California black oak response to N-amendment at an N-saturated site

Article *in* Environmental Pollution · November 2005

DOI: 10.1016/j.envpol.2005.01.039 · Source: PubMed

4 authors, including:

Nancy Grulke
US Forest Service
91 PUBLICATIONS **2,954** CITATIONS
SEE PROFILE

Mark Fenn
US Forest Service
203 PUBLICATIONS **5,485** CITATIONS
SEE PROFILE

Available online at www.sciencedirect.com
SCIENCE DIRECT®
Environmental Pollution 137 (2005) 536–545
ENVIRONMENTAL POLLUTION
www.elsevier.com/locate/envpol

California black oak response to nitrogen amendment at a high O_3, nitrogen-saturated site

N.E. Grulke *, W. Dobrowolski, P. Mingus, M.E. Fenn

USDA Forest Service, Pacific Southwest Research Station, 4955 Canyon Crest Drive, Riverside, CA 92507, USA

Received 10 December 2004; accepted 31 January 2005

Despite ecosystem-level N saturation, lower foliar respiration and significant photosynthetic gains under low light conditions resulted in greater wood production in black oak.

Abstract

In a nitrogen (N) saturated forest downwind from Los Angeles, California, the cumulative response to long-term background-N and N-amendment on black oak (*Quercus kelloggii*) was described in a below-average and average precipitation year. Monthly measurements of leaf and branch growth, gas exchange, and canopy health attributes were conducted. The effects of both pollutant exposure and drought stress were complex due to whole tree and leaf level responses, and shade versus full sun leaf responses. N-amended trees had lower late summer carbon (C) gain and greater foliar chlorosis in the drought year. Leaf water use efficiency was lower in N-amended trees in midsummer of the average precipitation year, and there was evidence of poor stomatal control in full sun. In shade, N-amendment enhanced stomatal control. Small differences in instantaneous C uptake in full sun, lower foliar respiration, and greater C gain in low light contributed to the greater aboveground growth observed.

Keywords: *Quercus kelloggii*; Gas exchange; Growth; Water use efficiency; Nitrogen fertilization; Stomatal behavior

1. Introduction

In Mediterranean forests east of Los Angeles, California, the primary form of atmospheric N deposition (95%) is dry deposition of nitric acid (HNO_3) and particulate nitrate (NO_3^-) (Bytnerowicz et al., 2001). The source of the N is fossil fuel combustion which is modified by subsequent photochemical reactions. Because of deposition kinetics of nitrogenous compounds, high N deposition is generally associated with high ozone (O_3) concentrations. The effects of these two concurrent pollutants on physiological responses in forest stands are poorly understood. Much of our understanding of their effects on forest tree species has been gained in chamber exposure studies (Sandermann et al., 1997), but results from several long term forest experiments better elucidate their interactive effects. The effects of O_3 alone are well known and include reduced CO_2 exchange rate (CER) accompanied by reduced conductance (g_s), greater respiration, reduced growth, whole plant biomass, and reduced allocation to roots (Heath and Taylor, 1997; Matyssek et al., 1995; Darrall, 1989). Even with concurrent O_3 exposure, N deposition generally improves gas exchange rates and whole plant carbon sequestration (Tingey et al., 2004; Grulke, 1999), but further exacerbates reductions in root growth (Andersen, 2003; Grulke et al., 1998). The interacting effects of O_3 exposure and N deposition in natural ecosystems are complex, but it is clear that N can exacerbate many of the effects of strong oxidants.

* Corresponding author. Tel.: +1 909 680 1556; fax: +1 909 680 1501.
E-mail address: ngrulke@fs.fed.us (N.E. Grulke).

0269-7491/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.envpol.2005.01.039

Dry deposition of nitrogenous compounds to foliage and litter layer is significant in the western San Bernardino Mountains. In contrast to N-saturated forests in more mesic climates, arid forests have less soil acidification and higher base saturation (Fenn et al., 1996). At this site, the foliar ratio of N to P is highly elevated relative to less polluted sites, with high foliar nitrate accumulation, especially in spring (Poth and Fenn, 1998). These forests also have low soil C:N ratios, high nitrate to ammonium in soil and soil solution, and high nitric oxide fluxes from the soil: all symptoms that characterize an N-saturated ecosystem (Fenn et al., 1996). Despite ecosystem-level N saturation, ponderosa pine and California black oak further amended with N had increased bole diameter growth (Fenn and Poth, 2001). In this study to directly test for the role of N deposition in physiological responses of California black oak, we used annual applications of slow release dry urea to the litter layer under trees as an analog of N deposition washed from foliage and litter into the soil in the first several autumn precipitation events.

To help understand how individual trees might respond to N amendment in an already highly N-enriched site, seasonal changes in gas exchange, foliar and branch growth, and foliar ozone injury were measured. At this site, long-term N-enrichment is accompanied by high O_3 exposure (80 ppb, hourly average for 24 h d^{-1}, over the 6 month growing season; Grulke, 1999). Physiological attributes were studied in a year of slightly below average precipitation (2003), as well as the most severe drought (2002) since instrumental records began in the region in 1849 (Minnich, 2005). The drought followed 3 years (1999–2001) of 20–30% below average precipitation[1] and coincided with the second year of heavy infestation of fruittree leaf-roller (*Archips argyrospilus* Walker), which has been present in the San Bernardino Mountains over the last several decades. The degree of leaf damage due to fruittree leaf-roller was also evaluated in the two treatments.

