Plant Biosystems

ISSN: 1126-3504 (Print) 1724-5575 (Online) Journal homepage: http://www.tandfonline.com/loi/tplb20

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To cite this article: P. Cudlin , B. Kieliszewska-Rokicka , M. Rudawska , T. Grebenc , O. Alberton , T. Lehto , M. R. Bakker , I. Børja , B. Konôpka , T. Leski , H. Kraigher & T. W. Kuyper (2007) Fine roots and ectomycorrhizas as indicators of environmental change, Plant Biosystems, 141:3, 406-425, DOI: 10.1080/11263500701626028

To link to this article: https://doi.org/10.1080/11263500701626028

Plant Biosystems, Vol. 141, No. 3, November 2007, pp. 406 – 425

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RECENT ADVANCES IN WOODY ROOT RESEARCH

Fine roots and ectomycorrhizas as indicators of environmental change

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Abstract

Human-induced and natural stress factors can affect fine roots and ectomycorrhizas. Therefore they have potential utility as indicators of environmental change. We evaluated, through meta-analysis, the magnitude of the effects of acidic deposition, nitrogen deposition, increased ozone levels, elevated atmospheric carbon dioxide, and drought on fine roots and ectomycorrhizal (ECM) characteristics. Ectomycorrhizal colonization was an unsuitable parameter for environmental change, but fine root length and biomass could be useful. Acidic deposition had a significantly negative impact on fine roots, root length being more sensitive than root biomass. There were no significant effects of nitrogen deposition or elevated tropospheric ozone on the quantitative root parameters. Elevated CO_2 had a significant positive effect. Drought had a significantly negative effect on fine root biomass. The negative effect of acidic deposition and the positive effect of elevated CO_2 increased over time, indicating that effects were persistent contrary the other factors. The meta-analysis also showed that experimental conditions, including both laboratory and field experiments, were a major source of variation. In addition to quantitative changes, environmental changes affect the species composition of the ectomycorrhizal fungal community.

Key words: *Environmental change, indicators, meta-analysis, temperate and boreal zones, woody plants*

Introduction

The productivity and vitality of forest trees depend on their access to soil resources. In forest ecosystems mycorrhizal associations constitute the interface between nutrients in the soil solution and the uptake organs of trees. Mycorrhizas are macroscopically prominently visible in the case of the ectomycorrhizal (ECM) symbiosis, where the fine roots are completely covered by a fungal mantle, and where water and soil nutrients usually pass through the fungus, there being no direct contact between plant root and soil solution. The ECM symbiosis is highly diverse: trees can be associated with a large number of ECM fungi, and individuals of ECM fungi can connect different trees of the same or different species. The composition of such plant – fungus associations is dependent on tree species composition, tree age, rooting depth, soil characteristics such as pH, the presence of organic and mineral layers, etc. (Erland & Taylor, 2002). Furthermore, natural and human-induced stress factors affect ECM roots, both quantitatively and qualitatively. Changes in fungal species composition can therefore be predicted to be correlated with altered tree responses to such stress factors. This relationship works in both

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ISSN 1126-3504 print/ISSN 1724-5575 online © 2007 Società Botanica Italiana
DOI: 10.1080/11263500701626028

directions: environmental factors could affect tree photosynthesis and thereby regulate carbohydrate availability to ECM fungi, leading to changes in fungal species composition on the roots. Similarly changes in soil conditions could affect the species composition of the ECM fungal assemblages, which subsequently alters plant nutrient uptake and photosynthetic performance (Leake, 2001; Kernaghan, 2005).

Forest decline, observed since the early eighties in Europe and North America, increased the interest of environmental research in bio-indication. Bio-indication provides a suitable means to evaluate the impact of stress factors on species and ecosystem properties and function. Bio-indicators are organisms or associations of organisms that react to environmental factors in ways that allow drawing conclusions on the state of the environment. Sessile organisms, including higher plants, mosses and fungi (including lichen-forming fungi), are acknowledged as suitable indicators with respect to tree performance and forest ecosystem health. Some authors (Arndt et al., 1987) differentiated between ecological indicators, organisms that give evidence on the state of entire ecosystems, and monitoring organisms that are used to monitor (harmful) substances in the environment and to detect their effects. However, many species or species groups (functional groups) can simultaneously fulfill both their bio-indication and monitoring roles. In this paper we therefore do not discriminate between both roles and use terms bio-indication and bio-monitoring interchangeably.

Decrease in abundance of sporocarps and a decrease in species richness of ECM fungi, which has been reported from various countries in Europe (Arnolds, 1988), provided the basis for the use of sporocarps of ECM fungi for bio-indication purposes (Fellner, 1989; Arnolds, 1991). Lilleskov et al. (2001, 2002) noted the same trends of changes in fungal genus composition along a gradient of nitrogen deposition. However, the use of sporocarps for biomonitoring purposes is not without difficulties, because abundance of sporocarps not only depends on these stress factors, but also on the prevailing meteorological conditions. Large variation in rainfall and temperature in the optimal season for sporocarps therefore makes the use of such bio-indication complicated (Arnolds, 1992).

The question thus is pertinent whether ectomycorrhizas (ECM root tips – the actual exchange organs of the mutualistic symbiosis) provide a better alternative for bio-indication purposes. On the one hand ectomycorrhizas are supposedly less sensitive, based on the observation that the fungal structure that is furthest from the carbon sink (the tree) is the most sensitive (Arnebrant, 1994; Wallander, 1995; Wallenda & Kottke, 1998). On the other hand, ectomycorrhizas are present in soil almost year round, showing a lower degree of variation and hence a higher sensitivity for demonstrating and assessing environmental change. Assessing changes in the ECM association on root tips through morphotyping and/or molecular methods is often quite time-consuming and expensive for applied monitoring purposes although the contribution to understanding below-ground processes might surpass the efforts (Horton & Bruns, 2001).

The question is therefore also pertinent whether aggregate measures, while disregarding species composition, are also applicable for monitoring purposes. Specific root length (SRL, root length per unit root weight) was proposed by Fitter (1976, 1985) as a parameter that both expresses nutrient uptake benefits (length scales with surface area over which nutrients are taken up) and construction and maintenance costs (which scales with biomass, being a function of root tissue density and root tip diameter, cf Ostonen et al., Pl Biosyst 2007, submitted). Other potentially useful aggregate parameters could include fractional colonization (the fraction of root tips that is ECM or the fraction of root length that is ECM), number of root tips per volume of soil, length of ECM roots, weight of ECM roots, and branching index (the number of mycorrhizal root tips per unit root length; Meyer, 1987). Finally, fungal characters referring to the ecological strategies of the fungi involved (e.g. exploration and exploitation strategies; Agerer, 2001) have been proposed.

Since global perturbations of the environment are increasing, it is very important to improve the predictive power, quality and combination of bio-indication methods (Tausz et al., 1996). In this review we evaluate the use of ECM root parameters as effective bio-indicators for the following processes of environmental change: (i) acid deposition (low pH, Al toxicity, low base saturation); (ii) nitrogen deposition; (iii) ozone; (iv) elevated CO_2 concentration; and (v) drought. This conceptual separation of the various environmental factors should not blind us to the fact that many forest ecosystems are exposed to various stress factors at the same time (e.g., acid rain in many parts of Europe is a cocktail that includes ammonium sulfate, which has the potential to both lead to N-enrichment and acidification, cf Van Breemen & Van Dijk, 1988) and that primary stress factors could induce subsequent stress (e.g., decreased root performance due to Al toxicity increases drought sensitivity; Manion, 1981). While experimental research can often single out individual factors and their impacts on the functioning of ECM roots, scaling up of such experimental results to global change in the real world may not be

straightforward (Read, 2002); O'Neill et al. (1991) proposed to use a modified hierarchy theory for this purpose. This review also takes an explicit phytocentric view – we look at changes in ECM roots as a monitoring tool for changes in tree and forest ecosystem functioning.

