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Below-ground competitiveness of adult beech and spruce trees: resource investments versus returns

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SUMMARY

The aim of the field study was to quantify the below-ground competitiveness of 50 to 60-year-old beech (*Fagus sylvatica*) and spruce (*Picea abies*) trees by means of space-related cost/benefit relationships. The study was conducted at the experimental site "Kranzberger Forst" within the framework of the interdisciplinary research program Sonderforschungsbereich 607 (SFB 607; Project B4) *"Growth and Parasite Defence – Competition for Resources in Economical Plants from Agronomy and Forestry".* It was postulated that costs (resource investments) and returns (resource gains) as based on soil volume have the potential to quantify the plant competitive ability below-ground. This idea relates to the definition of Begon *et al.* (1996) that the competitive success of plants depends on their ability to acquire efficiently resources shared with neighbours from external pools located in a given space. The below-ground competitive ability (i.e. competitiveness) of beech and spruce was quantified by using three types of space-related cost/benefit relationships (i.e. "efficiencies", cf. Grams *et al.*, 2002): (1) Efficiency of below-ground space occupation (occupied soil volume per unit C investment into standing fine-root biomass), (2) Efficiency of below-ground space exploitation (resource uptake as related to the occupied soil volume), and (3) Efficiency of below-ground "running costs" (occupied soil volume per unit of C costs of root respiration to sustain occupation and exploitation of the occupied soil volume). Here, tree response to free-air ozone fumigation at the crown level (the O_3 regime was experimentally raised by a factor of 2 relative to the ambient O_3 regime; i.e. $1xO_3$ and $2xO_3$, respectively) was related to different water availability across the three experimental years (including the extraordinary summer drought of 2003) to analyse the belowground responsiveness of both competitors to disturbance under forest stand conditions.

The following hypotheses were to be evaluated: (i) Limited carbon gain by the foliage, as caused by O_3 stress or water limitation, results in stimulation of compensatory fine-root production; (ii) Spruce being more conservative in resource turnover is less affected below-ground by O_3 stress than beech; conversely, relative to beech, the root system of spruce is more affected by drought; (iii) O_3 exposure enhances the CO_2 efflux from the soil, whereas drought reduces CO_2 efflux; (iv) "Autotrophic" soil respiration (i.e. CO_2 release from roots + mycorrhizosphere) and "heterotrophic" soil respiration (i.e. respiration of free-living soil micro-organisms) differ in their response to changing soil temperature and soil water content, with higher sensitivity reflected in "autotrophic" soil respiration ; (v) The responses of beech and spruce plants to O_3 stress and water limitation depend on the type of competition (i.e. intra or interspecific); (vi) Below-ground competitiveness of adult beech and spruce trees is determined by similar efficiency ratios as above-ground competitiveness.

Sampling and analysis were conducted within the uppermost 20 cm of the soil where most intense below-ground competition between the neighbouring trees was expected. In addition, within this soil depth two soil sub-samples were distinguished according to the existing gradient in nutrient and water supply: *organic sub-sample* (consisting of the humus layer, and the humic topsoil (A-horizon)); and *mineral sub-sample* (consisting of the loamy B-horizon). At mono-specific subplots, the space occupied by roots was derived from the volume of the organic or mineral soil sub-sample which was extracted with a soil coring cylinder. At mixed subplots, a factor $\boldsymbol{k_c}$ (i.e. defined at the monospecific sub-plots under control conditions as the ratio between the soil volume and the volume of contained root biomass) was used to split the soil volume into parts occupied by beech or spruce roots, respectively. Bio- and necromass of the fine roots was monitored using soil coring and in-growth coring methods. In addition, the natural variations of $\delta^{13}C$ signature were assessed in newly formed fine-roots as obtained by in-growth technique. For assessment of the physiological, biochemical and morphological parameters, the fine-root fraction was differentiated into three functional categories according to root position and anatomy. Water uptake was studied *in situ* on intact fine rootlets by using the non-destructive approach of Göttlein et al. (2001) adapted to field conditions. Root respiration was measured with a portable, integrated infrared gas analyzer (IRGA) and gas exchange assessment system throughout the annual course and in response to temperature. Total soil respiration was assessed accordingly throughout the annual courses of 2002 and 2003. In addition, the root exclusion method was employed to differentiate between the components in total soil respiration, i.e. “autotrophic” and “heterotrophic” respiration. Available soil water content (calculated by S. Raspe, LWF, through LWF-BROOK90; Hammel & Kennel, 2001) and soil temperature data were used to parameterize a modelling approach for estimation of the annual “autotrophic” and “heterotrophic” soil respiration.

At monospecific sub-plots, beech responded to both disturbing factors (drought or ozone) with enhanced fine-root production and turnover. Spruce, in contrast, showed inhibited root growth under dry conditions, and had no response to enhanced O_3. Hence, *hypothesis (i)* was corroborated for beech and rejected for spruce in that resource limitation stimulated fine-root growth. The reduced fine-root production in spruce shows that this species is more affected below-ground by drought than beech, thus confirming *hypothesis (ii)*. The contrasting physiological root responses in these tree species to drought may relate with the different extent of water limitation underneath mono-specific spruce and beech groups during 2003. In contrast to beech, spruce which has not responded below-ground to O_3 showed aboveground decrease in stem diameter increment of fumigated trees (Wipfler *et al.*, 2005). Possibly, the capacity for ensuring sufficient nutrient supply for growth and/or repair processes *via* enhanced fine-root turnover is the “strategy of success” in beech to cope with

O_3 stress. In beech, the combination of factors "O_3+drought" influenced fine-root dynamics in a way similar to that by drought or O_3 impact alone, whereas in spruce such scenario induced responses similar as that caused by drought. At mixed sub-plots, only spruce showed different response to the studied scenarios remaining non-affected by drought in any of the studied root parameters (i.e. *hypothesis (v)* was confirmed only for spruce). Apparently the shallow fine-root system of spruce has profited from a more effective re-charge and use of soil water in beech/spruce mixed sub-plots relative to monospecific sub-plots.

In both species, beech and spruce, and independent of the type of competition, drought of 2003 reduced and O_3 exposure increased the total CO_2 efflux from the soil thus corroborating *hypothesis (iii)* and rejecting *hypothesis (v)*. In the context of "global change" scenarios with increase of O_3 levels, the risk of chronic O_3 stress to promote CO_2 efflux from forests with sufficient water supply cannot be ruled out. In both species, beech and spruce, "autotrophic" rather than "heterotrophic" soil respiration was sensitive to changing soil temperature and soil moisture (i.e. *hypothesis (iv)* was corroborated in both tree species). Drought limitation of "autotrophic" soil respiration was accompanied, on an annual basis, in both tree species by decrease in radial stem growth (according to P. Wipfler, pers. comm.), with spruce being more sensitive than beech.

Under control conditions, the below-ground competitive advantage of beech within the uppermost 20 cm of the soil was indicated by higher efficiency of space occupation and space exploitation, whereas the efficiency of "running costs" remained similar in both tree species. The competitive success of beech was associated with the capacity to exploit available resources *rapidly* from soil (i.e. via constructing fine-roots with high specific fine-root length). This finding supports the theory of Grime (1977), that *the competitive success is a reflection of the individual capacity to exploit resources rapidly*. Additionally, the present study shows that beech which was the superior competitor for light (Reiter *et al*., 2005) was the superior competitor also for soil resources (i.e. soil water). These results are in agreement with the other hypothesis of Grime (1977), *that superior competitors for light would be equally successful in competing for soil resources* (cf. section 1.1.2).

When focusing on space occupation within both soil sub-samples, beech was more efficient than spruce within the organic soil sub-sample, whereas spruce was more efficient within the lower mineral soil. Such "habitat partitioning" between both competitors resulted in decreased competition for water: Beech was more efficient in space exploitation within the mineral, whereas spruce was more efficient in space exploitation within the organic soil sub-sample. Such "habitat partitioning" may represent the mechanism allowing beech and spruce to coexist in a short-term scale. On the other hand, such kind of partitioning may result in a shift towards a more superficially distributed fine-root system of spruce in mixture with beech,

which suppose spruce to be at higher risk than beech at prolonged drought or regarding hazards like wind-throw.

The competitive below-ground advantage of beech over spruce vanished under chronically enhanced O_3 exposure independent of the type of competition: The disturbance through elevated O_3 lowered the efficiency of beech in below-ground space occupation and the efficiency of "running costs" relative to the corresponding efficiencies in control sub-plots. Spruce, in contrast, showed similar below-ground space occupation under both O_3 regimes and types of competition.

The novel approach of a quantitative, space-related assessment of cost/benefit relationships proved suitable to analyse the below-ground competitive ability of forest trees. Within the studied soil depth of 20 cm and under control conditions, the higher below-ground competitive ability of beech over spruce was reflected by higher efficiency in space occupation and space exploitation. Both "efficiencies" can be explained with higher morphological plasticity (i.e. specific fine-root length, turnover) of the beech fine-root system relative to spruce. In contrast, spruce fine-roots, which appear to be more expensive than beech fine-roots in terms of their structural costs per root length, were less efficient in space occupation and exploitation within the studied soil depth. Independent of the type of disturbance (i.e. drought or O_3-fumigation) beech maintained an enhanced fine-root production. Although the enhanced fine-root production is related with additional structural costs (i.e. lower efficiency in space occupation), on a whole-tree level beech was less imperilled to such disturbances than spruce.

ABBREVIATIONS

Abbreviation	Unit	Parameter
A	cm^2	Surface root area;
A_N	cm^2	Rootlet surface area at the time of harvest;
AOT40	nl l^{-1}	Accumulated exposure to ozone per year above a threshold of 40 nl l^{-1} O_3 and 50 W m^{-2} of total global radiation;
ASW	mm m^{-2}	Available soil water;
BRC	m^3 $g^{-1}C$	Belowground "running" costs
BSE	ml l^{-1} day^{-1}	Belowground space exploitation
BSO	m^3 $g^{-1}C$	Belowground space occupation
D	mm	Root diameter;
DW	g	Dry weight;
FRB_{min}	mg l^{-1}	Minimum standing fine-root biomass;
FRP	mg l^{-1}	Fine-root production;
FRR	%	Fine-root recovery rate;
k		The ratio between a given soil volume and the contained volume of the root biomass;
k_c		*k* assessed under control conditions (monoculture under ambient ozone levels);
l	gCO_2 m^{-2} h^{-1} per 1 °C	Correction factor accounting for stimulation effect of shed foliage on soil respiration rate;
L	cm	Total root length;
L_0	cm	Initial rootlet length;
L_i	cm	Rootlet length at a recording date i;
L_{mean}	cm	Mean standing rootlet length;
L_N	cm	Rootlet length at the time of harvest;
LR_{prim}		Long lateral roots with primary xylem;
LR_{sec}		Long lateral roots with secondary xylem;
M_{mean}	g	Mean standing rootlet biomass;
M_N	g	Dry biomass of the rootlet at the time of harvest;
MycTD	N cm^{-1}	Number of mycorrhized root tips per unit root length;
N_{RT}		Number of root tips;
N_{WRT}		Number of the non-pigmented white root tips;

NSC	mg g^{-1}	Non-structural carbohydrate concentration (integrates sucrose, glucose, fructose, pinitol (in case of spruce) and starch concentrations);
P	mm	Precipitation;
P_{an}	mm yr^{-1}	Annual precipitation;
PTR	%	Proportion of each of a given fine-root category in the total rootlet biomass;
PSV	%	Proportion of soil volume occupied by roots of a given tree species within a given soil sub-sample;
Q_{10}		Change in root respiration rate in response to a 10°C change in temperature;
RB	g	Root biomass;
RD	mg l^{-1}	Fine-root density;
RL	yr	Fine-root longevity;
RM	%	Fine-root mortality rate;
RN	g	Root necromass;
RP	g	Fine-root production;
RR	nmol CO_2 g^{-1} s^{-1}	Root respiration rate;
RT	%	Root turnover;
RR^{10}	nmol CO_2 g^{-1} s^{-1}	Root respiration rate at a standard temperature of 10°C;
RR^{T}	nmol CO_2 g^{-1} s^{-1}	Root respiration rate at a sample temperature T;
$RR^{T(0)}$	nmol CO_2 g^{-1} s^{-1}	Root respiration rate at a temperature $T_{s(0)}$;
RR_{beech}	nmol CO_2 g^{-1} s^{-1}	Species-specific root respiration rate in beech;
RR_{spruce}	nmol CO_2 g^{-1} s^{-1}	Species-specific root respiration rate in spruce;
RV	cm^3	Root volume;
SDI	cm	Stem diameter increment measured at 1.30 m
ShR		Short mycorrhizal roots
SR_t	gCO_2 m^{-2} h^{-1}	Total soil respiration;
SR_a	gCO_2 m^{-2} h^{-1}	"Autotrophic" soil respiration rate;
SR_h	gCO_2 m^{-2} h^{-1}	"Heterotrophic" soil respiration rate;
SR^{10}	gCO_2 m^{-2} h^{-1}	Soil respiration rate standardized to a temperature of 10°C;
SRA	cm^2 g^{-1}	Specific root area;
SRL	cm g^{-1}	Specific root length;
STD	N cm^{-1}	Specific root tip density
SV	cm^3	Soil volume;

SV_{pr}	cm^3	Predicted soil volume which should to be occupied by roots of a given tree species in mixed cultures;
SWC	%	Volumetric soil water content;
SWU_M	ml g^{-1} day^{-1}	Daily water uptake rate of the rootlets per mean standing root biomass;
SWU_{RP}	ml g^{-1} day^{-1}	Daily water uptake per unit of newly produced fine roots;
SUM0	nl l^{-1}	Accumulated exposure to ozone per year;
T_{air}	°C	Air temperature;
T_s	°C	Soil temperature;
$T_{s(0)}$	°C	Mean daily soil temperature as monitored at 0 cm soil depth;
TGR	kWh m^{-2}	Total global radiation
TSC	mg g^{-1}	Total sugar concentration (integrates sucrose, glucose, fructose, and, in case of spruce, pinitol concentrations);
TSV_{pr}	cm^3	Predicted total soil volume;
V	cm^3	Root volume;
W	ml	Cumulative water uptake of the rootlets per rhizotrone;
W_i	ml	Water consumption by rootlets at a recording date i;
WU	ml day^{-1}	Daily water uptake rate of the rootlets;
WUE	mmol mol^{-1}	Water-use efficiency
$\delta^{13}C$	‰	$^{13}C/^{12}C$ ratio;

1 INTRODUCTION

1.1 Theories of plant competition

A series of influential works, ever since Darwin, suggest that species interactions such as competition are the major impediment to species coexistence and community diversity, and that competition plays a major role in shaping the structure of communities (Grace & Tilman, 1990). C*ompetition is an interaction between individuals, brought about by shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned* (Begon *et al*., 1996). According to this definition, the competitive success of the individual plant depends on the ability to efficiently acquire resources shared with neighbours. The competitive interactions between neighbours can be *intraspecific* (between individuals of the same species) or *interspecific* (between individuals of different species).

Burkholder (1952; after Grace & Tilman, 1990), in classifying the possible ways by which two species may interact, used the term *competition* for a reciprocal negative interaction *(- , -)* and the term *amensialism* for one-way negative interaction *(0, -).* The term amensialism was replaced later, according to Connell (1983), by the term *"asymmetrical" competition*. "Asymmetrical" competitive plant interactions were found by Connell (1983) in about 65% of the studied cases. Further, Keddy & Shipley (1989) distinctly defined plant-plant interactions as *asymmetric* and *symmetric competition*. *Asymmetric competition* takes place when the intraspecific competition is stronger for one species (the dominant one) than the interspecific competition, while for the other species (the subordinate one) the interspecific competition is stronger than the intraspecific competition. Consistently, *symmetric competition* in a two-species system occurs when the interspecific competition is stronger for both species than the intraspecific competition.

1.1.1 Mechanisms of competition

Goldberg (1990) developed a mechanistic framework for studying interactions between plants. The framework is based on the observation that most interactions between individual plants actually occur *indirectly* through some intermediary (e.g. resources) and consist of two distinct processes: one or both plants have an *effect* on the abundance of the intermediary and a *response* to changes in abundance of the intermediary (**Fig. 1**).

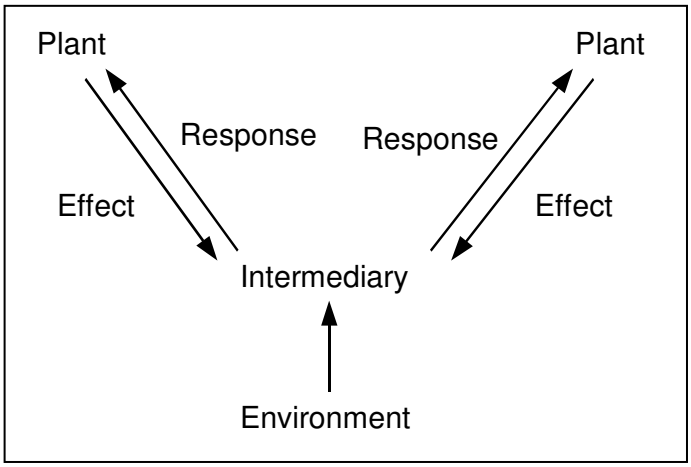

Figure 1*:* The effect and response components of indirect interactions between plants. The intermediary could be resources, mutualists, natural enemies or even toxins, (from Goldberg, 1990).

Effect on a particular resource is defined as the per-individual or per-unit size rate of change in the resource availability at a given abiotic supply rate. The most obvious mechanism through which the plant can affect resource availability is *depletion due to uptake.* Although depletion of light by plants has often been measured, less is reported about the magnitude of effects on nutrients or water in the field. The magnitude of uptake effects is determined by physiological activity rates and allocation to and spatial arrangement (architecture) of resource-acquiring organs. Caldwell & Richards (1986) have argued that allocation and architecture are of greater importance than physiological activity rates in determining relative effects on resources among similar-sized plants.

Response to resources is defined as the relationship of some components of fitness (growth, reserve storage, fructification and defence; Bazzaz & Grace, 1997) to resource availability, where availability is determined by one or both of the neighbouring plants along with the abiotic environment. When the resource is limiting, response will be determined by the excess of uptake over loss of the resource and the new biomass (or seeds) that can be produced per unit of internal stores. Assuming that growth is positively correlated with fitness, there are three possible ways in which a plant may increase its fitness at low resource levels: (1) increased resource uptake, (2) decreased resource loss, and/or (3) increased efficiency of conversion of internal stores into new growth (Chapin *et al*., 1987).

Mechanisms such as directly harming a neighbouring plant, e.g. release of toxic substances, mechanical abrasion or direct overgrowth are involved in the *direct interactions* between competing plants. The result of such interactions can also affect the abundance of the intermediary resource (Goldberg, 1990; Gersani *et al*., 2001; Reiter, 2004).

1.1.2 Determining the competitive success in plants

When competition is between individuals of similar size, *effect* on resources and *response* to resources of both species must be taken into account to determine their net interaction. The competitive success of each individual can be ranked in view of such effects and responses, depending on the extent of suppressing or tolerating the neighbour. Two classical theories exist on the determinants of competitive ability: The one was posed by Grime and the other by Tilman (both reviewed by Grace, 1990). **Grime** (1977) associates competitive ability with traits that maximize resource capture by individuals, *i.e. the competitive success is a reflection of the individual capacity to exploit resources rapidly.* In his scheme, those plants that during their live history are adapted to low levels of *stress* (defined as "the external constraints which limit the rate of dry-matter production of all or part of the vegetation") and *disturbance* (defined as "mechanisms which limit the plant biomass by causing its destruction") are referred to as "competitive". Additionally, Grime supports the idea that *superior competitors for light would be equally successful in competing for soil resources.* In contrast, **Tilman** (1982) *defines a superior competitor for a resource as one whose population can deplete the resource to a lower level at equilibrium.* The species with the lowest resource requirement will then competitively displace all other species at equilibrium. However, when the community is not at equilibrium, traits other than the ability of individuals to tolerate low resource levels become important. Moreover, Tilman supposed that plants face a trade-off between their efficiency to compete for above- and below-ground resources, and hence *good competitors for light would have a low ability to exploit soil nutrients.*

As shown above, the differences in concepts of expressing competitive ability between Grime and Tilman are consistent also with their different assumptions about trade-offs for different resources. These discussions so far have assumed that resource supplies are constant. However, in nature, soil resources are often supplied by pulses due to sporadic rainfall and the effects of temperature, moisture or organic deposition on microbial activity. When resources occur by pulses, species with rapid uptake are more likely to be able to take advantage of the pulse than are slower-growing species with low uptake rates but tolerance of low resource levels (Grace, 1990).

In addition to the allocation in primary metabolism (growth), plants have other resource demands related to the defence (secondary) metabolism (Herms & Mattson, 1992; Matyssek *et al*., 2002). Hence, the competitive success depends on the efficiency of plant "allocation strategies", i.e., the internal conflict (or trade-off) in the allocation of the internal resources (carbon, water, nutrients) to the different sinks (growth and/or defence; **Fig. 2**).

The conceptual model proposed by Herms & Mattson (1992) claims that increasing (external) resource availability from the level of limitation towards saturation does reduce the proportion of secondary metabolites along with an increase in primary production. This reduction is believed to occur at the expense of defence but in favour of a stimulated primary metabolism and, as a consequence, fostered plant competitiveness (www.sfb607.de). This view supports Grime's theory according to which the *abiotic stress* (defined as disturbance reflected, e.g. by increased allocation to secondary metabolism) is related to competition, whereas the *importance of competition* (concerning growth as an outcome of competition and indicator of individual fitness) decreases with increasing stress (Donovan & Richards, 2000). However, the long-lived woody plants may reflect a "defence strategy" that differs along gradients of natural productivity in quantitative and qualitative ways in relation to the primary and secondary metabolism (Ladd & Facelli, 2005).

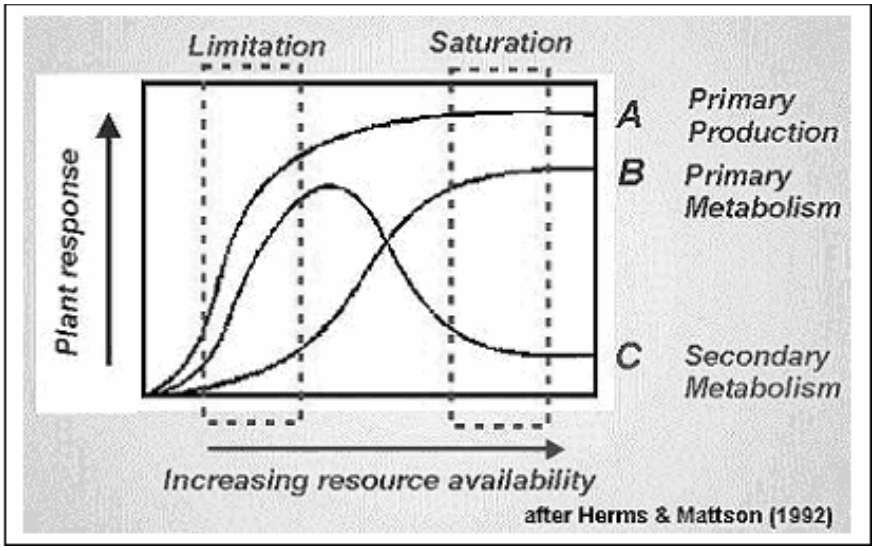

Figure 2*:* The conceptual model of resource allocation (adapted from Herms & Mattson, 1992; from Matyssek *et al*., 2002) along increasing resource availability, and the trade off between primary and secondary metabolism.

1.1.3 Quantifying the competitive success in plants: investments vs. returns

The competitive success in plants depends on the efficient allocation of nutrients and assimilates to the different resource sinks (Bazzaz & Grace, 1997). Plants must balance their functionality between (1) *resource costs (**investments**)*, i.e., investment of internal resources in structures for space sequestration (i.e. of the above- or belowground space that harbours the external resources) and maintenance of such structures (resource-capturing organs) within the occupied space, and (2) *resource benefits (**returns**)*, i.e., acquisition of resources from external pools which are shared with the neighbours. To understand competitiveness of

plants, quantitative assessments of the resource *cost/benefit* relationships are necessary (Matyssek *et al.*, 2002; Reiter *et al.*, 2005; Kozovits *et al.*, 2005a, b). To this end, three types of space-related investment-return ratios (called "efficiencies") were defined (Grams *et al.*, 2002):

(1) *space occupation* (occupied above or below-ground space per unit of resource investment, e.g. of biomass);
(2) *resource gain* (resource acquisition per unit of resource investment, or of occupied above and below-ground space);
(3) *"running costs"* by respiration and transpiration (i.e. per unit of sequestered volume) for sustaining the occupied space and the functionality of organs involved in competition.

Such efficiencies allow, in an economic context, the mechanistic and quantitative analysis of competitive success of hedgerow and woody species (Küppers, 1984; Küppers, 1985; Reiter *et al.*, 2005; Kozovits *et al.*, 2005a). However, such "efficiencies" have been assessed mainly for the aboveground plant organs (Küppers, 1984; Küppers, 1985; Reiter *el al.*, 2005; Kozovits *et al.*, 2005a). The definition of these efficiencies is based on the consideration that plants must to balance their resources between development and maintenance of structures responsible for occupation of space (above- and below-ground) and, through this, ensuring the effective acquisition of new resources within this space (Matyssek & Schulze, 1987).

1.2 Below-ground competition

Belowground competition occurs when plants decrease the growth, survival, or fecundity of neighbours by reducing available soil resources (Casper & Jackson, 1997). In contrast to the aboveground competition amongst plants which primarily involves a single resource, namely light, plants compete for a broad range of soil resources, including water and several mineral nutrients that differ in molecular size, valence, oxidation state, and mobility within the soil. According to Begon's definition of competition (cf. section 1.1) and Goldberg's mechanistic framework for resource-mediated competition (**Fig. 1**), the limited level of the intermediary (here, soil resources) has a negative impact on the performance of the competing plants measured per individual plant, or per unit plant size. Unlike competition for light, in which larger plants have a disproportionate advantage by shading smaller ones, competition for soil resources is apparently more *symmetric* (Casper & Jackson, 1997). However, below-ground, the ability to take up soil resources and the competitive ability are not necessarily correlated, e.g. as in the case of *habitat partitioning* by growth into deep soil horizons and tapping of water reserves which are unavailable to shallow-rooted neighbours (Casper & Jackson, 1997). This kind of partitioning may decrease competition for water. Plants also differ in their ability to convert soil resources to biomass, referred to as water-use efficiency or nutrient-use

efficiency (Nobel, 1991; after Casper & Jackson, 1997), which can affect relative plant growth rates across a soil resource gradient even in the absence of below-ground interactions. In addition, direct interference in plant competition through allelopathy (Olofsdotter *et al*., 2002), competition between plants and soil micro-organisms (Kaye & Hart, 1997), or mycorrhizae do alter interactions between root systems in complex ways (Bauhus & Messier, 1999).

1.2.1 Mechanism of below-ground competition

Since the mechanism through which plants can affect soil resource availability is depletion *due to resource uptake* (e.g. *indirect root interactions,* see **Fig. 1**), three general processes by which soil resources can pass the root surface are involved in below-ground competition (Casper & Jackson, 1997):

1. root interception: the capturing of water and nutrients as the root grows through the soil, physically displacing soil particles and clay surfaces;
2. mass flow of water and dissolved mineral nutrients: is driven by plant transpiration, and is a function of the rate of water movement to the root and the concentration of dissolved nutrients in the soil solution; is more important for uptake of nitrogen, especially nitrate;
3. diffusion: occurs when nutrient uptake exceeds the supply by mass flow, creating a local concentration gradient; is especially important for nutrients with large fractions bound to the solid matrix, such as potassium and phosphate.

Besides root interception (accounts for less than 10% of the resource uptake by roots and is the least important of the three processes), resource uptake (e.g. competition) via diffusion has received the most attention, since the neighbouring roots reduce nutrient uptake when nutrient depletion zones (i.e. the radius of the concentration gradient around roots; Walker *et al*., 2003) overlap. Soil moisture and soil type were predicted to be the major determinants of diffusive nutrients supply in the soil, and therefore the primary factors determining the mechanisms of below-ground competition (Volder *et al*., 2005; Raynaud & Leadley, 2004). This concept is less applicable to water and dissolved nutrients that are primary supplied by mass flow. Regarding such nutrients, aboveground characteristics, such as maximum transpiration rate or stomatal conductance, will both affect water uptake and will be affected by the rate of water uptake (Schulze *et al*., 1994). Therewith, the most efficient way for a plant to compete whit its neighbour is to take the resource before its neighbour does and such *indirect root interactions* may favour speed over efficiency of nutrient uptake (Nobel 1991).

In addition to competition through resource depletion, contest competition may occur where the roots of different individuals may *interact directly* by releasing organic compounds, such as: toxic exudates that inhibit the growth of the neighbouring plants (Bais *et al*., 2003) as well as releasing of non-toxic signals that indicate an individual's presence (Bruin *et al*., 1995). Such direct interactions may allow assessment of the origin of neighbouring roots (as self or non-self, Gersani *et al*., 2001). Schenk *et al.* (1999) expect such responses to ensure that root systems of different plants achieve a high degree of segregation (as shown for beech and spruce roots in Schmid & Kazda, 2005). Such "ownership" of space allows a plant to favour efficiency rather than speed of uptake when developing its root mass, architecture, and uptake kinetics (Gersani *et al*., 2001). Understanding the mechanisms that control plant competition for soil nutrients is an essential step in predicting the outcome of interspecific competition, the role of niche differentiation in plant competition, and the interactions between plant diversity and ecosystem functioning (Tilman, 1988).

1.2.2 Quantifying the competitive ability in plants below-ground

To understand the complex mechanisms of competition for soil resources, Casper & Jackson (1997) consider morphological and physiological root attributes which correlate with the below-ground competitiveness of plants (**Fig. 3**).

