Growth of five hybrid poplar genotypes exposed to interacting elevated CO_2 and O_3

R.E. Dickson, M.D. Coleman, D.E. Riemenschneider, J.G. Isebrands, G.D. Hogan, and D.F. Karnosky

Abstract: A wide variety of hybrid poplar clones are being introduced for intensive culture biomass production, but the potential clonal or genotypic response to increasing tropospheric carbon dioxide (CO_2), ozone (O_3), and their interactions are unknown. To study these effects, we exposed five different hybrid *Populus* clones to increased concentrations of CO_2, O_3, and CO_2 + O_3 in open-top chambers for one growing season and determined growth responses. Exposure to elevated CO_2 increased height growth, dry mass, and basal area; exposure to O_3 decreased all three of these growth responses. Exposure impact differed among the different plant parts (leaf, stem, and roots) and among the clones. These differences were associated with different growth strategies or carbon allocation patterns inherent in the different clones. The fastest growing clones had the greatest response to O_3 treatment. The addition of CO_2 to the O_3 exposure counteracted the negative impact of O_3 in all plant components except leaf mass (e.g., CO_2 + O_3 plant mass equaled control plant mass) in all of the clones. But correspondingly, added O_3 negated increased growth from CO_2. Genetic variation in response to atmospheric pollutants must be considered even in closely related genotypes found in *Populus* culture.

Résumé : Une grande variété de clones de peupliers hybrides sont introduits pour la production de biomasse en culture intensive mais leurs réactions clonale ou génotypique potentielles face à l'augmentation du dioxyde de carbone (CO_2) et de l'ozone (O_3) dans la troposphère ainsi qu'aux interactions entre CO_2 et O_3 sont inconnues. Dans le but d'étudier ces effets, nous avons exposé cinq clones différents de peupliers hybrides à des concentrations élevées de CO_2, de O_3 et de CO_2 + O_3 dans des chambres à ciel ouvert pendant une saison de croissance et nous avons mesuré les effets sur leur croissance. L'exposition à une quantité élevée de CO_2 a augmenté la croissance en hauteur, en masse sèche et en surface terrière; l'exposition à une concentration élevée de O_3 a réduit tous ces paramètres de croissance. L'impact de l'exposition variait selon la partie de la plante (feuilles, tige et racines) et selon le clone. Ces différences étaient associées à différentes stratégies de croissance ou patrons d'allocation du carbone inhérents aux différents clones. Les clones qui croissaient le plus vite ont réagi le plus à une exposition à O_3. L'addition de CO_2 lors de l'exposition à O_3 a contrecarré l'impact négatif de O_3 dans toutes les parties de la plante excepté dans le cas de la masse des feuilles (ex., la masse des plants exposés au CO_2 + O_3 était égale à la masse des plants témoins) chez tous les clones. Mais à l'inverse, l'addition de O_3 éliminait l'augmentation de croissance provoquée par le CO_2. La variation génétique dans la réaction aux polluants atmosphériques doit être considérée même chez les génotypes étroitement reliés qu'on retrouve dans la culture du peuplier.

[Traduit par la rédaction]

Introduction

Tropospheric carbon dioxide (CO_2) and ozone (O_3) are the two atmospheric pollutants generally considered to have the greatest impact on plant growth. Plant response to elevated CO_2 will be widespread because worldwide atmospheric concentrations are fairly uniform (Bazzaz 1990; Wittwer 1990; Bowes 1993). Plant response to elevated O_3 will be more localized because atmospheric concentrations vary widely in space and time (Chameides et al. 1994; Hogsett et al. 1997). Elevated CO_2 has the potential to increase productivity 20–50% in many agricultural crops and forest trees (Kimball 1983; Cure and Acock 1986; Eamus and Jarvis 1989; Wittwer 1990; Ceulemans and Mousseau 1994). The 25% increase in atmospheric CO_2 concentration within the last 150 years may have already significantly increased productivity of crop plants (Wittwer 1990) and trees (Eamus and Jarvis 1989; Ceulemans and Mousseau 1994).

Ozone is a potent atmospheric pollutant that causes widespread damage to plants. Peak diurnal background O_3 concentrations in pristine areas currently range from 20 to 40 $nL \cdot L^{-1}$ during the growing season. Summer daytime values of 50–70 $nL \cdot L^{-1}$ (seasonal 70–100 $\mu L \cdot L^{-1}$-h, 50 $nL \cdot L^{-1}$ ×

Received March 18, 1998. Accepted September 9, 1998.

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12-h day × 120-day growing season) are common over much of the eastern and southeastern United States (Taylor 1994; Hogsett et al. 1997) and southeastern Canada (Fuentes and Dann 1994) and are increasing by about 1–2% per year. More pessimistic estimates based on regional (eastern United States, Europe, China, and Japan) nitrogen oxide (NO_x) production indicate that O_3 concentrations may triple within the next 30–40 years (Chameides et al. 1994). Damage estimates based on current O_3 concentrations indicate billions of dollars in agriculture crop losses annually (Adams et al. 1989) and significant impacts on forest tree productivity (Pye 1988; Taylor et al. 1994). However, decreases in yield of forest trees from O_3 impacts are not well documented. Estimates for major regional forest ecosystems are highly variable but on average range from a 2 to 15% decrease in growth over the next 20 years (de Steiguer et al. 1990). Estimates for more sensitive species (trembling aspen, *Populus tremuloides* Michx.; black cherry, *Prunus serotina* Ehrh.) range from a 14 to 33% loss in yearly productivity over 50% of their range in years of high O_3 impact (e.g., 1988, 1995). We have found decreases in total dry mass as high as 45% in sensitive aspen clones after one 97-day growing season of episodic O_3 exposure (92 $\mu L \cdot L^{-1}$-h) and 39% in a square-wave exposure (52 $\mu L \cdot L^{-1}$-h) (Karnosky et al. 1996).

