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Hydraulic Properties and Water Relations of *Vitis vinifera* L. exposed to Elevated CO₂ Concentrations in a Free Air CO₂ Enrichment (FACE)

By

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Summary

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Plants of *Vitis vinifera* (cv. Sangiovese) were submitted to elevated carbon dioxide concentrations in the field, using a FACE array; the experiment took place in a vineyard in Central Italy, throughout two growth seasons. The effects of fumigation on stem hydraulic properties and leaf water relations were evaluated. A significant decrease in stomatal conductance did not result in marked differences in leaf water potentials of FACE plants. Apparently, embolism formation showed to increase and hydraulic sufficiency to decrease after two years of exposure to elevated CO₂. The allometric relationships between stem hydraulic conductivity, leaf area and stem cross-sectional area of xylem imply a physiological origin, though being unclearly affected by elevated CO₂. The effect of elevated CO₂ on water relations and hydraulic parameters of Sangiovese grapevine displayed variation reliant on fumigation time-span. Under these experimental conditions, changes in hydraulic properties in FACE plants did not provide a direct explanation for variations in leaf water relations in comparison with controls.

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Introduction

Global climatic change due to increasing atmospheric CO₂ concentration is likely altering physiological functions and growth rates of plants (KEELING & WHORF 1994). Many studies have been dealing with the effects of elevated CO₂ on agricultural crops (CURE & ACOCK 1986), forest trees (CEULEMANS & MOUSSEAU 1994) and other plant types (BAZZAZ 1990, POORTER 1993, IDSO & IDSO 1994). The great majority of these studies have concluded that increased atmospheric CO₂ enhanced net photosynthesis, biomass accumulation, seed yield, light and nutrient use efficiency, leaf water potential and plant water use efficiency. However, the interaction with other environmental factors, the fate of extra carbon assimilated during photosynthesis, the difficulty in discriminating long term adaptation and short term acclimation, and finally the typically species-specific response evidenced in many experimental studies, make any predictive analysis extremely difficult (AMTHOR 1995), in particular when data from single species are used to infer the behavior of whole systems.

Climate warming is expected to be particularly pronounced in the Mediterranean Basin, since Mediterranean-type agro-ecosystems will have to face an increase in the frequency and severity of drought periods (WIGLEY & al. 1984). These climatic effects may counteract the direct control of elevated CO₂ on photosynthesis and growth, while the influence on plant water relations may be critical in determining the overall response. Physiological adjustments of Mediterranean woody plants to summer drought may underline important tolerance and adaptation mechanisms that aid recovery from stress and crop productivity (TOGNETTI & al. 2001, 2002). During drought, progressive stomatal closure may play a significant role in preventing plants from reaching levels of water stress inducing runaway xylem cavitation (JONES & SUTHERLAND 1991), though it is not clear whether plants grown in high CO₂ are more or less prone to embolism formation (ATKINSON & TAYLOR 1996, HEATH & al. 1997). Studies documenting the effect of elevated CO₂ on fruit trees are rare (IDSO & KIMBALL 1997, ITO & al. 1999, TOGNETTI & al. 2001). In seedlings of fruit tree species, positive photosynthetic and growth responses have been evidenced in enriched glasshouse as well as field fumigated systems (CENTRITTO & al. 1999, PAN & al. 1998, KEUTGEN & CHEN 2001, SEBASTIANI & al. 2002). However, practical problems may arise when exposing adult trees in traditional enrichment tools, such as greenhouses and open top chambers.

The mosaic nature of European agriculture, climate, landscape and soil (as well as culture and land use) is expected to greatly affect the responsiveness to climate change (OLESEN & BINDI 2002). Mediterranean agro-ecosystems have, nonetheless, received less attention compared to crops of temperate regions, although they should be fairly responsive to global warming (MORENO & OECHEL 1995). The aim of the present study was to assess the effect of elevated CO₂ on hydraulic properties and water relations of adult *Vitis vinifera* L. plants fumigated in the vineyard by means of a Free Air CO₂ Enrichment (FACE) set-up. Since growth and development of grapevine are influenced by environmental factors, such as tem-

perature and radiation (MULLINS & al. 1992), whole plant performances may be affected by increased CO₂ through the stimulation of photosynthesis and plant growth when water resources are adequate. Nevertheless, this may make plants more vulnerable to cavitation and thus less likely to survive static drought stress due to soil dryness in the late season. Alternatively, if plants under elevated CO₂ avoid low water potentials for longer periods they may run into less xylem cavitation during Mediterranean summers.

