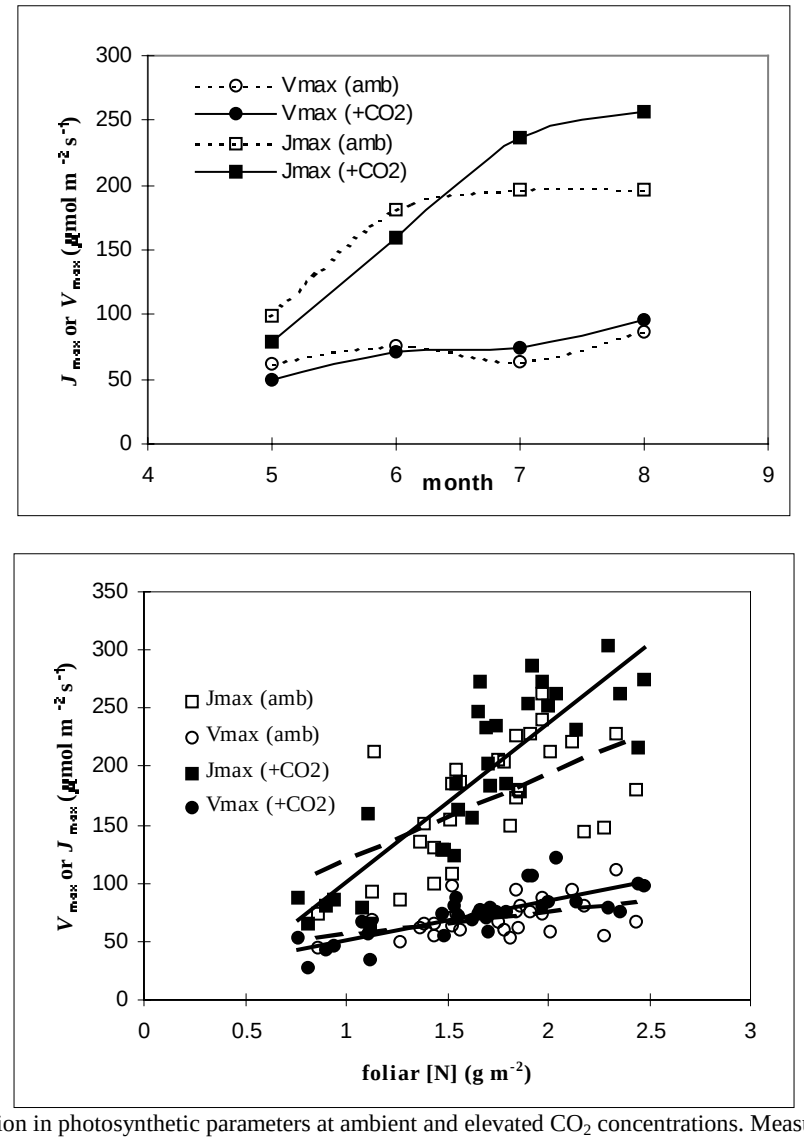

Fig. 1 a) Seasonal variation in photosynthetic parameters at ambient and elevated CO_2 concentrations. Measurements were made during the summer of 1997 using a CIRAS-1 (PP-Systems Ltd., UK) gas exchenge analysis system. Data were fitted to the model of Farquhar following the methods of De Pury. b) Observed relationships between photosynthetic parameters and foliar nitrogen concentration expressed on an area basis, for all individual analyses included in the mean data points shown in a). Linear regressions are shown.

Photosynthetic processes were parameterised according to the model of Farquhar and Von Caemmerer (1980) at four time-points during the course of the 1997 growing season. Large changes related to leaf development were observed in both V_{max} and J_{max}, but no down-regulation was evident; in fact, both parameters (particularly J_{max}) were higher in the ambient CO_2 treatment at the end of the growing season (Fig. 1a), possibly indicating a protective role of elevated CO_2 against ambient ozone pollution through reduced stomatal conductance (Broadmeadow *et al*., 1999). This hypothesis was supported by the large

reduction in both parameters observed for the elevated ozone treatments (data not shown) following the same time-course as the changes in the ambient ozone parameters. Highly significant relationships were observed between both J_{max} and V_{max} and [N], although in both cases, the linear fit was better for the ambient CO_2 treatment.

