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# Comparative stem-growth rates of Mediterranean trees under background and naturally enhanced ambient CO<sub>2</sub> concentrations

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## SUMMARY

Ring widths of five Mediterranean forest tree species (*Arbutus unedo*, *Fraxinus ornus*, *Quercus cerris*, *Quercus ilex* and *Quercus pubescens*) growing close to a natural source of CO<sub>2</sub> in Tuscany, Italy and at a nearby control site were compared. At the CO<sub>2</sub>-enriched site, trees have been growing for decades under elevated CO<sub>2</sub> concentrations. They originated from parent trees that also grew under elevated CO<sub>2</sub> in natural conditions, and they have been continuously exposed to elevated CO<sub>2</sub> throughout their growth. Tree-ring series from each of the species were prepared. Assigning calendar dates to rings was difficult but possible, and ring-width series were built for all species. The ring-width data were analysed using a two-sided *t*-test to assess if there was a difference between the radial growth at the CO<sub>2</sub>-enriched site and the control site. The cumulative basal area at the same cambial age at both sites was also compared using a Wilcoxon test. Radial growth of trees at the CO<sub>2</sub>-enriched site was not significantly different from growth at the control site. For each species, year by year, radial growth at the CO<sub>2</sub>-enriched site was tested against the control site and significant differences were found in only a few years; these differences were not synchronous with extreme climatic events. The expected increase in above-ground productivity, as one of the ecosystem responses to increasing CO<sub>2</sub> during drought stress, was not observed in this Mediterranean woody plant community, despite being water-limited. Other resource limitations, such as low nutrient availability (common in the Mediterranean region), may have counteracted the positive effect of elevated CO<sub>2</sub> under drought stress, or trees may have acclimated to the high CO<sub>2</sub>.

**Key words:** *Arbutus unedo* (strawberry tree), carbon sequestration, dendroecology, Mediterranean trees, natural CO<sub>2</sub> springs, *Quercus ilex* (holm oak), tree rings, water stress.

## INTRODUCTION

Atmospheric CO<sub>2</sub> mole fractions are rising at a rate of 1–2 μmol mol<sup>-1</sup> yr<sup>-1</sup>, largely as a result of the burning of fossil fuels (Keeling *et al.*, 1995), and are expected to reach more than 700 μmol mol<sup>-1</sup> by the year 2100 (Houghton *et al.*, 1995). Climate change associated with increases in CO<sub>2</sub>, as well as other

greenhouse-active gases, may result in higher temperatures and decreasing soil moisture (Mitchell *et al.*, 1990) if precipitation does not increase (Rind *et al.*, 1990). Plant communities in ecosystems that experience a combination of high temperatures, sub-optimal levels of soil moisture and the presence of airborne pollutants are expected to be particularly sensitive to elevated CO<sub>2</sub> (Moreno & Oechel, 1995). Many ecosystems in the Mediterranean Basin experience these conditions. Moreover, the whole

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Mediterranean region has been subject to human activities (coppicing, grazing, fire, etc.) since ancient times (Le Houérou, 1981), and as a result many of today's ecosystems are particularly fragile. Some Mediterranean ecosystems are therefore expected to react dramatically to global change.

Despite semi-arid woody ecosystems comprising 16% of the world's terrestrial biomass, and containing 23–25% of the area and net primary productivity of the world's terrestrial surface (Atjay *et al.*, 1979), they have not been extensively studied. Amongst other effects on woody plants and ecosystems, increasing CO<sub>2</sub> is expected to increase net primary productivity (Melillo *et al.*, 1993; Amthor, 1995; Loehle, 1995) and to stimulate biomass accumulation (Ceulemans & Mousseau, 1994; Saxe *et al.*, 1998). However, there is little information to date on the effects of elevated CO<sub>2</sub> on productivity and carbon sequestration in native woody ecosystems (Mooney *et al.*, 1991). The majority of studies with forest tree species are limited to seedlings or saplings growing in chambers, rather than mature trees growing under natural conditions for long periods (Eamus & Jarvis, 1989; Amthor, 1995). Consequently, the responses to elevated CO<sub>2</sub> of plants grown in communities should not be directly extrapolated from studies of individually grown plants (Körner *et al.*, 1996).

Tree stems represent the critical link between roots and leaves and assume a major role in the exploitation of above-ground resources (Hinckley & Schulte, 1995). Stem wood accounts for the largest proportion (20–40%) of total ecosystem C above ground in closed forests (Saxe *et al.*, 1998), but uncertainty still exists over the magnitude of C storage in forests (Dixon *et al.*, 1994). An early report of a possible CO<sub>2</sub> fertilization effect on stem wood increment was given by LaMarche *et al.* (1984) based on enhanced growth shown in tree-ring series obtained from high-elevation pine species. More recently, other authors (e.g. Hari & Arovaara, 1988; Kienast & Luxmoore, 1988; Graumlich, 1991; Graybill & Idso, 1993; Becker *et al.*, 1995; Nicolussi *et al.*, 1995) have reported some indications of enhanced tree growth, which has been attributed (in some cases) to CO<sub>2</sub> increases from pre-industrial levels to present values (Watson *et al.*, 1990). Schweingruber *et al.* (1993), through cross-continental surveys of tree rings, suggested that the most likely response of adult trees to current atmospheric CO<sub>2</sub> enrichment in the boreal zone is close to zero, while Phillips & Gentry (1994) showed that tropical forests may be stimulated. Tree rings in Mediterranean-type forested ecosystems, which represent a transition phase from tropical to boreal vegetation, could therefore provide important information on the responses of tropical and temperate environments to global change. However, they have seldom been used for dendroecological purposes,

primarily because of difficulties in the dating of individual tree rings (Fahn, 1953; Serre-Bachet, 1985; Liphshitz & Lev-Yadun, 1986; Guibal, 1996).

Although not ideal, the analysis of trees surrounding natural geological CO<sub>2</sub> degassing vents may provide the best available surrogate for long-term experiments (Amthor, 1995). Natural CO<sub>2</sub> springs have exposed terrestrial ecosystems to elevated CO<sub>2</sub> for generations in an otherwise natural or culturally modified environment (Miglietta & Raschi, 1993; Miglietta *et al.*, 1993; Körner & Miglietta, 1994; van Gardingen *et al.*, 1995). Natural CO<sub>2</sub> springs, being exposed to a combination of environmental forcing factors and human activities (Field *et al.*, 1992), may constitute a unique opportunity for CO<sub>2</sub> impact studies and may help the prediction of future ecosystem responses to global change (Raschi *et al.*, 1997).

Many studies have been made in the past decade at natural CO<sub>2</sub> springs in Italy, and the observed physiological responses under elevated CO<sub>2</sub> concentration (in terms of gas exchange and water relations) have confirmed experimental evidence: lower stomatal density and stomatal index (Jones *et al.*, 1995; Paoletti *et al.*, 1998); reduced stomatal conductance (Bettarini *et al.*, 1998); diminished superoxide dismutase activity (Schwanz & Polle, 1998); and smaller foliage area for a corresponding sapwood cross-sectional area (Tognetti *et al.*, 1999). Hättenschwiler *et al.* (1997a), through the analysis of tree-ring data from *Quercus ilex* trees growing around two separate natural CO<sub>2</sub> springs, reported that trees grown under high CO<sub>2</sub> for 30 yr showed a 12% greater final radial stem width than those growing at the ambient-CO<sub>2</sub> sites. However, this stimulation was largely due to responses when trees were young. By the time the trees were 25–30 yr old, the annual differences in tree-ring width between trees grown in background and elevated CO<sub>2</sub> had disappeared. At any given tree age, elevated CO<sub>2</sub> had a relatively greater positive effect on tree-ring width in years with a dry spring compared to years with more rainfall between April and May. Thus elevated CO<sub>2</sub> increased radial stem width when the trees were young, but positive responses disappeared in the annual rings when the trees were approx. 30 yr old. If this is generally true for other woody species, despite the initial acceleration of tree growth under elevated CO<sub>2</sub> (thus enhancing forest dynamics), long-term tree C stocks may not become greater.