Material and Methods

Site details and experimental design

The experiment was done on a vineyard of 20-year-old-grapevines (cultivar Sangiovese) in the Chianti Region in Italy (Santa Cecilia, Rapolano Terme, Siena, Lat. 43° 25' N, Long. 11° 35' E), throughout the growing seasons 1995 and 1996. Grapevines were grown at a spacing of 3 x 1.5 m, cordon trained (vertical trellised vines) and spur pruned.

Six FACE arrays, enclosing 7 plants each, were installed on three rows in March 1994 and fumigation started at bud break in both years. Two CO₂ exposure levels (ambient and 700 µmol mol⁻¹) were maintained. Each emission array was formed by a rectangular plenum (10 x 2 m) positioned at the soil surface, connected with 22 vertical pipes. The whole system was assembled from polyvinyl chloride (PVC), using pipes with an internal diameter of 20 cm for the plenum and 2 m long pipes with an internal diameter of 4 cm for the vertical vents. Each vent pipe had 4 emission holes with 2 cm diameter, placed in two groups of two holes each, approximately at 120 and 190 cm above the soil surface. High volume blowers (APEM, Firenze, Italy) were used to blow air into the plenum, through flexible pipes; pure CO₂ was mixed with ambient air by injecting it in the flexible pipes. The CO₂ injection rates were regulated using the Proportional Integral Differential (PID) algorithm described by LEWIN & al. 1994 and were controlled by motorized metering valves (Zone-master, Satchwell Control System). The algorithm makes use of both horizontal mass flow based on wind velocity and a PID component based on CO₂ concentrations read in the centre of the array to calculate output voltage used to control the metering valves. The CO₂ concentration in the FACE array was measured by an infra-red gas analyzer (WMA-2, PPS, Hitchin, UK) having a 0-2000 µmol mol⁻¹ range, with an accuracy of 20 µmol mol⁻¹ full scale and a temporal resolution of 1 s. The FACE system used geologic CO₂ obtained from a local company (Geogas S.p.A.) that extracts CO₂ for industrial and alimentary purposes. CO₂ fumigation was done only during daytime hours since natural CO₂ concentrations during nighttime were very often above 400 µmol mol⁻¹. Distances between arrays ranged from 10 to 20 m to avoid unintended CO₂ enrichment of the controls. Further details on the performance of the fumigation system are given elsewhere (BINDI & al. 2001).

Leaf water relations

Seasonal maximum daily stomatal conductance ($g_{s,max}$) and leaf transpiration ($T_{l,max}$) in morning hours were determined on the abaxial surface of six healthy, sun exposed leaves per treatment by using a steady-state porometer (LI-COR 1600, Lincoln, NE, USA). The natural inclination and azimuth of leaves were maintained during the measurements, each measurement was completed within 30 s and humidity inside the porometer chamber was kept near ambient values. Changes in leaf conductance were considered to reflect variation in stomatal conductance, assuming that boundary layer conductance inside the cuvette was constant and large.

In parallel to stomatal conductance measurements, water potentials at predawn (Ψ_{pd}) and midday (Ψ_{md}) were determined in the field on six leaves per treatment by using a portable pressure chamber (PMS 1000, Corvallis, OR, USA); again, sun exposed, healthy leaves were chosen. Shoot hydraulic conductance was calculated as: $K_{s-1} = T_{l,max} / (\Psi_{pd} - \Psi_{md})$.

