Elevated CO$_2$ mitigates the adverse effects of drought on daytime net ecosystem CO$_2$ exchange and photosynthesis in a Florida scrub-oak ecosystem

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Abstract

Drought is a normal, recurrent feature of climate. In order to understand the potential effect of increasing atmospheric CO$_2$ concentration (C_a) on ecosystems, it is essential to determine the combined effects of drought and elevated C_a (EC) under field conditions. A severe drought occurred in Central Florida in 1998 when precipitation was 88 % less than the average between 1984 and 2002. We determined daytime net ecosystem CO$_2$ exchange (NEE) before, during, and after the drought in the Florida scrub-oak ecosystem exposed to doubled C_a in open-top chamber since May 1996. We measured diurnal leaf net photosynthetic rate (P_N) of *Quercus myrtifolia* Willd, the dominant species, during and after the drought. Drought caused a midday depression in NEE and P_N at ambient CO$_2$ concentration (AC) and EC. EC mitigated the midday depression in NEE by about 60 % compared to AC and the effect of EC on leaf P_N was similar to its effect on NEE. Growth in EC lowered the sensitivity of NEE to air vapor pressure deficit under drought. Thus EC would help the scrub-oak ecosystem to survive the consequences of the effects of rising atmospheric CO$_2$ on climate change, including increased frequency of drought, while simultaneously sequestering more anthropogenic carbon.

Additional key words: air vapor pressure deficit; net ecosystem CO$_2$ exchange; open-top chamber; *Quercus myrtifolia*; stomatal conductance.

Introduction

Drought is one of the major environmental factors determining plant productivity and species distribution (Woodward 1987, Volkmar and Woodbury 1995). Drought may become more significant in the future with the predicted increases of atmospheric CO$_2$ concentration (C_a) and other greenhouse gases (Roeckner 1992, Hoerling and Kumar 2003). The interactive effects of drought and rising C_a are considered crucial for the prediction of the responses of forest trees to the global environmental change (Beerling *et al.* 1996, Norby and Luo 2004). Many studies on the responses of trees to elevated C_a (EC) under water stress have been reported (Morison 1993, Dixon *et al.* 1995, Roden and Ball 1996, Anderson and Tomlinson 1998), but most of these studies were carried out with seedlings under controlled environment and only relatively short-term C_a enrichment. There are several differences in the field compared to controlled environment regarding drought: (*a*) Drought stress evolves more gradually in the field and plants experience no root constriction from confinement in pots (Lawlor and Mitchell 1991, Ceulemans and Mousseau 1994, Körner 1995). (*b*) Plants acclimate to long-term water stress (Matthews and Boyer 1984, Bussis *et al.* 1998, Panković *et al.* 1999). (*c*) Atmospheric conditions concomitant to drought such as atmospheric vapor pressure deficit (VPD) are important factors determining the response of plants to drought (Maier-Maercker 1988, Panek and Goldstein 2001). For example, the daily sums of photosynthesis and transpiration in the field were more dependent on atmospheric conditions than on soil water potential in *Picea*

abies (Maier-Maercker 1998). For *Vicia faba*, relative humidity was the main environmental factor mediating the change in stomatal sensitivity to C_a (Talbott *et al.* 2003). It is essential to determine how the effects of drought will be altered by EC under field conditions (Mooney *et al.* 1991, Wullschleger *et al.* 2002, Norby and Luo 2004).

A long-term study of the effects of EC on the carbon, nutrient, and hydrologic cycles of a Florida scrub-oak ecosystem has been under way since May 1996. During the period of April to August 1998, Central Florida experienced a severe drought. This drought provided a unique opportunity to investigate the interactive effects of drought and EC on this ecosystem. We tested the hypothesis that EC mitigates the adverse effects of drought on daytime net ecosystem CO_2 exchange (NEE) of the Florida scrub-oak ecosystem.