2. Methods

2.1. Research site and experimental manipulations

Research was conducted during the summers of 2002 and 2003 in the mixed conifer zone (Minnich, 2005) near Camp Paivika (34°14′05″N, 117°19′12″W; 1800 m) in the western San Bernardino Mountains. The stand is composed of mature ponderosa pine (*Pinus ponderosa* Laws, averaging 100 years old), white fir (*Abies concolor* Gord. & Gord.) incense cedar (*Libocedrus decurrens* (Torrey) Florin), and sugar pine (*P. lambertiana* Douglas). In this stand, California black oak (*Quercus kelloggii* Newb.), canyon live oak (*Q. chrysolepis* Liebm.), tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehder), laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.), and chinquapin (*Chrysolepis sempervirens* (Kellogg) Hjelmq.) are common in the understory. Bracken fern (*Pteridium aquilinum* var. *pubescens* Underw.) dominates the herbaceous cover.

The western edge of the San Bernardino Mountains has been exposed to long-term atmospheric pollutant deposition (Miller et al., 1989; Miller and McBride, 1999) for over 50 years, and the site meets the criteria for ecosystem-level N saturation (Fenn et al., 1996). Total background N deposition averages 35 kg ha^{-1} $year^{-1}$ (Kiefer and Fenn, 1997). Nitrogen is deposited primarily in the form of dry particulate nitrate (NO_3^-; 60%) and dry nitric acid (HNO_3; 30%) at this site (Bytnerowicz et al., 2001), but nitrogen dioxide (NO_2) is also elevated at this site relative to less polluted sites in the San Bernardino Mountains (Grulke et al., 2004). Typical hourly averages (from 24 h active samplers) for dry HNO_3 concentrations are 4–6 μg m^{-3} and 6–7 ppb for NO_2, which are two- to three-fold greater than less polluted sites. Ozone concentrations are high, and average 80 ppb over June, July, and August during daylight hours (Grulke et al., 2004; Grulke, 1999).

2.2. Experimental manipulations and sampling frequency

A long-term project was initiated to elucidate the role that N deposition plays in ecosystem and tree response (ponderosa pine and California black oak) to oxidant exposure (Fenn and Poth, 2001). California black oak (*Quercus kelloggii* Newb.) trees (40–80 years old) were fertilized beginning autumn, 1997 and fertilization continues annually at the rate of 50 kg ha^{-1}, approximately 20% beyond the canopy drip line, a circle with a radius of approximately 5 m. Eight trees of comparable size, morphology, and relative distance to overstory trees in each of background-N and background plus N-amendment were chosen for intensive study. Nitrogen was applied as slow release urea (“Blue Chip”[2]) in dry form in the autumn to simulate the pulse of N input as the first precipitation events wash the summer deposition off leaf and branch surfaces (Fenn et al., 2000).

Soil moisture availability, growth, foliar health, and gas exchange rates were measured monthly through the growing season from May through October in 2002, and June through the end of September in 2003. Sampling

[1] Available on line from the San Bernardino County Water Resources Division web site: http://www.co.san-bernardino.ca.us/trnsprtn/pwg/.

[2] Mention of trade names is for information only and does not suggest endorsement.

generally took 1–2 days. Sampling of soil and foliage for carbon and N content was conducted in mid August both years.

2.3. Soil nutrient availability

Soil samples were collected approximately 1.5 m from the bole of each tree in the B_1 mineral horizon, generally at a depth of −10 to −15 cm. Samples were air dried for 5 days, sieved to pass a 2 mm screen, macerated, and analyzed on a NA 1500 Carlo-Erba C-N-S Analyzer. Carbon (C) and N content was expressed on an oven-dry basis. Foliar samples were collected in the field (5–7 leaves per tree), transported on ice packs to the lab, oven-dried at 65 °C for 2 days, ground to pass through a 40 mesh, and then analyzed.

2.4. Soil water availability

Gravimetric soil moisture was determined at −20 cm in mineral soil in 2002, and −20 and −50 cm in 2003 at the same time as intensive gas exchange measurements. Soil samples were collected within 1 m of the bole of the study trees on the south side. Soils were sieved to pass a 2 mm sieve, immediately placed in sealed soil tins, weighed, oven-dried at 65 °C to completion, then reweighed. Moisture content was reported as percent of dry weight.

2.5. Leaf xylem water potential

Leaf xylem water potential was measured at pre-dawn and solar noon for N-amended and background-N trees in 2003 only. For control trees, water relations was measured on the same days as intensive gas exchange measurements. For N-amended trees, water relations was measured only in early (6th) and late (22nd) July. Leaf water potential was determined on 2–5 detached leaves per tree inserted into a pressure chamber (PMS Instruments, Corvallis, OR) according to Pallardy et al. (1991). Statistical analyses (one-way analyses of variance) were conducted on mean leaf water potential per tree as the independent unit of measure.

2.6. Growth measurements

Current year branchlet elongation and diameter, and leaf expansion, retention, percent damage (from herbivory), and chlorosis (senescence) was measured monthly over both summers. Branch length was measured by age class to the nearest millimeter. Leaf length was measured to the nearest millimeter. Leaf retention was a count of the number of leaves remaining each month by leaf age. The percent damage and injury was recorded to the nearest 1% up to 5%, then by 10% increments thereafter for herbivory and chlorosis. Data from 5 to 6 branches per tree were averaged for each tree, with tree as the independent unit of measure for statistical evaluation.

2.7. Gas exchange measurements

An open photosynthetic system (model 6400, LiCOR, Inc., Lincoln, NE) was used at a light level of 1400 μmol m^{-2} s^{-1} (using red and blue light) and CO_2 level of 400 ppm, while matching ambient leaf temperature. Flow rates in the cuvette were varied to minimize the CO_2 draw-down in the sample air stream (dependent on gas exchange rates), but were constant during measurement. Air in the cuvette was almost always drier than that of the ambient air so that in general, no air was passed through the desiccant. For seasonal measurements, data from 2 to 3 leaves per tree were averaged, with the tree as the independent unit of measure.