Stem hydraulic parameters

Xylem embolism in apical twigs was quantified by determining the hydraulic conductivity (mass flow rate / pressure gradient) of the xylem before and after the removal of air emboli from cavitated vessels by the "flushing" method (SPERRY & al. 1988a). At different dates during the season, current-year apical vine-shoots were collected from each of six plants per treatment. Vine-shoots were immediately enclosed in polyethylene bags stored in a cooler in the dark and brought to the laboratory within 2 h of abscission. In the laboratory, vine-shoots were soaked for 15-30 min before measurement in order to release tension in the xylem, and to prevent artifacts in the measurement of hydraulic conductivity resulting from tissue capacitance (SPERRY & al. 1988b). From each vine-shoot, a segment about 250 mm long was cut under water and then, while still submerged, cut again to avoid further embolism and to obtain a final stem portion about 200 mm in length and 5-6 mm in diameter. Both ends of the stem section were fitted with rubber gaskets, trimmed with a razor blade in distilled water and mounted on rubber tubes. The perfusing solution was 0.1% HCl in distilled water (pH 1.8) to minimize microbial occlusions of xylem vessels. The perfusing solution was degassed by agitating under vacuum for 60 min and then introduced into an air-free plastic ball enclosed in a compressed gas tank. The solution, passing through a 0.2 μ m inline filter (POLYCAP-36AS, Arbor Technologies Inc., Ann Arbor, MI, USA), perfused the samples under a constant pressure gradient maintained by a pressure regulator. Stopcocks allowed selective influx for measuring the initial conductivity (K_i) on one sample at a time under a pressure gradient of 9-10 kPa. The maximum conductivity (K_m) was determined by pressurizing the solution through all the segments at 150 kPa for 60-90 min. The permeating solution flowed from the pressurizing reservoir across the samples and into a container on an analytical balance joined to a computer that automatically made the calculations. Measurements of hydraulic conductivity were recorded every 30 s and calculated by averaging ten readings after steady-state had been achieved. Embolism causing percent loss of hydraulic conductivity (K_{loss}) was assessed from: $K_{loss} = 100 (K_m - K_i)$. Specific hydraulic conductivity (K_s), as a measure of the porosity of the xylem on a cross-sectional area basis, was calculated from: $K_s = K_i / A_w$, where A_w is the cross-sectional area of xylem tissue. Leaf specific hydraulic conductivity (K_L), as a measure of xylem efficiency, was calculated from: $K_L = K_i / A_L$, where A_L is the area of foliage supplied by the branch. Huber value (H_v), as a measure of the investment of stem tissue per unit leaf area fed, was calculated from $H_v = A_w / A_L$.

Ultrasound acoustic emissions (UAE) from cavitating xylem conduits were recorded by ultrasonic transducers (PAC 1151) clamped on each plant. Signals from the transducer were amplified by 75 decibels, and logged with a 4615 Drought Stress Monitor (Physical Acoustic Corporation, Princeton, NJ, USA). The sensors were placed on the same stem portions. A portion of the bark was removed to expose a small area of xylem, onto which the transducer was tied. This area was coated with silicone grease to prevent evaporation from the tissue. The contact between the transducer and the xylem was improved by using an ultrasound transmitting gel. The transducers were scanned in turn, and the output of each was recorded for 4 min in 16 min cycles.

Statistical analysis

Measurements were conducted on several consecutive days per month, in late June, mid August and Early October. Data were averaged on a plant basis within each period, and temporal and treatment fluctuations in the data were analyzed by repeated analysis of variance (ANOVA, $\alpha = 0.05$).

Results

In general, $g_{s,max}$ and K_{s-1} differed clearly between the two treatments (Fig. 1), in both 1995 and 1996 growing seasons, being higher in control plants ($P < 0.05$). By contrast, Ψ_{pd} and Ψ_{md} never differed significantly between treatments (Fig. 2). Chronological differences in $g_{s,max}$ were negligible, though a decreasing

tendency within each season was somewhat observed. A marked decrease in K_{s-1} was observed from early to late summer 1995, though in 1996 values were consistently higher ($P < 0.05$) than the previous year regardless of the treatment. The seasonal course in Ψ_{pd} showed an opposite trend between the two years, increasing (absolute terms) with the season in 1995 while decreasing in 1996. Seasonal trends in Ψ_{md} were less obvious and, in general, differences between years were of minor importance. Values of Ψ_{pd} and Ψ_{md} did not indicate noticeable water stress conditions. Treatment effects on Ψ_{pd} and Ψ_{md} were never significant.

