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Seasonal growth, $\delta^{13}C$ in leaves and stem, and phloem structure of birch (*Betula pendula*) under low ozone concentrations

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Summary. The growth of potted birch cuttings (one clone of *Betula pendula*) was studied under low O_3 concentrations (0, 0.050, 0.075, 0.100 µl l^{-1}) throughout an entire growing season. With increasing O_3 dose, 20–50% of all leaves formed were prematurely shed, while 40–70% of the remaining foliage displayed advanced discoloration by the end of the season. Ozonation affected the S, P and N concentration of leaves and increased $\delta^{13}C$ in leaves and stem, while the CO_2 assimilation rate declined with increasing CO_2 concentration in mesophyll intercellulars. While whole-plant production correlated negatively with the O_3 dose, ozone increased the specific leaf weight (i.e. leaf weight/leaf area, SLW) but decreased the ratios of stem weight/stem length and root/shoot biomass. Neither the latter ratio nor SLW changed in experimentally defoliated control plants, whereas in ozonated plants starch accumulated along leaf veins and phloem tissue was deformed in the leaf petioles and the stem. Only in early summer was the relative growth rate higher in the ozonated than in the control plants. The ratio of whole-plant biomass production versus total foliage area formed was lowered under O_3 stress. However, when relating biomass to the actual foliage area present due to leaf loss, this ratio did not differ between treatments. Similarly the ratio of actual foliage area versus basal stem area in cross-section did not differ. Overall, whole-plant production was strongly determined by O_3-caused changes in crown structure and began to be limited at O_3 doses (approximately 180 µl l^{-1} h) similar to those of rural sites in Central Europe.

Key words: Ozone – *Betula pendula* – Growth analysis – $\delta^{13}C$ – Phloem structure

Introduction

Environmental factors are known distinctly to change the carbon allocation in trees (Schulze and Chapin 1987), but are non-detrimental as long as the tree metabolism copes with the stress (Waring 1987). While the understanding of mechanisms predisposing trees to injury is growing in relation to some natural stress factors, knowledge concerning the seasonal impact of low concentrations of air pollutants is limited (Winner et al. 1988). Trees with mesophytic leaves are thought to be prone to high pollutant uptake (Reich 1987). A recent study with mesophytic *Betula pendula* showed that under low O_3 concentrations the decline of carbon uptake and water-use efficiency of leaves was coupled with the gradual collapse of tissue structure (Matyssek et al. 1991). The relevance of such O_3 effects for tree growth can only be established through relating them to the production and carbon allocation in the whole plant (Mooney and Winner 1988). Even though the O_3 impact on the foliage seems to be coupled with favoured aboveground versus below-ground carbon allocation at declining whole-plant production, findings do not necessarily represent the low O_3 stress of many rural regions (Reich 1987). Findings on the O_3 effect on carbon allocation conflict (cf. Reich and Lassoie 1985), as the developmental state of plants at the harvest time may bias growth analysis.

Aiming to understand the seasonal O_3 impact on the whole plant (as requested by Mooney and Winner 1988), the present study follows the biomass development throughout the entire growing season of the same birch individuals, which in parallel were investigated at the leaf level (Matyssek et al. 1991). Mechanisms of plant response are addressed as to whether gas exchange and carbon allocation under low O_3 concentrations are associated with changes in $\delta^{13}C$ of leaves and stem (Farquhar et al. 1989) and in phloem structure (cf. Spence et al. 1990), and how partial defoliation in O_3-free air affects carbon allocation relative to O_3-caused leaf loss.

Materials and methods

Plants and treatments. From 14 April through 2 October 1989, cuttings of one birch clone (*Betula pendula,* Roth) were grown in 10-l pots filled with sand and a basal layer of inert synthetic clay beads (1 plant/pot,

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Table 1. Nutrient concentrations of birch leaves from mid-stem positions in August 1989 (μg g^{-1}; 5 trees per O_3 treatment)

	O_3 concentration of fumigation (μl l^{-1}):			
	0 (control)	0.050	0.075	0.100
Nutrient:				
Ca	10667 ± 1914	9504 ± 1100	10461 ± 848	10007 ± 628
K	17950 ± 606	*16149* ± 1288	17891 ± 396	17251 ± 1343
Mg	3485 ± 196	3432 ± 315	3498 ± 292	*3190* ± 111
Fe	64 ± 12	51 ± 4	69 ± 11	55 ± 3
P	2655 ± 268	2846 ± 212	2977 ± 367	*3237* ± 471
S	1671 ± 311	1863 ± 337	1847 ± 440	1918 ± 341

Values in italics differ significantly from control at 5% according to Wilcoxon *u*-test

fertilized, well-watered). When transferred into the field fumigation chambers on 16 May 1989, the plants (shoot 3 cm long) were separated into four O_3 treatments (20 plants/treatment, 4 plants/chamber). The O_3 concentrations were 0 (control), 0.050, 0.075, and 0.100 μl l^{-1}, and were monitored by a Monitor Labs 8810 instrument. Ozone was generated from pure oxygen (Fischer, model 502) and continuously added to charcoal-filtered air. Plants, fumigation chambers and O_3 regimes were the same as described in Matyssek et al. (1991; see also Landolt et al. 1989).

