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Ozone sensitivity of wild field layer plant species of northern Europe. A review

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Abstract

The increasing tropospheric ozone (O_3) concentration constitutes a potential threat to nature. Plants are known to react to O_3, but knowledge of the sensitivity and type of responses of different species and plant communities is widely lacking. This review focuses on the ecological effects of O_3 on northern wild field layer plant species. Most of the 65 species examined thus far have proven to be quite tolerant of O_3. Visible symptoms were observed in 54% of the 61 species studied, and growth reduction in 31% of the 55 species studied for growth. There were no signs to suggest that certain families or vegetation types are more sensitive or tolerant than others. There were, however, clear differences in sensitivity between the different species. It seems that forbs are usually more sensitive than grasses. It should be kept in mind, however, that we still lack knowledge on the responses of many common and abundant key species. The long-term effects are also far from clear. Hardly any field examinations have been carried out on the effects of O_3 on plant communities.

Introduction

Ozone (O_3) has progressively become the major air pollutant in many parts of the world. The fact that the tropospheric O_3 concentrations in Europe have at least doubled during the 20th century on account of human activities, and still continue to increase (Hough and Derwent 1990; Anfossi et al. 1991; Volz and Kley 1988), raises the question of how plants will react to the change. From southern and central Europe, there are field reports of visible injury symptoms on grasses and trees that can be attributed specifically to O_3. From Fennoscandia, where the summer daytime O_3 levels are lower, around 30–40 ppb, with occasional episodes of 60–100 ppb, there are no data on visible symptoms, but it has been demonstrated that the O_3 concentrations are high enough to reduce the growth of field-grown trees, and the current O_3 levels are generally regarded as being high enough to cause negative effects on plants (Laurila and Lättilä 1994; Skärby et al. 1994; Sellden et al. 1997).

An inverse dependence of stomatal resistance on ozone diffusivity is generally accepted. Usually, the uptake of O_3 through the cuticle is neglible compared to uptake through stomata (Grunhage and Haenel 1997). Under high humidity, stomatal opening increases and plants are thus more sensitive to air pollution. Actually, the areas experiencing the highest O_3 exposures, i.e., where the accumulated exposures over a threshold of 40 ppb (AOT40 values) (Fuhrer et al. 1997) are highest, are frequently not the same as the regions calculated as having the highest O_3 fluxes. The highest O_3 exposures (AOT40 values) occur in the Mediterranean region and central Europe. In contrast, it is apparent that the highest O_3 fluxes occur in southern Scandinavia and northern Europe (Emberson et al. 2000). Furthermore, our earlier studies suggest that northern Finnish (sub)species and populations may be more sensitive to O_3 than southern Finnish ones (Manninen et al. 1999, 2002).

After O_3 has entered the substomatal cavities and the apoplastic space, physical and chemical defence and tolerance processes acquire an essential role in the plant response (Reich 1987; Runeckles 1992; Guzy and Heath 1993; Nebel and Fuhrer 1994). Oxidative stress may result in stomatal closure (Davison and Reiling 1995; Pearson et al. 1996; Lyons and Barnes 1998), decline in the photosynthetic capacity of the leaf (Reich and Amundson 1985; Chappelka and Chevone 1992; Torsethaugen et al. 1999) or accelerated rates of leaf senescence (e.g., Pearson et al. (1996)). Disturbances of this kind may result in a reduction of the growth rate or changes in resource allocation and the reproductive performance (Reiling and Davison 1992a, 1992b, 1992c; Runeckles and Chevone 1992; Davison and Reiling 1995; Pearson et al. 1996; Lyons et al. 1997; Lyons and Barnes 1998)