Because an earlier onset of senescence was apparent during the drought year, and because trees in Mediterranean climates commonly experience late summer drought stress, we investigated photosynthetic attributes of senescing foliage between September 29th and October 7th, 2003, to test for differences in N treatment level. Steady state gas exchange measurements were conducted to test for N amendment effects on rubisco carboxylation, maximum photosynthetic rate under saturating CO_2 and light, and quantum efficiency. To test for the effects of N deposition on stomatal behavior, g_s response to changing levels of light (30 and 1000 μmol $m^{-2}s^{-1}$) were applied to leaves under otherwise ambient environmental conditions. For these experiments, the time required to reach equilibrium, and magnitude of change in stomatal conductance was recorded. A one-way analysis of variance was applied to test for differences between the two N-levels.

3. Results

3.1. Soil water content and leaf water potential

Soil water content (Fig. 1) was high as terminal buds were swelling in mid April, 2002 (8.9±0.7%). Soil water content had declined to 6.0±0.4% by mid June and to 3.2±0.2 by mid July, and remained low until autumn rains (3.0±0.1%) in 2002. By early October, soil moisture had recovered to 10.9±0.4%. In 2003, soil water content was 14.4±1.2% in mid June, and declined to 11.7±2.2% by mid July. In early September, soil water content had recovered to 14.9±2.1% due to reduced evapotranspiration at the site (frequent morning fogs in the month of August). Soil water content declined to 8.0±0.1 by the end of September, and further declined to 6.2±1.3% in October, 2003.

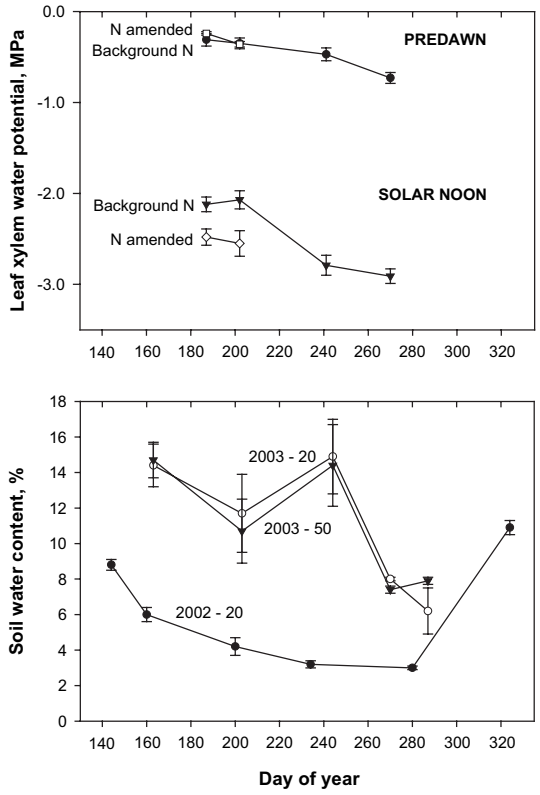

Fig. 1. Seasonal changes in leaf xylem water potential (above, given in MPa) for 2003, and soil water content (below, given in %) for 2002 and 2003. Leaf water potential was measured in predawn and at solar noon. Soil water content was measured at −20 cm and −50 cm. Symbols and bars represent means and ±1SE for eight trees at each N-level and for three pits for soil water content.

Pre-dawn leaf xylem water potential (Ψ_L) of background-N trees ranged from −0.3±0.1 MPa in early July to −0.7±0.1 MPa in late September (Fig. 1). Pre-dawn Ψ_L was not significantly lower for N-amended trees in early (−0.4±0.1 MPa) or late (−0.4±0.0 MPa) July. For background-N trees, solar noon Ψ_L was low in both early and late July (−2.1±0.1 MPa). In N-amended trees, solar noon Ψ_L was significantly lower than background N trees in both early (−2.5±0.1 MPa) and late (−2.6±0.1 MPa) July ($p=0.01$, 0.02, respectively). In background-N trees, solar noon Ψ_L further declined to −2.8±0.1 MPa in early September and −2.9±0.1 MPa in late September. No additional values were taken of N-amended trees.

3.2. Soil and tissue N content

Despite doubling the annual rate of N deposition, soil N content of the B_1 mineral horizon of N-amended trees did not significantly differ from that of background trees (Table 1). It is possible that available N had already been taken up, allocated or sequestered. Similarly, there were no statistically significant differences in foliar C, N, or C:N of N-amended or background-N trees.

3.3. Growth

In 2002, branchlet elongation and diameter growth were significantly greater in N-amended trees than in background N trees. Mean values presented in Table 2 are given on the date when growth was complete. In the year following drought, there were no differences in growth between treatments. The number of leaves produced per growing point did not differ between N-treatments in either year. Fewer leaves (one less per growing point) were initiated in the year following drought. In the drought year, background-N trees reduced leaf area soon after enlargement (Fig. 2). In the average precipitation year, there were no differences in leaf retention between N treatments.

3.4. Foliar herbivory and chlorosis

Leaf injury or damage due to herbivory was increased in the drought year and decreased in the average precipitation year by N-amendment relative to trees with background N levels (Table 2), but differences were not statistically significant. Once leaves reached full expansion, there was no further loss of leaf area due to herbivory. In the average precipitation year, herbivory

Table 1
Percent dry weight of carbon (C) and nitrogen (N) of B_1 mineral soil collected in May, 2002 and foliage collected in August in both 2002 and 2003

	2002			2003		
	C	N	C:N	C	N	C:N
Soil						
N-amended	1.9±0.2	0.10±0.01	18.9±0.5			
Background N	2.3±0.3	0.12±0.01	18.3±0.3			
p	0.38	0.25	0.30			
Foliage						
N-amended	45.1±0.5	2.48±0.07	18.9±0.5	49.0±0.4	2.7±0.4	18.1±2.5
Background N	46.1±0.2	2.53±0.06	18.3±0.3	48.9±0.6	2.7±0.4	18.3±1.9
p	0.06	0.64	0.31	0.61	0.78	0.87

Means±1SE have been tested with a one-way ANOVA.

