The impact of ozone on natural vegetation – An ecological discussion of European studies

Jürgen Franzaring, Elke Bergmann, Jürgen Bender and Hans-Joachim Weigel

Synopsis

In this paper results from ozone fumigation studies using plant species native to Europe are presented and discussed. Although several species have been included in environmentally-controlled experiments, generalisations on the negative effects of photosmog on natural vegetation can not yet be deduced. Apart from differences in sensitivities of individual species, the influence of environmental factors on the phytotoxicity of ozone must be taken into account. The importance of various response parameters is discussed and approaches to the classification of ozone sensitivities of plant species representing different ecological groups are presented.

natural vegetation, sensitivity, primary ecological strategies, climate, water-status, ozone exposure regimes

1 Introduction

In the 70's and 80's a large number of studies was conducted to determine the impact of ozone on crops and forest trees. Only recently native herbaceous plant species have been included in these studies (REILING & DAVISON 1992, ASHMORE & al. 1996, BERGMANN et al. 1997 and PLEIJEL & DANIELSSON 1997). Although many European species had been screened for their ozone sensitivity in terms of visible injury in short-term fumigation experiments, these results cannot simply be transferred to the field situation. Generally, the visual assessment of vegetation damage by air pollutants is an indication of acute phytotoxicity. In contrast, the chronic, invisible effects leading to growth reductions and a loss of competitive ability are considered to be of higher ecological significance.

Chronic effects are studied in long-term fumigation experiments, e.g. in open-top chambers (OTC) using near ambient ozone concentrations. There are currently several research groups in Europe investigating ozone impacts on the natural vegetation. Dose-response relationships for native plant species are generally difficult to establish because differences in sensitivity are strongly influenced by environmental modifiers like water status and atmospheric conductivity which vary within and between different vegetation types.

The aim of this paper is to summarise results of studies on the phytotoxicity of ozone and to discuss ecological approaches which might prove useful in interpreting the impact of ozone on natural vegetation.

2 Results of studies on the impact of ozone on native plant species

A **literature survey** revealed that in 1500 articles about 400 plant species have been studied to date for their ozone sensitivity. Of these species 16% are crops which are dealt with in the largest proportion of ozone literature. Plants from natural vegetations have only been studied in few of the articles, of which 53% are herbs and shrubs, 27% belong to the phanerophytes, 14% are grasses and only 5% are bryophytes and lichens. Of the studied species 12% belong to the family of Poaceae, 10% are Fabaceae, 8% Asteraceae, 6% Pinaceae and 5% Rosaceae.

Fourty-six percent (186) of the 400 considered plant species are native to the European flora; of these 44% are hemicryptophytes, 15% therophytes, 11% phanerophytes and 3% geophytes. Most of them belong to grassland ecosystems while experiments using species from extreme habitats are not present in the literature. These findings indicate that, based on plant systematics, life forms and autecology, plants used in ozone research have not comprised a representative sample.

Field studies on the effects of ozone on vegetation have often been focused on visual assessment of leaf injury, but a causal relationship between leaf damage and a specific environmental pollutant remains a generally difficult and strongly biased method. Field observations in natural ecosystems were conducted in the U.S. National Parks where several ozone-sensitive shrub and tree species were observed (SIMINI & al. 1992, HILDEBRAND 1996). In Europe, the active bioindicators *Nicotiana tabacum* cv. Bel W3, species of *Populus*, cultivars of *Phaseolus vulgaris* and clones of *Trifolium repens* are currently being used in routine field studies to evaluate the impact of ozone. Recently, other plant species (*Cirsium arvense* and *Malva sylvestris*) have also been utilised in a network which was established to assess the impact of ozone across Europe (ICP-CROPS 1997).