Response to atmospheric pollutants varies among species and genotypes within species. Current damage estimates are usually based on broad species classification such as northern hardwoods or southern pines (de Steiguer et al. 1990) or average species response based on seedling populations (Pye 1988). However, these estimates do not account for the potentially large impact on sensitive genotypes within a species. Sensitive genotypes have been identified in both agricultural crops and forest trees (Kozlowski and Constantinidou 1986; Wittwer 1990; Taylor 1994; Karnosky et al. 1996; Ballach 1997). Most genetically improved tree species (and many agricultural crops) are selected based largely on growth rate but also on disease and stress resistance (Adams et al. 1992; Stettler et al. 1996). Such selection criteria may inadvertently select for O_3 sensitivity as well.

Because elevated CO_2 exposure usually increases photosynthetic rates, decreases stomatal conductance, and increases resistance to other environmental stresses, it is generally believed that increasing atmospheric CO_2 concentrations will offset the detrimental effects of increasing O_3 concentrations (Allen 1990). However, results of recent studies on the interacting effects of CO_2 and O_3 are contradictory. Some studies with several different species show that exposure to elevated concentrations of CO_2 may counteract decreases in photosynthesis and growth caused by O_3 (McKee et al. 1995; Mortensen 1995; Volin et al. 1998). In contrast, other studies show that elevated CO_2 did not protect against O_3 (Balaguer et al. 1995; Barnes et al. 1995). These studies involved average responses of general plant populations and did not examine genotypic responses. However, there is a strong genotypic response to both CO_2 (Ceulemans et al. 1996) and O_3 exposure (Karnosky et al. 1996) in *Populus*. We found that added CO_2 did not ameliorate the detrimental effects of O_3 on photosynthetic parameters of aspen clones differing in sensitivity to O_3. In fact, the O_3-tolerant clone appeared more sensitive to O_3 (Kull et al. 1996).

Because hybrid poplar clones differing in genetic makeup are being widely planted in reforestation and intensive culture systems in Canada, the United States, and many other countries around the world (Palmer 1991; Zsuffa et al. 1996; Riemenschneider et al. 1997), it is important to gather information about clonal response to these interacting atmospheric pollutants. Tropospheric CO_2 and O_3 are probably already impacting growth in sensitive genotypes, and these impacts will become more severe in the near future as atmospheric concentrations increase. Because of the potential importance of this information, we conducted a study to examine growth responses to elevated CO_2 and (or) O_3 of five poplar hybrid clones that are widely planted in both Canada and the United States (Brown et al. 1996). Our objectives were to examine the impact of CO_2, O_3, and CO_2 plus O_3 on growth and carbon allocation of poplar hybrids that differed in growth rates and inherent carbon allocation patterns (early shoot or root growth favored). Our hypotheses were (*i*) the more rapidly growing hybrids would show the greatest response to both CO_2 and O_3 exposure, (*ii*) hybrids favoring leaf production and height growth would show most O_3 response in root growth, and (*iii*) increased concentrations of CO_2 would significantly decrease the negative impact of O_3 exposure.

Materials and methods

Plant material

The plant material consisted of five hybrid poplar clones selected for a range of growth rates and carbon allocation strategies. All of the clones are high-productivity hybrids tested for growth response in Canada and released for commercial production (Brown et al. 1996). Four clones (DN-33, DN-34, DN-70, and DN-74) are *Populus deltoides* Bartr. × *P. nigra* hybrids and one clone (NM-6) is a *P. nigra* × *Populus maximowiczii* A. Henry hybrid.

Dormant hardwood cuttings (about 5 cm long) were planted in 6.5-L pots (15 × 35 cm) filled with a peat–sand–vermiculite mix (2:1:1), fertilized with 3.5 g/L slow-release fertilizer (Osmocote, Sierra Chemical Corp., Milpitas, Calif, 17:6:10, plus minor elements, 9-month formulation) mixed throughout the potting medium. The pots were watered daily to run through with a trickle irrigation system.

Plant treatments and harvest

The experiment was conducted at Michigan Technological University's Ford Forestry Center in Alberta, Mich., during the summer of 1995. The four experimental exposure treatments were (*i*) charcoal-filtered control, (*ii*) elevated CO_2 (150 $\mu L \cdot L^{-1}$ above ambient), (*iii*) elevated ozone (100 $nL \cdot L^{-1}$ above the charcoal-filtered background), and (*iv*) elevated CO_2 plus elevated O_3 (at the above concentrations). The treatments were applied in open-top chambers (3.1 m wide × 4.6 m tall) (Karnosky et al. 1996) modified with frustums and rain exclusion caps. There were two chambers per treatment (total eight chambers) and 10 plants per clone in each chamber. The cuttings were planted on June 7, 1995, and exposures were started immediately so that the entire seasonal growth was under treatment. The elevated CO_2 treatment was applied for 24 h per day during the entire exposure period (June 7 to August 31; 86 days), and the square-wave O_3 treatment was applied for 6 h per day, 5 days per week (total 60 days). The total seasonal O_3 exposure was 12 $\mu L \cdot L^{-1}$-h for the charcoal-filtered (CF) treatment and 48 $\mu L \cdot L^{-1}$-h for the O_3 treatment.

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Table 1. Results of analyses of variance for whole plots.

Dependent variable	Source of variation: Whole-plot error MS	Whole-plot error F	$O_3 \times CO_2$ MS	$O_3 \times CO_2$ F	CO_2 MS	CO_2 F	O_3 MS	O_3 F
Height	19 165	5.01**	14 813	0.80ns	98 861	5.32†	147 396	7.94*
Total dry mass	4115.3	8.38**	588.2	0.15ns	19 833.6	4.99†	30 150.1	7.59*
Basal area	11 340	9.63**	264	0.02ns	43 532	3.98ns	75 670	6.91†
Leaf dry mass	358.5	9.44**	83.1	0.24ns	571.3	1.65ns	2386.6	6.90†
Stem dry mass	1267.0	8.80**	72.1	0.06ns	7060.6	5.77†	8016.8	6.55†
Root dry mass	66.71	7.59**	16.83	0.26ns	245.18	3.80ns	369.23	5.73†
Shoot dry mass	3014.3	9.39**	435.9	0.11ns	11 544.0	4.08ns	21 418.4	6.71†
Cutting dry mass	19.78	2.94*	6.51	0.34ns	297.35	15.43*	257.08	13.34*
Shoot/root ratio	106.8	8.70**	161.9	1.57ns	102.7	1.00ns	132.8	1.29ns
Leaf/mass ratio	0.014 64	5.46**	0.000 27	0.02ns	0.117 03	8.26*	0.000 32	0.02ns
Stem/mass ratio	0.015 46	2.12†	0.061 40	4.06ns	0.200 68	13.26*	0.101 93	6.73†
Root/mass ratio	0.007 41	8.11**	0.014 70	2.05ns	0.008 58	1.20ns	0.011 78	1.64ns
Shoot/mass ratio	0.030 05	3.33*	0.069 16	2.27ns	0.020 43	0.36ns	0.091 04	2.95ns
Cutting/mass ratio	0.016 03	1.09ns	0.148 60	11.44*	0.039 40	3.03ns	0.167 90	12.93*

