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Physiological and foliar symptom response in the crowns of *Prunus serotina*, *Fraxinus americana* and *Acer rubrum* canopy trees to ambient ozone under forest conditions

M. Schaub[a,1], J.M. Skelly[b,*], J.W. Zhang[c,2], J.A. Ferdinand[c], J.E. Savage[c], R.E. Stevenson[b], D.D. Davis[b], K.C. Steiner[d]

[a] *Graduate Ecology Program, Pennsylvania State University, University Park, PA 16802, USA*
[b] *Department of Plant Pathology, Pennsylvania State University, University Park, PA 16802, USA*
[c] *Penn State Institutes of the Environment, Pennsylvania State University, University Park, PA 16802, USA*
[d] *School of Forest Resources, Pennsylvania State University, University Park, PA 16802, USA*

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Within the heterogeneous environment of a mature forest, many factors in addition to soil moisture play a significant role in determining exposure/response relationships to ozone.

Abstract

The crowns of five canopy dominant black cherry (*Prunus serotina* Ehrh.), five white ash (*Fraxinus americana* L.), and six red maple (*Acer rubrum* L.) trees on naturally differing environmental conditions were accessed with scaffold towers within a mixed hardwood forest stand in central Pennsylvania. Ambient ozone concentrations, meteorological parameters, leaf gas exchange and leaf water potential were measured at the sites during the growing seasons of 1998 and 1999. Visible ozone-induced foliar injury was assessed on leaves within the upper and lower crown branches of each tree. Ambient ozone exposures were sufficient to induce typical symptoms on cherry (0–5% total affected leaf area, LAA), whereas foliar injury was not observed on ash or maple. There was a positive correlation between increasing cumulative ozone uptake (U) and increasing percent of LAA for cherry grown under drier site conditions. The lower crown leaves of cherry showed more severe foliar injury than the upper crown leaves. No significant differences in predawn leaf water potential (ψ_L) were detected for all three species indicating no differing soil moisture conditions across the sites. Significant variation in stomatal conductance for water vapor (g_{wv}) was found among species, soil moisture, time of day and sample date. When comparing cumulative ozone uptake and decreased photosynthetic activity (P_n), red maple was the only species to show higher gas exchange under mesic vs. drier soil conditions ($P < 0.05$). The inconsistent differences in gas exchange response within the same crowns of ash and the uncoupling relationship between g_{wv} and P_n demonstrate the strong influence of heterogeneous environmental conditions within forest canopies.

Keywords: Ozone; Canopy trees; Hardwood forest; Leaf gas exchange; Foliar injury; Environmental site conditions; Soil moisture

1. Introduction

Amongst air pollutants, anthropogenically produced tropospheric ozone continues to pose the most serious threat to the health and productivity of vegetation throughout the northeastern United States (US EPA,

* Corresponding author. Tel.: +1 814 865 7584; fax: +1 814 863 7217.
E-mail address: jms34@psu.edu (J.M. Skelly).
[1] Current address: Swiss Federal Research Institute WSL, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland.
[2] Current address: Pacific Southwest Research Station, USDA Forest Service, 3644 Avtech Parkway, Redding, CA 96001, USA.

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1996; Skelly et al., 1997; Lefohn et al., 1997; Heck et al., 1998). Ozone induces distinct foliar symptoms on sensitive species (Skelly, 2000; Innes et al., 2001), but perhaps of more importance, the pollutant causes significant pre-visual physiological effects (Kolb et al., 1997; Chappelka and Samuelson, 1998). Assessing the direct and indirect impacts of ozone within natural forests is a challenging task due to the various factors that affect exposure/response relationships (Chappelka and Chevone, 1992; Taylor, 1994; Hogsett et al., 1997; Lefohn et al., 1997; Chappelka and Samuelson, 1998; Samuelson and Kelly, 2001).

Under controlled open-top chamber conditions, Schaub et al. (2003) investigated the foliar response of black cherry, white ash and red maple seedlings under varying soil moisture and ambient ozone concentrations. Seedlings grown under irrigated conditions had similar (in 1998) and then significantly higher gas exchange rates (in 1999) than seedlings grown within non-irrigated plots under similar ozone exposures. Cherry and ash had similar ozone uptake but cherry developed more ozone-induced injury (ca. 34% LAA) than ash (ca. 5% LAA), whereas maple rarely showed foliar injury. Significantly more severe injury on seedlings grown under irrigated conditions than seedlings grown under non-irrigated conditions demonstrated that soil moisture altered seedling response to ambient ozone exposures.

Under natural forest conditions, within the Shenandoah National Park, VA, USA, Hildebrand et al. (1996) found that available soil moisture during periods of elevated ozone exposure played an important role in the development of foliar injury on mature canopy black cherry, white ash and yellow-poplar (*Liriodendron tulipifera* L.) growing on sites with naturally higher and lower available soil water content. During the summers of 1991, 1992 and 1993, more ozone-induced foliar injury was observed on yellow-poplar and black cherry growing on wetter forest soils as compared to drier sites.

The uptake of ozone affects leaf photosynthetic rates. In addition to the ozone concentrations, actual uptake may depend upon leaf position and light environment and several other environmental/site related parameters (Fredericksen et al., 1996c). High humidity, abundant sunlight, intermittent rains and available soil moisture characterize the mesophytic growing conditions across the range of many forest tree species known to be sensitive to ozone exposures; conditions that favor increased ozone uptake during the normal gas exchange process (Reich, 1987; Pye, 1988; Hildebrand et al., 1996; Wei et al., 2004a,b). Therefore, it is important to measure water relations, leaf physiology and other physiological response parameters that govern ozone uptake by sensitive species under ambient exposures and natural forest conditions.

The objective of this current research was to test for any influence of soil moisture on leaf gas exchange and visible foliar injury within canopy trees of black cherry, white ash and red maple growing under ambient ozone exposures and heterogeneous forest conditions.

2. Materials and methods

2.1. Study area and experimental design

The study was conducted within an 80-year-old mixed-hardwood stand in central Pennsylvania, USA (40°46′N, 77°37′W, elev. 466 m.a.s.l.). Dominant tree species included black cherry, white ash, red maple, sugar maple (*Acer saccharum* Marsh.), scarlet oak (*Quercus coccinea* Muenchh.), northern red oak (*Q. rubra* L.) and chestnut oak (*Q. prinus* L.); the forest was growing on a north-facing 5% slope and exhibited the physiognomy of a mature stand. The stand was characterized by an average canopy height of 20 m with a basal area of 2.6–3.4 m^2 per ha. Five cherry, five ash and six maple canopy trees were accessed with six scaffold towers of varying heights according to tree heights; towers were located within ca. 200 m of one another (Table 1). Within the same stand, three of the six towers were scattered on a drier site and three towers were located in a mesic site along a creek. The natural stream within the mesic site had running water throughout the summer seasons of 1997, 1998 and 1999. Other tree species grown at the mesic site included cucumber tree (*Magnolia acuminata* L.) and yellow-poplar. Other species, typically growing under drier site conditions were scarlet oak (*Q. coccinea* L.), chestnut

Table 1
Diameter and height of the sample trees at Penn Nursery, Bureau of Forestry, Centre County, PA

Tree #	Site	Scaffold	Diameter (cm)	Height (m)
BC-11	Drier	1	26.3	27.4
BC-21	Drier	2	50.8	29.3
WA-51	Drier	5	17.3	15.2
WA-52	Drier	5	21.6	15.5
RM-11	Drier	1	33.0	24.4
RM-21	Drier	2	46.2	29.3
RM-51	Drier	5	17.3	14.0
BC-41	Mesic	4	20.6	13.7
BC-61	Mesic	6	17.8	13.1
BC-62	Mesic	6	16.5	12.2
WA-31	Mesic	3	22.4	25.0
WA-32	Mesic	3	31.5	27.1
WA-33	Mesic	3	27.9	25.6
RM-41	Mesic	4	22.9	17.7
RM-42	Mesic	4	33.0	13.1
RM-61	Mesic	6	20.6	13.4

BC = black cherry; WA = white ash and RM = red maple.

oak (*Q. prinus* L.), blueberry (*Vaccinium* spp. L.) and trailing arbutus (*Epigea repens* L.).