As a first step in improving our knowledge on the bio-indicating and monitoring value of ECM roots, meta-analysis provides a quantitative statistical means of integrating independent results and of identifying aspects of experimental design that might contribute to variation among studies (Gurevitch & Hedges, 1999, 2001). Meta-analysis not only allows evaluation of the effects of the various parameters, but it also offers the possibility of testing whether variables of the system under study could impact on the outcome of the results. We therefore also tried to assess the importance of the following factors, that likely (co-)determine the usefulness of ECM roots as indicators of environmental change: (i) duration of study; (ii) age of plants (ranging from seedling to mature trees); (iii) field *versus* lab studies; (iv) controlled experiments *versus* natural experiments (where controlled experiments are often of the pulse type (Bender et al., 1984), where the environmental factor is changed at once, as in doubling atmospheric CO_2); and (v) conifers versus broad-leaved trees.

Materials and methods

Data collection

Literature data on ECM trees from boreal and temperate ecosystems were extracted and processed by meta-analysis. Arbuscular mycorrhizal trees were not part of the meta-analysis.

One crucial assumption for meta-analysis is independence of studies and data points (Gurevitch & Hedges, 1999, 2001). Independence in this case refers to biological independence and this often requires judgment by the authors. If publications reported data from more than one study system (different tree or ECM fungal species; plants of distinctly different age; soil types, etc.), those systems were considered independent data points. Also if data were collected from different soil horizons (organic *versus* mineral layer), we considered these data points as independent, based on the argument that response functions are often context-dependent (Van der Heijden & Kuyper, 2001) and that responses to stress factors could therefore show different directionality (positive in one layer, negative in the other).

Our study includes data from both true experiments (ranging from laboratory experiments under fully controlled conditions, via nursery experiments under partly controlled conditions to field experiments with a specified treatment and an untreated control) and natural experiments (Diamond, 1986), where, for example, years with different amount of precipitation were compared to evaluate the effects of water deficiency (Diamond, 1986). For elevated CO_2, treatments often consisted of an ambient level and around double ambient level (Alberton et al., 2005). For acidification and N deposition there was very substantial variation in used concentrations and doses. In all cases the highest level applied was used for the meta-analysis. However, in the case of ozone studies the highest level applied were often not realistic as such levels have up to now never been observed in the field. In that case we selected ozone levels that come close to the realistic conditions, i.e. approximately double ambient concentrations.

Bio-indicators must serve several, sometimes conflicting, demands. On the one hand they should allow early detection of environmental stress factors; on the other hand the organism's response to stress should not be rapidly reversible and show persistent and not only transients effects (Fränzle, 2006). If parameters were measured several times in the same study or were reported in studies that are considered as sequential reports on the same experiment, we used only the last sampling date. However, the implications of this choice for persistent effects can be evaluated because different experiments lasted for very different periods and we separated long-term (>1 year) from short-term (<1 year) responses; we analyzed different response parameters separately in order to determine their relative usefulness as indicators of environmental stress impact.

Data collection consisted of obtaining the means of the experimental and control group with their standard deviation (SD) and replicate number (n). Standard errors (SE) were transformed to SD. Unidentified error bars were assumed to represent SE. Papers where standard deviations were not indicated were exceptionally accepted, and an arbitrary value for SD (based on a coefficient of variation that was 1.5 times that of the average of other studies) was taken. We decided to include such data, because we wanted sufficient data points to evaluate the usefulness of certain parameters for bio-indication purposes. However, papers with number of replicates missing were excluded. When data were presented graphically, values were estimated from figures.

Literature search was the responsibility of the lead author for that environmental stress factor. We did not include an exhaustive search through Web of Science®. The literature search was ended on 2 April 2007.

Statistics

The units with which measurements were reported are not important because the response ratio (the

natural log of the ratio of the mean of the experimental treatment divided by the mean of the control) is dimensionless. However, because fractional colonization has an upper bound of 100% (and is often close to that value in both control and experimental treatments – see Discussion), we also looked at Hedges' g (the ratio between response difference and a pooled variance estimate) for fractional colonization under elevated CO_2 (Hedges et al., 1999; Rosenberg et al., 2000; Gurevitch & Hedges, 2001). In the Results section we report the weighted mean response ratio (R; back transformed), the 95% confidence interval for R (CI), and the number of observations (n). Mean response was considered significantly positive if the lower limit of the 95% CI was larger than one and significantly negative if the upper limit of the 95% CI was smaller than one. A random effect model was used if the value of pooled within-class variance (σ^2 pooled) was higher than zero, and a fixed effect model was used if that quantity was equal to or lower than zero. Means of response variables of n different subgroups (see subdivision above) were tested for significant differences based on the model heterogeneity test (Q-test), which is tested against a χ^2 distribution with $n-1$ degrees of freedom as implemented in MetaWin ($P \leq 0.05$). Calculations were performed using MetaWin 2.0 (Rosenberg et al., 2000) and in Microsoft Excel worksheets.

Results

Acidic deposition

There was a highly significant negative impact of acidification on ECM roots ($R = 0.66$, CI = 0.59 – 0.72) and also on non-mycorrhizal roots ($R = 0.72$, CI = 0.64 – 0.81; Table I).

For all fine roots combined (ECM plus non-mycorrhizal) the negative effect was significantly stronger for root length than on root biomass ($P = 0.03$). This was due to the significant effect ($P = 0.01$) of acidification on non-mycorrhizal fine root length compared to fine root biomass. For mycorrhizal roots the difference was not significant. Larger reduction in root length than in root biomass, which translates into a decrease in SRL, is consistent with the effect reported by Ostonen et al. (2007). The results also fit with the general observation that acidification (and increased Al bio-availability) leads to the formation of more stubby roots. The negative impact of acidification increased over time, as long-term experiments showed a significantly smaller R ($R = 0.59$) than short-term experiments ($R = 0.82$). There was no significant difference between laboratory and field studies.

Nitrogen deposition

The general effect size of increased N availability on ECM root tips was not significant ($R = 0.95$, CI = 0.79 – 1.13; Table II). Neither root biomass, nor number of ECM root tips, nor fractional colonization showed a significant response. However, there was a tendency for mycorrhizal parameters to decrease (R for number of ECM root tips and fractional colonization being 0.73 and 0.88 respectively), while fine root biomass increased ($R = 1.12$). In field experiments the effect of N-fertilization was much weaker than in laboratory experiments although the difference was not-significant ($P = 0.14$). However, there was a significant

Table I. Meta-analysis of the effects of acidification on tree roots and ectomycorrhizas.