Table 2
Summary of growth, and foliar chlorosis and herbivory

Days of year	200–210				291–295	280–290
	Branchlet diameter	Branchlet length	Leaf length	No. leaves/branchlet	% chlorosis	% herbivory
2002						
N-amended	2.3±0.1	59±6	111±5	5.9±0.5	55±5	23±4
Background N	2.0±0.1	41±6	95±6	5.3±0.5	46±5	16±4
p	0.03	0.04	0.06	0.33	0.23	0.26
2003						
N-amended	2.6±0.1	21±3	85±4	4.9±0.3	9±2	26±5
Background N	2.8±0.2	28±5	77±5	4.6±0.2	8±2	37±5
p	0.40	0.24	0.26	0.56	0.62	0.09

Due to herbivory later in the growing season, the number of leaves per branchlet is given for mid May in 2002 and early June in 2003. For all other parameters, growth and injury attributes are reported from the end of September (2002) or mid October (2003). Current year branchlet diameter and length, and leaf length are given in millimeters. Means±1SE were tested with a one-way ANOVA.

was greater in the background-N trees, but differences were not statistically significant. In the drought year, the percent foliar chlorosis was higher for N-amended trees for the last two sampling dates (day 295 and 311), but was significant only for the last date (96.8±1.1 vs. 86.4±2.4%, $p<0.01$; data not given in table). There were no differences in leaf chlorosis on any sampling date in the average precipitation year.

3.5. Seasonal gas exchange

Maximum seasonal CO_2 exchange rate (CER) in 2003 was 20% greater than in 2002 (Fig. 3). In 2003, maximum seasonal stomatal conductance (g_s) was three-fold higher than in the drought year. In a three-way analysis of variance with N-level (background-N and N-amended), seasonality (June through October), and year of measurement (2002, 2003), year, seasonality, and their interaction were statistically significant for CER, g_s, and C_i/C_a, a measure of leaf-level water use efficiency (Table 3). In a two-way analysis of variance, seasonality and N-level were statistically significant for g_s and C_i/C_a in 2003, but in the drought year, only the effect of seasonality on g_s was statistically significant.

Leaf-level water use efficiency was similar for both background-N and N-amended trees throughout the drought year (Table 3, Fig. 3). In an average precipitation year, fertilized trees were less water use efficient in mid-July. In late summer in the average precipitation year, the response to N-amendment was suppressed in full sun and seasonal gas exchange of both N-amended and background-N trees was similar. In late summer in the drought year, there was an earlier onset of senescence: gas exchange was significantly depressed in N-amended trees. Lower late summer gas exchange in N-amended trees was associated with greater foliar chlorosis (see above) in the drought year.

In the drought year, there were no differences in the relationship between stomatal conductance and leaf to air vapor pressure deficit (VPD) between N-amended and background-N trees (Fig. 4). In the average precipitation year, a power curve fit to stomatal response to increasing VPD suggested that the N-amended trees had poorer control relative to background-N trees.

Maximum CER under saturating CO_2 (2000 ppm in air) or ambient CO_2 (375 ppm in air) were greater in N-amended vs. background-N trees (Table 4), but differences did not differ statistically. Rubisco carboxylation rates were similar between N-amended and background-N trees. Light compensation point in N-amended trees was half that in background-N trees. Dark respiration in N-amended trees was half that in background-N trees, and these differences accounted for some of the differences observed in light compensation points. Apparent quantum efficiency did not differ between N-levels.

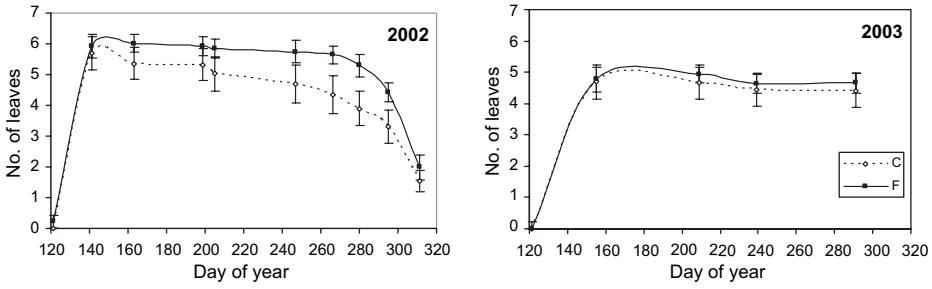

Fig. 2. Leaf production and retention in N-amended (F) and background-N (C) trees. Symbols and bars represent mean leaf number per growing point per tree for six trees per N-level in 2002 and eight trees per N-level in 2003, ±1SE.