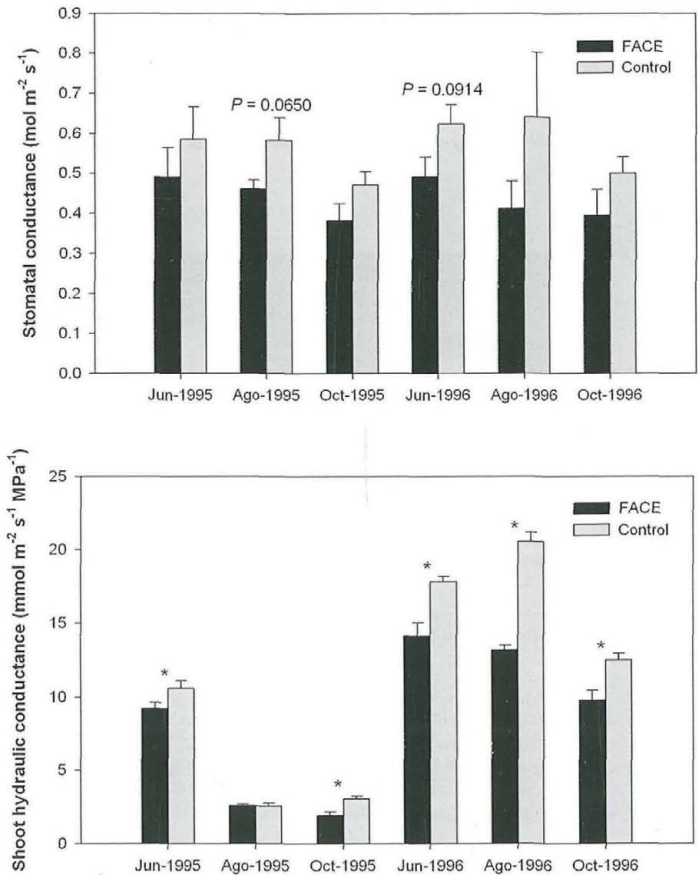


Fig. 1. Seasonal trends in stomatal conductance ($g_{s,max}$) and shoot hydraulic conductance (K_{s-1}) in grapevine grown at two CO_2 concentrations (ambient, control, and 700 ppm, FACE). Mean values are reported $\pm$ SE ($n = 6$). An asterisk (when present) indicates differences between treatments at the 0.05 significance level; when almost significant the P -level was directly reported, see text for overall significance. Treatments are referred to by symbols in the legend.

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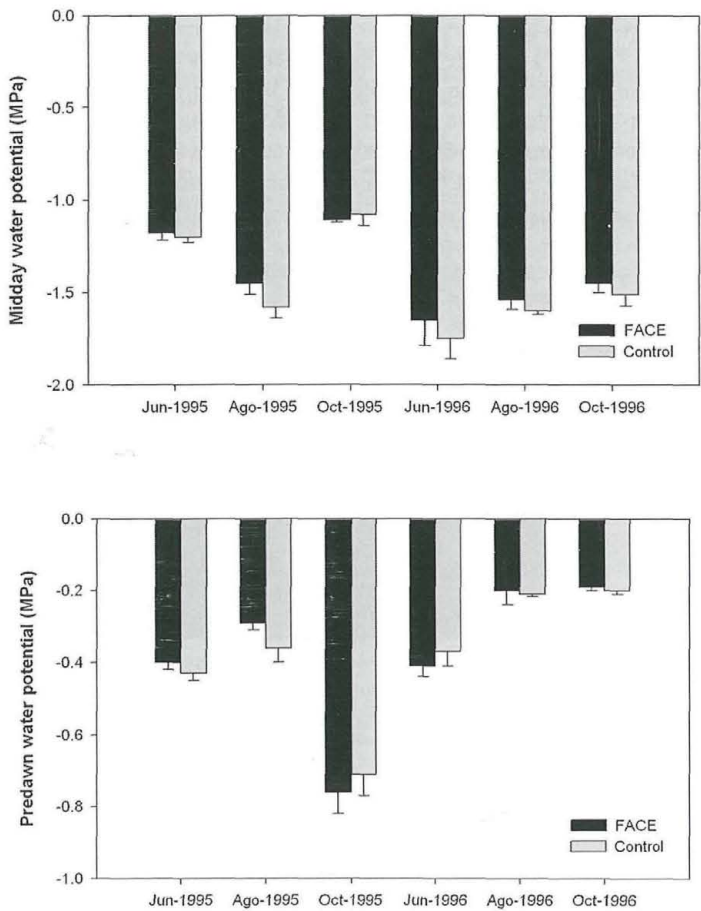


Fig. 2. Seasonal trends in predawn (Ψ_{pd}) and midday (Ψ_{md}) water potentials in grapevine grown at two CO_2 concentrations (ambient, control, and 700 ppm, FACE). Mean values are reported $\pm$ SE ($n = 6$). See text for overall significance. Treatments are referred to by symbols in the legend.