Note: Whole-plot error terms derived from chambers within $O_3 \times CO_2$ treatment combinations. ns, mean square not significant ($p > 0.10$).
†Mean square significant ($p < 0.10$).
*Mean square significant ($p < 0.05$).
**Mean square significant ($p < 0.01$).

Table 2. Results of analyses of variance for subplots assuming an all fixed-effects model.

Dependent variable	Source of variation: Subplot error MS	$O_3 \times CO_2$ clone MS	$O_3 \times CO_2$ clone F	$CO_2 \times$ clone MS	$CO_2 \times$ clone F	$O_3 \times$ clone MS	$O_3 \times$ clone F	Clone MS	Clone F
Height	3821	1041	0.27ns	1552.	0.41ns	4285	1.12ns	66 267	17.34**
Total dry mass	491.3	142.8	0.29ns	1156.6	2.35*	1371.1	2.79*	128 881.9	26.22**
Basal area	1177	609.	0.52ns	1245	1.06ns	1903	1.62ns	20 615.	17.51**
Leaf dry mass	38.0	14.3	0.38ns	54.8	1.44ns	91.9	2.42*	790.5	20.82**
Stem dry mass	144.0	62.3	0.43ns	381.6	2.65*	415.3	2.88*	2847.8	19.77**
Root dry mass	8.78	6.91	0.79ns	17.1	1.94ns	19.3	2.20†	71.7	8.16**
Shoot dry mass	315.0	124.5	0.40ns	694.9	2.21†	888.5	2.82*	6 272.2	19.91**
Cutting dry mass	6.73	4.43	0.66ns	15.02	2.23†	11.75	1.75ns	721.84	107.20**
Shoot/root ratio	12.3	36.5	2.98*	13.0	1.06ns	39.4	3.21†	146.2	11.90**
Leaf/mass ratio	0.002 68	0.001 50	0.56ns	0.000 77	0.29ns	0.004 27	1.59ns	0.113 66	42.40**
Stem/mass ratio	0.007 28	0.006 61	0.91ns	0.003 34	0.56ns	0.010 37	1.42ns	0.076 76	10.54*
Root/mass ratio	0.000 91	0.001 16	1.27ns	0.000 44	0.48ns	0.001 09	1.20ns	0.009 20	10.06**
Shoot/mass ratio	0.009 49	0.009 44	0.89ns	0.006 82	0.72ns	0.01161	1.22ns	0.043 67	4.60**
Cutting/mass ratio	0.011 94	0.007 63	0.64ns	0.009 54	0.80ns	0.018 50	1.55ns	0.064 57	5.41**

Note: Subplot error terms derive from trees within clones within chambers within $O_3 \times CO_2$ treatment combinations. ns, mean square not significant ($p > 0.10$).
†Mean square significant ($p < 0.10$).
*Mean square significant ($p < 0.05$).
**Mean square significant ($p < 0.01$).

Plants were harvested on September 6, 1995 (91 days from planting). During harvest, the height and diameter of each shoot on the cutting were measured (summed for each plant), and leaves, stems, cuttings, and roots were separated for each plant, dried at 70°C, and weighed.

Statistical analysis

Data were subjected to analyses of variance (ANOVA) according to a mixed-effect split-plot model. Whole-plot effects due to O_3, CO_2, and an $O_3 \times CO_2$ interaction were assumed fixed and tested against a random whole-plot error (chambers within $O_3 \times CO_2$ combinations) (Table 1). Subplot effects due to clone and the $O_3 \times$ clone, $CO_2 \times$ clone, and $O_3 \times CO_2 \times$ clone interactions were also assumed fixed and tested against a random subplot error (clones × chambers within $O_3 \times CO_2$ combinations) (Table 2). Unbalanced replication at the subplot level required complete least squares ANOVA and the use of least squares mean estimates for comparisons among treatment combinations. We did not adjust variance estimates or invoke special procedures to protect against type I error when making multiple comparisons, mostly because the validity of such procedures is unverified for unbalanced data sets (Steel and Torrie 1980). Some protection against type I error can be achieved by using simple least significant difference

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Table 3. Relative response of six growth parameters of five *Populus* hybrid clones to elevated CO_2 and (or) O_3 exposure.

Clones	Height	Total dry mass	Basal area	Leaf dry mass	Stem dry mass	Root dry mass
CO_2						
DN-33	+32.6	–16.2	+20.2	–18.6	–5.8	–22.8
DN-70	+5.0	+34.0	+41.0	+18.6	+42.2	+62.5
DN-34	+13.1	+28.6	+27.2	+16.7	+37.9	+10.7
DN-74	+7.8	+34.2	+22.8	+5.5	+51.1	+45.6
NM-6	+22.3	+35.6	+36.1	+24.1	+52.6	+35.6
Mean	+16.2	+23.2	+29.4	+9.3	+35.6	+26.3
O_3						
DN-33	–18.3	–46.7	–32.7	–38.4	–50.5	–51.1
DN-70	–29.5	–40.7	–36.3	–37.7	–45.9	–39.0
DN-34	–24.6	–44.0	–38.0	–40.8	–49.2	–62.8
DN-74	–36.6	–49.9	–41.8	–54.2	–50.6	–57.7
NM-6	–29.6	–50.4	–41.9	–46.3	–57.5	–69.2
Mean	–27.7	–46.3	–38.1	–43.5	–50.7	–56.0

Note: Values are the percent change. A plus or minus sign indicates an increase or decrease in percent response compared with the charcoal-filtered control. See Figs. 1 and 2 for statistically significant differences among treatments.

comparisons to variables where an ANOVA *F* test is significant for one or more whole-plot treatments or their interactions (Steel and Torrie 1980).