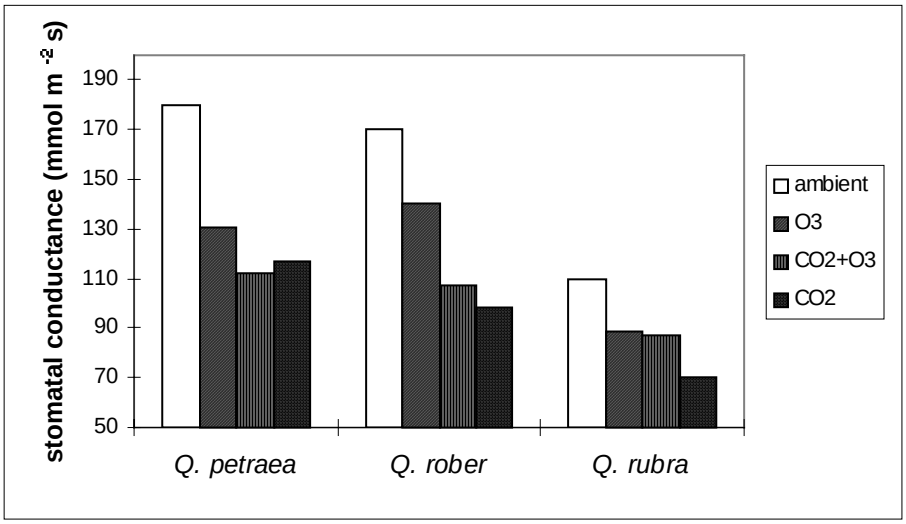

Figure 2. The effect of CO_2 and O_3 on stomatal conductance in for three species of oak. Measurements were made within one minute of placing the leaf within the cuvette using an LCA-3 gas exchange system and broad leaf cuvette. Values represent the mean of measurements made over twenty days during July and August 1998. Five measurements were made per species per chamber (four replicates) between 0800 and 1300 hr GMT.

The large reduction in g_s in response to elevated CO_2 was confirmed (Fig. 2) for all three species during an intensive assessment of stomatal conductance. Performance data were collected over the course of two months during the 1998 growing season to parameterise the conductance models of Jarvis and Ball-Berry. However, attempts to derive these parameters proved unsuccessful. As a result of the free draining nature of the soil, large diurnal variation in g_s (with complete stomatal closure during the afternoon: data not shown) acted as a confounding factor when analysing the data.

The seasonal course of leaf, root and branch respiration was determined from spring 1997 to summer 1998 (Fig. 3a). Minimum values of root and branch respiration observed in December and January, probably represent maintenance respiration, with varying proportions of growth respiration accounting for the higher rates through the rest of the year. In the case of leaf respiration, fully expanded leaves were chosen, and therefore the variation here may represent changes in metabolic activity, possibly dependent on available carbohydrate and therefore environmental (weather) conditions. The temperature response of respiration (Q_{10}) was also determined at all time-points by measuring respiration rates at 10 and 20^{o}C (Fig. 3b). Although there was considerable variation from month to month (Table 2a), assuming a Q_{10} of 2.0 provides a good average over the year as a whole, for all three plant tissues (Fig. 2b); here, the difference in slopes between the 10 and 20^{o}C data-sets was 1.92. Fig. 2b also demonstrates the close relationship observed between respiration rate and nitrogen concentration at a given temperature for all three plant tissues, providing good evidence for modeling maintenance respiration on tissue nitrogen concentration.