Categories, parameters	R	95% CI	n	P
ECM, general effect size (response ratio)	0.66	0.59 – 0.72	26	
ECM + not-ECM, general effect size (response ratio)	0.68	0.64 – 0.73	48	
Not-ECM, general effect size (response ratio)	0.72	0.64 – 0.81	22	
ECM, fine root length	0.60	0.43 – 0.82	5	0.36
ECM, fine root biomass	0.67	0.60 – 0.74	21	
ECM + not-ECM, fine root length	0.62	0.55 – 0.70	15	**0.03**
ECM + not-ECM, fine root biomass	0.72	0.66 – 0.78	33	
Not-ECM, fine root length	0.62	0.53 – 0.73	10	**0.01**
Not-ECM, fine root biomass	0.83	0.71 – 0.98	12	
ECM, experiments in laboratory conditions	0.62	0.55 – 0.71	19	0.20
ECM, experiments in field conditions	0.72	0.57 – 0.91	7	
Not-ECM, experiments in laboratory conditions	0.72	0.64 – 0.81	22	
ECM, experiments in short-term (< 1 year)	0.82	0.65 – 1.03	6	**0.00**
ECM, experiments in long-term (> 1 year)	0.59	0.52 – 0.66	20	

For each category we calculated the following: weighted mean of the response ratio (R), the 95% confidence interval (CI) for R, and the number (n) of observations. The final column indicates the probability (P) of the model heterogeneity test that both means are not significantly different. Values in bold are significant.

difference ($P = 0.01$) between short-term studies ($R = 0.61$) and long-term studies ($R = 1.05$).

Ozone

Table III gives the results of the meta-analysis of ozone effects on tree roots and ECM associations. There were in general very few significant effects. The general effect size was 0%. ECM colonization showed a small but significant decrease (−5%), whereas root mass showed an equally small but insignificant increase (+4%). Deciduous and coniferous trees did not show any significantly different reaction to ozone. Differences in root mass between field experiments (an increase of 10%) and laboratory experiments (a decrease of 15%) were marginally significant ($P = 0.06$). The abundance and mass of ECM root tips increased in field experiments (+9%) and decreased in laboratory experiments (−19%). Because lab experiments lasted less than one year, experimental duration also showed the same, non-significant ($P = 0.11$) effect.

Table II. Meta-analysis of the effects of eutrophication (N fertilization) on tree roots and ectomycorrhizas.

Categories, parameters	*R*	95% CI	*N*	*P*
General effect size (response ratio)	0.95	0.79–1.13	52	
Fine roots biomass	1.12	0.85–1.48	21	
ECM colonization	0.88	0.67–1.15	23	0.19
ECM biomass (tips)	0.73	0.43–1.24	8	
Field experiment	1.01	0.82–1.23	43	0.14
Laboratory experiment	0.71	0.43–1.16	9	
Short-term experiment (<1 year)	0.61	0.39–0.93	12	**0.01**
Long-term experiment (>1 year)	1.05	0.87–1.28	40	

For each category we calculated the following: weighted mean of the response ratio (*R*), the 95% confidence interval (CI) for *R*, and the number (*n*) of observations. The final column indicates the probability (*P*) of the model heterogeneity test that both means are not significantly different. Values in bold are significant.

Elevated CO_2

There was a significant positive effect of elevated CO_2 on ECM parameters ($R = 1.25$; CI = 1.18–1.32). Both fractional colonization ($R = 1.19$) and the number of ECM root tips ($R = 1.33$) responded positively to elevated CO_2 (Table IV). The difference in response between both parameters was significant ($P = 0.03$). Because fractional colonization has an upper bound of 100% (and field values are often close to that value, see Discussion), we also calculated Hedges' *g* statistic. For fractional colonization $g = 0.51$ (CI 0.19–0.86), implying that the change due to elevated CO_2 was around half the

Table III. Meta-analysis of ozone effects on tree roots and ectomycorrhizas.

Categories, parameters	*R*	95% CI	*n*	*P*
General effect size (response ratio)	1.00	0.94–1.05	144	
Root mass and length	1.03	0.93–1.13	45	0.44
ECM colonization, tips and mass	0.98	0.92–1.05	99	
Root length	0.96	0.64–1.45	4	0.55
Root mass	1.04	0.94–1.16	41	
Root mass in field condition (FACOS, OTC)	1.10	0.97–1.25	33	0.06
Root mass in lab condition (GH and GC)	0.85	0.64–1.14	8	
Root mass in short-term experiment (<1 year)	1.02	0.82–1.28	11	0.81
Root mass in long-term experiment (>1 year)	1.05	0.92–1.21	30	
Root mass of coniferous tree	1.04	0.91–1.18	30	0.83
Root mass of deciduous tree	1.07	0.81–1.42	11	
ECM colonization	0.95	0.92–0.98	33	0.35
ECM tips (abundance) and mass	1.01	0.93–1.11	66	
ECM (col., tips and mass) of coniferous tree	0.98	0.92–1.05	90	0.74
ECM (col., tips and mass) of deciduous tree	1.05	0.67–1.65	9	
ECM colonization in field condition (FACOS, OTC)	0.95	0.90–0.99	23	0.90
ECM colonization in lab condition (GH and GC)	0.95	0.91–0.99	10	
ECM col. in short-term experiment (<1 year)	0.96	0.92–1.00	18	0.52
ECM col. in long-term experiment (>1 year)	0.94	0.89–0.99	15	
ECM (tips, mass) in field condition (FACOS, OTC)	1.09	0.93–1.27	57	0.11
ECM (tips, mass) in lab condition (FACOS, OTC)	0.81	0.54–1.20	9	
ECM (tips, mass) in long-term experiment (>1 year)	1.09	0.93–1.27	57	0.11
ECM (tips, mass) in short-term experiment (<1 year)	0.81	0.54–1.20	9	

For each category we calculated the following: weighted mean of the response ratio (*R*), the 95% confidence interval (CI) for *R*, and the number (*n*) of observations. The final column indicates the probability (*P*) of the model heterogeneity test that both means are not significantly different.

Table IV. Meta-analysis of the effects of elevated CO_2 on tree roots and ectomycorrhizas.

Categories	*R*	95% CI	*n*	*P*
ECM response ratio on colonization	1.19	1.10 – 1.28	39	**0.03**
ECM response ratio on root tips	1.33	1.22 – 1.44	36	
ECM response ratio (colonization + root tips)	1.25	1.18 – 1.32	75	
Fungal identity				
ECM fungi species specific colonization	1.20	1.07 – 1.34	17	0.76
ECM fungal assemblage colonization	1.17	1.07 – 1.29	23	
ECM fungi species specific root tips	1.30	1.14 – 1.48	16	0.54
ECM fungal assemblage root tips	1.37	1.20 – 1.56	20	
Plant identity				
ECM fungi conifer tree colonization	1.17	1.09 – 1.26	33	0.59
ECM fungi broad-leaved tree colonization	1.22	1.01 – 1.49	6	
ECM fungi conifer tree root tip number	1.32	1.18 – 1.47	23	0.75
ECM fungi broad-leaved tree root tip number	1.36	1.15 – 1.61	13	
Experimental duration				
ECM fungi short-term (<1 year) colonization	1.10	0.98 – 1.25	11	0.09
ECM fungi long-term (>1 year) colonization	1.25	1.13 – 1.37	28	
ECM fungi short-term (<1 year) root tips	1.22	1.10 – 1.36	21	**0.01**
ECM fungi long-term (>1 year) root tips	1.49	1.30 – 1.71	15	
Experimental set-up				
ECM fungi in laboratory experiments colonization	1.19	1.08 – 1.31	21	0.78
ECM fungi in field experiments colonization	1.17	1.05 – 1.30	18	
ECM fungi in laboratory experiments root tips	1.38	1.24 – 1.54	28	0.18
ECM fungi in field experiments root tips	1.18	0.92 – 1.50	8	

For each category we calculated the following: weighted mean of the response ratio (*R*), the 95% confidence interval (CI) for *R*, and the number (*n*) of observations. The final column indicates the probability (*P*) of the model heterogeneity test that both means are not significantly different. Values in bold are significant.

standard deviation in colonization commonly observed in such experiments.

