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Leaf traits, shoot growth and seed production in mature *Fagus sylvatica* trees after 8 years of CO$_2$ enrichment

Qingmin Han[1],*, Daisuke Kabeya[2] and Günter Hoch[3]

[1]*Department of Plant Ecology, Forestry and Forest Products Research Institute (FFPRI), 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan,* [2]*Kiso Experiment Station, FFPRI, 5473-8 Kisofukushima, Nagano 387-0001, Japan and* [3]*Institute of Botany, University of Basel, Schönbeinstrasse 6, CH-4056 Basel, Switzerland*
* *For correspondence. E-mail* qhan@ffpri.affrc.go.jp

• *Background and Aims* Masting, i.e. synchronous but highly variable interannual seed production, is a strong sink for carbon and nutrients. It may, therefore, compete with vegetative growth. It is currently unknown whether increased atmospheric CO$_2$ concentrations will affect the carbon balance (or that of other nutrients) between reproduction and vegetative growth of forest species. In this study, reproduction and vegetative growth of shoots of mature beech (*Fagus sylvatica*) trees grown at ambient and elevated atmospheric CO$_2$ concentrations were quantified. It was hypothesized that within a shoot, fruiting has a negative effect on vegetative growth, and that this effect is ameliorated at increased CO$_2$ concentrations.
• *Methods* Reproduction and its competition with leaf and shoot production were examined during two masting events (in 2007 and 2009) in *F. sylvatica* trees that had been exposed to either ambient or elevated CO$_2$ concentrations (530 μmol mol^{-1}) for eight consecutive years, between 2000 and 2008.
• *Key Results* The number of leaves per shoot and the length of terminal shoots was smaller or shorter in the two masting years compared with the one non-masting year (2008) investigated, but they were unaffected by elevated CO$_2$ concentrations. The dry mass of terminal shoots was approx. 2-fold lower in the masting year (2007) than in the non-masting year in trees growing at ambient CO$_2$ concentrations, but this decline was not observed in trees exposed to elevated CO$_2$ concentrations. In both the CO$_2$ treatments, fruiting significantly decreased nitrogen concentration by 25 % in leaves and xylem tissue of 1- to 3-year-old branches in 2009.
• *Conclusions* Our findings indicate that there is competition for resources between reproduction and shoot growth. Elevated CO$_2$ concentrations reduced this competition, indicating effects on the balance of resource allocation between reproduction and vegetative growth in shoots with rising atmospheric CO$_2$ concentrations.

Key words: Beech, carbon autonomy, CO$_2$ enrichment, *Fagus sylvatica*, mast seeding, nitrogen, resource allocation, trade-off, vegetative growth.

INTRODUCTION

Plant life history functions, including growth, maintenance and reproduction, all require resources. If resources such as carbon (C) and nitrogen (N) are limited, their allocation to reproduction may occur at the expense of other functions, generally referred to as the 'cost of reproduction' (Obeso, 2002). In perennial woody plants, the cost of reproduction for the whole plant has been estimated from annual tree-ring increments (Obeso, 1997; Genet *et al.*, 2010), while local trade-offs, for single shoots, can be analysed by comparing current shoot elongation in fruit-bearing and non-reproductive shoots (Obeso, 1997; Suzuki, 2001; Kawamura and Takeda, 2006). Shoots can be considered as the modular unit of a tree crown. Resource allocation within branchlets might respond to local trade-offs (e.g. leaf size and number, shoot growth and fruit production) but is probably integrated at individual trees (as measured by tree-ring growth, for example) (Miyazaki *et al.*, 2002; Obeso, 2002; Ishihara and Kikuzawa, 2009).