The aim of this study was to extend the findings of Hättenschwiler *et al.* (1997a) to several neighbouring tree species that are dominant or codominant in the Mediterranean woody plant community. Our objectives were to assess whether tree-ring growth at natural CO<sub>2</sub> springs is enhanced, and to provide further information on the capability of stems in Mediterranean ecosystems to sequester C.

## MATERIALS AND METHODS

*Site description*

The study was carried out at a natural CO<sub>2</sub> spring near Lajatico, Pisa, Italy called 'I Borboi' (lat 43° 26' N, long 10° 42' E). The enriched area extends over 0.7 ha. The area is covered by a coppiced stand dominated by *Quercus ilex* L., in which *Quercus pubescens* Willd. and *Arbutus unedo* L. (as well as several other tree species, including *Quercus cerris* L. and *Fraxinus ornus* L., represented by scattered individuals) and a shrub layer (including, other than the species studied here, *Smilax aspera* L., *Cytisus scoparius* L., *Cistus salviifolius* L., *Genista* sp., *Ligustrum vulgare* L., *Pistacia lentiscus* L. and *Phyllirea latifolia* L.) constitute the bulk of the flora. No information is available about past mortality and stand dynamics.

The CO<sub>2</sub> spring is located on the north-facing slope (20%) of a hill near the bottom of a small valley at 210 m above sea level (Raiesi, 1998). A full description of the geology of the site is given by Panichi & Tongiorgi (1976). Almost pure CO<sub>2</sub> emissions occur from a series of vents located along a narrow seasonal creek, and the CO<sub>2</sub> tends to decrease up the slope. The vents emit small amounts of H<sub>2</sub>S, but H<sub>2</sub>S mole fractions never exceed 0.04 μmol mol<sup>-1</sup>, which is not considered to be harmful (H. Rennenberg, pers. comm.). Mole fractions were measured periodically throughout the year with a portable infrared gas analyser (EGM-1, PP-Systems, Hitchin, Herts, UK) and absorptive diffusion tubes (500/a-D, Dräger, Lübeck, Germany) (Fig. 1). Plants around the spring are exposed to daytime CO<sub>2</sub> mole fractions of approx. 700 μmol mol<sup>-1</sup> throughout the year, with short-term variations between 500 and 1000 μmol mol<sup>-1</sup> depending on wind speed and convective turbulence. The CO<sub>2</sub> at different heights within the canopy varies little.

Stem samples were obtained from trees growing in the proximity of the CO<sub>2</sub> spring. Additional measurements were made at a control site chosen along the same creek approx. 150 m downstream, outside the CO<sub>2</sub>-enriched area (Fig. 1). When working with natural vegetation, variability in characteristics within and between populations can exceed any response to CO<sub>2</sub> (van Gardingen *et al.*, 1997). At our site, soil water availability and CO<sub>2</sub> are co-varying factors, making the choice of control site critical. The control site was selected as close as possible to the CO<sub>2</sub> spring, on the same slope, with similar vegetation, soil type and environmental and biological characteristics. Our control site was 200 m closer to the CO<sub>2</sub> spring than that of the earlier study by Hättenschwiler *et al.* (1997a). The roots of selected plants experienced the same soil environment, and branches the same aerial environment, except for CO<sub>2</sub>. The seasonal mean leaf area index

(LAI) at both sites was approx. 3.5. The area has non-calcareous, brown, loamy, clayey soils, developed from calcareous marl (pH 6–7). Soil nutrient availability is similar between the control and the CO<sub>2</sub>-enriched site (Raiesi, 1998; Raiesi Gahrooe, 1998). The climate is typical Mediterranean, with cool, wet winters and hot, dry summers. The influence of climate on tree-ring width at the CO<sub>2</sub>-enriched and control site was assessed using meteorological data recorded at the Saline Meteorological Station, (72 m above sea level, approx. 12 km from the site): mean annual precipitation for the period 1958–95 was 882 mm (Fig. 2) and mean annual temperature was 13.7°C.

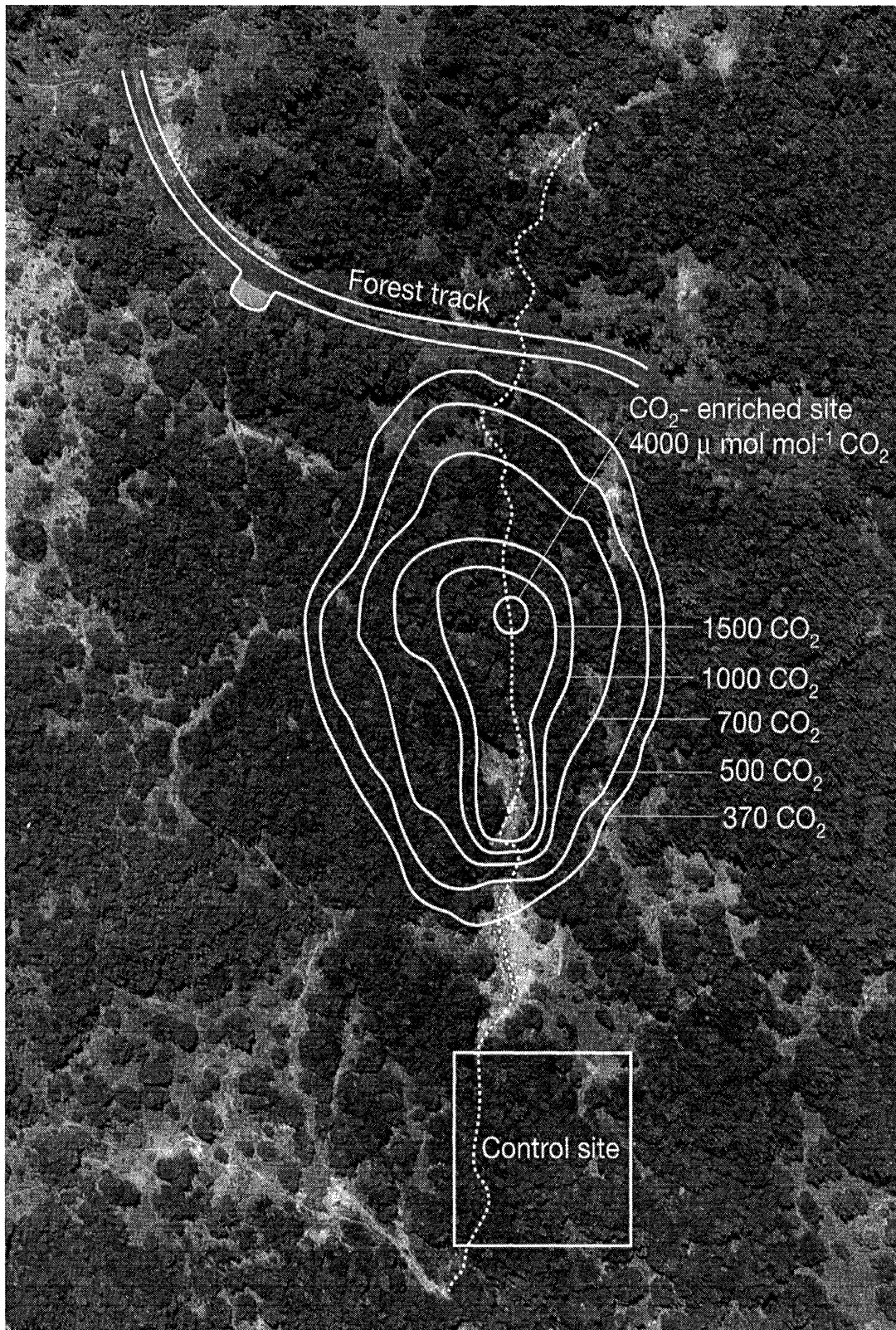
*Tree sampling and dendroecological analysis*

Approximately 10 dominant and codominant individuals for each of *A. unedo*, *F. ornus*, *Q. cerris*, *Q. ilex* and *Q. pubescens* were selected. As the location of our control site differed from that used by Hättenschwiler *et al.* (1997a) to look at *Q. ilex*, we also included this species in our sample. We selected single, erect stems, but were unable to distinguish between trees originating from seedlings and sprouts originating from stumps formed by coppicing.