In controlled **fumigation studies** those ozone concentrations having a specific phytotoxic effect can be determined. In short-term experiments, greenhouse or field grown plants were exposed to acute ozone concentrations in order to identify the occurrence of leaf injury. Ozone-screening experiments in closed chambers using unrealistically high concentrations and microclimatic conditions have been conducted by CORNELIUS & al. (1985) and ASHMORE & al. (1987). A field fumigation system was used for the same purpose by TRESHOW & al. (1973). More than 250 European plant species have been screened for acute ozone effects in these studies. Fabaceae were most sensitive whereas Gramineae and Compositae did not develop excessive leaf injury.

Long-term fumigation experiments generally reveal ecologically more meaningful results because they include reaction parameters other than visible injury. Growth rates, root:shoot ratios, carbon allocation, seed output and germination rates might assist in making preliminary predictions of vegetation changes by long-term exposure to ozone.

Table 1 summarises results of long-term fumigation experiments conducted with a number of European species considering visible injury and, more important, growth parameters. Additional information on root:shoot ratios seed output and germination can be found in REILING & DAVISON (1992a) and BERGMANN & al. (1997). Of the 96 species listed in Table 1, 40 reacted with leaf injury, while 42 species showed a more than 10% reduction of leaf biomass and 9 species, mainly grasses, developed a greater leaf biomass (>10%) under elevated ozone. A growth stimulation by ozone must be interpreted carefully as in most ozone studies, control plants are exposed to charcoal-filtered air, although a low ozone background concentration can be regarded as natural.

3 Ecological approaches to the interpretation of fumigation studies

The *ranking* of plant sensitivities to ozone using available data is difficult because different concentrations and conditions have been applied in the various studies. Because the relative ozone sensitivity of the large number of European species cannot be assessed in standardised experiments, it might be jusitified to apply functional approaches to explain the ozone sensitivity of **ecological groups**.

Relating ecophysiological characteristics to ozone sensitivities of different species, HARKOV & BRENNAN (1982) concluded that herbaceous species are generally more sensitive than woody plants. Different growth rates and ecological strategies to adapt to changing environmental factors can lead to different plant reactions to ozone (SELLDEN & PLEIJEL 1995). In Figure 1a the results of short-term screening experiments for visible injury are transferred to the **CSR-concept** of GRIME & al. (1988) along with a short description of the primary ecological strategies. Most of the 35 (out of ca. 200 tested) sensitive species follow mixed strategies with a slight shift to the competitor and ruderal components. There are only very few ozone sensitive species classified as stress-tolerators. This might indicate that slow-growing species from unfavourable (e.g. nutrient-poor) habitats are less endangered by ozone than fast-growing species thriving in productive ecosystems (e.g. grasslands) where the competition for resources is pronounced. This would be clearer if results from long-term fumigation studies were taken into account. The 33 species included in Figure 1b have shown an ozone-dependent reduction in leaf biomass by more than 10% in at least one publication (see Table 1). Again, most of the sensitive species follow the intermediate strategy, but also include 4 species which are described as stress tolerators. It is therefore believed that the concept of primary ecological strategies cannot fully explain differences in ozone sensitivities unless ozone-tolerant species are included as well. Other ecologically significant parameters like seed output and root:shoot ratios would also have to be examined as they too may determine a plant's long-term survival.

In his *unifying theory* REICH (1987) related the strong dependence of phytotoxic ozone effects to the plant's gas exchange properties. Gas exchange and transpiration are inherently coupled to the water status of a plant and it might be informative to relate ozone-sensitivities of plants to their **ecological water amplitude**. This approach is being applied in Figure 2 for the results of BERGMANN & al. (1996a,b, 1997). Visible injury (ranking) tends to be related to the ELLENBERG-moisture (F)-values. The slightly increased sensitivity in species from moist habitats supports the hypothesis that hygro- and mesomorphous species from moist sites may be more affected by ozone than the scleromorphous species adapted to dry sites. A similar relationship could not be established from results of short-term fumigation studies. Also, the proportional leaf biomass changes during long-term ozone fumigations showed no clear relationship to the ecological water amplitude of plants. Gas exchange rates would give a better explanation for ozone sensitivities than the F-values, which are valid under environmental but not experimental conditions.