Mast seeding or masting, i.e. synchronous, but highly variable, interannual seed production by plant populations, is a

characteristic of many perennial species globally, including tropical and temperate trees and temperate herbs (Shibata *et al.*, 1998; Kelly and Sork, 2002). This complex phenomenon, the results of many endogenous and exogenous factors, has been explained by ultimate evolutionary advantages and proximate causes (Kelly and Sork, 2002; Piovesan and Adams, 2005). Although the physiological mechanism behind the masting phenomenon is not fully understood, it is generally considered to be related to temporal variations in individual resource budgets and the associated costs of reproduction, which is strongly affected by climatic conditions (Hilton and Packham, 2003; Richardson *et al.*, 2005). It is assumed in most resource-driven models of masting that C is the main limiting internal resource for seed production (Isagi *et al.*, 1997; Satake and Iwasa, 2000). Only recently, mobile carbohydrate stores have been shown to control mast flowering in *Astragalus scaphoides*, a perennial herb (Crone *et al.*, 2009). Because masting is a consequence of physiological controls of reproduction, under environmental influence, differences in plant resource acquisition and allocation could dramatically change patterns of seed production. If C is the resource limiting masting in *Fagus sylvatica*, increased atmospheric carbon

dioxide (CO_2) concentrations could lead to a higher frequency of masting events and thus greater seed production. Interestingly, Övergaard *et al.* (2007) found that the average interval between masting events of *F. sylvatica* in Sweden has been reduced to 2·5 years during the last 30 years compared with an average of 5·0 years from the end of the 17th century up to the 1960s, although other environmental factors may also be involved. However, to date, only a few studies have experimentally tested the reproductive response of forest tree species to elevated CO_2 (LaDeau and Clark, 2001; Stiling *et al.*, 2004; Körner *et al.*, 2005; Way *et al.*, 2010). The competition between reproduction and shoot growth as atmospheric CO_2 concentrations increase has received little attention. Yet, seed production and seed quality are important determinants of natural regeneration and maintenance of species diversity.

Here, we describe an investigation of the effect of 8 years of continuous free-air CO_2 enrichment (530 μmol mol^{-1}) at the Swiss Canopy Crane (SCC) site on the reproductive effort and seed traits of *F. sylvatica* and the competition between reproduction and vegetative growth during the growing season. Previous studies at the SCC site found that net photosynthesis in fully sunlit, upper canopy foliage was stimulated by approx. 40 % compared with ambient controls (Zotz *et al.*, 2005; Bader *et al.*, 2010). However, the fate of these surplus C assimilates remained uncertain, since no significant increase in growth was found when evaluated as stem basal area increment (Körner *et al.*, 2005; Asshoff *et al.*, 2006). Fruits might be an additional C sink for surplus photoassimilates under elevated CO_2 conditions, although a previous coarse estimate of the biomass of seeds and vegetative infructescence tissues (e.g. cupules) at the SCC site, based on litter trap data, revealed no significant difference between trees growing at ambient and elevated CO_2 concentrations (Körner *et al.*, 2005). In the current study, seed production was quantified by investigating individual shoots of *F. sylvatica* trees at the SCC site. Therefore, the main objectives of this study were to: (*a*) investigate trade-offs between seed production and vegetative growth within individual shoots; and (*b*) evaluate effects of elevated CO_2 on these trade-offs in *F. sylvatica* 1 year after the end of an 8 year period of CO_2 enrichment.

MATERIALS AND METHODS

Study site and CO_2 enrichment

The study was conducted at the SCC site close to Hofstetten, 15 km south of Basel, Switzerland (47°28′N, 7°30′E, 550 m a.s.l.). It is a mature temperate deciduous forest, with trees ages between 80 and 120 years, tree heights between 30 and 35 m, a tree density (breast height diameter ≥0·1 m) of 415 trees ha^{-1} and a stem basal area of about 46 m^2 ha^{-1}. The stand is characterized by dominant *Fagus sylvatica* and *Quercus petraea*, with *Carpinus betulus*, *Tilia platyphyllos*, *Acer campestre*, *Prunus avium* and four conifers (*Abies alba*, *Larix decidua*, *Picea abies* and *Pinus sylvestris*) as companion species. The climate is typical of the humid temperate zone, characterized by mild winters and moderately warm summers. Soils are of the rendzina type on calcareous bedrock (a silty loam with an accessible profile depth of

approx. 30 cm and a pH of approx. 5·8 in the top 10 cm of the profile). Further details regarding the site are presented in Pepin and Körner (2002).