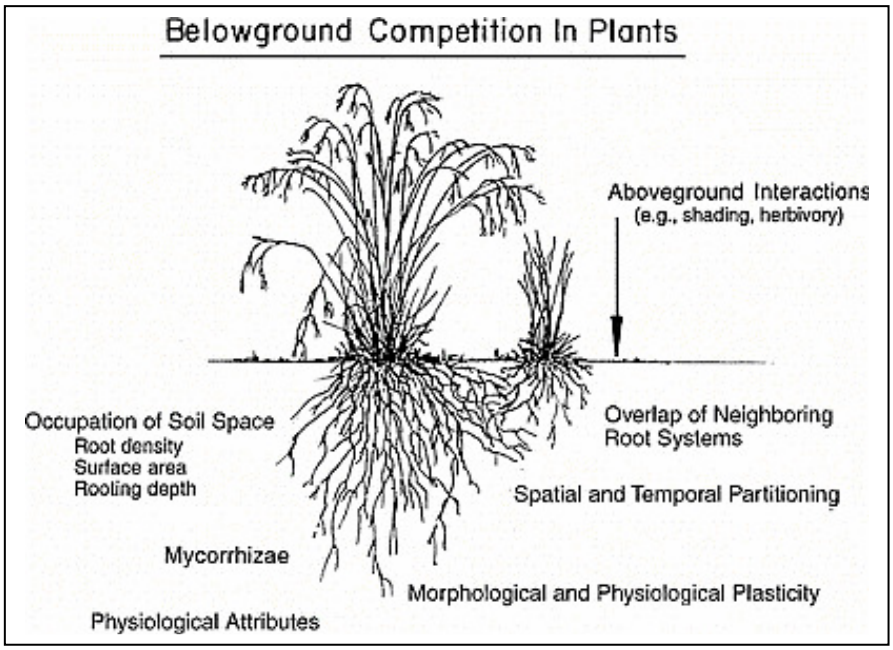

Figure 3: Plant traits that determinate below-ground competitive ability, from Casper & Jackson (1997).

The occupation of soil space is of primary importance in below-ground competition and is predicted to play a predominant role for uptake of nutrient ions that have a low diffusive supply in the soil (Raynaud & Leadley, 2004). The ability to occupy space is found to depend on several root characteristics related to root abundance, such as: relative growth rate,

standing biomass and fine root longevity (Leuschner *et al*., 2001); or to morphological root characteristics such as specific fine-root length (Grams *et al*., 2002; Kozovits *et al*., 2005a) and root surface area (Raghothama & Karthikeyan, 2005). However, root abundance alone is insufficient to explain the relative uptake rates among different tree species. In two grasses, Caldwell *et al.* (1991) found the same acquisition of phosphate from nutrient patches despite the difference in the root biomass. Other factors, such as *mycorrhizae* and their *spatial and temporal partitioning* may explain the lack of close relationships between root density and the outcome of competition. The ability to quickly adjust in *morphological* (demographic and architectural) or *physiological* terms (enzymatic alterations, osmoregulation) to changes in the local environment is defined as *plasticity* and is crucial for the competitive ability of plants (Bliss *et al*., 2002; Hodge, 2004). This feature allows plant roots to proliferate into nutrient-rich patches (Huang & Eissenstat, 2000); however, the costs of morphological plasticity, uptake kinetics and mycorrhizal activity should by taken into account (Gersani *et al*., 2001). For instance, Huang & Eissenstat (2000) report numerous evidences about considerable energy investments related to patch space exploitation below-ground.

Traditionally, below-ground competition is quantified by the extent of reduced resource uptake, vegetative growth or proliferation due to root interactions (Gersani *et al*., 1998; O'Brien *et al*., 2005). The methods which are used for estimating below-ground competition often affect soil environment, and hence, constrain sharing of resources. Another approach which involves less manipulation is based on the estimation of changes in shared resources, but problems of scaling may result. Casper & Jackson (1997) recommend combined approaches to document both the resource intermediary and the significance of root interactions on below-ground competition.

There is ongoing debate on the determinants by which species may be successful in competition under changing environmental conditions, and on the relative importance of competition *per se* in determining species composition of plant communities (Chesson, 2000). This question can be elucidated through productivity gradients as resulting from such in resource availability. Such a gradient was experimentally employed within the framework of the interdisciplinary research program Sonderforschungsbereich 607 (SFB 607) *"Growth and Parasite Defence – Competition for Resources in Economics of Plants from Agronomy and Forestry".* A twice-ambient O_3 regime (maximum level restricted to 150 nl l^{-1}) was employed to curtail carbon availability in plants upon O_3-induced reduction of photosynthesis. In this context, ozone was not regarded as an air pollutant, but as an analytical tool to experimentally invoke disturbance in the carbon allocation of trees – i.e., to derive regulatory mechanisms in allocation from the response to this kind of disturbance (Matyssek *et al*., 2002).

1.3 Competitiveness under the influence of ozone

The tropospheric O_3 concentration has been increasing for several decades (Fabian, 2002), and may nowadays reach peak concentrations of 100-200 nl l^{-1} in urban areas (Musselman *et al.*, 1994). It is widely recognised that this increase in ozone results from anthropogenic pollution (e.g., car traffic, industry) at the local or trans-regional scale, and that ozone can affect vegetation when exceeding natural, pre-industrial levels (Matyssek *et al.*, 1995). One important sink is the degradation and uptake of tropospheric ozone by plants.

1.3.1 Ozone impact on forest trees

Ozone enters plants by diffusion through stomata into the mesophyll. Injury to plant leaf tissue results from oxidation of biological compounds by O_3 and derivates like free radicals (Mittler, 2002; Edreva, 2004), adversely affecting biochemical and physiological processes (Polle, 1998). Ozone-induced alterations in plant growth and biomass allocation are documented in crops (McCrady & Andersen, 2000), seedlings (Andersen & Rygiewicz, 1995), and juvenile trees (Utriainen & Holopainen, 2001; Uddling *et al.*, 2004). The O_3 effects on above-ground plant parts may incite growth and crop reduction (Matyssek & Innes, 1999; Giles, 2005), stimulation of carbonyl emissions from leaves (Cojocariu *et al.*, 2005), enhanced low-molecular antioxidant concentrations in leaves (Grulke *et al.*, 2003), increased phenolics in leaves (Saleem *et al.*, 2001), enhanced 1-aminocyclopropane-1-carboxylate (ACC) level, reduction of gas exchange and accelerated foliar senescence in fall (Matyssek *et al.*, 1992; Grulke *et al.*, 2002; Nunn *et al.*, 2005a). O_3 injury is a consequence of the O_3 uptake exceeding the detoxification capacity of the leaf mesophyll (Matyssek *et al.*, 2004). However, ozone impact on mature forest trees has rarely been examined experimentally; in particular, (indirect) O_3 effects on below-ground processes are hardly understood.

Several studies in juvenile and adult forest trees suggest a reduction in C allocation to roots under both short-term and long-term ozone exposures (Scagel & Andersen 1997; Grulke *et al.*, 1998; Matyssek & Sandermann, 2003). The higher C demand in leaves under O_3 stress is reflected by C limitations within the root system which can disrupt their prominent function to store the carbohydrate reserves (Andersen, 2003). In controlled experiments, ozone fumigation of Ponderosa pine seedlings reduced the available starch reserves within fine and coarse roots during the following spring (Andersen *et al.*, 1991). Additionally, changes in the translocation of photosynthate to sinks in roots lead to altered interactions with rhizospheric micro-organisms (Andersen & Rygiewicz, 1995; Scagel & Andersen, 1997; McCrady & Andersen, 2000; Andersen, 2003). Often the observed stimulation in bacterial and fungal

biomass disappeared after two years of O_3 fumigation (Kasurinen *et al*., 1999), or decreased at higher O_3 levels compared to the control (Scagel & Andersen, 1997).

Although below-ground O_3 effects have been frequently observed in controlled conditions, ozone effects on roots of mature forest trees have rarely been documented. Most of the reports are from forest sites in the San Bernardino Mountains, California, where the specific climatic conditions combine with the air pollutants from Los Angeles, resulting in elevated chronic O_3 exposure at the local forest sites (Grulke *et al*., 1998). Ponderosa pine and Jeffery pine being most sensitive to O_3 showed depressed monosaccharide concentrations in fine and coarse roots (Grulke *et al*., 2001) and a strong reduction in root biomass at the most polluted relative to the least polluted site (Grulke *et al*., 1998). Simulated root dynamics of individual adult sugar maple trees using the TREEGRO model (Retzlaff *et al*., 1996) confirm the decline of fine and coarse root production as a response to ozone exposure. The reductions in above- and below-ground biomass, and decreases in root exudation, root and hyphal turnover due to elevated ozone levels can also significantly lower the C sink strength and C input into the soil (Loya *et al*., 2003). O_3 can alter C flux to soils also by changing leaf litter quality (Saleem *et al*., 2001). Since belowground C allocation drives soil respiration (Högberg *et al*., 2001), O_3 may induce changes in soil CO_2 efflux. Experimental studies on Ponderosa pine seedlings (Scagel & Andersen, 1997) show increasing soil CO_2 efflux in response to O_3. In forests, the response of soil respiration to ozone fumigation has not been documented so far. A detailed review that emphasises O_3 impact on physiological processes within the complex plant-soil continuum is presented by Andersen (2003). The conceptual diagram of this review (**Fig. 4**) shows the positions at which O_3 disrupts the carbon flow in a tree-soil system. Included is the transfer between below-ground biotic and abiotic components that influence soil physical and chemical properties. Andersen (2003) points out that future effort should be directed to quantifying changes that occur below-ground in response to O_3, and to their potential impact on the long-term stability of ecosystems. However, the simultaneous influence of a multitude of interacting factors (e.g., N deposition, drought events) makes it difficult to ascertain ozone specific reactions of forests (Grulke *et al*., 2002; Grulke *et al*., 2003).

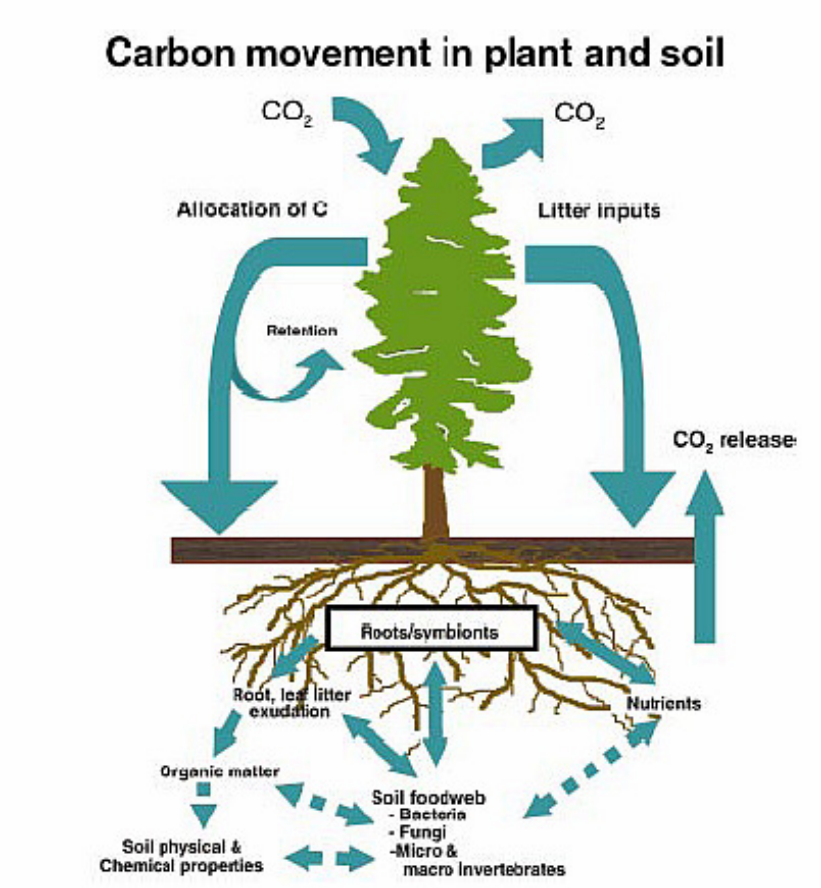

Figure 4*:* Ozone effects on the C flow in a tree-soil system: arrows denote carbon flux pathways that are affected by O_3. Dashed lines indicate where impact of O_3 is expected but unknown (from Andersen, 2003).

1.3.2 Ozone fumigation experiment at "Kranzberger Forst"

Investigations of the impact of ozone on young woody plants have typically been carried out in fumigation chambers (Saurer *et al*., 1995; Kozovits *et al*., 2005; Nunn *et al*., 2005b), where even minor ozone effects could be identified as a result of the well defined, controlled conditions. Even open-top chamber experiments (Blaschke, 1990; Isebrands *et al*., 2001; King *et al*., 2001) were limited to young trees. A novel free-air system for the O_3 fumigation of entire canopies was developed recently by Werner & Fabian (2002). This system is installed in a mixed stand "Kranzberger Forst" near Freising (Germany) consisting of about 25-30 m high spruce and beech trees which are 50 to 60 years old (Pretzsch *et al*., 1998). The system has been operated since May 2000 in the framework of the interdisciplinary research program Sonderforschungsbereich 607 (SFB 607) *"Growth and Parasite Defence – Competition for Resources in Economics of Plants from Agronomy and Forestry".* During the first phase of this program, the main aim of the research was to clarify the efficiencies by which space is being sequestered, exploited and sustained under contrasting environmental conditions (Reiter, 2004, Reiter *et al*., 2005). Nunn et al. (2005a) summarize responses of structural, phenological, physiological and biochemical parameters to high O_3 doses in beech and spruce at that site across three growing seasons (from 2000 to 2002). Responses of

some parameters (e.g. length of growing season, leaf injury) tended to decrease from 2000 to 2002 and showed large variations at the different scaling levels and between foliage types and growing seasons.

1.4 Competitiveness under the influence of drought

Drought represents the major constraint on plant growth and productivity in most terrestrial plant communities (Chaves *et al.*, 2002). Periods of soil and/or atmospheric water deficit often occur during a plant's life cycle even outside the arid/semi-arid regions, as reported for temperate forests (Law *et al.*, 2000). Water limitation can prove to be a critical constraint to primary production under future climate scenarios of global change (Kalvova & Nemesova, 1997; Ciais *et al.*, 2005). The plant's competitive ability strongly relies on the water availability during growth. In this way, the sequestration of the resource water is the pre-requisite for growing structures, occupying space, exploiting that space for resources and, as a consequence, out-competing neighbouring plants (Matyssek, 1999). In order to occupy and exploit space, the rapidity in space occupation (e.g. the growth rate) is crucial for the competitive success relative to neighbours. The implications of water shortage for the metabolism and growth of trees have been studied intensively with emphasis mainly on above-ground processes, and prognoses at the whole-tree level are greatly limited by the lack of below-ground investigations (Joslin *et al.*, 2000; Leuschner *et al.*, 2001). Furthermore, the root-growth strategies were found to differ distinctly between conifers and angiosperm tree species (Bauhus & Messier, 1999; Schmid & Kazda, 2005). Consequently, a multi-level whole-tree approach has to be adopted for quantifying drought responses of adult trees in context of plant competition (Bréda & Granier, 1996).

Plant strategies to cope with drought normally involve a mixture of stress *avoidance* (e.g. deep rooted perennials or winter/spring annuals) and *tolerance* "strategies" (e.g. drought-tolerant sclerophyls) that vary with genotype. Plants can also endure drought conditions by avoiding tissue dehydration, while maintaining tissue water potential as high is possible, or by tolerating low tissue water potential. Dehydration avoidance is associated with a variety of adaptive traits: (1) minimising water loss (e.g. by closing stomata, shedding of older leaves) and (2) maximising water uptake (e.g. by adjusting the allocation pattern, namely increasing investment in the roots; Jackson *et al.*, 2000). Plant adjustments to the low resources include altered leaf and/or root structure: whereas short-lived organs can be discarded in response to stress, long-lived organs must optimise their resource gain. This response results in lower turnover rates and therefore higher nutrient-use efficiency, which means that plants can partially compensate for lower rate of carbon gain by investing less in new constructions

(Casper *et al*., 2001). However, long-lived structures have to tolerate and survive periods of hostile environment, which require various protective mechanisms ranging from anatomical and morphological characteristics to the biochemical mechanisms as osmotic adjustment (Smirnoff, 1995). Another tolerance strategy to survive the dry season is the partial plant dormancy (Mittler *et al*., 2001). Acclimatory changes in the root/shoot ratio or the temporary accumulation of reserves in the stem under water deficit are accompanied by alterations in carbon and nitrogen metabolism, the fine regulation of which is still largely unknown (Pinheiro *et al*., 2001).

Under severe drought, it has been documented for soybean seedling experimental system (Matyssek *et al*., 1991) that the water capacitance of roots does not support the above ground growth, rather the roots exploit their own water storage and that of the shoot for assuring their own growth. This behaviour appears to be the reason for the typically enhanced root/shoot ratio of plants which grow under edaphically dry site conditions (Matyssek, 1999). For forest trees it has been reported that species with deeper root systems and higher root/shoot ratios are generally better adapted to dry climatic regimes than shallow-rooted species (Caldwell & Richards, 1986; Kozlowski *et al*., 1991). Additionally, several experimental studies indicate that, when trees experience moisture stress in one part of the rooting zone, root growth increases in areas where water is still available, usually at grater depths (Hendrick & Pregitzer, 1996). However, Osunubi & Davies (1981) found this to be the case for seedlings of a deep-rooted tree species, but not for a shallow-rooted species. Typically in dry habitats was found that taproots reaching deep and moist soil horizons or the groundwater table provide water to the horizontally growing, shallow fine-root zone underneath the soil surface, where root turn-over can be high (so called “hydraulic lift”, Caldwell & Richards, 1989). By this, the environment (rhizosphere) within the shallow root zone becomes favourable and stimulates for further root growth. The water released from roots has implications for biotic interactions with rhizospheric organisms and other plants attracted by the upper-most soil horizons.

In the southern part of Central Europe (where the experimental site is being situated) the summer of 2003 was characterised by above-average insolation, distinctly enhanced daily mean temperatures and exceptional drought conditions (Raspe, 2003). Such extremes regarding Central-European summer conditions set the stage for evaluating the below-ground responsiveness of both competitors to drought in a mixed beech-spruce stand “Kranzberg Forst” near Freising/Germany.

1.5 Aim of the study

The focal point was on the tree root activities at the experimental site “Kranzberger Forst”. In consistency with previous aboveground studies (from 1999 to 2002; Reiter *et al*., 2005), the main aim was to quantify the physiological basis of belowground competitiveness between deciduous broad-leaved *Fagus sylvatica* and evergreen coniferous *Picea abies* trees which grew in a mixed forest during the experimental period of 2002 through 2004. Both species are strong competitors according to comparable ecological power (Otto, 1994), and are of major economic interest in Central-European forestry. In the present work, the below-ground competitive ability of the experimental plants was investigated through combining conventional with novel approaches of a quantitative, space-related assessment of cost/benefit relationships. These latter approaches had successfully been used in previous studies of aboveground competitiveness (Grams *et al*., 2002; Reiter *et al*., 2005; Kozovits *et al*., 2005a, b). From main interests is to assert the explanatory power of the space-related “cost/benefit relationship” approach for competition-related below-ground studies. In the present work, tree response to free-air ozone fumigation at the crown level was related to different water availability across the three experimental years (including the extraordinary summer drought of 2003) to analyse the belowground responsiveness of both competitors to disturbance under forest stand conditions.

<u>The hypotheses to be examined were:</u>

(i) Limited carbon gain by the foliage, as caused by O_3 stress or water limitation, results in stimulation of compensatory fine-root production;

(ii) Spruce being more conservative in resource turnover is less affected below-ground by ozone stress than beech; conversely, relative to beech, the root system of spruce is more affected by drought;

(iii) Ozone exposure enhances the CO_2 efflux from the soil, whereas drought reduces this efflux;

(iv) “Autotrophic” soil respiration (SR_a: by roots and mycorrhizosphere) and “heterotrophic” soil respiration (SR_h: by free-living soil micro-organisms) differ in their response to changing soil temperature and soil water content, with higher sensitivity reflected in SR_a;

(v) The responses of beech and spruce plants to O_3 stress and water limitation depend on type of competition (i.e. intra- or interspecific);

(vi) Below-ground competitiveness of adult beech and spruce trees is determined by similar efficiency ratios as above-ground competitiveness.

2 MATERIAL AND METHODS

2.1 Site description

Measurements were made in a mixed forest of adult European beech *(Fagus sylvatica* L.*)* and Norway spruce *(Picea abies* [L.] KARST) at "Kranzberger Forst" (48°25'08''N, 11°39'41''E, 490 m a.s.l.; Pretzsch et al. 1998, http://www.sfb607.de) near Freising/Germany. Two groups of approximately 60-year-old beeches (60 to 100 individuals each) were surrounded by spruce trees which were seven years younger but overtopped beech in height. An understorey of *Rubus fruticosa agg., Oxalis acetosella* and the moss *Hylocomium splendens* (Hedw.) B.S.G. (ground coverage of 5 to15 %) was present only under spruce. Rooting depth was about 1m in a luvisol (FAO classification) which had developed from loess over tertiary sediments and provided ample water and nutrient supply. Local climate classified as temperate (sub-atlantic to sub-continental) was characterized by a mean daily air temperature and annual precipitation of 7.8°C and 785 mm, respectively (30-year record each, 1970 through 2000), with periods of snow cover between December and February. Climatic data during the 3-year study period (2002, 2003 and 2004) are shown in **Tab. 1**.

Table 1*:* Climatic data summarized for 2002, 2003, and 2004 and for the 30-year record 1970 through 2000. Air temperature (T_{air}) and precipitation (P) were measured at neighbouring Level II monitoring site "Freising", LWF. Soil temperature (T_s) was recorded at the border of the humus layer and mineral soil at the site "Kranzberger Forst". Growing season is defined as May 1 through September 30 (according to Otto, 1994).

Year	Mean annual T_{air} (°C)	Mean T_{air} of growing season (°C)	Mean T_s (°C)	Mean T_s of growing season (°C)	Annual P (mm)	P during growing season (mm)
2002	8.88	15.74	8.13	13.44	1015	539
2003	8.81	18.01	7.93	14.28	558	279
2004	8.07	15.13	8.09	13.04	779	373
1970-2000*	7.82	14.81	n.d.	n.d.	786	442

* Data from DWD station „Weihenstephan"; n.d. = not determined

The summer of 2003 was characterised by above-average T_{air} of the growing season and exceptional drought conditions. The climatic extremes across the study years regarding Central-European summer conditions set the stage for evaluating the responsiveness of both competitors to drought in the mixed beech-spruce stand of "Kranzberger Forst".

2.2 Species description

2.2.1 European Beech (Fagus sylvatica L.)

2.2.1.1 Area of distribution

Fagus sylvatica is assumed to be the widest-spread tree species in Central Europe if undisturbed by anthropogenic influences (**Fig. 5**, Schütt *et al*., 2002). It is a tree species of temperate and warm-temperate climate (sub-mediterranean), reaching the optimum in occurrence in Central Europe. After the last glacial period, European beech re-immigrated into Central Europe from the southern Balkan Peninsula and southern Apennines (Felbermeier & Mosandl, 2002). European beech predominates within sub-mountainous altitudes, extending to mountainous and colline elevations. Preferable is humid and mild climate during winter (minimum annual precipitation from 500 to 600 mm and mean annual air temperature from 4 to 15 °C). Beech can endure dry periods of up to 3 months, depending on topography and soil conditions, and can even tolerate high temperatures in the absence of prolonged drought.

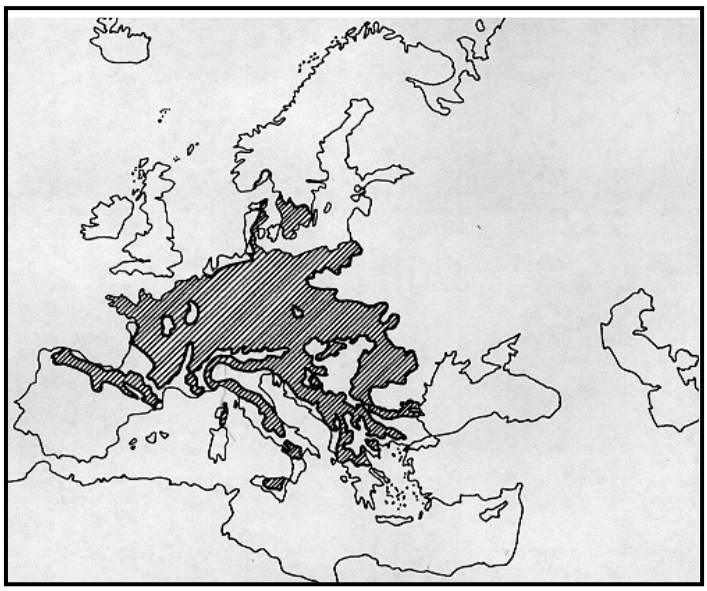

Figure 5*:* Natural distribution area (hatched) of *Fagus sylvatica* L. in Europe, (from Schütt *et al*., 2002).

2.2.1.2 Species characteristics

Above-ground: *F. sylvatica* is a deciduous tree reaching heights of up to 30 (40) m in forest stands of edaphically non-limiting site conditions. Beech can regenerate vegetatively by forming root and stool sprouts. At the timberline in the southern parts of the distribution area, beech can develop a shrub-like habit. The crown of young trees is pyramidal, and in adult trees it is oval to ball-shaped. When growing solitary in the open landscape beech trees develop a wide, spreading crown with live branches along the entire stem length (Kutschera & Lichtenegger, 2002).

Below-ground: Beech develops a typical “heart-root system”, occupying moderately deep soil layers as depending on topography and soil conditions. The majority of *coarse* roots (>2 mm in diameter) proliferate vertically in the proximity of the stem basis, reaching deeper soil layers. In beech stands, the numerous and densely packed root ramifications often show symphyses within or between root systems of individual trees. In adult beech trees, roots contribute little to the total plant biomass (13 to 17%, according to Möller *et al*., 1954), which is explained by the low fraction of large roots (diameter >20 mm). The widely reported high root density in beech is due to the high fraction of fine roots (diameter < 2 mm) which are located together with small roots (2-5 mm in diameter) within soil layers rich in organic matter. Coarse roots of the mineral soil rather than topsoil are characterised by low branching into fine roots (Kutschera & Lichtenegger, 2002). The fine roots of beech are highly colonised by ectomycorrhizal fungi (Leuschner *et al*., 2004).

Deep-rooting is not strongly pronounced in beech: The mean rooting depth is 120-140 cm (Köstler *et al*., 1968). In compacted loamy soils, as luvisoils, beech is rooting at a maximum depth of 80 to 90 cm. On poorly aerated and waterlogged soils, rooting depth can be restricted to 50-70 cm. At favourable site conditions (soil temperature > 0°C), root growth in beech can be maintained during the whole year with 2 periods of intense increment: in spring (April/May) and in fall, after a short break in summer (Göttsche, 1972). Beech fine roots are protected against pathogenic infection and drought due to cell-wall cutinisation in the rhizodermis (Kutschera & Lichtenegger 2002). Leuschner *et al*. (2001) reported increasing mortality of finest roots (diameter < 1mm) in beech during summer drought but compensatory production upon re-wetting of the soil.

2.2.2 Norway Spruce (Picea abies (L.) Karsten)

2.2.2.1 Area of distribution

Norway spruce is a tree of cool-temperate climate and has a natural area of distribution extending from Central Europe to the continental and eastern regions of Asia (**Fig. 6**). After the last glacial period, spruce re-immigrated into Central Europe from Central Asia (Otto, 1994), the Balkan Peninsula, the Apennines and the southern Carpathian Mountains (Schmidt-Vogt, 1989). Mountainous sites rich in precipitation (Alps, Carpathian Mountains) are optimal for the occurrence of spruce in Central Europe. During the growing season, spruce requires at least 40 mm precipitation per month and a mean annual air temperature that ranges between -10 and 10 °C. *Picea abies* is frost-resistant, but sensitive to late-frosts in spring. Since Norway spruce is a productive tree species of low site demands, it has been cultivated since two centuries outside its natural distribution area. The main limiting factor in Central European is low soil water supply during summer (Schütt *et al*., 2002).

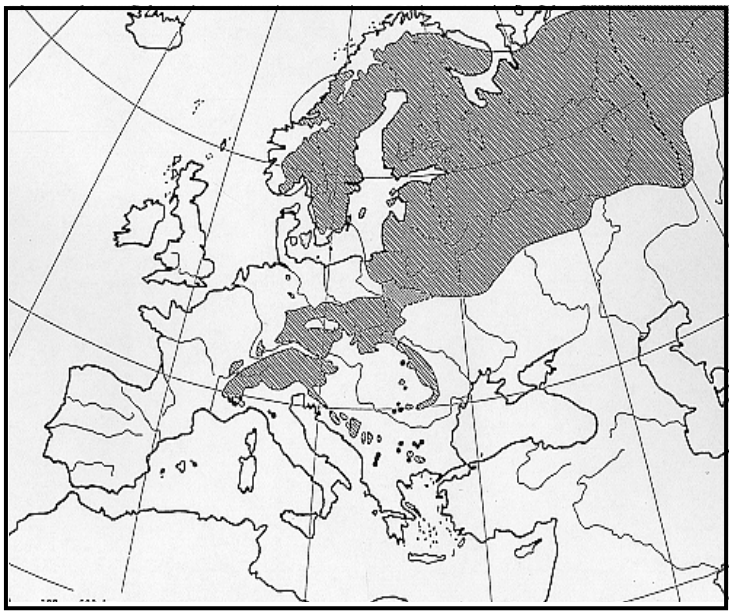

Figure 6*:* Natural distribution area (hatched) of *Picea abies* in Europe (from Schütt *et al*., 2002).

2.2.2.2 Species characteristics

Above-ground: *P. abies* is an evergreen tree that reaches heights of up to 40 (50) m on edaphically non-limiting sites. It grows in a monopodial way, forming a straight and cylindrical stem. The crown is pyramidal and its length and form depends on the stand structure and climate. Wide crowns are typical in trees growing at lower altitudes, and more tapered crowns are characteristic in northern Europe and in mountainous regions (Schmidt-Vogt, 1989). Three different branching patterns exist: the prevailing “brush” type, a “comb” type, and a “plate” type. All these types of branching are genetically fixed and can occur on different individuals within the same stand. Vegetative regeneration in spruce is rarely observed, but can occur at cold and N-exposed sites (Kutschera & Lichtenegger, 2002).

Below-ground: Spruce forms shallow root systems, characterized by a flat root plate with numerous vertical ramifications. In adult trees, this plate forms robust sinker roots. On poorly aerated, loamy or wet soils, the sinker roots are poorly developed and reach low depth only. Flat root plates are also formed in cold or warm but dry forest soils. However, on well aerated, nutrient-rich and moist soils, the sinker roots of spruce can reach a depth of 150 to 170 cm. Horizontally spruce roots can spread across 18 m (Köstler *et al*., 1968). Symphyses are often observed in spruce stands and may be present in 35% of the trees. Since 60 to 80% of the root system is located within the upper soil horizons, spruce is susceptible to wind-throw. Fine-root production depends on soil temperature, moisture and aeration. Fine-root density decreases rapidly with soil depth. In adult trees, roots amount to 15 and 25% in the total plant biomass depending on site conditions. Fine roots of Norway spruce are highly ectomycorrhizal (Göttsche, 1972).

