

Is the sensitivity of plants to tropospheric ozone related to their ecology?

Jürgen Franzaring

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Synopsis

An analysis of the results from ozone fumigation experiments with 166 European plant species was conducted to determine if a plant's sensitivity to ozone was associated with innate traits and/or its ecology. The studied species were reasonably representative of the Central European flora. Fabaceae were mainly affected by foliar injury, while growth reductions due to ozone frequently occurred in Asteraceae. In contrast, the growth of one third of the Sweet Grasses (Poaceae) was stimulated by ozone. Ozone responses also proved to be somewhat associated with ecological plant strategies. Species with a strong ruderal or competitive component were more likely to be negatively affected by ozone than species classified as stress tolerators. Ellenberg ecological indicator values describing habitat preferences of species were not well related to growth responses of plants to ozone. However, species with foliar injury due to ozone were often associated with base and nutrient rich habitats. Addressing inherent plant traits partly confirmed the importance of relative growth rate (RGR) and specific leaf area (SLA) in determining a plant's response to ozone. Slow growing plant species tend to be affected by ozone to a lesser extent than fast-growing species. While these relationships may be generally valid under standardised experimental conditions, ecological amplitudes of species in the field and of course above- and belowground competition are believed to disturb these relationships. Furthermore, plant responses in the field are determined by the canopy structure which governs the flux of air pollutants. Identifying ozone sensitive plant communities will thus afford further fumigation experiments in the resident canopy on site. The next generation of experiments should also address the interactions between the phytotoxic pollutant and the global fertilisation by CO₂ enrichment and nitrogen deposition.

1. Introduction

A relatively large number of plant species native to Europe have been screened in short-term or long-term experiments for their sensitivity to ozone. Visible injury and growth responses are the most commonly used parameters to describe interspecific variation in ozone sensitivity, while information on resource allocation, seed output, reproductive success, phenology and carry-over effects are widely lacking. However, these are all ecologically important determinants of plant survival in a changing world.

As it is unrealistic to test all plant species and their response parameters in experiments simulating various aspects of global change, the relevance of plant functional types has been frequently used to predict the outcome of ecosystem functioning, including changes in biodiversity (SMITH et al. 1997). Several attempts have already been made to determine which characteristics influence the relative sensitivity of plants to air pollution. In an ecophysiological analysis of plant responses to oxidants, HARKOV & BRENNAN (1982) addressed gas exchange and growth-rates as the primary determinants of air pollutant uptake.

They also noted the importance of genetic and ecological characteristics of plants necessary to survive in the succession of plant communities under oxidant stress. The authors concluded that fast growing species may be generally more susceptible to photo-oxidants than slow growing species which was elaborately postulated in the "unifying theory" of REICH (1987). In an attempt to differentiate plant responses to ozone with regard to "dose-regulating" and "response-regulating" factors, SELLDEN & PLEIJEL (1995) addressed the importance of plant strategies, which was the first ecological approach in addressing ozone effects on plants including the semi-natural vegetation. DAVISON & BARNES (1998) presented a first review on effects of ozone on wild plants collating some ecologically relevant information on the species' relative sensitivities with regard to growth responses and effects of ozone on allocation patterns and reproduction. The authors point out the problems in deriving relative rankings of species along ozone sensitivities and underline that great care must be taken when comparing results from different studies and growth stages.

A recent synopsis of experimental results on ozone effects on wild species taking into account most of these factors has been presented by HAYES et al. (2007). Their meta-analysis identified 83 species from existing publications suitable for inclusion in a database of sensitivity of species to ozone (UN ECE ICP Vegetation OZOVEG database). An index of relative sensitivity to ozone was calculated for each species based on changes in biomass in order to test for species traits associated with the ozone sensitivity. Some relationships were found; especially plants with the therophyte life form were identified as being sensitive to ozone. On the other hand, ozone sensitivities were uncorrelated to stomatal density, which determines the uptake of gaseous pollutants. The authors conclude to use such meta-analytical approaches to predict the sensitivity of untested species and plant communities to ozone. However, BASSIN et al. (2007) point out that risk assessments, based on results from individuals or immature mixtures exposed in chambers, are only applicable to intensively managed, productive ecosystems, and that the risk of ozone damage for most vegetations with lower productivity tends to be less than previously expected. Future approaches for identifying stocks at risk or EUNIS vegetation categories like the one presented by MILLS et al. (2007) will thus have to be supported by further field experiments in the undisturbed and natural canopies.