Mature canopy cherry was selected following climbing and a visual inspection of their crowns for the presence of ozone-induced foliar injury. Ash and maple trees were selected due to their proximity to the selected cherry trees and their accessibility for measurements from the top platform of the respective scaffolds.

2.2. Environmental monitoring

Ambient ozone concentrations (ppb) were continuously monitored with an ozone analyzer (TECO Model 49, Franklin, MA, USA) and a data logger. The monitoring shelter was located in an open field situated 0.5 km distance from the center of the canopy site (Schaub et al., 2003). Hourly average ozone concentrations were collected following the guidelines of the Pennsylvania Department of Environmental Protection, Bureau of Air Quality and the United States Environmental Protection Agency. Meteorological data inclusive of air temperature (°C), relative humidity (%), wind speed (m/s), wind direction and precipitation (mm) were recorded using a Campbell meteorological data system (Campbell Scientific Inc., Logan, UT, USA). In 1999, soil water potential (ψ_S) was calculated from electrical conductance measurements with Gypsum Soil Moisture Probes (Soil Moisture Tester Model KS-D1, Delmhorst Instr. Co., Towaco, NJ, USA) at each scaffold. Soil moisture probes were buried at a depth of 20–30 cm within the projected area of the tree crown and connected to a Campbell data logger for continuous measurements throughout the growing seasons.

2.3. Physiological measurements

During the 1998 and 1999 growing seasons, leaf water potential (ψ_L) of the canopy trees was measured using two pressure chambers (PMS Instruments, Inc., Corvallis, OR, USA). Daytime (09:00–16:00 EST) ψ_L was measured simultaneously to the gas exchange measurements on three sun exposed leaves, randomly identified from within the portion of the upper crown that was accessed for physiological measurements. During the driest periods of each season, predawn (01:00–04:00 EST) ψ_L was recorded eight times in 1998 and twice in 1999 in addition to the daytime ψ_L in order to determine if the upper crown leaves were experiencing drought stress.

Leaf gas exchange measurements were recorded concurrently on paired mesic and drier sites during 4-h sampling periods across both sites using two LiCor 6200 portable photosynthesis systems fitted with a 0.25-L cuvette (LiCor Inc., Lincoln, NE, USA). The two LiCor 6200 systems were cross-calibrated to one another and to known concentrations of CO_2 (0 and 360 ppm) at the beginning of each measurement period, i.e. morning and afternoon. Leaf gas exchange measurements were conducted twice per day (09:00–12:00 EST, 13:00–16:00 EST) over a time period of 116 days from 19 May to 13 September 1998 at 7 to 16 day intervals and over a time period of 106 days from 4 June until 13 September 1999 at 10–20 day intervals; measurement days were determined by favorably sunny and low wind conditions. There were 11 and 8 sampling periods during the 1998 and 1999 growing seasons of each year. During each morning and afternoon sampling period, eight randomly identified leaves from the same eight tagged and numbered shoots within the upper sun exposed crown of each tree were selected. Leaf gas exchange was measured on a total of 643/563 cherry, 452/526 ash, and 704/654 maple leaves for the 1998 and 1999 growing seasons, respectively.

Leaf gas exchange measurements were made only during optimal light and environmental conditions to avoid outliers and values measured under extreme ambient conditions. Measurements taken below in situ photosynthetically saturated light intensity levels (PAR $< 600\ \mu mol\ m^{-2}\ s^{-1}$) and high ambient CO_2 concentrations (>400 ppm) were omitted from the data analysis (Schaub et al., 2003).

2.4. Visible foliar ozone injury

Visible ozone-induced injury (%) was rated at the same time as leaf gas exchange and ψ_L measurements were made. Three branches were selected and tagged in the upper and lower outer crown on each of the 16 study trees. At the time of measurement, each leaf was rated for visible ozone-induced injury defined as dark adaxial stipple. The Horsfall-Barratt rating system (Horsfall and Barratt, 1945) as modified by Nash et al. (1992) was used to determine the ozone-induced foliar injury classes (HB), the average percent of leaves affected (% LA) and the average leaf area symptomatic of ozone injury (% LAA). Measurements were made during 18 weeks from the time of full leaf expansion in mid May until early September.

2.5. Data analysis

All data were tested for normality and homogeneous variance before the analysis of variance was performed. Values outside of determined plant physiological response limits and environmental conditions were omitted, resulting in an unbalanced dataset for gas exchange. Because of logistic difficulties, the experimental design was regarded as a confounded factorial design. To test for a site effect, we used tower as an experimental unit. Species and species by site interactions were tested with individual trees with site per species as an error term. Dependent variables measured at the different dates were treated as the repeated measures. All data recorded for leaf gas exchange, leaf injury and leaf and soil water potential were analyzed with the General Linear Model procedure of the Statistical Analysis System (SAS Institute Inc., 1989). Seasonal means were compared among species, soil moisture conditions and times of day (for leaf water potential) using Bonferroni's *t*-test ($\alpha = 0.05$). According to Bonferroni's mean separation procedure, the *P*-values were adjusted and divided by the number of comparisons leading to adjusted *t*-values.

3. Results

3.1. Ozone exposure

The canopy trees were exposed to seasonal 24-h ambient ozone averages of 42.1 ppb in 1998 and 40.6 ppb in 1999 and to seasonal 7-h (09:00–16:00 EST) ambient ozone averages of 52.8 ppb in 1998 and 46.5 ppb in 1999. One-hour peak values of ambient ozone were slightly higher in 1998 compared to 1999 (Fig. 1). The highest 1-h peak in 1998 was recorded on 13 May at 113 ppb and in 1999 on 17 August at 109 ppb ozone. During the 1998 growing season, there were seven episodes during which the revised NAAQS standard of 8 h above 84.9 ppb ozone (Federal Register, 2003) was violated (May 15–16, May 19, June 25, July 3, August 5, August 21, and September 6). In comparison, there were only two episodes with violations recorded in 1999 (July 16–18 and August 17). The seasonal SUM00 and SUM60 ozone values were higher in 1998 compared to 1999 with notable increase in exposures during 1998 occurring in the months of August and September.

3.2. Environmental conditions and soil moisture

From May to September, the total precipitation was lower in 1998 than in 1999 but monthly totals varied between years (Table 2, Fig. 2). During the early season of 1999, precipitation was lower in May and June and higher in July, August and September as compared to 1998. The seasonal average temperature was higher in 1999 compared to 1998. Thus, for the mid growing season of 1998 as well as for the seasonal average, weather conditions were slightly cooler but drier than for the same time period in 1999. Soil water potential differed between the mesic and drier soils during the mid season of 1999. Differences were small but became statistically significant during dry periods starting in mid July until the beginning of September (Fig. 3). Cycles of dry-down were evident where ψ_S values were as low as −0.12 MPa in mid August. The ψ_S values measured on the mesic site were never lower than −0.06 MPa. Relatively mesic and drier long-term soil conditions