The mean rooting depth of spruce is 80 to 100 cm, whereas the maximal fine root density is located at the transition between organic (Oh) and humic (Ah) topsoil layers (Göttsche, 1972; Ammer & Wagner, 2002). A remarkably low fine-root density was observed within the organic topsoil as a result of drought (Kutschera & Lichtenegger, 2002). Distorted vertical ramifications of coarse roots were present in loamy, poorly aerated mineral soil. Fine-root growth of Norway spruce is restricted in strongly compacted soil horizons (e.g. at soil density >1.3 kg l^{-1}; Köstler *et al*., 1968) or in waterlogged soils. Root growth of spruce initiates in spring before bud burst and reaches a maximum by early summer. In the absence of drought and at soil temperatures above 6°C (Ladefoged, 1939; from Puhe, 2003), intense root growth can occur in autumn and continue through early winter. Summer drought may disrupt root growth so that root tips become suberized and stay brownish as during winter, thus the discolouration rapidly extends to the root tip (Puhe, 2003). Fine roots of *P. abies* reduce growth when exposed to increased N input and increased soil acidity, being accompanied by reduced mycorrhizal frequency (Kutschera & Lichtenegger 2002).

2.2.3 Central European mixed forests with Fagus sylvatica and Picea abies

Central European forests tend to display homogeneous structure during the final stage of development (Schütz, 1990). Natural mixed forests prevail in the transition zone between different climate regions (**Fig. 7**). One example is the natural beech-fir-spruce forest, which is one of the most productive forests in Europe (Otto, 1994). However, mixed forests with only beech and spruce exist rarely in nature (e.g. predominantly in mountainous regions). The higher physiological power of beech may be one reason (Otto, 1994). The physiological power is defined by Otto (1994) as the interaction of three factors. One factor is related to the species-specific requirement for climate and soil properties. Beech typically grows on warmer sites with less annual precipitation in comparison with spruce (**Fig. 8**). The second factor is the species-specific competitive ability. At comparable shade tolerance, biomass production and regeneration capacity, beech shows higher stand stability than spruce. However, the below-ground competitive ability of both tree species, when growing under same stand conditions, has rarely been studied (Schmid & Kazda, 2002). This latter issue was, however, the aim of this present study. The third factor is related to the external hazards of the species. Spruce is more endangered from forest fire and biotic enemies than beech. As an example, a study in Switzerland showed that heartwood decay in spruce accelerated in mixed culture with beech, but decreased when spruce grew in mixture with fir (Schütz, 1990).

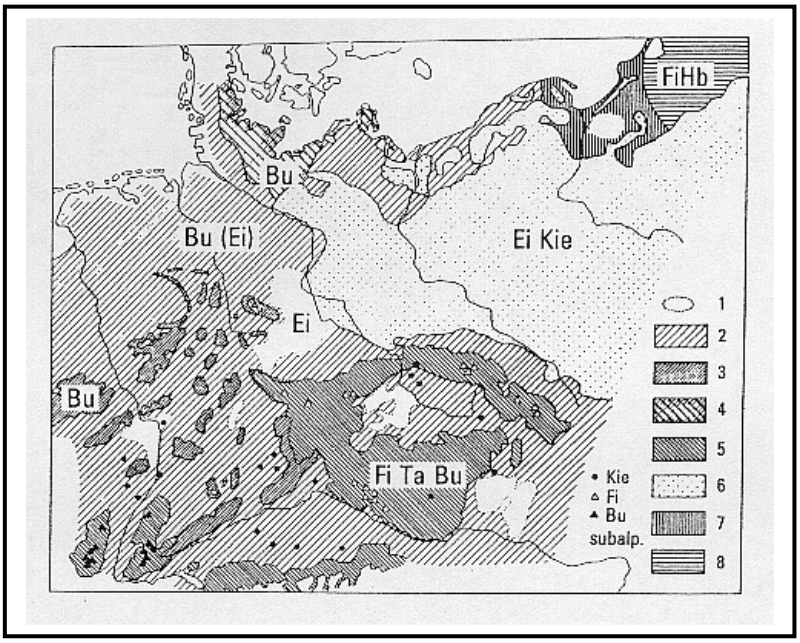

Figure 7*:* Natural forests in Central Europe (without Alps) with beech (Bu), spruce (Fi), fir (Ta), oak (Ei) and pine (Kie), (from Otto, 1994).

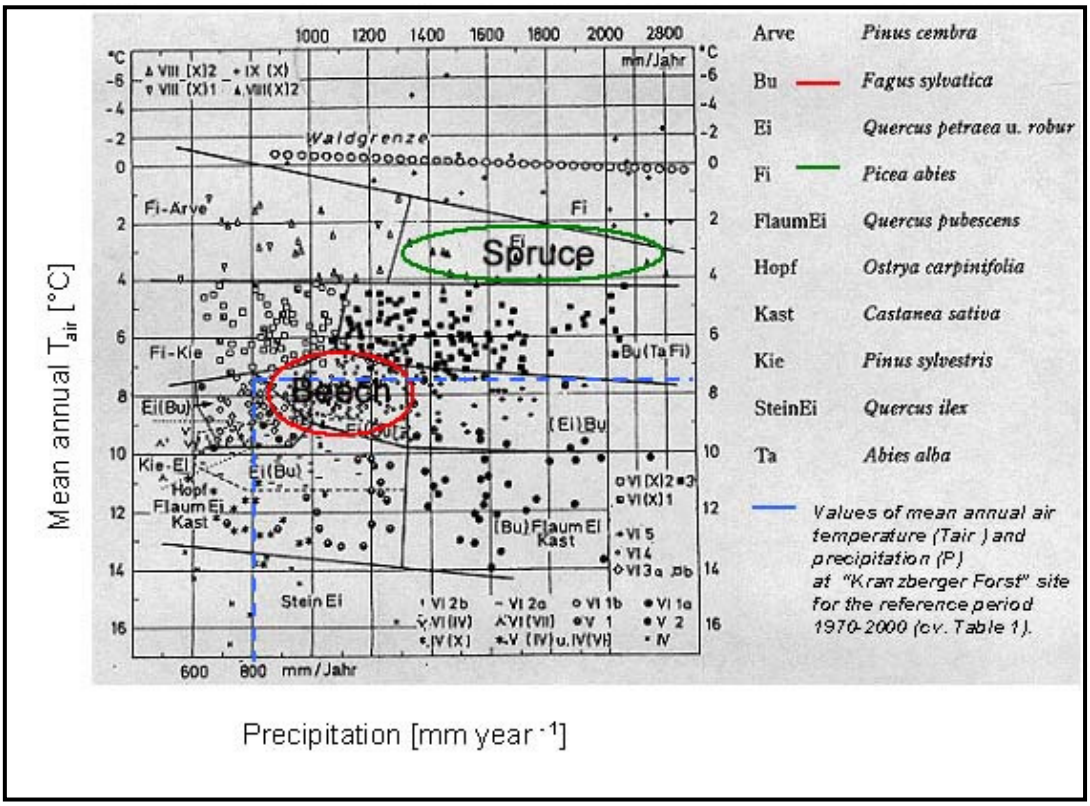

Figure 8*:* Dominating tree species within the natural vegetation of the Alps as placed in the co-ordinate system according to ecological characteristics: annual precipitation (P_{an}), and mean annual air temperature (T_{air}) (from Ellenberg, 1996). Red ellipse defines the range of pure beech forests, and the green ellipse denotes pure spruce forests. The blue dotted line shows the climate characteristics of "Kranzberger Forst" site as based on long-term averages (1970-2000; from **Tab. 1**).

Since spruce shows very high productivity in natural stands, spruce was planted on former beech stands across Central and Eastern Europe, as the need for timber increased during the 18th century. Nowadays, cultivation of pure spruce and mixed beech-spruce forests has become a major economic interest in Central-European forestry. Mixed beech-spruce forests are preferable because of their stabilising effect on biodiversity (Schütz, 1990). According to common silvicultural practice, beech trees are usually planted as small (500 to 1000 m^2) or big (1000 to 5000 m^2) groups in view of effective management (Ammer, pers. comm.).

2.3 The Kranzberg Ozone Fumigation Experiment (KROFEX)

KROFEX was installed at the experimental plot of the research site "Kranzberger Forst" (**Fig. 9** and **Fig. 10**), and has been operating continuously throughout the growing seasons (from May to the end of October) since early 2000 (Nunn *et al*., 2002; Werner & Fabian, 2002). Ozone is produced by a commercial ozone generator (Ozonia-CSI) which is operating with oxygen rather than air to prevent formation of oxides of nitrogen. The fumigation system is designed to maintain about 2 times ambient ozone levels ($2xO_3$) within the adjacent crowns of 5 beech and 5 spruce trees, but not exceeding 150 nl l^{-1}. The reference ambient ozone concentration ($1xO_3$) is recorded at about 25 m distance on a tower 5 m above the canopy. The spatial ozone distribution in the fumigated volume is continuously monitored by 6 ozone analysers and a dense array of 200 passive samplers which provide ozone doses integrated over weekly sampling periods. No fumigation is carried out below foliated crowns. Thus the control instrument mounted at 6 m above ground shows no elevated ozone levels (Werner & Fabian, 2002).

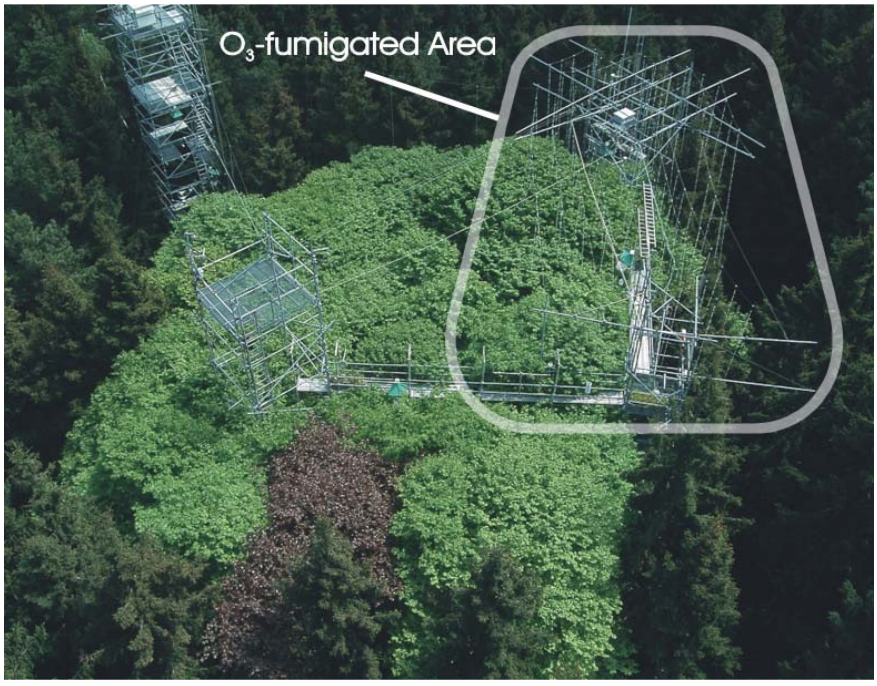

Figure 9:
Ozone fumigation area on the experimental plot at "Kranzberger Forst" site (cf. **Fig. 12**). Scaffoldings and a canopy crane (the crane is not shown in this picture) enable access to individual tree crowns (Häberle *et al*., 2003). The beech tree group established within spruce consists of about 60 individuals, (from Reiter, 2004).

Table 2*:* SUM0 (accumulated exposure to ozone per year) and AOT40 (accumulated exposure to ozone per year above a threshold of 40 nl l^{-1} O_3 and 50 W m^{-2} of total global radiation) of ambient ($1XO_3$) and twice ambient ($2XO_3$) ozone treatment for the year 2002 of beech and spruce branches in the sun and shade crown. According to Reiter (2004) and Nunn *et al*. (2005a), 10 study trees each of beech and spruce were selected, and in each study tree one branch in the sun and one in the shade crown was chosen to cover the extremes of the structural and ecophysiological variability within the crowns. Standard deviations of beech resulted from different lengths of the growing season of studied branches (data from Reiter, 2004).

Ozone treatment	Branch type	SUM0 [µl l^{-1}]	AOT40 [µl l^{-1} h]
beech			
1 x O_3	shade	123.2 (5.2)	16.0 (0.5)
2 x O_3	shade	180.7 (1.5)	48.0 (0.4)
1 x O_3	sun	126.4 (1.1)	16.3 (0.3)
2 x O_3	sun	234.0 (3.0)	67.2 (0.5)
spruce			
1 x O_3	shade	211.1	18.7
2 x O_3	shade	271.6	52.7
1 x O_3	sun	211.1	18.7
2 x O_3	sun	328.3	72.6

Accumulated exposure to ozone (SUM0) and AOT40 (accumulated exposure to ozone per year above a threshold of 40 nl l^{-1} O_3 and 50 W m^{-2} of total global radiation, VanderHeyden *et al*., 2001; Matyssek *at al*., 2004) within beech and spruce are shown in **Tab. 2** for the study year of 2002. The horizontal distribution of ozone in the sun crown (at 20 m above-ground) is exemplified in **Fig. 10**. The O_3 concentration distinctly decreased towards ambient levels with increasing distance from the fumigation system.

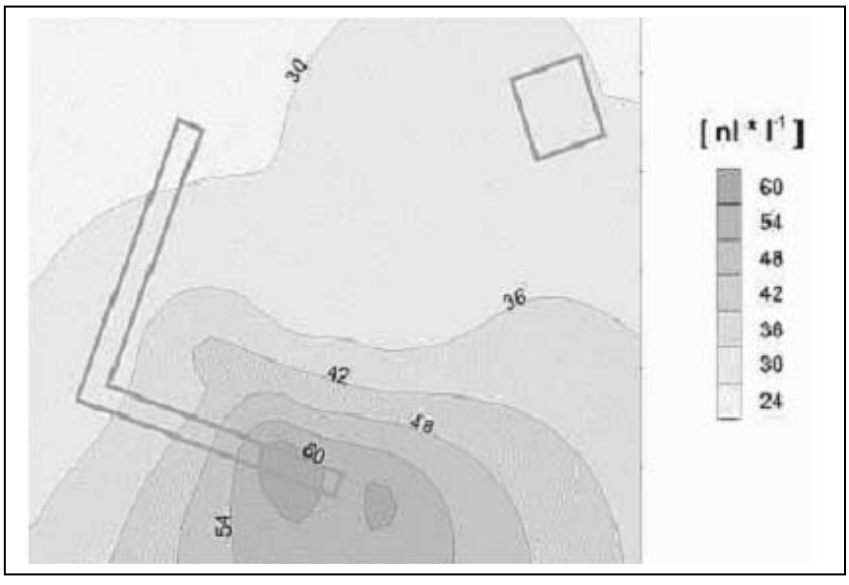

Figure 10*:*
Horizontal distribution of ozone in sun crowns. Isobars were created by the method of Kriging (from Nunn *et al*., 2002). Frames represent scaffolding.

2.4 Experimental design

In this study, the results were not quantified per individual tree, as the below-ground resources in a given soil volume are shared by the root systems of several surrounding trees (including soil organisms; Casper & Jackson, 1997). The focus here, however, is on the coexistence of beech and spruce, both being the only dominant tree species at the experimental site. The locations of below-ground analyses under the $2xO_3$ regime were chosen within the joint projection area of the ten O_3-fumigated tree crowns. Analyses at $1xO_3$ were conducted at locations outside the fumigation area (**Fig. 11**). Altogether, six subplots within the experimental plot were established:

B $1xO_3$ - intraspecific competition (beech, mono) under ambient ozone;
B $2xO_3$ - intraspecific competition (beech, mono) under elevated ozone;
S $1xO_3$ - intraspecific competition (spruce, mono) under ambient ozone;
S $2xO_3$ - intraspecific competition (spruce, mono) under elevated ozone;
BS $1xO_3$ - interspecific competition (beech and spruce, mixed) under ambient ozone;
BS $2xO_3$ - interspecific competition (beech and spruce, mixed) under elevated ozone;

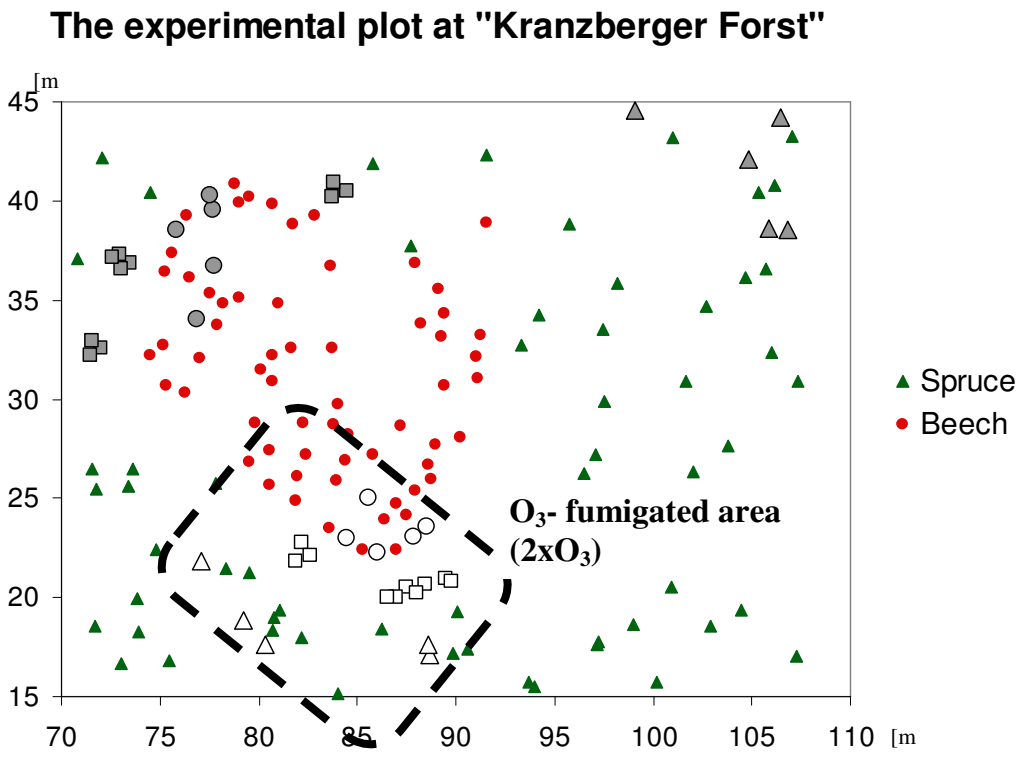

Figure 11: The experimental plot at "Kranzberger Forst" (cf. **Fig. 10**) with the "free-air" O_3 fumigation system. Small symbols mark the positions of spruce (green triangles) and beech (red circles) trees. Large closed symbols represent positions of soil cores taken within the $1xO_3$ area: circles for beech (B $1xO_3$), triangles for spruce (S $1xO_3$), and squares for mixed subplots (BS $1xO_3$). Large open symbols represent positions of corresponding experimental subplots within the $2xO_3$ area.

In the central zone of each B or S subplot, 5 measurement positions were selected per ozone treatment (5 under 1xO_3, and another 5 under 2xO_3, **Fig. 11**). The BS subplots were established between beech and spruce trees. Within each BS subplot 20 positions (10 under 1xO_3, and another 10 under 2xO_3) were marked at similar distances to neighbouring trees (positions at least at 50 cm distance to each other).

Within beech and spruce tree groups outside the experimental plot (**Fig. 12**), in addition one beech and one spruce subplot each were established, allowing complementary assessment of fine-root morphological and physiological parameters. At such subplots, the root exclusion technique was installed for studying the components on soil respiration.

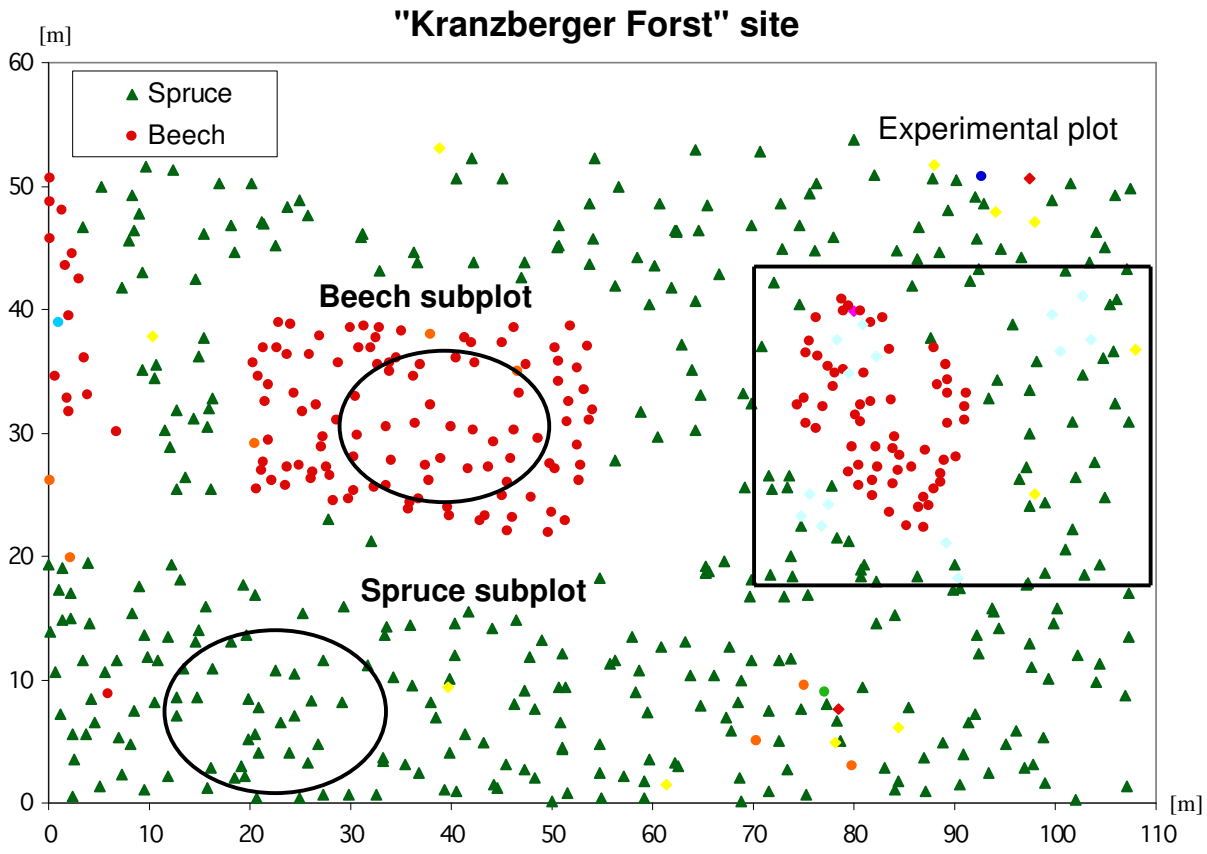

Figure 12: Individual positions of trees at the research site “Kranzberger Forst”: green triangles represent spruce, and red circles represent beech; the positions of other tree species are shown with other colours. The zone of “free-air” ozone fumigation is marked by a solid frame, and black ellipses show the additional beech and spruce subplots (B or S).

2.5 Diagnostics of the ozone impact below-ground

According to the conceptual diagram of Andersen (**Fig. 5**; Andersen, 2003), the ozone-effects on physiological parameters of the fine root system were analysed as shown in **Fig. 13**. Measurements were performed during 2002 and 2003, and compared with several root data sets from 1999 and 2000 (fine root biomass from in-growth cores, data processed by Dr. H. Blaschke).

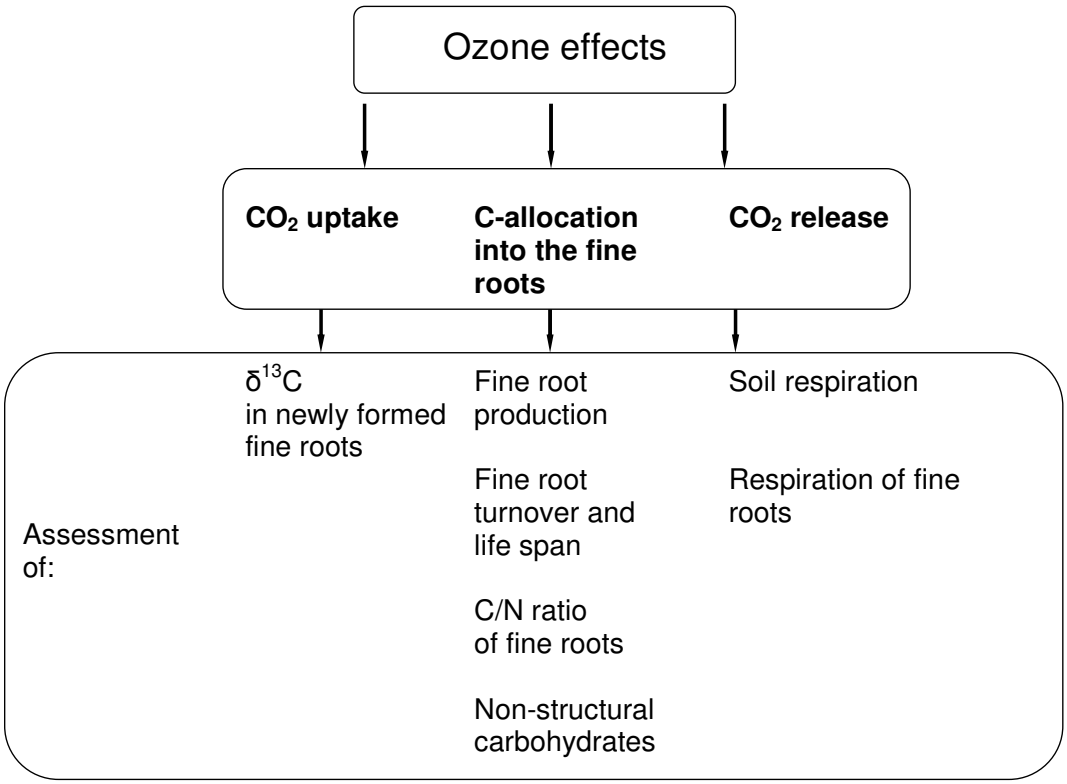

Figure 13*:* Physiological fine-root parameters assessed to examine for below-ground ozone effects on CO_2 uptake, C-allocation into fine roots and on CO_2 release (cf. **Fig. 5**).

2.6 Diagnostics of the drought impact below-ground

The methodology employed for assessing changes in below-ground competitive ability in response to drought was based on the conventional approaches by Casper & Jackson (1997; cf. **Fig. 3***)*. The morphological and physiological parameters were assessed in fine roots of beech and spruce as shown in **Fig. 14**. Measurements were performed during the growing seasons of 2002, 2004 (water non-limited) and 2003 (water limited).

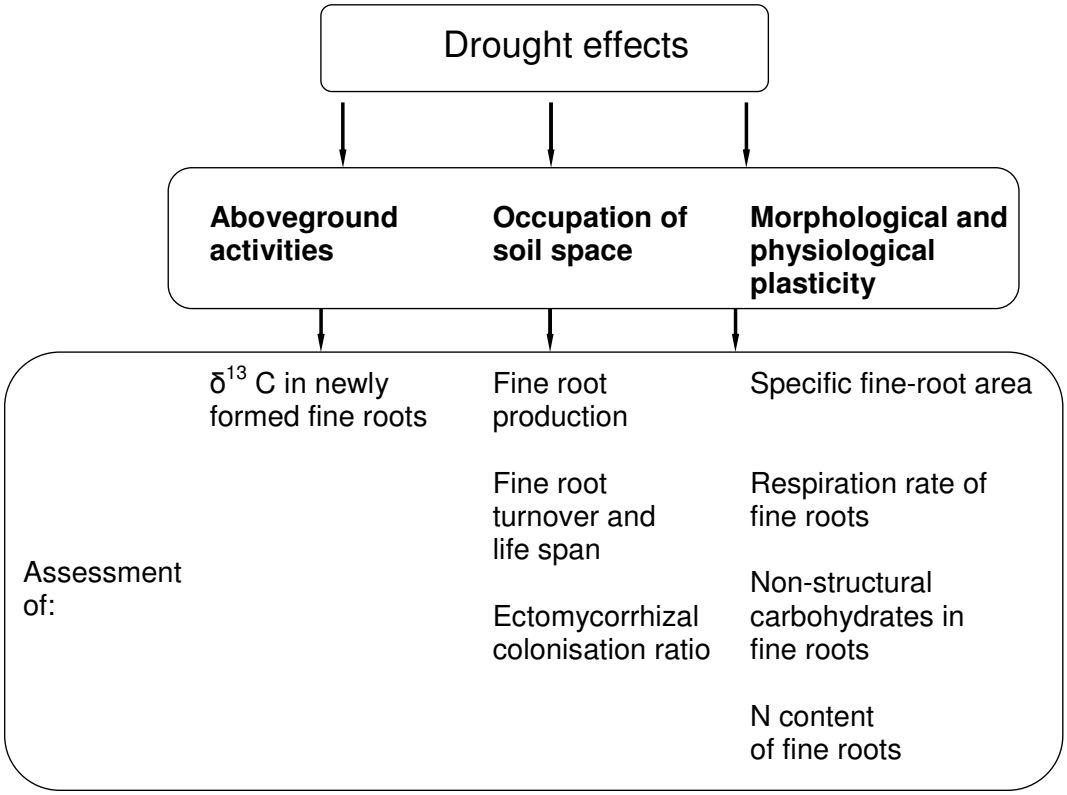

Figure 14*:* Fine-root parameters assessed to examine drought effects on aboveground activities, belowground space occupation and morphological and physiological plasticity.

2.7 Space definition below-ground

The identification of the discrete soil volume (e.g. space), surrounding the root system per individual tree, is not feasible. The soil volume surrounding roots (i.e. the *rhizosphere:* the zone where soil properties and microbial populations are influenced by root exudates) can be exploited simultaneously by several intermingling rootlets (inter- or intra-specifically) as depending on the root density so that the rhizosphere of such roots can strongly overlap (Hawkes & Casper, 2002). The competition for shared soil resources depends on gradients in resource availability within the soil depth and on the various patches in the spatial distribution of the soil resources (Huang & Eissenstat, 2000). The high degree of ectomycorrhizal infection in beech (Leuschner *et al.*, 2004) and spruce (Münzenberger *et al.*, 2004), and the different “exploration types” of mycorrhiza (Agerer, 2000) in addition alter the dimension of below-ground space exploited by roots and their symbionts.

