Responses of deciduous forest trees to severe drought in Central Europe

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Summary   In 2003, Central Europe experienced the warmest summer on record combined with unusually low precipitation. We studied plant water relations and phenology in a 100-year-old mixed deciduous forest on a slope (no ground water table) near Basel using the Swiss Canopy Crane (SCC). The drought lasted from early June to mid September. We studied five deciduous tree species; half of the individuals were exposed to elevated CO_2 concentration ($[CO_2]$) (530 ppm) using a free-air, atmospheric CO_2-enrichment system. In late July, after the first eight weeks of drought, mean predawn leaf water potential about 30 m above ground was −0.9 MPa across all trees, dropping to a mean of −1.5 MPa in mid-August when the top 1 m of the soil profile had no plant accessible moisture. Mean stomatal conductance and rates of maximum net photosynthesis decreased considerably in mid-August across all species. However, daily peak values of sap flow remained surprisingly constant over the whole period in *Quercus petraea* (Matt.) Liebl.*,* and decreased to only about half of the early summer maxima in *Fagus sylvatica* L. and *Carpinus betulus* L. (stomatal downregulation of flux). Although we detected no differences in most parameters between CO_2-treated and control trees, predawn leaf water potential tended to be less negative in trees exposed to elevated $[CO_2]$. Leaf longevity was greater in 2003 compared with the previous years, but the seasonal increase in stem basal area reached only about 75% of that in previous years. Our data suggest that the investigated tree species, particularly *Q. petraea*, did not experience severe water stress. However, an increased frequency of such exceptionally dry summers may have a more serious impact than a single event and would give *Q. petraea* a competitive advantage in the long run.

Keywords: drought, elevated CO_2 concentration, global climate change, sap flow, Swiss Canopy Crane, tree phenology, water relations, web-FACE.

Introduction

Drought represents a major constraint on plant growth and productivity in most terrestrial plant communities (Hinckley et al. 1979, Churkina and Running 1998). The record-breaking heat wave and low precipitation that Europe experienced in 2003 highlighted the potential consequences of drought events for temperate European forests. For desert and Mediterranean-type climates with hot dry summers, drought events are common and their impact on species assemblages and productivity has long been acknowledged (e.g., Mouillot et al. 2002). Fewer studies have addressed the role of severe drought in Europe, where such events have been reported in historic times but have been rare during the past century (Lloyd-Hughes and Saunders 2002), with the last severe drought in 1976. However, recent evidence suggests an increase in the frequency of extreme weather conditions in Europe related to global climate change (Schär et al. 2004). Given the economic importance of agriculture and forestry, and the potential impact of climatic change on these industries, the effects of drought have lately evoked interest beyond the scientific community.

Implications of temporal water shortage on temperate forest trees, e.g., with respect to leaf water status (Hinckley et al. 1981), stomatal conductance, photosynthesis (Epron and Dreyer 1993) and hydraulic conductivity (Bréda et al. 1993, Cochard et al. 1996), have been studied extensively. In the course of a drought, gradually decreasing stomatal conductance, predawn leaf water potential, assimilation and growth are commonly observed, accompanied by a stimulation of fine root growth. Tree organs (leaves, roots, stem) generally differ in their sensitivity to drought (Westgate and Boyer 1985, Bréda et al. 1993) and a whole-tree approach is needed rather than one restricted to the leaf level (Leuschner et al. 2001a). Furthermore, when investigating drought responses of plants in general, it is crucial to compare several species, as even closely related species may differ greatly in their drought responses (e.g., Gieger and Thomas 2002). Water relations also need to be studied together with growth because it is well known that cambial activity is much more sensitive to drought than leaf-level gas exchange (e.g., Macfarlane and Adams 1998). Species under investigation have predominantly been those of economic importance (e.g., *Picea abies* (L.) Karst., *Quercus petraea* (Matt.) Liebl., and *Fagus sylvatica* L.; Schwanz et al. 1996, Leuschner et al. 2001a). *Quercus petraea* was generally found to have a higher drought resistance than

F. sylvatica, its main competitor (Epron and Dreyer 1993, Backes and Leuschner 2000). However, *F. sylvatica* seems to outcompete *Q. petraea* over most of Western and Central Europe. Competitive superiority may thus depend rather on canopy architecture and leaf orientation (Leuschner et al. 2001*a*) or shade tolerance (Küppers and Schneider 1993) than on the ability to maintain growth and vitality under drought stress. The ultimate long-term reproductive success and hence species abundance and distribution is unlikely to depend on individual physiological processes that are impaired during a single drought period. Rather, it will be the duration and frequency of drought events over a number of years that will likely determine changes in community structure.

The combined effect of elevated CO_2 concentration ($[CO_2]$) and drought is of particular interest as their conjunction forms part of a likely scenario for summers in Europe in the near future (Schär et al. 2004). The multitude of studies on water relations in trees subjected to an elevated $[CO_2]$ has been reviewed by Chaves and Pereira (1992), Saxe et al. (1998), Pospisilova and Čatský (1999), Körner (2000) and Medlyn et al. (2001). These reviews suggest that deciduous trees may be less affected by drought stress when exposed to an elevated $[CO_2]$ and thus may extend their ranges into less favorable areas. Conifers, on the other hand, show little or no measurable stomatal response to an elevated $[CO_2]$ (Ellsworth 1999, Körner 2000), and hence may benefit less from reduced canopy transpiration in response to elevated $[CO_2]$. In potted *Q. petraea*, Guehl et al. (1994) found greater biomass production during water shortage in elevated $[CO_2]$. Similarly, greater biomass production was found for cherry and oak seedlings during exposure to drought at elevated $[CO_2]$ (Picon et al. 1996, Centritto et al. 1999). However, unlike their responses to controlled environments, plants in the field can respond to drought by exploring deeper soil horizons or by more intensive rooting in a given soil volume. For example, Chaves et al. (1995) found only a marginal reduction in water-use by *Q. ilex* exposed to drought. A previous study at the Swiss Canopy Crane (hereafter, SCC) site in Hofstetten, Switzerland, revealed a reduction in transpiration of only about 10% in response to drought as measured by sap flow, with *Q. petraea* and *F. sylvatica* showing the least reaction (Cech et al. 2003). These authors also found a reverse (positive) effect of elevated $[CO_2]$ on sap flow under dry conditions. Clearly, more in situ studies are needed, in which tall trees experience simulated atmospheric change under natural conditions. Here we used free-air, atmospheric CO_2-enrichment technology (FACE, Pepin and Körner 2002) in combination with a canopy crane to study the combined effect of $[CO_2]$ and drought on trees in a mature forest.