Materials and methods

Experimental site: The study site was located on the Merritt Island National Wildlife Refuge, Cape Canaveral, Florida, USA (28°38′N, 80°42′W). The climate is warm, humid, and subtropical. Annual precipitation averages 131 cm, with a dry period typically occurring from April to June. The mean daily maximum temperature is 22.3 °C for January and 33.3 °C for July, and the mean daily minimum temperature is 9.6 °C for January and 21.9 °C for July (Mailander 1990). Thunderstorms are common in the summer with frequent lightning strikes, which can cause wildfires.

The soil consists primarily of sand and sandy coquina deposited since the Pleistocene, and has a 2–5 cm O horizon and 10–20 cm A horizon. The composition of aboveground biomass at the research site was *Quercus myrtifolia* Willd. (76 %), *Q. geminata* Small (15 %), and *Q. chapmanii* Sarg (7 %). Additional species included *Myrica serifera* L., *Lyonia ferruginea* (Walt.) Nutt, and *Galactia elliotti* Nuttall (Dijkstra *et al.* 2002).

Before the start of the experiment, aboveground biomass was measured from 19 randomly selected plots with the size of the footprint of intended chambers. After the site was burned in January 1996, sixteen open-top chambers (eight at AC and eight at 350 µmol mol^{-1} above ambient C_a, EC) were erected on 16 of the 19 selected plots, and eight more plots were selected in the burned area as un-chambered control. The chambers were octagons, 3.6 m in diameter and 2.1 m in height having an area of 9.45 m^2. The AC and EC chambers had the same pre-burn aboveground biomass (Dijkstra *et al.* 2002). Shoots of plants that had begun to grow after the site had been burned were cut off at ground level before beginning CO_2 treatment on May 14, 1996. The numbers of shoots and aboveground biomass grown after the burning and prior to the beginning of CO_2 treatment did not differ significantly between the pots later assigned to AC and EC chambers (Dijkstra *et al.* 2002). Pure CO_2 was added to the air stream blown into the EC chambers. CO_2 concentration in each chamber was monitored continuously, 24 h a day.

NEE: The methods and calculation of NEE were described in detail by Dore *et al.* (2003). In brief, open-top chambers were used as gas exchange cuvettes. When the measurements were conducted, lids were added to prevent backflow of ambient air into the chamber. NEE was determined by multiplying the flow rate of air through the open-top chambers by the difference in CO_2 concentration between air coming into and air leaving the chambers. NEE measured using this method was not different from what measured in the same stand using an eddy covariance system (Dore *et al.* 2003). NEE was measured one week every month in 1998 and 1999.

Leaf gas exchange measurements: Leaf net photosynthetic rate (P_N) was measured on intact sunlit leaves using a *LI-COR 6400* photosynthesis system (*LI-COR*, Lincoln, NE, USA) under field conditions. CO_2 concentration in the air coming into the leaf chamber was controlled using a CO_2 cartridge in order to get stable CO_2 concentrations. Measurements were conducted in the field under full sunlight from six AC and six EC chambers every two hours from 06:00 to 20:00 h over two consecutive days on May 20 and 21, July 8 and 9, and August 24 and 25, 1998. For each day, plants from three AC and three EC chambers were measured. Exceptions from this schedule occurred due to clouds which were the periods 18:00–20:00 h on July 8 and 9; 06:00–08:00 h, 18:00–20:00 h on August 20 and 21. Each measurement took less than ten minutes.

Soil water content, temperature, and photosynthetic photon flux density (PPFD) measurements: Volumetric soil water content in the top 15 cm was measured in each chamber by water content reflectometers (*CS615*, *Campbell Scientific*, Logan, UT, USA). Air temperature above canopy at 0.5 m high and soil temperature at 10 cm depth inside chambers were continuously measured using copper-constantan thermocouples (*Omega Engineering*, Stanford, CT, USA). PPFD and wind speed and direction were measured every minute with a cross-calibrated quantum sensor (*LI-COR 190S*, Lincoln, NE, USA) and a cup-anemometer (R.M. Young Wind Sentry Set, *Campbell Scientific*, Logan, UT, USA). All those measurements were recorded with a data-logger (*CR7*, *Campbell Scientific*, Logan, UT, USA). Air VPD was calculated using water vapor concentration and air temperature from AC and EC chambers.