Trees growing in a Mediterranean climate are sometimes difficult to use in dendroecology because of the presence of false rings. Missing rings, which occur when a tree fails to put on any radial increment at the sampling height in a specific year, are relatively rare in the Italian macchia vegetation type, as there is sufficient winter rainfall to ensure that some growth occurs. However, because of the likely presence of false rings and the potential risk of missing rings, it is essential to have an adequate sampling programme, and great care needs to be taken to ensure that each measured ring width is assigned the correct calendar date. Dating of individual rings can be done by visual comparisons of series, using skeleton plots (Douglass, 1939) or by cross-dating (Fritts, 1976; Pilcher, 1990).

In this study, trees were sampled during May 1997 and May 1998. In 1997, trees were cored at 1 m height. To avoid reaction (tension) wood, two wood cores were taken at 180° to each other with an increment borer 0.5 cm in diameter. Cores were mounted on channelled wood, seasoned in a fresh-air dry store and sanded a few months later. As anticipated, some of the cores had false rings or were otherwise difficult to date. We therefore revisited the site in 1998 and took 31 cross sections at 1 m height for species that were difficult to date using tree cores (14 cross sections for *A. unedo*, 10 for *Q. ilex* and seven for *F. ornus*). In all, we analysed 89 series from 51 trees at the CO<sub>2</sub>-enriched site, and 81 series from 43 trees at the control site (Table 1).

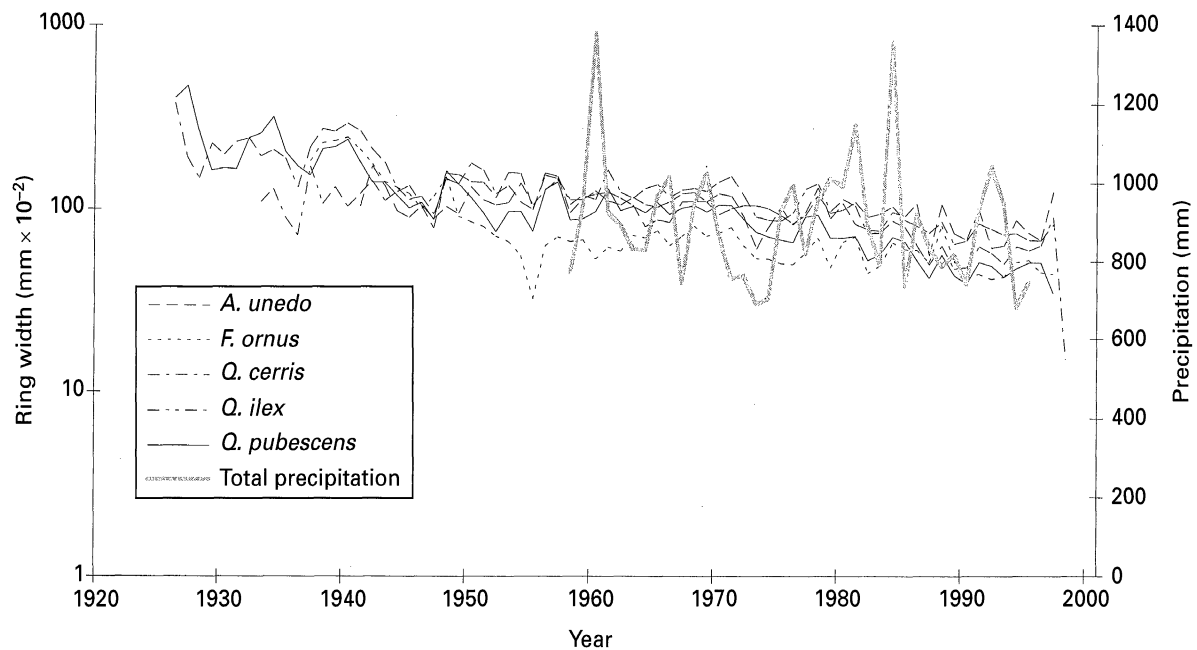
Ring-width measurements were made to the nearest 0.01 mm on the cores and on two radii on



**Fig. 1.** Map (1:2000) of the study area showing isolines of  $\text{CO}_2$  measured around the geothermic  $\text{CO}_2$  spring. Isolines were drawn using mean  $\text{CO}_2$  concentrations from several sampling dates during 1997 (absorptive diffusion tubes and infrared gas analyser) at approx. 50 locations within the study area. The location of the main point source of  $\text{CO}_2$  and where trees were sampled (rectangle) is indicated.

each of the cross sections, using TSAP measurement equipment and software package (Frank Rinn, Heidelberg, Germany). The results were examined using the DENS software package (Swiss Federal Institute for Forest, Snow and Landscape Research, WSL, Birmensdorf, Switzerland). The raw ring-widths of the single curves of each dated tree were

plotted, cross-dated visually and then cross-dated statistically by (i) the Gleichläufigkeit (there is no English equivalent to this term), which is the percentage agreement in the signs of the first differences of two time series; and (ii) Student's *t*-test which determines the degree of correlation between the curves.



**Fig. 2.** Mean ring-width chronologies for all trees (growing at the CO<sub>2</sub> spring and at the control site) of each species at Lajatico, and total annual precipitation at the meteorological station of Saline for the period 1958–95.

**Table 1.** Number of samples and of sample trees for each species at Lajatico, Italy

Species	No. of samples CO <sub>2</sub> -enriched	No. of trees CO <sub>2</sub> -enriched	No. of samples Control site	No. of trees Control site
<i>Arbutus unedo</i>	21	11	17	9
<i>Fraxinus ornus</i>	17	11	16	8
<i>Quercus cerris</i>	15	10	15	9
<i>Quercus ilex</i>	18	9	14	7
<i>Quercus pubescens</i>	18	10	19	10

Although standard methods were used to build an averaged series for each species at each site, details are provided here, as the development of such series can have an impact on any signal contained in the ring series. Ring-width measurements for a given calendar year from different trees were averaged into mean series. A series of mean annual ring width chronologies contains different signals that can be described by the following general model (Cook, 1987a, b):

$$R_t = G_t + C_t + D_{1,t} + D_{2,t} + E_t$$

( $R_t$  is the observed ring-width series measured along a single radius of an individual tree  $t$ ;  $G_t$  is the growth trend associated with increasing age and size of the tree;  $C_t$  represents the climatically related growth variations common to the whole stand, but excluding the effects of extreme events such as wind damage and severe frosts;  $D_{1,t}$  is the variance due to endogenous disturbances that have an impact that affects individual trees or a small subset of trees within the stand, which are essentially independent of the environment;  $D_{2,t}$  is the variance due to exogenous disturbances that have an impact across the whole stand, including the effects of fire, wind and frost;  $E_t$  is the random variance unique to each tree or radius. The  $_$  term associated with  $D_{1,t}$  and

$D_{2,t}$  is a binary indicator of the presence ( $_ = 1$ ) or absence ( $_ = 0$ ) of a subseries in  $R_t$  for some year or group of years.)

Different signal types may be detected over short time scales (i.e. affecting inter-annual variability or climate responses through time) or longer time scales (as underlying trends). Standardization, which is the removal of long-term variations from a time series of measured ring widths by dividing the measurements by a standardizing smoothing function and their conversion to a time series of ring-width indices (Fritts, 1976), is commonly used to remove age-related sample bias. However, we did not use standardization techniques because, although they effectively minimize or modify the effects of disturbances by removing the low-frequency variability attributable to stand dynamics (Cook *et al.*, 1990a,b), they also remove or change other low-frequency signals, such as evidence of pollution or long-term climate change (Briffa *et al.*, 1996).

For each tree, the mean ring-width cumulative curve was also computed. The mean cumulative basal area at the same cambial age (i.e. basal area produced by unevenly aged trees when having the same age) was computed for each species.