This review focuses on the O_3 responses of wild field layer plant species found in experimental studies in northern Europe. Ozone sensitivity has been mostly studied among forest trees and sensitive and tolerant cultivars, clones and populations of different economic plants. It has become clear that some wild herbaceous plants are equally sensitive to O_3 as the most sensitive crop species studied so far (Ashmore and Davison 1996; Ashmore et al. 1996; Kärenlampi and Skärby 1996; Davison and Barnes 1998; UN/ECE 1999). A recent review by Black et al. (2000) discussed the O_3 impact on growth and resource allocation and on the reproductive development of plants, showing that past research had been focused mainly on economic plants and less on natural or seminatural plants. With regard to northern wild plants, only a few new experiments have been documented since Davison and Barnes (1998) and Franzaring et al. (1998) published their reviews on the effects of O_3 on wild plants. Davison and Barnes (1998) discussed the difficulties involved in measuring relative O_3 resistance and considered the effects on growth, resource allocation and evolution without trying to find out which species would be sensitive or tolerant to O_3. Franzaring et al. (1998) tried to establish a connection between the CSR-strategy, ecological water amplitude, climate parameters and sensitivity of certain species. The aim of the present state of the art review is to find out if the known O_3 effects (occurrence of visible injuries, growth reductions) on northern wild forbs, grasses and dwarf shrubs allow any ecological conclusions. A further aim is to find out the ecological, anatomical and morphological characteristics that explain the differences in O_3 sensitivity.

Studied responses

Altogether 65 Scandinavian wild field layer plant species have been studied, which accounts for about 3.8% of the wild field layer flora in Scandinavia (Lid 1985). Forty of the species were studied in controlled-environment chambers (CEC), twenty in open-top chambers (OTC) and five in both CECs and OTCs (Tables 1, 2 and 3). Nussbaum and Fuhrer (2000) stated that in OTCs, ozone uptake differs between species because of the specific reactions to chamber conditions. The typical OTC effects on the chamber microclimate are filter effects, a 10–20% reduction of global and PAR radiation, an increase of long-wave radiation, a mean temperature increase, and a mean vapour pressure deficit (Jetten 1992). The temperature regime in the present CEC and OTC studies varied from cool to warm between 11 °C and 28 °C as mean daily maximum. Light intensity varied from 260 μmol m^{-2} s^{-1} to an average of 839 μmol m^{-2} s^{-1}. Relative humidity varied between 64 and 87%. Comparison of the climatic conditions in experiments was difficult, but all reviewed studies had tried to follow the natural climatic conditions when planning the studies. It was noteworthy that real studies *in situ* in Scandinavia are lacking. *In situ*, the light intensity is much greater than in many environmental chambers. Generally a level of 400 μmol m^{-2} s^{-1} for 12 h is considered to be enough for growing cool season plants in CECs (Lambers et al. 1998)

The effects of O_3 exposure have been documented to vary, depending on the genotype, species, population, origin, plant age, developmental stage and physiological state of the plant and also on the interaction with other species, insects, pathogens and the abiotic environment (Chappelka and Chevone 1992; Manning and Krupa 1992; Bungener et al. 1999; Reiling and Davison 1992a, 1992b, 1992c; Davison and Reiling 1995; Kärenlampi and Skärby 1996; Pearson et al. 1996; Lyons et al. 1997; Krupa and Manning 1988; Lyons and Barnes 1998; Whitfield et al. 1998; UN/ECE 1999).

The vast majority of O_3 studies have been performed on seedling state perennials (Tables 1 and 2). Leaves are most sensitive (decrease in photosynthesis) to O_3 when they have just reached full size (UN/ECE 1999). Lyons and Barnes (1998) noticed that

Table 1. Summary of some experiments designed to study the effects of O_3 on wild forb species. Visible symptoms: concentration and significance. Growth parameters: + increase, – decrease, 0 no effect. In the case of no study, the cell is blank.