More contradictory were results on hydraulic architecture, K_{loss} being to some extent higher in FACE than control plants in 1996 ($P < 0.05$), but not in 1995 (Fig. 3). A general reduction of K_{loss} , though vague, was observed during the seasonal course. Fumigation and seasonal effects were even less evident on K_s , with regularly high values (Fig. 3). Values of K_L showed a slight increase with the season in both years and treatments (Fig. 4). Fumigation effects were reverse in 1995 with respect to 1996, K_L being to some extent higher ($P < 0.05$) in FACE plants

during 1995 and in control plants at some stages in 1996. The same tendency, though less clear, was shown for H_V (Fig. 4). In FACE plants, K_i increased significantly ($P < 0.05$) as a function of A_L (after log transformation to linearize the data) and the latter considerably augmented ($P < 0.05$) with increasing A_W , while this was not the case of control plants (Fig. 5). Instead, K_i increased significantly ($P <$

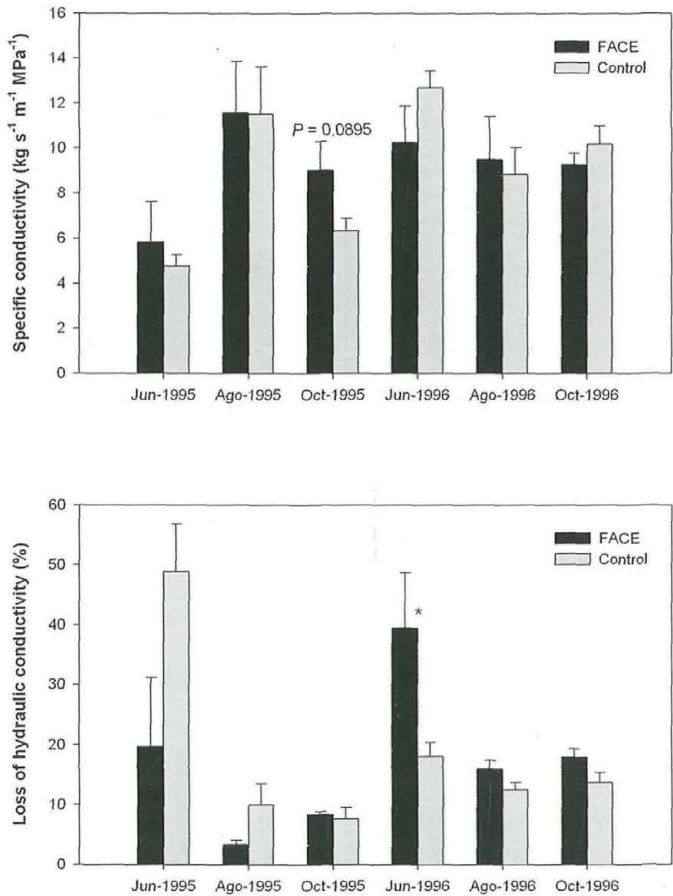


Fig. 3. Seasonal trends in percent loss of hydraulic conductivity (K_{loss}) and specific hydraulic conductivity (K_s) in grapevine grown at two CO_2 concentrations (ambient, control, and 700 ppm, FACE). Mean values are reported $\pm$ SE ($n = 6$). An asterisk (when present) indicates differences between treatments at the 0.05 significance level; when almost significant the P -level was directly reported, see text for overall significance. Treatments are referred to by symbols in the legend.

0.05) as a function of A_w in both treatments (Fig. 5). The daily course of UAE counts displayed an irregular pattern (Fig. 6), with wide fluctuations in all representative days, regardless of the treatment. However, absolute values of UAE counts decreased in late summer, FACE plants showed lower UAE counts than control plants in early and mid summer, while the opposite was true in late summer. A year-to-year variation between FACE and control plants was observed in cavitation events recorded.