Mean sensitivity, which could be considered as an indicator of the responsiveness of trees to climate

and other exogenous factors, was analysed for all the averaged chronologies and for all the single trees within a specific chronology. Sensitivity is defined as the mean percentage change from each measured ring-width value to the next, namely the average relative difference from one ring width to the next, calculated by dividing the absolute value of the differences between each pair of measurements by the average of the paired measurements, then averaging the quotients for all pairs in the tree-ring series (Fritts, 1976). Two forms of sensitivity exist.

(i) Annual sensitivity:

$$S_{i+1} = \{[(x_{i+1} - x_i) \times 2] / (x_{i+1} + x_i)\}$$

( $x_i$  is the observed value of ring-width series at moment (yr)  $i$ ; and  $S_{i+1}$  is the sensitivity in interval  $i+1$ .)

(ii) Mean sensitivity:

$$\bar{S} = \frac{\sum_{i=1}^{n-1} |S_{i+1}|}{n-1}$$

( $n$  is the number of observations.)

The interval trend was analysed for all the mean chronologies (i.e. the number of intervals of individual ring width exhibiting the same tendency, expressed as a percentage of ascending intervals) (100% indicates that all the intervals are ascending, while 0% indicates that all are falling) (Kaennel & Schweingruber, 1995).

For all the mean chronologies, the pointer years (Cropper's values; Cropper, 1979) were analysed. Cropper's values were obtained using the formula

$$(x_i - x_{\text{mean of a 5 yr window}}) / \text{SD of a 5-yr window}$$

Skeleton plots were used to determine stem age and the life history of the trees. Analyses were carried out with the help of a stereomicroscope (Wild M3Z, Leica, Germany), using the methods described by Stokes & Smiley (1968) and Schweingruber *et al.* (1990). During the skeleton plot analyses, the age of the innermost rings (situated immediately next to the pith) and the presence of any abrupt growth changes were recorded. An abrupt growth change is defined as a sudden change (increase or decrease) in increment at least 40% above or below the average increment over the previous 4 yr.

#### Statistical analyses

Climate influence on tree-ring width at the site was assessed using meteorological data recorded at the Saline Meteorological Station. In a first step, the ageing effect was removed by modelling cambial age of ring-width series with a Hughschhoff function and indexing procedure. Afterwards, stepwise regressions and response functions were performed with Precon5<sup>®</sup> software package to assess the influence of climate on ring-width growth. Further

analyses were made of the role of intra-annual climatic variables on radial growth (Otto U. Bräker, personal communication). Prior growth was also taken into account in the models, as although the climate of a given year can have a large effect on the ring width for the same year, it can also affect ring width for a number of subsequent years (the autocorrelation function) (Fritts, 1976).

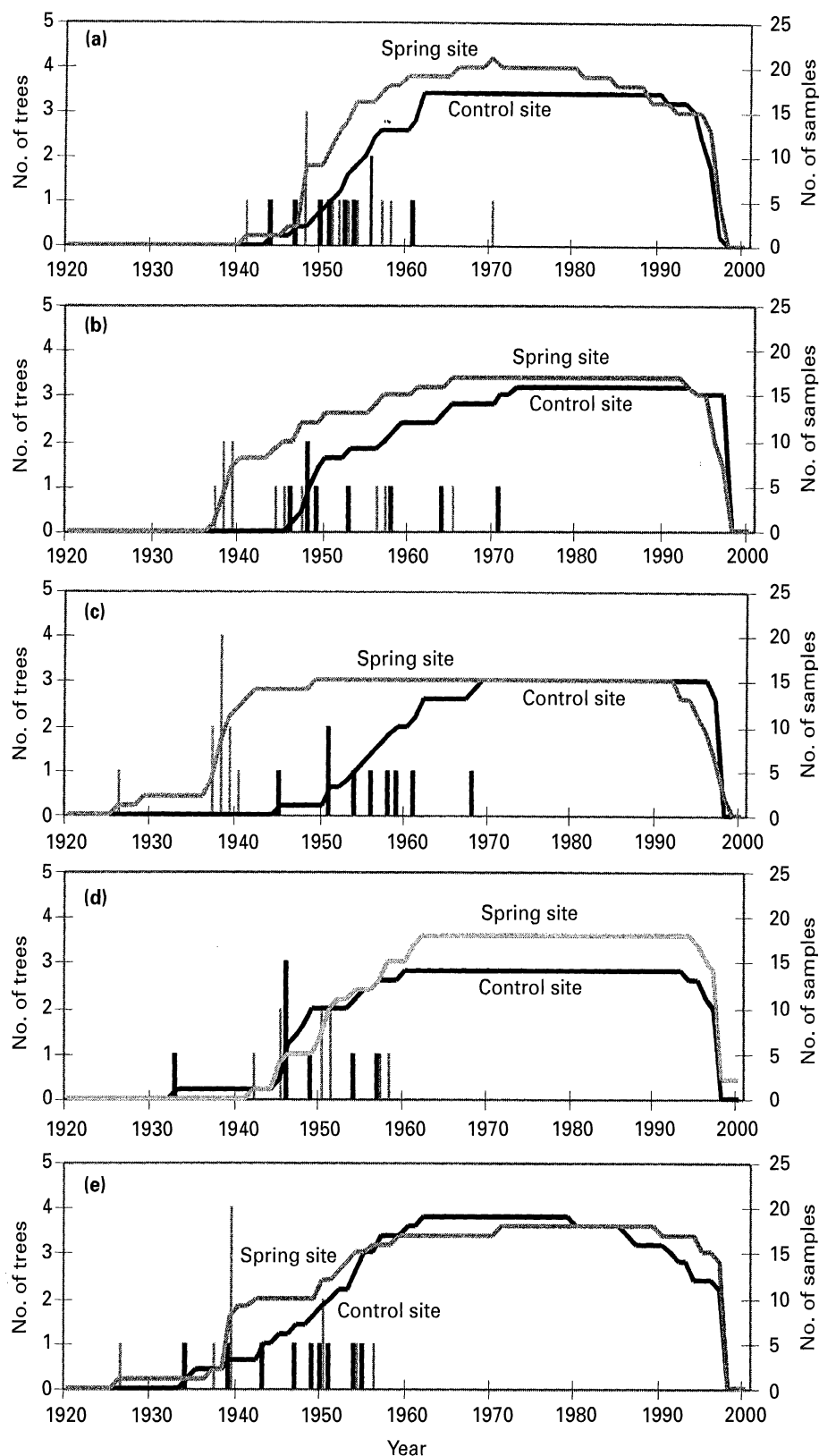
Statistical analyses were undertaken using the SAS System (SAS Institute, 1989) to determine any differences in radial growth between the CO<sub>2</sub>-enriched and control sites. First, we checked if variances were significantly different. The variance was equal in all cases except two. The data were then analysed using a two-sided *t*-test. For each species, year by year, radial growth at the CO<sub>2</sub>-enriched site was tested against the control site. The hypothesis was that the difference was not significant and the means were tested for equality. Furthermore, the cumulative basal area at same cambial age was analysed. We performed both a two-sided *t*-test and a Wilcoxon (rank sums) test.

## RESULTS

### Tree-ring width chronologies

Dating tree rings was very difficult, but possible, as shown by the synchronous occurrence of pointer years – years in which particularly narrow or wide rings are formed – in the mean ring-width chronologies of different sites and species (Fig. 2). This indicates that the annual rings were assigned the correct calendar years. A climatic signal may be present in tree-ring patterns. Although a strong correlation between ring width and total annual precipitation was not found, some dry periods (1972–75, 1982–83, 1989–90) have influenced the ring-width growth, as shown by ring widths and climatic records (Fig. 2).