Species	Age	Ozone treatments	Visible symptom	Growth	Ref.
Alchemilla alpina L.	A (t.)	CEC, 15, 40 or 80 ppb, 8 h/day, 66 days.		0	Mortensen and Nilsen (1992)
Angelica archangelica L.	S	CEC, 20, 45 or 90 ppb, 8 h/d, 41 days.	(45 and 90 ppb ***)	– (90 ppb ***)	Mortensen (1993)
Antennaria dioica (L.) Gaertn.	S	CEC, 12, 40 or 86 ppb, 8 h/d, 65 days.	(86 ppb ***)	– (86 ppb ***)	Mortensen (1993)
Anthyllis vulneraria L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Astragalus frigidus (L.) A. Gray	S	CEC, 15, 43 or 78 ppb, 8 h/d, 8 weeks.	(78 ppb *)	0	Mortensen (1994)
Campanula rotundifolia L.	S	CEC, 5 or 50 ppb, 8 ? h/d, 42 days.	0	0	Mortensen and Nilsen (1992)
Centaurea jacea L.	S	CEC, 5 or 50 ppb, 8 ? h/d, 42 days.	(50 ppb ***)	0	Mortensen and Nilsen (1992)
Cirsium palustre (L.) Scop.	S	CEC, 20, 45 or 90 ppb, 8 h/d, 42 days.	(45 and 90 ppb ***)	0	Mortensen (1993)
Dianthus deltoides L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Epilobium angustifolium L.	S	CEC, 12, 40 or 86 ppb, 8 h/d, 65 days.	(40 and 86 ppb ***)	– (86 ppb ***)	Mortensen (1993)
Erigeron borealis (Vierh.) Simm.	S	CEC, 15, 43 or 78 ppb, 8 h/d, 8 weeks	(78 ppb *)	– (78 ppb *)	Mortensen (1994)
Fragaria vesca L.	S	CEC, 20, 45 or 90 ppb, 8 h/d, 41 days	(45 and 90 ppb ***)	– (90 ppb ***)	Mortensen (1993)
Geranium sylvaticum L.	S	CEC, 15, 43 or 78 ppb, 8 h/d. 8 weeks.	(78 ppb *)	0	Mortensen (1994)
Gnaphalium norvegicum Gunn.	S	CEC, 15, 43 or 78 ppb, 8 h/d, 8 weeks	0	0	Mortensen (1994)
Hypericum perforatum L.	S	CEC, 5 or 50 ppb, 8 ? h/d, 42 days.	(50 ppb ***)	0	Mortensen and Nilsen (1992)
Hypochoeris radicata L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Leontodon autumnalis L.	S	CEC, 20, 45 or 90 ppb, 8 h/d, 40 days.	(45 and 90 ppb ***)	– (90 ppb **)	Mortensen (1993)
Leontodon hispidus L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Leucanthemum vulgare Lam.	S	CEC, 5 or 50 ppb, 8 ? h/d, 46 days.	(50 ppb ***)	0	Mortensen and Nilsen (1992)
Lotus corniculatus L.	S	CEC, 5 or 50 ppb, 8 ? h/d, 33 days	0	0	Mortensen and Nilsen (1992)

Table 1. Continued

Species	Age	Ozone treatments	Visible symptom	Growth	Ref.
Melampyrum pratense L.	S	OTC, 5, 75 or 150 ppb, 8 h/d, 2–6 days.	(75 and 150 ppb)		Nygaard (1994)
Oxalis acetosella L.	S	OTC, 5, 75 or 150 ppb, 8 h/d, 2–6 days.	(75 and 150 ppb)		Nygaard (1994)
Oxyria digyna (L.) Hill.	A (t.)	CEC, 15, 40 or 80 ppb, 8 h/d, 30 days.	0		Mortensen and Nilsen (1992)
Oxyria digyna (L.) Hill.	S	CEC, 12, 40 or 86 ppb, 8 h/d, 50 days.	(86 ppb ***)	– (86 ppb *)	Mortensen (1993)
Pilosella officinarum F.W. Schultz & Sch. Bip. (coll.)	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Plantago lanceolata L.	S	CEC, 5 or 50 ppb, 8 ? h/d, 42 days.	(50 ppb ***)	– (50 ppb **)	Mortensen and Nilsen (1992)
Plantago lanceolata L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Plantago major L.	S	CEC, < 5 or 70 ppb, 7 h/d, 2 weeks.	0	– (70 ppb *)	Lyons et al. (1997)
Plantago media L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Polygonum viviparum L.	S	CEC, 15, 40 or 80 ppb, 8 h/d, 66 days.		+ (40 ppb **) – (80 ppb **)	Mortensen and Nilsen (1992)
Potentilla erecta (L.) Raeusch.	A (t.)	CEC, 15, 40 or 80 ppb, 8 h/d, 60 days.	(80 ppb)		Mortensen and Nilsen (1992)
Potentilla palustris (L.) Scop.	S	CEC, 15, 43 or 78 ppb 8 h/d, 8 weeks.	(78 ppb *)	– (43 and 78 ppb *)	Mortensen (1994)
Prunella vulgaris L.	S	CEC, 5 or 50 ppb, 8 ? h/d, 33 days.	0	0	Mortensen and Nilsen (1992)
Ranunculus acris L.	S	CEC, 20, 45 or 90 ppb, 8 h/d, 41 days.	(90 ppb ***)	– (90 ppb **)	Mortensen (1993)
Rumex acetosa L.	S	CEC, 5 or 50 ppb, 8 ? h/d, 37 days.	0	0	Mortensen and Nilsen (1992)
Rumex acetosa L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Rumex acetosa subsp. Lapponicus Hiit.	S	CEC, 12, 40 or 86 ppb, 8 h/d, 32 days.	(86 ppb ***)	+ (40 ppb ***) – (86 ppb ***)	Mortensen (1993)
Saussurea alpina (L.) DC.	S	CEC, 20, 45 or 90 ppb, 8 h/d, 42 days.	(90 ppb ***)	+ (45 ppb *)	Mortensen (1993)
Saxifraga cernua L.	S	CEC, 15, 40 or 80 ppb, 8 h/d, 44 days.	0	0	Mortensen and Nilsen (1992)
Saxifraga cespitosa L.	S	CEC, 15, 40 or 80 ppb, 8 h/d, 66 days.	0	0	Mortensen and Nilsen (1992)
Silene acaulis (L.) Jacq.	S	CEC, 15, 40 or 80 ppb, 8 h/d, 66 days.		– (40 and 80 ppb *)	Mortensen and Nilsen (1992)