On 27 July 1989, when the control had reached about one-quarter of its final biomass (see Fig. 4A), five further control plants were partially defoliated by excising 66% of all leaves on stem and branches (beginning at the basal axis ends). This treatment is denoted as defoliated control (DC plants).

Biomass analysis. On 17 July, 15 August, and 3 October (before autumnal discoloration), 5–10 individual trees in each O_3 treatment were harvested (the 5 DC plants on 3 October) for the biomass analysis of the whole plant. The *actual* foliage area was determined from one-sided area measurements of all leaves attached at each harvest (Delta-T areameter MK2), while the *potential* foliage also includes the shed leaf area. The latter was calculated from the missing leaf number and the mean leaf area on both stem and branches. Basal stem area in cross-section was calculated from diameter measurements (with calipers) at 10 cm above the stem basis. The plant organs were dried at 65° C to constant weight (4 days). The ratio of root/shoot biomass comprises only plant organs developed from the originally planted cutting (about 13 cm long, 0.6 g in April); otherwise the cutting increment is part of the whole-plant dry weight. The relative growth rate (RGR) is derived from the mean whole-plant biomass in a treatment at each harvest as $\Delta W/\Delta t * (W)^{-1}$, where ΔW is the increment of mean biomass during the time interval Δt between two harvests; $W = (W_1+W_2)/2$ is calculated from the mean biomass at the beginning (W_1) and at the end (W_2) of the interval Δt. The efficiency of production in terms of foliage availability was estimated by basing whole-plant biomass either on the actual or the potential foliage area at each harvest (reciprocal of leaf area ratio). The specific leaf weight (SLW) of the foliage is given as dry weight/area of the actual (= attached) foliage.

The extent of O_3-induced discoloration in the attached foliage was determined by counting and assigning leaves to three classes of visual injury: (1) no symptoms, (2) early symptoms (little, light-green yellowish or black dots), and (3) established yellowish-bronze discoloration including large necroses.

The concentration of cations, S and P in leaves from similar stem position was assessed by ICP-AES (inductive coupled plasma-atomic emission spectroscopy) ICP, that of N with a Carlo Erba NA1500 analyser.

Gas exchange experiments. These were conducted on attached complete leaves with a thermo-electrically climate-controlled cuvette system (Walz) as described by Matyssek et al. (1991). The steady-state rates of net CO_2 uptake and transpiration were determined after 90 min of constant cuvette conditions (see legend of Fig. 2).

$\delta^{13}C$ analysis. A 50 mg aliquot was prepared from the ground total stem axis of each tree. Cellulose was separated from wood (Brenninkmeijer 1983) by the following steps: Soxhlet extraction with toluene-enthanol azeotrope, delignification with acidified $NaClO_2$ solution at 70° C (3 times 8 h), incubation in NaOH (4%) and washing in distilled water (24 h, 70° C). Heating of the cellulose samples occurred at 950° C (2 h), and the isotopic composition of the released and purified CO_2 was determined with the mass spectrometer MAT 250 (Finnigan MAT) as described by Becker et al. (1989). $\delta^{13}C$ values of the samples were calculated by comparing the relative abundance of ^{13}C with that in the PDB standard (Craig 1957). The $\delta^{13}C$ of the leaves investigated by gas exchange experiments (see Matyssek et al. 1991) was determined without preceding cellulose extraction.

Light microscopy. At each harvest date, discs were excised in the afternoon from two fully developed leaves at the stem of each tree (disc diameter = 8 mm; 2 discs each from the central left and right half of one lamina). After fixation and bleaching in hot methanol the starch in these samples was stained with JJK solution. Phloem tissue was investigated in samples cut from the central part of the leaf petiole and from the mid-position of the stem internode underneath that leaf. Sections (2.5 μm thick) were prepared after sample fixation in glutaraldehyde solution (2.5%, at 5° C) and embedding in Technovit 7000. Acid fuchsin and toluidine blue solution were used for staining.

Results

Nutrient and carbon relations of leaves

The cation concentrations of leaves did not clearly respond to ozone (Table 1), whereas P and S tended to increase with the O_3 concentration. Compared with the leaves formed in spring (Fig. 1A, lower stem), N of leaves formed in summer increased in parallel with the leaf area in all but the 0.1 μl l^{-1} O_3 treatment (Fig. 1A, upper stem). However at 0.1 μl l^{-1}, SLW was raised in the summer leaves (Fig. 1B). By August, mainly the (older) leaves at the lower stem had developed visual O_3 injury and declined in photosynthetic capacity, depending on the O_3 dose (Fig. 2; see Matyssek et al. 1991). This decline was coupled with a raised c_i/c_a ratio (i.e. CO_2 concentration of the mesophyll intercellular spaces versus that of ambient air; Fig. 2), while the $\delta^{13}C$ of the O_3-injured leaves was higher (–31.5 ± 0.4‰) than in the control (–34.4 ± 0.4‰). Visual O_3 injury spread from the lower stem, and by September about two-thirds of the foliage displayed advanced discoloration in the 0.075 and 0.1 μl l^{-1} treatments (Table 2).