We took advantage of the unique combination of drought and an exceptional heat wave that occurred in Europe in the summer of 2003, the heat wave having a mean return period of more than 10,000 years (according to traditional climate models, Schär et al. 2004). Drought responses were explored at the SCC site in Hofstetten, Switzerland, where some of the experimental trees are subjected to an elevated $[CO_2]$. The aims of the study were twofold: (1) to compare drought responses in adult specimens of five common deciduous tree species using a multilevel approach including measurements of water potential, maximum net photosynthesis, leaf conductance, sap flow, growth and phenology; and (2) to investigate the influence that atmospheric CO_2-enrichment exerts on these parameters in situ.

Materials and methods

Site description and study species

The study site is located in a diverse mixed forest stand about 15 km south of Basel, Switzerland (47°28′ N, 7°30′ E, 550 m a.s.l.), with the SCC providing access to the canopy. The forest is 80–100 years old; tree height ranges from 30 to 35 m; tree density (diameter = 0.1 m) is 415 trees ha^{-1}; and stem basal area is 46 m^2 ha^{-1}. The leaf area index (LAI) of the canopy in the experimental area is about 5. The dominant stand species are *F. sylvatica* L. and *Q. petraea*. Deciduous broad-leaved *Carpinus betulus* L., *Tilia platyphyllos* Scop., *Acer campestre* L. and *Prunus avium* L., and three species of conifers (not included in this study), occur as companion species. *Quercus petraea, F. sylvatica, C. betulus, A. campestre* and *T. platyphyllos* were selected for observations, as abundant deciduous species typical of a Swiss lowland forest. Soils are of the rendzina type on calcareous bedrock (a silty loam with an accessible profile depth of about 30 cm and a pH of about 5.8 in the top 10 cm of the profile). The site is situated on a slope with no access to the ground water table and has an essentially rocky subsoil at 40 to 90 cm below the surface.

The typical humid temperate zone climate is characterized by mild winters and moderately warm summers. Mean January and July air temperatures are 2 and 19 °C, respectively. Long-term mean annual precipitation for the region is 990 mm, two thirds of which commonly falls during the growing season. The previous years (2001 and 2002) were average with respect to temperature and precipitation. In the study year (2003), the growing season for deciduous trees lasted from the beginning of April (bud break) to the beginning of November. Most measurements were started on June 1 and ended on September 11.

Canopy access and atmospheric CO_2 enrichment system

Access to the tree canopy was achieved by a 45-m free-standing tower crane equipped with a 30-m jib. Of the 64 trees in the crane area, 14 broad-leaved trees (four *F. sylvatica*, three *Q. petraea*, four *C. betulus*, one *T. platyphyllos*, one *A. campestre* and one *P. avium*, the last not used for this experiment) were selected for the elevated $[CO_2]$ treatment in autumn of 2000 (all within a continuous plot). A similar number of control trees were located in the remaining crane area at a sufficient distance from the CO_2 release zone. Atmospheric CO_2 enrichment of the forest canopy was achieved by a free-air, pure CO_2 release system (Pepin and Körner 2002), which consisted of a web of 4-mm plastic tubes (about 0.5 km per tree) with laser-punched holes emitting pure CO_2 into the tree canopy (web-FACE). The rate at which CO_2 was injected into the tubing system and released around the tree crowns was set by computer-controlled magnetic valves to maintain a target $[CO_2]$

of 550 ppm as closely as possible (details in Pepin and Körner 2002). The system was set up in late September 2000 and operated in the three subsequent growing seasons (from budbreak until leaf fall) every day from dawn to dusk. The overall mean seasonal daytime [CO_2] within the canopy deviated slightly from the set point and was 520 ppm in 2001 and 530 ppm in 2002 and 2003.

Environmental data

Rain, throughfall precipitation, air humidity, potential evapotranspiration, temperature and soil humidity were monitored by weather stations located above the tree canopy at the top of the crane and in the understory. Tipping bucket rain gauges (RG1, Delta-T, Cambridge, U.K.) were used to monitor rain, and throughfall precipitation was quantified with 22 evenly spaced funnel-type rainwater collectors. Potential evapotranspiration was measured with two evaporometers (ET gauge, Spectrum Technologies, Plainfield, IL). Data were recorded as 10-min means with data loggers (DL3000, Delta-T). Soil moisture data were obtained at 15-cm depth from hourly measurements with theta-probes (ML2x, Delta-T) located within and immediately outside of the atmospheric CO_2-enrichment zone and connected to another data logger (DL2e, Delta-T). Additional soil water content across a 90-cm profile (the lower 50 cm representing eventual water in rock crevices) was monitored every 7–14 days during the 2003 growing season at four locations using time domain reflectometry (MP-917 and probes PRB-F, Environmental Sensor, Victoria, BC, Canada).