Table 1. Continued

Species	Age	Ozone treatments	Visible symptom	Growth	Ref.
Silene vulgaris (Moench) Garcke	S	CEC, 12, 40 or 86 ppb, 8 h/d, 65 days.	(86 ppb ***)	+ (40 ppb ***)	Mortensen (1993)
Silene vulgaris (Moench) Garcke	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Solidago virgaurea L.	S	CEC, 5 or 50 ppb, 8 ? h/d, 35 days.	(50 ppb **)	0	Mortensen and Nilsen (1992)
Solidago virgaurea L.	S	CEC, 12, 40 or 86 ppb, 8 h/d, 65 days.	(40 or 86 ppb ***)	– (86 ppb **)	Mortensen (1993)
Thalictrum alpinum L.	S	CEC, 15, 43 or 78 ppb, 8 h/d, 8 weeks.	0	0	Mortensen (1994)
Trientalis europaea L.	S	OTC, 5, 75 or 150 ppb, 8 h/d, 2–6 days.	(75 or 150 ppb)		Nygaard (1994)
Viola riviniana Reichenb.	S	OTC, 5, 75 or 150 ppb, 8 h/d, 2–6 days.	(75 or 150 ppb)		Nygaard (1994)
Plant age:	Ozone treatments				
A (t.): transplant from the field	CEC: controlled environment chamber				
S: seedling	OTC: open-top chamber, CF: charcoal-filtered air, F: filtered air, NF: non-filtered air, NF + supplemental O_3				

The nomenclature follows Hämet-Ahti et al. (1998). nl l^{-1} and µg m^{-3} was converted into ppb by the authors. AOT40s are given in ppb.h. Question mark (?): duration of daily exposure was not given.

Table 2. Summary of some experiments designed to study the effects of O_3 on wild grass species. Visible symptoms: concentration and significance. Growth parameters: + increase, – decrease, 0 no effect. In the case of no study, the cell is blank.