Table 1

Summary of results from long-term fumigation experiments using species from the European flora according to the reaction parameters visible injury and growth parameters.

x	incidence of foliar injury	+	growth stimulation of leaf biomass by more than 10%
±	difference in leaf biomass <10%	-	reduction of leaf biomass by more than 10%

reaction parameter: / tested plant species:	visible injury	ref.	leaf biomass (deviation from control)	ref.
Achillea millefolium			-	3
Agrostis capillaris			±	6
Agrostemma githago			±	2
Agrostis stolonifera			±,-	2,6
Alopecurus pratensis			±,±	2,6
Anthoxanthum odoratum			±	2
Anthyllis vulneraria			±	2
Arrhenatherum elatius	x	3	±,-,-	3,5,6
Betula pubescens	x	4	±	4
Brachypodium pinnatum			±	6
Briza media			±,-	2,6
Bromus arvensis			±	2
Bromus erectus			+	3
Campanula rotundifolia			-	6
Capsella bursa-pastoris			±	1
Carum carvi	x	3	±	3
Centaurea cyanus			±	2
Centaurea jacea	x	3	-	3
Cerastium fontanum			-,±	5,6
Crepis biennis			±	3
Chamomilla recutita	x	1	-	1
Chenopodium album	x	5	+,±	1,2
Chrysanth. leucanthemum	x	3,4	-	3
Chrysanthemum segetum			±	2
Cirsium arvense	x	1	±	1
Cynosorus cristatus			±	6
Dactylis aschersonii	x	2	±	2
Dactylis glomerata	x	2	±,-,-,-	2,3,4,6
Danthonia decumbens			+	6
Daucus carota	x	1	±	1
Deschampsia flexuosa			+	6
Dianthus deltoides			±	2
Epilobium hirsutum	x	5	±	5
Euphorbia peplus			-	1
Festuca ovina			+,-	2,6
Festuca pratensis			±,-	2,4
Festuca rubra			-,-,±	3,4,6
Galinsoga parviflora	x	1	-	1
Galium saxatile			-	6
Hieracium pilosella			±,-	2,6
Holcus lanatus			-	6
Hordeum murinum	x	5	±	5
Hypochoeris radicata			±	2
Hypericum perforatum	x	4	±	4

References:	chamber:	concentration:	control:
1) BERGMANN & al. 1996/97	OTC	0.6*AA+30 ppb	30 ppb
2) PLEIJEL & al. 1997	OTC	1.5*AA	CF
3) GRUB & al. 1997	OTC	1.5*AA	CF
4) MORTENSEN & al. 1992	closed	15-80 ppb	CF
5) REILING & al. 1992a	closed	70 ppb	CF
6) ASHMORE & al. 1996	closed	80 ppb	CF