In this contribution, we will use information from ozone fumigation studies on over 160 species from the native European flora and address two questions: a) do the plant species that have been studied represent the European flora, and more important b) are plant taxonomy, functional plant types, ecological behaviour and plant traits of value in explaining differences in ozone sensitivity between European herbaceous plant species? A valuable output of this approach could be to identify the most sensitive groups of species and taxa on which future research should concentrate.

2. Classification and analysis of data

Information on the sensitivity to ozone (foliar injury and growth responses) was extracted from the literature and incorporated in a database along with the type of fumigation used, the duration of experiments and the exposure regime. Data for growth responses of herbaceous species due to ozone was normalised in a way enabling the comparison of results from the different studies: The relative shoot biomass response to ozone was calculated as shoot or leaf biomass in the highest ozone treatment relative to that in charcoal-filtered air (CF), so that percentage changes in biomass (in analogy to ASHMORE et al. 1996 and HAYES et al. 2007) could be calculated. Data for these comparisons came exclusively from studies using pot grown seedlings and exposing them to more or less realistic exposure regimes. To somewhat make good for differences in experimental setup of the various fumigation experiments, only growth responses of larger than 5 % were taken into account in our comparisons.

Data on relative growth rate (RGR) and specific leaf area (SLA) were taken from GRIME et al. (1975), POORTER & REMKES (1990), HUNT & CORNELISSEN (1997) and VAN DER WERF et al. (1998). Information on primary ecological strategies (C=competitors, S=stress tolerators and R=ruderals) was extracted from FRANK & KLOTZ (1990), as their study comprises a list of more than 2200 species native to Europe. In contrast to GRIME et al. (2007), who developed the CSR-concept for only 1000 species differentiating between 19 ecological types, FRANK & KLOTZ (1990) used only seven ecological types, excluding the mixed strategies. Ecological indicator values for moisture preference (F-values) and for basophily (R-values) of plant species were taken from ELLENBERG et al. (2001). These data are ordinally-scaled, so that a Spearman rank correlation analysis between indicator values and relative growth response to ozone had to be performed. Data presented in tables, diagrams and the text are expressed as proportions along categories of life forms, plant families and ecological strategies. The sample sizes of total species numbers for which these comparisons were possible are indicated as well. In order to describe the representativeness of the studied wild species with regard to the Central European flora, information on the averages of ecological traits of the different groups was included and evaluated as well. These groups were the total Central European Flora, the studied wild plant species, the group of species with foliar injury and the group with growth responses of larger than 5 %.

3. Results

A list of 166 herbaceous plant species and grasses native to Europe was generated to which information on their life form, taxonomy (for all species) and ecological strategies (for 158 species) was added. In addition, values on relative growth responses due to ozone were available for 110 species, on ozone-related foliar injury for 95 of the species, on relative growth rates (RGR) for 104 species and on specific leaf area (SLA) for 72 of the 166 species. Eco-

logical indicator values for moisture preference (F-value), basophily (R-value) and nutrient preference (N-value) were available for 147, 106 and 138 species, respectively.

Life forms

Table 1 indicates that the species studied in ozone fumigation experiments appear to represent the Central European flora quite well. Only the phanerophytes (woody species) are over-represented, which can be explained by the strong interest in the causes of forest-dieback in the 1980 and early 1990's. On the contrary, geophytes (perennial bulb plants) have hardly been included in ozone studies to date although they represent 12 % of the European plant species. Lower plants (algae, lichens and mosses) have not at all been addressed in ozone fumigation experiments.

Table 1: Central European plant species mentioned in the ozone literature classified according to life forms and taxonomy (plant families). N = number of species.

Life-forms (all plant species)	Taxonomy (herbs and grasses only)				
	In ozone-literature N=169	In Central Europe ¹ N=2725	Families	In ozone-literature N=166	In Central Europe ² N=2209
Hemicryptophytes	44 %	50 %	Poaceae	27 %	8 %
Therophytes	15 %	17 %	Asteraceae	18 %	11 %
Phanerophytes	11 %	3 %	Fabaceae	11 %	5 %
Geophytes	3 %	12 %	Rosaceae	3 %	5 %

¹ after ELLENBERG (1988) ² after FRANK & KLOTZ (1990)

Because of the poor representation of some life-forms in the ozone literature, comparisons of ozone sensitivity between life-form classes were thought to be inconclusive. The question whether herbaceous species are generally more sensitive to ozone than are woody species therefore still remains unanswered. Potential differences in sensitivity between annuals (therophytes) and perennials (hemicryptophytes, geophytes) will be addressed in the ecology section.