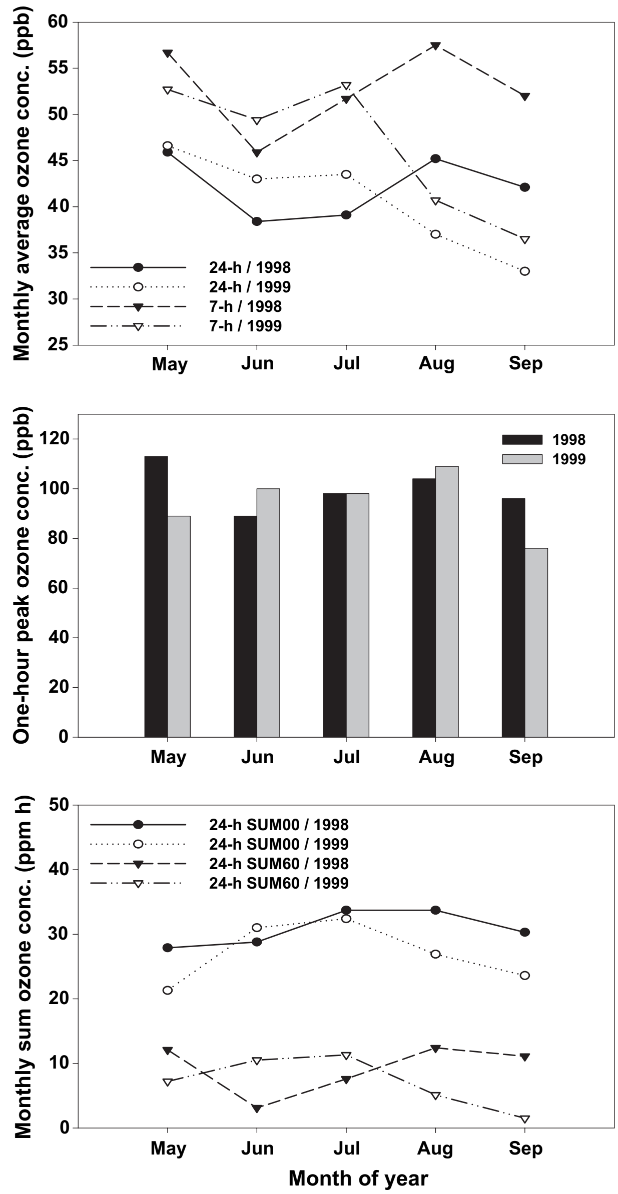

Fig. 1. Monthly average (ppb), 1-h peak (ppb) and monthly sum (ppm h) ozone concentrations from 6 May to 30 September 1998 and from 13 May to 30 September 1999 at Penn Nursery, Bureau of Forestry, Centre County, PA.

were also characterized by the presence or absence of certain plant species.

3.3. Leaf water potential

Leaf water potential differed significantly among species and date during both seasons (Table 3). Canopy trees grown on the drier site tended to have a more negative or similar ψ_L compared to trees grown under mesic soil conditions for all three species during predawn, morning and afternoon-measurements in 1998 and 1999 (Fig. 4). During both seasons, cherry expressed the lowest average ψ_L under both drier

Table 2
Monthly mean air temperature (°C), total precipitation (mm), and mean soil water potential (MPa) from the 1998 and 1999 seasons for the research facility at Penn Nursery, Bureau of Forestry, Centre County, PA

Time	Temperature (°C)	Precipitation (mm)	Soil water potential (MPa)	
			Mesic site	Drier site
1998				
May	16.7	91.7	–	–
June	19.8	142.2	–	–
July	19.7	50.8	–	–
August	17.5	94.0	–	–
September	16.8	50.8	–	–
Mean	17.9	85.9		
Total		429.5		
1999				
May	21.2[a]	68.6[a]	–	–
June	18.3[b]	69.6[a]	0.0252	0.0260
July	22.3	77.9	0.0237	0.0344
August	19.1	137.2	0.0281	0.0401
September	16.0	161.0	0.0242	0.0289
Mean	19.4	102.9	0.0254	0.0321
Total		514.3		

[a] Pennsylvania State Climatology Center, State College.
[b] June 10–30, 1999.

(−1.72 MPa) and mesic soil conditions (−1.42 MPa). With the exception of maple in 1999, the ψ_L of trees grown under drier soil conditions decreased more drastically than for trees grown under mesic soil moisture conditions from predawn to afternoon during both seasons.

3.4. Physiological gas exchange

During both seasons of the investigation, species, date and the interaction between date and soil moisture were significant sources of variance for gas exchange indicating significant changes of P_n and g_{wv} over the course of each season and between the differing soil moistures (Table 3). However, g_{wv} showed a significant interaction between date and species indicating a species specific seasonal trend of g_{wv}. During both seasons, cherry grown on mesic soil conditions had a lower seasonal average of gas exchange than cherry grown under drier soil conditions (Figs. 5 and 6). Ash showed the same trend but differences in gas exchange between the mesic and drier sites were not apparent in 1999. The significant increase of gas exchange as measured in the three white ash trees at scaffold tower 3 (Table 1) from 1998 to 1999 may simply reflect our ability to measure more leaves which were positioned in the upper crown (the scaffold height had been increased by 2.5 m from 1998 to 1999) under higher photosynthetic active radiation. Maple showed the opposite gas exchange response to the mesic and drier sites but differences were significant only in 1998. For both, white ash and red maple, the significance in differing gas exchange values between both sites disappeared in 1999.

Ash and cherry grown under drier conditions had the highest gas exchange values with a seasonal average g_{wv} of 0.27 mol m^{-2} s^{-1} and an average P_n of 13.24 µmol m^{-2} s^{-1}. On average, maple had ca. 50% less g_{wv} than ash and cherry, but maple had the highest water use efficiency (P_n/g_{wv}) during both seasons. At the beginning of both seasons (i.e. 18 May 1998 and 5 June 1999), gas exchange values were the same or similar for all three species grown under mesic and drier soil conditions (Figs. 7 and 8). In 1998, trees of all three species started with g_{wv} of 0.05–0.09 mol m^{-2} s^{-1} and with P_n of 6.0–7.0 µmol m^{-2} s^{-1}. At the beginning of 1999, 18 days later then in 1998, gas exchange values were ca. 100% higher than those at the beginning of the 1998 measurement campaign. Cumulative ozone uptake (U) was calculated as the product of the seasonal 7-h (09:00-16:00 EST) average of g_{wv} and seasonal cumulative ambient ozone exposures (SUM00) (Reich, 1987). According to the highest g_{wv} values, ash and cherry grown under drier conditions showed the highest seasonal average U of 35.8 mmol m^{-2} but only cherry developed ozone-induced visible foliar injury.

3.5. Visible foliar ozone injury

Ambient ozone concentrations and the duration of exposures were sufficiently high within the forest canopy to induce typical adaxial foliar stipple on cherry during both years of the investigation. Initial injury developed between August 3 and 20 in 1998 and August 2 and 14 in 1999 on cherry grown under drier conditions and remained more severe throughout both seasons compared to cherry grown under mesic conditions. The lower crowns of cherry exhibited a higher percentage of affected leaves, higher injury classes and a higher affected leaf area index than the upper crowns under both soil moisture conditions in 1998 and 1999 (Fig. 9). In 1998, cherry leaves expressed more severe visible ozone injury than in 1999. The highest observed percentage of LAA across all four cherry trees was 12% throughout both seasons. Ash and maple were asymptomatic of ozone-induced injury during both seasons.