For a better understanding of the role played by climate, models were run to examine the percentage of variance explained by prior growth. Prior growth explained more than 20% of the variance for radial growth of *F. ornus*, more than 30% for *Q. ilex*, more than 50% for *Q. cerris* and more than 60% for *Q. pubescens*, but did not affect radial growth of *A. unedo*. No clear differences were observed between the CO<sub>2</sub>-enriched and control site. More detailed analyses (P. Cherubini *et al.*, unpublished) show that the precipitation regime for May affected radial growth of all species at Lajatico. Only the precipitation in May significantly influenced the ring width of all species. Winter precipitation plays a role for all *Quercus* species (December of previous year for *Q. cerris*, February for *Q. ilex*, and January for *Q. pubescens*). Precipitation in August of the current year plays a positive role on tree-ring growth for *Q. cerris* and *Q. pubescens*. These species do not stop



**Fig. 3.** Sample depth through time and distribution of innermost rings (i.e. number of rings situated immediately next to the pith on cross sections) which gives approximate age of each tree, for all the species at the CO<sub>2</sub> spring site and at the control site. (a) *Arbutus unedo*; (b) *Fraxinus ornus*; (c) *Quercus cerris*; (d) *Quercus ilex*; (e) *Quercus pubescens*.

growing in summer and therefore are adversely affected by very dry months, i.e. August. *Quercus ilex* is the only species that reacts significantly to late summer or early autumn precipitation (September) of the current year. Growth of *A. unedo* is influenced by the precipitation in April, May and June of the current year.

#### Age structure

The age of the innermost ring gives an approximate age for each tree (Fig. 3). At this site trees grow fast, and typically reach 1 m height when they are 2–3 yr old (unpublished results), so that the error in assessing the establishment date of each tree, caused



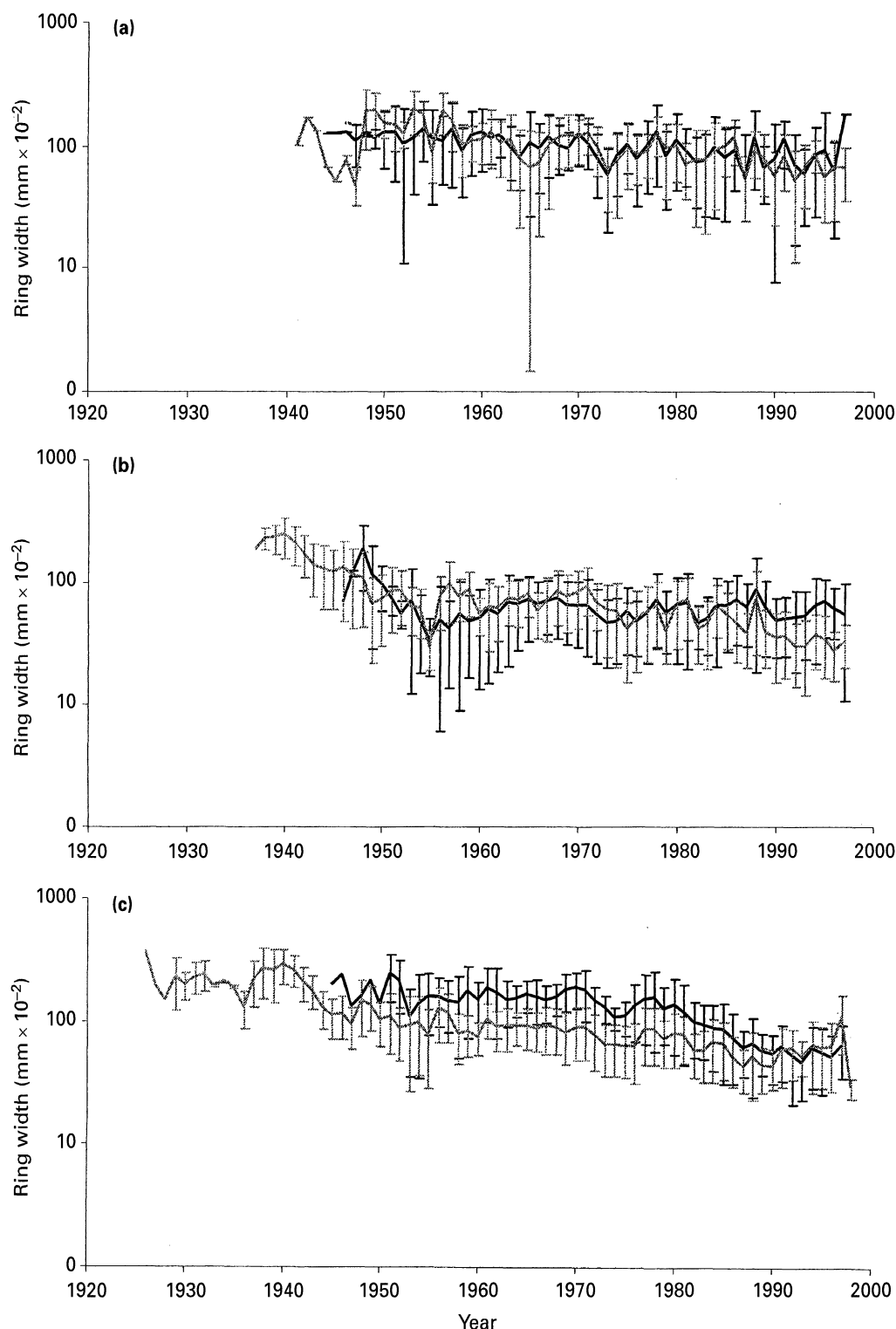


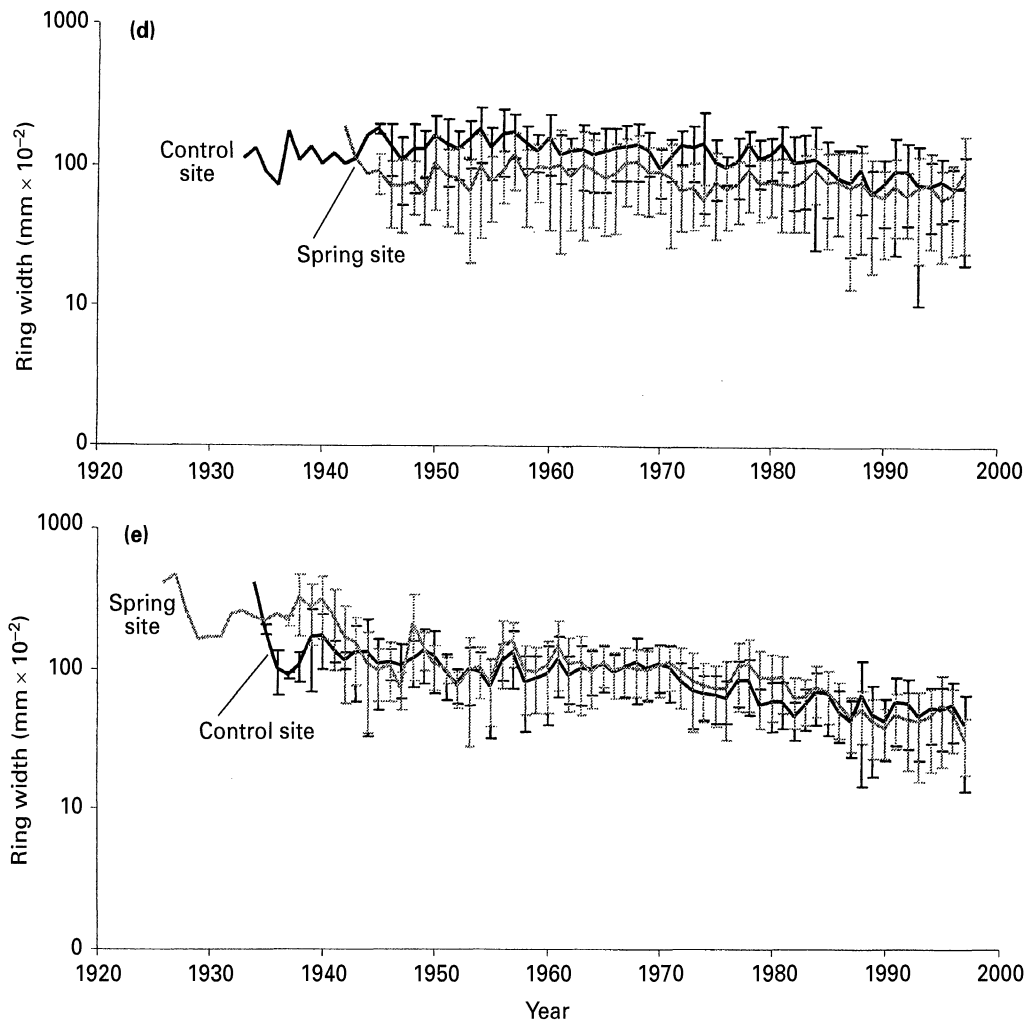
Fig. 4. For legend see opposite.

by the cores and cross sections being taken at 1 m height rather than at the stem base, is negligible. The age given by the innermost ring can be considered as the actual age.