Results

Growth responses

Whole-plant responses

Compared with control plants, exposure to elevated CO_2 increased height growth, total dry mass, and basal area; while elevated O_3 decreased all three of these growth parameters (Table 3, Fig. 1). Total dry mass and basal area changed the most in response to treatment while height was less responsive. Compared with the control plants, total dry mass and basal area of the treated plants increased 23 and 29% with CO_2 exposure and decreased 46 and 38% with O_3 exposure, respectively (Table 3). Height increased 16% with CO_2 exposure and decreased 28% with O_3 exposure. Response to the exposure treatments differed among the clones. In most cases, significant differences were found for all dependent variables measured (Tables 1 and 2). In some cases, however, pooled main effects were not significantly different (for example, basal area response to CO_2 treatment; Table 1) but were significantly different when the individual treatments were compared (Fig. 1). These apparently contradictory results arise because the *F* values in Table 1 come from pooled treatment comparisons (e.g., CO_2 and CO_2 + O_3 vs. control and O_3). Such pooled comparisons mask the strong and opposing growth responses to CO_2 and O_3 and the complex clonal interactions to elevated CO_2 and O_3.

In Fig. 1, the clones are placed in order of their relative growth response. The greatest response to treatment was associated with the fastest growing or most productive clones. Note that total dry mass production with O_3 exposure was similar for all clones, except DN-33 (Fig. 1B); while total mass in the CO_2 treatment was greater for NM-6 compared with all other clones. However, the percent increase in mass in response to CO_2, compared with the control treatment, was essentially the same in all clones (DN-70, 34%; NM-6, 36%) except in DN-33, which showed a slight but nonsignificant decrease in growth with the CO_2 exposure (Table 3). The decrease in mass in response to O_3 was greater in the more productive clones (e.g., NM-6, 50% and 31.3 g vs. DN-70, 41% and 16.5 g). In contrast to mass, the decrease in height in response to O_3 was similar (NM-6, 30%; DN-70, 30%) (Table 3), but the increase in height in response to CO_2 was greater in the more productive clones (NM-6, 22% vs. DN-70, 5%). Exposure of the different poplar clones to CO_2 plus O_3 alleviated the detrimental response to elevated O_3. There were no significant differences between the control treatment and the CO_2 plus O_3 treatment in height, total dry mass, and basal area in any of the clones tested (Figs. 1A–1C). However, O_3 exposure negated the increase in growth from CO_2.

Leaf, stem, and root response

Growth of different plant parts (leaf, stem, and roots) also increased with CO_2 exposure and decreased with O_3 exposure (Table 3, Fig. 2). However, the relative response differed with the part in question and among the clones. These differences were associated with the different growth strategies or carbon allocation patterns inherent in the different clones. For example, DN-34 and NM-6 allocate considerable carbon to leaf growth, and exposure to elevated CO_2 increased leaf dry mass 17 and 24%, respectively (Table 3, Fig. 2A). Exposure to O_3 decreased leaf mass 41 and 46% in DN-34 and NM-6, respectively. In contrast, DN-74, allocating more carbon to stem and root growth, responded to elevated CO_2 with an increase in leaf mass of only 6% and responded to O_3 with a decrease of 54%. Conversely, exposure to elevated CO_2 increased root growth 11 and 36% in DN-34 and NM-6, respectively, while exposure to O_3 decreased root growth 63 and 69% (Table 3, Fig. 2C).

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Fig. 1. Whole-plant response to exposures of elevated CO_2, O_3, and CO_2 + O_3: (A) total height growth, sum of all shoots on the cutting; (B) total plant dry mass; and (c) total basal area, sum of all shoots on the cutting. Treatments with the same letter are not significantly different at the 10% level based on the least significant difference test. Error bars are 1SE.

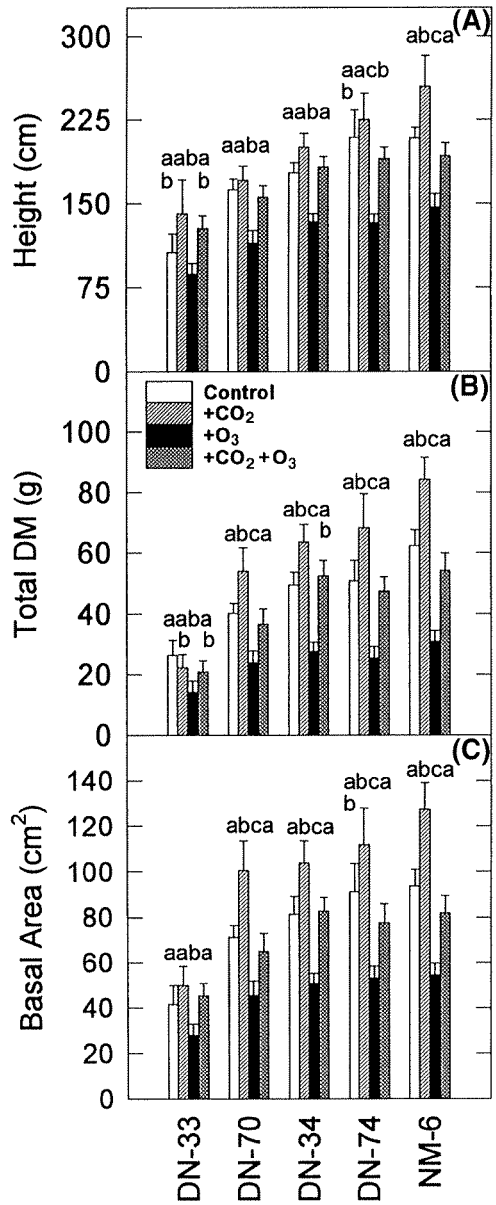
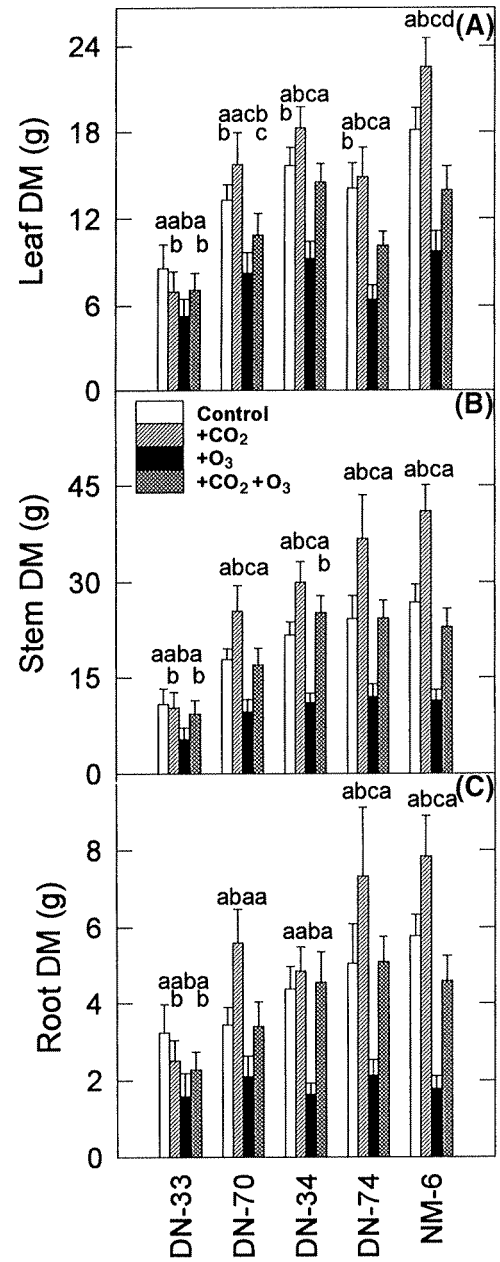