At the SCC site, 13 of the 64 broad-leaved trees within the reach of the crane were exposed to elevated CO_2 between late September 2000 and October 2008, using the so-called web-FACE technology (Pepin and Körner, 2002). On average, the treated trees experienced CO_2 concentrations of 530 μmol mol^{-1} during daytime hours throughout the growing season (March–October; Körner *et al.*, 2005). Control trees, which grew in the crane area but at sufficient distance from the CO_2 release to avoid elevated CO_2, were permanently at ambient atmospheric CO_2 concentrations. The CO_2 enhancement ended at leaf fall of the deciduous species in October of 2008.

Three *F. sylvatica* trees previously exposed to elevated CO_2 concentrations and four individuals exposed to ambient CO_2 concentrations were selected for this study. In autumn 2008, the presence of floral buds was confirmed on all selected trees, indicating mast fruiting in 2009. All of the leaves of *F. sylvatica* trees are pre-formed in the winter buds (Eschrich *et al.*, 1989). Thus, the numbers of leaves per shoot and even the numbers of cell layers in the palisade tissues within the leaves on the trees in 2009 were fixed during summer 2008, i.e. while still exposed to elevated CO_2 concentrations. Trees under both elevated and ambient CO_2 concentrations mast fruited in 2007, and this was followed by a non-fruiting year in 2008, and a masting year again in 2009. The biomass of seeds and vegetative infructescence tissues (e.g. cupules) collected from litter traps was 30·8 ± 9·6, 0·36 ± 0·14 and 31·2 ± 5·3 g m^{-2} in 2007, 2008 and 2009, respectively.

Shoot and fruit sampling

All shoots were investigated and sampled by means of a crane gondola. In July 2009, four 5-year-old fully sunlit branches from the upper crown of each tree were chosen, within which all shoots were classified according to their age. The numbers of leaves and fruits per shoot were counted directly for shoots in 2009 and indirectly from petiole scars for shoots from the 2007 and 2008 seasons. All measurements in July 2009 were conducted non-destructively *in situ*.

In September 2009, two 5-year-old branches were harvested from each tree and kept under cool conditions during transport. In the laboratory, each branch was separated into shoot segments developed in 2009, 2008 and 2007. The numbers of leaves and fruits per shoot for the year 2009 were counted, and total leaf areas per shoot were measured using a leaf area meter (Li-3100, LI-COR, Lincoln, NE, USA). In addition, the length of each terminal shoot was measured for the years 2007–2009. All samples were dried at 80 °C for 48 h and the dry mass was recorded for each. For chemical analyses, the same tissues of both sampled branches were pooled for each tree before grinding in a steel ball mill (MM2000, Retsch, Haan, Germany). The C and N concentrations were measured after combustion in a CHN Analyzer (Vario EL III, Elementar, Hanau, Germany).

Statistical analyses

The effects of all of the independent variables (i.e. elevated CO_2, fruiting and year) on all dependent variables measured
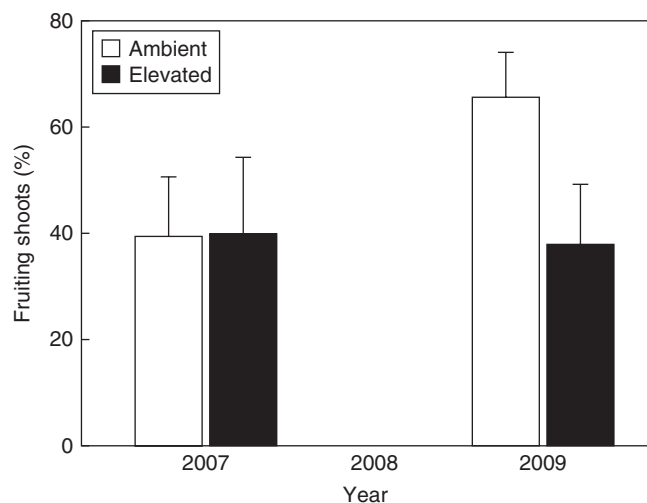

FIG. 1. Comparison of the estimated percentage of fruit-bearing shoots of *Fagus sylvatica* trees (means $\pm$ s.e.) exposed to ambient ($n = 4$) and elevated ($n = 3$) CO_2 concentrations, as indicated. Masting occurred in 2007 and 2009, whereas 2008 was a non-masting year. The results of the statistical analysis are shown in Table 1.

were evaluated by fitting generalized linear mixed models (GLMMs) on the basis of restricted maximum likelihood, using SAS/STAT 9·1 software (PROC GLIMMIX, SAS Institute, Cary, NC, USA). Poisson (count data), binomial (binary data), log-normal (length and dry mass data) or normal (C and N concentrations) distributions were assumed for the errors of the dependent variables, and the effect of individual trees and that of branches within individuals were included in the models as random effects. The degrees of freedom of the denominator in type III tests of the fixed effects (Wald-type tests) were approximated using the method of Kenward and Roger (1997). Results were considered significant when the *P*-value was <0.05 unless otherwise mentioned.