In the present work, for methodological reasons (in favour of less destructive techniques), below-ground studies were concentrated on the fine-root system within the uppermost 20 cm

of the soil. Here, the strongest competition is to be expected between the fine roots of neighbouring trees for space occupation and resource capturing, since the topsoil (0 to 20 cm depth) is the densely rooted and the nutrient-richest zone at this site (Schuhbäck, 2004; Mainiero, pers. comm.). Additionally, a gradient in the nutrient and water supply exists within this soil depth (Schubäck, 2004). Therefore, two sub-samples were distinguished: *(1) organic sub-sample* (O+Ah), consisting of the litter layer (L), the organic fermentation layers (Of1 and Of2), the organic humus layer (Oh), and the humic topsoil horizon (Ah); and *(2) mineral sub-sample* (B), consisting of a loamy subsoil horizon (Bv). The boundary between both sub-samples was defined visually by the change in colour (black to dark-brown in O+Ah and brown in B), supported by several differences in the soil properties. For example, sub-sample (O+Ah) compared to sub-sample (B) showed higher pH-values, lower soil density and higher C/N ratio (for more detailed description of soil properties at "Kranzberger Forst" see Schuhbäck, 2004). On the other hand, surface soil layers integrated within (O+Ah) are typically characterised by higher fluctuations in the soil water content. During prolonged drought, a higher mortality rate of the shallow fine-root system was recorded underneath the soil surface, as compared to fine-roots that grew in the mineral subsoil (Wells *et al*., 2002).

2.8 Assessment of climate conditions

Air temperature, volumetric soil water content and precipitation for the experimental period 2002-2004 were obtained on daily basis from the adjacent Level II monitoring site "Freising", located at "Kranzberger Forst" (48°24'24''N 11°39'22''E; data are provided by Waldklimastation, Sachgebiet II, Bayerische Landesanstalt für Wald und Forstwirtschaft, Freising). Additionally, soil temperature (T_s) was recorded at the experimental site by 10-minute intervals at 0, 10, 20 and 30 cm depth through a PTC thermistor set (Thermor-1, UP, Germany). Daily averages were calculated, and the most shallow soil temperature measured at the boundary between the humus layer and the mineral soil (defined as 0 cm soil depth) was used for further analysis. Volumetric soil water content (SWC) was recorded by time-domain reflectometry ("TDR"; field measuring devise TRIME-FM2, two-rod probe, length 10 cm; IMKO GmbH, Germany) in July 23 of 2002 at each position of total soil respiration measurement (section 2.20), and continuously from June 12 through July 24 of 2003 at 3 positions within beech and spruce tree group (TRIME-MUX6, IMKO GmbH, Germany). Two-rod probes (P2Z, length 16 cm, measurement range 0-50%, accuracy $\pm$1%) were vertically placed into the humus layer and the mineral soil. A calibration curve was used to convert soil dielectricity into volumetric soil water content SWC [%]. Averages of the 3 positions were used for comparison with modelling of available soil water (ASW, mm m^{-2}; section 2.21.2).

2.9 Assessment of standing fine root biomass

Standing fine root biomass was assessed at the experimental plot by *sequential soil coring* (SC), (Vogt *et al.*, 1998). This technique was used to estimate the amount of root standing biomass at a given time for a given soil volume. Fine root sampling was conducted with sharp soil cores (length 20 cm, diameter 3.8 cm) that were manually driven into the topsoil. Soil cores were collected in four sampling dates: the last week of March 2002, the second week of August and November 2002, and during the first week of April 2003. For each sampling date new coring positions were chosen in a distance of about 20 cm around the measurement positions of total soil respiration (SR_t) (see **Fig. 11**, 40 cores per sampling date). During the measurement period (one year) it was expected to document the maximal standing fine root biomass in August and the minimal in winter or spring months (according to Göttsche, 1972; for both beech and spruce). The soil cores were transferred to plastic bags and stored at 4°C until processing (maximal for four weeks). In the laboratory, each soil corer was divided in two sub-samples: organic (O+Ah) and mineral (B), the thickness and volume of each were recorded. Both soil sub-samples were processed separately: roots were extracted by hand and only fine roots (diameter < 2mm) were considered in the analysis. Living (RB, biomass) and dead (RN, necromass) roots were distinguished (in case of doubt under microscope) using degree of cohesion of stele and periderm, root elasticity, and colour according to Hertel (1999). For distinguishing the two species, differences in colour (beech: dark reddish brown; spruce: yellow to brown), and ramification (beech: smooth and numerously; spruce: chunkier and more evenly) were used. RB and RN were dried at 65°C for 48 h, and the data were expressed as root density RD (e.g. dry mass per unit soil volume [mg l^{-1}]).

2.10 Annual fine-root production

2.10.1 "Minimum-maximum" method

This method was used for estimation of the annual fine root production (FRP) calculated as a difference between the maximum and the minimum fine root mass (RB+RN) assessed by SC during the measuring period of one year (McClaugherty *et al.*, 1982). For calculation the annual FRP root mass data assessed for both soil sub-samples according to section 2.9 were pooled and presented as fine-root density [mg l^{-1}] (e.g. as the pooled root dry mass in the total volume of the soil corer). The method assumes that arbitrary size classes (e.g., < 2.0 mm) accurately reflects the dynamic portion of the root system over the time of interest, and that pools of live and dead roots are near steady-state (Pregitzer, 2002). Only significant

differences between minimum and maximum values have to be considered for this calculation approach (McClaugherty *et al*., 1982).

2.10.2 In-growth coring method

In-growth coring (IC) technique was used additionally to sequential soil coring for estimating the annual fine-root production (Vogt *et al*., 1998; Hertel & Leuschner, 2002). The holes of the SC extracted in March 2002 (soil volume 227 ml) served as in-growth cores. Each coring hole was re-filled with mineral soil and organic layer (Bv and O+Ah, respectively), using homogenised substrate from the site according to the natural profile. Positions of in-growth cores were marked at the soil surface with PVC rings of the same diameter. Annual fine-root production was assessed by sampling the in-growth cores in December 2002 and extracting the newly formed fine-roots. The rootlets were manually removed from each sample and oven-dried (at 65°C for 48 h) to estimate root density as dry mass per unit soil volume [mg l^{-1}]. Simultaneously, the coring holes were re-filled and marked again as described above, and re-sampled in December 2003. Additionally, fine root recovery rate (FRR; in percent of initial root density) was calculated. To do so, fine root density in the in-growth cores at harvests (in December 2002 and in December 2003) was related to the initial fine root density as assessed by *SC* in March 2002 (Hertel & Leuschner, 2002). The method assumes that recovery of roots is unbiased (Pregitzer, 2002).

2.11 Fine root dynamics

2.11.1 Fine-root turnover

Fine root turnover (RT) refers to the process by which roots are produced, die and decompose (Eissenstat, 2002). It has been defined as the ratio of annual fine-root production to either the maximum, mean or minimum belowground standing biomass of fine roots (different methods are referred in Gill & Jackson, 2000). Here, fine-root turnover was calculated according Hendrick & Pregitzer (1993), who defined turnover as fine root production (FRP; mg l^{-1}) related to the minimum standing root biomass (FRB_{min}; mg l^{-1}). For this calculation FRP was obtained from IC during 2002 and 2003; FRB_{min} in 2002 was the minimum standing fine root biomass obtained by SC along the period from March 2002 to April 2003, and in 2003 FRB_{min} was the biomass assessed by SC in April 2003. This method calculates the average RT and is based on roots of approximately the same age, and is a good alternative to a single-root model, which requires studies on individual rootlets (e.g. by

using minirhizotrons). When expressed in %, RT shows the proportion of fine-root biomass that is renewed (newly produced or dies) during a certain period (in this study one year).

2.11.2 Root longevity

Root longevity, or life span (RL, yr), represents in this study the length of the time period for which the fine roots of a given tree species were present *alive* in the soil. RL is calculated for 2002 and 2003 as the inverse value of root turnover (Eissenstat, 2002).

2.11.3 Root mortality rate

Root mortality rate (RM, %) was calculated as the proportion of the necromass (RN, g) in the total standing fine root mass (e.g. RM = RN / (RB + RN) x 100), both assessed by means of sequential soil coring during fine-root samplings as in section 2.9.

2.12 Functional categories of fine roots

Recent studies report about differences in form and function within fine roots of the same diameter (Pregitzer, 2002; Wells & Eissenstat, 2001). The position and age of an individual root is directly related to its life-span and physiological function and seems to be more important than the mere diameter. However, root diameter size classes (Vogt & Peterson, 1991) are still used in most root studies, because they can be quite easily detected by automatic scanning techniques. To avoid large variations and misinterpretations when results are scaled to the stand level, three functional categories were established within beech and spruce fine roots (**Fig. 15**) according to their position at the root system and anatomical differences:

LRprim: long lateral roots with primary xylem (distal root parts);
LRsec : long lateral roots with secondary xylem (proximal root parts);
ShR : short roots, which were predominantly mycorrhizal.

Eight to ten individual rootlets per tree species, ozone treatment and sampling date (samplings made during April, June, August, October and December 2003) were extracted from the humus layer plus the uppermost 5 cm of the mineral soil and served for determination of the dry weights DW [g] of roots from each fine-root category (DW_{LRprim}, DW_{LRsec} and DW_{ShR}; cf. Appendix: **Tabs. 1A** & **1B**), and of the proportion PTR [%] of each of the three fine-root categories in the total rootlet biomass (PTR_{LRprim}, PTR_{LRsec} and PTR_{ShR}; cf.

Appendix: Tab. 1A & **1B**). DW was used for calculation of the assessed fine-roots parameters (XX), such as fine-root respiration RR, N-content, C content etc. of the individual cuttings according to:

$$XX_i = (XX_{LRprim} \times DW_{LRprim} + XX_{LRsec} \times DW_{LRsec} + XX_{ShR} \times DW_{ShR}) / DW_i \quad \text{Eq. 1}$$

where:

XX_i is the calculated parameter of the individual fine rootlet i in beech or spruce respectively, and DW_i is the total dry fine rootlet weight [g];

XX_{LRprim}, XX_{LRsec} and XX_{ShR} are the values of the parameter assessed on roots from categories LR_{prim}, LR_{sec} and ShR;

DW_{LRprim}, DW_{LRsec} and DW_{ShR} are the dry weights [g] of roots from each category within the individual fine rootlet.

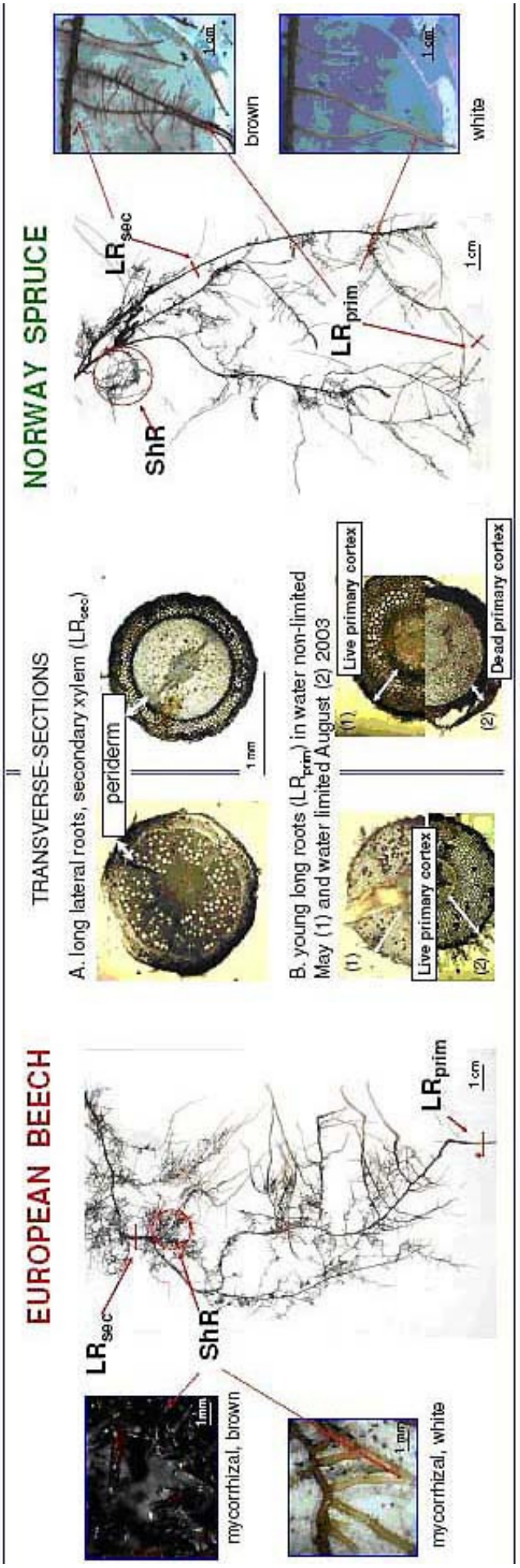

Figure 15: Both long lateral roots with secondary xylem LR_{sec} (A.) and long lateral roots with primary xylem LR_{prim} (B.) have similar mean diameters but their transverse-sections show different anatomical properties. During water limited August of 2003 LR_{prim} in spruce stop to grow: the primary cortex suberize and the inactive roots develop a metacutinized apex to prevent dormant root tips from desiccation.
Classification based only on root colour is also misleading, because “white“ fine roots can be either slowly growing short mycorrhizal roots ShR (beech, left site, bottom) or fast growing LR_{prim} (spruce, right, bottom). Similarly, “brown” colour comprises ShR (beech, left, top), primary dormant long roots LR_{prim} and secondary long roots LR_{sec} (spruce, right, top).
* Red lines show positions of the transverse-sections.

2.13 Morphological parameters of fine roots

The stored images of fine-roots extracted from soil corers (cf. section 2.9) and in-growth cores (cf. section 2.10.2), used before for root respiration measurements (cf. section 2.18), or developed in the rhizotrones (cf. section 2.19), were later processed in a batch mode using WhinRHIZO® (Regent instruments, Canada) to assess root morphological parameters as: surface area (A, cm^2), total length (L, cm), total volume (V, cm^3), mean diameter (D, mm), and number of root tips (N_{RT}). The dry weight of each sample was defined after 48 h desiccation at 65°C, and the following key fine-root parameters were calculated:

Specific fine-root surface area (SRA):

$$\frac{\text{Fine-root surface area}}{\text{Fine-root biomass}} \quad [cm^2\ g^{-1}] \qquad \text{Eq. 2}$$

Specific fine-root length (SRL):

$$\frac{\text{Fine-root length}}{\text{Fine-root biomass}} \quad [cm\ g^{-1}] \qquad \text{Eq. 3}$$

Specific root tip density (STD):

$$\frac{\text{Number of root tips}}{\text{Fine-root length}} \quad [N\ cm^{-1}] \qquad \text{Eq. 4}$$

The three specific parameters, which are connected with the physiological activity of fine roots and characterise the root-soil contact (Ostonen *et al.*, 1999), were used for studying the root ecomorphology, e.g. the variability of the root morphology to changes in environmental or soil characteristics.

2.14 Assessment of ectomycorrhizal colonisation rate

Species living in symbiosis with ectomycorrhizal fungi, such as beech and spruce, generally have short, swollen lateral roots resulting in a distinctive root system (Blaschke & Weiss, 1990; Frank, 2005). Mycorrhized fine-roots develop a stronger tendency to branching, so that the lateral rootlet branches occur at short intervals close behind the tip. These characteristic lateral roots can be visible without a microscope and have been used to identify mycorrhized parts. Scanned images (five per tree species) of short roots (ShR, cf. section 2.12) used before in fine-root respiration measurements (seven sampling dates between August 2002 and December 2003, cf. section 2.18) were analysed using the *gridline interception method*

for recording the number and the rate of ectomycorrhizal colonisation of this fine root category. The vertical and horizontal lines of the grid were followed, and intersect with root tips and intersect with mycorrhizal root tips were counted separately (http://www.ffp.csiro.au/research/mycorrhiza/root.html). However, this method provides information about the present but not about the vitality of the ectomycorrhizal associations. The *ectomycorrhizal colonisation rate* was calculated as the percentage of mycorrhizal to total root tips.

2.15 Nutrient analysis in the fine roots

(Co-operation with the partner group of Prof. A. Göttlein, Chair of Forest Nutrition and Water Resources, TUM)

Aliquots of each fine-root category (fine roots were sampled in May and in August 2003, and were first used in root respiration measurements as described in section 2.18) served for analysis of micro-and macroelements (inclusive C). Previously dried and milled root samples were digested with HNO_3, and analysed for major elements by ICP-AES. Total carbon and nitrogen concentrations of plant samples were measured by combustion using an elemental analyser (Leco, USA). The concentration of C and N were used to define the C/N ratio for each fine-root category as well as to calculate efficiency ratios of competitiveness (see below section 2.22).

2.16 Non-structural carbohydrate analysis

In August 2002, and in April, June, August and October 2003 in parallel to the sampling of roots for root respiration measurements, other 5 rootlets per tree species were extracted from the humus layer plus the uppermost 5 cm of the mineral soil and prepared for analyses of sugar and starch content. Cut rootlets were covered with wet paper and transported in a plastic bag to the lab to avoid root damage and desiccation. Three fine-root categories were distinguished in beech and spruce: long roots with primary xylem (LR_{prim}), long roots with secondary xylem (LR_{sec}), and short myccorrhized roots (ShR) (cf. section 2.12). Fine roots were carefully cleaned from soil particles and dead root ramifications by brushing, frozen in liquid nitrogen, and stored in a –80°C freezer until analysis. The samples were ground by hand under liquid N and lyophilized. Extraction of sugars and starch was done after Fleischmann (pers. comm.). Aliquots of samples (20 mg dry weight) were extracted with twice-distilled water in three steps (each 10 min with gentle shaking at 80°C). The supernatants were centrifuged, decanted, pooled and frozen until the measurement by

HPLC. The residual pellet was dried over 3 hours by low pressure desiccation. Starch in the insoluble residue was extracted by amylase-incubation at 85°C for 30 min, centrifuged, and an aliquot of the supernatant was incubated with amyloglucosidase at 37°C for 16 hours to ensure complete hydrolysis to glucose, which concentration was measured by HPLC (technical details are shown in **Tab. 3**). The peaks were quantified by comparing peak height with a range of external standards (glucose, fructose, sucrose). Additionally, in spruce samples, a content of pinitol was identified after analytical expertise by Prof. M. Popp (University of Vienna, Austria).

Table 3: Technical parameters of the HPLC system used for analysis of sugars and starch (as glucose).

Parameter	Sugars	Starch (glucose)
Column	Aminex HPX-87C (BIORAD, München, Germany), column 300x7.8 mm, working temperature 85°C	Aminex HPX-87H (BIORAD, München, Germany), column 300x7.8 mm, working temperature 60°C
Mobile phase	H_2O	5 mM H_2SO_4
Pump	L-6200A, Merck-Hitachi, München, Germany	
Autosampler	AS-96C (BIORAD, München, Germany)	
Detector	Model 1755, Refractive Index Monitor (BIORAD, München, Germany)	
Flow rate	0.6 ml/min	
Injection volume	20 µl	
Analysis Software	Gold Nouveau (Beckmann, München, Germany)	

2.17 Analysis of $\delta^{13}C$ of newly produced fine-roots

(Co-operation with the partner group of Prof. H. Schnyder, Chair of Grassland Science, TUM)

During 1999, 2002 and 2003 the natural variations of $\delta^{13}C$ [‰] were assessed in newly formed fine-roots as obtained by in-growth technique (see section 2.10.2). Dried root material was ground and 1 mg per sample was analysed for total N and C contents as well as the $^{13}C/^{12}C$ ratio, using an elemental analyser (Carlo Erba NA1110, Milan, Italy) interfaced to a mass spectrometer (FinniganMAT Delta Plus, Thermo Electron Corporation, Bremen, Germany). Similarly to leaf or wood tissues (Warren *et al*., 2001; Macfarlane & Adams, 1998; Ferrio *et al*., 2003), high $\delta^{13}C$ values in fine roots indicates stomatal limitation on photosynthetic CO_2 uptake during the period in which the carbon has been fixed. However, carbon isotopes only correlate with WUE above a critical concentration of available nitrogen (Hobbie & Colpaert, 2004), e.g. plants have to be N non-limited during assimilation.

2.18 Assessment of fine root respiration rate

The respiration rate (RR) of fine roots was measured by means of a differential infrared gas analyser IRGA (CIRAS-2, PP-Systems, UK, http://www.ppsystems.com) in combination with an open-chamber system (PLC Conifer, PP-Systems, UK). The measuring cuvette with a window size 70 mm x 50 mm allowed RR assessment of fine root aliquots (parts) with fresh weight 0.4 - 0.6 g. Making allowance for the high morphological and functional heterogeneity of fine roots (diameter < 2 mm; Pregitzer, 2002) which resulted in high heterogeneity of the measured RR values, so that the following sampling and measuring procedure was chosen:

(1) For measuring RR three functional fine-root categories were distinguished in beech and spruce: long roots with primary xylem (LR_{prim}), long roots with secondary xylem (LR_{sec}), and short mycorrhizal roots (ShR) (cf. section 2.12).

(2) Five to ten fine rootlets per tree species and sampling date were harvested at the experimental plot from the topsoil (the uppermost 5 cm of the mineral soil plus humus layer) and used for RR assessment. Another seven to ten rootlets per tree species and sampling date were sampled in parallel and served for determination of the proportion of each of the three functional fine-root categories in the total rootlet biomass (cf. section 2.12).

(3) Roots from each sample (4 to 6 replications) were carefully cleaned by brushing off soil particles and dead root ramifications. An aliquot of 0.4 - 0.6 g fresh weight was put in a mesh bag (mesh size 50 µm, window size of the bag 60 mm x 40 mm) which was then immediately placed in the cuvette of the CO_2-analyser. Mesh bag was used to protect the IRGA and showed no influence on the RR during preliminary tests.

(4) Cuvette environment parameters were set as follows: air humidity of 90 % of the ambient air humidity, flow rate of 0.2 l min^{-1}, and the input CO_2 concentration of the cuvette was set to 400 µl l^{-1}. Root sub-samples were tested for a possible effect of the CO_2 concentration by determining respiration rates at both 400 and 1000 µl l^{-1}, but no effect of CO_2 on RR was detected over that concentration range (in agreement with Burton et al. 2002). Cuvette temperature was chosen according to the task (see 2.18.1 and 2.18.2). Respiration readings of each root sample were taken manually 2 to 4 min after closing the cuvette when respiration rates had stabilized. Since root cuttings have not been rinsed before RR measurement, microbial respiration in the adhering soil and organic debris was measured as root respiration, but rates of microbial respiration per gram of forest soil material are often orders of magnitude less than those we measured per gram of root tissue. Thus the contribution of these materials to measured RR should be less than 5% of the values (Zak *et al.*, 2000).

(5) After finishing the measurements, root samples were covered with wet paper and transported in plastic bags to the lab. They were rinsed and spread out in plastic trays filled

with distilled water, and scanned in colour using a desktop scanner (HP Laserscanjet 4L) at 300 dpi for assessment of the SRA by means of WhinRhizo® (cf. 2.13). Respiration rates of each sample were determined on a root dry weight basis [nmol CO_2 g^{-1} s^{-1}].

2.18.1 Assessment of the ozone impact on root respiration rate

In August 2002 the ozone impact on root respiration was tested at the experimental plot on individual fine rootlets (five per tree species and O_3-treatment) which were sampled and measured as described in section 2.18. Respiration measurements were performed at a cuvette temperature of 18°C and reported as respiration rates [nmol CO_2 g^{-1} s^{-1}].

2.18.2 Seasonal dynamics in fine-root respiration rate

The seasonal dynamics in RR was assessed on fine-roots as obtained at beech and spruce subplots outside the "experimental plot" (**Fig. 12**). In April, June, August, September and October 2003 the measurements were performed within each fine-root category and tree species at three temperature levels (7, 15 and 22°C) for determining the response of RR to change in temperature. The sampled fine rootlets were covered with wet paper and transported to the lab in plastic bags where they remained until measuring at 10-15°C. Respiration rates have been assessed within 3 hours after root excision, a time period which had been prooved to show constant respiration rates of trenched fine-roots during preliminary tests. At each temperature level 4 to 6 replications were measured per root category and tree species, using always newly prepared root samples. The environmental cuvette parameters during all measurements were set as described above (see section 2.18, step 4).

Regression analysis was performed to examine the temperature response of fine-root respiration during 2003. Fine-root categories and tree species were analysed separately. Exponential regressions were developed by plotting the averaged RR against temperature by using *van't Hoff* equation:

$$RR = \rho e^{\theta T} \qquad \text{Eq. 4}$$

where ρ and θ are regression coefficients, and T is the sample temperature.

For each root category and each sampling date the respiratory Q_{10} *values* were determined (Q_{10} is defined as the change in respiration in response to a 10°C change in temperature) by using the equation:

$$Q_{10} = e^{10\theta} \qquad \text{Eq. 5}$$

By means of Eq. 4, the measured RR of each root category was transformed:

(1) relating RR data to the mean daily soil temperature as monitored at 0 cm soil depth ($T_{s(0)}$) during the day of the measurement (e.g. $RR^{T(0)}$). $T_{s(0)}$ was characterized by the highest annual amplitudes and was chosen as a basic T_s for recalculations.

(2) relating RR data to a standard temperature of 10°C (e.g. RR^{10}) which is the mean $T_{s(0)}$ for the period from April to October when fine roots are active.

The transformed RR were used for estimation of the respiration rates of the individual fine-root cuttings (RR_I) both at $T_{s(0)}$, and at 10°C. RR_I was calculated for each sampling date as the sum of the respiration rates of all fine-root categories according to their proportion in the total rootlet (cf. Eq.1):

$$RR^T_I = (RR^T_{LRprim} \times DW_{LRprim} + RR^T_{LRsec} \times DW_{LRsec} + RR^T_{ShR} \times DW_{ShR}) / DW_I \qquad \text{Eq. 6}$$

where:

RR^T_I is the respiration rate [nmol CO_2 g^{-1} s^{-1}] of the individual fine rootlet in beech or spruce $RR^{T(0)}_I$ or RR^{10}_I, respectively, and DW_i is the total dry fine rootlet weight (g);

RR^T_{LRprim}, RR^T_{LRsec} and RR^T_{ShR} are the respiration rates $RR^{T(0)}$ or RR^{10} [nmol CO_2 g^{-1} s^{-1}] of the roots from categories LR_{prim}, LR_{sec} and ShR;

DW_{LRprim}, DW_{LRsec} and DW_{ShR} are the dry weights [g] of roots from each category within the individual fine rootlet.

During September 2004 a measurement of RR was made with all categories in beech and spruce fine roots at sample temperature of 10°C. RR^{10}_I was calculated according Eq. 6 and was used for comparison with the RR^{10}_I values assessed during September 2003.

The mean value of RR^{10}_I for April, June and October 2003, and September 2004 was taken as species-specific RR^{10} [nmol CO_2 g^{-1} s^{-1}] of beech (RR_{beech}) and spruce (RR_{spruce}) fine roots. Since August and September 2003 were months with strong limitation of soil water content, RR^{10} assessed during both months were not included in the calculation of the species-specific RR^{10}. RR_{beech} and RR_{spruce} were used to calculate the efficiency ratio of competitiveness (e.g. “Belowground running costs”, see section 2.22).

2.19 Measurement of water uptake by fine roots

The experimental approach for studying the water uptake of intact tree fine roots was modified according to a non-destructive *in situ* method by Göttlein *et al*. (2001) for

investigating rhizosphere chemistry and nutrient uptake. Customized rhizotrones (**Fig. 16A**) allowed documentation of individual fine root development during the process of water uptake. To this end, four rhizotrones per tree species were installed horizontally into the soil surface on June 1, 2003, so that one intact rootlet (consisting of fine roots only) was captured within each rhizotrone. The rhizotrones (volume of 900 ml each) had been filled before with about 800 g of forest soil from the (Ah+Bv) horizons (soil water content 10 to 12 vol. %, soil density about 1 g/ml). Inside the rhizotrones, roots were supplied with water through a miniaturized ceramic cell (Rhizon SMS, length of the porous material 10 cm, Wageningen, Netherlands), connected via PE tubing (inner diameter of 2 mm) to a water reservoir (non-transparent 1.5 l plastic bottle). After placing the rootlets into the rhizotrons, the soil-root system was irrigated for 24 h by placing the water bottles on the soil surface. Thereafter, the bottles were positioned within a 50 cm deep hole in the soil so that the vertical difference between the rootlet within the rhizotrone and water surface in the bottle was about 30 cm. Via the "hydraulic soil – micro-cell – tube system", roots sucked water according to their demand from the bottle along a water potential gradient of 0.03 MPa. Three additional rhizotrones were installed in the same way, although without roots, to serve as control. Water loss *via* evaporation was prevented by sealing the rhizotrones with Terostat-IX^{TM} (Henkel KGaA-Teroson, Germany) and quartz sand (**Fig. 16A**). Rhizotrones and bottles were covered with styropor plates and PVC trays for protection from sun light and rainfall. The suction tubes were checked at least once a week to remove potential embolies. The water in the bottles was regularly re-filled to 1.0 l upon dropping to below 0.5 l.

Water consumption by the rootlets WU_i [ml] was recorded since mid-June 2003, after an equilibration period of two weeks, by 2 to 4-week intervals (altogether 6 recordings; $i = 6$) by means of assessment of the water table in the bottles. Water uptake of individual roots was corrected during same intervals by the averaged uptake of the control rhizotrons without roots (n=3), as necessary. Cumulative water uptake (W, ml) of each rootlet per rhizotrone was recorded from June 18 through October 29 (134 days). In parallel, roots were documented by same time intervals through digital imaging, and the number of the non-pigmented white root tips (N_{WRT}, **Fig. 16B**) of roots growing along the upper transparent plates of the rhizotrones was determined. In addition, the initial rootlet length (L_0, cm) had been assessed on June 1, 2003, by processing root images in black-white mode (Adobe Photoshop®, Germany) by WhinRHIZO® (Regent instruments, Canada). On October 29, 2003, rootlet length (L_N, cm) and rootlet surface area (A_N, cm^2) were assessed upon root excision through scanning in the lab at 300 dpi (Laserscanjet 4L, HP, Germany) and processing by WhinRHIZO®. Dry mass of each rootlet at the time of harvest (M_N, g) was assessed after 48 h at 65°C, and the specific fine-root length (SRL) of this rootlets were calculated according to Eq. 3.