#### Radial growth

Annual ring widths of each species were compared between the CO<sub>2</sub>-enriched and control sites. The periods considered were 1948–96 for *A. unedo*, 1948–97 for *F. ornus*, 1951–97 for *Q. cerris*, 1946–97 for *Q. ilex*, and 1939–97 for *Q. pubescens*. There were

no significant differences in the mean ring-width chronologies between the control and enriched sites for any of the species (Fig. 4). Some trends between sites were observed, but not always in the expected direction. Ring widths at the CO<sub>2</sub>-enriched site were higher for young *A. unedo*, *F. ornus*, and *Q. pubescens*, but these differences decreased with increasing tree age, and *F. ornus* growth has been higher at the control site in recent years. This is consistent with expectations (Hättenschwiler *et al.*, 1997a). However, ring widths of *Q. cerris* and *Q. ilex* were higher at the control site than at the CO<sub>2</sub>-enriched site, although these differences also decreased with time.



**Fig. 4.** Mean ring-width chronologies (log-transformed) of *Arbutus unedo*, *Fraxinus ornus*, *Quercus cerris*, *Quercus ilex* and *Quercus pubescens* at the CO<sub>2</sub> spring and control site. Vertical bars indicate SE. (a) *A. unedo*; (b) *F. ornus*; (c) *Q. cerris*; (d) *Q. ilex*; (e) *Q. pubescens*.

The interval trend for all the mean chronologies was 100% in 1967, 1977, 1984, 1988 and 1991, while it was 0% in 1979, 1987 and 1989. These data do not seem to be controlled by total annual precipitation (e.g. 1967 was a very dry year).

Within each species, the interval trend was analysed for all trees for the period 1950–96. All species at the control site showed higher interval trend values than at the CO<sub>2</sub>-enriched site. Regardless of the site, *Q. ilex* showed the lowest values (always less than 80%) and *A. unedo* the highest (21% of the years with more than 80%).

Pointer years (Cropper's values), which indicate the trees' reactions to extreme environmental conditions (at this site negative pointer years are triggered by droughts), were analysed for all the mean chronologies. In all species the negative pointer years (narrow rings) rarely differed between the control and CO<sub>2</sub>-enriched sites (6 yr in *Q. ilex*, 5 in *A. unedo*, 4 in *Q. cerris*, 2 in *Q. pubescens* and 1 in *F. ornus*), indicating similar responses irrespective of the CO<sub>2</sub> concentrations. This is an interesting result. At our site, pointer years are triggered by drought events. Our hypothesis was that dry conditions should have a less pronounced effect on trees growing

under elevated CO<sub>2</sub> concentrations, because in such conditions trees should save water through stomatal closure due to enriched CO<sub>2</sub>, and therefore respond with a higher water use efficiency (WUE) through increased photosynthetic rates and decreased stomatal conductance. Our findings show that even trees growing under elevated CO<sub>2</sub> concentrations are affected by severe droughts.

#### *Cumulative basal area at same cambial age*

Studies of annual growth differences do not take into account long-term changes that may only be apparent in the form of cumulative effects. Considering the data shown in Fig. 5, in all cases there were no significant differences in the cumulative basal areas between sites. The curves for *Q. cerris* and *A. unedo* are almost identical. Those for *F. ornus* and *Q. pubescens* suggest that given a longer time series, a significant difference in cumulative growth might become apparent, with growth being greater at the CO<sub>2</sub>-enriched site. The curve for *Q. ilex* indicates that long-term growth at the CO<sub>2</sub>-enriched site may eventually be lower than at the control site. This hypothesis was confirmed by statistical analyses.

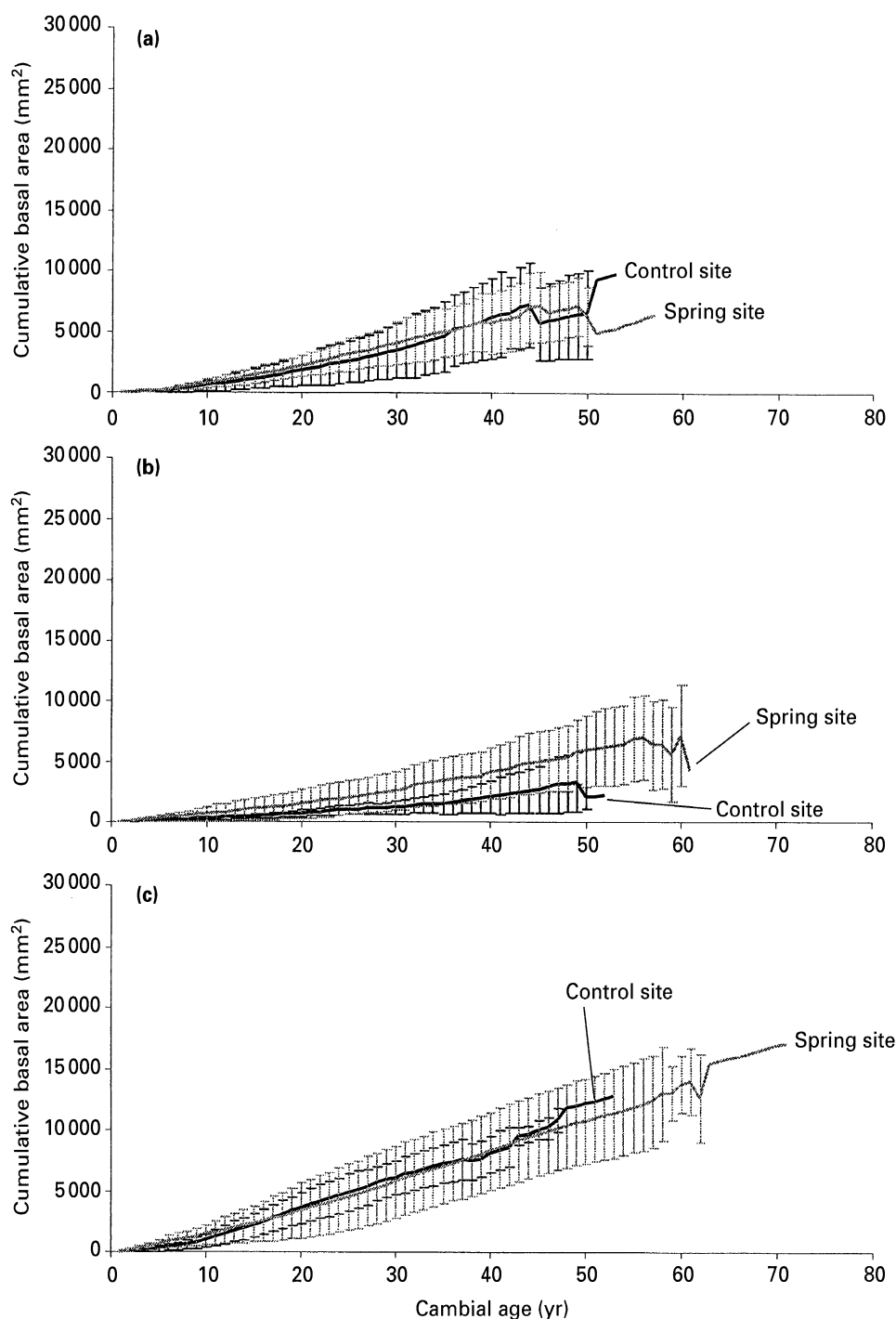


Fig. 5. For legend see opposite.