RESULTS

Fruiting efforts and seed traits

The proportion of fruit-bearing shoots was significantly greater in 2009 than in 2007, but only for trees growing at ambient CO_2 before 2009, i.e. there was a significant interaction between CO_2 treatment and year (Fig. 1, Table 1). In contrast, the number of fruits per fruit-bearing shoot was similar between the two recorded masting years for trees growing at both ambient and elevated CO_2 (data not shown). CO_2

TABLE 1. *Summary statistics for the type III test of fixed effects (Wald-type test) and the estimated random effects in the generalized linear mixed model for data presented in Table 3 and Figs 1–3*

Variables in Table 3 and Figs 1-3	Fixed effect	d.f.	den d.f.	F	P	Random effect Individuals	Random effect Branches in individuals
Table 3							
Leaf number	Fruiting	1	239·0	19·16	**<0·0001**	0	0
	CO_2	1	239·0	1·04	0·308		
	Fruiting × CO_2	1	239·0	1·74	0·189		
Leaf area	Fruiting	1	229·5	16·97	**<0·0001**	0·0355	0·0127
	CO_2	1	5·0	0·85	0·399		
	Fruiting × CO_2	1	229·5	0·14	0·704		
LMA	Fruiting	1	230·0	32·88	**< 0·0001**	0·0224	0·0040
	CO_2	1	5·1	1·23	0·318		
	Fruiting × CO_2	1	230·0	2·14	0·145		
Figure 1							
Fruiting shoot	Year	1	982·0	7·28	**0·007**	0·5360	0·0369
	CO_2	1	5·1	1·64	0·255		
	Year × CO_2	1	982·0	5·25	**0·022**		
Figure 2							
Leaf number	Year	2	1297·0	14·29	**< 0·0001**	0·0121	0·0023
	CO_2	1	5·3	0·12	0·747		
	Year × CO_2	2	1297·0	1·22	0·296		
Figure 3							
Length	Fruiting	2	24·0	8·02	**0·002**	0·0297	0·0117
	CO_2	1	5·0	2·22	0·196		
	Fruiting × CO_2	2	24·0	0·31	0·739		
Biomass	Fruiting	2	24·0	22·20	**< 0·0001**	0	0·1330
	CO_2	1	12·0	3·21	0·098		
	Fruiting × CO_2	2	24·0	0·61	0·549		
Biomass per length	Fruiting	2	24·0	205·73	**< 0·0001**	0	0·0363
	CO_2	1	12·0	1·98	0·185		
	Fruiting × CO_2	2	24·0	4·03	**0·031**		

The degrees of freedom of the denominator (den d.f.) were approximated using Kenward and Roger's method.
Significant values are highlighted in bold.

TABLE 2. *Dry mass (DM), and nitrogen (N) and carbon (C) concentrations of individual seeds and cupules of trees exposed to ambient or elevated CO_2 concentrations sampled on 8 September 2009*

	Seeds			Cupules		
CO_2 concentration	DM (g)	N (%)	C (%)	DM (g)	N (%)	C (%)
Ambient	0·17 ± 0·03	3·45 ± 0·14	58·0 ± 0·8	0·76 ± 0·06	0·21 ± 0·02	46·8 ± 1·0
Elevated	0·20 ± 0·02	3·21 ± 0·17	56·4 ± 0·9	1·01 ± 0·17	0·25 ± 0·00	45·9 ± 0·7
d.f.	1	1	1	1	1	1
den d.f.	5·0	5·0	5·0	5·0	5·0	5·0
F	0·95	1·19	1·86	3·88	2·62	0·49
P-value	0·373	0·325	0·231	0·106	0·167	0·514

Values shown are means ± s.e. from four trees exposed to ambient CO_2 and three trees previously exposed to elevated CO_2. A generalized linear model was used for statistical analysis.