In accordance with studies on the relationship between root pigmentation and root growth dynamics (Withington *et al*., 2003), it was assumed in the present study that high number of non-pigmented root tips reflects the periods of fast growth (here length increment) of the rootlets. This assumption allowed determining, in addition, the following rootlet parameters:

1. Total rootlet length (L_i, cm) for each recording date:

$$L_i = L_{i-1} + r_i(L_N - L_0); \quad \text{Eq. 7}$$

where:
L_i is the rootlet length [cm] at the recording date *i*;
L_{i-1} is the rootlet length [cm] assessed at the previous recording date (for the first recording $L_{i-1} = L_0$);
$(L_N - L_0)$ represent the length increment [cm] of each rootlet from June 1 through October 29 in 2003.
r_i is the proportion of white root tips (N_{WRT}) at the recording date *i* in the total number of white root tips determined during the whole experimental period:

$$r_i = N_{WRTi} / \sum_{i=1}^{6} N_{WRTi}; \quad \text{Eq. 8}$$

2. The mean standing rootlet length (L_{mean}, cm) of the study period was calculated based on the individual rootlet lengths L_i as:

$$L_{mean} = [\sum_{i=1}^{6} N_{days} (L_i + L_{i-1}) / 2] /150; \quad \text{Eq. 9}$$

where:
$(L_i + L_{i-1}) / 2$ is the mean root length of the period between recordings *i*-1 and *i* ;
N_{days} is the number of days of the time period between recordings *i*-1 and *i* ;
150 is the number of days from the June 1 (rootlet length L_0) through October 29, 2003 (rootlet length L_N).

3. The mean standing biomass (M_{mean}, g) of each rootlet of the study period was calculated as:

$$M_{mean} = L_{mean} / SRL; \quad \text{Eq. 10}$$

where L_{mean} [cm] is the mean standing rootlet length (Eq. 9) and SRL [cm g^{-1}] is the specific root length assessed at the end of the exposure in the rhizotrons.

4. The root production (RP, g) of each rootlet was assessed for the period of recorded water consumption as:

$$RP = (L_N - L_1) / SRL; \quad \text{Eq. 11}$$

where $(L_N - L_1)$ is the length increment [cm] of the rootlets from June 18 through October 29 of 2003.

5. Fine root daily water uptake rate WU [ml day^{-1}] for the periods between recordings was assessed as:

$$WU_{daily} = WU_{(i\text{-}1) \text{ to } i} / N_{days} ; \quad \text{Eq. 12}$$

where:
WU_{daily} is the daily fine-root uptake rate [ml day^{-1}] for the period between recordings *i*-1 and *i*;
$WU_{(i\text{-}1) \text{ to } i}$ is the total water uptake for the period between recordings *i*-1 and *i*;
N_{days} is the number of days between recordings *i*-1 and *i*.

6. The daily specific water uptake rate SWU [ml g^{-1} day^{-1}] during the period of recorded water consumption was calculated for each rootlet as:

$$a) \; SWU_M = W / 134 / M_{mean}; \quad \text{Eq. 13}$$

$$b) \; SWU_{RP} = W /134 / RP; \quad \text{Eq. 14}$$

where W [ml] is the cumulative water uptake of each rootlet recorded from June 18 through October 29 (the whole experimental period), and 134 is the number of days included in this period.

For the whole experimental period, SWU_M represents the daily water uptake rate of the rootlets per mean standing root biomass (M_{mean}, g), and SWU_{RP} represents the daily water uptake per unit of newly produced fine roots (RP, g). The SWU_M is used to calculate efficiency in competitiveness (see below).

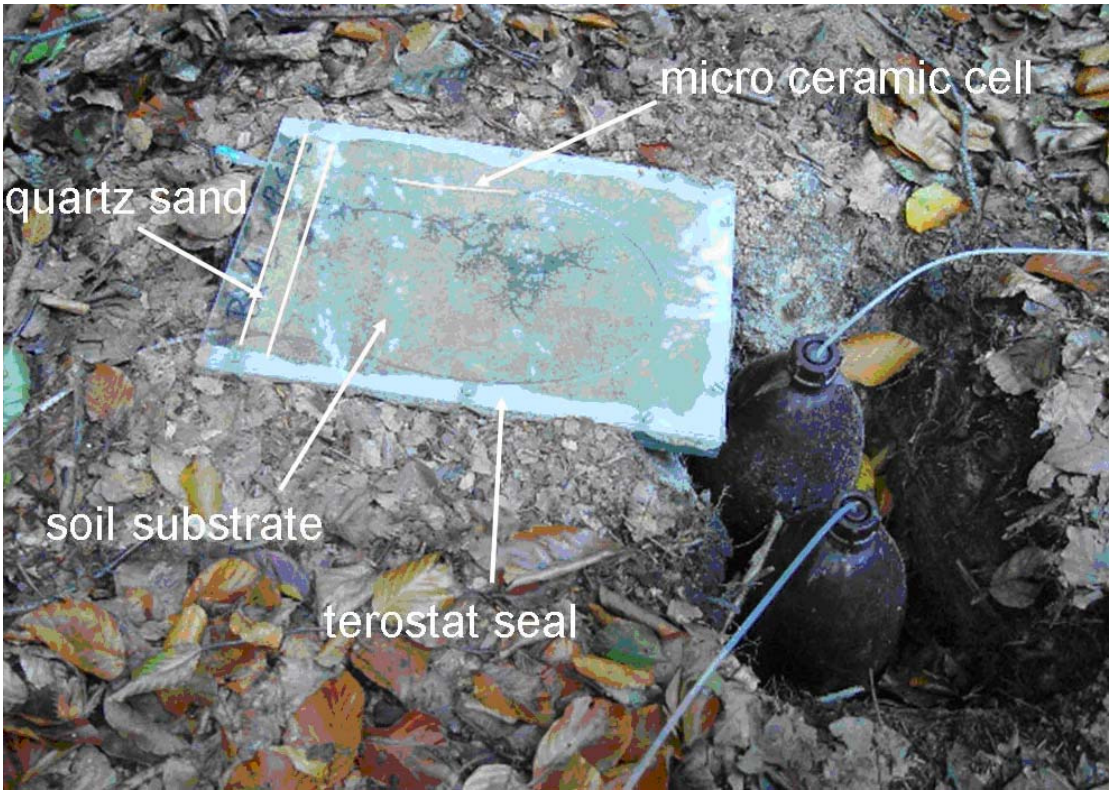

Figure 16A: Miniaturized ceramic cells installed in rhizotrons as customized for studying, *in situ,* the water uptake of intact tree fine roots.

Figure 16B: Intact fine rootlet in beech: Non-pigmented fine root tips (marked by white circle) are well distinguished from the older root parts (marked in black). Photo: September 30 of 2003.

2.20 Assessment of total soil respiration

Measurements of SR_t were performed at the experimental plot on 40 measurement positions (see **Fig. 11**) by monthly intervals from May through November 2002, and from March through November 2003. B, S and BS subplots under $1xO_3$ (20 measurement positions) were compared to the correspondent subplots under $2xO_3$ (other 20 measurement positions) to study the impact of ozone fumigation on soil respiration. The SR_t positions were permanently marked by PVC-rings (length 2 cm and inner diameter 10 cm) clipped on the soil surface (**Fig. 17**). For implementation, measurement rings were removed from their positions and placed back after completion of respiration measurements. The moss layer was removed from inside the rings when present. Soil respiration rate was assessed as CO_2 release by means of differential IRGA in combination with a closed-chamber system (EGM-3 with SRC-1, PP-Systems, UK; see Parkinson 1981 and Blanke 1996 for details). SR_t was calculated from the increase in CO_2 (by a maximum of 60 ppm) over time (maximum of 120 s), the volume of the chamber system (1170 cm^3) and the enclosed soil surface area (78 cm^2). The rate of CO_2 efflux from the soil (gCO_2 m^{-2} h^{-1}) was followed until steady-state, when three readings were averaged to yield representative SR_t. Measurements of SR_t and soil temperature at 3 cm depth (soil temperature probe STP-1, PP-Systems, UK) were made between 10 a.m. and 2 p.m. (time of average CO_2 efflux during the day, cf. Davidson *et al.*, 1998). Soil temperature typically varied by less than $\pm$ 1.0°C across the site.

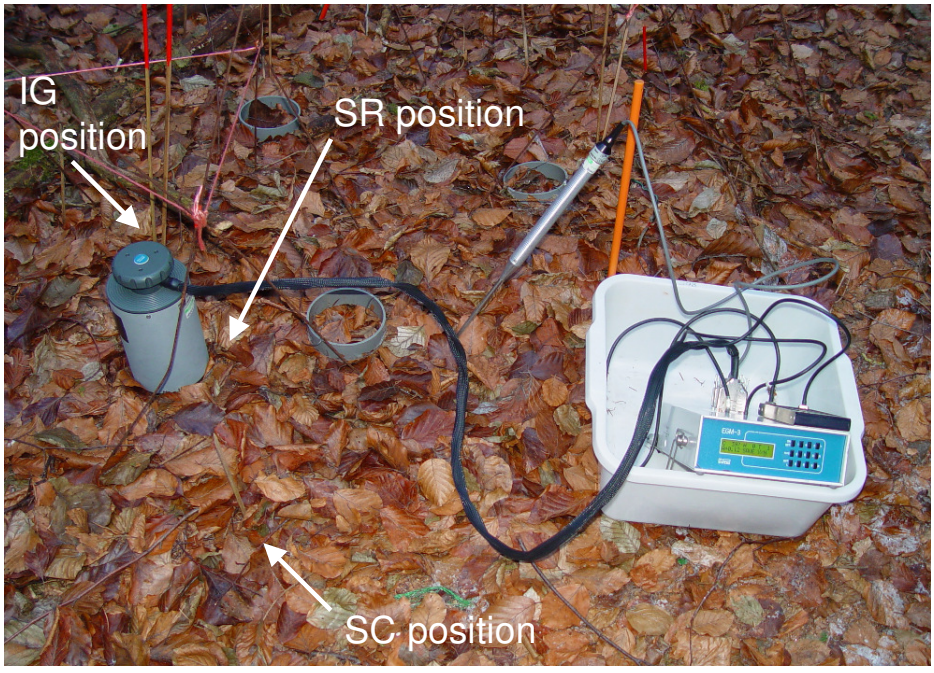

Figure 17*:* Experimental set-up of the measurement positions: from *IG* position was extracted an in-growth core, SC position was used for sequential coring technique, and at SR_t position was measured the soil total respiration rate.

2.21 Assessment of "autotrophic" and "heterotrophic" soil respiration

2.21.1 Root exclusion technique

This approach was used to resolve total soil respiration (SR_t) into "autotrophic" (SR_a) and "heterotrophic" (SR_h) soil respiration. To this end, SR_t was measured on undisturbed reference and SR_h was measured on other nearby positions (e.g. root exclusion positions where roots were removed 3 weeks before the first measurement) by monthly intervals from July through November 2002, March through November 2003, and March through July 2004. In June 2002, ten measurement positions were selected in each group of trees (distance between group centres about 25 m): five for employing the root exclusion procedure, and another five that stayed unchanged as reference. However, ground vegetation (i.e. mosses), when present, was removed on all measurement positions. At the positions of root exclusion, metal soil corers (length 10 cm, inner diameter 10 cm) were inserted into the forest floor to allow soil excavation and removal of roots from a defined volume (785 ml). Live roots of each soil core were sorted, and the fine root density (FRD, root diameter < 2mm) in each position of root exclusion was determined as dry mass per unit of soil volume. Upon live root removal, soil including root necromass was refilled into the coring holes (stabilized by PVC tubes: length 10 cm, inner diameter 10 cm), accounting for the original position of soil material along the corer length. The PVC tube also prevented lateral in-growth of roots, while the top and bottom areas of tubes were kept open to ensure aeration as well as wet and dry deposition and drainage. A re-equilibration period of 3 weeks was required after soil refilling to minimise disturbance artefacts and re-attain respiratory steady-state conditions. SR_a was calculated as:

$$SR_a = SR_t - SR_h, \qquad \text{Eq. 15}$$

where SR_h is on positions upon fine-root removal, and SR_t on undisturbed reference positions. The proportion of SR_a in SR_t was calculated at each sampling date as $(1 - SR_h / SR_t) \times 100$.

Soil volumes within tubes were checked at the end of the experiment (after two years) for in-growth of fine-roots from below, which stayed confined, on average, to 3% in spruce, and 5% in beech in relation to initial root mass each. At the same time, i.e. in July 2004, fine root density was assessed at the reference positions by soil coring (corer length 10 cm, inner diameter 10 cm).

2.21.2 Modelling of "autotrophic" and "heterotrophic" soil respiration

(Co-operation with Dr. S. Raspe, LWF, Freising)

From the periodic SR measurements the continuous CO_2 release of the different measurement positions was modelled with respect to the dependency of SR_a and SR_h on soil temperature and available soil water (ASW, mm m^{-2}), and – in the case of beech – on litter fall. Therefore, SR_t was split into the proportions of SR_a and SR_h in view of their dynamics under varying temperature and soil moisture regimes. In addition, survey data were separated into a "soil water non-limited" data set (including 2002 and 2004), and a "soil water limited" one, only comprising 2003. An exponential function described the *temperature dependency* of SR underneath beech and spruce, respectively:

$$SR^{pr} = a\, e^{b(Ts-10)} \qquad \text{Eq. 16}$$

where:
SR^{pr} is the predicted autotrophic or heterotrophic soil respiration rate ($gCO_2\ m^{-2}\ h^{-1}$);
T_S is soil temperature in 3 cm soil depth (°C);
a and *b* are coefficients as estimated from measured SR through non-linear least square fit.

When subtracting 10°C from T_S, the coefficient *a* is an estimate of the respiratory CO_2 efflux at temperature of 10°C (Lavigne *et al.*, 2004). The coefficient *b* is the temperature coefficient, which is related to Q_{10} ($Q_{10} = e^{10b}$). Differences in *a* and *b* between "soil water non-limited" and "soil water limited" scenarios were analyzed for each tree group through *t*-test with Bonferroni correction (Bärlocher, 1999).

To assess the variation of SR in response to *plant-available soil water content,* SR value of each observation was standardised to a temperature of 10°C (Lavigne *et al.*, 2004), modifying Eq. 16:

$$SR^{10} = SR / e^{b(Ts-10)} \qquad \text{Eq. 17}$$

where:
SR is autotrophic or heterotrophic SR;
b the corresponding temperature coefficient.

Available soil water was modelled for the period 2002 through 2004 within the uppermost 40 cm of the soil profile by Dr. Stephan Raspe (LWF, Freising) through LWF-BROOK90

(Hammel and Kennel, 2001) for site conditions underneath groups of beech and spruce trees each. Normalised SR_a and SR_h were related to the mean daily ASW throughout the study period by means of linear response functions for independent analysis of beech and spruce. When SR_h was studied, the positive relationship at low ASW levels changed into negative at high ASW, or vanished, as observed in spruce. In determining the species-specific thresholds in ASW dependence of SR_h[10], an iterative approach was applied, repeating linear analysis until yield of highest R^2.
Equation 18 combines the effects of T_s and ASW on respiration:

$$SR^{pr} = (c + d\,ASW)\, e^{b(Ts-10)} \qquad \text{Eq. 18}$$

with *c* and *d* being coefficients (examined through *t*-test with Bonferroni correction for statistically significant differences between species).

SR_a and SR_h measured in beech during November were excluded from modelling as the T_s dependence on SR was interfered by additional C and N supply released from the shed foliage in mid-October (Meier *et al.*, 2005). The litter deposition stimulated SR_t and SR_a, for which phenomenon was accounted for by correcting modelled SR_h and SR_a according to:

$$SR^{cor} = SR^{pr} + I(T_s-2), \qquad \text{Eq. 19}$$

where SR^{pr} are predicted SR_h or SR_a from Nov. 2 (in agreement with the end of the "late autumn" phenological phase; DWD, http://www.dwd.de) through the end of each year (whenever mean daily $T_s > 2$°C at 0 cm depth), 2 is the threshold T_s in °C. Below this threshold, all other environmental factors, but temperature, are believed to lose influence on the belowground microbial activity (cf. Tibbett *et al.*, 1998).

The correction factor *I* was calculated separately for 2002 and 2003 each as:

$$I = (SR^{sh} - SR^{pr}_{(t\leq 2)})/(T_s^{sh} - T_{s(t\leq 2)}), \qquad \text{Eq. 20}$$

where SR^{sh} is measured SR_h or SR_a during one week after complete fall of the foliage, $SR^{pr}_{(t\leq 2)}$ is predicted SR_h or SR_a during the first day past Nov. 2 with mean daily $T_s \leq 2$°C, and T_s^{sh} and $T_{s(t<2)}$ are corresponding means of subsequent days.
Factor *I* of 2004 and 2002 were set equal to each other. Given the large inter-annual variation of litter fall and slow decomposition in spruce stands (Pedersen & Bille-Hansen 1999; Hayes 1979), factor *I* was not included in the SR model for spruce.

SR_a and SR_h predicted for the days of SR measurement were re-calculated by means of Eq. 16 for the T_s (recorded in parallel at 3 cm soil depth) of such days. Model precision was evaluated by comparison between re-calculated predicted and measured SR_a and SR_h each.

2.22 Efficiency ratios of competitiveness

Efficiency ratios have been defined to compare the competitiveness of beech and spruce quantitatively (Grams *et al*., 2002). However, such "efficiencies" have been assessed mainly for the aboveground plant organs (Reiter *el al*., 2005; Kozovits *et al*., 2005a).

2.22.1 Belowground space occupation

Belowground, the objects of plant competition (e.g. soil water and nutrients) are located along gradients within the soil volume. Space occupation requires C investment into root structures (e.g. "structural costs"). The soil volume (previously defined in section 2.7) per unit of C investment into standing fine-root biomass was taken as a measure of the "efficiency of belowground space occupation" (BSO):

$$BSO = \frac{\text{Occupied soil volume}}{\text{C-investment into standing fine-root biomass}} \quad [m^3\ g^{-1}] \qquad \text{Eq. 21}$$

In mono-specific subplots, covered by trees of only one species (i.e. beech or spruce), the space occupied by roots was the mean soil volume (i.e., of the three sampling campaigns during March, August and December of 2002) of each soil sub-sample (organic O+Ah or mineral B) as determined by the *SC* technique. C investment into fine roots was defined by the mean standing fine-root biomass (i.e., of the three sampling campaigns in March, August and December of 2002; for details see section 2.9) and the C content of fine roots (45,4 % and 46,6 % of dry mass in beech and spruce, respectively; assessment see section 2.15).

In mixed subplots, the soil volume within each soil sub-sample was shared by both tree species. To assess the portion of the soil volume which was occupied by spruce or beech fine roots, the following approach was applied separately for each tree species:

(1) Annual means of soil sub-sample volume ($SV_{(O+Ah)}$ or $SV_{(B)}$, cm^3) and the respective root volume ($RV_{(O+Ah)}$ or $RV_{(B)}$, cm^3) were calculated for all subplots based on samplings in March, August and December of 2002.

(2) The ratio between a given soil volume and the contained volume of the root biomass was defined as the **factor *k***. It was assumed that beech and spruce trees, when growing in monoculture and under $1xO_3$ (undisturbed control conditions), develop a root structure ensuring "optimal resource exploitation" of the surrounding space and this structure avoids overlapping zones of nutrient depletion (e.g. adjusting exploitation rates to approach short-term *steady state*; Tsur & Zemel, 2004). Hence, the factor $\boldsymbol{k_c}$ for fine-roots under control conditions was defined as:

$$k_c = SV_c / RV_c; \qquad \text{Eq. 22}$$

where:
SV_c [cm^3] is the annual mean volume of the soil sub-sample O+Ah ($SV_{c(O+Ah)}$) or B ($SV_{c(B)}$), as assessed by the *SC* technique in the control beech or spruce group;
RV_c is the annual mean volume of the living roots extracted from the correspondent soil sub-sample O+Ah ($RV_{c(O+Ah)}$, cm^3) or B ($RV_{c(B)}$, cm^3) in the control beech or spruce group.
The factor $\boldsymbol{k_c}$ yields the space per unit of root volume in which plants including mycorrhizae and associated bacteria exploit available resources (Casper *et al.*, 2003: "zone of influence"). Roots with far-reaching mycorrhizae can be characterized by wide ratios of soil versus root volume.

(3) The factor $\boldsymbol{k_c}$ was used to predict the soil volume SV_{pr} which should be occupied by beech ($SV_{pr\ beech}$) or spruce ($SV_{pr\ spruce}$) roots in mixed subplots (according to the root volume while assuming similar efficiency as for roots growing in monoculture):

$$SV_{pr} = \boldsymbol{k_c}\, RV; \qquad \text{Eq. 23}$$

where:
SV_{pr} [cm^3] is $SV_{pr\ beech}$ or $SV_{pr\ spruce}$ within soil sub-samples *O+Ah* or *B*;
RV [cm^3] is RV_{beech} or RV_{spruce} within soil sub-samples *O+Ah* or *B* as assessed by *SC* in the mixed subplots;

(4) The soil volume predicted to be occupied by beech or spruce fine roots in mixed subplots (Eq. 23) was assessed in proportion [PSV, %] to the predicted total soil volume TSV_{pr} ($TSV_{pr} = SV_{pr\ beech} + SV_{pr\ spruce}$) of each sub-sample:

$$PSV = SV_{pr} / TSV_{pr} \times 100; \qquad \text{Eq. 24}$$

where:
PSV is the proportion of soil volume [%] occupied by beech (PSV_{beech}) or spruce (PSV_{spruce}) within soil sub-sample O+Ah or B;

SV_{pr} is $SV_{pr\ beech}$ or $SV_{pr\ spruce}$ within the corresponding soil sub-sample;
TSV_{pr} is the corresponding total soil sub-sample volume [cm^3] which was predicted to be shared by beech and spruce. An overlapping of the zones of nutrient depletion of beech and spruce roots from mixed plots was expected when TSV_{pr} was calculated higher than the total SV assessed by *SC*.

(5) The calculated PSV were set equal to the *in situ* portions of soil volume occupied with respect to beech and spruce fine-roots each when growing in mixture. Therefore, the soil volume occupied by beech fine roots ($SV_{(O+Ah)beech}$ for soil sub-sample O+Ah and $SV_{(B)beech}$ for soil sub-sample B) was assessed as:

$$SV_{(O+Ah)beech} = PSV_{(O+Ah)beech} \times SV_{(O+Ah)}; \quad \text{Eq. 25}$$

$$SV_{(B)beech} = PSV_{(B)beech} \times SV_{(B)}; \quad \text{Eq. 26}$$

where:
$SV_{(O+Ah)}$ and $SV_{(B)}$ are the annual mean volumes assessed by *SC* of the soil sub-samples O+Ah and B, respectively (see step 1). The same calculation was performed for spruce.
The approach presented here served to divide the measured volume of soil sub-samples $SV_{(O+Ah)}$ or $SV_{(B)}$ into two parts: one occupied by beech and the other one occupied by spruce fine-roots. These soil volumes were inputs in Eq. 21 to assess the "efficiency of belowground space occupation" (BSO) of beech and spruce within mixed subplots. The C investment into fine roots (cf. Eq. 21) was defined in mixed subplots as explained for the mono-specific subplots (see above).
This approach is relatively simplified, since the "zone of influence" becomes a fixed, circular shape, which represents fine-roots as a homogeneous system. The below-ground zone of influence was characterized here in a field setting, both in intra- and interspecific competition, where, as advantage compared to pot studies, lateral root growth was not constrained by the size of the plot.

2.22.2 Belowground space exploitation

The "overlapping concept" model outlined by Fitter *et al*. (1991) implies that the increase in root branching (or changes in root morphology) can lead to decrease in exploitation efficiency. Similarly, Casper *et al*. (2003) demonstrated that decreases in inter-branch distances would result in decreases in exploitation efficiency. Therefore, it is important to quantify the space exploitation (e.g. the benefit from the root structure present in a given soil volume) as well – not only the space occupation (e.g. the physical presence of roots within the soil volume). Here, the "efficiency of belowground space exploitation" (BSE) is

accounting for root function in terms of resource uptake as related to the occupied soil volume:

$$BSE = \frac{\text{Resource uptake}}{\text{Occupied soil volume}} \quad [\text{ml l}^{-1}\ \text{day}^{-1}] \qquad \text{Eq. 27}$$

BSE here is the Daily specific water uptake rate SWU [ml g $^{-1}$ day^{-1}] along the annual mean standing fine-root biomass of beech or spruce assessed during 2002 as fine-root density [mg l^{-1}] for both sub-samples of the soil cores. To this end, SWU was multiplied by the annual mean fine root density [g l^{-1}] in beech or spruce as assessed for both soil sub-samples.

2.22.3 Belowground "running costs"

The efficiency of "running costs" (BRC) is related to the maintenance of the present root structures (e.g. to the "functional costs") and is determined here by dividing the volume of already occupied soil by carbon "costs" for root growth and respiration to sustain occupation and exploitation this soil volume:

$$BRC = \frac{\text{Occupied soil volume}}{\text{C investment into root respiration}} \quad [\text{m}^3\ \text{g}^{-1}] \qquad \text{Eq. 28}$$

Occupied soil volume is defined here as previously described in section 2.22.1.
Carbon costs of root respiration were calculated for one growing season from April 1 through October 31 by using the annual mean (species-specific) standing fine-root biomass of the year 2002 (from *SC* technique) and the mean fine-root respiration rate at 10°C ($RR^{10}_{\text{l beech}}$ and $RR^{10}_{\text{l spruce}}$, for more details see section 2.18.2).

2.23 Statistical analyses

Statistical evaluation was made by using SPSS (version 13.0, SPSS INC., Chicago, IL, USA). Differences between means, factorial effects and factorial interactions were tested with the General Linear Model procedure (GLM: repeated measures, univariate or multivariate analysis with or without covariates) of the SPSS software. Data had been tested for homogeneity using Lavene Test for Equality of Variances, and in case of unbalanced design a non-parametrical Mann-Whitney-*U*-test (for independent samples) or Wilcoxon test

(for dependent samples) has been applied. Significance was determined at $p<0.05$ in all analyses. Graphics design, correlation and regression analyses were performed by Origin (version 6.0, Microcal Software Inc., USA). The differences between regression coefficients were tested by *t*-tests (using SPSS) and by adjusting the alpha level (e.g. Bonferroni method; Bärlocher, 1999).

3 RESULTS

3.1 Climatic variation at "Kranzberger Forst" during 2002-2004

Climate conditions at "Kranzberger Forst" varied largely during the three study years between extremely moist conditions during 2002 and extreme drought during 2003 (annual means of climatic parameters during 2002 through 2004 see **Tab. 1**, and seasonal dynamics of air temperature T_{air}, soil temperature, T_s, precipitation, P_a, and soil water content, SWC, see **Fig. 21***).* T_s at 0 cm soil depth was generally above 0°C throughout the three study years, rising gradually between February and August, and declining between September and January of the subsequent year. Mean annual T_s only slightly varied across the study period (**Tab. 1**), however, was highest during the growing season of 2003, and lowest in 2004 because of cool conditions in May and June (**Fig. 21**). P_a of both 2002 and 2003, but not so of 2004, differed significantly from the average of the reference period (RP, i.e. 1970-2000; **Tab. 1**). P_a in 2002 was enhanced by 30% relative to the long-term average due to intense rainfall during March and August. As a consequence, volumetric soil water content (SWC, %) at 5 cm soil depth remained, throughout the growing season, above 14% which is the minimum level of plant-available water in this soil (Raspe *et al.*, 2004). On the contrary, extreme summer drought prevailed in 2003 as a result of a 30% reduction in P_a and an increase in air temperature by 3.2°C (during the growing season) relative to the respective long-term averages. Water reserves at 5 cm soil depth were depleted until mid-July, when SWC declined to the minimum of 14% (**Fig. 21**). Recovery of SWC did not occur before the end of December 2003. During 2004, SWC at 5 cm depth was lower than during 2002, but never reached the minimum of 14%. In summary, 2002 had highest P_a (1015 mm) and highest mean air temperature (8.88°C) during the study period and contrasted with 2003 which displayed exceptionally low P_a (558 mm) at similar temperature; conditions in 2004 were representative of the long-term averages.

Comparing total monthly precipitation with mean monthly air temperature by means of a Walter's climate diagram (**Fig. 22**) indicates the temperature level to overpass that of precipitation during March through April and August through September of 2003. Drought is reflected, in particular, during the second half of the growing season. The extremely dry and warm summer of 2003 set the stage for evaluating the responsiveness of the two competing tree species, beech and spruce, to water limitation under the mixed-stand conditions of "Kranzberger Forst".

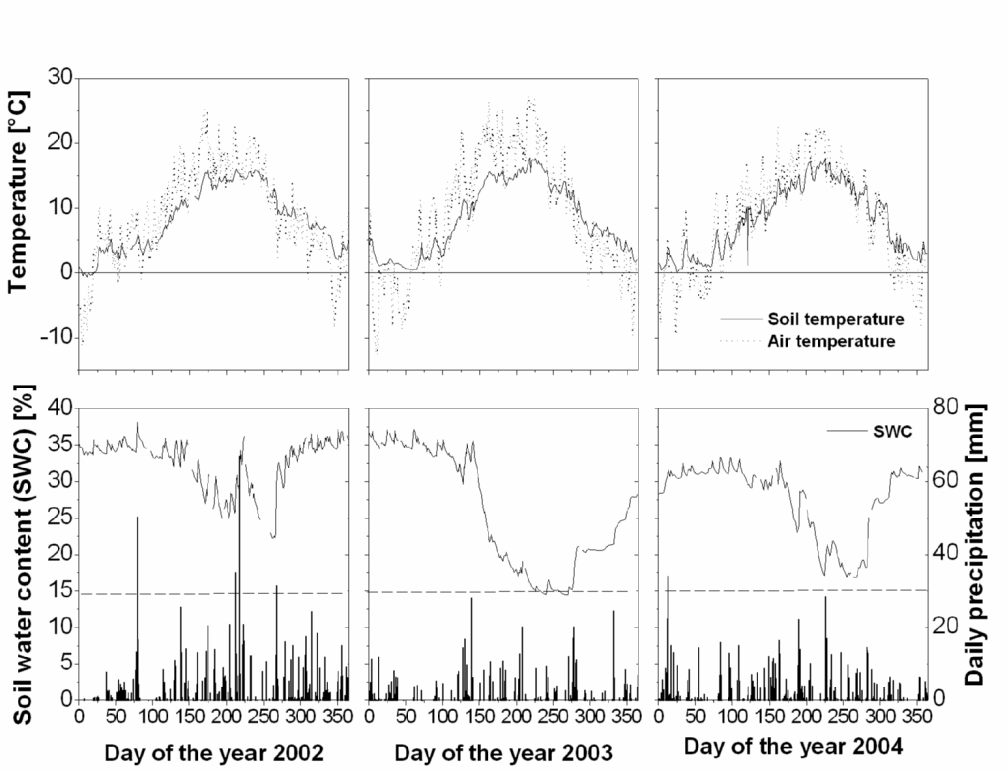

Figure 21: Soil temperature (T_s), air temperature (T_{air}), daily precipitation (P_a) and volumetric soil water content (SWC) at "Kranzberger Forst" during study years 2002, 2003 and 2004. Soil temperature is shown at 0 cm soil depth (measured at the study site), and SWC refers to 5 cm soil depth (measured at neighbouring Level II monitoring site "Freising", LWF). Solid horizontal lines of the upper graphs represent the zero-level of Celsius temperature; dotted lines of the lower graphs represent the threshold of 14 % SWC below which soil water is not available to plants.