Taxonomy

The herbaceous species and grasses most frequently studied in the ozone literature belong to the Poaceae, Asteraceae and Fabaceae and together account for 56 % of the studied species. All three families appear to be over-represented compared to their relative proportion of the European flora (table 1). The largest over-representation was observed in the Poaceae (Sweet Grasses), indicating the strong interest of ozone researchers in grasslands.

The taxonomy of the listed 166 species serves to explain in part the ozone sensitivity of European herbaceous species and grasses. Occurrence of visible

foliar injury was observed in 40 % of the Poaceae and 53 % of the Asteraceae in the list, but was most frequent (89 %) in the Fabaceae (Fig. 1). The leguminos (e. g. clover), certainly comprise an ozone-sensitive family, which was also noted in the extensive short-term screening experiments of ASHMORE et al. (1988) and the Open Top Chamber based study of BERMEJO et al. (2003). However, the relative insensitivity of Asteraceae observed by ASHMORE et al. (1999) is in contrast to our summary, which indicated visible injury in more than half of the species of this family used in fumigation experiments.

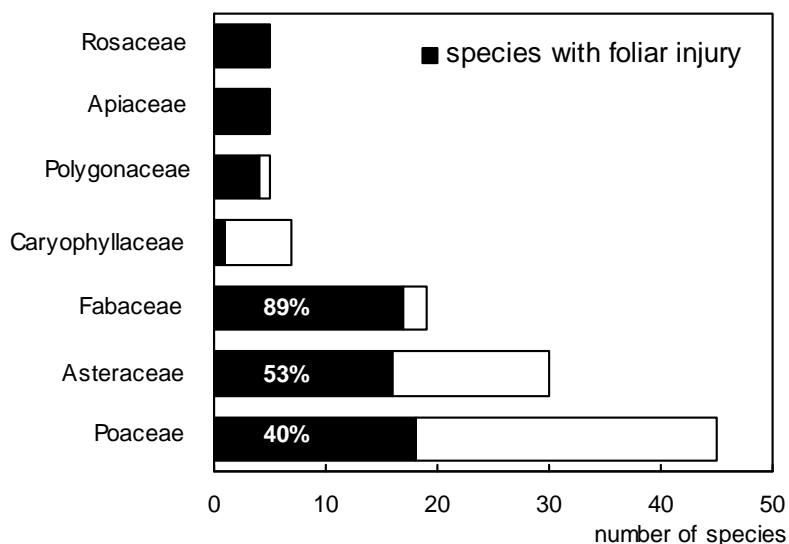


Figure 1: The occurrence of foliar injury due to ozone in seven plant families. White bars represent the number of species in a plant family, while black bars represent the number of species showing foliar injury due to ozone.

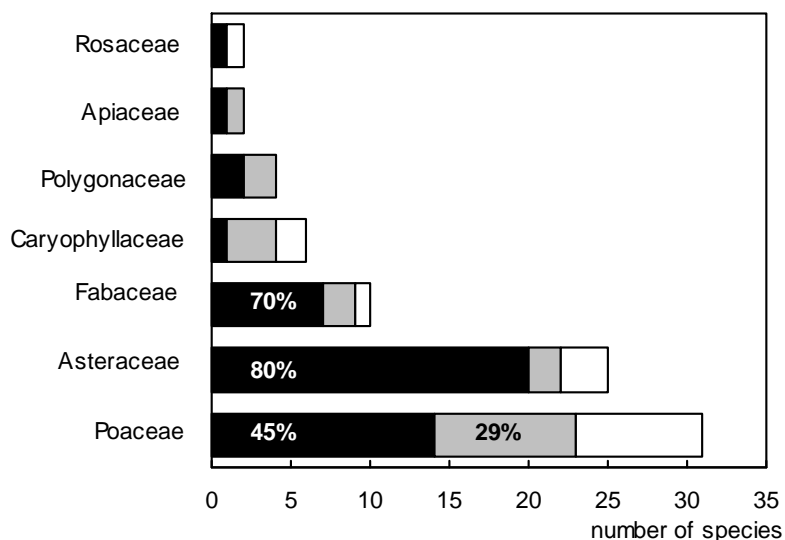


Figure 2: The occurrence of growth responses (>5 %) to ozone in seven plant families based on 110 species. White bars indicate the number of species in each family without adverse effects; black bars indicate the number of species reduced in growth while grey bars represent the number of species stimulated in growth due to ozone.