Leaf water potential measurements

Predawn leaf water potential was measured with a pressure chamber (SKPM 1400, Skye Instruments, Powys, U.K.) from the canopy crane gondola on 5 days from July to September (July 22, July 23, August 14, August 20 and September 12). The weather was clear on all five days with light availabilities up to 1600 mmol m^{-2} s^{-1}. On three occasions, daily courses of water potential were recorded. Samples were taken at similar heights above ground to avoid variability due to hydrostatic water potential and samples were wrapped with scotch tape immediately after cutting to prevent further transpiration. We sampled three to four individuals of *Q. petraea, F. sylvatica* and *C. betulus* and two of *A. campestre* and *T. platyphyllos*.

Sap flow measurements

Sap flux density within the xylem was measured by the constant heat-flow technique described by Granier (1985, 1987). Each sensor (UP, Kolkwitz, Germany) consists of two 20-mm-long probes (2 mm in diameter), each equipped with a copper-constantan thermocouple and wrapped with heating wire. The upper probe was inserted radially into the sapwood at breast height into bore holes lined with thin-walled aluminum tubing. The bore holes were separated vertically by about 15 cm. The upper probe was heated at a constant power of 200 mW, while the lower reference probe remained unheated. During conditions of zero sapflow, e.g., at night or during prolonged rain events, the temperature difference, ΔT, between the probes reaches a maximum (about 9–15 K). Sap flow dur-

ing the day causes a decrease in ΔT by cooling the upper probe. Sap flux density within the xylem (J_S) measured in m^3 H_2O m^{-2} was calculated from an empirical relationship validated for several species by Granier (1985), and recently revalidated by Clearwater et al. (1999). We tested for azimuthal variability in sap flux densities, which revealed differences of up to a factor of three between six sensors in *Q. petraea,* whereas almost no differences were found between sensors in *F. sylvatica*. We also compared sap flux densities among trees and among species. Maximum sap flux density was between 30 and 90 J_S (10^{-6} m^3 H_2O m^{-2} s^{-1}) for *Q. petraea*, between 80 to 140 J_S for *F. sylvatica* and about 60 to 100 J_S in *C. betulus*. Given these large differences in absolute sap flow rates and the difficulty of calibrating and converting sap flow signals of mature trees with uncertain sapwood widths into absolute flow rates, we considered relative values only in the present study.

Measurements of J_S were performed from June 21 to October 1, 2003, on three dominant tree species (*Q. petraea*, *F. sylvatica* and *C. betulus*, $n = 2$, only one tree per species at the beginning of the season) using three to six sensors per tree (equally spaced around the stem). Sensors were protected against rain and external thermal influences by aluminum covers filled with polyester wool. Readings were taken at 30-s intervals and recorded as 10-min means using a multi-channel data logger (DL2e, Delta-T). The signals per tree were averaged over all sensors per stem.

Leaf gas exchange measurements

Instantaneous rates of CO_2/H_2O gas exchange were measured in situ in the first half of the day in early (mid-June), mid- (August) and late summer (early September 2003) on mature leaves fully exposed to the sun in the outer canopy of 25 trees (13 trees exposed to elevated [CO_2] and 12 controls) with a portable gas exchange system (Li-6400, Li-Cor, Lincoln, NE). From each tree, eight (June), four (August) and four (September) leaves from different branches were selected for gas exchange measurements, which were conducted at saturating photosynthetic photon flux (PPF) (1200 µmol m^{-2} s^{-1}; from an LED light source; Li-Cor 6400-02). Trees grown in an elevated [CO_2] were measured at about 530 ppm, control trees at about 360 ppm. Chamber temperature (June: 27.1 ± 1.5 °C; August 30.1 ± 0.9 °C; September: 20.9 ± 0.8 °C; mean ± SD) and relative humidity (June: 64 ± 9%; August 37 ± 2%; September: 60 ± 4%) tracked ambient conditions. A data set was recorded once the net rate of photosynthesis and stomatal conductance remained constant. Individual measurements lasted less than 5 min.

Growth and phenology data

Each month, from 2001 to 2003, we measured the breast-height diameter of 22 trees randomly distributed within the study site with fixed "Permanent Tree Girth-Tape" (D1-L, UMS GmbH, Munich, Germany; accuracy of measurement 0.1 mm). Trees measured were as follows: *Q. petraea*: $n = 6$, 3 ambient, 3 elevated [CO_2]; *F. sylvatica*: $n = 6$, 3 ambient, 3 elevated [CO_2]; *C. betulus*: $n = 6$, 3 ambient, 3 elevated [CO_2];

T. platyphyllos: $n = 2$, 1 ambient, 1 elevated [CO_2]; and *A. campestre*: $n = 2$, 1 ambient, 1 elevated [CO_2]. Leaf longevity, defined by the time span from 75% bud break to 75% leaf fall was documented in 2002 and 2003, based on observations on a total of 24 individuals of the dominant tree species (*C. betulus*: $n = 8$; *F. sylvatica*: $n = 6$; *Q. petraea*: $n = 6$; *T. platyphyllos*: $n = 2$; and *A. campestre*: $n = 2$; half of the individuals of each species being subjected to elevated [CO_2]).

Data analysis

Leaf water potential, photosynthesis parameters and sap flow data were evaluated by repeated-measures analysis of variance (ANOVA). Datasets that were not normally distributed (according to the Kolmogorov-Smirnov test for normality) were log-transformed before analysis. Tukey's HSD post hoc test for unequal sample size was used to detect differences between CO_2 treatments. Data analysis was performed with the software package STATISTICA Version 5.0 (Statsoft, Tulsa, OK). Error terms represent standard errors unless otherwise stated.