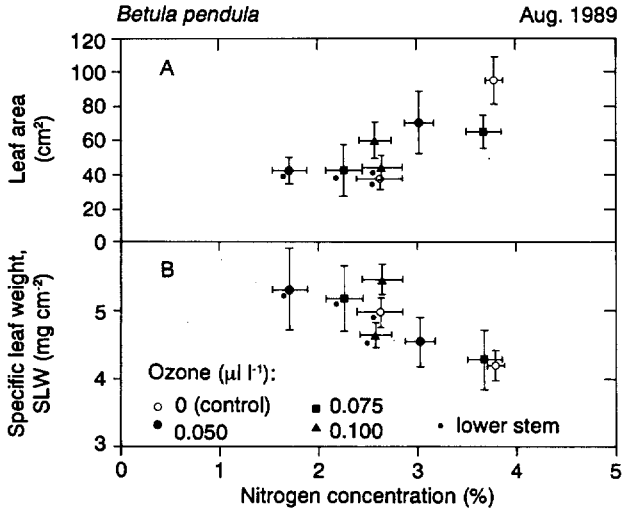

Fig. 1. A Leaf area, and **B** specific leaf weight (i. e. leaf weight/leaf area) of single leaves in relation to the nitrogen concentration. Two leaves each from the lower stem (formed in spring) and the upper stem (formed in summer) were analysed per plant. Thus, data points are means ± SD of 10 leaves (from 5 plants) per treatment and stem position *(little dots beside symbols mark* leaves from lower stem; *symbols without dots* represent upper stem)

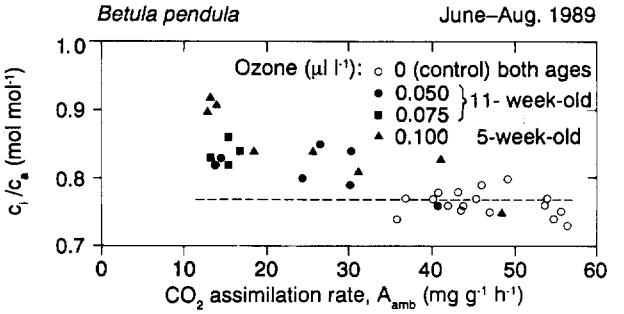

Fig. 2. Ratio of the CO_2 concentration in the mesophyll intercellular spaces of the leaf, c_i (cf. Farquhar and Sharkey 1982), versus that in the ambient air, c_a, as related to the CO_2 assimilation rate per unit of single-leaf dry weight $A_{a\ m\ b}$ (at $c_a = 340$ µl l^{-1}). Steady-state response after 90 min of single leaves from the lower stem to constant light intensity (>1200 µmol photons m^{-2} s^{-1}), leaf temperature (20° C), and leaf/air difference in vapor mole fraction (10 mmol mol^{-1}); each data point represents one plant. The O_3 dose (84 µl l^{-1} h) in 5-week-old leaves at 0.100 µl l^{-1} was similar to that in 11-week-old leaves at 0.050 µl l^{-1} (92 µl l^{-1} h) but 139 µl l^{-1} h for 11-week-old leaves at 0.075 µl l^{-1} (cf. Matyssek et al. 1991)

Biomass development. The mean whole-plant biomass produced in each O_3 treatment by October declined linearly with the O_3 dose accumulating over the growing season (Fig. 3). Remarkably, the production of this birch clone was inhibited by a similar O_3 dose to that of the ambient air of the experimental site. The annual course of growth resulting in the relation of Fig. 3 differed strongly between treatments (Fig. 4A). While the biomass of the control increased throughout the experiment, production of the ozonated plants mostly stagnated as the foliage area declined after mid-summer (Fig. 4A, B). The decline resulted from the premature loss of O_3-injured leaves (Fig. 4C). In October, the DC plants displayed a biomass and foliage area similar to the 0.05 µl l^{-1} O_3 treatment, although the proportional leaf loss equalled that at 0.1 µl l-1 (Fig. 4A–C).

Ozone not only reduced production but also changed the carbon allocation: SLW of the attached (= actual) foliage was enhanced by October in all O_3 treatments (Fig. 5A; cf. Fig. 1B); the weight/length ratio of the stem and the root/shoot biomass ratio were, however, higher in the control (Fig. 5B, C). These differences in allocation were established during the second half of the season. In the DC plants, only the weight/length ratio of the stem showed a similar decrease to that under the 0.05 µl l^{-1} O_3 regime (Fig. 5). At the given O_3-induced leaf loss (cf. Fig. 4B, C), the decreased root biomass related to proportionally more foliage area in ozonated than in control plants (including DC plants; Fig. 6A). In parallel, the root biomass was more strongly limited than that of stem and branch axes, as SLW of the attached foliage increased with the O_3 concentration (Fig. 6B).