Analysis of data: Results were statistically analyzed using *SYSTAT 8.0* (*SPSS*, Chicago, IL, USA). Repeated

measures' analysis of variance (ANOVA) was used for NEE data. In all cases, growth C$_a$ – the C$_a$ treatment to which the plants were normally exposed – was considered the main effect, or between-subjects contrast. The decline rate of NEE from its maximum to its minimum around noon (*i.e.* midday depression) was calculated using linear regression for each of the sixteen chambers on May 14–17, June 6–9, 1998, and July 7 and 9, 1999. For comparing the CO$_2$ effect on decline rate, day was the repeated measure (within-subjects contrast). The decline

Results

Drought conditions: Low precipitation during the spring of 1998 resulted in a severe drought (Fig. 1). The precipitation recorded at the experimental site for the period of April to June was 88 % less than the average for the 18 year period of 1984–2002. In 1999, the precipitation was close to normal in May, June, and August but not in July. In the drought year 1998, soil water content declined from March to June (Fig. 2). The soil water content in May and June was 64 % lower than that in the normal year 1999. EC did not significantly affect soil water content during the measurement periods in 1998 (*p*=0.261) and 1999 (*p*=0.254).
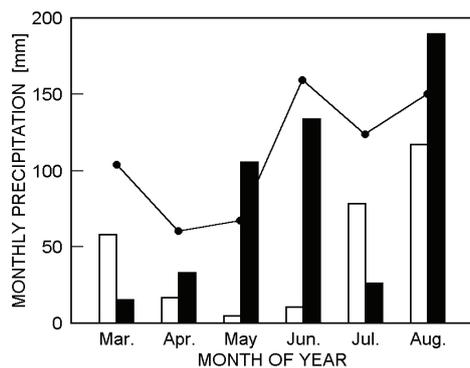
Fig. 1. Monthly precipitation in 1998 (□) and 1999 (■), and the averages from 1984 to 2002 (–●–) at the experimental site.

NEE: The average diurnal courses of NEE and the corresponding PPFD and air VPD from 2–4 d in April through August 1998 are shown in Fig. 3. Because EC did not significantly affect PPFD and VPD, the averages from AC and EC are presented for brevity. In April and August, NEE increased as PPFD increased to the maximum value before decreasing as PPFD declined in the afternoon (Fig. 3). The same diurnal pattern appeared in wet May, June, and August 1999 (Fig. 4). Under drought conditions in May, June, and July 1998 and July 1999, NEE reached the highest rate in the morning long before PPFD was maximum, and declined thereafter. This decline continued until nearly constant, usually around noon, or rose again as PPFD gradually decreased. NEE exhibited a mid-day depression at both AC and EC under drought.

rate with increase of air VPD (*i.e.* sensitivity of NEE to VPD) was analyzed using the same method for the decline rate with time. The soil water content was analyzed with repeated ANOVA. The daily average of soil water contents was used for the analyses with month as repeated measure. Two- and three-way ANOVAs were used to determine the significance of effects of C$_a$, drought, time of day and their interactions on leaf P$_N$ and stomatal conductance (g$_s$).
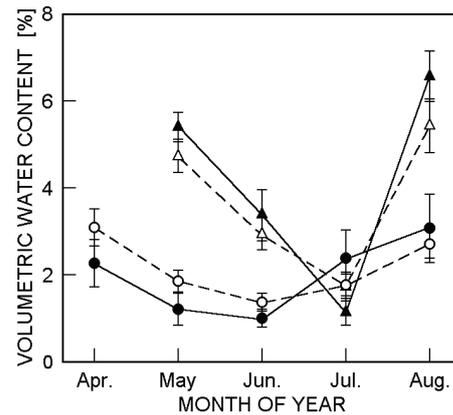
Fig. 2. Volumetric soil water content over the top 15 cm as determined by reflectometer in the 2–4 d of net ecosystem exchange measurements in 1998 (ambient CO$_2$ --○--, elevated CO$_2$ –●–), and in 1999 (ambient CO$_2$ --△--, elevated CO$_2$ –▲–). Means ± standard errors (*n* = 8).