Results

Environmental data

At the SCC site, total accumulated rain during the study as defined above was less than 50% of the 10-year mean from 1989 to 1999, and spring precipitation was also well below the mean (Figure 1). Moreover, throughfall precipitation amounted to approximately half of the above-canopy precipitation of 188 mm, while potential evapotranspiration was 559 mm, i.e.,

exceeding throughfall precipitation almost sixfold during the same period. Mean monthly temperatures exceeded the long-term mean (1989–1999) dramatically (e.g., + 6.8 °C for June). Soil water content at 15-cm depth dropped from around 30 Vol.% in early June to 8 Vol.% within the first five weeks of drought and remained low with no plant accessible moisture throughout the rest of the study (Figure 1). Because of the stony subsoil at the study site, soil water between 15- and 90-cm depth as derived from TDR was low and spatially variable (6 to 18 Vol.%). However, irrespective of the absolute values, the signals remained mostly constant during the drought, indicating that none of the remaining moisture was taken up by trees from the monitored soil horizons. There was no significant difference in soil water between the elevated [CO_2]-treated area and the control area in the explored soil horizon (constant minimum readings; data not shown).

Rate of net photosynthesis and leaf conductance

Both net photosynthesis (*A*) and leaf conductance (*g*) decreased significantly, by 60 to 80%, from June to August in all species (Figures 2A and 2B). Intraspecific variation was large in both parameters, but nonsignificant in August when all species were strongly affected. Only *Q. petraea* (and to some extent *T. platyphyllos*) resumed *g* and *A* values in September comparable with those of June (Figures 2A and 2B), whereas the other species showed only partial recovery. Elevated [CO_2] had no significant effect on *g*. In contrast, elevated-[CO_2]-treated trees (all species pooled) assimilated more (12.7 ± 0.9 µmol CO_2 m^{-2} s^{-1}) than trees growing in ambient [CO_2] (8.3 ± 0.8 µmol CO_2 m^{-2} s^{-1}; repeated-measures ANOVA, $P < 0.002$, $F_{1,9} = 18.7$).
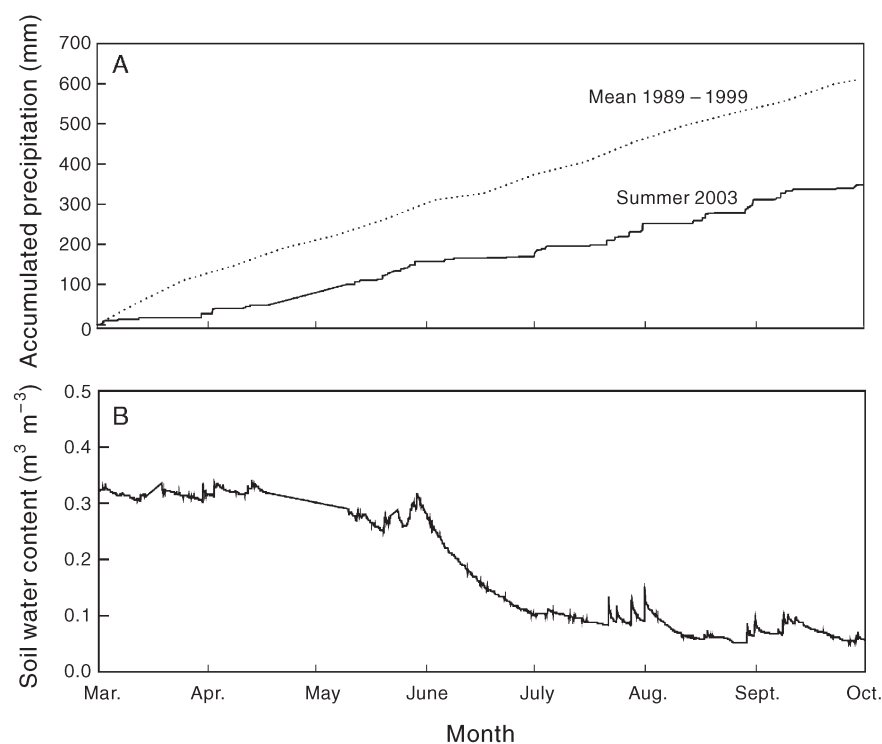