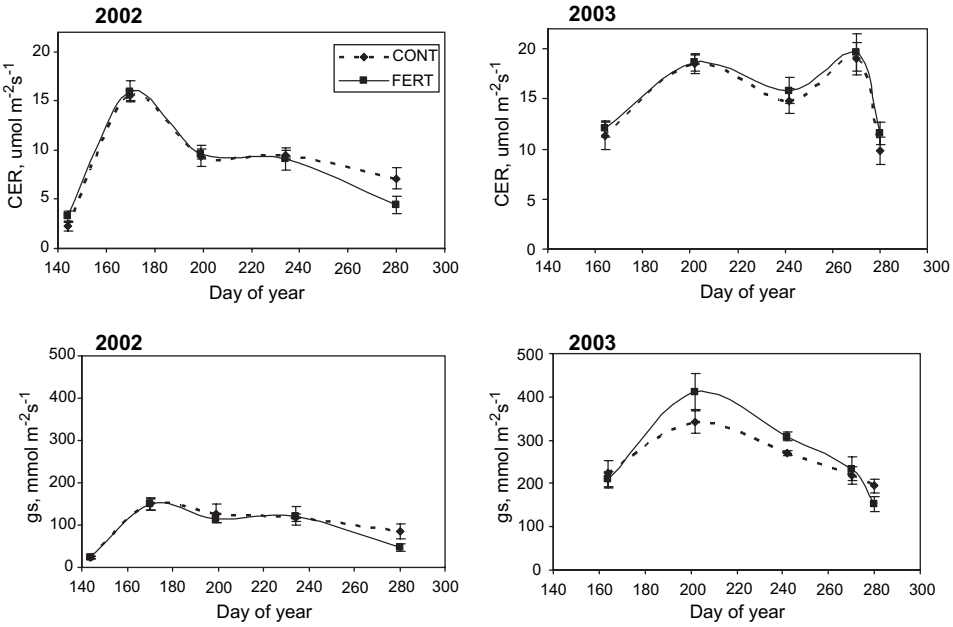

Fig. 3. Seasonal patterns in CO_2 exchange rate (CER) and stomatal conductance to water (g_s) in 2002 (drought year) and 2003 (average precipitation) for background-N (CONT) and N-amended trees (FERT). Symbols and bars represent means of six trees in 2002 and eight trees in 2003, ±1SE.

In order to test responses of stomata to rapid changes in light as commonly occurs in canopies, the time to reach equilibrium, either increased g_s due to increased light (1000 μmol $m^{-2}s^{-1}$) or decreased g_s due to decreased light (30 μmol $m^{-2}s^{-1}$), was tested between N-amended vs. background-N trees (Fig. 5). These tests were conducted on branches shaded by the overstory. Despite shading foliage on the primary branch measured, light on adjacent branches influenced the lowest level of g_s observed. For this reason, the overall change in g_s was tested in response to increasing and decreasing light. In June, only stomatal closure in response to reduced light was tested. In both June and September, no differences observed between N-levels were statistically significant (Table 5) although several trends supported greater water use efficiency in N-amended trees in early autumn. Stomatal opening in response to increased light was slightly faster (18%) for N-amended trees, and stomata did not open as much as in background-N trees. The time required for stomatal closure in response to decreased light was also faster (32%) for N-amended trees, and a greater change in g_s occurred. It is possible that high within population variability in the onset of autumn senescence contributed to lack of statistical significance between N-levels.

Table 3
Summary statistics for between year, seasonality, and N-level treatment on gas exchange attributes: CO_2 exchange rate (CER), stomatal conductance (g_s), and C_i/C_a (substomatal CO_2 concentration/ambient CO_2 concentration, an indicator of leaf-level water use efficiency)

	CER	g_s	C_i/C_a
2002 2-factor ANOVA			
Seasonality (A)	<0.01	0.01	<0.01
N-level (B)	0.82	0.63	0.51
A×B	0.88	0.94	0.96
2003 2-factor ANOVA			
Seasonality (A)	<0.01	<0.01	0.01
N-level (B)	0.15	0.01	0.05
A×B	0.52	0.55	0.54
3-factor ANOVA			
Year (A)	<0.01	<0.01	<0.01
Seasonality (B)	<0.01	<0.01	<0.01
N-level (C)	0.68	0.09	0.14
A×B	<0.01	<0.01	0.02
B×C	0.82	0.69	0.81
A×C	0.10	0.01	0.99
A×B×C	0.20	0.49	0.99

Values given in boxes are *p* values for the analysis conducted.

4. Discussion

Despite ecosystem-level N saturation, California black oak responded to N-amendment via increased elongation and enlargement growth of branchlets. The effects of both pollutant exposure and drought on gas exchange characteristics were complex, and were further modified by light level. For example, in average precipitation years under full light, N-amended trees were less water use efficient in mid-summer and had poor stomatal control in response to declining VPD. In contrast, the variation in the form (nitrate, ammonium, or both) and amount of supplied N did not affect the instantaneous water use efficiency in peduncular oak seedlings (*Quercus robur*) (Thomas and Gehlen, 1997).

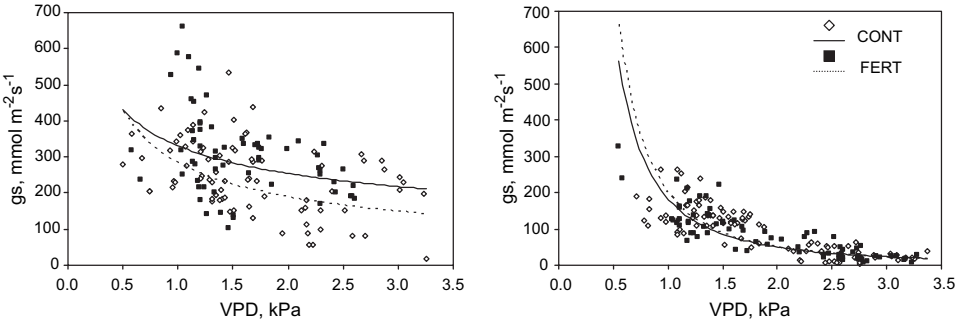

Fig. 4. Stomatal response to vapor pressure deficits (VPD) experienced during seasonal gas exchange measurements in 2002 (left) and 2003 (right). Square symbols represent the mean stomatal conductance of two leaves on N-amended trees and diamond symbols represent background-N trees. A power function was used to fit a regression line to the data.

In full light, CER under saturating or ambient CO_2 concentrations was elevated when compared to background-N trees, but the differences were not statistically significant near the end of the growing season when such differences are least likely to be detected. N-amendment of cork oak seedlings (*Quercus suber* L.) significantly increased the maximum observed photosynthetic rate under saturating CO_2 and light (Maroco et al., 2002). In our study, rubisco carboxylation did not significantly differ between background-N and N-amended trees, but foliar N content (and foliar chlorosis) also did not differ. N amendment of cork oak seedlings led to significantly greater carboxylation rates, but foliar N was also significantly improved (Maroco et al., 2002).