Species	Age	Ozone treatments	Visible symptom	Growth	Ref.
Agrostis capillaris L.	S	CEC, 15, 43 or 78 ppb, 8 h/d, 8 weeks.	(78 ppb *)	0	Mortensen (1994)
Alopecurus pratensis L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Anthoxanthum odoratum L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Briza media L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Carex atrofusca Schkuhr	S	CEC, 15, 43 or 78 ppb, 8 h/d, 8 weeks	(78 ppb *)	– (43 and 78 ppb *)	Mortensen (1994)
Dactylis glomerata L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	(73 ppb)	0	Pleijel and Danielsson (1997)
Eriophorum angustifolium Honck.	S	CEC, 15, 43 or 78 ppb, 8 h/d, 8 weeks.	(78 ppb *)	0	Mortensen (1994)
Festuca ovina L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	+ (73 ppb *)	Pleijel and Danielsson (1997)
Festuca pratensis Hudson	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Melica nutans L.	S	CEC, 15, 43 or 78 ppb, 8 h/d, 8 weeks.	(78 ppb *)	0	Mortensen (1994)
Phalaris arundinacea L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Phleum alpinum L.	S	CEC, 12, 40 or 86 ppb, 8 h/d, 64 days.	(40 and 86 ppb ***)	– (40 and 86 ppb ***)	Mortensen (1993)
Phleum alpinum L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	(73 ppb)	0	Pleijel and Danielsson (1997)
Phleum alpinum L.	3 w	OTC, CF, ambient or ~ 75 ppb,12 h/d = 1290 or 20 000 ppb.h, respectively, 7 weeks.	(~ 75 ppb *)	– 75 ppb *)	Danielsson et al. (1999)
Poa alpina var. vivipara L.	S	CEC, 15, 43 or 78 ppb, 8 h/d, 44 days.	0	0	Mortensen and Nilsen (1992)
Poa annua L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)
Poa palustris L.	S	OTC, CF, NF 49, NF + 73 ppb, 7 h/d = 3913 or 11450 ppb.h, respectively, 1 month.	0	0	Pleijel and Danielsson (1997)

Table 2. Continued

Species	Age	Ozone treatments	Visible symptom	Growth	Ref.
Plant age:	Ozone treatments				
S: seedling	CEC: controlled environment chamber				
3 w = three weeks old seedlings	OTC: open-top chamber				
	CF: charcoal-filtered air, NF::non-filtered air, NF + supplemental O_3				

The nomenclature follows Hämet-Ahti et al. (1998). nl l^{-1} and µg m^{-3} was converted into ppb by the authors. AOT40s are given in ppb.h.

resistance to O_3 increased with plant age in *Plantago major* L., and the decline in final plant dry weight was entirely due to the sensitivity of the seedlings to O_3. The fact that seedling state shows visible injuries and growth reduction but not adult *Oxyria digyna* (L.) Hill. individuals (Table 1) may also be due to the 20 days longer duration of the experiment with seedling state plants.

There is usually only a small correlation between relative sensitivity in terms of visible symptoms and growth reduction or seed production (Reiling and Davison 1992a; Davison and Barnes 1998). In trees, however, reduced radial growth correlates with visible O_3 injury (Chappelka and Chevone 1992). In the experiments discussed in this review, visible symptoms form the most frequently studied response. In half of the cases with visible symptoms, there is also another response. The rarest case is to have growth reduction without any visible injury symptoms.

Visible symptoms

Of the 40 forb species studied for symptoms of visible injury, 25 species (63%) showed such symptoms. In the CEC experiments the percentage was 70% and in the OTCs 31%. (Table 1). The short-term high concentrations most readily cause visible injury symptoms in plants (Treshow and Stewart 1973; Krupa and Manning 1988; Nygaard 1994), but there are differences between species. Bergmann et al. (1999) found that some species show high sensitivity to daily AOT 40 peak values: a mean daily maximum AOT 40 of > 270 ppb.h appears to be critical, while in some other species, e.g., *Rumex acetosa* L., symptoms become apparent with a daily maximum of AOT40s of > 320 ppb.h. Missing daily high peak concentrations could be associated with some species not showing visible injuries.

The readiness of plants to show visible symptoms in the present experiments may be due to the fact that most were still in the juvenile phase. According to Heath (1994), growing leaves are most sensitive for showing visible injuries, as the area of the leaf is just beyond the half-way point to maximum size, before expansion ceases. This might explain the fact that *Oxyria digyna* (L.) developed visible injury symptoms in seedlings but not in the adult state (Table 1). Plants grow most rapidly and, consequently, are most vulnerable to environmental stress during the seedling and juvenile phase.

Table 3. Summary of some experiments designed to study the effects of O_3 on wild dwarf shrubs. Visible symptoms: concentration and significance. Growth parameters: + increase, − decrease, 0 no effect. In the case of no study, the cell is blank.