Measurement of NEE every 16 min provided clear evidence of a midday depression. The decline in NEE was linear with time in the morning after reaching the maximum. For example, on May 17, 1998, NEE declined linearly after reaching the maximum rate at 09:11 h until 12:13 h (*r* = 0.988[**] at AC; *r* = 0.982[**] at EC) (Fig. 5*A*). The slope of the regression was taken as the decline rate of NEE, and we took the slope to indicate the intensity of the midday depression. A linear regression was applied to each of sixteen chambers in May and June 1998 and July 1999. Because of cloudiness in the morning during the measurement period, the midday depression was not calculated in July 1998. The slopes labeled as reduction of NEE per hour are presented in Fig. 5*B*. EC decreased the slope. On average, the slope was 58 % (*p*<0.003), 60 % (*p*<0.025), and 66 % (*p*<0.032) lower at EC than AC, respectively, in May and June 1998 and July 1999.

High air VPD is usually a typical feature of drought. Under drought, NEE was linearly correlated to air VPD during the period starting from the time NEE reached the highest value at about 09:00 h and ending at the time NEE reached the lowest value around noon. In this period PPFD was always over 1 000 μmol m^{-2} s^{-1}, which saturated leaf P$_N$, except when it was cloudy. For example,

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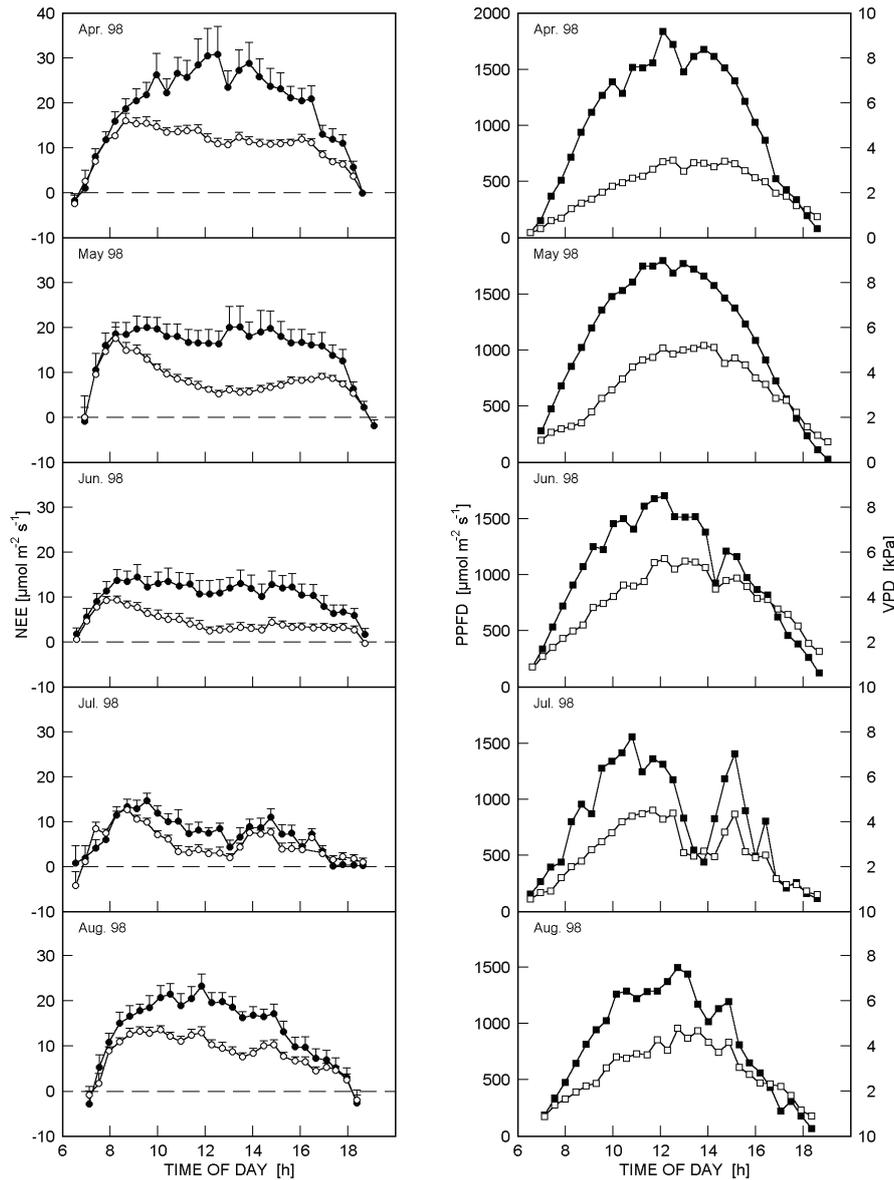
Fig. 3. Diurnal net ecosystem CO_2 exchange (NEE) at ambient, AC $(-○-)$ and elevated, EC $(-●-)$ CO_2, photosynthetic photon flux density (PPFD) $(-■-)$, and air vapor pressure deficit (VPD) $(-□-)$ in April–August 1998. Means over 2–4 d. The standard errors indicate variation among chambers ($n = 8$). PPFD and VPD were not affected by EC. Their averages from AC and EC are presented for brevity.