Fig. 2. Individual plant part response to exposures of elevated CO_2, O_3, and CO_2 + O_3. (A) leaf dry mass; (B) stem dry mass; (C) root dry mass. Significant differences are shown as in Fig. 1.



Response of the more root-oriented DN-70 showed an increase of 62% in root mass with CO_2 exposure and a decrease of 39% with O_3 exposure. These results show large clonal differences in carbon allocation within the plant in response to these environmental changes (Tables 1 and 2).

As with total plant growth, elevated CO_2 added to the elevated O_3 exposure largely counteracts the O_3 response, particularly in stems and roots (Figs. 2B and 2C). Average leaf mass was less, however, in the CO_2 plus O_3-treated plants compared with the controls but was significantly (statistically) smaller only in NM-6, the most productive clone (Fig. 2A).

Allometric responses

Carbon allocation patterns within the plant differ with clone, CO_2, and O_3 treatments. These different allometric responses are clearly shown when the different mass ratios are compared (Figs. 3 and 4). Shoot/root ratio is an allometric response that indicates important changes in carbon allocation within the plant and is often quite sensitive to changing environmental stresses. Ozone exposure increased the shoot/root ratio in DN-34 and NM-6 because root growth was impacted more than leaf and stem growth in these clones (Fig. 3A). Similarly, the shoot/root ratio decreased in DN-70 with CO_2 exposure because this clone allocates more available carbon to the root system. All other treatments had

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Fig. 3. Allometric responses of leaves, stems, and roots to exposures of elevated CO_2, O_3, and CO_2 + O_3. (A) shoot/root ratio; (B) leaf/mass ratio (leaf mass divided by total plant dry mass); (C) stem/mass ratio. Significant differences are shown as in Fig. 1.

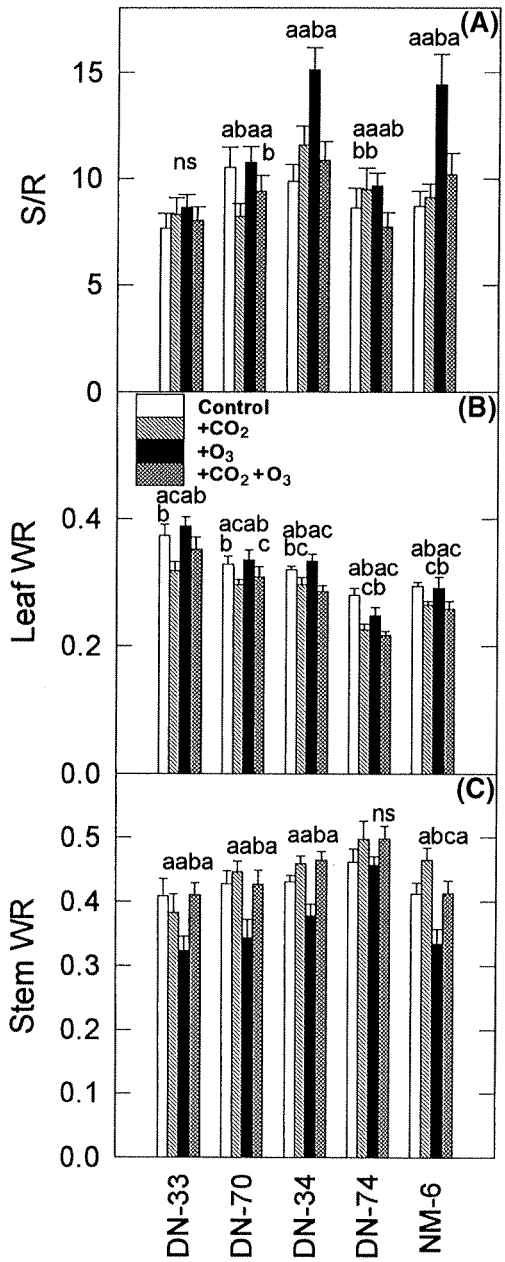
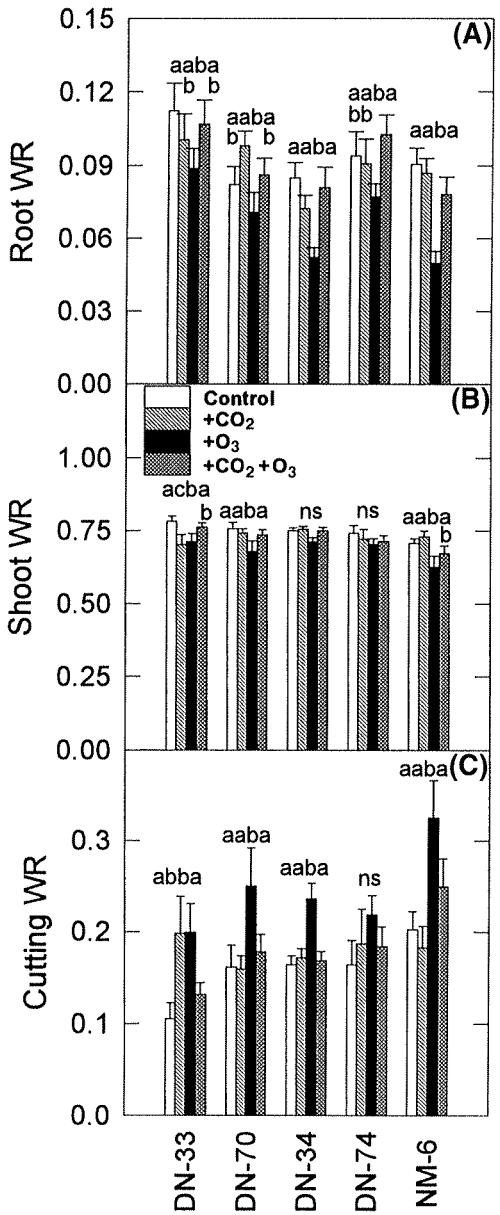