Species	Age	Ozone treatments	Visible symptom	Growth	Reference
Andromeda polifolia L.	A (t.)	CEC, 15, 40 or 80 ppb, 8 h/d, 60 days	0		Mortensen and Nilsen (1992)
Betula nana L.	S	CEC, 15, 40 or 80 ppb, 8 h/d, 43 days.	(80 ppb ***)		Mortensen and Nilsen (1992)
Calluna vulgaris (L.) Hull.	A (t.)	CEC, 15, 40 or 80 ppb, 8 h/d, 30-90 days.	0		Mortensen and Nilsen (1992)
Empetrum nigrum L.	A	OTC, 35, 45 or 75 ppb, 8 h/d, 16 months.		0	Johnsen et al. (1991)
Rubus chamaemorus L.	A (t.)	CEC, 15, 40 or 80 ppb, 8 h/d, 40 days.	0		Mortensen and Nilsen (1992)
Vaccinium myrtillus L.	A (soil)	OTC, 5, 75 or 150 ppb, 8 h/d, 2 months.	(75 and 150 ppb)		Nygaard (1994)
Vaccinium myrtillus L.	S	CEC, 15, 43 or 78 ppb, 8 h/d, 8 weeks.	(78 ppb *)	0	Mortensen (1994)
Vaccinium vitis-idaea L.	A (t.)	CEC, 15, 40 or 80 ppb, 8 h/d, 60 days.	0		Mortensen and Nilsen (1992)
Vaccinium vitis-idaea L.	S	CEC, 15, 43 or 78 ppb, 8 h/d, 8 weeks.	0		Mortensen (1994)

Plant age:	Ozone treatments
A (t.): adult, transplant from the field	CEC: controlled environment chamber
A (soil): adult, soil block from the forest	OTC: open-top chamber
S: seedling	

The nomenclature follows Hämet-Ahti et al. (1998). nl l^{-1} and µg m^{-3} was converted into ppb by the authors.

Of the 15 grass species studied, visible injury symptoms were observed in 6 species (40%). In the CEC experiments the percentage was 83% and in the OTCs 20% (Table 2). The corresponding percentages for all species were 67% in the CECs and 29% in the OTCs (Tables 1, 2 and 3). The injured species were commonly grasses with smooth, hairy leaves. The lowest O_3 concentration found to cause injuries was 40 ppb in 64 days, which caused *Phleum alpinum* L. to be injured (Mortensen 1993). In two OTC studies, *P.alpinum* revealed visible symptoms in 78 ppb in 4 weeks, and visible symptoms and growth decrease in 75 ppb in 7 weeks, when the experiment was started after 3 weeks without ozone. Approximately 80 ppb concentrations in 8 weeks caused injuries to *Agrostis capillaris* L., *Carex atrofusca* Schkur, *Dactylis glomerata* L. (only 4 weeks), *Eriophorum angustifolium* Honck. and *Melica nutans* L.

Among the boreal field layer key species, the responses of a few dwarf shrubs have been studied (Table 3). Visible symptoms were observed in *Betula nana* L. and *Vaccinium myrtillus* L. at the level of 80 ppb. This is in accordance with the observation on birch and other broad-leaved trees (Mortensen and Nilsen 1992; Matyssek et al. 1995; Gunthardt-Goerg et al. 1997; Mortensen 1999).

Growth

In the experiments covered in this review, growth was one of the studied parameters in 61 cases. Aboveground biomass dry weight is a common measure of growth. Even slight exposure to O_3 may alter the ability of plants to translocate carbohydrates to roots, seeds and fruits (Black et al. 2000). Allometric root/shoot coefficient was one of the studied parameters only in the case of *Plantago major*, and there was no effect. In the CEC experiments, 44% of the 39 species studied showed growth reduction, while only one of the 20 species in the OTCs, *Phleum alpinum* L., showed such reduction. Forbs seem to be more sensitive to O_3 than grasses as far as growth is concerned. In 39% of the forb species studied, O_3 reduced growth, while the corresponding percentage in grasses was 13%.