The response ratio of ECM root tip number between conifer and broad-leaved trees was not significantly different ($P = 0.75$). There were also no significant differences in cases where studies with one fungal species were compared to studies with fungal assemblage ($P = 0.54$). Bio-indicator value is therefore independent of those factors. The response in long-term experiments was significantly higher than that in experiments of shorter duration ($P = 0.01$), suggesting that this response is not transient but persistent and even increases over time. The difference between field experiments and laboratory experiments was not significant ($P = 0.18$), suggesting that the differences due to experimental duration are not due to covariation between experimental duration and experimental set-up.

Drought

Drought (Table V) had a significant negative effect on ECM roots ($R = 0.68$, CI = 0.55 – 0.85). This effect was due to the highly negative effect of drought on fine root biomass ($R = 0.54$), whereas fractional colonization showed small, insignificant increase ($R = 1.10$). The difference between fine root biomass and fractional colonization was significant ($P = 0.00$). Drought stress had the same effects in short-term and long-term experiments ($P = 0.99$). Contrary to acidic and N deposition, drought stress had a significantly larger ($P < 0.00$) negative impact in the field than in laboratory experiments. The impact of drought was somewhat larger in long-term experiments ($R = 0.56$) compared to short-term experiments ($R = 0.73$), although that difference was not significant.

Discussion

Advantages and problems of the use of meta-analysis

Meta-analysis is a combination of data from independent studies to estimate the magnitude of the effect across such studies and to test for potentially causative factors in the magnitude of effect among these studies (Gurevitch & Hedges, 2001). As many factors, besides the main factor analyzed in the different tables, could have caused the different responses (choice of mycorrhizal fungal and plant species, duration of the experiment, field and laboratory conditions, etc.), we subdivided experiments in a number of separate classes to test for these subsidiary factors. Not always was the database large enough to allow such subdivision. For instance, the

Table V. Meta-analysis of drought effects on tree roots and ectomycorrhizas.

Categories, parameters	*R*	95% CI	*n*	*P*
General effect size (response ratio)	0.68	0.55–0.85	31	
Fine root biomass	0.54	0.41–0.71	20	**0.00**
ECM colonization	1.10	0.72–1.67	11	
Fine root biomass in laboratory experiments	0.89	0.52–1.52	6	**0.00**
Fine root biomass in field experiments	0.43	0.31–0.59	14	
Fine root biomass in short-term experiments (<1 year)	0.54	0.39–0.74	15	0.99
Fine root biomass in long-term experiments (>1 year)	0.54	0.26–1.11	5	
Laboratory experiment	1.10	0.82–1.45	15	**0.00**
Field experiment	0.46	0.35–0.60	16	
Short-term experiment (<1 year)	0.73	0.57–0.93	24	0.27
Long-term experiment (>1 year)	0.56	0.34–0.93	7	

For each category we calculated the following: weighted mean of the response ratio (*R*), the 95% confidence interval (CI) for *R*, and the number (*n*) of observations. The final column indicates the probability (*P*) of the model heterogeneity test that both means are not significantly different. Values in bold are significant.

role of tree age (which very likely is a major factor that influences plant responses to environmental stress factors) could not yet be investigated. Only further studies (and hence an expanded database) will allow such testing for the effect of tree age in the future. Furthermore, while for experimental purposes the causative factors are treated as independent causes, this will unlikely be the case for the real world, where global change simultaneously affects several of the causative factors. For instance, deposition of acidifying substances ('acid rain') often co-occurs with N-deposition (Van Breemen & Van Dijk, 1988). Simultaneously drought (Matyssek et al., 2007) or acid rain and acid mist (Cairney & Meharg, 1999) often co-occur with increased ozone levels. Plant responses (also below-ground responses) to elevated CO_2 are constrained by the level of N-availability (Luo et al., 2004; Hu et al., 2006; Johnson, 2006). Although a factorial meta-analysis is in principle possible (Gurevitch et al., 2000), there were too few studies available to apply this technique.

Two major complicating issues of meta-analysis are publication bias and research bias (Gurevitch & Hedges, 2001) Publication bias (underreporting of experiments without significant results) will likely lead to an overestimation of the number of significant results. It also leads to an overestimation of effect size. However, if experiments that refute the original hypothesis are still reported, the effects of publication bias may be mitigated to some extent by larger confidence intervals. Research bias can be manifested through the tendency to preferentially choose certain organisms or experimental conditions under the expectation of obtaining significant results or through the choice of model species and experimental conditions that are easy to handle. It is not possible to estimate the magnitude of the effect. Research bias may also result in investigating parameters that are easier to assess, such as fractional colonization (see following), even if such parameters are unsuitable. Finally, research bias could manifest itself through the preferential use of pulse experiments where levels of the experimental factor under investigation are elevated instantaneously instead of gradually – as would happen with the deposition of acidifying and eutrophying substances or with elevated CO_2. Considering that trees can show substantial plasticity in root characteristics, pulse experiments, especially if combined with experiments of relatively short duration, may lead to overestimation of effect size; and hence to an overoptimistic judgment as to the suitability of root parameters for bio-monitoring and bio-indication purposes.

Ratios as indicators of environmental change

Fractional colonization has an upper bound of 100%. In systems where fractional colonization is high (>90%), the response ratio is inevitably constrained to values that are close to, though possible still significantly different from, unity. In natural forest ecosystems in Europe a high fractional colonization (>99%) was established (Kraigher et al., 1996, 2007; Kraigher, 1999; Taylor et al., 2000). These high values are not always found in nurseries, greenhouse or pot studies, where experimental conditions may result in substantially lower levels of colonization. It has also been suggested that reported much lower colonization levels might be explained by instances where a fungal species with a conspicuous mantle was replaced by other fungal species (often of Ascomycete origin) with a much thinner mantle. In cases where root anatomy was not systematically checked under the microscope (presence of Hartig net and sheath), such observations could distort the interpretation of fractional

colonization as an indicator of environmental stress and change. Fractional colonization is also the result of plant root growth and fungal growth on or around roots. A differential effect of environmental stress factors on both parameters can be positive or negative (Allen, 2001). It is a serious argument against the use of fractional colonization for bio-indication purposes.

The usefulness of SRL as indicator has been discussed by Ryser (2006) and Ostonen et al. (Pl Biosyst 2007, submitted). However, ECM fungi have an impact on root anatomy and morphology. From data in Bauhus & Messier (1999) it seems likely that this problem with SRL may be especially large in the case of ECM conifers. Van Der Heijden & Kuyper (2003) identified two ECM strategies, such as root replacement and root manipulation. They showed that the presence of different ECM fungi on the roots of *Salix repens* had a major impact on root length, and through the thickness of the fungal mantle on root diameter. However, there was no relationship between root length and nutrient uptake, so an economic cost–benefit analysis for roots was not applicable due to the fungal effects on root morphology.

These strategies have a large impact on SRL and on uptake expressed per unit root. In such cases SRL could not be used without problems.

Persson (1980) suggested the use of the live to dead fine root ratio as an indicator. At present, too few data-points are available to test the usefulness of this ratio. Further research is evidently needed. Similarly the branching index (Meyer, 1987) was suggested to decline under the influence of environmental stress (acid rain, N deposition). There were too few data available to judge the usefulness of this indicator.