4. Discussion

Overall, average ambient ozone concentrations were slightly higher in 1998 than in 1999. In addition, monthly ozone means varied between years. The seasonal SUM00 ozone exposure of 135.2 ppm h in 1998 and of 154.4 ppm h in 1999 were similar to those reported in the combined data set of Chappelka et al. (1999b) within the Shenandoah National Park (SHEN)

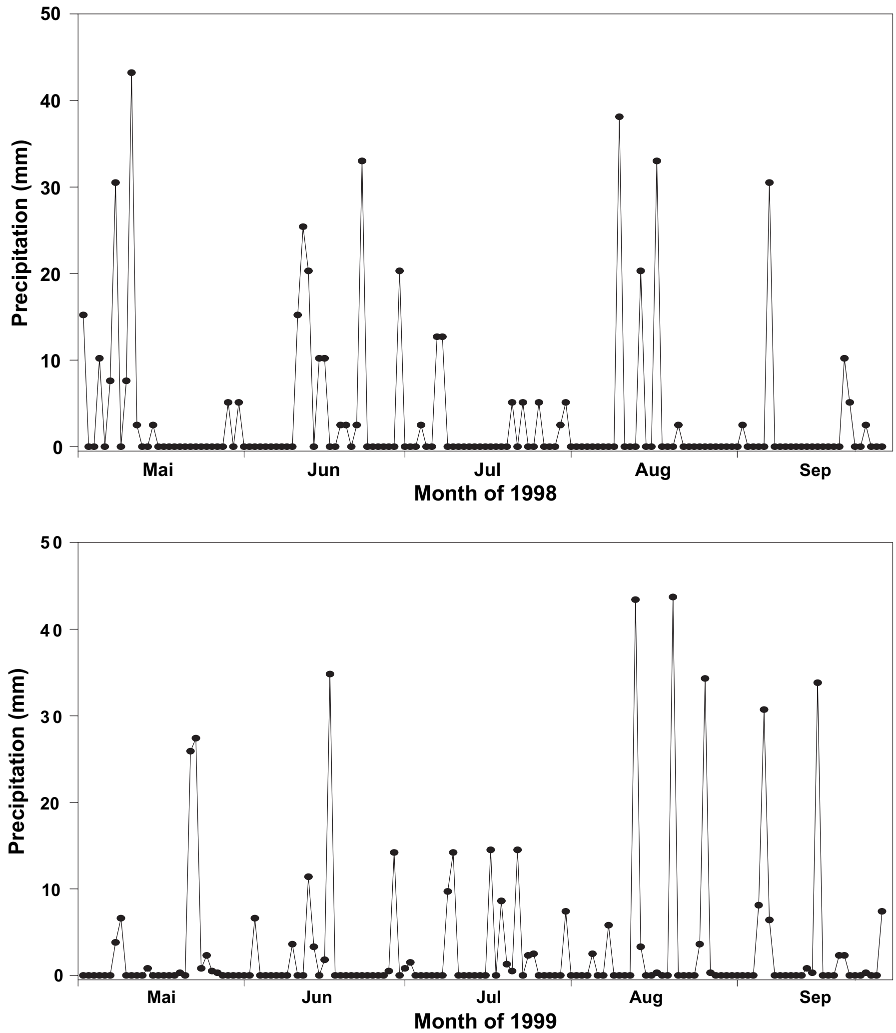

Fig. 2. Seasonal precipitation distribution (mm) during the 1998 and 1999 seasons at Penn Nursery, Bureau of Forestry, Centre County, PA.

in the Appalachian Mountains and the Great Smoky Mountains National Park (GRSM) during the summers of 1991, 1992, and 1993. The SUM00 ozone exposure statistics in our study (466 m.a.s.l.) were similar to the SUM00, which are typical of Big Meadows (SHEN) (1067 m.a.s.l.). The SUM60 ozone exposures in our study at 46.3 ppm h in 1998 and of 35.6 ppm h in 1999 were similar to the SUM60 statistics of Look Rock (GRSM) (823 m.a.s.l.). The 7, 12 and 24 h averages were very similar to the commonly occurring ozone exposures (30–50 ppb) and episodic peaks (> 80 ppb) that typically occur during the summer months in Pennsylvania (Simini et al., 1992; Comrie, 1990, 1994). Even though the ozone data were obtained from a station situated 0.5 km distant from the forested area, a recent study by Wei (2004b) employed Ogawa passive monitors within an open field at only 100 m distance from the canopy trees of this current study and weekly average exposures during two summer seasons of monitoring showed that the passives were comparable ($P < 0.05$) with the TECO ozone monitor. Furthermore, an increasing vertical gradient of ozone has been reported within forest canopies with the upper portions of tree crowns being exposed to ozone concentrations comparable to those found within more open areas (Skelly et al., 1996). Thus, the ambient ozone exposures encountered for trees in this study were found to be comparable to those recorded elsewhere within forested areas of eastern United States. The comparability between our central Pennsylvania ozone exposures and those observed elsewhere in the central Appalachian Mountains permits meaningful exposure/response relationships to be further extrapolated.

Ozone concentrations and the duration of exposures were sufficient during both years to induce typical ozone injury on black cherry (Fig. 9), which is consistent with the previous mature-tree studies described by Chappelka et al. (1992, 1994, 1999a,b), Hildebrand et al. (1996) and Lee et al. (1999). However, maple and ash did not develop ozone-induced injury in either the 1998 or 1999 growing season. Hildebrand et al. (1996) confirmed the sensitivity of cherry and ash to ambient ozone exposures

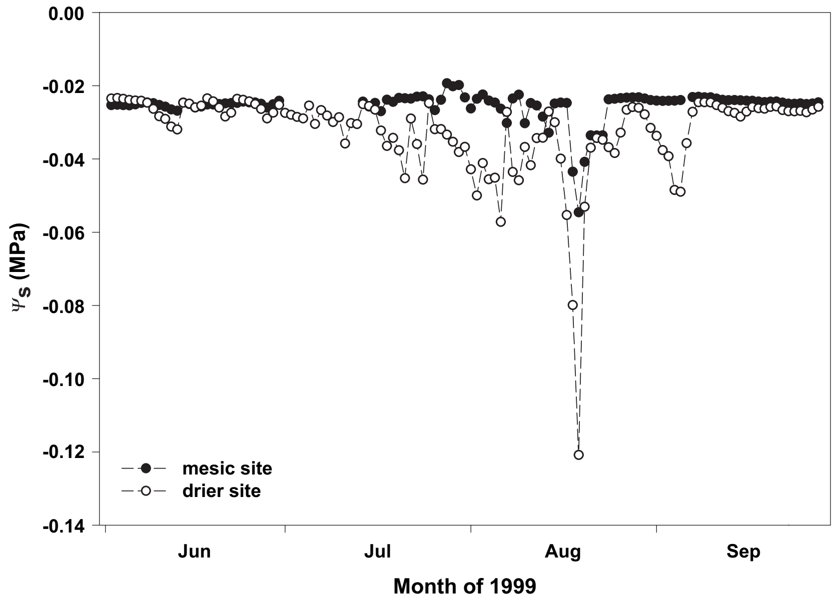

Fig. 3. Seasonal soil water potential (ψ_S) measured at a rooting depth of 20–30 cm during the 1999 season for all trees grown under naturally mesic vs. natural drier site conditions at Penn Nursery, Bureau of Forestry, Centre County, PA.

Table 3
Degree of freedom (d.f.), mean square (MS) and F values (F) for the analysis of variance for stomatal conductance to water vapor (g_{wv}), net photosynthesis (P_n), leaf water potential (ψ_L) and leaf area symptomatic of ozone injury (LAA) among three tree species grown under naturally mesic and drier soil conditions from 1998 and 1999

Source of variation	d.f.	g_{wv} (mol m^{-2} s^{-1})		P_n (μmol m^{-2} s^{-1})		ψ_L (MPa)		LAA (%)[a]	
		MS	F	MS	F	MS	F	MS	F
1998									
Site	1	0.787	29.16*	190.31	1.35	13.69	7.44	0.01	0.72
Tower (Site)	3	0.027		141.04		1.84		0.05	
Species	2	2.817	42.00***	1817.94	45.97***	87.71	133.69***		
Sp × Site	1	0.364	5.43	630.40	15.94*	1.01	1.54		
Tree (Site × Sp)	5	0.067		39.55		0.66			
Date	11	0.934	53.68***	814.98	48.66***	7.05	18.52***	0.07	1.48
Date × Site	11	0.127	7.29***	38.68	2.31*	0.67	1.77	0.01	0.17
Date × Tower (Site)	31	0.017		16.75		0.38		0.05	
Date × Sp	20	0.084	3.74***	25.58	1.07	1.67	7.05***		
Date × Sp × Site	10	0.022	0.98	11.80	0.49	0.21	0.91		
Date × Tree (Site × Sp)	50	0.023		23.92		0.24			
Error	1641[b]	0.007		8.62					
1999									
Site	1	0.049	1.94	6.76	0.03	1.88	3.43	0.16	0.37
Tower (Site)	3	0.025		198.55		0.55		0.43	
Species	2	1.576	11.80*	1696.17	12.75*	59.37	55.53**		
Sp × Site	1	0.149	1.11	46.08	0.35	3.01	2.82		
Tree (Site × Sp)	5	0.134		133.06		1.07			
Date	7	0.413	75.52***	622.08	23.33***	15.63	66.97***	0.63	2.72*
Date × Site	6	0.043	7.85***	73.72	2.76*	0.51	2.17	0.12	0.5
Date × Tower (Site)	19	0.006		26.66		0.23		0.23	
Date × Sp	13	0.070	2.92**	71.08	1.07	1.86	4.61***		
Date × Sp × Site	6	0.021	0.89	14.20	0.21	0.79	1.96		
Date × Tree (Site × Sp)	31	0.024		66.72		0.40			
Error	1638[b]	0.006		15.13					