reaction parameter: / tested plant species:	visible injury	ref.	leaf biomass (deviation from control)	ref.
Hypericum pulchrum			-	6
Knautia arvensis	x	3	-	3
Koeleria macrantha			+	6
Leontodon hispidus			±,-	2,6
Lolium perenne			+,±	3,6
Lotus corniculatus	x	3	+,-	3,6
Lychnis flos-cuculi			+	3
Malva sylvestris	x	1	-	1
Malva moschata			±	1
Matricaria discoidea	x	1	-	1
Matricaria perforata			+	1
Onobrychis sativa	x	3	-	3
Papaver argemone			±	1
Papaver dubium			-	1
Papaver rhoeas			±,±	1,2
Phalaris arundinacea			±	2
Phleum alpinum	x	2	±	2
Phleum pratense	x	4	-	4
Plantago lanceolata	x	3,4	±,±,-,-,-	2-6
Plantago major	x	1	+,-	1,5
Plantago media			±	2
Poa annua			±,±	2,5
Poa palustris			±	2
Poa pratensis			-,-,±	3,4,6
Polygonum viviparum			±	4
Potentilla erecta	x	4	±	4
Rumex acetosa	x	1,5	-,±,±	1,2,6
Rumex acetosella	x	5	-	5
Rumex crispus	x	1	±	1
Rumex obtusifolius	x	1	+,+,±	1,3,5
Salvia pratensis			±	3
Sanguisorba minor			±	6
Senecio vulgaris			-,±	1,2
Silene acaulis			-	4
Silene dioica			+	3
Silene vulgaris			±	2
Sinapis arvensis	x	1	±	1
Solanum nigrum			-	1
Solidago virgaurea	x	4	±	4
Sonchus asper	x	1	-	1
Stellaria media			±	1
Tanacetum vulgare	x	1	±	1
Tragopogon orientalis	x	3	-	3
Taraxacum officinalis	x	3	-	3
Teucrium scorondonia			-	5
Trifolium arvense	x	1	-	1
Trifolium dubium	x	6	-	6
Trifolium pratense	x	3,6	-,-	3,6
Trifolium repens	x	3,6	-,-	3,6
Trisetum flavescens			±	3
Urtica dioica			-,-	1,5
Vicia sativa	x	6	-	6