TABLE 3. *Effects of fruiting and CO_2 treatment on number of leaves per shoot, individual leaf area and leaf dry mass per area (LMA) from non-fruiting and fruiting shoots sampled on 8 September 2009*

Shoot type	No. of leaves per shoot	Leaf area ($m^2 \times 10^{-4}$)	LMA ($g\ m^{-2}$)
Ambient CO_2			
Non-fruiting	3·2 ± 0·2	7·88 ± 0·56	85·59 ± 5·98
Fruiting	4·7 ± 0·2	8·52 ± 0·51	96·83 ± 6·81
Elevated CO_2			
Non-fruiting	3·3 ± 0·3	9·18 ± 1·57	100·66 ± 9·97
Fruiting	4·5 ± 0·2	10·30 ± 1·69	107·57 ± 7·48

Values shown are the means ± s.e. from four trees exposed to ambient CO_2 and three trees previously exposed to elevated CO_2. The results of the statistical analyses are shown in Table 1.
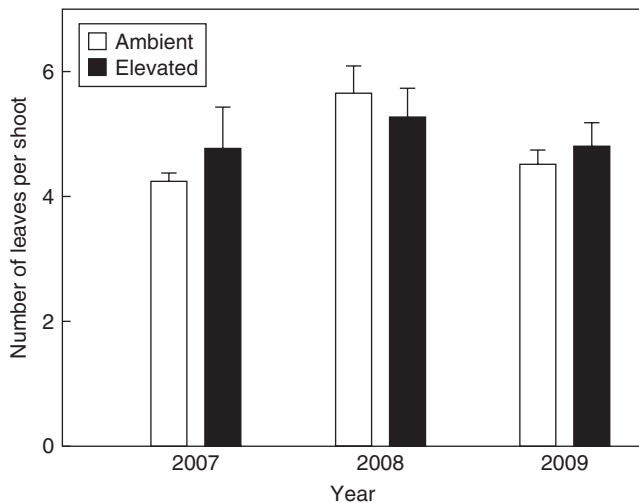

FIG. 2. Interannual variations in number of leaves per current-year shoot of *Fagus sylvatica* trees (means ± s.e.) exposed to ambient ($n = 4$) and elevated ($n = 3$) CO_2 concentrations, as indicated. Masting occurred in 2007 and 2009, whereas 2008 was a non-masting year. The results of the statistical analysis are shown in Table 1.

enrichment in the preceding years had no significant carry-over effect on either dry mass of seed and cupule or their respective N and C concentrations (Table 2).

Leaf traits

In 2009, fruit-bearing shoots had significantly more leaves with greater individual leaf area and leaf dry mass per area (LMA) than non-fruiting shoots (Table 3). Since this difference in leaf traits between fruiting and non-fruiting branches also persisted within a 5-year-old branch of an individual tree (data not shown), they are unlikely to be due to factors associated with different crown positions (e.g. sun exposure). The interannual comparison revealed that there were fewer leaves per shoot in the masting years than in the non-masting year (Fig. 2, Table 1). Leaf number per shoot was not affected by CO_2 enrichment (Fig. 2, Table 3).

Leaf N concentrations on a dry mass basis were significantly lower for fruiting shoots than for non-fruiting shoots in September (Tables 4 and 5). This difference in leaf N persisted when the comparison was made on a leaf area basis (mg N cm^{-2}; data not shown). Moreover, leaf N decreased significantly between the two occasions, and this decline was greater for fruit-bearing shoots than for non-fruiting shoots. In contrast, leaf C concentrations were similar for fruiting and non-fruiting shoots. Neither leaf N nor leaf C concentrations were affected by previous CO_2 enrichment.