*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.
[a] Due to a different sample size the error term for ψ_L and foliar injury equals 1362 and 155 in 1998, 509 and 300 in 1999.
[b] Foliar injury for *Prunus serotina*.

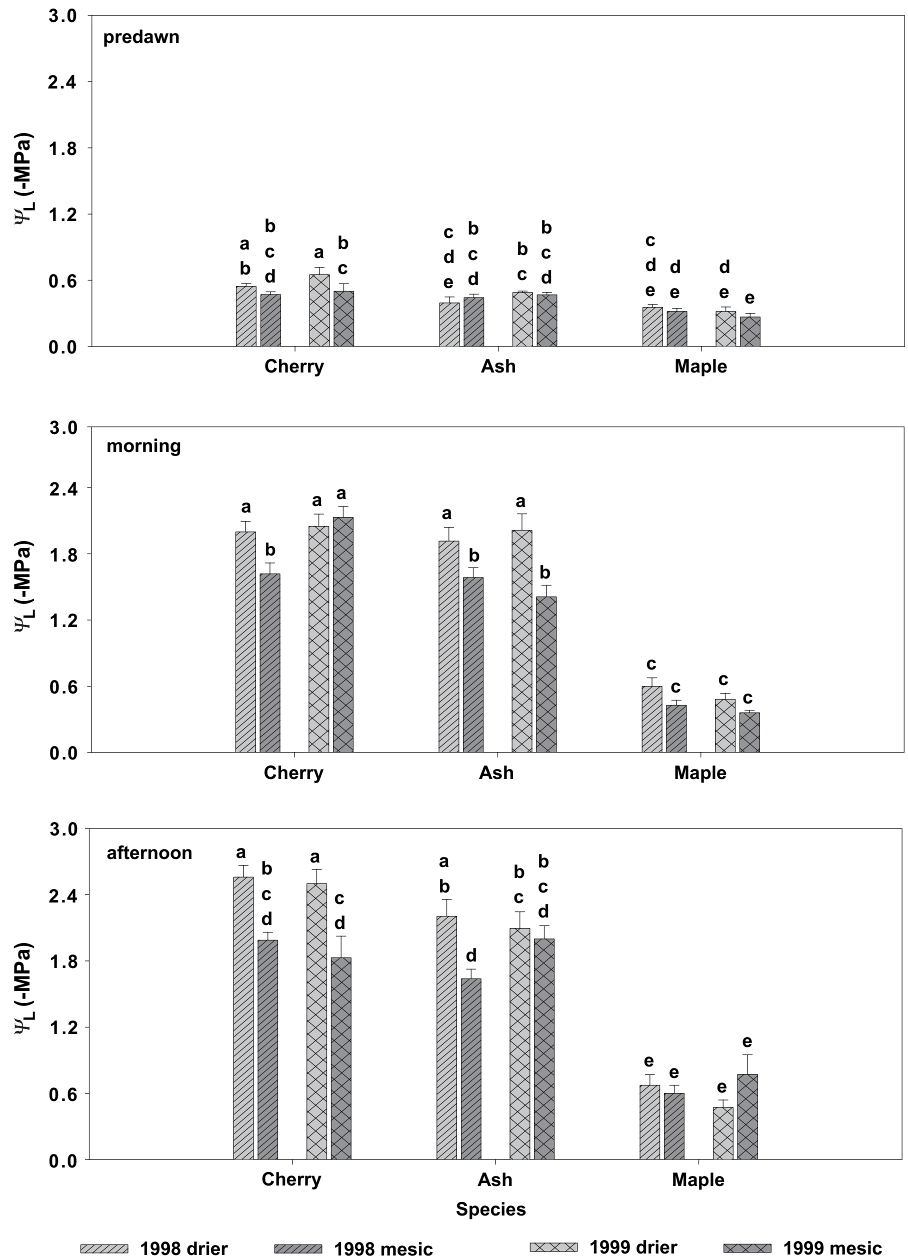

Fig. 4. Seasonal average of predawn-, morning-, and afternoon-leaf water potential (ψ_L) measured in 1998 and 1999 on upper crown leaves of black cherry, white ash and red maple trees grown under naturally mesic and drier soil moisture conditions. Significant differences are designated by differing lower case letters based on Bonferroni's *t*-test ($\alpha = 0.05$) across all species and both sites for predawn-, morning- and afternoon-measurements separately.

within the SHEN and observed a significant ozone exposure–plant response relationship with cherry but not with ash. In the combined data from both national parks (Chappelka et al., 1999b), the total LAA for cherry in both the GRSM and SHEN ranged from 1 to 8%; injury correlated with SUM00 ozone ($r = 0.87$) and SUM60 ozone ($r = 0.40$) exposures, respectively. In the current study, similar observations were recorded with the LAA ranging from 1 to 5% in 1998 and from 0.4 to 1% in 1999 for the lower crown of cherry grown under drier or mesic site conditions. During both seasons, the percent of LAA was greater for cherry grown under drier soil conditions than for trees grown under mesic conditions.

Visible foliar symptoms were first observed on 20 August 1998 with SUM00 ozone of 39.7 ppm h (17.1 ppm h SUM60 ozone) and on 14 August 1999 with SUM00 ozone of 37.3 ppm h (19.5 ppm h SUM60 ozone). The lower number of ozone episodes as defined by the new NAAQS in 1999 compared to 1998 in accord with lessened symptoms during the 1999 season suggests that reaching the goals of the new NAAQS may be sufficient to protect ozone-sensitive tree species such

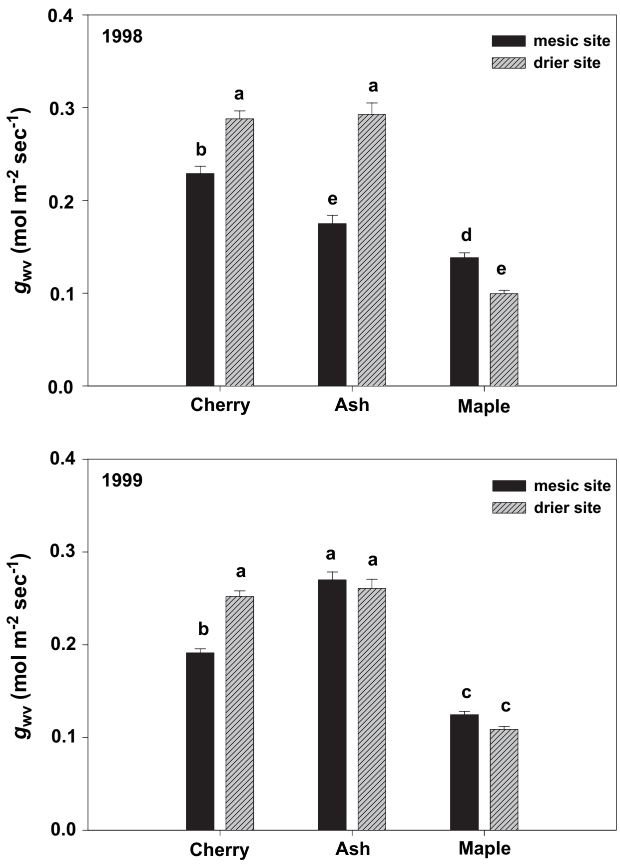

Fig. 5. Seasonal average of stomatal conductance (g_{wv}) in 1998 and 1999 for black cherry, white ash and red maple grown under naturally mesic and drier soil conditions. Significant differences are designated by differing lower case letters based on Bonferroni's *t*-test ($\alpha = 0.05$) across all species and both sites for 1998- and 1999-measurements separately.