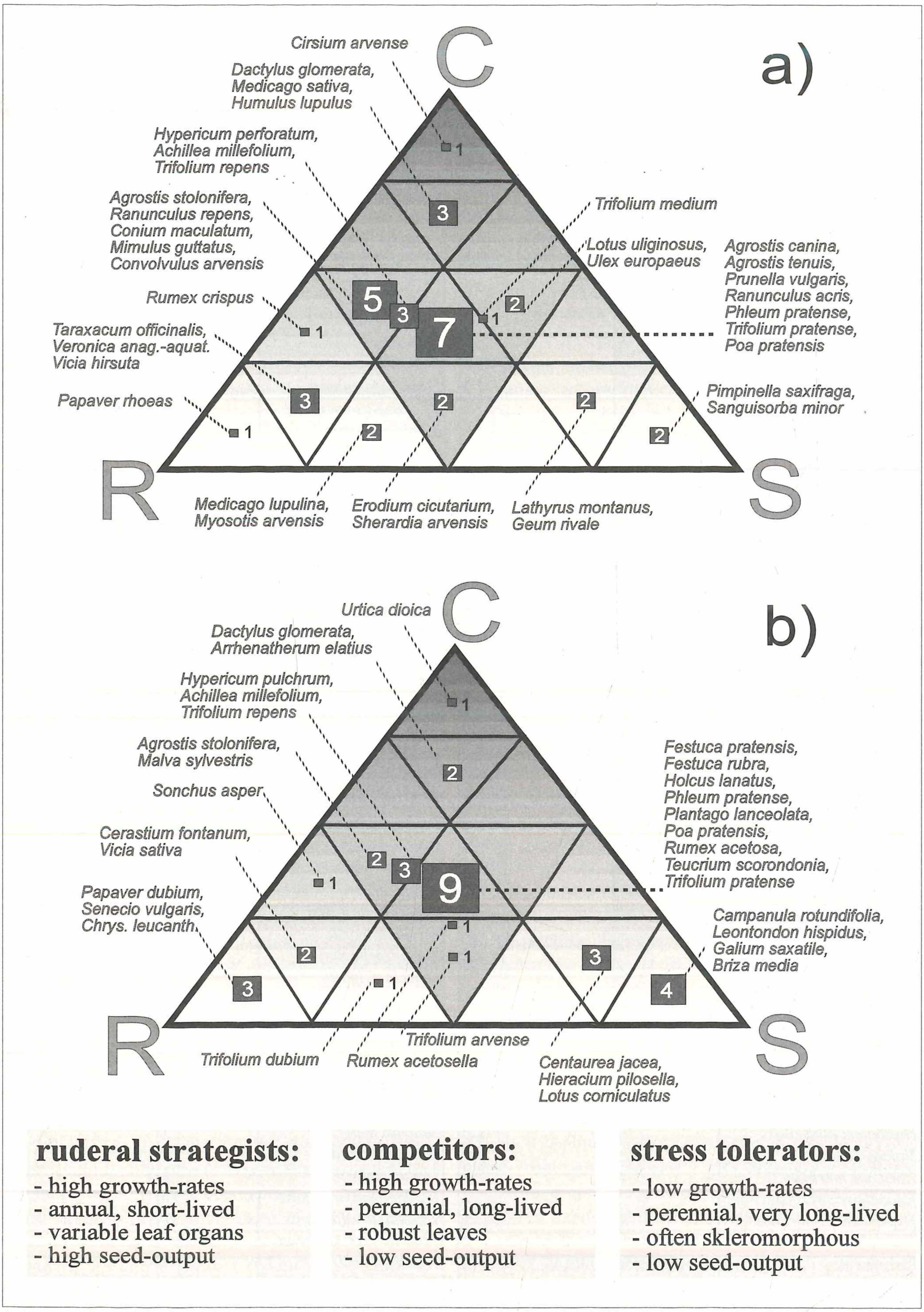

Fig. 1

Classification of ozone-sensitive plant species after primary ecological strategies (GRIME & al. 1988) for the reaction parameters a) visible injury and b) leaf biomass reductions >10%. Data for visible injury based on TRESHOW & al. (1973), CORNELIUS & al. (1985) and ASHMORE & al. (1987). Data for leaf biomass reductions based on Table 1.

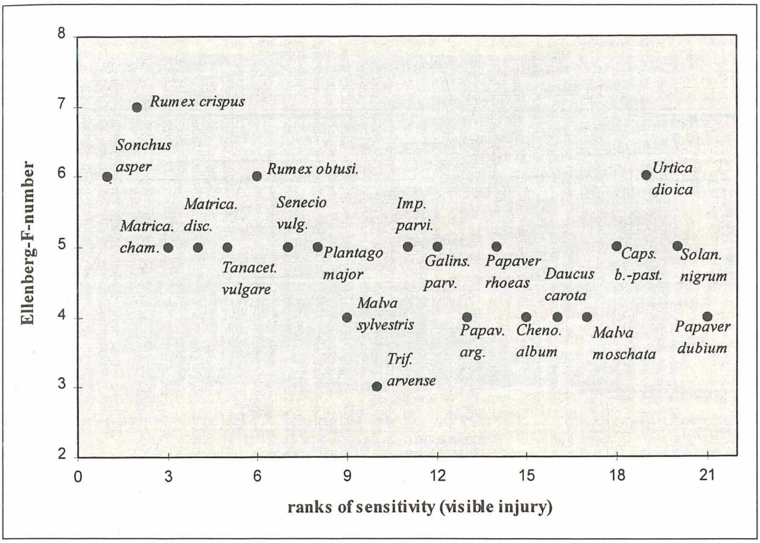

Fig. 2
Relationship between ozone sensitivity and ELLENBERG-moisture numbers. The results of BERGMANN & al. (1997) show a tendency that moisture preferent species seem to develop greater leaf injury.

4 The importance of modifying environmental factors: ozone exposure regimes, climatic factors and water status

Results from fumigation experiments cannot simply be transferred to the field because plants tend to be more sensitive to ozone in chambers than outside due to an optimal water supply, high humidity and ventilation rates (= high stomatal conductivity). Having described a few of the ecological mechanisms by which some plant species tend to be more ozone sensitive than others the above mentioned modifying factors must be taken into consideration as well.