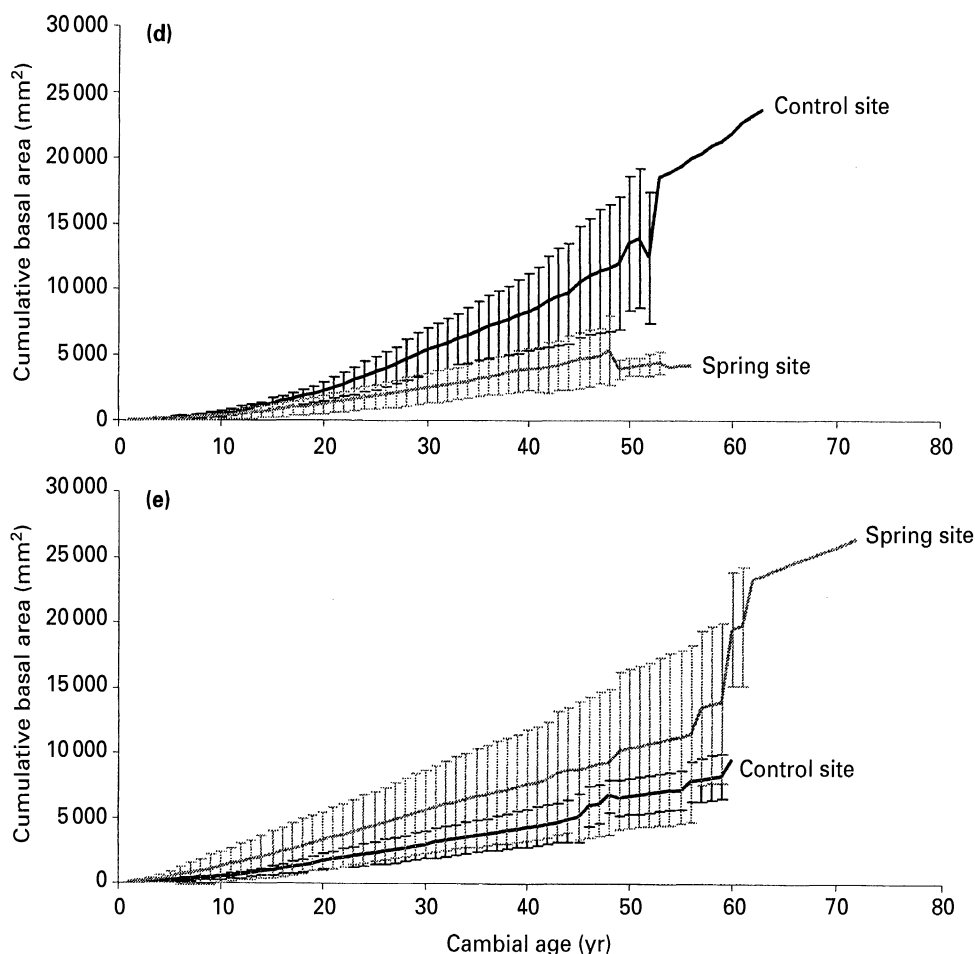
The *t*-test and the Wilcoxon test gave similar results. Using the Wilcoxon test, for *A. unedo*, *F. ornus*, *Q. cerris* and *Q. pubescens* no consistently significant (at  $P = 0.05$ ) difference was found, whereas for *Q. ilex* from cambial age 18 onwards, the cumulative basal area was for each year significantly different ( $P = 0.044$ – $0.003$ ) (Table 2).

#### DISCUSSION

In this paper we present the first tree-ring series for a widespread Mediterranean species (*A. unedo*). It was possible to date tree rings for all the species included in the study. In Mediterranean environments, cross-dating of ring-width time series is

difficult and time-consuming, but is possible. Whole-stem disks are preferable when sampling because of missing and/or false rings and unclear ring boundaries.

All trees had similar ages and life histories, regardless of site. Establishment occurred mostly after 1935, indicating a common origin, probably triggered by increased light following coppicing. The only exceptions were *Q. cerris* and *Q. pubescens*, which had trees that were 10–20 yr older at the CO<sub>2</sub>-enriched site. Consequently, although growth at a specific cambial age was comparable, the overall series in relation to calendar date for these species were not compared. The trees at the enriched site became established earlier (in 1927), probably having



**Fig. 5.** Mean cumulative basal area of five tree species close to the CO<sub>2</sub> spring and at the control site. (a) *Arbutus unedo*; (b) *Fraxinus ornus*; (c) *Quercus cerris*; (d) *Quercus ilex*; (e) *Quercus pubescens*.

**Table 2.** Differences (expressed as *P* values determined using the Wilcoxon test) between cumulative growth at the elevated CO<sub>2</sub> site and the control site

Cambial age (yr)	<i>Arbutus unedo</i> ( <i>P</i> )	<i>Fraxinus ornus</i> ( <i>P</i> )	<i>Quercus cerris</i> ( <i>P</i> )	<i>Quercus ilex</i> ( <i>P</i> )	<i>Quercus pubescens</i> ( <i>P</i> )
10	0.11	0.17	0.19	0.09	0.02
15	0.15	0.13	0.65	0.09	0.04
20	0.13	0.23	0.27	0.03	0.07
25	0.21	0.13	0.21	0.02	0.05
26	0.21	0.13	0.21	0.01	0.05
30	0.42	0.06	0.31	0.004	0.07
35	0.60	0.03	0.56	0.006	0.08
40	1.00	0.05	1.00	0.004	0.11

No significant ( $P \leq 0.05$ ) long-term differences were observed, except for older *Quercus ilex* and younger *Q. pubescens*. In the latter case, the differences disappeared after 15 yr. *Q. ilex* growth was significantly lower at the CO<sub>2</sub>-exposed site.

been present in the understorey before coppicing. Tree establishment of all species at both sites continued until 1972, showing that establishment in such stands is not restricted to a few years following the coppicing, but is possible under the canopy. No positive abrupt growth changes (i.e. growth releases after suppression) occurred, so it is unlikely that the stands were subjected to any major disturbances after establishment (such as coppicing or natural tree fall). All trees showed the same life history, regardless of the site.

The sample depth curve showing the number of specimens of each species indicated that further analyses of the ring-width data should be restricted to the period 1950–96.

Annual radial increment at the CO<sub>2</sub>-enriched site was significantly greater than at the control site in only three individual cases (1956 for *A. unedo*; 1957 and 1959 for *F. ornus*), and no synchronicity with particularly dry climatic conditions, as expected for trees with a higher WUE, was found. The frequency with which growth was significantly greater at the

**Table 3.** Sensitivity values (for single trees within a specific chronology and mean chronologies) for five tree species

Species	Mean sensitivity		Mean sensitivity of mean curves	
	CO <sub>2</sub> spring	Control	CO <sub>2</sub> spring	Control
<i>Arbutus unedo</i>	42.39	46.04	27.84	23.45
<i>Fraxinus ornus</i>	33.78	30.52	20.62	18.06
<i>Quercus cerris</i>	23.97	28.46	17.75	19.77
<i>Quercus ilex</i>	38.38	35.90	16.38	16.64
<i>Quercus pubescens</i>	25.37	29.62	18.65	17.92
Average	32.78	34.11	20.25	19.17

See text for details. Differences between CO<sub>2</sub> spring and control site were never significant for all the species.

control site decreased with time (i.e. with increasing ring-width age, and more recent calendar date). The very low percentage of years in which growth was higher at the CO<sub>2</sub>-enriched site strongly suggests that CO<sub>2</sub>-enrichment does not lead to a significant enhancement of radial increment in this Mediterranean woody plant community.

At our site *Q. ilex*, the only species studied by Hättenschwiler *et al.* (1997a), grew more slowly at the CO<sub>2</sub>-enriched site compared to the control site. A number of differences between the two studies may account for this. Different trees were selected. Hättenschwiler *et al.* (1997a) selected reproductive individuals with single and erect stems, and with similar ranges in height and ages, avoiding multi-stemmed trees. We selected dominant and co-dominant individuals, and we were not able to assess if trees originated from coppice or not. Further differences included the location of the control site (which in our case was 200 m closer to the CO<sub>2</sub>-enriched site); the number of plants sampled (at least seven trees for each of the five species at each site in this study, instead of five trees of one species); and the sampling methodology (cores plus cross sections in this study, instead of only cores). Hättenschwiler *et al.* (1997a) state that their stands were coppiced approx. 40–50 yr ago. At our sites the age structure suggests that trees became established from approx. 1940–60, and the stand was coppiced approx. 40–60 yr ago. It seems likely, therefore, that the trees in both studies experienced the same coppicing history.