Figure 1. Accumulated seasonal rainfall (mean of 1989 to 1999, dotted line) compared with rainfall during the summer drought of 2003 at the SCC site in Hofstetten, Switzerland (solid line). Total rainfall during the study period (June 1 to September 11) was less than half the 10-year mean (188 versus 415 mm). Subsequently, substantial rainfall caused soil water content to increase as shown in the upper panel (soil water content at a depth of 15 cm).
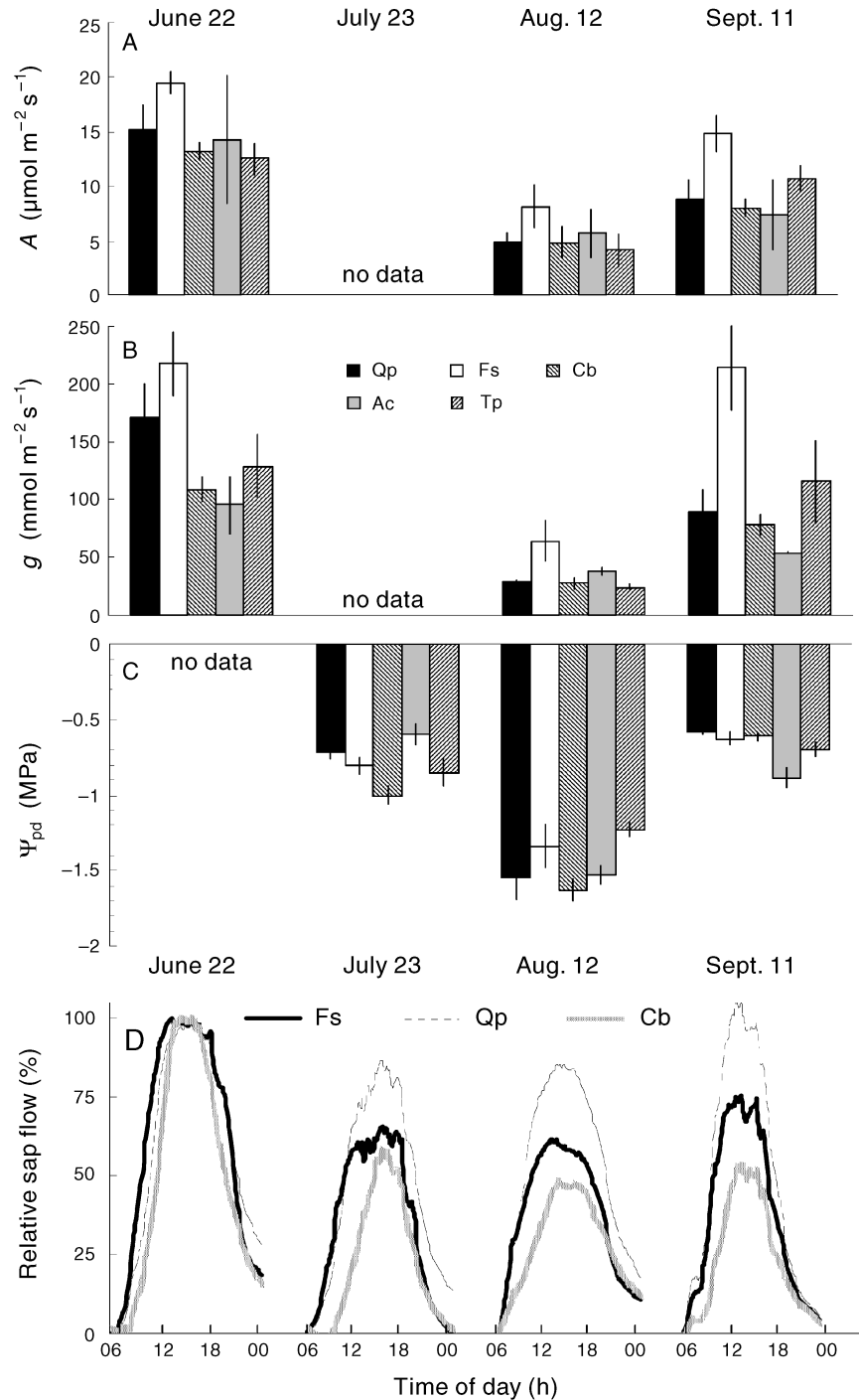
Figure 2. Net rate of maximum photosynthesis, *A* (A), stomatal conductance, *g* (B), predawn leaf water potential, Ψ_{pd} (C) and sap flow (relative to initial peak values; D) of three to five species (*Quercus petraea* (Qp), *Fagus sylvatica* (Fs), *Carpinus betulus* (Cb), *Acer campestre* (Ac) and *Tilia platyphyllos* (Tp), all in ambient [CO_2]) at the beginning (22 June), in the middle (23 July and 12 August) and towards the end (11 September) of the 2003 summer drought (means ± SE). Maximum standard errors for data in panel D are: 12.6 (*Q. petraea*), 18.0 (*F. sylvatica*) and 11.1 (*C. betulus*). All measurements were made on clear days and vapor pressure deficit reached 45, 18, 38 and 12 hPa on the four days shown.

Leaf water potential

At the end of the completely dry period between August 1 and August 14 (Figure 1), predawn leaf water potential (Ψ_{pd}) ranged from −1.7 MPa in *C. betulus* to −1.3 MPa in *Q. petraea* and −1.1 MPa in *T. platyphyllos* (Table 1 and Figure 2C). Over the course of the drought, Ψ_{pd} declined across all species (repeated-measures ANOVA, $P < 0.001$, $F_{4,24} = 82.2$) from a mean of about −0.8 MPa in mid-July to below −1.4 MPa in mid-August, reflecting severe soil desiccation. Mean Ψ_{pd} then

recovered to about −0.9 MPa in the second half of August and about −0.7 MPa in mid-September. Predawn leaf water potential tended to be less negative in elevated [CO_2] (3-way ANOVA for all species, $P = 0.06$, $F_{1,6} = 5.3$), but there was no significant effect of [CO_2] on the diurnal minimum of leaf water potential ($P = 0.22$, $F_{1,6} = 1.8$). Trees started the day from different predawn leaf water potentials, but because of differences in daytime flux control, they arrived at similar minima by the afternoon.

Table 1. Leaf water potential (Ψ) of five tree species during the summer drought (2003) in Hofstetten, Switzerland. Shown are means (SE in parentheses) of predawn (Ψ$_{pd}$) and daily minimum (Ψ$_{min}$, early afternoon) leaf water potentials for each species. Measurements were on two to four individuals per species and treatment, except for A. campestre and T. platyphyllos. Abbreviations: A = trees grown under ambient [CO$_2$]; E = trees subjected to elevated [CO$_2$]. Different letters indicate significant differences between species (with CO$_2$ treatment and sampling date pooled, repeated-measures ANOVA, P < 0.05).

Ψ$_{pd}$	F. sylvatica[a]		Q. petraea[b]		C. betulus[a]		T. platyphyllos[c]		A. campestre[a]		All species	
	A	E	A	E	A	E	A	E	A	E	A	E
July 22	−0.83 (0.03)	−0.66 (0.02)	−0.80 (0.03)	−0.79 (0.10)	−1.13 (0.07)	−1.00 (0.24)	−0.80	−0.63	−0.68	−0.56	−0.94 (0.09)	−0.80 (0.08)
July 23	−0.72 (0.06)	−0.70 (0.10)	−0.80 (0.02)	−0.82 (0.12)	−1.10 (0.07)	−0.90 (0.07)	−0.94	−0.76	−0.67	−0.54	−0.86 (0.06)	−0.78 (0.05)
Aug. 14	−1.44 (0.25)	−1.66 (0.14)	−1.42 (0.16)	−1.26 (0.26)	−1.71 (0.08)	−1.54 (0.10)	−1.07 (0.22)	−1.16	−1.54 (0.06)	−1.59	−1.50 (0.08)	−1.47 (0.09)
Aug. 20	−0.82 (0.11)	−0.86 (0.05)	−0.92 (0.03)	−0.89 (0.12)	−1.14 (0.08)	−0.91 (0.04)	−0.95 (0.05)	−0.80	−0.92 (0.03)	−1.01	−0.94 (0.04)	−0.88 (0.03)
Sept. 12	−0.57 (0.04)	−0.58 (0.02)	−0.67 (0.06)	−0.58 (0.05)	−0.61 (0.04)	−0.62 (0.04)	−0.72 (0.10)	−0.68	−0.93 (0.08)	−0.81	−0.68 (0.04)	−0.62 (0.02)