Ozone concentrations show a strong temporal (diurnal, seasonal and inter-annual), spatial and altitudinal variation. Up to now insufficient information on the phytotoxic importance of different **ozone exposure** regimes is available, e.g. short-term peak concentrations or enhanced seasonal means. LEFOHN & MANNING (1995) suggest »biologically based exposure indicators« to better quantify the possible risk associated with ozone affecting the vegetation in U.S. wilderness areas. Results from fumigation studies of BERGMANN & al. (1997) indicate that plants are better able to compensate for negative effects under fluctuating ozone exposures compared to constantly high concentrations. Temporal differences in exposure regimes are super-imposed by a strong geographical variation in ozone concentrations which might lead to a regional difference in ozone sensitivities between plant populations, too (see chapt. 5).

The steep diurnal ozone profiles at urban locations are not parallelled by the flat profiles from rural locations where high ozone concentrations at night can occur due to the lack of ozone scavengers. The highest seasonal means are identified in high elevation regions.

Apart from the ozone exposure regimes, the **climate parameters** humidity and temperature must be regarded because they influence the ozone dose passing through the stomata of a plant leaf. At high temperatures and low air humidities (high VPD, vapour pressure deficit) plants will partially close their stomata to avoid water loss. By this mechanism the uptake of ozone is reduced as well. Figure 3 shows the relationship between ozone levels and VPD at four locations. At the location Mannheim high ozone concentrations are always coupled with a high evaporative stress whereas at the other locations high ozone concentrations may well coincide with low VPD (<1kPa). Thus, one could hypothesize that the (zonal) vegetation of a warm/dry climate region (e.g. Mannheim, SW-Germany) may be potentially less responsive to ozone than the vegetation of a cool/moist region (e.g. Emden, NW-Germany) in spite of the higher ozone levels in the first region. Additionally, higher wind speeds in an oceanic region might favour uptake of ozone into the leaf canopy by reducing the atmospheric/canopy resistances. Another related hypothesis is that the azonal vegetation of wetlands might be generally more sensitive to ozone than the vegetation of dry habitats because meso- and hygrophytic plants from moist environments generally maintain high transpiration rates, thus possibly taking up more ozone than the xerophytic vegetation from dry habitats. The notion of differences in plant exposure to ozone in different climatic regions should also be transferable to the temporal level. Indeed, SHOWMAN & al. (1991) observed less leaf damage on plants in dry summers with high ozone concentrations compared to moist summers with lower ozone concentrations.