Looking at the taxonomy of the 110 species for which information was available on growth responses due to ozone, the Fabaceae also proved to be a

family in which growth reductions due to ozone are widespread (70 %). However, by far the greatest proportion of growth reductions (80 %) was noted in the Asteraceae (Fig. 2). Interestingly, growth stimulations due to ozone were reported in 29 % of the Poaceae (Sweet Grasses). Examples for this are *Danthonia decumbens*, *Deschampsia flexuosa* and *Koeleria macrantha* (ASHMORE et al. 1996), *Molinia caerulea* (FRANZARING et al. 1999) and *Bromus erectus* (GRUB et al. 1997). The actual invasion of competitive grasses into semi-natural vegetations in the past decades has been previously related to increasing nitrogen deposition (BOBBINK et al. 1996). However, the survey of ozone studies indicates that rising concentrations of ozone might already be, or become an additional factor leading to growth stimulations and hence a spread of grasses in semi-natural vegetations in the future.

Ecology

Results on ecological strategies indicate that the CSR distribution of species studied in fumigation experiments differs to some extent from that of the ecological spectrum of the Central European Flora (table 2). Relatively more R- and S-strategists have been used in ozone experiments than C- and CS-strategists. It thus follows that the species used in fumigation studies are not an adequate reflection of the ecological spectrum of the European flora.

Of the species visibly injured by ozone, relatively more species follow the C- and R-strategy than the S-strategy. Compared to the Central European ecological spectrum CSR-, R- and S-strategists are over-represented in the experiments examining growth responses, in contrast to the C- and CS strategists. Throughout the group of species in which growth was studied (i. e. 110 species), growth of CSR- and R-strategists is more likely to be reduced by ozone, while growth stimulations due to ozone are more frequent in S- and CS-strategists. It must be noted, however, that the sample size of species with growth increases (n=24) might not be fully representative of the European flora.

Still, the results suggest a relationship between plant ecological strategy and plant responses to ozone. Species with a strong ruderal or competitive component are more likely to be negatively affected by ozone with respect to growth and foliar injury, while growth increases due to ozone are more likely in stress tolerators.

Another ecological approach was used to identify relationships between ozone sensitivity and Ellenberg ecological indicator values. The use of habitat related information (ELLENBERG et al. 2001) in artificial neural networks (ANNs) by BALL et al. (1999) showed a better performance than the CSR model to explain the ozone sensitivity of native European species. Looking at the ecological behaviour and species amplitudes might help to explain their reaction to environmental stress. A hygromorphous species adapted to a wet habitat presumably takes up large doses of ozone as a result of its high transpiration rates. In theory there should then be a positive relationship between ozone sensitivity and the

F-moisture preference-index. A correlation calculated between these values and the relative ozone response of shoot or leaf biomass of the species, however, yielded no significant correlation.

Table 2: Number of species in lists (for Central Europe and ozone literature) and proportion of species (%) after CSR strategies, classified according to the ozone responses visible injury and growth.

	Species recorded in		Species with	Species studied in growth experiments		
	Central Europe ¹	Ozone literature	Visible injury	All species	Growth reductions >5%	Growth increases >5%
Nr. of species in list	2209	166	95	110	66	24
Total nr.	>2700 ³	>2700	166	166	110	110
Data available for ²	2209	157	91	105	61	24
C	24	18.5	22.0	18.1	14.8	25.0
CSR	27.5	25.5	19.8	31.4	37.7	20.8
CR	11.7	15.9	18.7	13.3	14.8	12.5
CS	18.4	8.9	7.7	6.7	1.6	12.5
R	9.8	19.7	23.1	17.1	24.6	8.3
SR	5.5	1.9	3.3	1.9	1.6	4.2
S	3.1	9.6	5.4	11.4	4.9	16.7

¹ based on FRANK et al. (1990), ² no. of species for which CSR data were available, ³ ELLENBERG et al. (2001)

Comparing the mean moisture preference of species showing foliar injury with species not injured by ozone indicated that species from dry habitats are affected by acute injury more frequently than species from wet habitats (figure 3a). This finding is opposed to expectation, but may be attributed to the high relative humidity and water availability in screening studies, which causes higher gas-exchange/ozone uptake in dryland plants in the experiments compared to the field situation.