Acidic deposition

The meta-analysis in this paper showed that tree fine roots, ECM as well as non-mycorrhizal, respond negatively to acidification of soil substrate and that the most suitable, significant indicators of the negative impact of acidity were fine root length and fine root biomass. The fine root responses were more distinct in experiments conducted in laboratory than in the field conditions and the negative effects of acidification were more pronounced in long-term than in short-term experiments. It is necessary to add that the level of soil acidity and the concentrations of available Al causing statistically significant reduction of tree root growth (elongation and biomass) in laboratory conditions depended on seedling species and age and on the cultivation method (hydroponic system/sand culture/soil culture). Roots of seedlings of *Picea* spp. were reported to be more sensitive to the impact of aluminum ions than roots of *Pinus* spp. in hydroponic system (McCormick & Steiner, 1978; Williams, 1982; Evers, 1983; Thornton et al., 1987), as well as in peat-perlite cultures (Kieliszewska-Rokicka et al, 1998; Heim et al., 2003). On the other hand, different authors reported variable responses of root growth of one species (*Picea abies*) to similar concentrations of Al (e.g. Rost-Siebert, 1983; Abrahamsen, 1984; Ingestad et al., 1985).

Under laboratory conditions ECM colonization of tree roots was reported as not affected by acidification (Cumming & Weinstein, 1990; Ericsson et al., 1998), decreased (e.g. Stroo & Alexander, 1985; Entry et al., 1987; Meier et al., 1989; Blaschke, 1990; Kieliszewska-Rokicka et al., 1998; Rudawska et al., 2000) or increased (Horubia & Diaz, 1996; van Schöll et al., 2005). The different findings may result from variable tolerance of ECM symbionts to acidity and Al. According to meta-analysis, in laboratory conditions the negative impact of acidification on ECM fine roots was more significant ($R = 0.62$) than on non-mycorrhizal fine roots ($R = 0.72$). However, this statistical method cannot include such qualitative responses of ectomycorrhiza as a decreased thickness of fungal mantle and inhibited development of the Hartig net (e.g. Kieliszewska-Rokicka et al., 1998), that are essential for ectomycorrhizal function.

The meta-analysis showed that the biomass of tree fine roots was a good indicator of the soil acidification caused by artificial acid rain in field experiments (e.g. Blaschke, 1990; Qian et al., 1998a), as well as of a amelioration of acid stress after 'clean rain' treatment (Bredemeier et al., 1995; Lamersdorf & Borken, 2004). However, the negative influence of acidification to tree fine roots were less significant in the field than in laboratory conditions ($R = 0.72$/ $R = 0.62$). It is obvious that in the field condition many various factors, such as nitrogen deposition, organic matter content, heavy metals, ozone, temperature, drought etc., can interfere with acidification, influencing fine root growth. On the other hand, some anthropogenic stress factors (i.e. aluminum, heavy metals, ozone) require soil acidification as a necessary condition to exert significant effects on living organisms.

Interactive responses of the composition of community of ECM fungi to combined stress factors have been observed in many studies under forest conditions, such as simulated acid rain and ozone (Walker & McLaughlin, 1991; Roth & Fahey, 1998), increased temperature, different levels of organic matter and important ions (Cullings & Makhija, 2001).

Although the meta-analysis indicated clearly the significance of the quantitative features of fine roots, some important qualitative characteristics, such as

differences in composition of ECM communities between the control and the treated plots in field experiments, were passed over, because of descriptive results, difficult to put into the rigid frames of mea-analysis.

ECM fungi (species and strains within species) indicated variable preferences for pH of culture medium when grown *in vitro* (Dennis, 1985; Willenborg et al., 1990). Consequently, ECM morphotypes developed by various ECM fungi differ in the tolerance to acidification (Qian et al., 1998a). This fungal feature probably contributes in a shift in composition of ECM community in forest stands subjected to acidification (e.g. Gronbach & Agerer, 1986; Kraigher et al., 1996; Qian et al., 1998b; Roth & Fahey, 1998; Rudawska et al., 2003). Among ECM mycobionts of relatively low tolerance to acidification and increased availability of Al ions were reported *Amanita crocea, A. vaginata, Hydnum repandum, Hygrophorus postulatus, Russula ochroleuca, R. cyanoxantha, R. olivacea, Tylospora sp., Tuber puberulum, and Piceirhiza nigra* (Agerer et al., 1998; Kraigher et al., 1996; Qian et al., 1998a). A high tolerance to acidification and increased concentrations of Al ions revealed *Amanita muscaria, Cenococcum geophilum, Paxillus involutus, Pisolithus tinctorius, Suillus luteus, S. bovinus, S. variegates, Xerocomus badius* (Marx & Zak, 1965; Hintikka, 1988; Agerer et al., 1998; Danielson & Visser, 1989; Leski et al., 1995; Kieliszewska-Rokicka et al., 1996; Kraigher et al., 1996; Qian et al., 1998a).

The meta-analysis indicated that the long-term influence of acidification (>1 year) had a more significant impact on ECM fine roots ($R=0.059$) than the short-term experiments (<1 year) ($R=0.82$), however, many details were missed. Generally, acidification did not reduce degree of mycorrhization of tree roots in forest plots and mostly was reported as almost 100% of fine root tips colonized; however the total number of ECM root tips per soil volume and the number of morphotypes were reduced (e.g. Rudawska et al., 1995, 1996, 2003; Kieliszewska-Rokicka et al., 1997; Nowotny et al., 1998; Kraigher, 1999; Bojarczuk et al., 2002; Erland & Taylor, 2002). Moreover, the life span of ectomycorrhizas was observed lower, the turnover rate was higher (Wöllmer & Kottke, 1990; Kottke et al., 1993; Godbold et al., 2003; Leuschner & Hertel, 2003) and the ratio between dead and dying to fully active, growing mycorrhizas was increased in acidified soils, when compared to untreated or previously limed plots (Qian et al., 1998a; Vanguelova et al., 2005).

In acidic soils, characterized by low base saturation, a decrease in relative length of fine roots was accompanied by enhanced formation of adventitious roots (Braun et al., 2005). However, variable responses of tree fine roots to acid stress in humic and mineral soil horizons were reported. In mature Norway spruce stands a decrease of fine root production and biomass with increasing soil acidity was observed both, in humic and upper mineral soils (Hahn and Marschner, 1998) or a decrease of root biomass in deeper mineral soils, coincident with an increased root production in the humic layer (Jentschke et al., 2001). Inverse correlation between fine root biomass and Al content in fine roots indicated a compatibility of the growth and chemical indicators (Oleksyn et al., 1996; Carnol et al., 1999).

Nitrogen deposition and fertilization

Nitrogen (N) deposition has increased across a large number of temperate conifer and deciduous ecosystems affecting tree growth and nutrient cycles (Vitousek et al., 1997; Kochy & Wilson, 2001). Increased soil N concentrations are often correlated with changes in a number of ECM community attributes, such as decreased sporocarps production, lower community diversity, and shifts in the relative abundance of ECM community members. Several excellent review articles on the response of fine roots, mycorrhizas and ECM sporocarps to nitrogen fertilization and deposition have appeared (Dighton & Jansen, 1991; Wallenda & Kottke, 1998; Cairney & Meharg, 1999; Nadelhoffer, 2000; Erland & Taylor, 2002; Lilleskov, 2005). These reviews made clear that nitrogen deposition can lead to diverse, sometimes contradictory consequences.