Shoot traits

Both length and biomass of terminal shoots increased less when fruiting occurred, with significantly longer shoots in the non-masting year 2008 than in the two masting years 2007 and 2009 (Fig. 3, Table 1). The length of terminal shoots was not affected by the CO_2 treatment irrespective of masting. In contrast, the biomass of terminal shoots was marginally affected by elevated CO_2, with about half the biomass in the masting year 2007 compared with the non-masting year 2008 for trees at ambient CO_2 but not at elevated CO_2. However, since the biomass of an individual shoot depends on its length, and shoot length was affected by fruiting, CO_2 effects on biomass increment were also analysed with respect to biomass per length. There was a significant interaction between CO_2 enrichment and fruiting when the biomass per length of terminal shoots was considered.

As with the leaves, N concentrations in the xylem of 1- to 3-year-old branches were significantly smaller for fruiting than non-fruiting shoots in trees exposed to both ambient and elevated CO_2, while they were unaffected by CO_2

TABLE 4. *Effects of fruiting and previous CO_2 treatment on nitrogen (N) and carbon (C) concentrations of leaves and xylem tissue of 1- to 3-year old branches from fruiting and non-fruiting shoots sampled on 22 July and 8 September 2009*

| | Leaf | | | | Xylem of branches | | | |
| | N (%) | | C (%) | | N (%) | | C (%) | |
Shoot type	July	September	July	September	July	September	July	September
Ambient CO_2								
Non-fruiting	2·41 ± 0·19	2·21 ± 0·13	51·0 ± 0·5	50·8 ± 1·1	0·67 ± 0·17	0·62 ± 0·07	48·6 ± 0·6	44·7 ± 0·3
Fruiting	2·40 ± 0·11	1·58 ± 0·07	53·0 ± 0·8	48·1 ± 0·6	0·43 ± 0·04	0·28 ± 0·05	48·8 ± 0·3	45·8 ± 0·8
Elevated CO_2								
Non-fruiting	2·56 ± 0·08	2·19 ± 0·13	52·0 ± 0·4	49·6 ± 0·4	0·83 ± 0·05	0·72 ± 0·06	48·6 ± 0·4	45·5 ± 0·8
Fruiting	2·13 ± 0·20	1·65 ± 0·25	48·9 ± 2·4	51·4 ± 0·6	0·42 ± 0·03	0·56 ± 0·10	47·9 ± 1·1	46·3 ± 0·2

Values shown are the means ± s.e. from four trees exposed to ambient CO_2 and three trees previously exposed to elevated CO_2. The results of the statistical analyses are shown in Table 5.

TABLE 5. *Summary statistics for the type III test of fixed effects (Wald-type test) and the estimated random effects from individuals in the generalized linear mixed model for the data in Table 4*

| | | N (%) | | | | | C (%) | | | | |
Tissue	Fixed effect	d.f.	den d.f.	F	P	Random effect	d.f.	den d.f.	F	P	Random effect
Leaf	Fruiting	1	16	35·19	**< 0·0001**	0·0517	1	21	0·32	0·576	0
	CO_2	1	5	0·01	0·932		1	21	0·08	0·782	
	Fruiting × CO_2	1	16	1·53	0·235		1	21	0·03	0·867	
	Date	1	16	47·25	**< 0·0001**		1	21	2·09	0·163	
	Date × CO_2	1	16	0·47	0·503		1	21	2·19	0·154	
	Fruiting × date	1	16	8·99	**0·009**		1	21	0·16	0·689	
Xylem	Fruiting	1	16	36·73	**<0·0001**	0·0151	1	16	0·67	0·424	0·0978
	CO_2	1	5	1·60	0·261		1	5	0·02	0·894	
	Fruiting × CO_2	1	16	0·01	0·942		1	16	0·55	0·468	
	Date	1	16	0·78	0·390		1	16	48·87	**<0·0001**	
	Date × CO_2	1	16	1·52	0·236		1	16	1·58	0·227	
	Fruiting × date	1	16	0·28	0·605		1	16	2·15	0·162	

The degrees of freedom of the denominator (den d.f.) were approximated using Kenward and Roger's method.
Significant values are highlighted in bold.

treatment (Tables 4 and 5). In contrast, total C concentrations were unaffected by shoot type or CO_2 treatment.