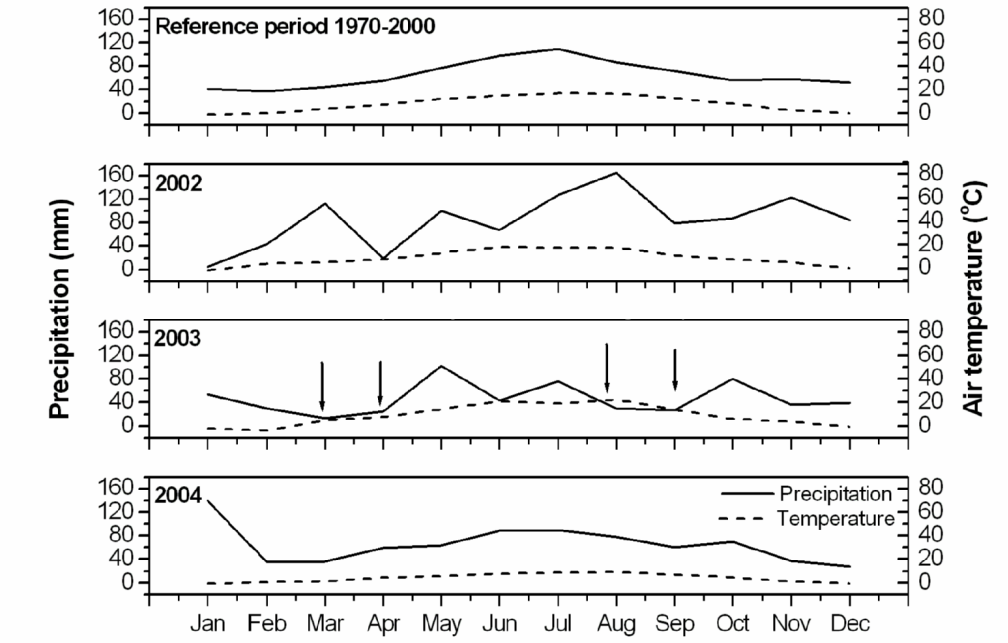

Figure 22*:* Walter's climate diagrams at „Kranzberger Forst" for the long-term average of the reference period of 1970-2000 and during the study years of 2002 to 2004. Precipitation and temperature are given as a 2:1 ratio, i.e. 20 mm of precipitation corresponds to 10°C temperature. Arrows mark periods of severe drought during 2003.

3.2 Dynamics of the fine-root biomass

3.2.1 Seasonal dynamics of the standing fine root biomass

In 2002, the standing fine root biomass of beech and spruce within the uppermost 20 cm of the soil showed seasonal dynamics with highest fine root densities in August, and lowest in winter or spring months (**Fig. 23**). When assessed at mono-subplots, both tree species showed similar total root densities (e.g. bio + necro-mass of fine-roots) ranging between maxima of 2000 to 2700 mg l^{-1} to minima of 900 to 2000 mg l^{-1}. At some sampling locations of "mono-subplots" also root biomass was present of the other tree species. Such an intrusion of alien fine-root mass was restricted to 5 to 10% of the total fine-root mass of a mono-subplot and neglected in further calculations. When growing in mixed subplots, maximum and minimum total standing fine-root mass accounted in both competitors each nearly for 50 % of the respective, species-specific fine-root densities found at mono-subplots (**Tab. 4**). Fine-root mortality rate (RM) in beech was about two times higher than in spruce, ranging within the study period between 22 and 48 % in beech, and between 4 and 22 % in spruce of the total fine-root mass each. No clear seasonal patterns of RM were found in both tree species.

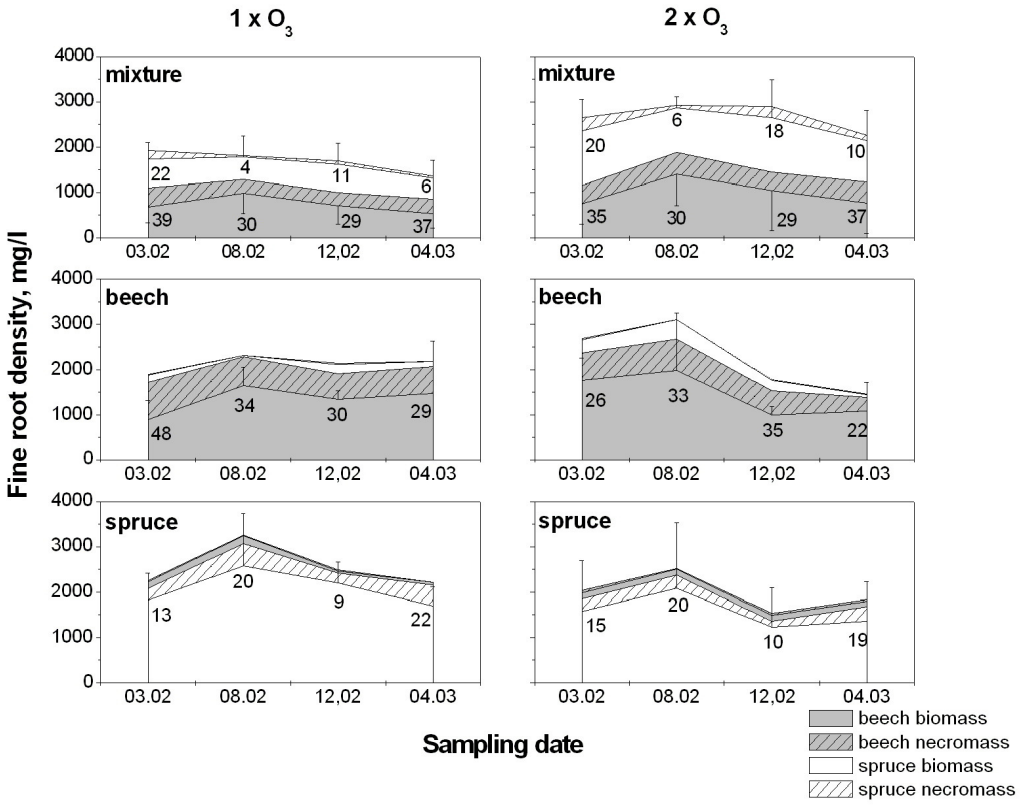

Figure 23*:* Standing fine-root biomass at "Kranzberger Forst" given as fine-root density within the uppermost 20 cm of the soil. Numbers show the averaged fine-root mortality rate as percentage of the standing fine-root mass (RM, %) in beech (placed on a grey background) and in spruce (placed on a white background) at sampling dates in 2002 and 2003. RM is presented on mono subplots only for the dominating tree species. Data represent mean + standard deviation (n = 5-10).

3.2.2 Annual fine root production

With the exception of beech growing in mixture under 2xO_3 the minimum and maximum levels of total fine-root mass did not differ significantly during the study period, by this, do not comply with the substantial pre-requisite of the "minimum-maximum" method (see section 2.10). Nevertheless, this assessment was compared with FRP as derived from the in-growth coring approach (IC, **Tab. 4**). Both methods yielded similar FRP in beech and spruce each. Since the agreement between both methods was high, further assessment of fine-root turnover and fine-root life span was based on the in-growth approach.

The in-growth data from the present study were completed with in-growth data from a previous comparable investigation at "Kranzberger Forst" (Dr. H. Blaschke, unpubl.) conducted during 1999 (the year prior to the start of the free-air O_3 fumigation experiment) and 2000 (**Fig. 24**). Locations of core extraction had been close to the positions of the present study. The additional data allow clarification if heterogeneity in FRP relates to the ozone fumigation. For 1999, univariate analysis was performed (General Linear Model GLM, SPSS, v.13.0) using as factors "treatment" (1xO_3 and 2xO_3 subplots), "tree species" (beech and spruce subplots) and "type of competition" (mixed and mono-subplots). As a result, no significant differences between the two O_3 regimes were found in either tree species or type of competition. Similarly, ozone did not cause differences in fine-root mass during the first year of fumigation (i.e. 2000). During 1999 and 2000, "type of competition" was found to determine the higher fine-root production at mono-subplots than at mixed subplots in both beech and spruce ($p=0.025$; GLM, SPSS 13.0). Since "tree species" x "treatment" and "type of competition" x "treatment" were found to interact significantly during 2002, the effect of each factor on fine-root biomass production was tested separately within this year. In contrast to the two preceding years, enhanced FRP was detected in beech and spruce under 2xO_3 during 2002, the third year upon starting the O_3 fumigation experiment. However, these differences were significant only in beech growing at mono-subplots and in spruce at mixed subplots ($p<0.05$, Wilcoxon test). During the extreme drought of 2003, the effect of the ozone fumigation on FRP vanished in both tree species. When FRP of 2003 was compared to that of the previous years, strong decreases were found under drought in spruce when growing at mono-subplots ($p<0.05$, Wilcoxon test). Any changes in beech FRP were found to be significantly affected by drought.

Across the entire study period (1999-2003), the factor "time" (e.g. the year of measurement) was found to have highly significant influence on FRP ($p=0.005$, repeated measures procedure of GLM, SPSS). There were no significant effects of "treatment", i.e. O_3 regime ($p=0.180$), and "tree species" ($p=0.660$) on annual FRP when tested for the whole study

period. The main factor leading to changes in FRP in both tree species, however, was the "type of competition". In mixed culture, FRP was reduced significantly in both beech and spruce each (p=0.003).

Table 4*:* Fine-root production (FRP; mg l^{-1}) at "Kranzberger Forst" in 2002 as assessed by the "Minimum-Maximum" or "In-growth" approach. Asterisks denote significant differences (p<0.05, Wilcoxon test) in FRP between $1xO_3$ and $2xO_3$ regime as assessed by the "In-growth" approach. Data represent means ± standard errors (n = 5 to 10).

Tree species	O_3 regime	Maximum and minimum of fine-root mass [mg l^{-1}]		FRP "Minimum-Maximum" method [mg l^{-1}]	FRP "In-growth" method [mg l^{-1}]
		Maximum	Minimum		
Beech, mixed subplots	$1xO_3$	1095 ± 165	939 ± 125	156	158 ± 41
	$2xO_3$	1871 ± 244	1156 ± 161	715	*413 ± 101
Spruce, mixed subplots	$1xO_3$	818 ± 115	628 ± 116	190	232 ± 80
	$2xO_3$	1491 ± 254	948 ± 83	543	*520 ± 115
Beech, mono subplots	$1xO_3$	1946 ± 299	1380 ± 296	566	255 ± 83
	$2xO_3$	2673 ± 648	1909 ± 154	764	*794 ± 160
Spruce, mono subplots	$1xO_3$	2697 ± 378	2085 ± 277	612	641 ± 145
	$2xO_3$	2368 ± 644	1699 ± 361	669	687 ± 215

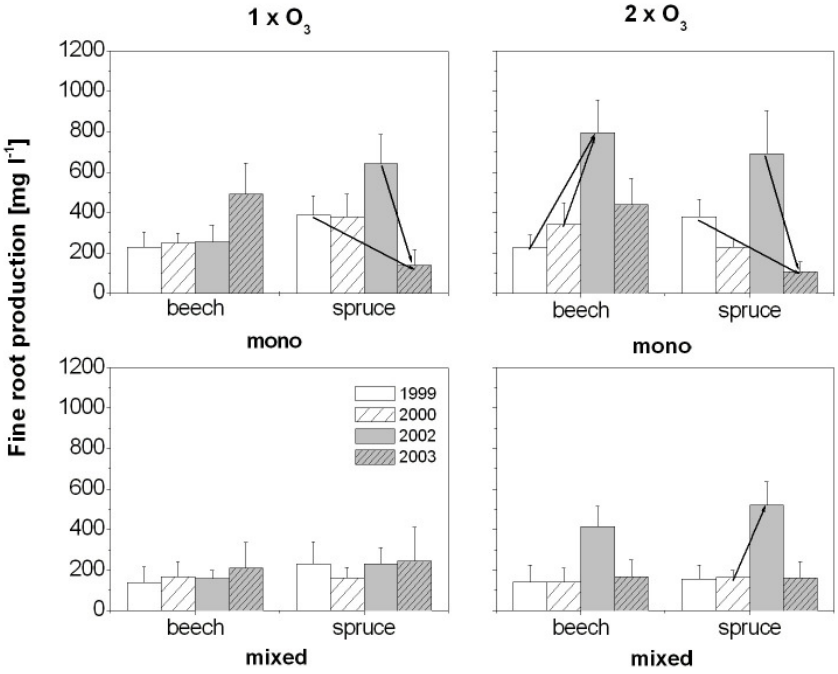

Figure 24: Fine-root production at "Kranzberger Forst" assessed by the "In growth" method during 1999, i.e. the year prior to the start of the free-air O_3 fumigation experiment, and during the three subsequent years of O_3 fumigation 2000, 2002 and 2003. Arrows indicate significant differences between years (p<0.05). Data represent means ± standard errors (n = 4 to 10).

3.2.3 Stand heterogeneity

The fine-root production as assessed during 2002 and 2003 was related to the mean distance between in-growth coring positions and the boles of the closest trees (**Fig. 25**; three distances were averaged within mono-subplots and four within mixed subplots). For each species, data from $1xO_3$ and $2xO_3$ were pooled. For all subplots the mean distance to the boles ranged between 1.0 m (e.g. high stem density) and 3.4 m (e.g. low stem density).

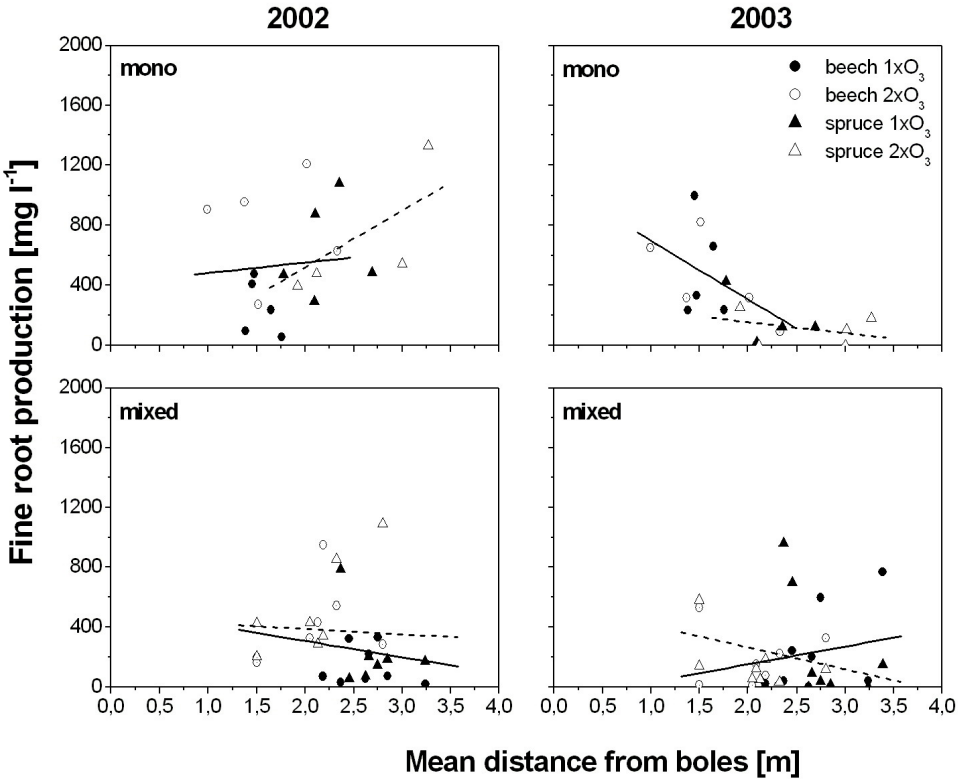

Figure 25*:* Relationship between fine-root production (assessed by in-growth coring within the uppermost 20 cm of the soil) and mean distance from boles (details are given in text) in beech (circles) and spruce (triangles). Closed symbols represent $1xO_3$ and open symbols $2xO_3$. Solid line represents the linear fit in beech, and dotted line the linear fit in spruce (for each species, data from $1xO_3$ and $2xO_3$ were pooled). All regressions are non-significant (p>0.10).

Since fine-root density was patchy, no significant pattern existed in relation to stand density within all subplots. However, the trends indicated a drought-induced reaction of beech and spruce fine roots. At mono subplots, during 2002, beech produced fine roots more uniformly than did spruce, as the latter species tended to produce two to tree times more fine roots at positions with low stem density. During 2003, fine-root production in beech was highest at positions with high stem density (mean distance to boles 1.5 m) and remained similar to that in 2002, whereas in spruce FRP was reduced by a factor of four to six in 2003 at positions with low stem density when compared to the preceding year. At mixed sub-plots, FRP was

uniform in 2002 in both tree species. However in 2003, spruce tended to produce more fine roots than beech at positions with high stem density, whereas beech fine-roots dominated at positions with low stem density. Compared to mono subplots, spruce was apparently less affected by drought when growing in mixture with beech.

SWC assessed on July 23 of 2002 within the uppermost 10 cm of the soil ranged widely between 7 % and 33 % (**Fig. 26**; data from $1xO_3$ and $2xO_3$ pooled for regression analysis). Highest levels were measured within beech sub-plots, where the mean SWC at $2xO_3$ (25.8%) was lower than at $1xO_3$ (31.9%; p=0.032, n=5). Lowest SWC was measured within spruce subplots (mean SWC of 14 to 16%; no significant differences between $1xO_3$ and $2xO_3$; p>0.10, n=5). Mixed subplots showed no significant pattern in relation to the mean distance from boles (**Fig. 26**), however, mean SWC at $2xO_3$ (14.2%) was significantly lower than at $1xO_3$ (22.1%; p=0.016, n=10). In sum, the highest SWC in beech was assessed at positions with high stem density (mean distance from boles 1.5 m) where FRP remained unaffected by drought during 2003 (**Fig. 25**), whereas in spruce the highest SWC was monitored when stem density was low. At such positions, spruce displayed highest FRP during the humid year of 2002, but lowest FRP during the drought of 2003; **Fig. 25**).

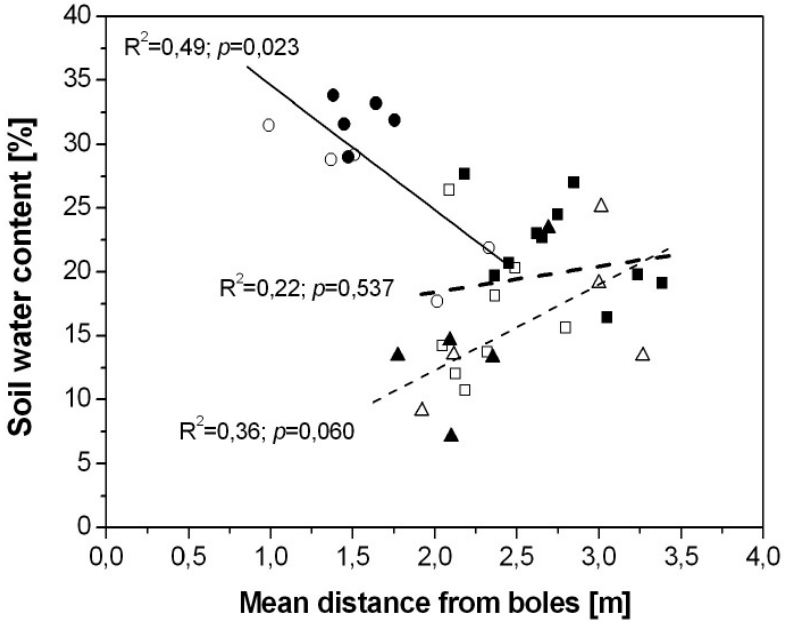

Fig. 26*:* Relationship between volumetric soil water content (SWC, %) and mean distance from boles [m] in beech (circles), spruce (triangles) and mixed sub-plots (squares). For linear regression analysis data of $1xO_3$ (closed symbols) and $2xO_3$ (open symbols) were pooled. R^2 represents measure of determination, and p gives levels of significance of the regression equations (ANOVA).

3.2.4 Fine-root turnover

During 2002, in both tree species the turnover rate (RT, %) of fine roots was found to be higher under $2xO_3$ than under $1xO_3$ (**Tab. 5**). Under $1xO_3$, about 30 % of beech fine roots were renewed at both mono and mixed subplots. In spruce, about 40% (at the mono-subplot) to 50% (at the mixed subplot) of fine roots died and were newly produced, showing higher dynamics of fine-root biomass at $1xO_3$ compared to beech. Under $2xO_3$, the turnover rate of beech fine roots was found to be two to three times higher compared to$1xO_3$, with higher RT levels at mono than mixed subplots (79% and 55% respectively). In spruce growing under $2xO_3$, renewal of fine roots was found to increase less distinctly than in beech. At $2xO_3$, RT in spruce was enhanced by 7% (mixed subplots) and by 20% (mono subplots) relative to $1xO_3$.

As affected by drought during 2003, RT of fine roots produced under $1xO_3$ increased (beech at mono and mixed subplots) or remained at a level similar (spruce at mixed subplots) to that in 2002. RT of spruce growing at mono subplots declined dramatically to 8% in 2003. The combination of drought and $2xO_3$ caused, in general, a decline of RT by a factor of two to three in relation to 2002. Hence, spruce responded again with strong reduction in RT dynamics, renewing only 8% of the standing fine-root biomass.

3.3.5 Life span of fine roots

Root life span (RL) similarly to fine-root turnover differed in this study largely between tree species, O_3 regimes, types of competition and years (**Tab. 5**). However some pattern in its dynamics could be found. The non-limiting water supply combined with $2xO_3$ resulted in the shortest life span of fine roots (1.3 to 2 years) of both beech and spruce trees, independent of the type of competition. The limited water supply combined with $2xO_3$ enhanced the longevity of both beech and spruce fine roots when growing in mixture (RL of 4.5 to 5.6 years). When growing at mono subplots, the combination of both $2xO_3$ and severe drought induced different responses in beech and spruce: in beech RL was lowered compared to the mixture (by up to 2.5 years), but in spruce RL increased strongly by up to 12 years. During 2003, fine-root longevity of about 12 years was detected also in spruce mono-subplots even under $1xO_3$, which indicates the dominating role of drought in limiting fine-root dynamics in spruce. Conversely, in beech the neighbourhood with spruce was likely to be a crucial factor in stimulating high fine-root longevity when water became limiting under $2xO_3$.

Table 5*:* Growth parameters assessed in beech and spruce fine roots during 2002 and 2003. Data representing minimum standing fine root biomass (RB_{min}) and fine root production (FRP) are presented as mean ± standard error (n = 5 to 10). Fine-root turnover (RT) is calculated from averages of RB_{min} and FRP. Root life span is the inverse of the root turnover rate.

Tree species	O_3-treatment	RB_{min} "Soil coring" [mg l^{-1}]		FRP "In-growth" [mg l^{-1}]		RT [yr^{-1}]		RL [yr]	
		2002	2003*	2002	2003	2002	2003	2002	2003
Beech, mixed sub-plots	1xO_3	533 ± 100	533 ± 100	158 ± 41	212 ± 126	0.29	0.39	3.4	2.6
	2xO_3	751 ± 143	766 ± 203	413 ± 101	167 ± 83	0.55	0.22	1.8	4.5
Spruce, mixed sub-plots	1xO_3	473 ± 120	473 ± 120	232 ± 80	244 ± 166	0.49	0.51	2	2
	2xO_3	922 ± 207	922 ± 207	520 ± 115	161 ± 79	0.56	0.18	1.8	5.6
Beech, mono sub-plots	1xO_3	878 ± 189	1468 ± 516	255 ± 83	492 ± 148	0.29	0.33	3.4	3
	2xO_3	995 ± 84	1079 ± 283	794 ± 160	439 ± 131	0.79	0.40	1.3	2.5
Spruce, mono sub-plots	1xO_3	1692 ± 189	1692 ± 189	641 ± 145	139 ± 76	0.38	0.08	2.6	12.5
	2xO_3	1224 ± 367	1350 + 393	687 ± 215	107 ± 49	0.57	0.08	1.8	12.5

* assessed in April 2003

3.4 $\delta^{13}C$ signature of newly formed fine roots

The $\delta^{13}C$ signature of beech and spruce fine roots produced during 2002 and 2003 was compared with the signature of fine roots obtained from in-growth cores in November 1999, the year before the O_3 fumigation experiment at "Kranzberger Forst" had been started (fine-root samples from 1999 provided by Dr H. Blaschke). For the 1999 data (**Fig. 27**), a univariate analysis was performed (General Linear Model GLM, SPSS, v.13.0) using as factors: "O_3 treatment", "tree species" and "type of competition". Only "tree species" showed a significant effect (p<0.001) on the observed differences in $\delta^{13}C$ signature of fine roots formed during 1999, as spruce had less negative $\delta^{13}C$ compared to beech. This finding is consistent with the documented higher $\delta^{13}C$ in the wood of the conifer *Pinus halepensis* as compared with the angiosperm *Quercus ilex* (Ferrio *et al.*, 2003) and reflects the higher water use efficiency (WUE, e.g. the molar ratio of CO_2 uptake to transpiration) of conifers. Since "O_3 treatment" x "tree species" interacted significantly (p=0.027), differences in 1999 in "O_3 treatment" effect were tested, in addition, for each tree group by non-parametrical Mann-Whitney-*U*-test. Spruce was found to have significantly less negative $\delta^{13}C$ in 1999 when growing at the 2xO_3 area of the subsequent years in both mono (p=0.014) and mixed (p=0.014) subplots. In beech fine roots of mono and mixed subplots, no significant differences in $\delta^{13}C$ were found in 1999 between the 1xO_3 and 2xO_3 areas of the subsequent years.

During the third year upon starting the O_3 fumigation experiment (i.e. during 2002), beech fine roots from mono subplots under $2xO_3$ had less negative $\delta^{13}C$ (p=0.004) than when produced under $1xO_3$, whereas no change in $\delta^{13}C$ was found in beech fine roots of mixed subplots (Mann-Whitney-*U*-test). The same was found for spruce (p=0.016). Since $\delta^{13}C$ of spruce fine roots differed in 1999 at the $2xO_3$ area of the subsequent years, the effect on $\delta^{13}C$ during 2002 under $2xO_3$ could not be interpreted as a response of spruce to enhanced O_3 stress. During 2003, no O_3 effect was detected on $\delta^{13}C$ of newly produced beech or spruce fine roots. Spruce fine roots produced under $1xO_3$ had less negative $\delta^{13}C$ than under $2xO_3$, however, this difference was not significant. Similarly to the observations during 1999, ^{13}C in fine roots was found to be less discriminated during 2002 and 2003 in spruce than in beech at both mono and mixed subplots (p<0.001).

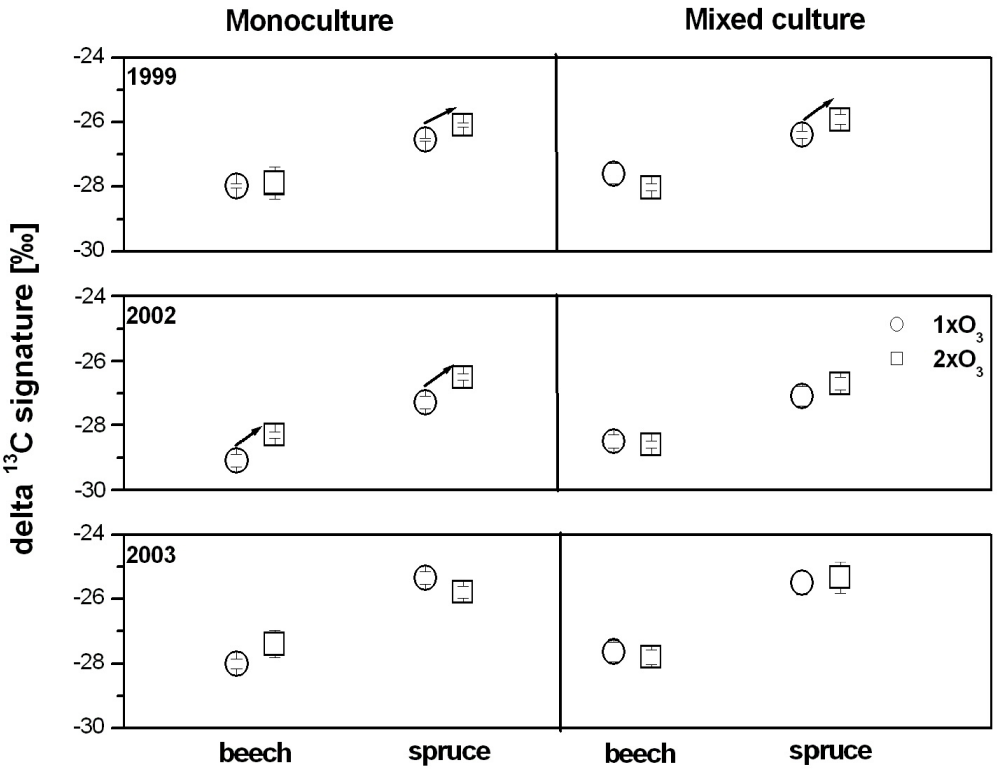

Figure 27*: $\delta^{13}C$* signature of newly produced fine roots during the year 1999 (prior to start of free-air O_3 fumigation) and during subsequent years with ozone fumigation 2002 and 2003. Arrows indicate significant differences between O_3 regimes (*U*-test); *p*-values are cited in text. Data represent means ± standard errors (n = 5 -10).