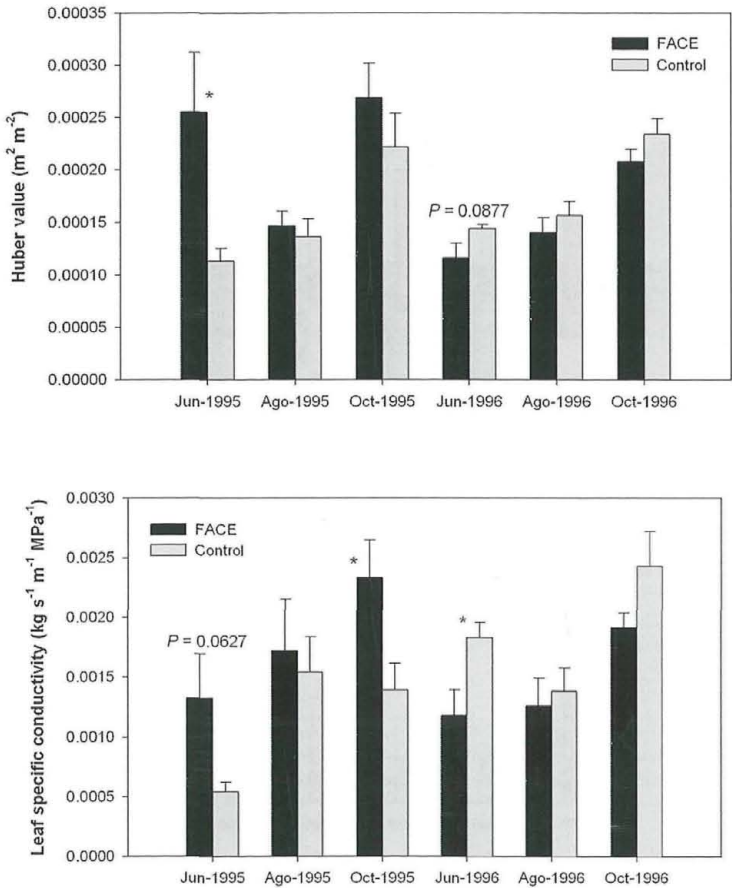


Fig. 4. Seasonal trends in leaf specific hydraulic conductivity (K_L) and Huber value (H_V) in grapevine grown at two CO_2 concentrations (ambient, control, and 700 ppm, FACE). Mean values are reported $\pm$ SE ($n = 6$). An asterisk (when present) indicates differences between treatments at the 0.05 significance level; when almost significant the P -level was directly reported, see text for overall significance. Treatments are referred to by symbols in the legend.