The first documented biological effect of nitrogen deposition on the diversity of ECM fungi has mainly been limited to observations made in sporocarps surveys of ECM fungi in nitrogen-supplemented plots, a rapid and substantial decrease in the diversity and production of ECM sporocarps of most species was observed. This issue was recently thoroughly reviewed by Lilleskov (2005). Response to fertilization seems to vary among species with certain taxa declining in abundance and diversity (*Cortinarius*, *Hydnum*, *Russula* and *Suillus*) and some continuing to fruit at higher deposition levels (*Lactarius rufus*, *L. theiogalus*, *Paxillus involutus*, *Laccaria* species).

Along with sporocarps surveys, research based on below-ground ECM observations provided new information about richness or diversity in response to N inputs and revealed the lack of direct correspondence between both approaches. They also showed notable discrepancies between different studies. Several reports indicated a decrease in fractional colonization by ECM fungi or total numbers of ECM roots (Tetreault et al., 1978; Alexander & Fairley, 1983; Rudawska 1986; Taylor & Alexander, 1989; Haug et al., 1992) or showed a

decline in the abundance and diversity of ECM fungi or a shift in ECM community composition (Alexander & Fairley, 1983; Taylor & Alexander, 1989; Kraigher et al., 1996, Taylor et al., 2000; Peter et al., 2001; Lilleskov et al., 2002; Parrent et al., 2006). However, a decrease in ECM colonization was sometimes rather short-lived and disappeared after few years after treatment (Menge et al., 1977). This time-dependent response was also clear from our meta-analysis.

Other authors observed smaller changes in response to nitrogen fertilization. Arnebrant & Söderström (1989) noted little change for *Pinus sylvestris* that had received N fertilization 13 years prior to sampling. Similarly, Kårén & Nylund (1997) and Nilsen et al. (1998) observed no decline in fractional ECM colonization of *Picea abies* following continued fertilization (around 5 years), although the total number of short lateral roots, and hence the total ECM number, decreased in the former study. A similar pattern emerged for *Pinus ponderosa* seedlings in experiment reported by Walker et al. (1997). Nitrogen fertilization has further been reported as having no significant effect on rates of ECM root tip turnover (Rygiewicz et al., 1997). Exposure of *Pinus sylvestris* seedlings to oxides of nitrogen (NOx) for short periods (<39 days) also had no significant effect on ECM colonization levels (Näsholm et al., 1991). No effects on mycorrhizal colonization, total number of mycorrhizas or frequencies of four common morphotypes of *Picea abies* were evident after 5 years (Brandrud, 1995; Brandrud & Timmermann, 1998). The addition of nitrogen also did not affect the species richness or diversity of below-ground ECM fungal species in an oligotrophic Swedish *Picea abies* forest (Jonsson et al., 2000).

Recent advances in the field of molecular identification of mycobionts of ectomycorrhizas have led to a rapid increase in our knowledge about below-ground ECM communities (Gardes & Bruns, 1996), together with information about taxa that do not form conspicuous fruiting bodies (thelephoroid fungi, *Tylospora* sp.). Certain *Cortinarius* and *Russula* species declined when N increased (Peter et al., 2001; Lilleskov et al., 2002), and *Tylospora* species abundance has been shown to either increase (*T. asterophora*; Peter et al., 2001) or not to change (*T. fibrillosa*; Lilleskov et al., 2002) between plots with greater N concentrations relative to low N sites. These results also suggest that certain fungal lineages may show large species-specific differences in their physiological tolerance to various soil chemical properties, limiting our ability to predict the response of individual species to environmental variation given the response of co generic species to the same environmental factors.

The physiological and ecological mechanisms behind so wide-ranging reactions of fine roots and their mycorrhizas to N deposition are still debated (Chalot & Brun, 1998; Wallenda & Kottke, 1998; Lilleskov & Bruns, 2001; Lilleskov, 2005) and are often interpreted as a consequence of adaptations of ECM fungi to N-limited forests.

The question arises whether some ECM fungal community attributes may find application in the bio-indicating and monitoring of nitrogen deposition in forest ecosystems. Due to great variability of information and experimental outcomes, finding any consistent pattern of responses in fine roots and ECM attributes under N enrichment seems difficult. The meta-analysis was performed on data from laboratory and field experimental studies with fertilizer treatments as well as gradient observations. Due to this wide-range approach the general effect size of increased N availability on ECM root tips was not significant ($R = 0.95$, $\mathrm{CI} = 0.79 - 1.13$) and neither root biomass, nor number of ECM root tips, nor fractional colonization showed a significant response. Treseder (2004) included in her meta-analysis only field-based manipulations of N and found that across studies fractional colonization significantly decreased (15%). In our analysis, we noted a similar decrease in fractional colonization ($R = 0.88$), but the effect was not significant. Also for ECM root tips the effect was not significant ($R = 0.73$). However, a decrease in ECM root tips combined with an increase in root biomass would translate into a decrease in SRL, as indeed observed by Ostonen et al. (Pl Biosyst 2007, submitted). The decrease in number of root tips (and hence in branching index – but there were too few data for that parameter) and in fractional colonization suggests that the mycorrhizal fungus is more sensitive to N deposition than the plant – as has been stated before by Wallenda & Kottke (1998). However, there is an issue to what extent N fertilizer experiments can be used to assess the effect of N deposition (ammonium deposition usually has also acidifying effects). N-deposition often occurs under conditions of already N-sufficiency or even N-saturation and there the negative effects will certainly prevail. Therefore, we may have to reflect to what extent N-fertilizer studies are a good proxy to assess the effect of atmospheric N-deposition. The database is unfortunately insufficient to subdivide the data on levels of N addition as a function of N availability under control conditions. Threshold conditions for potential ECM fine root impacts from nitrogen stress could therefore not be estimated. The effects greatly depend on the amount and form of fertilizer (Persson & Ahlström, 1994), as well as on site conditions, tree species and the age of the stand. Wiemken et al. (2001) showed that increased nitrogen input caused

a slightly reduced production of fine root biomass in a calcareous soil but increased it by 33% in a siliceous soil. In other studies nitrogen fertilization resulted in increased fine-root biomass when it was applied on a nutrient-poor site (Helmisaari & Hallbäcken, 1999).

The effect of N-fertilization in field experiments was much weaker than in laboratory experiments although the difference was not significant ($P = 0.14$). Laboratory approaches with nutrient pulses generally provide a higher degree of control but often less realism as a result of high doses of fertilizers that are usually higher than applied in forestry practices. A significant difference was found ($P = 0.01$) between short-term studies ($R = 0.61$) and long-term studies ($R = 1.05$), which suggests that trees show a transient negative effect to increased N-availability, but that such effects are most likely not persistent. In conclusion, meta-analysis indicates considerable robustness and stability of ECM fine roots under conditions of nitrogen fertilization.

The leading question of this review, whether under nitrogen deposition below-ground ECM fine root attributes may provide an alternative to above-ground sporocarps for bio-indication purposes, remains unanswered. The large variation in N responses among studies indicates that predictability of N deposition effects on fine roots and their mycorrhizas for any given ecosystem is relatively low. One of the possible reasons may also derive from different methods used. In general, with increasing nutrient availability, sequential coring shows decreased fine root production but nondestructive methods show increased fine root production (Nadelhoffer, 2000), even though there are important exceptions (Eissenstat & Yanai, 1997). Ostonen et al. (Pl Biosyst 2007, submitted) also showed that method of assessing fine roots has a major impact on observed changes in SRL. In addition to differing methodologies, variation in N treatment regimes and N sources makes comparisons among studies difficult. More research is still needed including other tree species, especially deciduous ones and other regions of the world, besides Europe, to propose some characteristics of fine roots and mycorrhizas for bio-indication purposes.