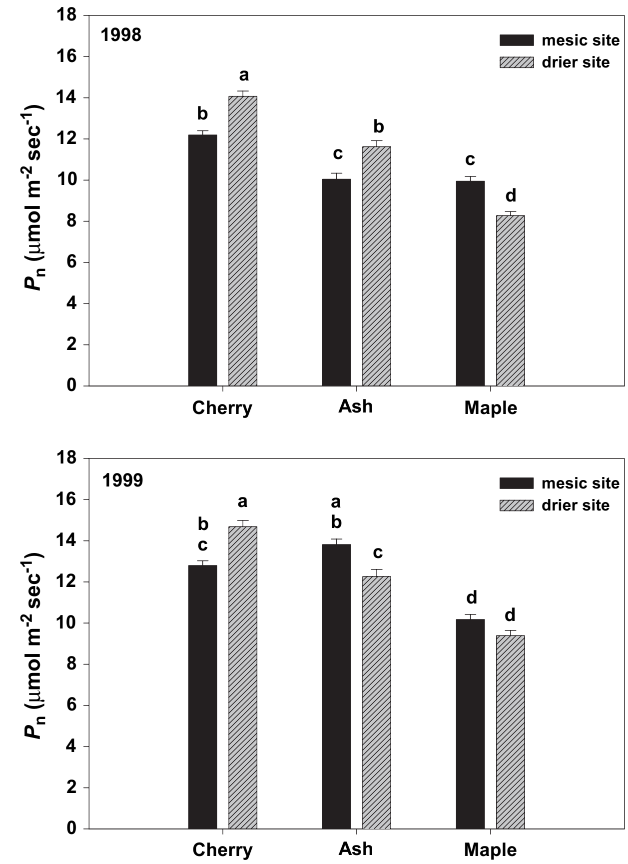

Fig. 6. Seasonal average of net photosynthesis (P_n) in 1998 and 1999 for black cherry, white ash and red maple grown under naturally mesic and drier soil conditions. Significant differences are designated by differing lower case letters based on Bonferroni's *t*-test ($\alpha = 0.05$) across all species and both sites for 1998- and 1999-measurements separately.

as black cherry from visibly present ozone injury. However, considering the small sample size and possible environmental and genetic influence factors, broader conclusions about the effectiveness of the NAQQS in protecting against foliar injury must be made with caution. The higher percent of total leaf area affected by ozone stipple within the lower crown compared to the upper crown was expected (Fredericksen et al., 1996a; Hildebrand et al., 1996).

Within mature canopy trees of the Shenandoah National Park, Hildebrand et al. (1996) found the fewest symptomatic yellow-poplar at a west-facing dry site (with the highest ozone exposures at high elevation) near Big Meadows and the most symptomatic yellow-poplar at a wetter site (with the lowest ozone exposures and low elevation) at Sawmill Run. They hypothesized that the differences in visible foliar injury were due to variation of g_{wv} and subsequently ozone uptake according to Reich's (1987) theory. Because g_{wv} is strongly related to soil water availability, trees at the wetter sites would be expected to develop more severe foliar injury. In this current study, g_{wv} of black cherry was consistently greater for trees at the drier site in comparison to trees at the mesic site (Figs. 6 and 8). Therefore, it was not surprising that cherry expressed a greater percent of LAA under drier soil conditions than under mesic soil conditions (Fig. 9). The positive correlation between ozone uptake and injury development for cherry confirms the findings of previous studies (Samuelson, 1994; Fredericksen et al., 1996b; Hildebrand et al., 1996).

Although precipitation was slightly higher during the 1999 measurement period (514.3 mm) than in 1998 (429.5 mm), measurements of ψ_L were similar between both seasons. For each species, there were no differences among predawn measurements of ψ_L between trees grown under mesic or drier soil conditions. Cherry showed the most negative ψ_L ranging from −0.47 MPa during predawn to −2.6 MPa in the afternoon, followed by ash (−0.40 MPa to −2.2 MPa), and maple (−0.26 MPa to −0.7 MPa). These values correspond to the values where black cherry canopy trees were investigated under mesic soil water conditions (Fredericksen et al., 1995) and where red maple and black

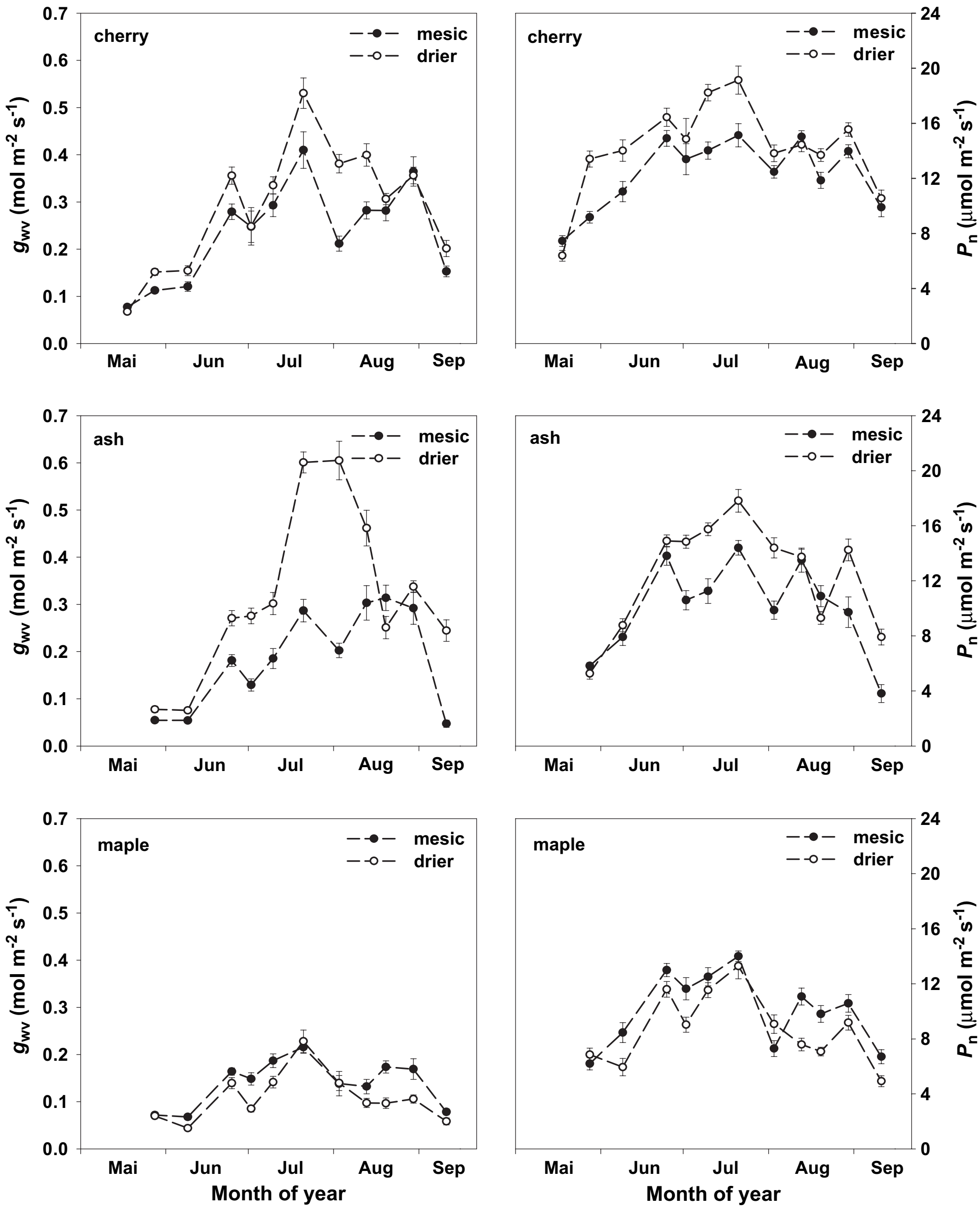

Fig. 7. Daily average of stomatal conductance (g_{wv}) and net photosynthesis (P_n) in 1998 for black cherry, white ash and red maple canopy trees grown under naturally mesic and drier soil conditions.