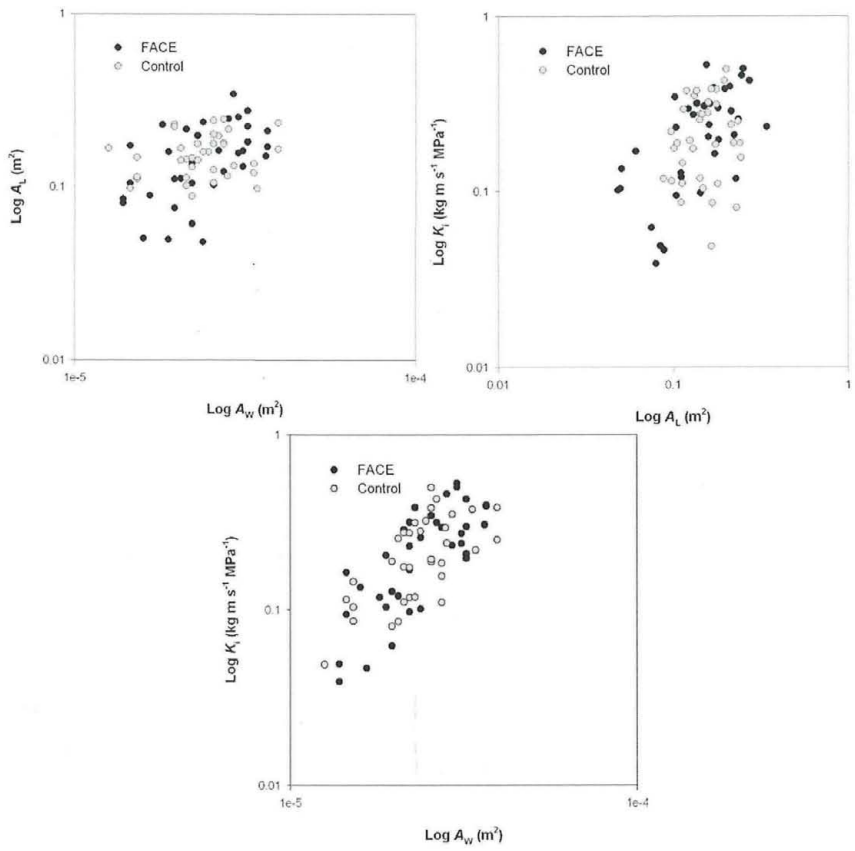


Fig. 5. Relationships between initial hydraulic conductivity (K_i), foliage area (A_L) and cross-sectional stem area (A_w) on a log scale in grapevine grown at two CO_2 concentrations (ambient, control, and 700 ppm, FACE). Treatments are referred to by symbols in the legend.

Discussion

The lack of marked drought conditions was reflected in the minor seasonality of xylem functionality and stomatal behavior. The present study confirms that stomatal conductance generally decreases under elevated CO_2 and that the effect is not transitory but persists over the long-term (MORISON 1998). No significant differences in predawn and midday water potential were evidenced between the two treatments, suggesting a scarce effect of the reduced transpiration (due to elevated CO_2) on plant water status, in absence of strong water stress. In

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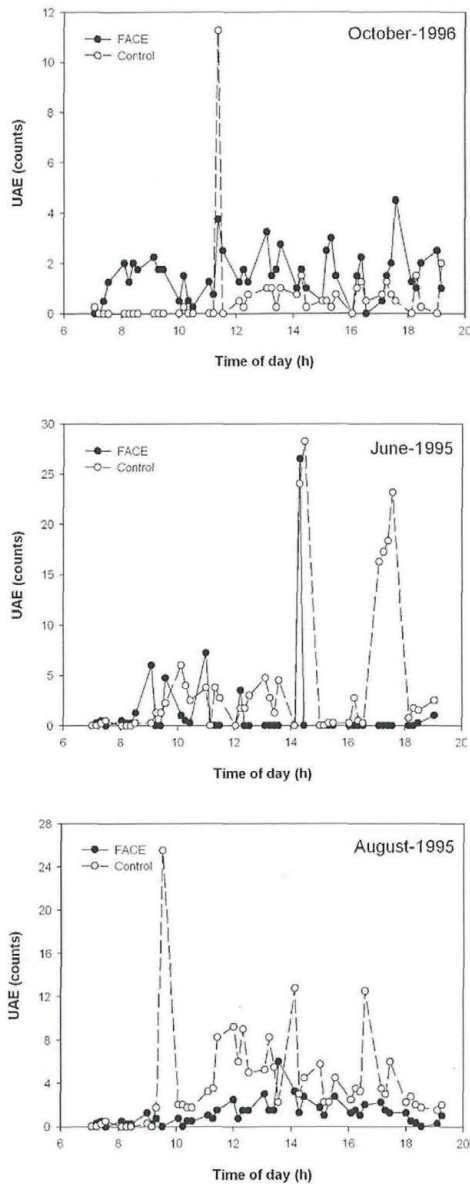


Fig. 6. Representative diurnal and seasonal trends of ultrasound acoustic emission (UAE counts) in grapevine grown at two CO₂ concentrations (ambient, control, and 700 ppm, FACE). Treatments are referred to by symbols in the legend.

general, it is assumed that a large genetic range exists in stomatal responsiveness of grapevine to environmental factors (CHAVES & al. 1987, SCHULTZ & al. 1999), and that cultivars adapted to stressful conditions usually display a higher stomatal sensitivity; therefore, extrapolation of results to different cultivars, typical of diverse pedoclimatic environments, may be misleading. Nevertheless, a marked reduction in shoot hydraulic conductance of FACE plants compared to controls was evident in the second year of study reflecting changes in water use in Sangiovese grapevine under elevated CO₂. HEATH & al. 1997 found that exposure to elevated CO₂ reduced shoot hydraulic conductance in *Quercus robur* but not in *Fagus sylvatica*.