Ozone

Tropospheric ozone (O_3) is a secondary atmospheric pollutant, generated from oxides of nitrogen and volatile organic compounds reacting in the presence of sunlight. It has been recognized as an increasing and damaging agent to plants (Karnosky et al., 2005). O_3 triggers physiological changes in leaves that affect carbon source strength, i.e. the amount of carbon available for allocation to sink tissues (Matyssek & Sandermann, 2003). Decreased carbon assimilation, increased metabolic costs for repair mechanisms, and decreased phloem loading, all lead to decreased carbon allocation below-ground, thus affecting roots, root symbionts, rhizodeposition, litter quality and quantity, and consequently the whole soil food web (Andersen, 2003). Carbon source–sink relationships or functional balance of roots and shoots were reported as primary factors in continuous adjustments between root and shoot growth (Tingey et al., 1976), possibly acting through root to shoot signaling, including hormonal regulation of root proliferation. In this context, the effects of ozone-fumigation on the cytokinins (CK) of beech trees (Winwood et al., 2007) can be related to mycorrhiza-associated changes in cytokinin concentrations in the host plants (Kraigher et al., 1991, 1993) and ozone-induced changes in fine root growth and ECM community structure (Grebenc & Kraigher, 2007a).The sensitivity to ozone has been reported to differ between species (for review see Andersen & Rygiewicz, 1991, 1995; Bortier et al., 1999, 2000a,b; Andersen 2003), between different clones and populations (Ballach et al., 1992; Coleman et al., 1996; Ottossen et al., 2003; Vanhatalo et al., 2003), experimental growth conditions, such as duration of the fumigation, light regime, irrigation, mineral nutrition and combination of different stress factors (McLaughlin & Downing, 1995; Roth & Fahey, 1998; Topa et al., 2004; Löw et al., 2006; Železnik et al., 2007) and between the age-related physiological differences within the same species (Matyssek et al., 2007). Ozone induced root growth reductions were found to alter the functioning of the rhizosphere organisms and to make them more susceptible to drought or nutrient deficiency (Woodbury et al., 1994). Also carryover effect was established (Andersen & Rygiewicz, 1991). With respect to the length of the fumigation, it should be considered with the view to the life span of the fumigated plant.

In adult beech trees a significant increase of number of vital ectomycorrhizas, non-turgescent short roots and of number of types of ectomycorrhiza was observed. Species richness was affected only in regularly humid years and not under conditions of drought stress (Grebenc & Kraigher, 2007a). The same treatment was effective also on individual ECM species abundance. The increased abundance of *Cenococcum geophilum*, Russula *fellea* and *Russula illota* pointed to their tolerance to the changed physiology of the beech trees under ozone, while *Xerocomus* sp., *Russula cyanoxantha, Russula ochroleuca* and *Lactarius* sp.1 decreased in abundance under increased ozone treatment or were only found with control trees (Grebenc & Kraigher, 2007b). In terms of nutrient status of roots $\delta^{15}N$ measurements

indicated a reduction of total nitrogen in fine roots from ozone treated adult trees (Haberer et al., 2007) while in seedlings Mg concentration was reduced under the same conditions (Železnik et al., 2007). Opposite to the results from adult trees, in beech seedlings a significant reduction of number of vital ECM types and number of ECM root tips was observed (*ibid*).

As shown by meta-analysis (Table III) the general effect size of ozone fumigation was zero. It showed a small but significant effect on decreased ECM colonization (−5%) and a small and insignificant increase on root biomass (+4%). The largest effects were noted in laboratory conditions (decrease of root mass by 15% and of ECM root tips by 19%). On the contrary the response in the field conditions was positive with 10% and 9%. Therefore ozone was shown to affect below-ground processes especially through the change in community structure, which could not take part in the meta-analysis. The laboratory conditions, which were all based on fumigation of tree seedlings, have revealed a decrease in root biomass and active ECM root tip numbers. Therefore in young plants a fast response to ozone fumigation could be predicted, implying a discussion on the relative length of the impacts of stress with respect to the total plant life-time. On the other hand in adult trees the increased growth of fine root biomass and number of active ECM root tips after several years of fumigation (in total the fumigation period might represent merely 5–10% of the adult tree's lifespan) might indicate a transient response of a tree to different source-sink relationships in the ecosystem. A shift in ECM community can lead to different mycelial networks providing the fluxes of water and nutrients between different components in the ecosystem. Forest soils and the mycelial networks can provide a buffering system for the relatively 'short episode' of ozone fumigation within the lifespan of a tree. Also, the transient higher root biomass and number of root tips in adult trees should be considered in the view of carbon dynamics of the ecosystem under elevated ozone.

Because the ozone effects on the analyzed root parameters were different and the overall effects as detected by meta-analysis were equal to zero, these parameters do not seem to be appropriate bio-indicators to be used for revealing early effects of ozone on forest trees and forest ecosystems. However, they should nevertheless be studied in order to provide functional insights in different forest stands, forest tree mixtures and different developmental phases, since the long-lasting effect on forest stability and regeneration processes (impact on seedlings was negative!) seems to be predictable. Also shifts in ECM community structure were noted in both adult trees and young plants (Grebenc & Kraigher 2007a,b; Železnik et al., 2007).

Through its indirect effects ozone provides a general stress to the below-ground community, often occurring in combination with other stresses; therefore a clear differentiation to ozone-sensitive and ozone-tolerant ECM species, such as proposed in acidic and nitrogen deposition studies (i.e. Kraigher et al., 1996), might be problematical. A step forward might be in establishing functional groups of ECM types (exploration types as proposed by Agerer, 2001), more or less sensitive to changes in carbon allocation below-ground, and in further revelation of the physiology, and thus bio-indication value, of each of the ECM types or groups.

Elevated CO_2

The meta-analysis, which expands on the earlier meta-analysis by Alberton et al. (2005), showed that ECM roots respond positively to elevated CO_2. An increase in root tip abundance under elevated CO_2 is consistent with reported changes in root: shoot ratio, especially under conditions of severe nutrient limitation (Poorter & Nagel, 2000; Ågren & Franklin, 2003). It is important to note, though, that such an increased carbon allocation to ECM roots does not automatically translate into an increased uptake of limiting nutrients and hence to increased forest productivity. ECM forests could already be 'saturated' with ectomycorrhizas (O'Neill, 1994) and any further increase in ECM roots and mycelia would only increase nutrient limitation of the system. This phenomenon has been described as the Progressive Nitrogen Limitation (PNL) hypothesis (Luo et al., 2004; Hu et al., 2006; Johnson, 2006). Ostonen et al. (Pl Biosyst 2007, submitted) noted that under elevated CO_2 concentration SRL of the finest root class (which mainly consists of ectomycorrhizas) hardly changed ($R = 0.97$); the difference is much smaller than the response of the ECM root tip abundance. However, their study included only 3 data points. We cannot therefore address the question which parameter should be preferred for bio-indication or monitoring perspectives. It should be noted, though, that the various parameters do not have to show the same direction and magnitude. SRL could also be effected through changes in species composition (if fungi with a thicker mantle replace those with thinner mantles, as suggested by Godbold & Berntson (1997) or changes in mantle thickness because the fungus is less constrained by C-availability, as suggested by Gorissen & Kuyper (2000). However, there are too few data available as to how elevated CO_2 affects species composition and/or properties of the fungal mantle.