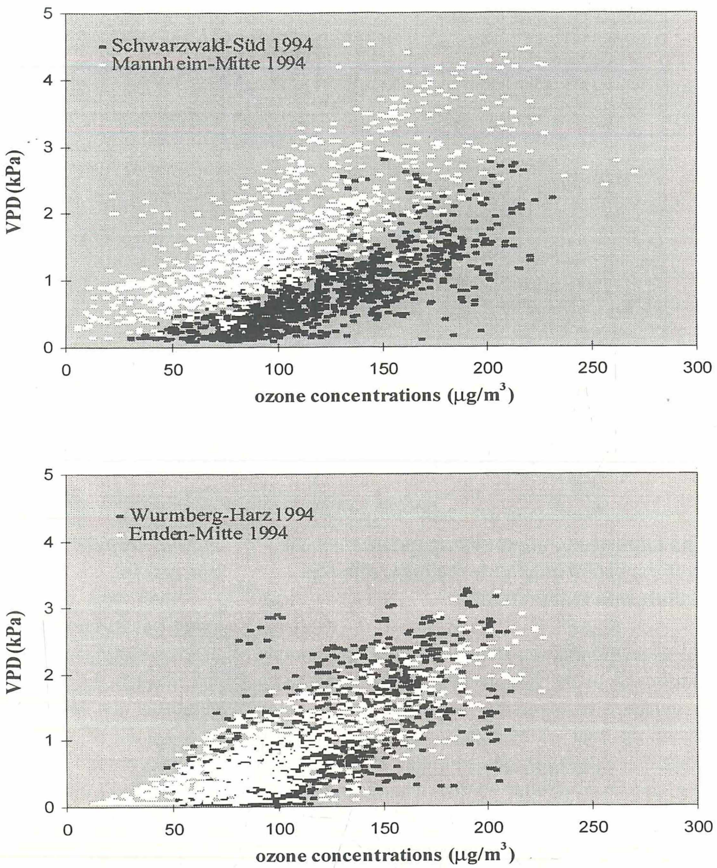

Fig. 3
Relationship between daytime (9–17:00 CET) ozone concentrations and vapour pressure deficit (VPD) at an urban lowland and a rural mountain site of southwest (a) and northwest Germany (b). Regional differences in ozone concentrations and climate result in a strongly varying exposure regime where plants growing under high evaporative stress might be less susceptible to the uptake of photooxidants. (Data from LfU Baden-Württemberg and LÜN Niedersachsen as 0.5h-values from May to August 1994).

Interactions between soil **water status** and ozone damage have often been found in chamber experiments using crops as test plants. The general idea is that plants growing under a slight drought stress will take up less ozone. For plants in natural communities this has not been systematically proven but a model on the influence of the soil moisture deficit on the sensitivity of plants to ozone is being prepared (ICP-CROPS 1997).

5 Conclusions and prospects

Although several European plant species have been included in fumigation studies, general conclusions on the impact of ozone on the natural vegetation can not be drawn. Results from such fumigation experiments can not yet be transferred to the ecosystem level so that the classification of the sensitivity of species belonging to ecological groups may prove meaningful. Generally, species with high growth rates are more likely to be affected by ozone than slow-growing scleromorphous species. Apart from the genetically fixed sensitivity of a plant species, the environmental conditions at the site where a plant becomes established in a community must be regarded more closely. In different regions with different exposure regimes and climatic and edaphic conditions plants might respond differently to ozone, which results in regional differences in sensitivities of plant populations. Examples for this have been shown for *Populus* (BERRANG & al. 1989) and *Plantago major* (REILING & al. 1992b and LYONS & al. 1997). Little information exists so far on the impact of ozone on plant communities in natural ecosytems which requires long-term field-fumigation systems and the study of competitive balances within the natural community.

Acknowledgements

The authors would like to thank Drs. A.E.G. Tonneijck and Dr. Th.A. Dueck (both AB-DLO Wageningen, The Netherlands) for reading the manuscript and valuable comments.

References

ASHMORE, M.R., DALPRA, C., TICKLE, A.K., 1987: Effects of ozone and calcium nutrition on native plant species. In: Air Pollution and ecosystems, edited by MATHY, P. 1987, p. 647–652.

ASHMORE, M.R., PRANGE, R.K., COUSINS, D.A., AINSWORTH, N., 1996: Effects of ozone on native grass and forb species: a comparison of responses of individual plants and artificial communities. In: Critical levels for ozone in Europe: testing and finalising the concepts, edited by KÄRENLAMPI, L. and SKÄRBY, L., Kuopio, p. 193–197.

BERGMANN, E., BENDER, J., WEIGEL, H.J., 1996a: Ozone and the natural vegetation: Native species sensitivity to different ozone exposure regimes. In: Critical levels for ozone in Europe: testing and finalising the concepts, edited by KÄRENLAMPI, L. and SKÄRBY, L., Kuopio, p. 205–210.

BERGMANN, E., BENDER,J., WEIGEL, H.J. 1996b: Effects of chronic ozone stress on growth and reproduction capacity of native herbaceous plants. In: KNOPFLACHER, M., & al. (eds.): Exceedance of critical loads and levels – spatial and temporsal interpretation of elements in landscape sensitivity to atmospheric pollutants. Congress Report 15. Vienna.

BERGMANN, E., BENDER, J., WEIGEL, H.J. 1997: Reproductive responses and sensitivities of native wild plant species to ozone stress. Report No. 108 03 047, German Umweltbundesamt, Berlin.

BERRANG, P., KARNOSKY, D.F., BENNETT, J.P., 1989: Natural selection for ozone tolerance in Populus tremuloides: field verification. Can. J. For. Res. 19: 519–522.