Since "tree species" was the main factor contributing significantly to the differences in $\delta^{13}C$ signature of newly-produced fine roots within the study years (univariate analysis of GLM; SPSS), $\delta^{13}C$ data were pooled across the O_3 regimes and types of competition in two sub-samples (beech and spruce) and correlated with the mean annual precipitation of the year in which roots were produced (**Fig. 28**). Highly significant linear correlations were found in both

beech (p=0.008) and spruce (p<0.001) sub-samples indicating the decrease in annual precipitation to cause enhanced water use efficiency (WUE) and to limit the CO_2 uptake in both tree species. In spruce, annual precipitation explains 80% of data variation, whereas in beech annual precipitation accounted for 53%. Testing the coefficients of both correlations revealed a significant difference between slopes of both tree species (p=0.05, t-test).

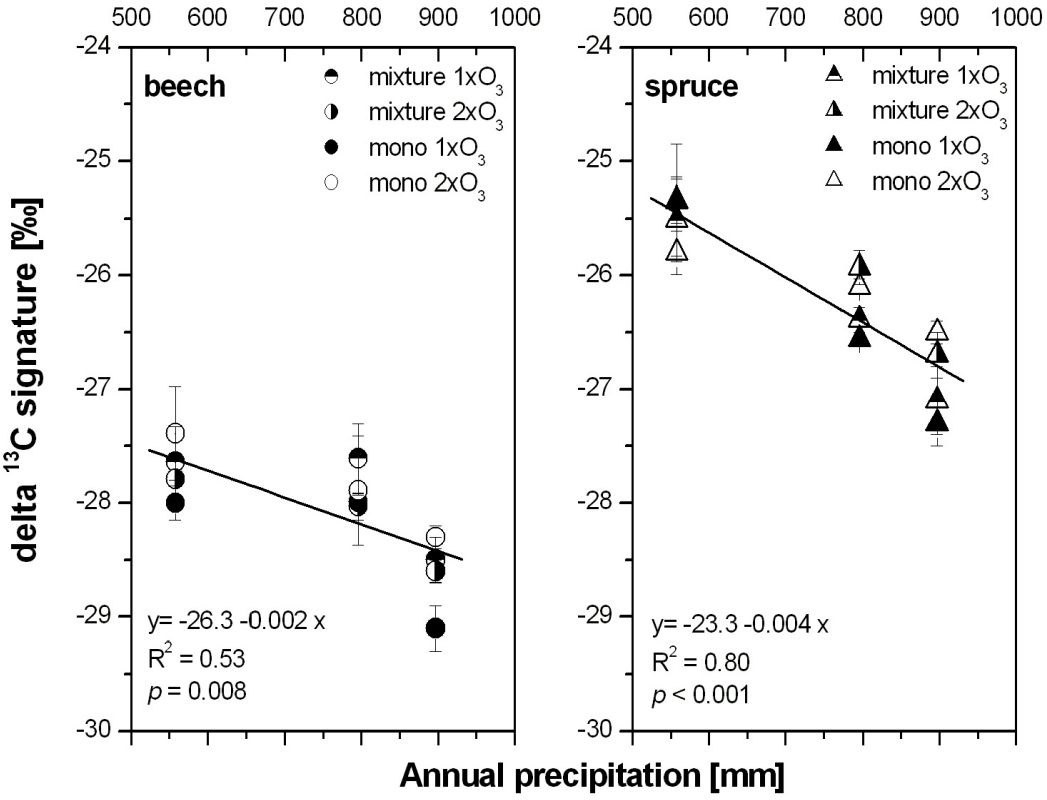

Figure 28: Correlation between $\delta^{13}C$ signature of fine roots in beech (A., circles) and spruce (B., triangles) and the annual precipitation at "Kranzberger Forst" during 1999, 2002 and 2003. Filled symbols represent $1xO_3$ and open symbols $2xO_3$. Big symbols represent mono subplots, and small symbols represent mixed subplots. Correlation equations are shown for pooled beech and spruce sub-samples (n=12). Data represent means $\pm$ standard errors (n = 5 -10).

3.4 Total soil respiration

3.4.1 Seasonal dynamics in total soil respiration

During the humid year of 2002, total soil respiration (SR_t) followed soil temperature under both O_3 regimes (T_s; **Fig. 29**). Maximum SR_t was assessed in June under $2xO_3$: 1.1 g CO_2 m^{-2} h^{-1} within the beech sub-plot, 0.78 g CO_2 m^{-2} h^{-1} within the spruce sub-plot, and 1.0 g CO_2 m^{-2} h^{-1} within the mixed sub-plot. In November 2002, SR_t tended to increase in all subplots

compared to the measurements in October substantially despite decreasing T_s, as a consequence of the C and N input of the recently shed leaves to the soil surface. In early spring of 2003, before fine root proliferation was started at T_s of about 2.5°C, lowest SR_t was found under beech (0.1 g CO_2 m^{-2} h^{-1}), while rates were 0.2 g CO_2 m^{-2} h^{-1} under spruce and 0.18 g CO_2 m^{-2} h^{-1} under mixed culture. During the exceptionally dry second half of the growing season of 2003, SR_t was reduced in all subplots as compared to the corresponding period of 2002. In particular under spruce, this reduction was the strongest under both O_3 regimes, and during July and August of 2003, SR_t was two times lower (0.4 g CO_2 m^{-2} h^{-1}) compared to levels during same months in 2002 ($p<0.05$). During July and August of 2003, SR_t was by 15 to 20 % lower at the mixed and beech sub-plots compared to levels during the same period in 2002 (although not being statistically significant). The increase in SR_t during November despite lowered T_s was less pronounced in 2003 than in 2002.

3.4.2 Ozone impact on total soil respiration

In general, total soil respiration assessed under $2xO_3$ was higher compared to $1xO_3$ within mono- and mixed sub-plots across the entire study period. Since "treatment" (i.e. $1xO_3$ and $2xO_3$ sub-plots) and "type of competition" (i.e. mixed, beech and spruce -subplots) interacted significantly (p=0.015), a univariate analysis with main factors "treatment" and "year" (i.e. 2002 and 2003), and with a covariate "soil temperature" (**Fig. 29**) was provided separately for each "type of competition". "Treatment" had a significant effect on SR_t within each "type of competition", whereas "year" was significant only for the beech subplot, tended to influence SR_t within spruce, and had no significant effect on SR_t within the mixed sub-plot (p values are shown on **Fig. 29**). Both main factors did not interact significantly in any "type of competition" indicating that the detected O_3-impact on SR_t was independent on the climatic differences between both study years.

To check the potentially confounding effect of the fine-root biomass on the detected ozone effect on SR_t, soil respiration rates assessed in July of 2002 were tested (univariate analysis) when "treatment" and "type of competition" were set as main factors, and "fine-root density" (assessed by soil coring during August of 2002 and set as representative for July of 2002) was used as covariate. Both main factors did not interact significantly (p=0.135) and, again, only "treatment" had a significant effect on SR_t (p=0.001), whereas "type of competition" did not show impact on SR_t (p=0.791). The covariate (i.e. "fine-root density") had no significant effect on SR_t (p=0.134).

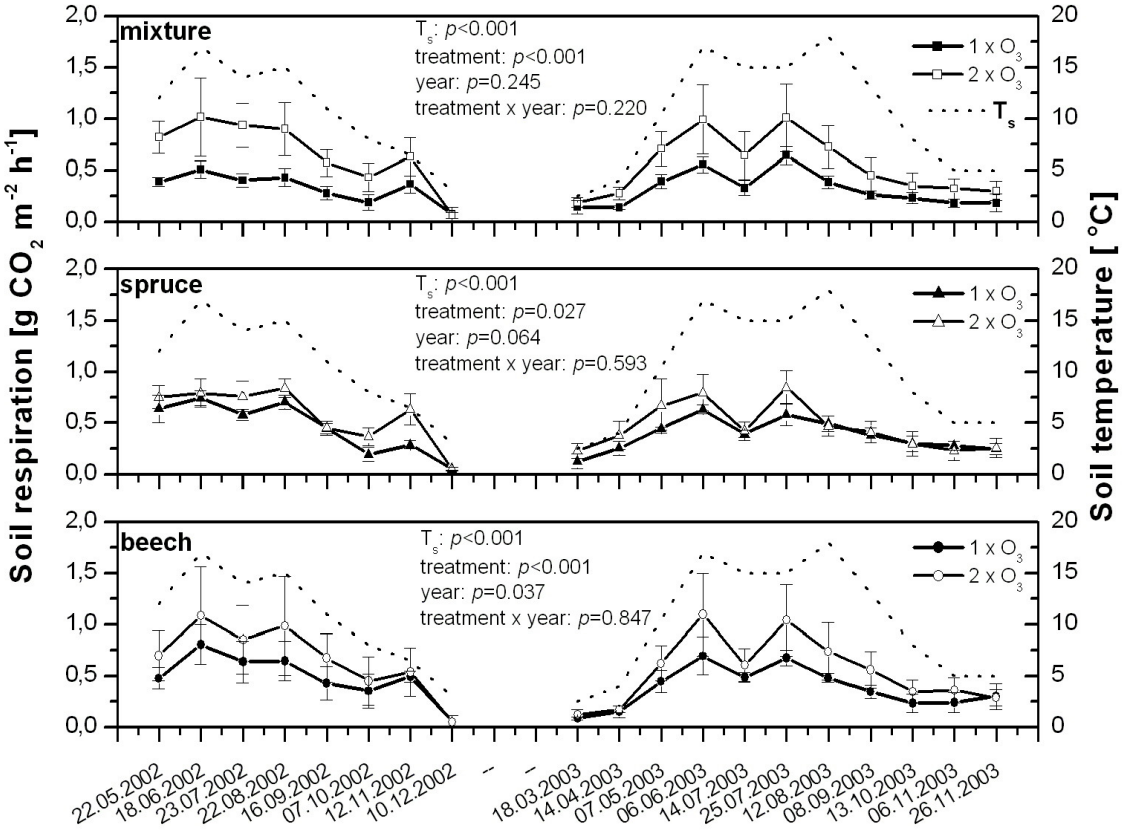

Figure 29: Total soil respiration (SR_t) and soil temperature (T_s, at 3 cm soil depth) assessed at "Kranzberger Forst" during the study period of May 2002 through November 2003. Data represent means ± 95% confidence interval (n = 5 or 10).

3.4.3 Components of total soil respiration under drought

3.4.3.1 Seasonal dynamics in "autotrophic" and "heterotrophic" soil respiration

Under the moist conditions of 2002 and 2004, SR_t tended to follow T_s (**Fig. 30**). In November of 2002, SR_t measured at the beech and spruce subplots (**Fig. 12**) increased underneath beech at lower T_s than in October, as a consequence of autumnal leaf litter input (cf. section 3.4.1). A similar, but smaller effect was detected in spruce. At the exceptionally low SWC during the second half of the growing season in 2003, SR_t was reduced under beech and spruce compared to the corresponding period of 2002 and 2004. Under spruce, SR_a contributed significantly less to SR_t during drought than under beech, where the ratio of SR_a to SR_h stayed unaffected (**Fig. 30**).

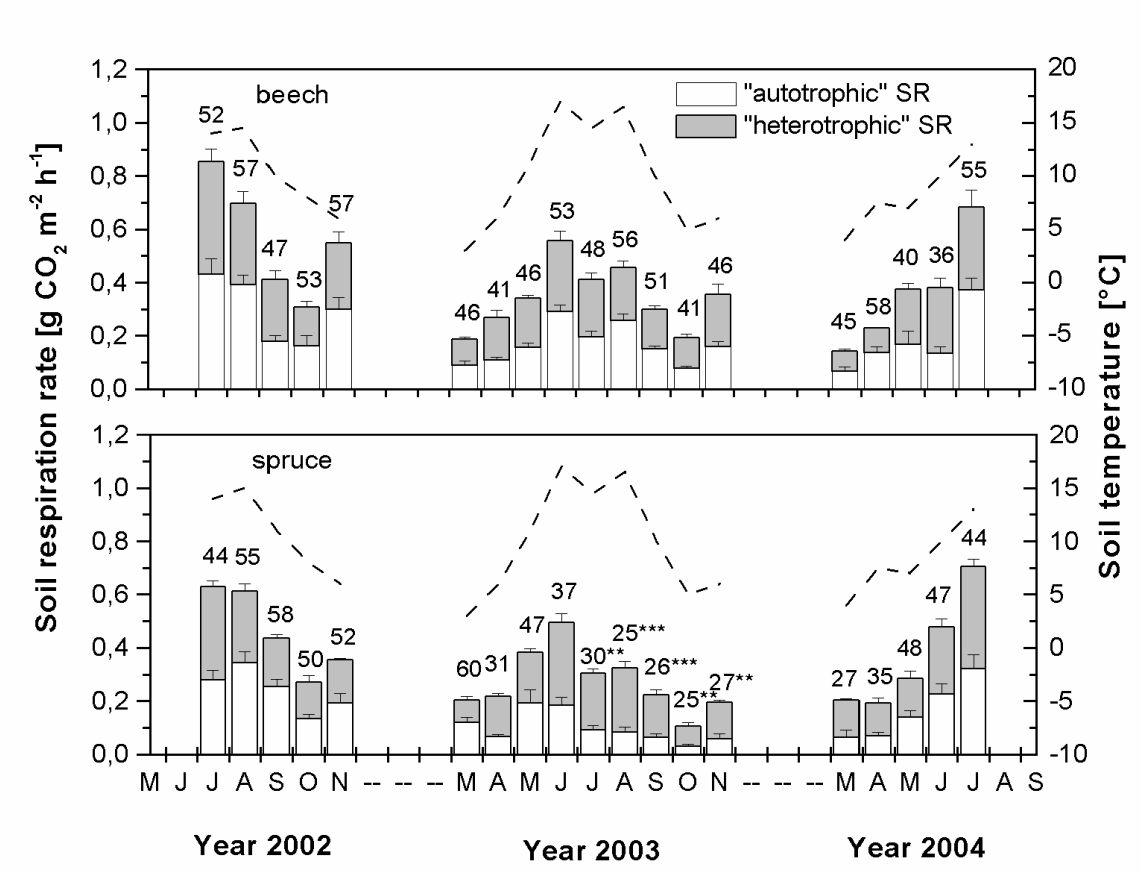

Figure 30: Seasonal courses of SR_t (total length of bars), SR_a (white portion of bars) and SR_h (grey portion of bars) underneath beech and spruce groups from July 2002 through July 2004 (no data between December 2002 and February 2003, and between December 2003 and February 2004). Dotted line represents soil temperature at 3 cm depth. Numbers above bars give percentage of SR_a in SR_t and differ significantly in 2003 compared to 2002/2004 underneath spruce during August and September at $p<0.01$ (***), and during July, October and November at $p<0.05$ (**); means (n=5) $\pm$ standard errors. Significance levels between months were assessed by means of *Wilcoxon*-test.

Table 6: Fine root density (FRD) at positions of the root exclusion assay and at reference positions underneath beech and spruce; one-sided standard errors of means (n=5) shown in brackets.

Date	FRD [mg l^{-1}]*	
	Beech	Spruce
June 28, 2002 at positions of root exclusion	852.6 (83.0)	1922.4 (193.5)
July12, 2004 at reference positions	912.8 (105.0)	1653.3 (212.9)

*calculated as the fine-root dry mass per unit of soil volume [mg l^{-1}]

Fine root density (FRD), determined in June 2002 and July 2004 did not differ between years underneath either tree species (**Tab. 6**) although fine root biomass was 2 times higher in spruce than beech within the uppermost 10 cm of the soil.

3.4.3.2 Modelling plant-available sol water

Annual courses of modelled plant-available soil water (ASW) strongly varied across the three study years within the uppermost 40 cm of the soil, where fine-root density was highest in both tree species (**Fig. 31**). In 2002, both tree groups displayed similar seasonal courses in ASW. Minor differences occurred at lowered ASW levels in June (90 and 75 mm m^{-2} underneath beech and spruce, respectively), although differences were greatest in 2003. ASW was already low in the spring underneath spruce, and low P_{an} in combination with high T_{air} induced severe soil drought during summer compared to the beech group. As a consequence, estimates indicated depleted ASW underneath spruce by mid-July. Soil moisture depletion was delayed by one month underneath beech, which had 20% less fine-root length relative to spruce within the uppermost 40 cm of soil depth. Although autumnal precipitation in 2003 increased ASW underneath both tree species, levels comparable to 2002 were not reached. ASW was completely re-charged by February 2004 underneath beech, whereas spruce experienced lowered ASW at that time relative to the preceding years. During the summer of 2004, ASW was roughly 10-15 mm m^{-2} lower under beech than spruce; however, low levels as experienced in 2003 were not reached at any time. Daily mean SWC was highly correlated with ASW in beech and spruce during the period of soil desiccation in 2003 (**Figs. 31 & 32**), reflecting higher ASW under beech than spruce (up to 7% and 20 mm m^{-2} higher SWC and ASW, respectively), and exhaustion of ASW underneath spruce.

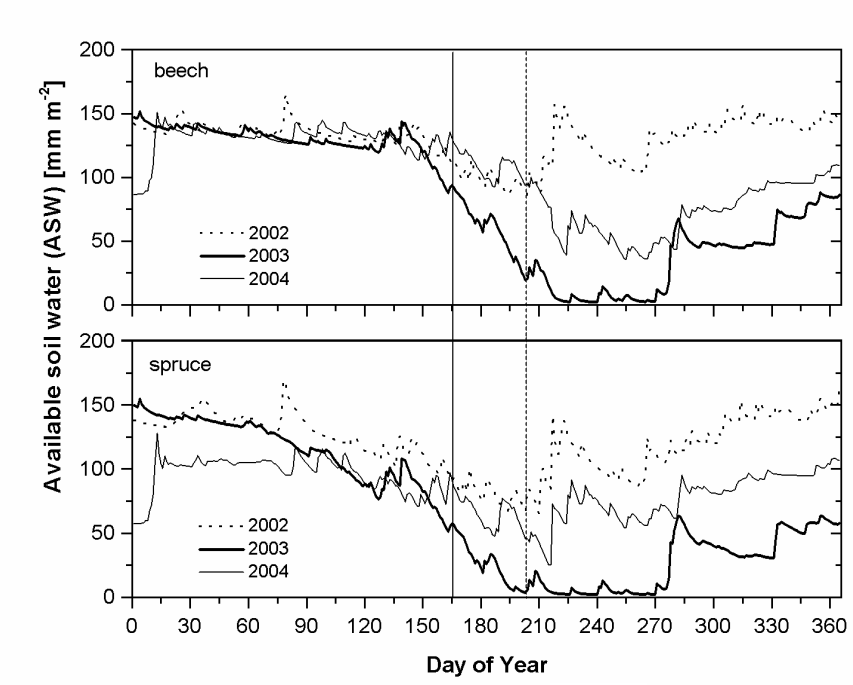

Figure 31*:* Seasonal dynamics of ASW as modelled by "LWF-BROOK90" for the groups of beech and spruce at "Kranzberger Forst". Levels represent integrals across the uppermost 40 cm of the forest soil during 2002, 2003 and 2004. The vertical dotted lines show the time period in 2003 during which modelled ASW was compared to measured volumetric soil water content (SWC) underneath beech and spruce (**Figure 32**).

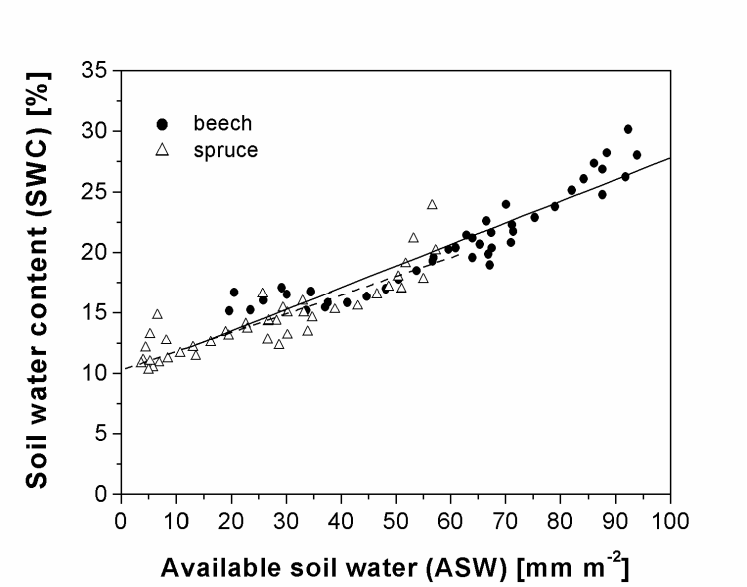

Figure 32*:* Relationship between plant-available soil water (ASW, modelled by LWF-BROOK90 on a daily basis, from **Fig. 31**) and measured volumetric soil water content (SWC, daily basis, averaged across 3 measurement positions) from day 165 through day 202 of 2003, underneath beech (solid line, $R^2 = 0.94$) and spruce (dotted line, $R^2 = 0.82$).

3.4.3.3 Responses of "autotrophic" and "heterotrophic" soil respiration to soil temperature and plant-available soil water

SR_a and SR_h were highly correlated with T_s (**Fig. 33**). However, the relationship between SR_a and T_s was atypical during drought under spruce. In spite of increasing T_s, SR_a remained constant in June 2003 and then dropped to levels which are typical for the cold season. A different exponential fit was required from June through October 2003 to quantify the temperature dependence of SR_a underneath spruce during drought (**Tab. 7**). Under drought, SR_a was significantly lower in spruce than during moist conditions at a reference T_s of 10°C (coefficient *a, p*=0.05). By comparison, in beech the temperature response (coefficient *b*) was lowered significantly, both in the case of SR_a and SR_h (*p*=0.05), in response to drought (**Tab. 7**). In general, SR_a tended to be more sensitive to T_s than was SR_h, independent of the study year or tree species, as expressed by Q_{10} ($Q_{10} = e^{10xb}$). Drought conditions reduced the Q_{10} of both SR_a and SR_h only in beech.

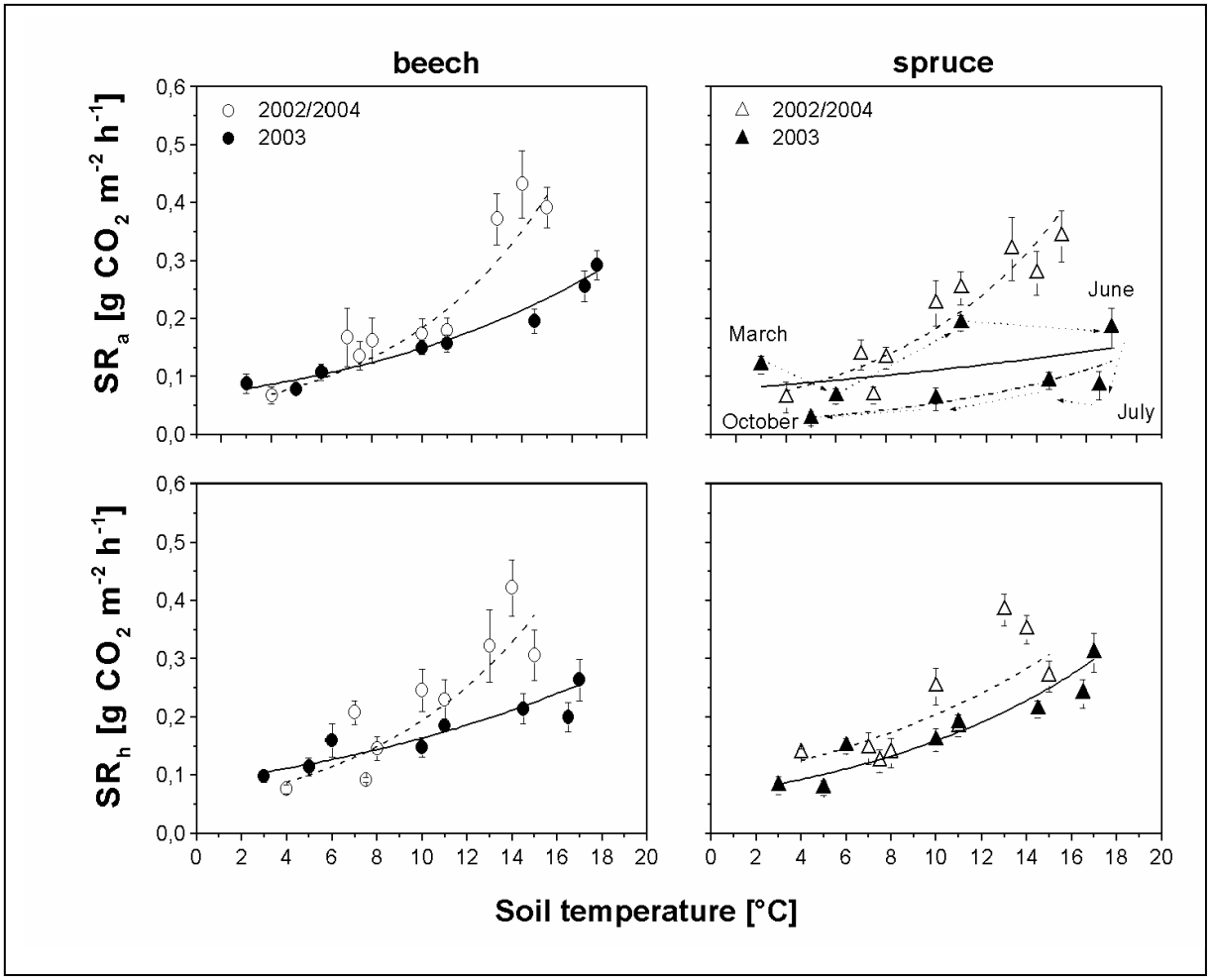

Figure 33: Relationship between soil respiration (SR_a, SR_h) underneath beech and spruce and soil temperature at 3 cm depth during the years 2002 and 2004 (pooled data) with non-limited water supply (dotted line) and the year 2003 with limited water supply (solid line). Arrows denote hysteresis in the time course of the temperature response of SR_a underneath spruce. The function fitted in spruce (dashed line) covers the period of June through October 2003; means (n=5) ± standard errors. Regression statistics is provided in **Tab. 7**.

SR_a^{10}, SR_h^{10} (SR_a and SR_h normalized in relation to T_s), were linearly related to ASW during the entire study period (**Fig. 34A, B**). Spruce showed a stronger decrease in SR_a than beech at low levels of ASW, which is reflected by the different coefficients *c* and *d* in both species (*p*=0.10, **Tab. 8**). In determining the ASW dependence of SR_h^{10}, a break-point was assessed iteratively at 100 mm m^{-2} in beech, at which the positive correlation turned into negative. In spruce, no such relationship between SR_h^{10} and ASW was found above 80 mm m^{-2} (R^2=0.06, *p*=0.61, see **Tab. 8**) so that no ASW response function was employed in modelling SR_h above this ASW level. Coefficients *c* and *d*, regarding the SR_h^{10} dependence on low ASW, did not differ significantly between the tree species.

Table 7: Statistical treatment of the data shown in **Fig. 33**. Exponential fit (SR = *a* e $^{b(t-10)}$) describes the relationship between "autotrophic" soil respiration (SR_a), "heterotrophic" soil respiration (SR_h) and soil temperature (T_s) at 3 cm soil depth, with *a* and *b* being regression coefficients, R^2 representing measure of determination, Q_{10} calculated from *b* ($Q_{10} = e^{10xb}$), and *p* giving levels of significance of the regression equations (ANOVA). Standard errors of *a* and *b* are shown in brackets.

Year	Species	Component of soil respiration	a [g CO_2 m^{-2} h^{-1}]	b [°C]	n	R^2	Q_{10}	*p*
2002 and 2004 (pooled data)	beech	"autotrophic"	0.184 (0.010)	0.161 (0.015)	9	0.92	5.0	<0.001
		"heterotrophic"	0.194 (0.009)	0.132 (0.014)	9	0.90	3.7	0.001
	spruce	"autotrophic"	0.184 (0.010)	0.148 (0.015)	9	0.88	4.4	0.001
		"heterotrophic"	0.204 (0.009)	0.081 (0.012)	9	0.63	2.2	0.007
2003	beech	"autotrophic"	0.149 (0.011)	0.090 (0.011)	8	0.97	2.4	<0.001
		"heterotrophic"	0.164 (0.009)	0.064 (0.010)	8	0.92	1.9	0.001
	spruce	"autotrophic" (March-Oct)	0.111 (0.010)	0.043 (0.015)	8	0.20	1.5	0.362
		second „autotrophic" (June-Oct)	0.051 (0.025)	0.142 (0.079)	5	0.85	4.1	0.027
		"heterotrophic"	0.159 (0.010)	0.090 (0.011)	8	0.94	2.5	0.001

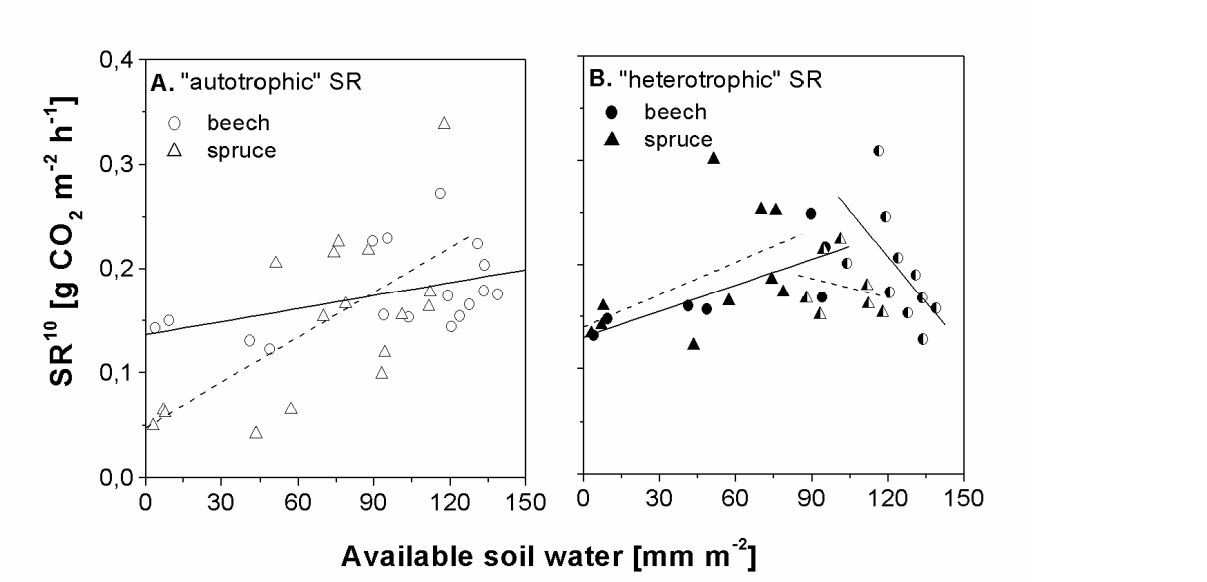

Figure 34*:* Relationship between soil respiration at 10°C (SR^{10}) and plant available soil water (ASW). A, "autotrophic" SR^{10} correlated positively with ASW underneath both tree species. B, "heterotrophic" SR^{10} correlated positively in beech at ASW < 100 mm m^{-2} (filled circles), and negatively at ASW > 100 mm m^{-2} (half-filled circles). "Heterotrophic" SR^{10} under spruce correlated positively at ASW < 80 mm m^{-2} (filled triangles), whereas the correlation was not significant at ASW > 80 mm m^{-2} (half-filled triangles). Regression lines of beech are solid, and of spruce dotted. Regression statistics is provided in **Tab. 8**.