Throughout the experiment, the ratio of actual (= attached) foliage area to basal stem area in cross-section

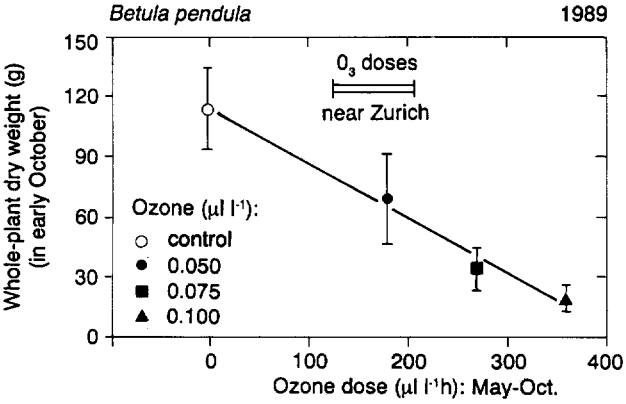

Fig. 3. Whole-plant dry weight in early October (before autumnal leaf loss) in relation to the O_3 dose of the growing season (means ± SD of 7–10 plants/O_3 treatment). *Horizontal bar* marks the range of the O_3 doses in the ambient air of the experimental site and in the nearby rural vicinity of Zurich (see Matyssek et al. 1991)

Table 2. Leaves with visual O_3 injury in relation to the total number of leaves attached to a tree (%); values given as means ± SD of 5 trees/O_3 treatment in September

	O_3 concentration of fumigations (µl l^{-1})			
	0 (control)	0.050	0.075	0.100
Symptoms:				
(1) None	100±0	9±4	5± 4	1± 2
(2) Early	–	50±8	33±11	30±15
(3) Established discoloration	–	42±7	62±12	69±14

The three classes of O_3 injury are: (1) no visual symptoms, (2) early visual symptoms (little, light-green yellowish or black dots), (3) established yellowish-bronze discoloration including large necroses

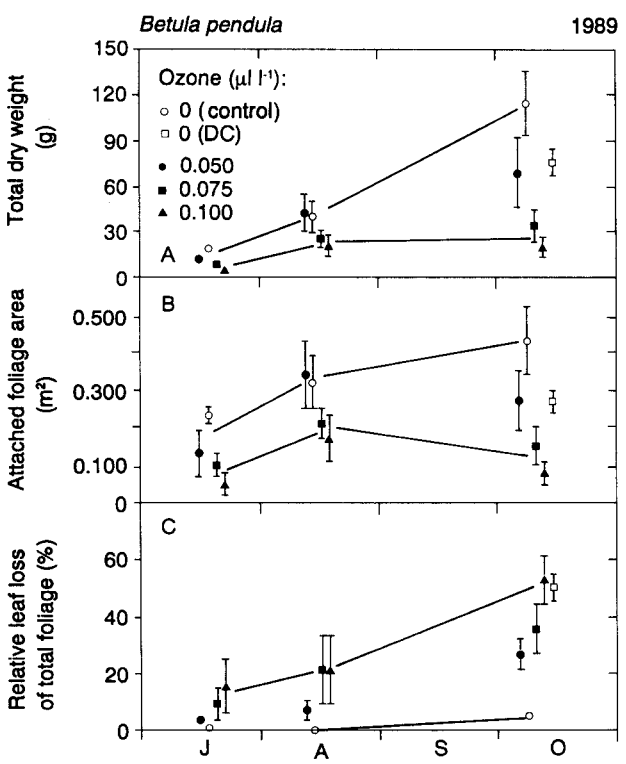

Fig. 4. Seasonal courses of **A** whole-plant dry weight, **B** foliage area attached, and **C** proportional leaf loss of the total leaf number formed. Data points are means ± SD of 5–10 plants/treatment at each harvest. At *points without bars*, SD falls within symbol size; treatment symbols are grouped around each harvest date for graphical reasons. *Straight lines* connect data populations with either no or strongest response to ozone

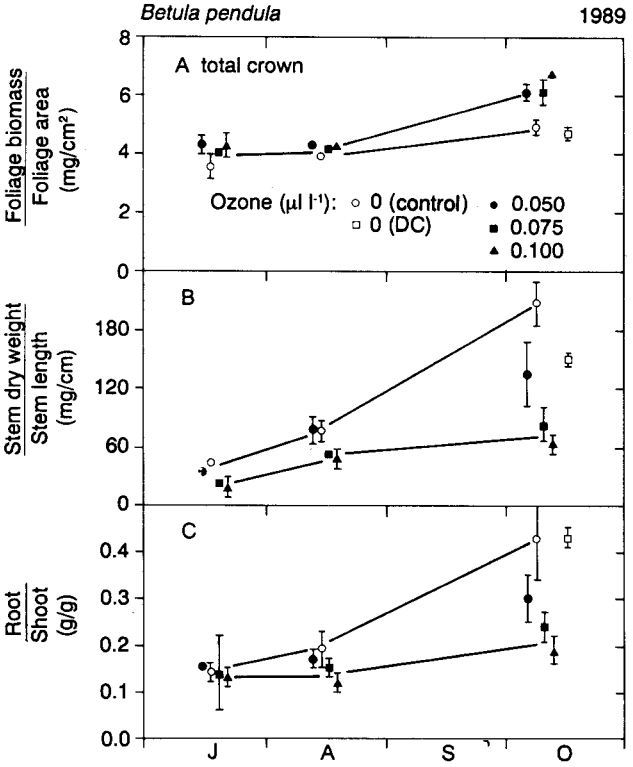

Fig. 5. Seasonal courses of **A** dry weight/area of the attached foliage (SLW), **B** stem dry weight/stem length, and **C** the biomass ratio of the root versus the shoot (data points, arrangement of symbols and straight lines as in Fig. 4)

(Fig. 7A) did not differ among all treatments (including DC plants), nor did the ratio of whole-plant biomass versus actual foliage area (Fig. 7B; see Materials and methods). This is remarkable, as growth (reflected in biomass and stem diameter) integrates over time, but actual foliage area is accidentally determined by the time of O_3-caused leaf loss. However, when relating the biomass to the potential foliage area, this ratio was reduced in ozonated and DC plants (Fig. 7C). This latter ratio reflects carbon investments into green tissue, which did not pay off due to the reduced life span of leaves. The chronic O_3 exposure of the foliage was recorded in the cellulose of the stemwood by increased $\delta^{13}C$ (Fig. 7D).