CORNELIUS, R., FAENSEN-THIEBES, A., MEYER, G., 1985: Immissions- und Wirkungserfassung in einem Berliner Bioindikationsprogramm. Einsatz von *Nicotiana tabacum* L. Bel W3. Staub Reinhaltung Luft 45(1): 59–61.

ELLENBERG, H., WEBER,E.H., DÜLL, R., WIRTH, V., WERNER, W., PAULISSEN, D. (1991): Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18: 248 S.

GRUB, A., BUNGENER, P., CONTAT, F., NUSSBAUM, S., ENDTNER, V., FUHRER, J., 1997: Pollution atmospherique et biodiversite floristique. Revue Suisse Agric. 29(4): 165–171.

GRIME, J.P., HODGSON, J.G., HUNT, R., 1988: Comparative plant ecology: a functional approach to common British species, London: Allen & Unwin, 742 pp.

HARKOV, R.S., BRENNAN, E.G.,1982: An ecophysiological analysis of the response of woody and herbaceous plants to oxidant injury. Journal of Environmental Management 15: 251–261.

HILDEBRAND, E., SKELLY, J.M., AND FREDERICKSEN, T.S., 1996: Foliar response of ozone sensitive hardwood tree species from 1991 to 1993 in the Shenandoah National Park, Virginia. Can. J. Forest Res. 26(4): 658–669.

ICP-CROPS, 1997: Progress report for the ICP-Crops (International Cooperative Programme on effects of air pollution and other stresses on crops and non-wood plants). ICP-Crops Coordination Centre. The Nottingham Trent University.

LEFOHN, A.S. & MANNING, W.J., (1995): Ozone exposures near Class I Wilderness areas in New Hampshire and Vermont. Atmospheric Environment 29: 601–606.

LYONS, T.M., BARNES,J.D., DAVISON, A.W., 1997: Relationships between ozone resistance and climate in European populations of *Plantago major*. New Phytol. 136: 503–510.

MORTENSEN, L.M., NILSEN, J., 1992: Effects of ozone and temperature on growth of several wild plant species. Norw. J. Agric. Sciences 6: 195–204.

PLEIJEL, H., DANIELSSON, H., 1997: Growth of 27 herbs and grasses in relation to ozone exposure and plant strategy. New Phytologist 135: 361–367, 1997.

REICH, P.B., 1987: Quantifying plant response to ozone: a unifying theory. Tree Physiology 3: 63–91.

REILING, K., DAVISON, A.W., 1992a: The response of native herbaceous species to ozone: growth and fluorescence screening. New Phytologist 120(1): 29–37.

REILING, K., DAVISON, A.W., 1992b: Spatial variation in ozone resistance of British populations of *Plantago major* L. New Phytologist 122(5): 699–708.

SHOWMAN, R.E., 1991: A comparison of ozone injury to vegetation during moist and drought years. Journal of the Air & Waste Management Association 41(1): 63–65, 1991.

SELLDEN, G., PLEIJEL, H., 1995: Photochemical oxidant effects on vegetation- response in relation to plant strategy. Water, Air and Soil Pollution 85(2): 111–122.

SIMINI, M., SKELLY, J.M., DAVIS, D.D., SAVAGE, J.E., COMRIE, A.C., 1992: Sensitivity of 4 hardwood species to ambient ozone in North Central Pennsylvania. Can.J.Forest Res. 22: 1789–1799.

TRESHOW, M., STEWART, D., 1973: Ozone sensitivity of plants in natural communities. Biological Conservation 5(3): 209–214.

Adressen

Dr. Jürgen Franzaring
Research Institute for Agrobiology
and Soil Fertility (AB-DLO)
P.O. Box 14
NL-6700 AA Wageningen

Dipl. Biol. Elke Bergmann
Dr. Jürgen Bender
Dir. u. Prof. Dr. Hans-Joachim Weigel
FAL-Institut für Agrarökologie
Bundesallee 50
38116 Braunschweig-Völkenrode