Fig. 4. Allometric responses of shoots, roots, and cuttings to exposures of elevated CO_2, O_3, and CO_2 + O_3. (A) root/mass ratio; (B) shoot/mass ratio (leaf and stem dry mass divided by total plant dry mass); (C) cutting/mass ratio. Significant differences are shown as in Fig. 1.



no effect on shoot/root ratios of the different clones compared with controls. Leaf mass in relation to total plant mass decreased with CO_2 exposure and CO_2 plus O_3 exposure, but O_3 exposure had little effect on the leaf mass ratios (Fig. 3B). This decrease in relative leaf mass was largely a CO_2 effect that was not counteracted by O_3 because the leaf mass ratio in the CO_2 plus O_3 treatment did not differ from that in CO_2 alone. Leaf mass in relation to whole-plant dry mass was smallest in DN-74 compared to the other four clones. In contrast to the leaf/mass ratio; stem/mass (Fig. 3C) and root/mass (Fig. 4A) ratios were significantly decreased by O_3 exposure in all clones except DN-74 (stem/mass ratio) and DN-70 and DN-74 (root/mass ratio). The decrease in root growth from O_3 exposure was particularly severe in the clones DN-34 and NM-6 (Fig. 4A).

Shoot/mass ratio decreased in the O_3-exposed plants but changed relatively little with the other treatments (Fig. 4B). This lack of shoot response in the CO_2 treatment reflects the average of leaf and stem response to treatment. For example, relative leaf mass decreased and stem mass increased with CO_2 exposure in clone NM-6 (Figs. 3B and 3C). While shoot/mass ratio decreased with O_3 exposure, cutting/mass ratio increased significantly with O_3 exposure in all clones

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(except DN-74) (Fig. 4C). Although cutting dry mass decreased with O_3 exposure compared with the control treatment (data not shown), the initial cutting mass modified the relative decrease in cutting growth in response to O_3, resulting in a greater relative contribution to total plant dry mass.

Discussion

Based on the projected tropospheric concentrations of CO_2 and O_3 expected in 50–100 years (Bowes 1993; Taylor 1994), the CO_2 and O_3 exposures of this experiment were moderate. The CO_2 exposure was 150 $\mu L \cdot L^{-1}$ above ambient or 510 $\mu L \cdot L^{-1}$ for 86 days or slightly less than a full growing season (100–120 days in Alberta, Mich.), and the O_3 exposure summed for the treatment period was 48 $\mu L \cdot L^{-1}$-h. The daily O_3 exposure of 100 $nL \cdot L^{-1}$ 6 h per day is relatively high but not unusual for many areas in the eastern United States and southern Canada, where 70–100 $nL \cdot L^{-1}$ daily maximum concentration is common and 150–190 $nL \cdot L^{-1}$ for several hours during the day may occasionally occur (Fuentes and Dann 1994; Gillian and Turrill 1995). The summed experimental exposure of 48 $\mu L \cdot L^{-1}$-h, if extended to a 100- to 120-day growing season, is well within the range of current seasonal ambient exposures (60–100 $\mu L \cdot L^{-1}$-h) over much of the eastern United States and Canada (Fuentes and Dann 1994; Taylor 1994; Taylor et al. 1994; Hogsett et al. 1997). In addition, based on the current rate of increase of CO_2 and O_3, our experimental concentrations will equal ambient concentrations in about 50 years, if not sooner.

The square-wave O_3 exposure of 100 $nL \cdot L^{-1}$ for 5 days per week may appear excessive. We have found, however, that such exposures provide several hours per day and 2 or 3 days per week for recovery in relatively low O_3 concentrations (20–30 $nL \cdot L^{-1}$) but plant response to these square-wave exposures is greater than that obtained with episodic exposures that provide a similar accumulated O_3 dose (Karnosky et al. 1996). The greater impact probably results from more days of 100 $nL \cdot L^{-1}$ O_3 exposure in the square-wave compared with the episodic treatment. Chronic ozone response of plants is determined by daily maximum concentration, total accumulated dose, and method of exposure (Taylor et al. 1994). The CO_2 concentration of 150 $\mu L \cdot L^{-1}$ above ambient or 510 $\mu L \cdot L^{-1}$ was chosen because this concentration more closely represented projected atmospheric CO_2 concentrations expected within the next 40–50 years. This time frame and CO_2 concentration is more realistic for hybrid poplar response (5 or 6 rotations in 50 years) than the 700 $\mu L \cdot L^{-1}$ CO_2 concentrations projected within 100–150 years.