Greater CER would support the growth stimulation observed in our study. Although long term N deposition at this site has led to greater whole tree biomass in ponderosa pine (Tingey et al., 2004; Grulke and Balduman, 1999), both high N-deposition and O_3 exposure are believed to have significantly altered within-plant carbon and carbohydrate allocation. Relative to other sites with lower N-deposition, pine trees at this site had reduced root biomass, but greater bole mass and carbohydrate content (Grulke et al., 2001). It is possible that the additional N in this experiment altered within-plant allocation of carbon resources, not total biomass accumulation, to effect greater aboveground growth. The lack of photosynthetic responses to N-amendment may also have been related to P limitation. Plants in Maroco et al.'s (2002) high N treatment had the lowest P contents. Soil N availability had only a minor effect of foliar N content of California black oak in a field survey of mature trees (Knops and Koenig, 1997). Soil P was much more highly correlated with foliar N content. California black oak had the highest foliar N content of native deciduous oaks, but had the lowest foliar N content at the time of abscission (retranslocation). Foliar P was not analyzed in this study.

In low light conditions, N-amended trees had a more positive C balance, in part due to lower foliar respiration. The light compensation point of N-amended trees was half that of background-N trees. Stomatal closure in response to a rapid change from moderate to low light for N-amended trees took 30% less time of background-N trees, although differences were not statistically significant. Individual leaves even in open-grown trees are shaded two-thirds of the time (Grulke, unpublished data), and low light responses may be important to whole plant carbon and water balance.

Table 4
Photosynthetic attributes of California black oak measured at a high background N-deposition and O_3 exposure site in early autumn, 2003

	N-amended	Background-N	*p*
CO_2 and light saturated CER	25.28±1.61	21.78±0.99	0.10
Rubisco carboxylation	0.057±0.007	0.058±0.007	0.99
Light saturated CER, ambient Ca	11.52±1.13	9.85±1.39	0.38
Light compensation point	13.45±0.65	24.46±4.55	0.05
Apparent quantum efficiency	0.040±0.002	0.036±0.002	0.29
Dark respiration, at 28 °C	−0.57±0.12	−1.01±0.11	0.05

CO_2 exchange rates are given in μmol CO_2 $m^{-2}s^{-1}$. Light levels are given in μmol $m^{-2}s^{-1}$. Means±1SE were tested with a one-way ANOVA.

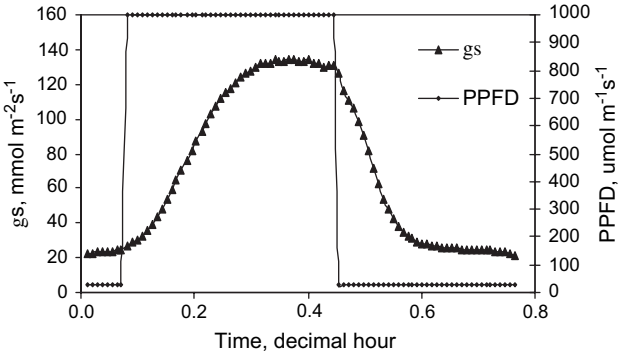

Fig. 5. Example of stomatal conductance to water (g_s, right hand *y*-axis) in response to two light levels: 30 and 1000 μmol $m^{-2}s^{-1}$ (left hand *y*-axis) Summary of differences between foliage on N-amended and background-N trees is given in Table 3.

Table 5
Stomatal behavior of California black oak measured in early summer and autumn, 2003 (see Fig. 5)

	Time to open (h)	Change in g_s	Time to close (h)	Change in g_s	Max g_s	Min g_s
June						
N-amended			0.99±0.13	42±9	56±12	15±6
Background-N			1.10±0.11	53±15	82±24	29±10
p			0.58	0.50	0.35	0.26
September						
N-amended	0.38±0.06	146±17	0.49±0.09	145±22	194±27	46±11
Background-N	0.45±0.07	168±15	0.72±0.09	112±19	231±16	99±35
p	0.52	0.37	0.12	0.33	0.26	0.12

Leaves were equilibrated to 30 μmol $m^{-2}s^{-1}$, then exposed to 1000 μmol $m^{-2}s^{-1}$, followed by 30 μmol $m^{-2}s^{-1}$ (September only). The time (in hours) required to reach stable stomatal conductance (g_s, in mmol H_2O $m^{-2}s^{-1}$) and the difference between g_s at low and moderate light are given below. Sample size was four trees for nitrogen (N)-amended and three trees for background-N in June, and six trees for N-amended and five trees for background-N in September. Means±1SE were tested with a one-way ANOVA. The time to open stomata with light challenges was not determined in June.

With drought, N-amendment and background-N trees had very similar gas exchange rates throughout most of the summer. At the end of the growing season N-amended trees experienced an earlier onset of senescence, with reduced gas exchange rates that were accompanied by significantly greater foliar chlorosis. These results are similar to those reported for birch (*Betula pendula* L.): low nutrition maintained the life span of O_3-exposed leaves through the growing season whereas highly fertilized trees exhibited symptoms earlier in the growing season (Maurer and Matyssek, 1997). Our results contrasted with increased foliar O_3 injury in wetter vs. drier years reported in the mid-1970s in Miller et al. (1980), but O_3 concentrations were twice as high then as they are now for the same site.

The growth stimulation by N-amendment was not apparent in the year following drought. Leaf growth rates and maximum size were also lower in the year following a drought (1976) for white oak (*Quercus alba* L.) in Missouri (Hinckley et al., 1979). The number of leaves initiated in the year following drought was reduced (by one leaf per growing point on average) in both N-amendment and background-N trees. Leaf primordia are formed in the year prior to growth, and the drought affected the number of leaf buds formed or that were promoted to grow in the following year (2003). In the drought year, both N-amendment and background-N trees initiated the same number of leaves, but the background-N trees began to drop leaves as soon as leaf expansion was complete. This may reduce whole-tree transpiration and thus enhance survival under extreme environmental stress.