on May 17, 1998, NEE declined linearly ($r = 0.992$[**] at AC; $r = 0.975$[**] at EC) after reaching the maximum at 09:00 h and until 12:00 h (Fig. 6*A*). The slope of the regression was used to evaluate sensitivity of NEE to VPD. Such linear regression was done for each of sixteen chambers in May and June 1998, and July 1999 but not in July 1998 because of cloudiness. EC reduced the slope of NEE to VPD by 59 % ($p<0.008$), 58 % ($p<0.046$), and 79 % ($p<0.038$), respectively, in May and June 1998 and July 1999 (Fig. 6*B*).

Leaf P_N: Interactions between EC and drought on diurnal leaf P_N were evident in the data for May, July, and August 1998 (Fig. 7). Generally, EC increased P_N ($p<0.001$) and drought decreased it ($p<0.001$). In May and July, P_N declined after reaching the highest value before 09:00 h. This decline continued until noon, after

which it either continued nearly constant or rose again as PPFD and VPD gradually decreased. The course for P_N thus formed a shallow depression, the midday depression. This effect increased as the drought intensified from May through July. This midday depression could not be evaluated using linear regression since P_N was measured every two hours, but was assessed by the relative reduction of leaf P_N at 12:30 h compared with that at 08:30 h. In May, P_N was reduced by 77 % from 08:30 h to 12:30 h at AC but by only 48 % at EC. In July, P_N was reduced by 82 % at AC and by 69 % at EC.

g_s: The effect of EC on g_s varied with drought (Fig. 7). Drought decreased g_s at either AC or EC ($p<0.001$). EC decreased g_s throughout the day in May ($p<0.044$) but not in July and August.

Discussion

In this study, drought clearly altered the diurnal courses of NEE and caused a midday depression in NEE. Although the midday depression occurred at both AC and EC, it appeared later in the day, ended sooner, and was much less severe at EC (Figs. 3 and 4). In May and June 1998, the midday depression was 58 and 60 % less at EC

than at AC. In July 1999, it was 66 % (Fig. 5). We used midday depression of P_N at AC as a sign of drought because it is a typical and widespread response of plants (Epron *et al*. 1992, Damesin and Rambal 1995, García-Plazaola *et al*. 1997).