Ecological significance

Plant functional types proved largely unsatisfactory in the effort to generalize change responses in the Arctic (Dormann and Woodin 2002). Hunt et al. (1993) concluded that high CO_2 responsiveness is normal only within the competitive functional type. This conclusion might also be applicable to ozone responses. Plant functional types proved largely unsatisfactory in the effort to generalize climate some extent. Plant species characteristic in unfavourable environments often exhibit inherently low maximum relative growth rates (RGR) compared to species from more favourable environments (Atkin et al. 1996; Hunt and Cornelissen 1997). Specific leaf area seems to explain the variation in the RGR of alpine, subalpine and lowland species (Atkin et al. 1996). However, the most ozone-sensitive species have not been widely used in RGR studies, and most results are from lowland sites. Among the few tested ozone-sensitive plants, *Plantago major* is a high-RGR species (RGR from 240 to 320 mg g^{-1} d^{-1}, Dijkstra and Lambers (1989) and Poorter and Remkes (1990)), while ozone-tolerant *Festuca ovina* is a low-RGR species (Poorter and Remkes 1990), But many other species are indifferent to ozone sensitivity and may be highly variable in their RGR, e.g., *Briza media* and *Poa annua*. Some species may show visible symptoms (*Hypericum perforatum*), while others do not (*Oxyria digyna*), and may still have quite equal relative growth rates (Poorter and Remkes 1990).

In the ozone experiments, the high-RGR species (Hunt and Cornelissen 1997) *Agrostic capillaris* showed visible symptoms and *Plantago lanceolata* showed growth reductions, whereas *Pilosella officinarum* was unresponsive.

The main criterion in sensitivity screening could be the effect of O_3 on plant growth, which is indicative of the ecological fitness of the species. The effect on seed output would be a very important parameter to study, especially in the case of annual or monocarpic species. Both species studied with respect to flowering, i.e., *Plantago lanceolata* L. and *Plantago media* L., were unfortunately perennials in the seedling state, and there were no observations on reproductive effects.

Sensitive species, such as *Antennaria dioica* (L.) Gaertn., *Epilobium angustifolium* L., *Plantago major* L.(after only two weeks) and *Potentilla palustris* (L.) Scop. and *Phleum alpinum* L., showed severe growth reduction after 50 days or more at concentrations between 70 and 80 ppb. At such concentrations, growth is also somewhat reduced in *Angelica archangelica* L., *Erigeron borealis* (Vierh.) Simm., *Fragaria vesca* L., *Leontodon autumnalis* L., *Ranunculus acris* L., *Silene acaulis* (L.) Jacq., *Solidago virgaurea* L., *Agrostis capillaris* L. and *Carex atrofusca* Schkuhr. Tolerant species including *Alchemilla alpina* L., *Gnaphalium norvegicum* Gunn., *Saussurea alpina* (L.) DC., *Saxifraga cernua* L., *Saxifraga cespitosa* L., *Thalictrum alpinum* L., *Poa alpina* var. *vivipara* L. and *Festuca ovina* L., seem to stand high concentrations for several weeks without any injury.

The few studies carried out so far on plant communities suggest that forbs are generally more sensitive than grasses, showing a proportional decrease of the biomass of the community upon increasing O_3 exposure. The total biomass of the community remains about the same, as the biomass of grasses grows due to the diminishing competition and/or the stimulating effect of O_3 on the growth of some grass species. This may lead to systematic shifts in species composition. The species that have been found to diminish in plant communities with increasing O_3 include *Leontodon hispidus* L., *Trifolium repens* L. and *Festuca ovina* L. Some less sensitive species, such as *Festuca rubra* L., seem to increase their portion of the community biomass (Ashmore et al. 1995, 1996). This is quite interesting, since *Leontodon hispidus* L. and *Festuca ovina* L. have proven to be quite tolerant of O_3 when screened in monocultures (Tables 1 and 2). Generally speaking, greater biodiversity seems to mean more biomass in grassland ecosystems (Tilman et al. 2001).

There is no common trend in sensitivity that is identifiable on the basis of family. After the classification of species according to habitat (forest, dry site, wet site, arctic or indifferent), tolerance seemed to be most common among the arctic and indifferent species. Interestingly, there are observations from Switzerland showing that fewer species are sensitive to O_3 at subalpine sites than at lower altitudes (Nebel and Fuhrer 1994). This may be explained by specific responses of the well-developed antioxidative systems in mountain plants (Wildi and Lütz 1996). On the other hand, the O_3 sensitivity of the mountain birches compared to two other birch species seem to be related to its rapid determinate growth pattern (Manninen et al. 2002).