During summer, RGR was first enhanced in ozonated plants (Table 3) but was then strongly depressed relative to the control. For the total period observed (July–October), RGR of DC plants was about the same as for the 0.075 and 0.100 µl l^{-1} O_3 regimes but lower than in the control and 0.05 µl l^{-1} treatments (Table 3).

Phloem structure

When leaves were sampled in the afternoon, starch was found accumulated along the veins of leaves with early visual O_3 injury (Fig. 8A) but not in the control (Fig. 8B). The phloem tissue of ozonated plants was deformed in the petioles of leaves with established discoloration (Fig. 8C) and in the stem axes (Fig. 8E; see corresponding controls in Fig. 8D, F).

Discussion

How does ozone determine whole-plant production? Total foliage area and arrangement of leaves usually more strongly define undisturbed plant growth than does the CO_2 assimilation rate, *A*, as based on leaf weight or area (Gifford 1974; Lange et al. 1987; Matyssek and Schulze 1987). When compensating ozonated birches for premature leaf loss and reduced *A* (Fig. 9, step 1, see legend), a similar whole-plant dry weight is calculated for the 0.05 µl l^{-1} O_3 treatment to that in the control. However, for the other O_3 treatments, increases in branch number (step 2) and mean leaf size (step 3) are additionally required to obtain the production of the control. Obviously, the changed crown structure (reduced number of branches, leaf size and premature leaf loss) due to ozone more drastically limits growth than does the decline in *A*, as the latter is only part of step 1 and strongly varies between leaves, depending on leaf age and thus O_3 dose (Table 2, Fig. 2; Matyssek et al. 1991). The above-mentioned principles determining undisturbed plant growth apparently also hold for O_3 stress.

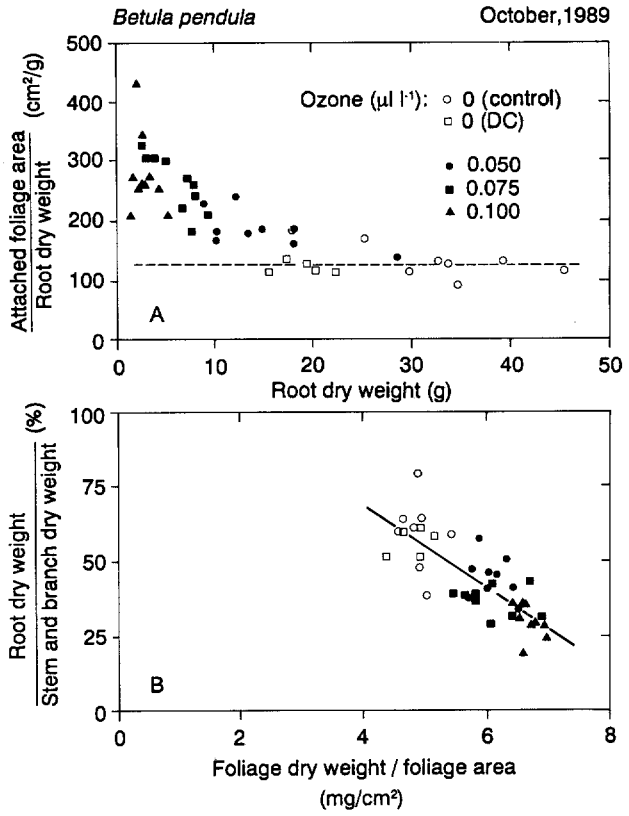

Fig. 6. October harvest, **A** ratio of foliage area versus root dry weight in relation to root dry weight, and **B** ratio of root by the sum of stem and branch dry weight (without leaves) in relation to SLW (dry weight/area) of the attached foliage