Ψ$_{min}$	F. sylvatica[a]		Q. petraea[a]		C. betulus[b,c]		T. platyphyllos[a,c]		A. campestre[a,c]		All species	
	A	E	A	E	A	E	A	E	A	E	A	E
July 22	−1.77 (0.14)	−1.76 (0.05)	−2.18 (0.08)	−2.03 (0.06)	−2.27 (0.02)	−2.07 (0.09)	−1.53	−1.32	−2.00	−1.92	−1.95 (0.10)	−1.95 (0.09)
Aug. 20	−1.54 (0.20)	−1.52 (0.06)	−2.20 (0.09)	−2.03 (0.14)	−1.95 (0.13)	−1.88 (0.12)	−1.49 (0.10)	−1.35	−1.94 (0.13)	−1.75	−1.89 (0.09)	−1.82 (0.09)
Sept. 12	−1.21 (0.35)	−1.07 (0.08)	−1.55 (0.08)	−1.63 (0.09)	−1.40 (0.06)	−1.43 (0.16)	−1.29 (0.01)	−1.00	−1.32 (0.01)	−1.40	−1.35 (0.07)	−1.41 (0.10)

Sap flow

Relative sap flow became progressively lower as the drought advanced in *F. sylvatica* and *C. betulus*, although in *Q. petraea*, sap flux density decreased by only 15% on August 12 compared to June 22, versus 40 and 50% in *F. sylvatica* and *C. betulus*, respectively (Figure 2D). In mid-September, sap flux density in *Q. petraea* recovered fully, whereas in *F. sylvatica*, it recovered only slightly, and in *C. betulus*, sap flow continued to decrease. *Quercus petraea* and *C. betulus* reached maximum sap flow rates at higher vapor pressure deficits (around 8 to 9 hPa) than *F. sylvatica* (about 6 hPa), i.e., *F. sylvatica* started to control transpiration at a lower VPD, reducing transpiration by overcompensating stomatal regulation above a VPD of about 18 hPa (Figure 3). *Quercus petraea* showed the smallest decrease in transpiration during conditions of high VPD (flow stabilized by stomatal control), whereas *C. betulus* reduced sap flow considerably (about 50%) above a VPD of 30 hPa. After minor rain events during the drought, relative sap flow rates increased rapidly in *C. betulus* only, decreasing again shortly afterwards, which may explain, in part, the discrepancy between Figures 2D and 3.

Growth and phenology

In 2003, the seasonal increase in tree basal area was reduced by about 25% over all 22 trees monitored compared with the two previous years (2001 and 2002 versus 2003, P = 0.06) and basal area growth virtually ceased by early August (Figure 4). Surprisingly, we observed increasing stem diameters late in the year, which was most likely caused by wetting of the bark after the first extensive rainfalls. There were clear differences between species: *F. sylvatica* and *T. platyphyllos* were affected most, whereas *A. campestre, C. betulus* and *Q. petraea* did not differ as much in growth rates from the two previous years. In 2003, leaf longevity was prolonged by a mean of 22 days across all trees compared with the previous year (one-way ANOVA, P < 0.001). This difference was mainly due to delayed discoloration and leaf fall, whereas earlier bud break in spring 2003 accounted for only about 5 days of the increased leaf longevity. Although leaves looked more yellow than normal in some species (mainly *C. betulus*) at the peak of the drought in August, they became green again after the September rains and none of the monitored species showed signs of accelerated senescence or leaf fall. There was also no mid-season leaf shedding.