ASHMORE et al. (1988) found that adverse effects of ozone increased with increasing calcium nutrition. Relating R-numbers (soil reaction) to the relative ozone response of the biomass of species did not reveal a relationship between ozone sensitivity and basophily of a species, whereas using foliar injury as a response parameter, confirmed the findings of ASHMORE et al. (1988). Foliar injury was more frequently observed in the basophilous species, which is indicated by higher average R-values in this group (figure 3b). At the same time foliar injury was more widespread in species preferring nutrient rich soils, indicated by the slightly higher N-values (figure 3c) of visibly injured species.

While these findings give some general insights in the association of adverse effects due to ozone with ecological groups of plants, it must be noted that the species used in fumigation experiments are not necessarily representative of the European flora. On the average, species from drier, less base-rich and nutrient

richer habitats appeared to be over-represented in ozone fumigation experiments (see broken lines in figure 3a-c).

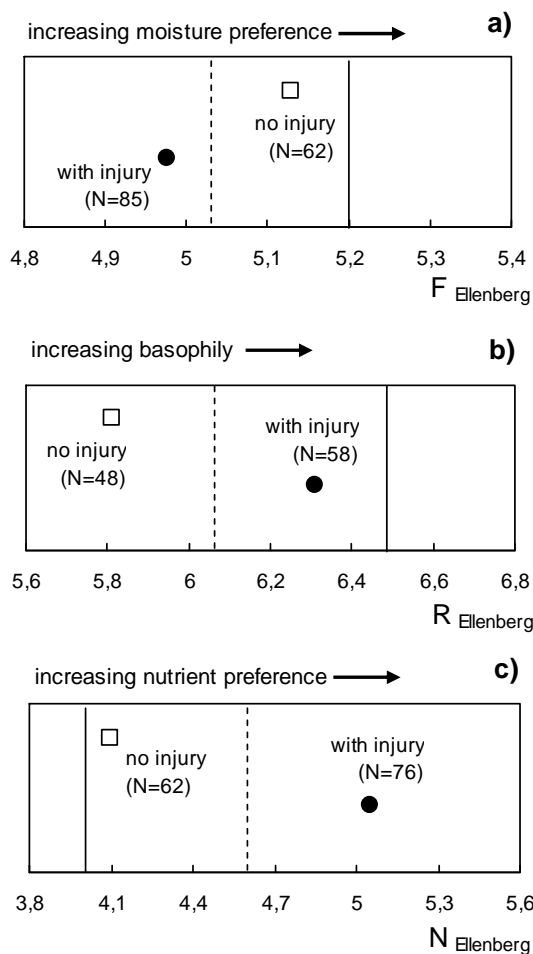


Figure 3: Mean ecological indicator values of plant species with (●) and without foliar injury (□) due to ozone after moisture preference (a), basophily (b) and nitrophily (c). Solid lines indicate means for central European Flora and broken lines those of wild species studied in fumigation experiments.

Plant traits

HARKOV & BRENNAN (1982) and REICH (1987) postulated that fast-growing species are more sensitive to oxidants than slow-growing species because of their higher gas exchange and metabolic rates. Similar relationships had been confirmed in fumigation studies with respect to SO_2 (ASHENDEN et al. 1996) and CO_2 (POORTER 1998). We examined whether this principle was also valid for ozone and assumed that plant traits are more suitable than functional groups in describing the ozone sensitivity of species as they relate to genetically-fixed characteristics. Species with a high mean relative growth rate (RGR) are supposed to take up higher ozone doses than slow-growing species and should therefore show a stronger response to ozone. Species with high mean specific leaf area (SLA), i. e. large, thin leaves, might show greater response to ozone than species with compact leaves, because the higher internal air volume in the

stomatal cavity and mesophyll causes higher concentrations of ozone reaching the apoplast.