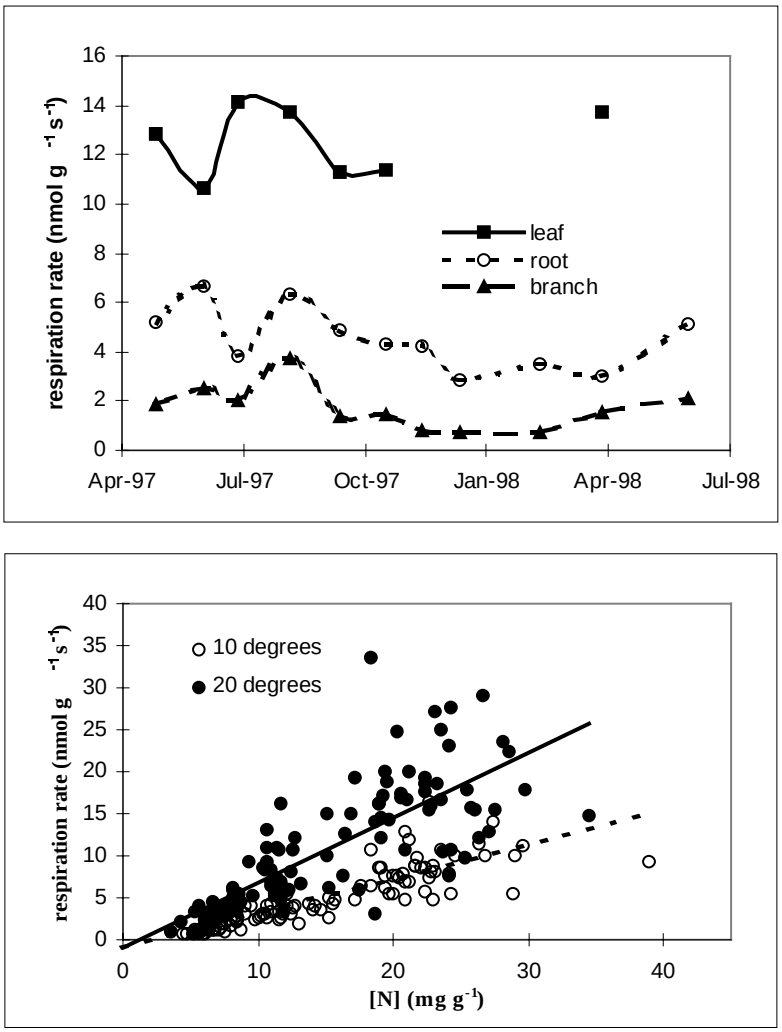

Fig. 3 a) Seasonal variation in respiration rate corrected to 15^{o}C for excised leaf, branch (stem) and root tissue, assuming the temperature coefficients shown in Table 2a. b) Relationship between respiration rate expressed on a dry weight basis and nitrogen content for leaf branch and root. The data represent analyses made throughout the year with measurements made at 10 and 20^{o}C.

Respiration parameters were derived throughout the year, expressed the results on fresh weight, dry weight area and nitrogen bases where possible (Table 2a). An analysis of the effects of elevated CO_2 on respiration was carried out in January and July 1998 (Table 2b) to include both maintenance and total respiration. This work only addressed root and branch respiration, since the effect of elevated CO_2 on leaf respiration had been determined alongside the photosynthesis parameterisation in 1997. For all analyses, there was no significant effect of elevated CO_2, irrelevant of whether the data were expressed on an area, weight or nitrogen basis. This intensive, and long running analysis also demonstrated no reductions in nitrogen concentration in any of the elevated CO_2 treatments. This therefore indicates that in a system supplied with adequate nitrogen , elevated atmospheric CO_2 does not lead to a reduction in respiration rate. This contrasts with the conditions in Headley II, where a slight reduction in respiration rate was observed, alongside the onset of nitrogen limitation. (Table 1).

month	root			branch				leaf			
	R_{15}(m)	**R_{15}(N)**	**RTBE**	**R_{15}(m)**	**R_{15}(N)**	**R_{15}(a)**	**RTBE**	**R_{15}(m)**	**R_{15}(N)**	**R_{15}(a)**	**RTBE**
may	5.23	0.44	0.073	1.87	0.29	0.60	0.119	12.8	0.62	0.68	0.085
june	6.63	0.54	0.086	2.48	0.38	0.69	0.067	10.6	0.53	0.66	0.061
july	3.81	0.29	0.050	2.07	0.28	0.59	0.052	14.1	0.41	0.64	0.050
sept	6.32	0.53	0.077	3.71	0.41	1.06	0.079	13.7	0.57	0.97	0.053
oct	4.85	0.48	0.076	1.42	0.22	0.56	0.039	11.3	0.46	0.85	0.063
nov	4.30	0.40	0.085	1.49	0.17	0.65	0.064	11.4	0.59	0.89	0.087
dec	4.24	0.29	0.048	0.84	0.09	0.35	0.139	-	-	-	-
jan	2.86	0.21	0.037	0.71	0.07	0.29	0.087	-	-	-	-
mar	3.46	0.23	0.075	0.75	0.07	0.28	0.082	-	-	-	-
apr	3.01	0.23	0.060	1.52	0.174	0.55	0.100	-	-	-	-
jun (o)	5.15	0.61	0.065	2.11	0.38	0.78	0.075	13.7	0.64	0.73	0.079
jun (n)	-	-	-	4.72	0.69	1.10	0.087	-	-	-	-

Table 2a. Seasonal variation in respiration parameters of *Quercus petraea*. Ten measurements were made at 10°C and 20°C on excised tissue at each time-point. Parameters were derived for the standard relationship $R=R_{15} * e^{((15-T)*RTBE)}$. Values are expressed on mass (m; nmol m^{-2} s^{-1}), area (a; µmol m^{-2} s^{-1}) and nitrogen content (N; µmol m^{-2} s^{-1}) bases.