Despite the extreme drought, none of the study plants died (as of winter, 2005). Perhaps one of the reasons the species is so drought-tolerant is that trees are able to draw water from deep within the weathered bedrock. Tritiated water was injected deep into bedrock interstices at the base of a cliff along a road cut. The next day, tritiated water was recovered from leaves of several species of oaks including California black oak growing on top of the cliff, 25 m above the injection point (Lewis and Burgy, 1964). In a germination experiment, seedling survival and growth rates of California black oak were unaffected by summer watering (vs. no watering) (Roberts and Smith, 1982). Root growth of five Californian oak species[3] is significantly greater and the supported leaf area lower than that of Japanese oak species from similar physiognomic groups[4] (Matsuda et al., 1989). When compared to other native co-occurring trees, oak has higher predawn Ψ_L than other genera (Abrams, 1990). These attributes all promote survival in long and extreme periods of summer drought.

Within-stand frequency of attack by fruittree leafroller is greater at higher pollution sites (Eatough-Jones, 2004). The combined effects of drought and fruittree leaf roller probably contributed to increased tree mortality in some areas across the San Bernardino Mountains (Grulke, unpublished data), but not at the site studied. In central Europe, two consecutive years of defoliation in combination with a climatic extreme contributed to oak decline in simulations (Thomas et al., 2002). The authors cited excess N, possibly in combination with drought stress, and decreased foliar concentrations of allelochemicals in peduncular oak, as contributing factors in increasing susceptibility to insect attack. However, air pollution and excess N-induced nutritional imbalances were not important causal factors in European oak decline. Defoliation of cork oak saplings had no effect on (the following) spring carbohydrate reserves in coarse roots (Cerasoli et al., 2004). Cork oak saplings recovered lost leaf area in 127 days. California black oak recovered lost leaf area in 20 days in this study.

Despite ecosystem N-saturation from long term atmospheric inputs, California black oak responded to

[3] *Q. dumosa*, *Q. douglasii*, *Q. lobata*, *Q. kelloggii*, *Q. agrifolia*.
[4] *Q. phillyraeoides*, *Q. serrata*, *Q. myrsinaefolia*.

N-amendment with greater growth. Small differences in instantaneous C uptake, lower foliar respiration, and lower light compensation point contributed to the greater aboveground growth observed. Drought combined with N-amendment to reduce late summer C gain and increase foliar chlorosis. Water use efficiency was lower in N-amended trees, and there was evidence of poor stomatal control in full light in an average precipitation year. In shade, N-amendment enhanced stomatal control. The effects of both pollutant exposure and drought were complex: both leaf- and whole-tree level water use efficiency were affected.

Acknowledgements

The authors are much appreciative of Dr Jim Sedell who provided support for the presentation of this research at the 21st International Meeting for Specialists in Air Pollution Effects on Forest Ecosystems, Environmental Stressors Working Group, 7.04, International Union of Forestry Research Organizations, Oulu, Finland. This article was written and prepared by US government employees on official time and is therefore in the public domain and not subject to copyright.

References

Abrams, M.D., 1990. Adaptations and responses to drought in *Quercus* species of North America. Tree Physiology 7, 227–238.

Andersen, C.P., 2003. Source-sink balance and carbon allocation below ground in plants exposed to ozone. New Phytologist 157, 213–228.

Bytnerowicz, A., Padgett, P.E., Parry, S.D., Fenn, M.E., Arbaugh, M.J., 2001. Concentrations, deposition, and effects of nitrogenous pollutants in selected California ecosystems. In: Galloway, J.N., Cowling, E.B., Erisman, J.W., Wisniewski, J., Jordan, C. (Eds.), Optimizing Nitrogen Management in Food and Energy Production and Environmental Protection. Proceedings, 2nd International Nitrogen Conference on Science and Policy. Potomac, MD, 14–18 October 2001. The Scientific World 1, pp. 304–311. <http://www.thescientificworld.com>.

Cerasoli, S., Scartazza, A., Brugnoli, E., Chaves, M.M., Pereira, J.S., 2004. Effects of partial defoliation on carbon and nitrogen partitioning and photosynthetic carbon uptake by two-year-old cork oak (*Quercus suber*) saplings. Tree Physiology 24, 83–90.

Darrall, N.M., 1989. The effect of air pollutants on physiological processes in plants. Plant Cell Environment 12, 1–30.

Eatough-Jones, M., 2004. Insect herbivore communities and air pollution: Focusing on the effects of nitrogen and ozone on herbivores of brackenfern, California black oak, and ponderosa pine in dry temperate forests. PhD dissertation, Entomology Department, University of California, Riverside, CA, pp. 376.

Fenn, M.E., Poth, M.A., 2001. A case study of nitrogen saturation in western U.S. forests. In: Galloway, J.N., Cowling, E.B., Erisman, J.W., Wisniewski, J., Jordan, C. (Eds.), Optimizing Nitrogen Management in Food and Energy Production and Environmental Protection. Proceedings, 2nd International Nitrogen Conference on Science and Policy. Potomac, MD, 14–18 October 2001. The Scientific World 1(S2), pp. 433–439. <http://www.thescientificworld.com>.

Fenn, M.E., Poth, M.A., Johnson, D.W., 1996. Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. Forest Ecology and Management 82, 211–230.

Fenn, M.E., Poth, M.A., Schilling, S.L., Grainger, D.B., 2000. Throughfall and fog deposition of nitrogen and sulfur at an N-limited and N-saturated site in the San Bernardino Mountains, southern California. Canadian Journal of Forest Research 30, 1476–1488.

Grulke, N.E., 1999. Physiological responses of ponderosa pine to gradients of environmental stressors. In: Miller, P.R., McBride, J. (Eds.), Oxidant Air Pollution Impacts in the Montane Forests of Southern California: The San Bernardino Mountain Case Study. Ecological Studies, vol. 134. Springer-Verlag, New York, pp. 126–163.