Responses of ECM root tips to elevated CO_2 in long-term experiments were significantly larger than in short-term experiments. This observation seems

to contradict the generally held view of down-regulation of photosynthesis under elevated CO_2, when enhanced photosynthesis does not lead to a similarly enhanced nutrient uptake. However, a persistent effect of elevated CO_2 on the abundance of ECM root tips is consistent with the progressive nitrogen limitation hypothesis.

Drought

There are several physiological short term indicators of drought such as stomatal conductance and water potential (Irvine et al., 1998). The time scale of changes to occur in the fine root biomass, root tip numbers, or the community structure of ECM fungi is weeks, which can be compared to the time scale of the use of carbon isotope ratios to indicate integrated water use efficiency (Warren et al., 2001). Making use of fine root and mycorrhiza characteristics as environmental indicators is complicated because of high variability, and low specificity, due to susceptibility to a number other natural and anthropogenic factors. Furthermore, determining root characteristics is very time-consuming. On the other hand, as fine roots and mycorrhizas are the first parts of the plant that are in contact with the drying soil, they are very sensitive (Konôpka et al., 2005). Also, in many soils these roots are concentrated in the topmost parts of the soil, which are the first to dry out.

The clearest effect found in the meta-analysis was the decrease in fine root biomass during drought. The relative allocation of growth to below-ground organs at the expense of above-ground ones during a mild drought has often been found, and even the absolute root growth may increase by a mild drought (Becker et al., 1987). However, when the water stress continues, reduction in root growth is a usual response (Joslin et al., 2000). By contrast to fine root biomass, the fractional colonization of ectomycorrhizas did not show a reduction but a slight (non-significant) increase. This may be due to a negative effect of drought on the total number of root tips. This kind of effect was expressly shown in Norway spruce by Feil et al. (1988).

In the meta-analysis in this paper, only fine root biomass and mycorrhizal colonization were mentioned in the table as separate variables. However, root tip number, fine root density and branching index, were probably responsible for the difference found between short-term and long-term experiments. There were too few data sets to make conclusions of these. There was only one paper with data on fine root density (fine root length per unit soil volume; Vanguelova et al., 2005). In short-term pot experiments (not included in meta-analysis) (Lehto, 1992a,b; Möttönen et al., 2001) a reduction in the number of root tips was the first morphological response to a drought treatment. In future studies the fine root density and the number of root tips per unit soil volume, or per unit root length or dry weight could be more frequently used as indicators of drought effects.

The rates of recovery of root indices from drought have been studied even less than the drought responses. Fine root growth and root tip formation can respond very quickly to resumed soil moisture (Joslin et al., 2000). Although the results of the meta-analysis here suggest that the drought effects were somewhat larger in longer-term experiments, this result was not significant. The papers in the meta-analysis included long-term drought experiments where there were probably very strong drought events (Swaty et al., 2004; Vanguelova et al., 2005). Studies with other types of approaches such as the examination of fine root regeneration potential in different levels of drought stress in a modified ingrowth bag technique study, could give new light to this (Cudlin & Chmelíková, 1999).

Cenococcum geophilum (*C. graniforme*) is often mentioned as a particularly drought-tolerant fungus. However, with a few exceptions (Worley & Hacskaylo, 1959), there are few reports based on solid experimental work. Pigott (1982) carefully showed that *Cenococcum* survived better than other mycorrhizal fungi during a drought episode. It is also possible that the mycelium of *Cenococcum* is more persistent to decomposition than that of some other species (Meyer, 1987). Furthermore, the concepts of taxonomy of this fungus have varied with time, and the morphological identification is not easy because of easy confusion with other fungi. *Cenococcum* may also be tolerant to other stresses such as to increased ozone (Grebenc & Kraigher, 2007a,b) or salinity (Saleh-Rastin, 1976). Therefore its use as drought indicator has limitations. While the mycorrhiza formation by other species was strongly delayed in drought-treated plants, *Thelephora terrestris* formed abundant mycorrhizas irrespective of watering treatment (Lehto, 1992c). Differences in community structure in drought conditions can therefore be expected also in forests.

Conclusions

- Fractional colonization of ectomycorrhizas in natural systems was weakly or not reduced under any of the stressors. In laboratory and pot experiments; however, the reduction was significant under most if not all stressors.
- Tree fine roots length and biomass may be proposed as good indicators of soil acidification. According to the meta-analysis, these parameters respond to acidification with a significant decrease both in laboratory conditions and in field

experiments, regardless of whether the roots are mycorrhizal or non-mycorrhizal. However, besides the quantitative features of fine roots, some qualitative characteristics of ECM should be considered.

- The large variation in N responses among studies indicates that predictability of N deposition effects on fine roots and their mycorrhizas for any given ecosystem is relatively low. Meta-analysis indicates considerable robustness and stability of ECM fine roots under conditions of nitrogen fertilization.
- All effects of ozone on below-ground processes are indirect, acting through carbon source–sink regulation, and chronical effects have been found to differ in the age and time-scale of the exposed plants and length of fumigation. The overall effects on root and ECM as detected by meta-analysis were equal to zero. Therefore these parameters do not seem to be appropriate bio-indicators used for revealing early effects of ozone on forest trees and forest ecosystems. However, they should nevertheless be studied to provide functional insights in different forest stands, forest tree mixtures and different developmental phases, since the long-lasting effect on forest stability and regeneration processes (impact on seedlings was negative!) seems to be predictable. Also shifts in ECM community structure were detected, but not subjected to meta-analysis, both in adult trees and young plants. A clear differentiation to ozone-sensitive and ozone-tolerant ECM species might not be determined; however, a step forward might be in establishing functional groups of ECM types, more or less sensitive to changes in carbon allocation below-ground, and in further revelation of the physiology, and thus bio-indication value, of each of the ECM types or groups.
- The consistent increase in below-ground allocation due to elevated CO_2 makes fine roots and ectomycorrhizas suitable for monitoring purposes. However, this measurable larger carbon flow below-ground will in most cases not translate into increased tree growth and forest productivity.
- The drought response of fine root biomass was the clearest result found in meta-analysis in this work, in addition to acidic deposition. Although studies on fine root and mycorrhiza responses to drought are very labour-intensive, they can yield very useful information about the damage caused by drought.

Acknowledgements

This collaborative effort was made possible by EU/ESF funding to COST action E38, Woody Root Processes. O. Alberton thanks the Graduate School PE&RC of Wageningen University for support. The research of P. Cudlin was supported by the Research Plan of the Institute of Systems Biology and Ecology, v.v.i.: AVOZ60870520 and research project of the Ministry of Education OC38.001. H. Kraigher and T. Grebenc contributed through the research programme P4-0107 and several projects, funded by the Slovenian Ministry for Higher Education, Science and Technology and the State Agency for Research and Development.

Literature data were extracted and commented on by B. Kieliszewska-Rokicka (acidic deposition), M. Rudawska (nitrogen deposition), T. Grebenc and H. Kraigher (ozone), elevated CO_2 (O. Alberton and T.W. Kuyper, for which the meta-analysis by Alberton et al., 2005 formed the basis), and drought (P. Cudlin and T. Lehto). M.R. Bakker, I. Børja, B. Konôpka and T. Leski provided additional data for meta-analysis. The meta-analyses were executed by O. Alberton and T.W. Kuyper. P. Cudlin, H. Kraigher and T.W. Kuyper took the lead in drafting and editing the paper.

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