DISCUSSION

In our investigations of individual shoots, fruit-bearing shoots had more leaves with a larger surface area and greater LMA than non-fruiting shoots. These results suggest that fruits develop preferentially on shoots that can provide sufficient assimilates from current photosynthesis for seed production. This is in agreement with the hypothesis of carbon autonomy for fruiting of branchlets, as had already been suggested in an experimental study at the SCC site (Hoch, 2005). However, in contrast to the current study, numbers of leaves per shoot did not differ between fruiting and non-fruiting shoots in two other masting temperate tree species: *Styrax obassia* and *Fagus crenata* (Miyazaki *et al.*, 2002; Han *et al.*, 2008). These differences in results may be because a resource is autonomic at a different size or age of branchlets among different species, which may also depend on nutrient availability which would depend on the sites. In our study the differences in

reproductive efforts between masting years are mainly controlled by the proportion of fruit-bearing shoots within the whole crown, but not by the number of fruits per fruiting shoot. This corroborates previous findings, which showed that cupules are more abundant on upper and/or outer branches in a moderate masting season, while they occur within the entire crown in a very heavy masting year (Hilton and Packham, 1997).

Competition between reproduction and vegetative growth in shoots

The numbers of leaves per shoot in masting years was smaller than in non-masting years, a relationship that also occurs in *F. crenata* (Han *et al.*, 2008). The length of terminal shoots was also shorter in the masting years than in the non-masting year in trees grown in both ambient and elevated CO_2. This might indicate that vegetative growth is suppressed by the high sink strength of reproductive structures. Biomass increase for an individual shoot results from both elongation and radial growth. Therefore, the ratio of biomass to shoot
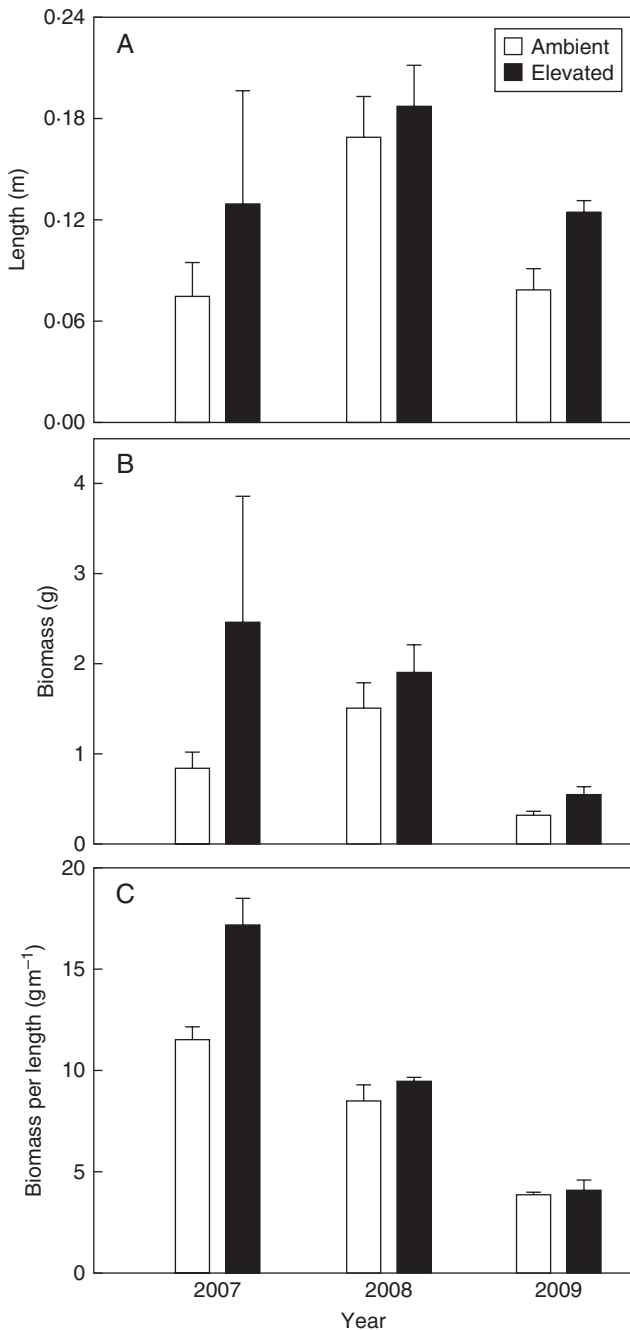
FIG. 3. Comparison of (A) length, (B) dry mass and (C) dry mass per length of terminal shoots of *Fagus sylvatica* trees (means ± s.e.) exposed to ambient ($n = 4$) and elevated ($n = 3$) CO₂ concentrations, as indicated. Masting occurred in 2007 and 2009, whereas 2008 was a non-masting year. The results of the statistical analyses are shown in Table 1.