At leaf level, the effects of drought on P_N of
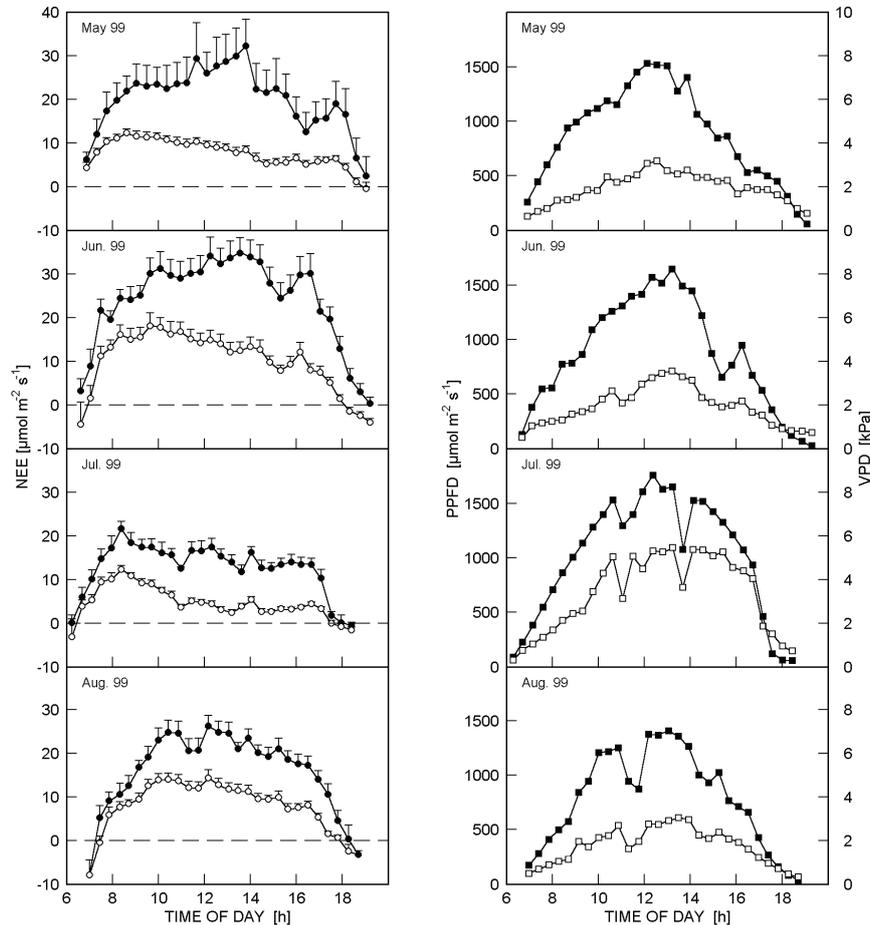
Fig. 4. Diurnal net ecosystem CO$_2$ exchange (NEE) at ambient, AC (–○–) and elevated, EC (–●–) CO$_2$, photosynthetic photon flux density (PPFD) (–■–), and air vapor pressure deficit (VPD) (–□–) in May–August 1999. Means over 2–4 d. The standard errors indicate variation among chambers (n = 8). PPFD and VPD were not affected by EC. Their averages from AC and EC are presented for brevity.

Q. myrtifolia were very clear in this study as indicated by reduction of P_N and mid-day depression of photosynthesis (Fig. 7). Compared to AC, EC alleviated the midday depression in *Q. ilex* in a Mediterranean climate (Scarascia-Mugnozza *et al*. 1996). In our study, the mitigation on midday depression by EC at leaf level was similar to the same effect at whole ecosystem level (Figs. 3 and 4).