Although a clear trend between growth reductions and plant traits does not exist across the various studies, the data of GRUB et al. (1997), FRANZARING (1999) and BUNGENER et al. (1999) support the mentioned theories. Moreover, a weak relationship between SLA and relative growth response to ozone can be observed in the data of ASHMORE et al. (1996), indicating that leaf thickness, i. e. their leaf morphology, might also play some role in determining the relative ozone sensitivity of plants. The same trend could be observed when plant traits were related to acute foliar injury (figure 4).

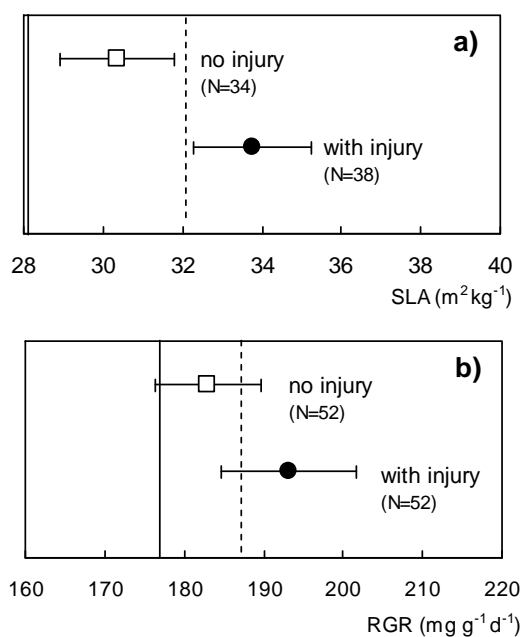


Figure 4: Specific leaf areas (a) and relative growth rates (b) of plant species with (●) and without foliar injury (□) due to ozone. Error bars indicate \pm SE and numbers in brackets represent sample size for which information was available. Solid lines indicate means for the central European Flora and broken lines those of wild species studied in fumigation experiments.

Species developing foliar injury tend to have thinner leaves than those species unaffected by ozone and injured plant species have also a slightly higher RGR on the average. As with respect to other ecological traits, the studied species are not a precise reflection of the central European Flora. Species with higher SLA and RGR are over-represented in the ozone literature.

It must be pointed out that the significance of these preliminary observations needs to be tested for a greater number of species. Furthermore, basic research on the underlying physiological mechanisms will have to be performed and future work will then have to prove whether general relationships between responses to ozone and the plant's ecology can be derived which hold true in the field.

4. Conclusions

The native European plant species studied in ozone fumigation experiments do not fully represent the taxonomic and ecological spectrum of the European flora. There is a large demand for fumigation studies with plant species from "extreme" habitats, including the xerophilous and hydrophilous vegetation. These specially adapted species make a large contribution to the red data books in Europe and are likely to be affected by anthropogenic alterations of their niches, including the adverse effects of air pollution. While the ozone sensitivity of plants seems to be related to their taxonomy, the ecological behaviour of plants or their habitat preference only partly assists in explaining the plants' sensitivity to ozone. Moreover, functional types and plant traits were shown to have some value in understanding differences in ozone sensitivity between plant species, although they cannot be used to fully predict species' reactions to rising levels of ozone or other climate change components. While a plant functional type is a question of definition, plant traits are variable to some extent with respect to various plant populations and varying habitats. Apart from functional and anatomical characteristics, a plant's performance in a stressed environment will also be a function of its ability to activate defence mechanisms on a cellular level. Finally, the long-term survival of plant species or populations will also greatly depend on the genetic potential to adapt to environmental stress. The physiological and ecological amplitude and the genetic flexibility of a species under ozone stress are not necessarily similar. This notion is of importance in the discussion of critical levels and proves decisive in the study of effects of air pollutants on plant biodiversity.

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Address of author:

Jürgen Franzaring
 Universität Hohenheim
 Ökologiezentrum 2
 Institut für Landschafts- und Pflanzenökologie -320-
 Fachgebiet Pflanzenökologie und Ökotoxikologie
 August-von-Hartmann Str. 3
 D - 70599 Stuttgart
 Tel. +49 (0)711 459 22329, Fax +49 (0)711 459 23044
 e-mail: franzari@uni-hohenheim.de