Traits affecting the response to ozone

Leaf anatomy features, e.g., stomatal density and resistance, the percentage of intercellular spaces among palisade cells and the size of palisade parenchymal cells have been found to affect O_3 sensitivity (Evans and Ting 1974; Evans et al. 1996a, 1996b). Many weeds and seminatural plant species, e.g., *Rumex obtusifolius* L. and *Plantago major* L. reported to be sensitive to O_3 (Reiling and Davison 1992a, 1992a; Lyons et al. 1997) have thin cuticles. For example, the amount of epicuticular wax is low in *Plantago major* (Martin and Juniper 1970; Baker 1982).

Based on comparative leaf conductance measurements (Janke 1970; Körner et al. 1979; Körner 1995) and the sensitivity considerations made in this review, it appears that the gas exchange rate correlates with the response to O_3 in many cases. Tolerant species, such as *Phalaris arundinacea* L. and *Alopecurus pratensis* L., and also *Vaccimium myrtillus* L. as an intermediate species, have moderate leaf conductance values (Janke 1970; Körner et al. 1979). On the othern hand, *Oxalis acetosella* L. and *Vaccinium vitis-idaea* L. have low conductances (Körner et al. 1979; Körner 1995), but *O. acetosella* L. shows readily visible injuries (Table 1).

There is evidence to suggest that, on account of their higher gas exchange rates accompanied by a higher uptake of O_3 or a low ability to allocate resources when exposed to stress, genotypes and species with a high growth rate are more sensitive to O_3 than slow-growing ones (Reiling and Davison 1992a; Danielsson and Pleijel 1999; Manninen et al. 1999; Bortier et al. 2000). There are exceptions to this even within a genus, such as the fact that *Phleum alpinum* L. has a slower growth rate than *Phleum pratense* L. but still shows more sensitivity to O_3 (Danielsson et al. 1999). Furthermore, differences in O_3 sensitivity within species may also be attributed to O_3 climate at the sites from where the populations originate (Lyons et al. 1997; Manninen et al. 2002). In other words, populations and species originating from areas where the ambient O_3 levels are low may be expected to be more sensitive to O_3 than those growing in areas with higher O_3 levels.

Conclusions

The influence of O_3 on plants can be positive, negative or not measurable. In most OTC experiments, fumigation had no effect on the response under study. Identification of the varying sensitivities of taxa, communities and ecosystems is quite complicated. There is variation due to such factors as plant functional types, species, genotype, plant age and the O_3 history of the plant, as it has been shown so clearly in *Plantago major* L. Differences in the experimental protocols (facilities, exposure regimes, etc.) and parameters used to measure the O_3 response may also cause differences in the results of sensitivity screening. In forests, field and ground layer plants are under tree canopies, which restrain a notable part of the O_3 load and reduce the dose to which the field layer is exposed. The exposure is often short, only some weeks in duration. It would be preferable to examine the responses of plants for a whole season or at least up to the state of reproduction in the field.

Knowledge of the effects of O_3 on the composition, diversity and stability of plant communities is widely lacking. Skärby et al. (1994) have pointed out that only a few species are likely to be affected by the current O_3 levels in Norway. This review warrants a similar conclusion pertaining to whole Fennoscandia. At any rate, our results suggest that a wild strawberry population from eastern part of central Finland was more sensitive to O_3 than a population from southern Finland and responded to an O_3 exposure far below the proposed critical level of 7000 ppb.h (Manninen et al. 2002). It must also be kept in mind that only a small portion of the species have been examined. Many important and prevalent ones have not been studied yet. Above all, there is a need for community studies in field conditions.

It seems that Arctic species may be even more tolerant of O_3 than boreal ones, but it must be kept in mind that relatively few species have been tested. It seems possible, from the studies of Ashmore et al. (1996) and the fact that forbs appear to more sensitive to O_3 than grasses, that O_3 may influence the species composition in grasslands.

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