The sensitivity of NEE of plants exposed to EC to air VPD under drought was reduced compared with those at AC. In May or June 1998, soil water content varied very little in four consecutive days. The large date-to-date variation in NEE was due to VPD. On average, the sensitivity of NEE to VPD was 59 and 58 % lower at EC than at AC, respectively, in May and June 1998 (Fig. 6). Similar results appeared in July 1999. This supports the conclusion that atmospheric conditions concomitant to

drought such as atmospheric VPD are important factors determining the response of plants to water stress (Maier-Maercker 1988, Panek and Goldstein 2001).

The CO$_2$ effect on g_s depended on drought intensity. EC decreased g_s in May but not in July 1998. This implies that EC may help the plant save water at moderate drought but not at severe drought. This is similar to the conclusion from an intensive review (Curtis 1996). For 83 independent experiments with 41 woody species, unstressed plants showed a modest but significant reduction in g_s at EC, while stressed plants showed no CO$_2$ effect on g_s (Curtis 1996). The stomatal responses of oak species are clearly dependent on environmental conditions because different results with the same species were reported from different experiments. For example, reduction of g_s in *Quercus robur* and *Q. rubra* at EC were reported in some studies (Beerling *et al*. 1996, Will and

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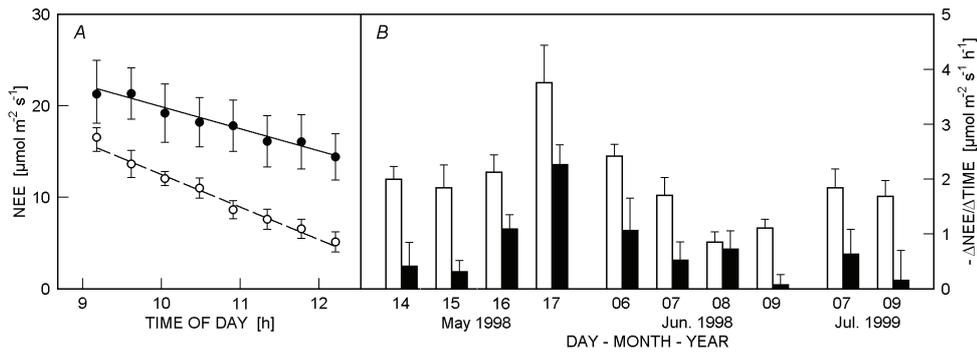
Fig. 5. Net ecosystem CO_2 exchange (NEE) at ambient, AC (--O--) and elevated, EC (−●−) CO_2 after reaching the highest rate until the lowest rate around noon on May 17, 1998, and decline rates of NEE (*i.e.* midday depression) at AC (□) and EC (■) after reaching the highest rate until the lowest rate around noon, which were calculated using linear regression for each chambers. Means ± or + standard errors (*n* = 8).
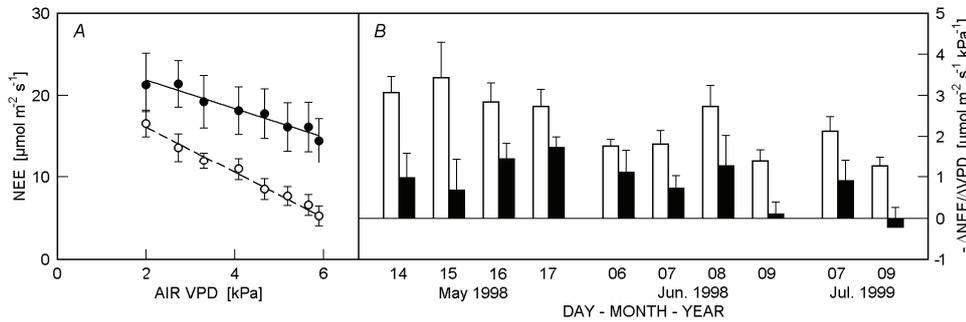