cherry canopy trees were investigated under mesic and drier soil water conditions (Patterson et al., 2000). The similar values of ψ_L and of ψ_S between the drier vs. mesic sites indicate that most likely there were no significant differences in soil water availability which could have affected the physiological leaf response as a driving factor.

When considering the dimensions of the sample trees (Table 1), most likely the root system of ash, cherry and maple trees may have penetrated the soil to a depth of 40 cm or more depending on soil water availability. Despite the fact that we were able to detect peaks of decreasing soil water potential at 20–30 cm below the soil surface, sufficient soil water may have been available at 40–50 cm rooting depth throughout the summer seasons to provide the necessary water flow for the maintenance of virtually non-restrictive gas exchange even during periods of extended dry weather. In shallow soil, every rain event generates a pulse of moisture that depending on the event size and evaporative demand of the atmosphere can last a few or more hours. However, single events may not recharge the soil below 20–30 cm. In this study soil water potential was recorded at a depth of 20–30 cm where single precipitation events may not recharge the soil. Despite the presence of typical mesic and drier plant species and despite the fact that there was

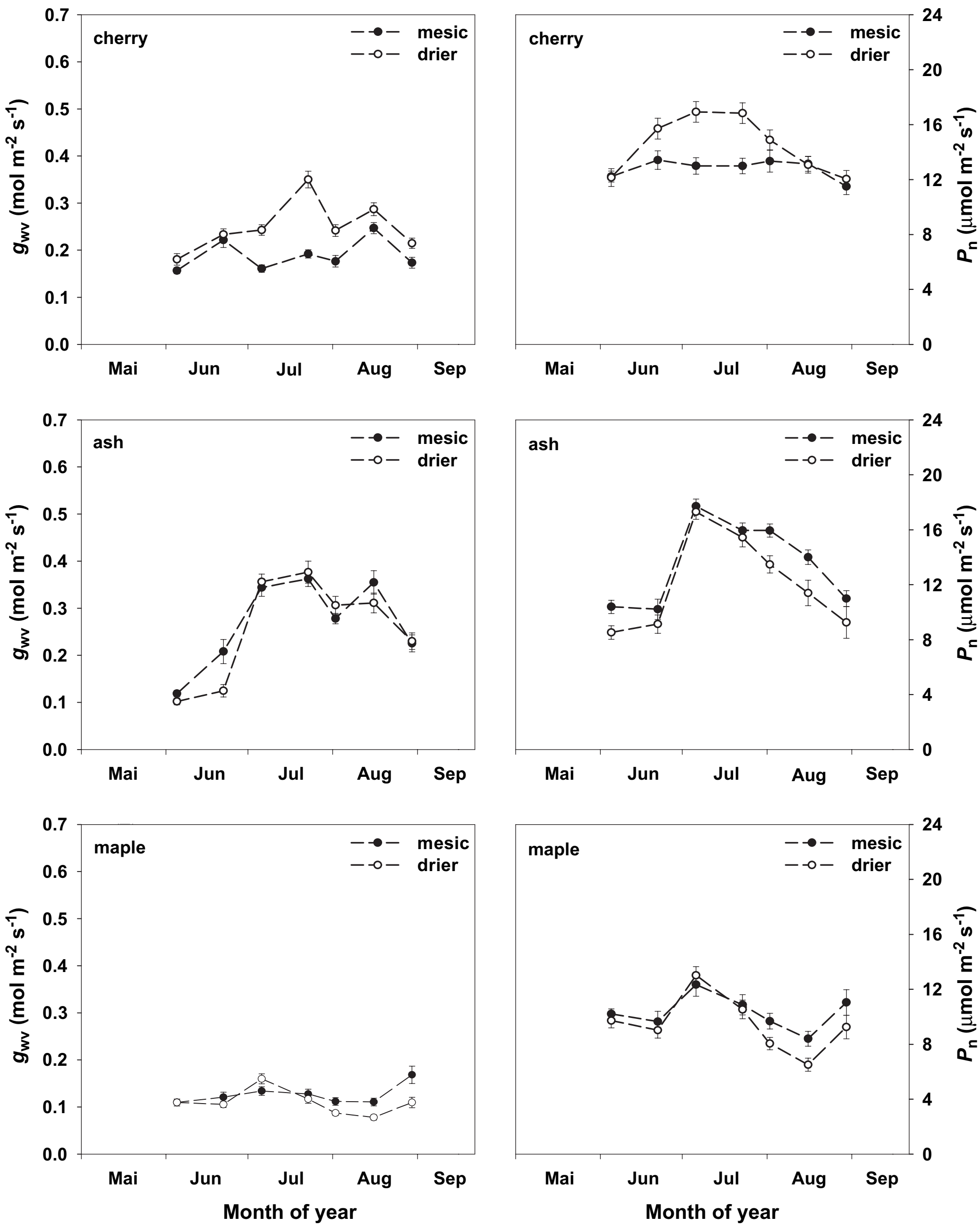

Fig. 8. Daily average of stomatal conductance (g_{wv}) and net photosynthesis (P_n) in 1999 for black cherry, white ash and red maple canopy trees grown under naturally mesic and drier soil conditions.

a small creek continuously running through the mesic site, it became obvious that the differences in soil water potential were not large enough to have a significant effect on the physiological response of the canopy trees.

Significant variance across species and sample date and sample date × soil moisture during both seasons were observed for stomatal conductance. On average, g_{wv} was highest for cherry in 1998 and for ash in 1999. Maple always had the lowest g_{wv} and ozone uptake. Although these ash trees had similar rates of ozone uptake as did cherry in 1998 and a higher seasonal ozone uptake than cherry in 1999, ash never showed visible foliar ozone injury; this was in contrast to ash studied in 1991–1993 in the Shenandoah National Park, VA (Hildebrand et al., 1996). These differences in injury development and ozone uptake between cherry and ash indicate that plant response to ozone may collectively be controlled by biotic and abiotic factors that are species specific. This suggests that an interpretation of ozone sensitivity based on only g_{wv} would underestimate plant response to ozone (Zhang et al., 2001). Considering the small sample size and the diversity of biotic and microclimatic influence factors such as PAR and vapor pressure deficit, further canopy investigations are