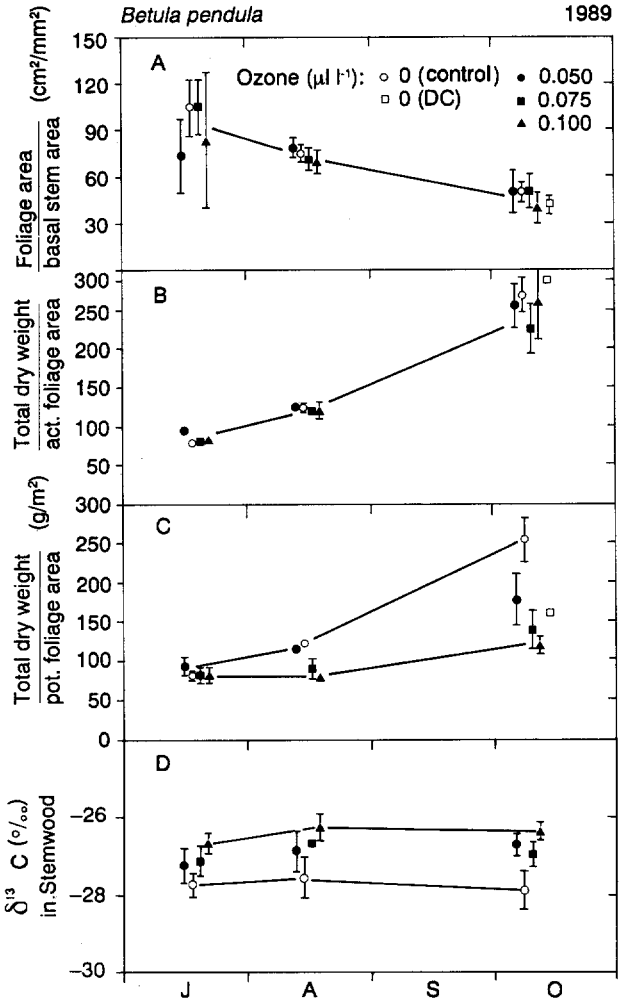

Fig. 7. Seasonal courses of **A** attached foliage area by basal stem area in cross-section, **B** whole-plant dry weight in ratio to the attached (actual) foliage area, **C** whole-plant dry weight in ratio to the potential foliage area (see Materials and methods), and **D** $\delta^{13}C$ of the cellulose in the stemwood (data points, arrangement of symbols and straight lines as in Fig. 4)

Nevertheless, the impact of O_3 on *A* was well reflected in disturbed leaf gas exchange and raised $\delta^{13}C$ of leaves and stems. This change in $\delta^{13}C$ seems to be a bioindication of even low stress by air pollutants (Becker et al. 1989; Greitner and Winner 1988) and to provide a long-term stress record in the wood formation (Martin et al. 1988). However, the increasing $\delta^{13}C$ was not related in the birch leaves to decreasing c_i, as might be expected from stomatal closure due to air pollutants (Farquhar et al. 1989). We found a more rapid decline in *A* than in stomatal conductance (Matyssek et al. 1991), resulting in raised c_i (Fig. 2). Thus, the raised c_i may indicate that $\delta^{13}C$ was less affected by stomatal limitation than perhaps by changes in carbon fixation (e. g. by raised PEP-carboxylase activity relative to that of rubisco as found in ozonated pine and poplar; Lüthy-Krause et al. 1990; Landolt, personal communication).

Although the calculations of Fig. 9 reconstruct the total production, they cannot reflect changes of carbon allocation in the plant. Compensating the DC plants for leaf loss

Table 3. Relative growth rate, RGR = $\Delta W/\Delta t * (W)^{-1}$ (mg g^{-1} day^{-1}), as calculated from the mean whole-plant biomass per treatment at each harvest; ΔW = increment of mean biomass during time interval Δt between two harvests; $W = (W_1+W_2)/2$ with W_1 as the mean biomass at the beginning and W_2 at the end of the time interval Δt

	Ozone concentration of fumigation (µl l^{-1})				
	0 (control)	0.050	0.075	0.100	Defoliated control (DC)
July 17 – August 15:	24	38	35	44	
August 15 – October 2:	20	10	6	0	
July 17 – October 2:	19	19	16	15	15