Species	January 1998						July 1998					
	350 ppm CO_2			700 ppm CO_2			350 ppm CO_2			700 ppm CO_2		
branch	**R_5(m)**	**R_5(a)**	**R_5(N)**	**R_5(m)**	**R_5(a)**	**R_5(N)**	**R_{15}(m)**	**R_{15}(a)**	**R_{15}(N)**	**R_{15}(m)**	**R_{15}(a)**	**R_{15}(N)**
Q. petraea	0.45	0.16		0.59	0.29		1.80	0.74		1.45	0.71	
Q. robur	0.53	0.19		0.41	0.21		1.75	0.78		1.43	0.62	
Q. rubra	0.33	0.22		0.39	0.22		1.26	0.82		1.66	1.16	
root												
Q. petraea	1.99	-	0.100	1.94	-	0.115	4.26	-	0.357	4.84	-	0.357
Q. robur	1.85	-		2.00	-		4.43	-		5.23	-	
Q. rubra	1.85	-	0.110	1.79	-	0.096	2.36	-	0.200	2.74	-	0.246

Table 2b. The effect of CO_2 on root and branch maintenance (January measurements) and total (July measurements) respiration in three species of oak. Values represent the mean of two measurements per chamber, with four replicate chambers per treatment. January analysis was carried out at 5°C, and July analysis at 15°C. Units are as in Table 2a.

2.2 Tree level observations

Headley II: Final harvest data are shown for the three species in Figure 1, which indicates a relatively small CO_2-fertilisation effect on growth, and for irrigated ash, a small negative effect. However, if the effect of CO_2 on total biomass is meaned across all other treatment combinations (including ozone), a CO_2 fertilisation effect of 76% is apparent for oak. In the case of Scots pine, the value is 60%, and only 20% for ash. Furthermore, If allometric relationships derived from height, diameter and biomass are used to estimate relative growth rate for 1996, three different responses are observed for the three species (data not shown): oak continued to show a positive CO_2 effect, no effect was observed in Scots pine, and relative growth rate in ash was smaller in the elevated CO_2 as compared to the ambient treatments. The negative CO_2 response observed in ash may reflect nitrogen limitation which was confirmed by lower foliar nitrogen contents in the elevated CO_2 treatments (Table 1). The disappearence of the RGR CO_2 effect in Scots pine might be explained by the determinate nature of its growth, suggesting that the observed growth effects are predominantly at the seedling stage. This contrasts with the response of oak, which flushed throughout the year, and the CO_2-induced promotion of RGR was maintained in the final year, even though the irrigated CO_2 treatments showed a reduced foiliar nitrogen content. Spring phenological development was assessed in 1995 and 1996 using a standard IUFRO scoring system, although no effects of elevated CO_2 were observed (data not shown).