Plant growth usually increases when plants are exposed to increasing CO_2 concentrations because photosynthetic rates increase (Eamus and Jarvis 1989; Bazzaz 1990; Bowes 1993; Ceulemans and Mousseau 1994; Gunderson and Wullschleger 1994), respiration rates decrease (Bunce 1994; Wullschleger et al. 1994), and other stress effects may be alleviated (Cure and Acock 1986; Allen 1990; Wittwer 1990). Ozone exposure, in contrast, decreases photosynthetic rates, increases respiration rates, increases leaf senescence and leaf loss, and therefore, decreases plant growth and productivity (Pye 1988; Darrall 1989; Taylor 1994; Taylor et al. 1994; Coleman et al. 1995a; Karnosky et al. 1996). Both CO_2 and O_3 responses may be modified by cultural conditions, particularly nitrogen and water availability (Greitner et al. 1994; Pell et al. 1994; Curtis et al. 1995; Tschaplinski et al. 1995; Lloyd and Farquhar 1996). The poplar clones in this open-top experiment were grown in large pots with adequate fertilization and water to minimize stress and to provide rapid growing conditions so that response to CO_2 and O_3 exposure would not be confounded by other stresses. Poplar hybrids and *Populus* species in general are very responsive to environmental manipulation because of their inherent rapid growth rates and growth strategy designed to take advantage of favorable environmental conditions. Perhaps because of these characteristics, poplars are sensitive to increased CO_2 exposure and O_3 damage (Reich 1987; Laurence et al. 1994; Winner 1994; Karnosky et al. 1996).

The poplar clones in this experiment were no exception. Growth in all parameters measured (i.e., height; total dry mass; basal area; and leaf, stem, and root dry mass) increased with CO_2 exposure and decreased with O_3 exposure in all clones except DN-33 (Table 3, Figs. 1 and 2). An increase in plant mass is usually the result of an increase in photosynthetic rate or net carbon fixation rate. Reviews of the response of tree species to increasing CO_2 found that, depending on the experimental CO_2 concentration, average photosynthetic rates were 40–50% greater at the higher CO_2 concentrations than at ambient CO_2 concentrations (Gunderson and Wullschleger 1994; Curtis 1996). The response of all species was not positive and photosynthetic rates ranged from 40% less than that at ambient to three times ambient. Although increases in photosynthetic rates are not always directly related to increases in plant mass, a recent review found that average tree growth increased by about 40% (range 20–120%) with increased CO_2 concentration (Eamus and Jarvis 1989).

Reported responses to O_3 exposure are more variable than responses to CO_2. Dry mass responses ranged from a stimulation of 41% at low to moderate O_3 concentrations (1.5 times ambient) to decreases of 60–70% (Pye 1988). This large variability in response results from the extreme differences in experimental conditions and the use of species and genotypes that range widely in sensitivity. Differences in species response to O_3 have been frequently documented (Reich 1987; Mortensen and Skre 1990; Taylor et al. 1994). For example, studies with moderate levels of O_3 exposure (82 $nL \cdot L^{-1}$, 7 h per day, 50 days or 29 $\mu L \cdot L^{-1}$-h) showed that *Betula pubescens* Ehrh. was more sensitive than *Betula verrucosa* Ehrh., and the birches were more sensitive than alder (*Alnus incana* (L.) Moench). Total dry mass decreased 64 and 42% for birch and alder, respectively, with the 29 $\mu L \cdot L^{-1}$-h treatment (Mortensen and Skre 1990). We found similar impacts of O_3 on our poplar clones as total dry mass decreased 46% (Table 3).

Plants respond to stress not only with changes in photosynthetic rates and growth rates but also with changes in carbon allocation within the plant. Carbon allocation within a plant depends on inherent growth strategy and response to varying environments (Chapin 1991; Lee and Jarvis 1995; Loehle 1996). Plant growth strategy differs widely among species. Species found in harsh environments commonly grow slowly and allocate most fixed carbon to root growth, storage, chemical defenses, or other functions that maximize

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gains of limited resources and improve survival. Species found in rich environments often grow rapidly and allocate carbon to leaf and root development, organs that increase the capacity to acquire resources and increase growth rates, but rapidly growing species may be susceptible to stress. Within species and even within a genotype, carbon allocation may shift in response to environmental changes. A common response is the increased allocation of carbon to root growth when nitrogen or water is limited (Chapin 1991). Given the large number of species and hybrids involved in current *Populus* cultural and production studies (Stettler et al. 1996), it is not surprising that some genotypes vary widely in growth strategy and in response to environmental stress. Thus, carbon allocation within the plant and the resulting allometric patterns will also vary (Scarascia-Mugnozza et al. 1997). Early growth studies and tracer studies with photosynthetically fixed ^{14}C clearly showed that during the first year of growth the hybrid "Tristis" allocated more carbon to root growth and developed larger root systems than Eugenei (DN-34), while Eugenei allocated more carbon to leaf development and height growth (Isebrands and Nelson 1983; Michael et al. 1988). Thus, Tristis growth strategy favored early root growth while Eugenei favored leaf production and height growth. We found similar differences in growth response in this current study with *Populus* hybrid clones that differed much less in parentage than Tristis and Eugenei. While DN-34 (Eugenei), DN-74, and NM-6 were all fast-growing hybrids, DN-74 had a smaller leaf/mass ratio than DN-34 and NM-6 (Fig. 3B), and a greater root/mass ratio (Fig. 4A). These genetically controlled growth responses are significant factors in the individual clonal response to elevated CO_2, O_3, and other environmental stresses.

The shoot/root ratio is probably the most common allometric parameter measured in studies of O_3 or CO_2 response of plants. Shoot/root ratios usually increase in plants exposed to O_3 (Cooley and Manning 1987). This increase in shoot/root ratio is particularly common in indeterminate growing plants such as hybrid poplars (Matyssek et al. 1993; Woodbury et al. 1994). Both shoot and root growth usually decrease with O_3 exposure. However, root growth is impacted more than shoot growth because lower leaves provide most of the photosynthate required for root growth and these lower or older leaves are the first leaf cohort damaged by O_3 (Coleman et al. 1995*a*; 1996). Upper or recently mature leaves supply most of the photosynthate for new leaf and height growth and are least damaged by O_3; thus, new leaf and shoot growth usually decrease less than root growth (Coleman et al. 1995b). The increase in shoot/root ratios of DN-34 and NM-6 (Fig. 3A) are actual allometric changes in carbon allocation and not a result of different growth rates (Gebauer et al. 1996) because total dry mass of all of the clones (except DN-33) were the same after ozone exposure.