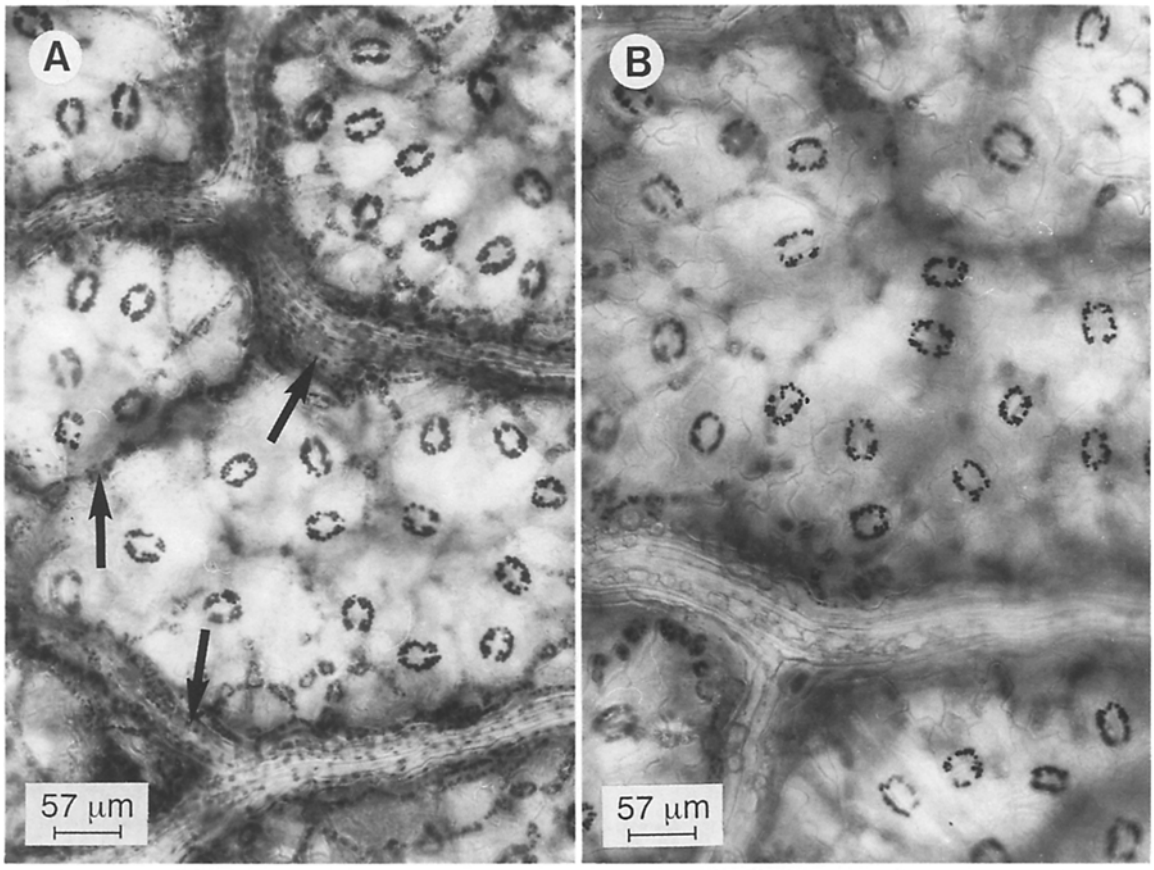

Fig. 8. Lamina of 9-week-old birch leaves sampled in the afternoon (3 p.m.); **A** 0.05 µl l^{-1} O_3 treatment, O_3 dose = 79 µl l^{-1} h, starch (*arrows*) accumulating along leaf veins; **B** control. **C** and **D** show phloem in the leaf petioles of birch, **C** 0.075 µl l^{-1} O_3 treatment, O_3 dose = 135 µl l^{-1} h, leaf with established O_3-induced discoloration; **D** control. **E** and **D** show phloem in the stem axis of birch; **E** O_3 concentration and dose as in **C**; **F** control. Petiole and stem section depicted in **C** and **E**, and in **D** and **F** from adjacent positions each; *white arrows* = deformed cells; *black arrows* = declining cell contents (**C**–**F** by Ig. Kälin)

(Fig. 9, step 1) raised the production to that of the intact control, though the ratio stem weight/length was lowered (cf. Ericsson et al. 1980) as in the ozonated plants (Fig. 5). This limitation in both DC and ozonated plants may result from the reduced foliage density along the stem; otherwise, unlike ozonated plants, the allocation in DC plants did not differ from the intact control. Thus, other causes than leaf loss per se reduced the root/shoot biomass ratio and enhanced SLW of the foliage in ozonated plants.

Phloem transport may play a key role in changing the carbon allocation under O_3 stress. Tracer experiments have shown reduced assimilate concentration and transport in the phloem and to the roots of ozonated pine (Spence et al. 1990). As ozone may have a direct impact on the phloem in the mesophyll, a disturbed phloem loading may result in the starch accumulation observed along the veins of the birch leaves (Fig. 8A), even though phloem seems to be less prone to complete disintegration than mesophyll cells (Fink 1989). Ozone probably does not act directly inside the petioles and stems. Therefore, the deformed phloem seen here (Fig. 8C, E) may arise from limited tissue growth and maintenance due to the reduced amount of available assimilates (reduced photosynthesis, starch retention in leaves). Thus, similar to findings on the effects of SO_2 (Michin and Gould 1986), inhibited phloem loading in the leaf by ozone may limit root growth and may affect leaf differentiation as suggested by increased SLW and changes in S, P and N.

In parallel with problems in phloem transport, root growth may be limited due to a favoured carbon allocation into the green biomass under O_3 stress (Mooney and Winner 1988). In fact, RGR tended to be raised in ozonated plants but only during the early growing season, whereas the foliage area based plant production as well as *A*, size and total number of leaves were *not* enhanced as compared with the control. Perhaps O_3 stress requires high carbon costs for leaf growth (Reich 1983) and for a potential delay of premature leaf loss in order to prevent an even stronger decline in whole-plant production than that observed (cf. Mooney et al. 1988). The unchanged foliage area based plant production (referring to the attached foliage) and area ratio between stem sapwood and attached foliage found in the ozonated plants may thus be part of such potential acclimation to O_3 stress.