Grulke, N.E., Balduman, L., 1999. Deciduous conifers: High nitrogen deposition and ozone exposure effects on ponderosa pine. Water, Soil, Air Pollution 116, 235–248.

Grulke, N.E., Andersen, C.P., Fenn, M.P., Miller, P.R., 1998. Ozone exposure and N deposition reduces root biomass in ponderosa pine across the San Bernardino Mountains, California. Environmental Pollution 103, 63–73.

Grulke, N.E., Andersen, C.P., Hogsett, W.E., 2001. Seasonal changes in carbohydrate pools of ponderosa pine in stands under differing environmental stress. Tree Physiology 21, 173–184.

Grulke, N.E., Alonso, R., Nguyen, T., Cascio, C., Dobrowolski, W., 2004. Stomata open at night in pole-sized and mature ponderosa pine: Implications for O_3 exposure metrics. Tree Physiology 24, 1001–1010.

Heath, R.L., Taylor Jr., G.E., 1997. Physiological processes and plant responses to ozone exposure. In: Sandermann, H., Wellburn, A.R., Heath, R.L. (Eds.), Forest Decline and Ozone: A Comparison of Controlled Chamber and Field Experiments. Ecological studies, vol. 127. Springer-Verlag, Berlin, pp. 317–368.

Hinckley, T.M., Dougherty, P.M., Lassoie, J.P., Roberts, J.E., Teskey, R.O., 1979. A severe drought: Impact on tree growth, phenology, net photosynthetic rate, and water relations. American Midland Naturalist 102, 307–316.

Kiefer, J.W., Fenn, M.E., 1997. Using vector analysis to assess nitrogen status of ponderosa and Jeffrey pine along deposition gradients in forests of southern California. Forest Ecology and Management 94, 47–55.

Knops, J.M.H., Koenig, W.D., 1997. Site fertility and leaf nutrients of sympatric evergreen and deciduous species of *Quercus* in central coastal California. Plant Ecology 130, 121–131.

Lewis, D.C., Burgy, R.H., 1964. The relationship between oak tree roots and groundwater in fractured rock as determined by tritium tracing. Journal of Geophysical Research, Washington 69, 2579–2588.

Maroco, J.P., Breia, E., Faria, T., Pereira, J.S., Chaves, M.M., 2002. Effects of long-term exposure to elevated CO_2 and N fertilization on the development of photosynthetic capacity and biomass accumulation in *Quercus suber* L. Plant, Cell, and Environment 25, 105–113.

Matsuda, K., McBride, J.R., Kimura, M., 1989. Seedling growth form of oaks. Annals of Botany 64, 439–446.

Matyssek, R., Reich, P., Oren, R., Winnter, R.E., 1995. Response mechanisms of conifers to air pollutants. In: Smith, W.K., Hinckley, T.M. (Eds.), Ecophysiology of Coniferous Forests. Academic Press, San Diego, CA, pp. 255–308.

Maurer, S., Matyssek, R., 1997. Nutrition and the ozone sensitivity of birch (*Betula pendula*) II. Carbon balance, water-use efficiency and nutritional status of the whole plant. Trees 12, 11–20.

Miller, P.R., McBride, J.R., 1999. Assessment of ecological risks and implications for policy and management in the San Bernardino Mountains. In: Miller, P.R., McBride, J. (Eds.), Oxidant Air Pollution Impacts in the Montane Forests of Southern California:

The San Bernardino Mountain Case Study. Ecological Studies, vol. 134. Springer-Verlag, New York, pp. 397–404.

Miller, P.R., Longbotham, G.J., Van Doren, R.E., Thomas, M.A., 1980. Effect of chronic oxidant air pollution exposure on California black oak in the San Bernardino Mountains. In: Plumb, T.R. (technical coordinator), Proceedings, Symposium on the Ecology, Management and Utilization of California Oaks, June 26–28, 1979, Claremont, CA. General Technical Report, PSW-44, US Department of Agriculture, Albany, CA, pp. 220–229.

Miller, P.R., McBride, J.R., Schilling, S.L., Gomez, A.P., 1989. Trend of ozone damage of conifer forests between 1974 and 1988 in the San Bernardino Mountains of southern California, pp. 309–324. In: Olson, R.K., Lefohn, A.S. (Eds.), Effects of Air Pollution on Western Forests. Proceedings, 1989 June, Transactions, Air and Waste Management Association, No. 16. Anaheim, CA, Pittsburgh, PA, p. 577.

Minnich, R.A., 2005. Southern Californian coniferous forests. In: Barbour, M.G., Billings, W.D. (Eds.), North American Terrestrial Vegetation, third ed. Cambridge University Press, New York, in press.

Pallardy, S.G., Pereira, J.S., Parker, W.C., 1991. Measuring the state of water in tree systems. In: Lassoie, J.P., Hinckley, T.M. (Eds.), Techniques and Approaches in Forest Tree Ecophysiology. CRC Press, Boca Raton, FL, pp. 27–76.

Roberts, T.A., Smith, C.H., 1982. Growth and survival of black oak seedlings under different germination, watering, and planting regimes. Tree Planters' Notes 33, 10–12.

Sandermann, H., Wellburn, A.R., Heath, R.L. (Eds.), 1997. Forest Decline and Ozone: A Comparison of Controlled Chamber and Field Experiments. Ecological studies, vol. 127. Springer-Verlag, Berlin, pp. 400.

Thomas, F.M., Blank, R., Hartmann, G., 2002. Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. Forest Pathology 32, 277–307.

Thomas, F.M., Gehlen, R., 1997. Effects of different forms of nitrogen supply on the gas exchange of young peduculate oaks. Zeitschrift-fur-Pflanzenernahrung und Bodenkunde 160, 209–215 (from abstract).

Tingey, D.T., Hogsett, W.E., Lee, E.H., Laurence, J.A., 2004. Stricter O_3 ambient air quality standard has beneficial effect on ponderosa pine in California. Environmental Management 34, 397–405.