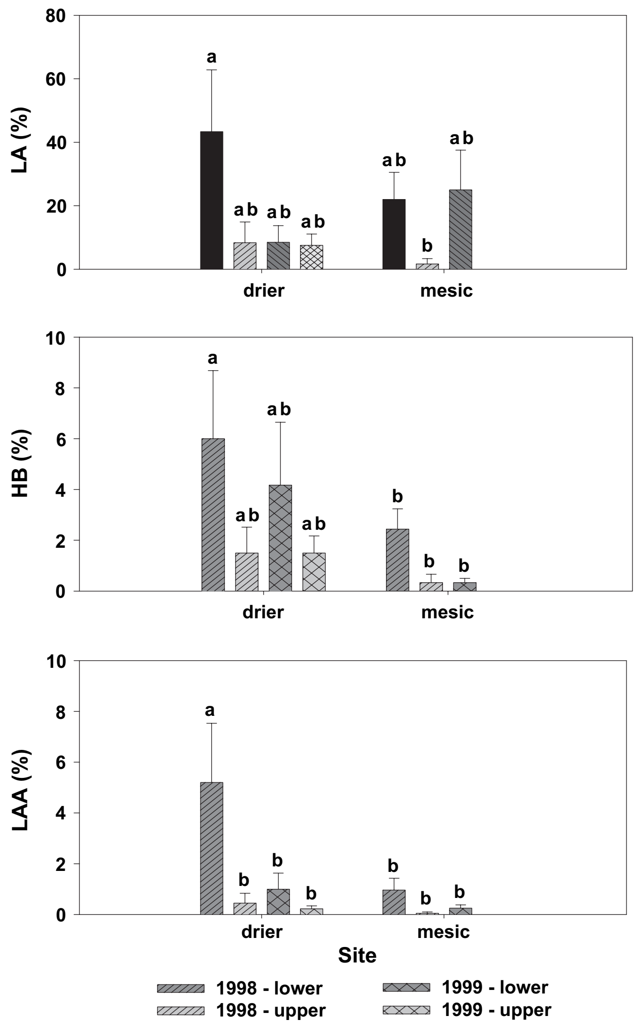

Fig. 9. Average of percentage of leaves affected (LA) by visible foliar injury, modified Horsfall-Barratt injury class (HB) and average leaf area affected (LAA), measured at the end of the 1998 and 1999 seasons in early September in the upper and lower crown of black cherry grown under naturally mesic and drier soil conditions. Significant differences are designated by differing lower case letters based on Bonferroni's *t*-test ($\alpha = 0.05$) among both canopy levels, sites and seasons.

needed to gain a better estimate of the species specific canopy response to elevated ambient ozone exposures. However, maple seedlings (Schaub et al., 2003) and mature trees showed the lowest ozone uptake during both seasons of 1998 and 1999; low ozone uptake rates may be the most important cause for ozone tolerance within red maple.

When comparing P_n and g_{wv} among the three species, it becomes obvious that across both growing seasons and across both the mesic and drier sites, cherry had the highest P_n although ash showed higher g_{wv} than cherry in 1999. Comparing the three species in 1999, the seasonal average of g_{wv} was highest for ash grown under both drier and mesic soil conditions but photosynthetic rates were highest for cherry when averaging among trees grown under drier and mesic soil conditions. Similar trends were found in 1998. In 1999, cherry grown under the two conditions had a lower ratio of the seasonal average of g_{wv} and P_n than the ash grown under similar conditions. Others have observed similar physiological responses and stated that a number of different environmental variables influence the gas exchange processes, which collectively affect ozone uptake and injury development (Arndt and Seufert, 1990; Davison and Barnes, 1998). For example, low PAR influences P_n and may increase plant sensitivity to ozone injury (Volin et al., 1993), but PAR may have much less of an effect on g_{wv} (Fredericksen et al., 1996c; Wei et al., 2004a,b). It seems that the heterogeneous light environments as they are typically found within the crown of canopy trees account most likely for the uncoupling of net photosynthesis and stomatal conductance as found in this current and several previous studies (Kozlowski et al., 1991; Fredericksen et al., 1996c; Zhang et al., 2001).

In 1999, a strong increase of gas exchange for ash grown under the mesic soil conditions was found after we increased the height of the canopy access scaffold which permitted more gas exchange measurements to be made at higher irradiance than in 1998. Since we only considered measurements taken at PAR > 600 μmol m^{-2} s^{-1} the increased gas exchange may not only be a response to higher irradiance but also due to the higher photosynthetic capacity of the upper sun exposed leaves vs. the lower partially shaded leaves. Fully sun exposed leaves have a higher light saturation point and enables them to take advantage of the higher photon flux compared to the lower crown leaves. This strong response in gas exchange to increased PAR from 1998 to 1999 within the upper crowns of ash demonstrates the strong influence of the heterogeneous light conditions on the differing photosynthetic capacities as they occur in the tree crowns. In this study, it is very likely that the varying light conditions within the tree crowns had a stronger influence on the gas exchange measurements than did the varying soil moisture conditions—even when only considering measurements above PAR of 600 μmol m^{-2} s^{-1}. The strong influence of light on P_n and the assumption that the root system of the cherry grown under drier soil conditions could provide sufficient soil water to maintain an uninhibited gas exchange process during both seasons of 1998 and 1999 may explain the unexpected higher rate of gas exchange and ψ_L for the drier site cherry compared to those on the mesic site. Indeed, the dominant cherry grown under drier soil conditions were considerably taller than the cherry grown under constantly mesic soil conditions; it is important to note however that sample trees were dominants and co-dominants on all sites.

Within the current study, maple showed the lowest gas exchange compared to cherry and ash throughout both seasons and on both sites. Although maple seemed to be the most ozone tolerant tree species by avoiding a higher uptake of ambient ozone exposures, it may also be possible that maple leaves have internal properties which react more sensitively to inner-leaf ozone concentrations. Kolb et al. (1997) suggested that it is necessary to consider assessing a plant's sensitivity to ozone in one or more of four possible responses: avoidance, compensation, defense, and repair. Whether or not avoidance (mediated by stomatal closure) is the dominant source of variance in ozone response, as Reich (1987) suggested and Taylor and Hanson (1992) dispute, it is certainly possible that compensation (i.e., increase in specific leaf area), defense (i.e., increase in the presence of anti-oxidant enzymes) (Pell and Pearson, 1983), or repair (i.e., allocation of carbon) may be of equal or greater importance in some instances (Kolb et al., 1997). However, usage of the terms sensitivity and tolerance, without reference to underlying mechanisms, may imply greater understanding of physiological condition than actually exists (Kolb et al., 1997). Based on our current findings of site and ozone effects on maple, the species specific behavior in stomatal conductance and the fundamental avoidance mechanism may be the dominant factor regulating the response to ozone, but that internal metabolic processes such as those responsible for the production of Rubisco may have a significant effect on sensitivity to ozone. The results and interpretations further suggest that investigations on the internal metabolic processes of so called ozone tolerant species are required in order to gain a better understanding of the effect of ambient elevated ozone concentrations on the physiological processes and long-term effects of ozone exposures within canopy trees while growing under natural forest conditions.

This study demonstrates the variability of responses in situ in the forest canopy with heterogeneous environments and that the relation between soil moisture and foliar injury expression are not as straightforward as reported in previous studies. Seedlings, when grown under irrigated and non-irrigated conditions, showed a positive relationship between soil water potential and ozone-induced visible injury (Schaub et al., 2003). Although seedling studies reveal important information about the influence of micro site conditions to the plant response under elevated ambient ozone exposures, results of this current study suggest that it is questionable to predict responses of mature trees to ozone based upon controlled seedling studies. To assess the sensitivity of canopy trees to ozone and to validate the principles found from seedling studies, it is important to take into account the diverse microclimatic conditions as they occur in a natural heterogeneous forest stand. Although higher stomatal conductance has been proven to reveal more injury due to a higher ozone uptake, responses appear to be species specific. Furthermore, an interpretation of ozone sensitivity based on only stomatal conductance would underestimate plant response to ozone as internal morphological leaf characteristics play an important role in the overall plant response to ozone (Bennett et al., 1992; Ferdinand et al., 1999). Soil water content may alter the response of canopy trees to ozone as it has been demonstrated for seedlings (Schaub et al., 2003) and canopy trees (Hildebrand et al., 1996; Patterson et al., 2000). But the question as to how strong the influence of soil moisture may be in relation to other micro site factors such as available PAR and vapor pressure deficit requires further investigations under natural forest conditions.

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