Discussion

Our study yielded three major findings: (1) *Q. petraea* maintained a consistently better water status during the drought than the other four species. Despite the high interspecific variability in drought response, no species showed signs of drought-induced leaf mortality; (2) across all trees, the summer drought of 2003 caused reduced basal stem area growth of all investigated species compared with growth in the two previous years; and (3) elevated [CO$_2$] resulted in less negative predawn leaf water potentials. However, we observed neither significantly lower stomatal conductance in trees exposed to elevated [CO$_2$] during the drought (though there was a small
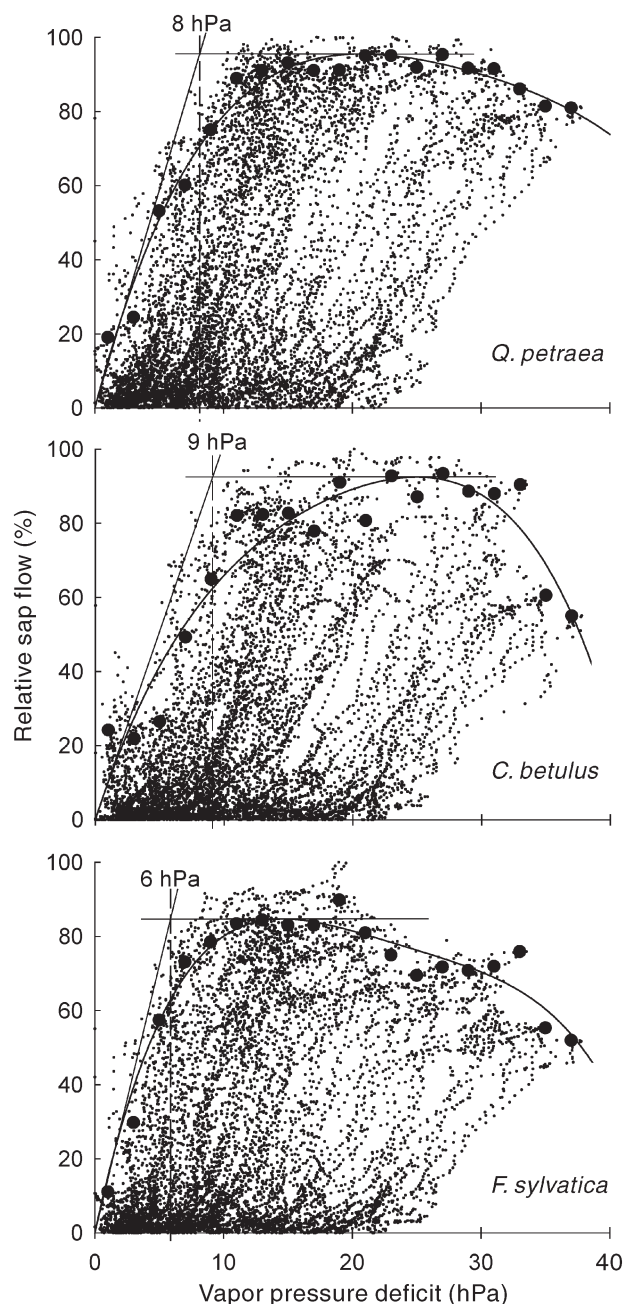
Figure 3. Vapor pressure deficit (VPD) plotted against relative sap flow for *Q. petraea*, *C. betulus* and *F. sylvatica*. Bold lines show best 4th order polynomial fit (least squares) for 95 percentiles of classes of 2 hPa VPD (bold dots). R^2_{adj} values are 0.97, 0.90 and 0.94 for *Q. petraea*, *C. betulus* and *F. sylvatica*, respectively, $P < 0.001$ for all three species, $n = 2$ (except for June and July $n = 1$).
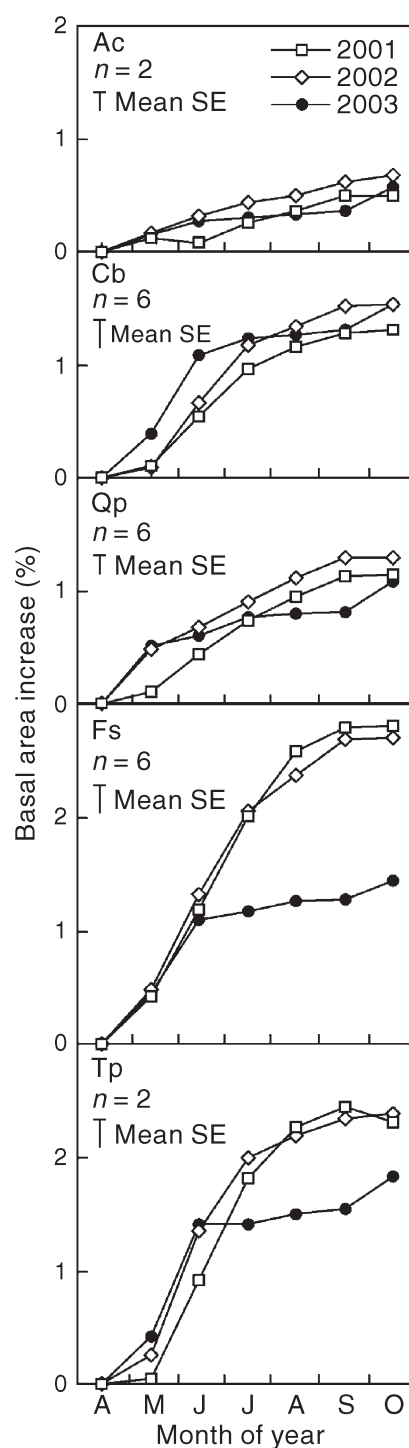

Figure 4. Stem basal area increase (%) in the drought year 2003 compared with the two previous years with mean precipitation (2001 and 2002) for the five species *Acer campestre* (Ac), *Carpinus betulus* (Cb), *Fagus sylvatica* (Fs), *Tilia platyphyllos* (Tp) and *Quercus petraea* (Qp). For clarity, the SE is averaged over the vegetation period (mean SE). Differences between trees grown under elevated CO_2 and ambient conditions were not significant, hence data were pooled for analysis.

trend in this direction) nor a significant [CO_2]-related increase in diameter growth across all species compared with controls.

Water relations during drought

The effect of severe drought as experienced in 2003 was aggravated by the heat wave which reduced the ratio of precipitation to evaporation further. Subtracting mean throughfall precipitation (about 100 mm) from potential evapotranspiration

(559 mm) results in a negative water budget of about 460 mm during the study period, or a potential water loss of 4.5 mm per day. Even if actual evapotranspiration was substantially lower

because of stomatal down-regulation, we estimate severe soil dessication down to at least 2.5 to 3 m, given the extremely rocky subsoil. In fact, many understory plants such as *Mercurialis perennis* L. wilted permanently. Canadell et al. (1996) reviewed the rooting depths of 21 temperate deciduous forest trees and arrived at 1.8 to 4.3 m, with a mean of 3.0 ± 0.2 m. *Quercus petraea* was found to have somewhat deeper rooting (max. 1.5 m) than *F. sylvatica* (1.1 m) (Leuschner et al. 2001*b*). Based on the estimates above, we expected much more severe signs of water shortage in the study trees. Surprisingly, this was not the case. This suggests that trees had access to deeper soil water through deep-reaching fine root systems, which may have been overlooked in excavation studies.