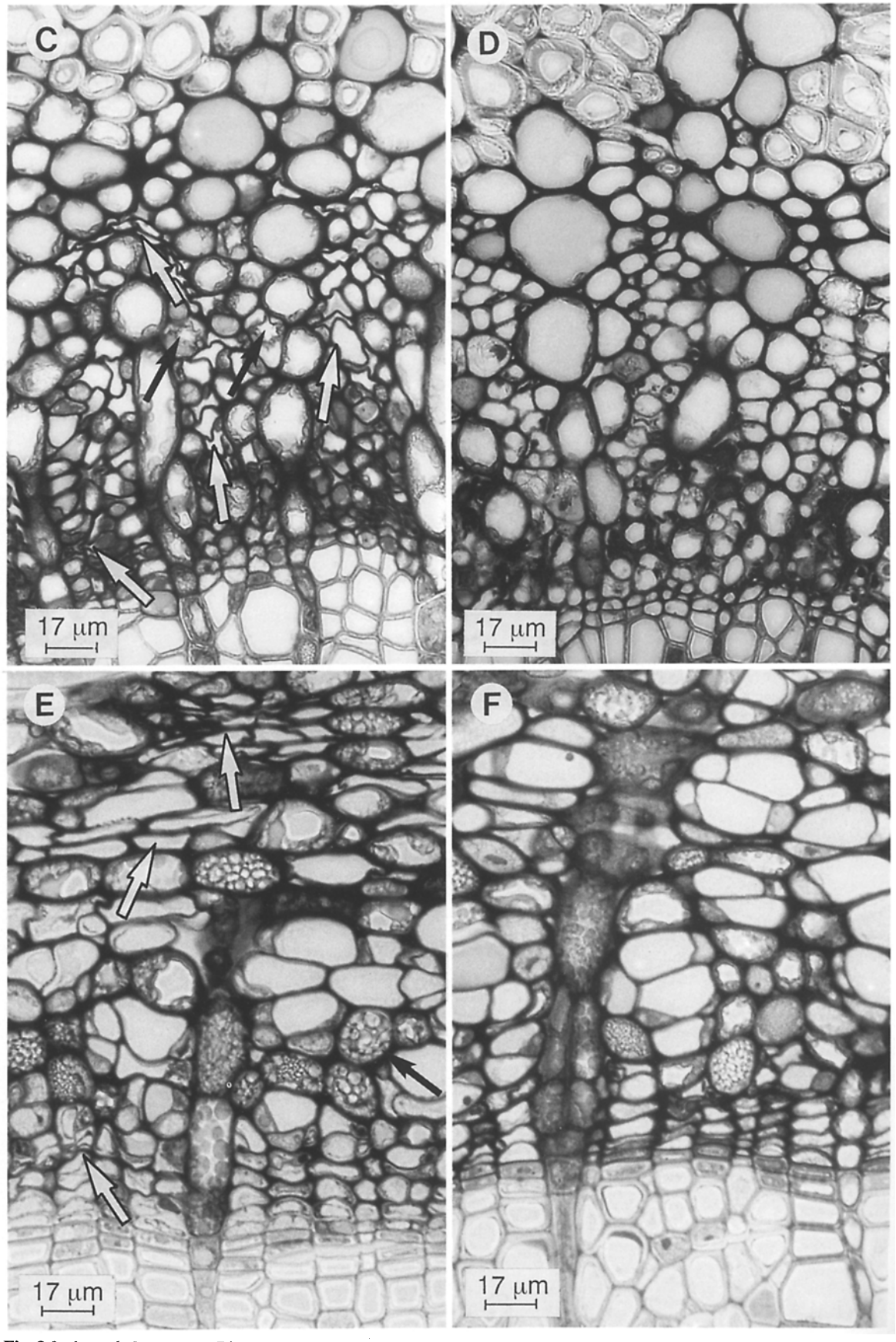

Fig. 8 for legend please see p. 74

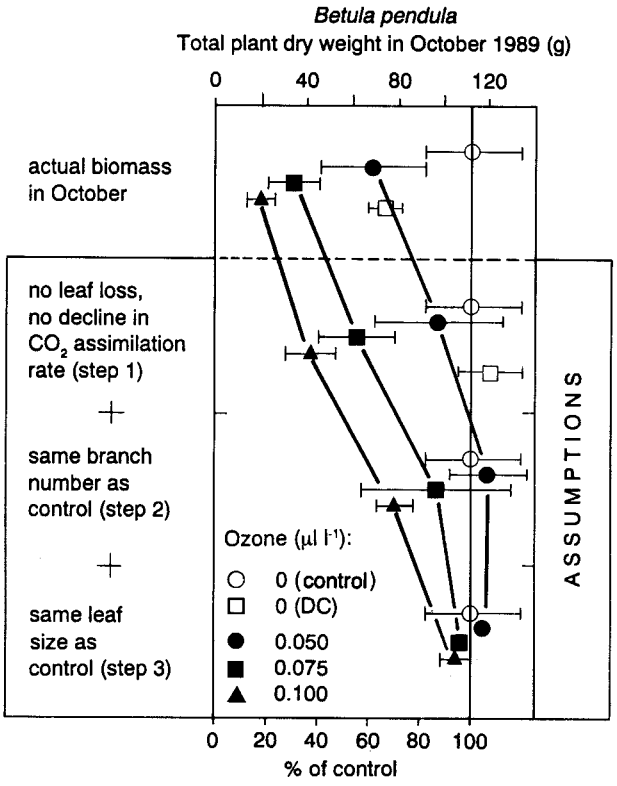

Fig. 9. Of each treated (i.e. ozonated or DC) tree harvested in October, the whole-plant production is converted into that of the control by three calculations (results given as means ± SD); step 1: the potential foliage area multiplied by the mean foliage area based plant production of the control (i.e. whole-plant biomass/attached foliage area) provides the whole-plant production of treated trees as corrected for leaf loss and reduced CO_2 assimilation rate, A; the obtained production is then enhanced by enlarging the potential foliage area as dependent on the branch number (step 2) and leaf sizes (step 3) of the corresponding means in the control:

O_3 (µl l^{-1}):	0	0.05	0.075	0.100
Branch number:	5±2	3±2	2±2	1±1
Stem leaf (cm^2):	65±6	66±7	56±5	48±6
Branch leaf (cm^2):	37±4	36±5	32±5	25±1

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