length is a proxy for the radial growth of a shoot, excluding its shortened length in masting years. If radial growth of shoots is the same in different years, one would expect that the same mass is added to terminal shoots each year for a given shoot length. However, dry mass per length of terminal shoots in trees at ambient CO₂ was reduced in masting years (see Fig. 3C). *Fagus* is considered to be a flush-type genus, so most of the shoot elongation is completed early in the

growing season, while shoot radial growth continues until late into the season (Kikuzawa, 2003). A previous study demonstrated that, in a masting year, non-structural carbohydrate in branches was significantly reduced during mid-season in *F. sylvatica* (Hoch et al., 2003), probably indicating an increased demand for carbon for fruiting, placing constraints on individual branches.

The N concentrations in dry matter of leaves were significantly smaller in fruiting shoots than in non-fruiting shoots in September. Moreover, between the two occasions, leaf N decreased more in fruiting than in non-fruiting shoots. These results suggest that the reduction in N concentration was not caused by leaf senescence, but by the high N sink strength resulting from seed production. Neighbouring foliage might serve as an N source for reproductive tissues, as has been demonstrated in *Pseudotsuga menziesii* and *S. obassia* (McDowell et al., 2000; Miyazaki et al., 2002). In addition, xylem N concentration of fruiting shoots was distinctly smaller than in non-fruiting shoots, implying that N for fruiting is supplied from the fruiting branchlets, but not from neighbouring non-fruiting parts of the crown.

CO₂ effects on reproduction–growth trade-offs

In contrast to trees growing at ambient CO₂, there was no decrease in dry mass per length of terminal shoots in the 2007 masting year compared with the 2008 non-masting year in trees exposed to elevated CO₂. It is likely that enhanced photosynthesis at elevated CO₂ concentrations (Zotz et al., 2005; Bader et al., 2010) alleviated the competition between seed production and shoot growth, of which the former is the strongest sink for newly produced photoassimilates in many species such as herbs and trees (Wardlaw, 1990; Hoch and Keel, 2006; Kudo and Ida, 2010). In contrast, CO₂ enrichment had no effect on the numbers of leaves or fruits per shoot, which is consistent with previous results from the same site based on litter trap collections (Körner et al., 2005). In addition, no significant increase in tree-ring increment of *F. sylvatica* has been recorded under elevated CO₂ at the SCC site (Körner et al., 2005; Asshoff et al., 2006). Our findings for small branchlets support the hypothesis of module specialization and physiological integration for reproductive events (Obeso, 2002): resource allocation within branchlets might respond to local autonomy and trade-offs (e.g. leaf number, shoot growth, fruiting effort and seed production), but is probably integrated at individual trees (e.g. degree of fruit loading or tree-ring growth).

It has been reported that the average frequency of masting in *F. sylvatica* has increased during the last 30 years (Hilton and Packham, 1997; Övergaard et al., 2007). Moreover, masting of *F. sylvatica* in two consecutive years, which was considered impossible in older literature, has recently been recorded by litter trap collections (Hilton and Packham, 1997; Körner et al., 2005; Övergaard et al., 2007). In the current study, both C and N resources were found to be autonomous within small branchlets, and elevated CO₂ alleviated the competition for C between reproduction and vegetative growth, as indicated by some leaf and shoot traits. If resource balance controls masting in *F. sylvatica*, the ongoing rising atmospheric CO₂

concentrations and N deposition may already have led to a higher frequency of masting events as observed over recent decades.

In conclusion, when masting in *F. sylvatica* occurred there were fewer leaves per shoot, and the increase in elongation and biomass of shoots was decreased, indicating competition for resources between the development of reproductive structures and growth within the shoot; the effect of elevated CO_2 was to lessen the decrease in biomass of shoots caused by masting, so the competition may be ameliorated in the future as a result of rising atmospheric CO_2 concentrations.

ACKNOWLEDGEMENTS

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