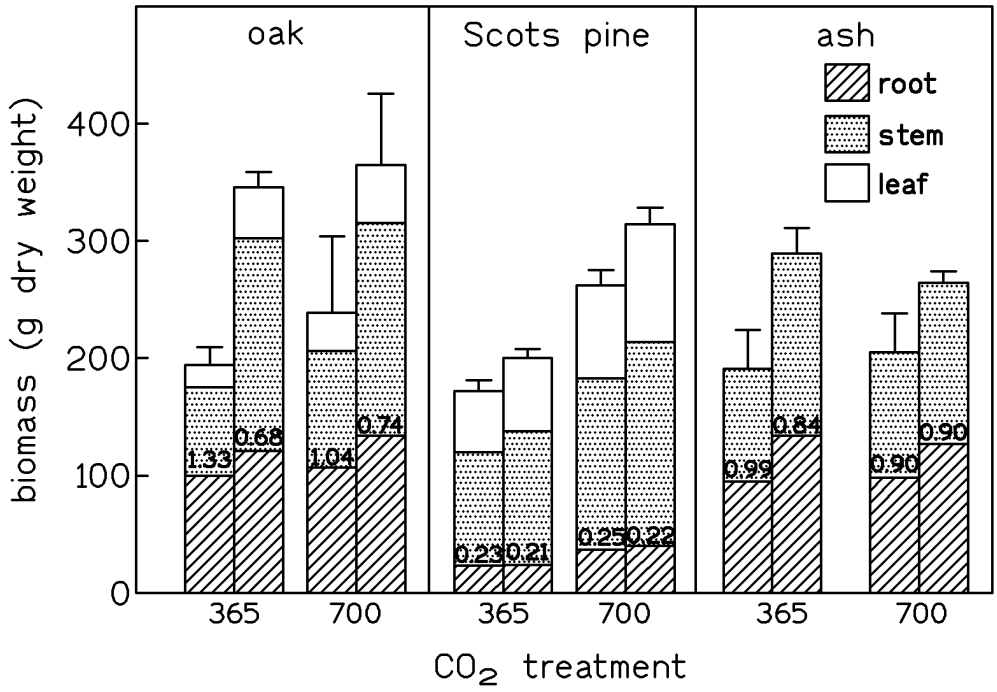

Fig. 4 Growth responses of oak, ash and Scots pine to three years treatment with ambient or elevated CO_2, and two years with and without irrigation, expressed on an individual tree basis. Leaf biomass of oak was determined by litter collection prior to the final harvest; needles were removed from Scots pine during drying; leaf litter of ash was not collected as a result of rapid deterioration whilst on the ground. Root:shoot allocation is given on the figure.

Headley III:

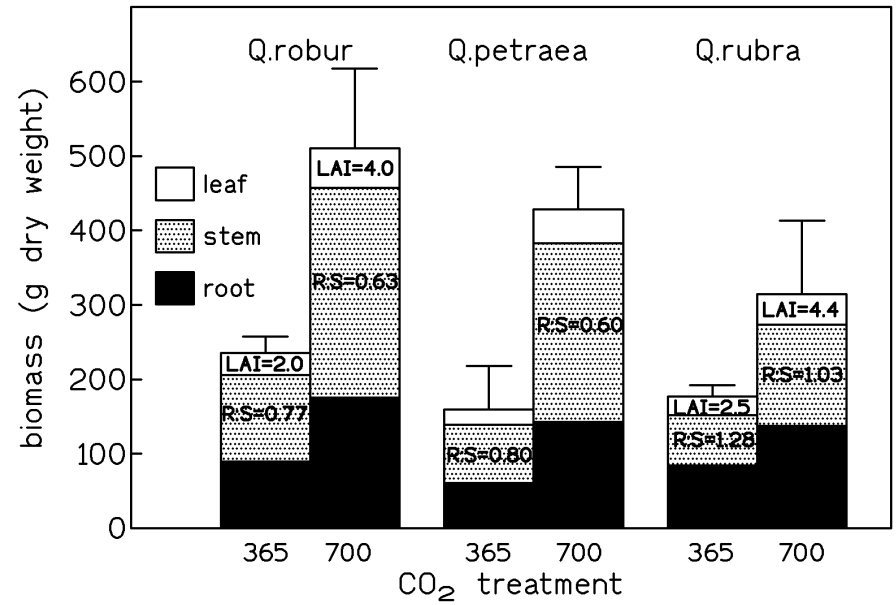

Fig. 5 The effect of two years growth in elevated or ambient CO_2 on biomass production in three species of oak. Leaf biomass was determined from litter collection in winter 1998-99. Leaf litter from the two native species (*Q. robur* and *Q. petraea*) could not be distinguished, and leaf has been apportioned according to stem biomass for those species. Leaf area index was calculated by determining specific leaf area for a sub-sample of 100 leaves from each treatment (data not shown). Root:shoot ratios are also given.

The CO_2 fertilisation of biomass increment was larger for all three species of oak than any species in the Headley II experiment. Of the two UK native species, *Q. petraea* showed the largest growth rate, and also the largest growth response to elevated CO_2, as would be expected given the natural preference for heavy, moist soil types of *Q. rober*. *Q. rubra* showed the poorest growth, and also, the smallest response to elevated

CO_2. Both the high growth rate, and large response to elevated CO_2 (Fig. 2) may result from the soil preparation prior to planting: the soil was not improved prior to the planting of Headley II, whilst the soil was replaced to a depth of 30 cm with soil from the nursery which had been improved with hop waste (to increase the organic matter content) and given a base NPK fertiliser dressing, along with 200 g dolomitic lime to reduce soil acidity, and prevent a magnesium deficiency developing. For all three species, there was a large reduction in root:shoot allocation, or alternatively, the CO_2 fertisation effect was predominantly on shoot growth. In addition, leaf area index was approximately double in the elevated CO_2 treatment, and in combination with the reduction in root allocation described above, this has serious implications for tree stability.