Fig. 6. Correlation of net ecosystem CO_2 exchange (NEE) at ambient, AC (--O--) or elevated, EC (−●−) CO_2 concentrations to air vapor pressure deficit (VPD) after NEE reached the highest rate until the lowest rate around noon on May 17, 1998, and the sensitivity of NEE to VPD at AC (□) and EC (■), which was calculated in each chambers by linear regression of NEE to VPD starting from the time NEE reached the highest rate and ending at the time NEE reached the lowest rate around noon. Means ± or + standard errors (*n* = 8).
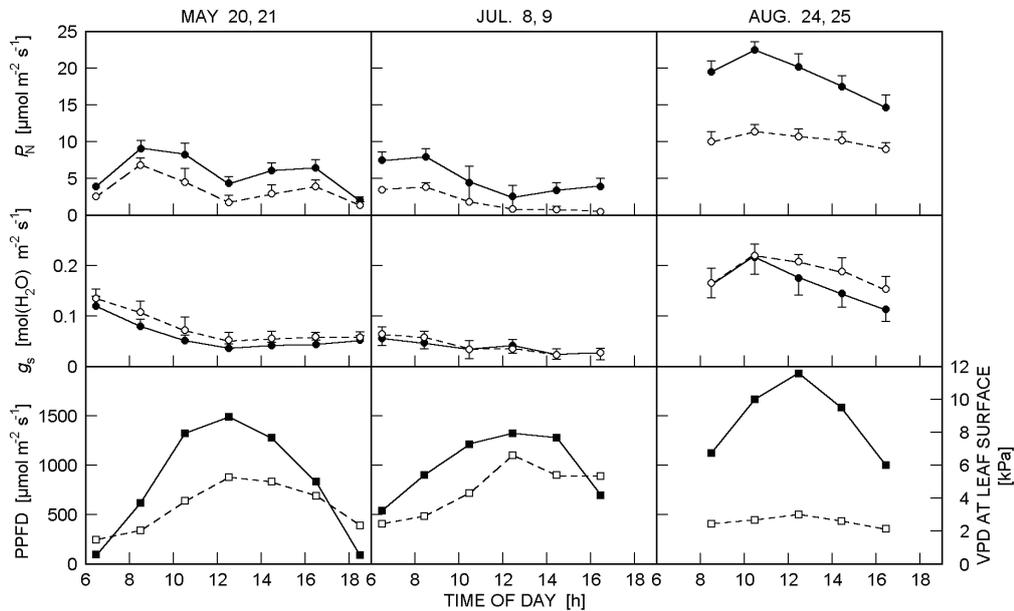
Fig. 7. Diurnal courses of leaf net photosynthetic rate (P_N) and stomatal conductance (g_s) of *Q. myrtifolia* grown and measured at ambient, AC (--O--) and elevated, EC (−●−) CO_2 concentrations on May 20, 21, July 8, 9, and August 24, 25, 1998. The PPFD (−■−) and vapor pressure deficit at leaf surface (−□−) were not affected by EC. Their averages from AC and EC are presented for brevity. Means ± standard errors (*n* = 6).

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Teskey 1997) but not in others (Bunce 1992, Dixon *et al.* 1995, Atkinson *et al.* 1997). The mitigation of the effects of water stress by EC was reflected in the aboveground biomass growth in 1998. The increment in total aboveground oak biomass in the drought year 1998 was 51 % lower than that in non-drought 1997 (Dijkstra *et al.* 2002) but the relative effect of EC on biomass accumulation of the dominant species *Q. myrtifolia* was higher during the drought year (210 % for 1998) compared to the non-drought years (67 % for 1997) (Dijkstra *et al.*

2002). Drought may become more significant in the future (Roeckner 1992, Hoerling and Kumar 2003). If so, rising atmospheric CO$_2$ will mitigate some of its effects with the result that the scrub-oak ecosystem will sequester more carbon. Whether this will also occur in other woody ecosystems remains to be seen, but studies such as the one reported here strongly support the conclusion that the effects of rising atmospheric CO$_2$ on plant and ecosystem processes are likely to be greater during drought.

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