Overall, we found important differences in drought response among species, particularly between the co-dominant species *Q. petraea* and *F. sylvatica*. In essence, *Q. petraea* maintained surprisingly high transpiration rates (estimated by sap flow) although assimilation and stomatal conductance were depressed substantially (but were still twice as high as in *F. sylvatica* and *C. betulus* at the peak of the drought). There are two possible explanations for this: (1) both *F. sylvatica* and *Q. petraea* had access to deep water, but *F. sylvatica* did not tolerate such high flux rates and thus down-regulated transpiration by stomatal closure, or (2) *Q. petraea* had access to deep water that was inaccessible to *F. sylvatica*. We favor the first explanation, as we measured minimum leaf water potentials (Ψ_{min}) of –2.2 MPa in *Q. petraea* but values no lower than –1.8 MPa in *F. sylvatica* under the same conditions (Table 1).

According to Hacke and Sauter (1995), embolism occurs at leaf water potentials below –1.9 MPa in *F. sylvatica*, and Bréda et al. (1993) state that both beech and oak can be considered water stressed when leaf water potential drops below –2.0 MPa. Although there is one study reporting Ψ_{min} values below –3.0 MPa for both *F. sylvatica* and *Q. petraea* in Greece (Raftoyannis and Radoglou 2002), such low leaf water potentials have never been reported from Central or Western Europe. We argue that with a minimum predawn leaf water potential (Ψ_{pd}) of –1.66 MPa at the peak of drought, *F. sylvatica* trees were considerably water stressed, as such low Ψ_{pd} values have never been found previously in tall adult trees (Aranda et al. 2002, Peuke et al. 2002). However, *Q. petraea* showed higher Ψ_{pd} together with lower Ψ_{min} values, which suggests that this species suffered less from water shortage. The greater abundance of *F. sylvatica* across most of Central and Western European lowlands contrasts with the higher drought resistance of *Q. petraea*, indicating that drought has not been the dominant selective force so far. This issue has been amply discussed by Leuschner et al. (2001*a*, 2001*b*). These authors observed drought-stimulated fine root growth as well as generally high competitive ability in fine root growth in *F. sylvatica* but not in *Q. petraea*. The diffuse-porous *F. sylvatica* also seems to operate at lower sap flux densities than the ring porous *Q. petraea*, possibly because of its higher Huber-value (Lösch 2001). Nevertheless, we observed *F. sylvatica* trees down-regulating transpiration by stomatal closure at atmospheric vapor pressure deficits above about 10 hPa, thereby mitigating cavitation risk. Cavitation risk is higher in *F. sylvatica* than in *Q. pubescens*, an oak species closely related to the one studied

here (Lösch 2001). Lower cavitation risk may thus explain the greater drought resistance of oak.

Carpinus betulus raised sap flow rates quickly after even minor rain events with little throughfall precipitation. This suggests that *C. betulus* features an effective fine root system in the shallowest soil horizon, allowing it to rapidly use small quantities of water that become available during otherwise dry periods (Figure 3). *Acer campestre* did not differ in *A* and *g* from the more drought-sensitive species *F. sylvatica* and *C. betulus*, whereas *T. platyphyllos* seemed to recover particularly well in September reaching pre-drought *A* and *g* values. Thus, *T. platyphyllos* may be a relatively drought-tolerant species, not previously recognized as such, whereas *A. campestre* seems to be more susceptible to drought.

The surprisingly low sap flow rates in all species at high VPD (e.g., almost zero flow at 20 hPa VPD; Figure 3) were a consequence of many extraordinarily hot nights (flow approaches 0) in August when predawn temperatures remained well above 20 °C and relative humidity was as low as 30%.

Growth and phenology

Intraspecific differences in physiological responses to drought matched patterns of basal stem area increase quite well. As expected, *Q. petraea* showed the least difference in growth reduction compared with the two previous years, whereas in *F. sylvatica*, water shortage had an unambiguous effect on basal area increase (Figure 4). *Carpinus betulus* showed rapid basal area growth during the spring when soil water availability was still high, but ceased growth almost completely during the drought. For *A. campestre* and *T. platyphyllos,* sample sizes are too low to allow interpretation of growth responses. Drought has generally been associated with reduced leaf longevity in deciduous species (Jonasson et al. 1997), depending on length and severity of the drought. In contrast, increases in leaf longevity as in our particular case have rarely been reported (but see Casper et al. 2001). The increase in stem basal area in October following the first autumn rains (Figure 4) is unlikely to have been caused by late season growth. The difference in thickness of fresh and air-dried bark samples (compare Zweifel et al. 2000, Asshoff et al., unpublished data) indicates that the apparent increase in basal area can be fully explained by bark swelling after rain.

Drought–CO₂ interactions

Elevated CO_2 in combination with drought caused less negative predawn leaf water potentials. As predawn leaf water potential is the sum of the (constant) hydrostatic potential plus the soil matrix potential, this indicates water savings of trees exposed to a high [CO_2] during drought. However, trees exposed to an elevated [CO_2] showed no measurable reduction in stomatal conductance during the drought, but small reductions may have escaped our assessment. A study by S.G. Keel et al. (Laboratory of Atmospheric Chemistry, Paul Scherrer Institute, Villigen, Switzerland, personal communication), which was conducted at the same site, indicated that there is such a difference, but the mean reduction across species is small (about 10–15%) compared with the variation in the data.

We conclude that a drought as severe as that in Europe during 2003 exerts no damage on the tested tree species. The visual impression during this summer suggests that this applies to most lowland forests in this area, where obvious drought damage was restricted to hill tops, ridges or rock escarpments. However, we identified a pronounced differentiation in the impact of the drought on water consumption, leaf photosynthesis and growth across the studied species. Adult *Q. petraea*, it appears, copes best with drought events, but it is too early to predict a possible shift in species composition in mixed forests of the kinds studied.

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