The effect of increasing CO_2 concentration on shoot/root ratios is much less certain. Shoot/root ratios may increase, decrease, or show no change in response to increasing CO_2 depending on the species involved and experimental conditions (Eamus and Jarvis 1989; Ceulemans and Mousseau 1994; Tschaplinski et al. 1995; Gebauer et al. 1996; McConnaughay et al. 1996). Elevated CO_2 often decreases the shoot/root ratio because increased photosynthetic rates provide excess carbohydrate that is preferentially utilized for root growth. We found relatively little effect of CO_2 on shoot/root ratios compared with that found with O_3 (Fig. 3A), although shoot/root ratio did decrease in DN-70, a more root-oriented hybrid. A similar lack of change in shoot/root ratio and other allometric responses with elevated CO_2 exposure was found with several other hybrid poplar clones, although increases in total dry mass with CO_2 exposure differed among these clones (Radoglou and Jarvis 1990; Bosac et al. 1995). The slowest growing clones often gave the greatest proportional increase in total dry mass with elevated CO_2 compared with ambient (Radoglou and Jarvis 1990; Ceulemans et al. 1996). However, the fast-growing clones were always larger than the slow-growing clones in both ambient and elevated CO_2. We found relatively little difference among the clones in percent dry mass increase with CO_2 exposure compared with control plant dry mass (Table 3). However, this dry mass increase was not evenly distributed among the leaf, stem, and root fractions, indicating different allometric response to CO_2 among the clones (Figs. 2 and 3).

Information on potential allometric changes in the different hybrids could be valuable because clones could be selected for different environmental conditions. For example, clones that favored root growth might be more drought tolerant or better able to utilize site nutrients. Such information would also be valuable if mixed hybrid plantings were desirable (Knowe et al. 1994).

Studies on the response of different species to CO_2 exposure are more frequently reported than studies with O_3 because of simplified experimental protocols and the concern about species and ecosystem response to increasing atmospheric CO_2 concentrations (Bazzaz 1990). Most such studies report large differences in species response (Rochefort and Bazzaz 1992; Ackerly and Bazzaz 1995; Groninger et al. 1995; Tschaplinski et al. 1995; McConnaughay et al. 1996), and in family or seed source response within species (Mebrahty et al. 1993). Although recognized for some time, this within-species, genotypic response of forest trees to O_3 or CO_2 exposure has only recently been seriously considered (Taylor 1994; Taylor et al. 1994; Karnosky et al. 1996).

The range of genotypic response may be great. For example, the photosynthetic response to O_3 exposure of 16 *P. trichocarpa* × *P. deltoides* F_2 hybrids ranged from 5% of or equal to that found for the charcoal-filtered controls after 38 $\mu L \cdot L^{-1}$-h exposure (Hinckley 1996). Similar ranges in increased photosynthetic rates and growth rates may be expected in response to CO_2 exposure (Eamus and Jarvis 1989; Radoglou and Jarvis 1990; Ceulemans and Mousseau 1994; Ceulemans et al. 1996). Given the wide genotypic range in O_3 response found in sensitive tree species such as poplars, it is probable that considerable losses in productivity are already occurring at current ambient levels of O_3 and that these losses will increase in the future.

In our study with hybrid poplars, the 48 $\mu L \cdot L^{-1}$-h O_3 exposure decreased average dry mass of the five clones by 46% (Table 3). Similar responses to O_3 were found for birch (Mortensen and Skre 1990) and aspen (Karnosky et al. 1996). The threshold for significant decreases in growth for sensitive genotypes will be considerably less than that found in average seedling populations or natural stands. Taylor (1994) reported that response of sensitive genotypes of

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loblolly pine would begin around 30–40 $\mu L \cdot L^{-1}$-h O_3 exposure and response of average seedling populations would be expected above 60–85 $\mu L \cdot L^{-1}$-h. Growth response to our experimental O_3 exposure (48 $\mu L \cdot L^{-1}$-h), when compared with current seasonal ambient O_3 exposures (60–100 $\mu L \cdot L^{-1}$-h) found in much of the eastern United States and Canada indicate that sensitive genotypes are frequently severely impacted and whole populations are occasionally impacted by current O_3 concentrations, although decreases in growth may be less with ambient episodic exposures compared to our square-wave exposure. If tropospheric O_3 concentrations double in the near future as predicted (Chameides et al. 1994), actual yields of hybrid poplars and other fast-growing species in high O_3 impact areas will be much less than projected.

Most genetically improved tree species are selected based largely on growth rate, although disease and stress resistance are also important (Adams et al. 1992; Stettler et al. 1996). Selection based on growth rate alone may inadvertently select for O_3 sensitivity as well. In this study, the most rapidly growing hybrids had the greatest response to O_3 exposure. Although the percent productivity losses to O_3 exposure were similar (total dry mass decrease was 50.4% in NM-6 and 46.7% in DN-33), total dry mass losses were much greater in NM-6 than in DN-33 (e.g., 31.4 vs. 12.4 g). Based on our current knowledge of genetic control of O_3 resistance, selecting for O_3 resistance will be secondary to selecting for rapid growth rate. The most rapidly growing genotypes may do well in the future, however, because rapid growth may allow for rapid recovery after periodic O_3 stress and for greater productivity during years of low overall O_3 impact (Bazzaz and McConnaughay 1992; Wang et al. 1994). It should be possible in the near future to select for both rapid growth rate and resistance to various environmental stresses (e.g., O_3, drought, insects) (Robison and Raffa 1997) if clones are tested in both controlled environments (growth chambers, open-top chambers) and in the field. Multiyear field selection of clones planted in a number of different environments or sites along an O_3 gradient would be very useful. Genetic variation in response to atmospheric pollutants must be considered even in closely related genotypes found in *Populus* cultures because these pollutants will be a significant component of total environmental stress in the near future and may have significant silvicultural and management implications.

Acknowledgments

We gratefully acknowledge the technical support of Zophie Gagnon and Pritt Pechter in managing the Alberta open-top sites and we thank Gary Hogan for supplying the poplar cuttings. Funding was provided in part by the USDA Forest Service's Northern Global Change Program and by the National Council of the Paper Industry for Air and Stream Improvement, Inc.

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