2.3. Digest of results: The two experiments carried out at Headley from 1994-1998 (Headley II and Headley III) have demonstrated varying responses of biomass increment to elevated CO_2 concentrations. The CO_2 fertilisation effect ranged from -10% in the case of irrigated Fraxinus excelsior (Headley II), to +175% for Quercus petraea (Headley III). Much of the variation can be explained by water and nutrient limitation, especially nitrogen limitation which is probably the basis for the large difference in results between the two experiments. Although there was variation in the magnitude of the growth response to elevated CO_2, there was a consistent change in allocation resulting in lower root:shoot partitioning. Physiological analysis of Headley II indicated a down-regulation of photosynthesis in the final year of the experiment as evidenced by the reduction in J_{max} and V_{max} of oak, although an assessment of CO_2 and light limited photosynthesis rates in the two previous years indicated no down-regulation earlier in the experiment This down-regulation coincided with a reduction in foliar N and chlorophyll concentration in the elevated CO_2 treatments, whilst modest reductions were also observed in respiration parameters. Although photosynthesis was not assessed in *Pinus sylvestris*, this was the one species to demonstrate a large positive response to elevated CO_2, and also showed no nitrogen deficiency. The non-nutrient limited trees in Headley III demonstrated larger growth responses to elevated CO_2, and no down-regulation (in fact a small increase) of photosynthesis or reduction of respiration in response to elevated CO_2. The effect of CO_2 on stomatal conductance, was however consistent between experiments, and indicated conservation of water at elevated CO_2 concentrations , particularly when increased rates of carbon assimilation are taken into account by expressing the results as instantaneous water use efficiency. Seasonal variation in respiration, both the basal rate and temperature coefficient have been demonstrated, and the responses parameterised. This process has also been carried out for photosynthesis, and to a limited extent, stomatal conductance. Phenological development (spring bud-burst) was followed during the course of both experiments, and on the whole, indicated no effect of elevated CO_2. However, for *Q. petraea*, there was a suggestion of a slight delay in budburst.

2.4 Conclusions: The growth response to elevated CO_2 is variable, depending on species and growth conditions, and is considerably influenced by nitrogen availability. The response to elevated CO_2 cannot therefore be treated in isolation. Photosynthetic and respiration parameters vary considerably through the course of the year, although for both, tissue nitrogen content acts as good surrogate for these parameters. Both the physiological parameters derived here, and the observed responses of growth to elevated CO_2 will enable predictive models of tree growth to be validated under conditions of elevated carbon dioxide concentrations.

2.5. Outlook: The open-top chamber facility will continue to run for the forseeable future: in the short-term, a four month experiment is planned to identify the location of the genes which are expressed under conditions of elevated CO_2 using a QTL mapped half-sib population of *Populus americana*. This work is in collaboration with Gail Taylor of Southampton University, UK. In the longer term, it is planned to modify the chambers by adding a roof and removing a section of glass at the side to maintain ventilation, but prevent natural rainfall from entering the chambers. This will then allow the interactions between elevated CO_2, and ozone to be elucidated for droughted trees, under the conditions of soil moisture that are expected over the course of the next century. Six forest tree species will be planted in the chambers, covering a range of production (or potentially productive) conifer and broadleaf species.

Experimental work will also concentrate on basic physiological parameterisation of six poplar and willow clones for a process-based yield model, which will be validated with biomass data from a network of 49 sites within an experimental yield trial.

Impact studies and experimental work will therefore continue to support the programme of yield model development, both for using process modelling as a tool in forest management (ultimately in the form of a decision support system), and to predict the effects of rising atmospheric CO_2 concentrations and climate change on UK forest growth.

2.6 Publications:

Broadmeadow MSJ, Ludlow, AR Randle TJ (1996) Modelling the effects of global change on European forests. In: *Report on Forest Research 1996*. Forestry Commission, Edinburgh, UK.

Crookshanks M, Taylor G, Broadmeadow MSJ (1998) Elevated $CO_2$and tree root growth: contrasting responses in *Fraxinus excelsior, Quercus petraea* and *Pinus sylvestris. New Phytologist* 138: 241-250.

Broadmeadow MSJ, Heath J, Randle TJ (1999) Environmental limitations to physiologically effective ozone exposure. *Water, Air and Soil Pollution*. In press.