There were no differences between mean sensitivity at the CO<sub>2</sub>-enriched and the control sites (Table 3). *Arbutus unedo* had the highest sensitivity. This species has the shallowest root system of the species that were sampled and is the least tolerant of prolonged drought. *Quercus* species (e.g. *Q. pubescens*) and *F. ornus* have a deep root system so they are less affected by the precipitation regime, and this is reflected in their lower sensitivities. The sensitivities can be related to the ecological characteristics of the trees, but are not influenced by long-term elevated CO<sub>2</sub>.

In all species, the negative pointer years at the control site differed from those at the CO<sub>2</sub>-enriched site in only a few cases. This suggests that the elevated CO<sub>2</sub> has not affected the response of cambial activity to extreme climatic events (e.g. droughts). Experimental work suggests that tree-ring growth should be more affected by drought at the control site than at the CO<sub>2</sub>-enriched site. No such response was found for any of the species. Elevated CO<sub>2</sub> has been shown to reduce stomatal conductance and transpiration rates in most tree species (Ceulemans & Mousseau, 1994; Saxe *et al.*, 1998). Photosynthetic rates are generally enhanced by elevated CO<sub>2</sub> leading, in combination with decreased water loss, to an increase in instantaneous WUE (Amthor, 1995). As a result, elevated CO<sub>2</sub> has been found to ameliorate the effects of water stress to such an extent that the percentage increase in biomass accumulation following a period of drought is greater than in ambient CO<sub>2</sub> (Eamus & Jarvis, 1989). Decreasing stomatal conductance and enhanced instantaneous WUE were observed at the CO<sub>2</sub> springs in Italy for *A. unedo* (Jones *et al.*, 1995), *Q. ilex* and *Q. pubescens* (Johnson *et al.*, 1997; Tognetti *et al.*, 1998a). Thus tree-ring growth at the CO<sub>2</sub>-enriched site was expected to be less affected by drought than at the control site. However, no such response was found for any of the species in dry years.

The unresponsiveness of tree-ring growth to elevated CO<sub>2</sub> during dry years may be explained by a complex of several interacting factors. Hättenschwiler *et al.* (1996) attributed the lack of response in the growth of *Picea abies* saplings to a partial downregulation of photosynthesis, lower leaf area ratios, decreased LAI and increased allocation of C to below-ground sinks. In some cases, significant downregulation of photosynthesis and homeostatic adjustments to elevated CO<sub>2</sub> have been observed in trees at the CO<sub>2</sub> spring sites (F. Miglietta, personal communication). At our site, however, water should be considered as the limiting factor and water stress, interacting with other factors, may drive physiological processes. Drought may

alter the growth response of tree species growing in an elevated CO<sub>2</sub> atmosphere (Tschaplinski *et al.*, 1995). Thus consistent changes in the rainfall or temperature regime, rather than in CO<sub>2</sub>, might be necessary before differences in tree-ring growth become evident, because of the reduced soil-water depletion at the CO<sub>2</sub>-enriched site. Furthermore, studies of *Q. ilex* and *Q. pubescens* at another CO<sub>2</sub> spring (called 'Bossoleto') have indicated that the decrease in stomatal conductance caused by elevated CO<sub>2</sub> may be less evident during severe summer drought stress at high vapour pressure deficits (Tognetti *et al.*, 1996, 1998b, 1999) than during periods of relatively low drought stress (Chaves *et al.*, 1995). *Quercus ilex* and *Q. pubescens* also showed a lower foliage area at the corresponding sapwood area under elevated CO<sub>2</sub> (Tognetti *et al.*, 1998b, 1999). This may counterbalance the increased assimilation rate at the leaf level. The absolute growth rate can only persist as long as leaf area increases, which is unlikely to continue indefinitely in a true forest (Saxe *et al.*, 1998). Hättenschwiler *et al.* (1997b) found that *Q. ilex* trees growing at the natural CO<sub>2</sub> spring of Bossoleto had a moderate, age-dependent increase in stem biomass production, but had lower biomass of 6-yr-old branches, decreased branching, and lower leaf area per unit branch biomass, compared to trees at a nearby control site. Although a reduced transpiring surface in trees at the CO<sub>2</sub> spring site might be as effective as stomatal closure in reducing plant water loss under elevated CO<sub>2</sub>, this can partially offset the advantage of greater C fixation per unit leaf area and thus limit C storage through canopy assimilation.

Mediterranean-type ecosystems (including our site) are characterized by low soil N availability, and the complexity of the multi-species system studied may also explain the absence of above-ground growth responses to elevated CO<sub>2</sub> in these trees (Körner & Arnone, 1992; Norby *et al.*, 1992; Loehle, 1995; Egli *et al.*, 1998; Poorter, 1998). A photosynthetic acclimation response has frequently been observed under N-limited conditions (Wolfe *et al.*, 1998). Telewski & Strain (1987) found positive CO<sub>2</sub> effects on tree-ring growth in seedlings of *Pinus taeda* and *Liquidambar styraciflua* but, as in other studies (e.g. Eamus & Jarvis 1989), these results apply to isolated seedlings grown in fertile soils. Our results indicate that nutrient-stressed plants show a relatively weak growth response to increased atmospheric CO<sub>2</sub>, as suggested by Poorter (1998).

It is possible that mature trees show greater root-growth responses than above-ground responses to elevated CO<sub>2</sub>, particularly on sites with recurrent water deficits or N deficiency (Luxmoore, 1981). High root-to-shoot ratios are associated with environments where water and nutrients are limited (Chapin, 1980). However, in a controlled-environment study on chaparral woody species, Oechel *et al.*

(1995) found that elevated CO<sub>2</sub> resulted in increased shoot and root biomass, with plants showing similar root : shoot ratios, and that such effects were relatively greater for plants under drought than for well watered plants. Although significant increases in mean total root length and biomass under elevated CO<sub>2</sub> have been detected (Janssens *et al.*, 1998), the below-ground C dynamics remain almost completely unknown in relation to global climate change (Norby, 1994; Hilbert & Canadell, 1995).

Extra C can also be diverted to secondary metabolites (Peñuelas *et al.*, 1996; Lawler *et al.*, 1997) and/or re-emitted as volatile compounds (Seufert *et al.*, 1995; Johnson & Allen, 1996), which may be more convenient than the investment in stemwood in semi-arid environments such as the Mediterranean. This has also been observed for *Quercus* species at the Bossoleto CO<sub>2</sub> spring (Johnson *et al.*, 1997). A high proportional allocation of biomass to stem may improve water relations in dry climates, but as the number of ray cells in the sapwood is larger, the respiratory costs may be high (Callaway *et al.*, 1994). The ability to sustain increases in growth under elevated CO<sub>2</sub> is dependent on the interaction between C assimilation, carbohydrate status, plant respiration and plant's chemical composition, as well as on the availability of nutrient resources and limiting factors.

In conclusion, there is no convincing evidence for CO<sub>2</sub>-enhanced stem growth of the dominant species in this woody plant community, as also observed for mature trees in other environments in recent decades (Luxmoore *et al.*, 1993). We stress that we have documented the absence of evidence for a CO<sub>2</sub>-effect at this site, and not evidence of a general absence of an effect. The question of whether Mediterranean forests have the capacity to store a larger amounts of C in stemwood under elevated CO<sub>2</sub> may have an indirect answer in our results. The possibility of increased C storage in wood with rising CO<sub>2</sub> may not result in net C storage in Mediterranean ecosystems if ontogenetic development is accelerated and stem turnover rates increased, as hypothesized by Hättenschwiler *et al.* (1997a). The expected greater ecosystem response to elevated CO<sub>2</sub> during drought stress, in terms of above-ground productivity, was not observed in this Mediterranean woody-plant community, despite it being water-limited. Other resource limitations, such as nutrient availability (suboptimal concentrations of N are common in the Mediterranean region) may have counteracted the potential positive effect of elevated CO<sub>2</sub> during drought stress.

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