Changes in native embolism Mediterranean shrubs indicated clear seasonal segregation by species and by growth CO₂ concentration (TOGNETTI & al. 2001, 2002). In *Erica arborea*, *Myrtus communis* and *Juniperus communis* hydraulic properties varied as a function of shoot biomass and leaf area, and the latter increased with increasing sapwood area, but differences between control plants and those grown for long term under elevated CO₂ were of minor importance except for *M. communis*. In the present experiment, year-to-year variations existed in percentage embolism between FACE and control grapevine, reinforcing the hypothesis of a different xylem structure in shoots developed under long-term elevated CO₂. In fact, larger vessels due to increased growth rates may be expected (ATKINSON & TAYLOR 1996), and consequently altered pit membrane permeability might influence water stress-induced cavitation within a species (TYREE & EWERS 1991). Indeed, cavitation events in grapevine shoots were apparently increasing from the first to the second year of exposure to elevated CO₂, as compared to control plants. The allometric nature of relationships between initial hydraulic conductivity, leaf area and stem cross-sectional area of xylem demonstrates a physiological basis, since the amount of conduit tissue was somewhat related to the supplied foliage area. The pipe diameter is size-dependent and varies with stem diameter (TYREE & EWERS 1991), though these relationships were unclearly affected by elevated CO₂.

As a consequence of year-to-year variation, the porosity of the xylem on a cross-sectional area basis and xylem efficiency of FACE plants tended to decrease with time of exposure as compared to controls. The investment of stem tissue per unit leaf area fed changed accordingly. If positive effects of hydraulic conductivity on growth efficiency holds true under changing environmental conditions, then Sangiovese grapevine could be relatively disadvantaged in terms of productivity, in consequence of the decrease in the intrinsic capacity to supply leaves with water. However, this stomatal and hydraulic behavior might result in a slower exhaustion of soil moisture during particularly dry summers, and further studies on grapevine responses to drought while growing under elevated CO₂ conditions are warranted for modeling future scenarios of this important woody crop (BINDI & al. 1996). Indeed, under severe drought stress, an elevated CO₂-induced decreased hydraulic efficiency in Sangiovese grapevine might reduce the risk of runaway xylem embolism. Contrasting results on the effect of elevated CO₂ on hydraulic efficiency of various woody plants have been reported by ATKINSON & TAYLOR 1996, and TOGNETTI & al. 1999, 2001, 2002. Leaf specific hydraulic conductivity is affected by specific hydraulic conductivity, and variation in Huber value (relative allocation

to conductive and foliage tissue) after fumigation with elevated CO₂ may act as compensation. The inability of Sangiovese grapevine to increase leaf specific hydraulic conductivity in FACE plants (which also showed similar or less leaf area at corresponding stem cross-sectional area) may balance for differences in growth in comparison with controls. A relatively larger wood investment may increase xylem redundancy while buffering higher cavitation rates.

In a companion paper, BINDI & al. 2005 report that the FACE treatment stimulated Sangiovese grapevine production without any negative or positive consequence on grapes and wine quality. However, any positive CO₂-fertilisation effect on grapevine yield may be reduced or completely cancelled by negative effects of warmer temperatures, as expected to be associated with elevated CO₂ concentration under future climatic scenarios. In this sense, year-to-year variations in eco-physiological responses to elevated CO₂ must be considered when modeling crop performances, particularly in climates characterized by strong variability, such as those at Mediterranean latitudes. Overall, elevated CO₂ might alter hydraulic properties and water relations of Sangiovese grapevine, though differences between FACE and ambient CO₂-grown plants in the proportional investment in conducting or non-conducting tissues, which strongly influence xylem hydraulic efficiency throughout the life cycle of a plant, showed variation reliant on fumigation time-span. Under the experimental condition, the link between stomatal functions and hydraulic capacities was not clear throughout the two years and the homeostatic regulation of leaf water potential at constant values for these plants could not be verified. Differences in stomatal conductance only partially reflected variations in hydraulic architecture between CO₂ treatments, and relations with crown structure and root system warrant further studies.

A c k n o w l e d g e m e n t s

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