Table 8*:* Regression statistics of the linear relationship between "autotrophic" and "heterotrophic" soil respiration at 10°C (SR_a^{10} and SR_h^{10} , respectively) and ASW (**Fig. 34**), where *c* and *d* are regression coefficients, R^2 is the coefficient of determination, and *p* gives the levels of significance of the regression equations (ANOVA). Standard errors of the coefficients *c* and *d* are shown in brackets.

Plots	Component of soil respiration	c [g CO_2 m^{-2} h^{-1}]	d *10^3 [mm m^{-2}]	n	R^2	*p*
beech	"autotrophic"	0.136 (0.022)	0.420 (0.217)	17	0.20	0.071
	"heterotrophic" <100 mm m^{-2}	0.130 (0.019)	0.820 (0.262)	7	0.62	0.034
	"heterotrophic" >100 mm m^{-2}	0.559 (0.182)	-2.920 (1.360)	10	0.33	0.083
spruce	"autotrophic"	0.048 (0.029)	1.400 (0.391)	17	0.44	0.003
	"heterotrophic" <80 mm m^{-2}	0.140 (0.025)	0.946 (0.471)	10	0.30	0.079
	"heterotrophic" >80 mm m^{-2}	0.241 (0.11)	-0.600 (0.674)	7	0.06	0.610

3.4.3.4 Modelling in "autotrophic" and "heterotrophic" soil respiration

SR_a and SR_h were modelled on a daily basis throughout the study period (cf. Eq. 12), accounting for T_s (coefficient *b*) and ASW (coefficients *c* and *d*) as driving factors. The correction factor *L* was set in beech (according to Eq. 14) to L_h=L_a=0.02, both in the case of 2002 and 2004, and to L_h=0.02 and L_a=0.015 in the case of 2003. Predicted SR_a and SR_h showed higher agreement with observed levels in beech than in spruce (R^2=0.89 in spruce vs 0.93 in beech for SR_a, and 0.85 in spruce vs 0.90 in beech for SR_h ; **Fig. 35**).

Based on modelling, annual SR_a, SR_h and SR_t were calculated underneath beech and spruce during the study period (**Tab. 9**). SR_t of the beech group was lowest during the drought of 2003 (789 g C m^{-2} a^{-1}), and highest during the humid year of 2002 (945 g C m^{-2} a^{-1}). SR_a amounted to 398 g C m^{-2} a^{-1} in 2003, and to 476 g C m^{-2} a^{-1} in 2002, accounting in both years for about 50 % of SR_t. In spruce, similar to beech, the lowest SR_t occurred during 2003 (613 g C m^{-2} a^{-1}), and the highest (928 g C m^{-2} a^{-1}) during 2002. SR_a of spruce nearly reached 51% (471 g C m^{-2} a^{-1}) of SR_t in 2002, but was lowered to 38% (234 g C m^{-2} a^{-1}) in 2003. The year 2004 was characterised by intermediate levels of SR_t in beech (888 g C m^{-2} a^{-1}) and spruce (804 g C m^{-2} a^{-1}), with SR_h being slightly higher in spruce (55 % of SR_t), but remaining near 50 % of SR_t in beech.

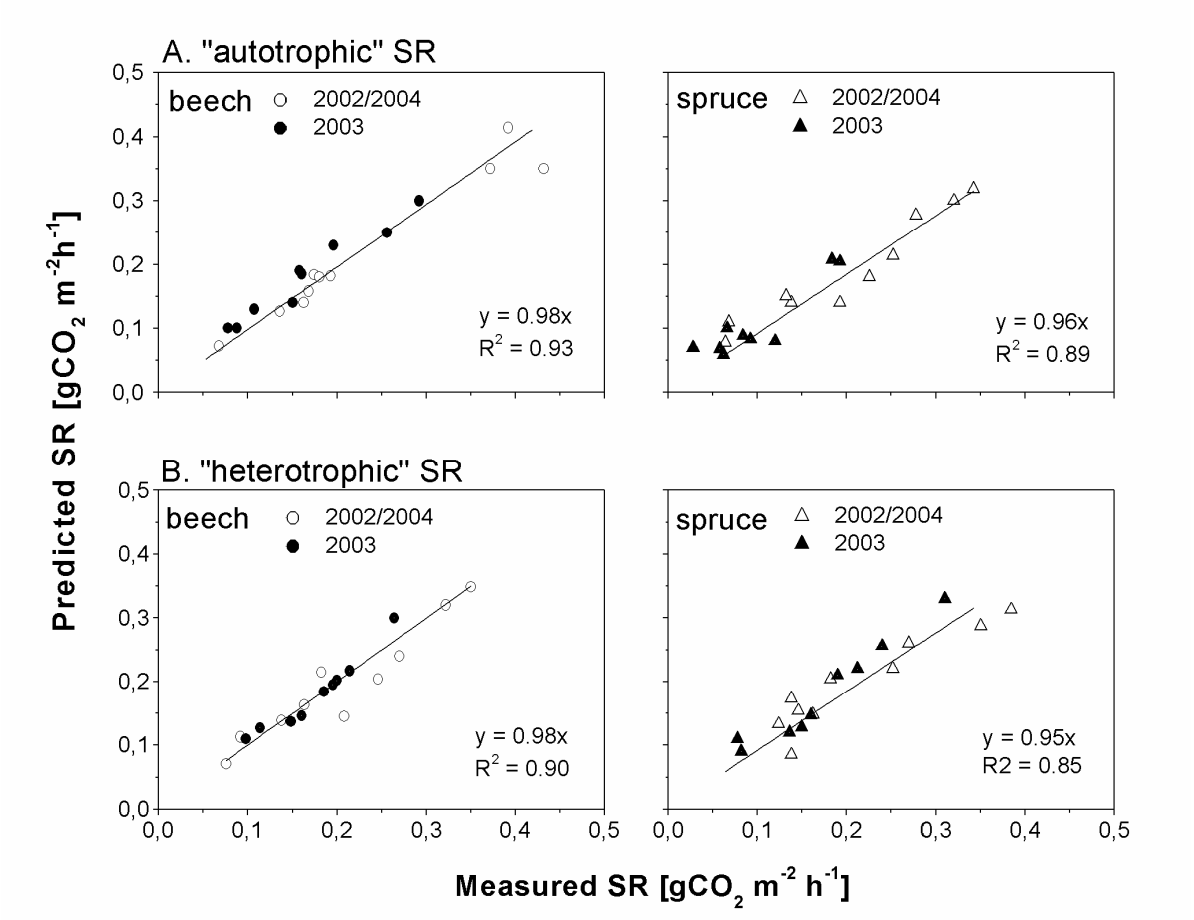

Figure 35: Parameterisation of modelled SR_a and SR_h in beech and spruce: relationship between measured A, "autotrophic" and B, "heterotrophic" SR (means, n=5) and predicted SR_a and SR_h (according to eqn. 4 and eqn. 5) throughout 2002-2004. Open symbols represent data from years 2002 and 2004 with non-limited water supply, and filled symbols from water-limited year 2003.

Table 9*:* Annual "autotrophic" (SR_a), "heterotrophic" (SR_h) and total (SR_t) soil respiration, [g $Cm^{-2}a^{-1}$] underneath beech and spruce during the study years at "Kranzberger Forst". Numbers in brackets represent SR_a/SR_t.

Year	Annual soil respiration [g C m^{-2} a^{-1}]					
	Beech			Spruce		
	SR_a	SR_h	SR_t	SR_a	SR_h	SR_t
2002	476 (50%)	469 (50%)	945	471 (51%)	457 (49%)	928
2003	398 (50%)	391 (50%)	789	234 (38%)	379 (62%)	613
2004	437 (49%)	451 (51%)	888	365 (45%)	439 (55%)	804

3.5 Respiration of fine roots

3.5.1 Ozone impact on root respiration rate

Root respiration rate (RR) assessed in August 2002 did not differ between $1xO_3$ and $2xO_3$ in any tree species or fine-root category (**Fig. 36**). These results indicate no response in respiratory activity of beech and spruce fine-roots after three seasons of chronic O_3 fumigation.

Pooling the data from both O_3 regimes, highest RR was measured on long lateral roots with primary cortex (LR_{prim}; 35 nmol CO_2 $g^{-1}s^{-1}$ in beech and 30 nmol CO_2 $g^{-1}s^{-1}$ in spruce), and lowest RR on long lateral roots with secondary cortex (LR_{sec}; 2.9 nmol CO_2 $g^{-1}s^{-1}$ in beech and 4.7 nmol CO_2 $g^{-1}s^{-1}$ in spruce). However, significant differences between beech and spruce were found only in RR of LR_{sec}. Both tree species showed similar RR in short roots (ShR) at a level of 10 nmol CO_2 $g^{-1}s^{-1}$.

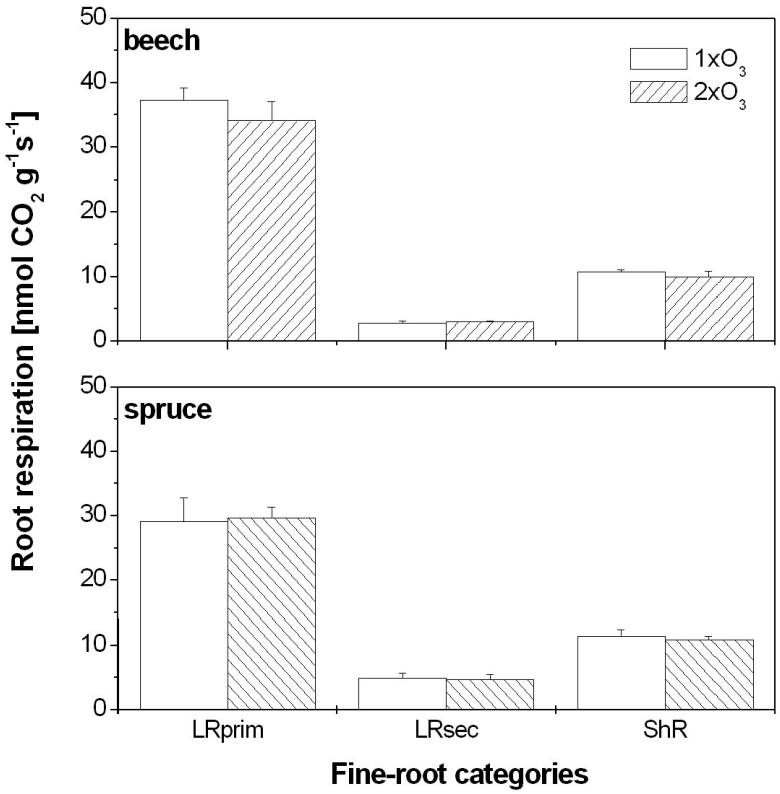

Figure 36*:* Respiration rate (RR) at 18°C of fine root categories in beech and spruce as assessed in August 2002 under $1xO_3$ and $2xO_3$. Data represent mean ± 95% confidence interval (n = 5).

3.5.2 Seasonal dynamics in temperature sensitivity of RR

In beech, the highest respiration rates and sensitivity to temperature were assessed during 2003 in LR_{prim} (**Fig. 37A & Tab. 10A**): RR at 10°C (RR^{10}) ranged between 9.46 nmol $CO_2\,g^{-1}\,s^{-1}$ in October and 17.06 nmol $CO_2\,g^{-1}\,s^{-1}$ in April, while Q_{10} ranged between 1.2 and 2.2 in September and June, respectively. Within the three fine-root categories, LR_{sec} displayed the lowest RR^{10} (from 2.4 nmol $CO_2\,g^{-1}\,s^{-1}$ in October to 4.14 nmol $CO_2\,g^{-1}\,s^{-1}$ in April) and the lowest temperature sensitivity***:*** Q_{10} ranged between 1.05 (in the dry September) and 1.24 (in October, when SWC recovered to 20%, see **Fig. 21**). Both LR_{prim} and LR_{sec} show high respiratory activity in June (after completion of leaf flush completed) and towards the end of October (after leaf shedding). Short roots (ShR) in beech showed medial levels of RR^{10} and Q_{10} throughout the study period when compared to both long root categories (LR_{prim} and LR_{sec}).

During water limitation in August and September, RR^{10} of LR_{sec} and ShR was reduced by near 50% compared to April and June, whereas RR^{10} of LR_{prim} remained on comparable level (**Tab. 10A**). Q_{10} of LR_{sec} and ShR showed a strong decrease during both dry months declining to 1.05 in September, than increased after rain events in October.

In spruce, contrary to beech, highest RR^{10} and highest sensitivity to temperature were found in ShR (**Fig. 37B & Tab. 10B**). Except for August, Q_{10} of this latter fine-root category ranged between 1.2 during drought in August and 1.8 in October when SWC recovered to 20%. RR^{10} in ShR was between 2.95 nmol $CO_2\,g^{-1}\,s^{-1}$ (August) and 8.15 nmol $CO_2\,g^{-1}\,s^{-1}$ (April). Spruce long lateral roots with secondary periderm (LR_{sec}) displayed, similarly to beech LR_{sec}, less C release: RR^{10} ranged between 2.64 and 3.7 nmol $CO_2\,g^{-1}\,s^{-1}$; Q_{10} here was between 1.0 and 1.37 (**Tab. 10B**). Compared to beech, LR_{prim} in spruce had 2 to 3 times lower RR^{10} and lower seasonal dynamics of Q_{10}, an indication of lower energy costs relative to beech for root length increment during the study period of 2003. In general, spruce displayed lower seasonal dynamics of Q_{10} than beech, but also lower variation in RR^{10} between fine root categories (**Tab. 10**).

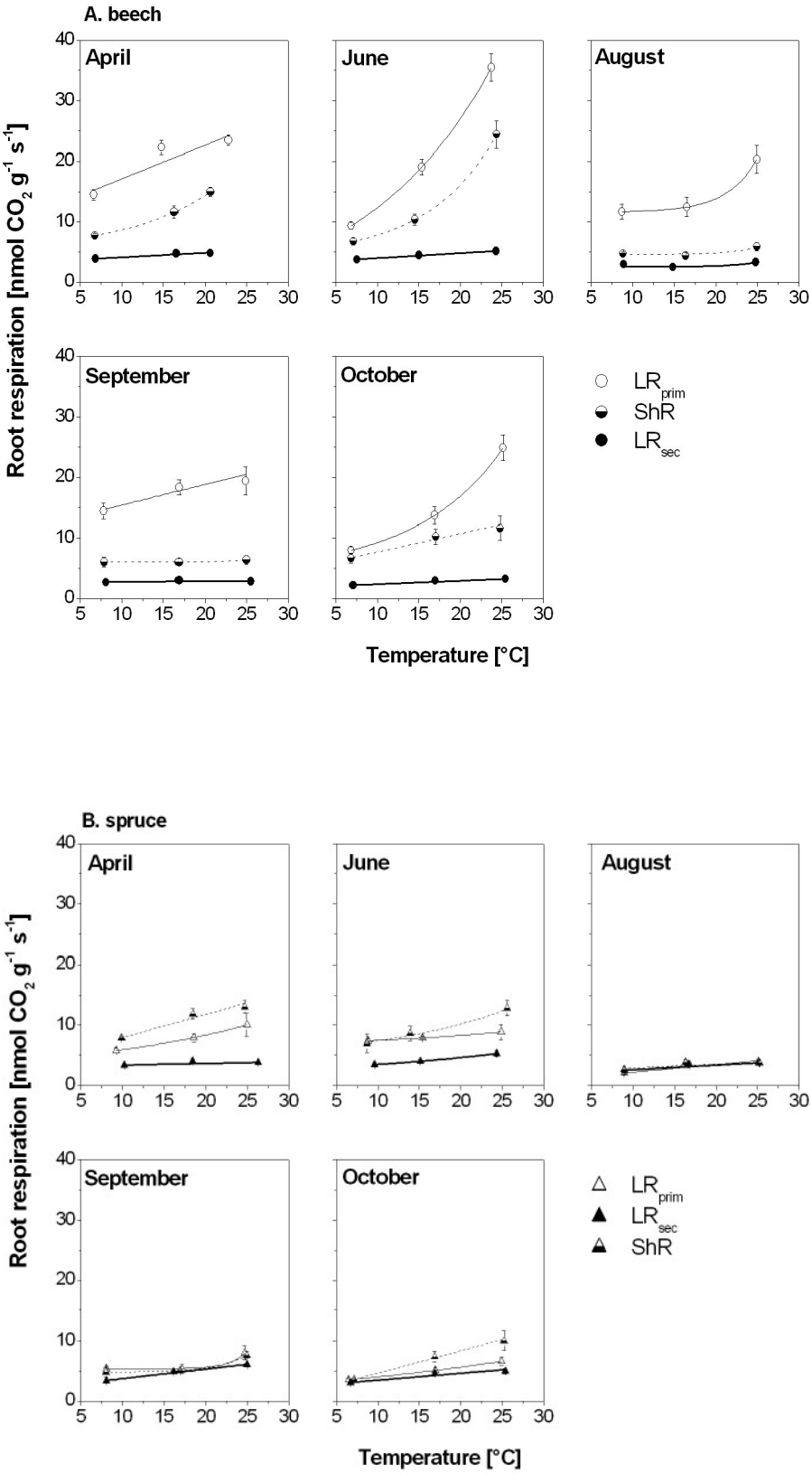

Figure 37*:* Temperature response of respiration (RR, according to Eq. 4) in, A, beech and B, spruce fine roots. Lines represent the response curve of LR_{prim} (solid thin line), LR_{sec} (solid bold line) and ShR (dashed line). Data shown as means ± standard errors (n = 4 to 6). Regression statistics is provided in **Tab. 10**.

Table 10*:* Statistical treatment of the data shown in **Fig. 37***,* A, beech and B, spruce. Exponential fit ($RR = \rho e^{\theta T}$) describes the relationship between root respiration (RR) and temperature, with ρ and θ being regression coefficients, Q_{10} calculated from θ ($Q_{10} = e^{10x\theta}$), R^2 representing measure of determination, and RR^{10} giving RR data at a standard temperature of 10°C.

A. beech

Sampling date	Fine-root category	Intercept, ρ [nmol $CO_2 g^{-1} s^{-1}$]	Slope, θ [°C]	Q_{10}	R^2	RR^{10} [nmol $CO_2 g^{-1} s^{-1}$]
April 24 (day 114)	LR_{prim}	12.66	0.029	1.35	0.83	17.06
	LR_{sec}	3.51	0.047	1.18	0.96	4.14
	ShR	5.58	0.017	1.60	0.99	8.90
June 27 (day 178)	LR_{prim}	5.53	0.079	2.20	0.99	12.16
	LR_{sec}	3.33	0.018	1.20	0.97	4.04
	ShR	3.79	0.075	2.12	0.99	8.02
August 22 (day 234)	LR_{prim}	8.06	0.035	1.41	0.85	11.38
	LR_{sec}	2.54	0.009	1.09	0.25	2.77
	ShR	3.90	0.015	1.16	0.60	4.50
September 18 (day 261)	LR_{prim}	12.88	0.018	1.20	0.92	15.36
	LR_{sec}	2.65	0.004	1.05	0.38	2.75
	ShR	5.78	0.004	1.05	0.78	5.99
October 30 (day 303)	LR_{prim}	5.11	0.062	1.85	0.99	9.46
	LR_{sec}	1.94	0.022	1.24	0.93	2.40
	ShR	5.55	0.031	1.37	0.95	7.59

B. spruce

Sampling date	Fine-root category	Intercept, ρ [nmol $CO_2 g^{-1} s^{-1}$]	Slope, θ [°C]	Q_{10}	R^2	RR^{10} [nmol $CO_2 g^{-1} s^{-1}$]
April15 (day 105)	LR_{prim}	4.18	0.035	1.42	0.99	5.93
	LR_{sec}	3.28	0.007	1.10	0.43	3.52
	ShR	5.75	0.035	1.42	0.94	8.15
June 26 (day 177)	LR_{prim}	6.79	0.010	1.11	0.68	7.53
	LR_{sec}	2.61	0.029	1.37	0.99	3.49
	ShR	4.90	0.039	1.47	0.99	7.19
August 21 (day 233)	LR_{prim}	1.52	0.041	1.50	0.88	2.28
	LR_{sec}	2.03	0.026	1.30	0.82	2.64
	ShR	2.43	0.019	1.20	0.61	2.95
September 17 (day 260)	LR_{prim}	4.18	0.023	1.26	0.67	5.25
	LR_{sec}	2.62	0.035	1.41	0.97	3.70
	ShR	3.66	0.027	1.30	0.82	4.77
October 28 (day 301)	LR_{prim}	2.85	0.04	1.40	0.99	4.00
	LR_{sec}	2.62	0.027	1.30	0.89	3.44
	ShR	2.47	0.058	1.80	0.96	4.41

3.5.3 Respiration rate of individual fine rootlets (RR_l) in beech and spruce

The respiration rate of individual beech and spruce fine rootlets (RR_l) was assessed according to Eq. 6 (section 2.18.2). Both $RR^{T(0)}_l$ (i.e. RR_l at mean daily soil temperature $T_{s(0)}$ monitored at 0 cm soil depth) and RR^{10}_l (i.e. RR_l at a standard temperature of 10°C) were significantly higher in beech than in spruce during the whole study period of 2003 (**Fig. 38**). In August of 2003, $RR^{T(0)}_l$ decreased significantly underneath trees of both species relative to June at higher $T_{s(0)}$, as a consequence of advanced summer drought. In beech, RR^{10}_l showed no significant differences between the harvests except for April of 2003 when the seasonal maximum of 9.9 nmol $CO_2 g^{-1}s^{-1}$ was assessed. In spruce, only in August of 2003, RR^{10}_l decreased significantly (2.75 nmol $CO_2 g^{-1}s^{-1}$) compared to the other samplings, and represented the seasonal minimum in RR^{10}_l during the study year.

During September of 2004, RR^{10}_l in beech was 8.9±0.9 nmol CO_2 $g^{-1}s^{-1}$ and in spruce 7.1±0.6 nmol CO_2 $g^{-1}s^{-1}$. In both species, levels were higher as compared to RR^{10}_l when assessed during September of 2003 (7.1±1.5 and 4.3±0.1 nmol CO_2 $g^{-1}s^{-1}$ for beech and spruce, respectively; **Fig. 38**). However, only the difference in spruce was significant. The species-specific respiration rate in beech (RR_{beech}) was found to amount to 8.14±0.89 nmol CO_2 $g^{-1}s^{-1}$ while the species-specific respiration rate in spruce (RR_{spruce}) was 5.74±0.64 nmol CO_2 $g^{-1}s^{-1}$ (calculation according to section 2.18.2; data as means ± standard errors). RR_{beech} and RR_{spruce} served to define the "running costs" (e.g. the efficiency ratio of competitiveness) of beech and spruce fine-roots.

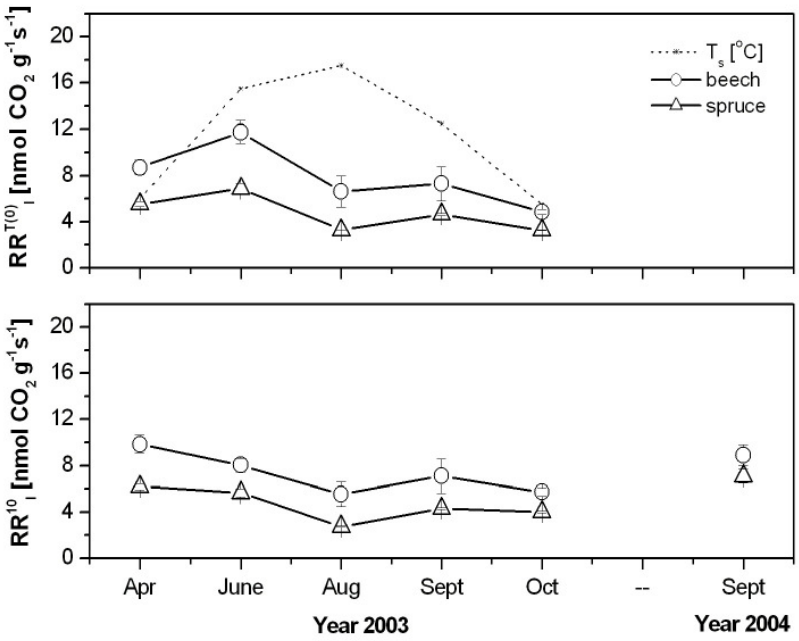

Figure 38*:* Respiration rates (RR_l) calculated for individual beech and spruce fine rootlets. The upper graph represents respiration rates $RR^{T(0)}_l$ at mean daily soil temperature $T_{s(0)}$ (monitored at 0 cm soil depth); the lower graph shows respiration rates RR^{10}_l at a standard temperature of 10°C. Data as means ± 95% confidence interval (n=5-10).

3.6 Morphological parameters of fine roots

3.6.1 Seasonal dynamics of the specific fine-root area

In beech, the lowest specific fine-root area (SRA, cm^2g^{-1}) was found in long lateral roots with secondary xylem (LR_{sec}; ranging between 58 $cm^2\ g^{-1}$ in August 2003 and 105 $cm^2\ g^{-1}$ in November 2002), relative to long lateral roots with primary xylem (LR_{prim}) and short roots (ShR). SRA of both latter fine-root categories was similar and 5 to 8 times higher than that of LR_{sec} (**Fig. 39**). In general, SRA tended to be lowered in all fine-root categories during the drought period of 2003; however, only SRA of ShR assessed in October of 2003 was significantly different compared to the level in October 2002 ($p<0.05$).

In spruce, the lowest SRA was found in the LR_{sec} (SRA ranging between 78 $cm^2\ g^{-1}$ and 140 $cm^2\ g^{-1}$; **Fig. 39**). SRA ranges of LR_{prim} and ShR were 140 $cm^2\ g^{-1}$ to 222 $cm^2\ g^{-1}$ and 263 $cm^2\ g^{-1}$ to 405 $cm^2\ g^{-1}$, respectively, which showed a strong morphological differentiation of these both categories. Under the drought of 2003, spruce tended to reduce SRA in all fine-root categories, although significant differences existed only in ShR between August 2003 and August 2002. Only SRA of ShR lay on a similar level in both tree species. SRA of LR_{prim} and ShR in beech were two to three times higher compared to SRA of the corresponding fine-root categories in spruce.

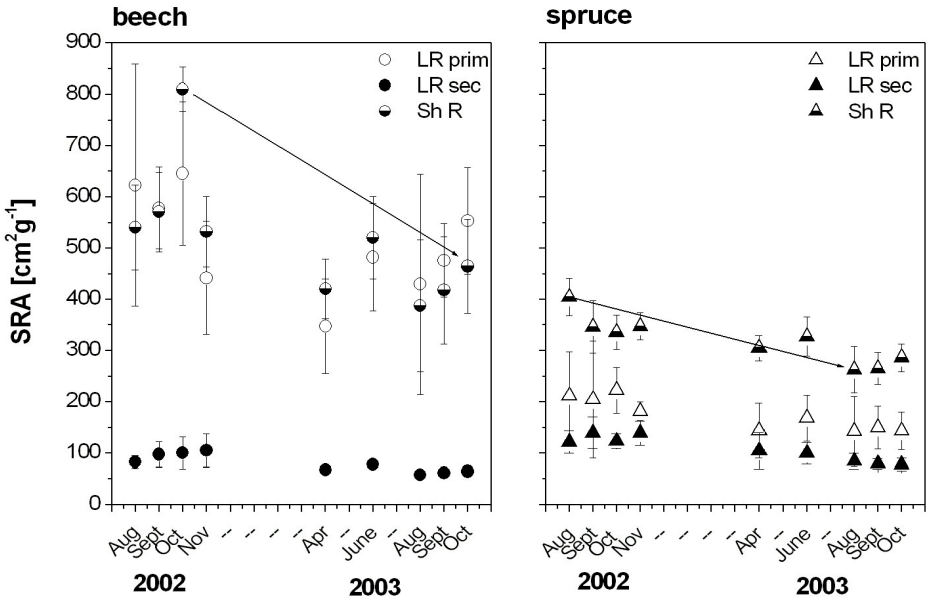

Figure 39: Seasonal dynamics in specific fine root area (SRA) of the three fine-root categories of beech and spruce as assessed during 2002 and 2003: long lateral roots with primary xylem (LR_{prim}; open symbols), long lateral roots with secondary xylem (LR_{sec}; filled symbols) and short roots (ShR; half-filled symbols). Arrows show significant differences in SRA at $p<0.05$. Data represent mean $\pm$ 95% confidence interval (n = 5 to 7).

3.6.2 Ozone impact on fine-root morphology

As in the case of root respiration rate (**Fig. 36**), SRA did not differ in August 2002 between $1xO_3$ and $2xO_3$ within each fine-root category of either tree species (**Fig. 40**). In beech, root mortality rate (RM) did not differ between the two O_3 regimes, regardless of the type of competition, while amounting to 30 - 34% of the total standing fine-root mass (**Tab. 11A**, coring in August of 2002). Also in spruce, enhanced ozone had no effect on RM, whereas fine-root density (RD) was reduced by 50 % and RM by a factor of 3 to 4 in the spruce/beech sub-plots compared to spruce monoculture. A multivariate analysis (GLM, SPSS) weighted the impact of "O_3 regime" and "type of competition" on RD, SRA and STD (specific root tip density) of beech and spruce fine-roots, using RM as a covariate to account for potential confounding effects on RD, SRA and STD. In beech, RD was enhanced and STD lowered under $2xO_3$, while RD was decreased in mixture with spruce (**Tab. 11B**). RM significantly correlated in beech in a positive way with SRA and STD, and in a negative way with RD. In spruce, ozone effects were absent in root morphology and root density, however, STD and RD were significantly decreased in beech/spruce mixed sub-plots. RM of spruce fine-roots was negatively related to RD. In summary, RM is not a confounding factor of O_3 effects in both tree species. However, RM does not only relate to morphological parameters (as in beech), but also to the standing biomass (i.e. root density, in both tree species).

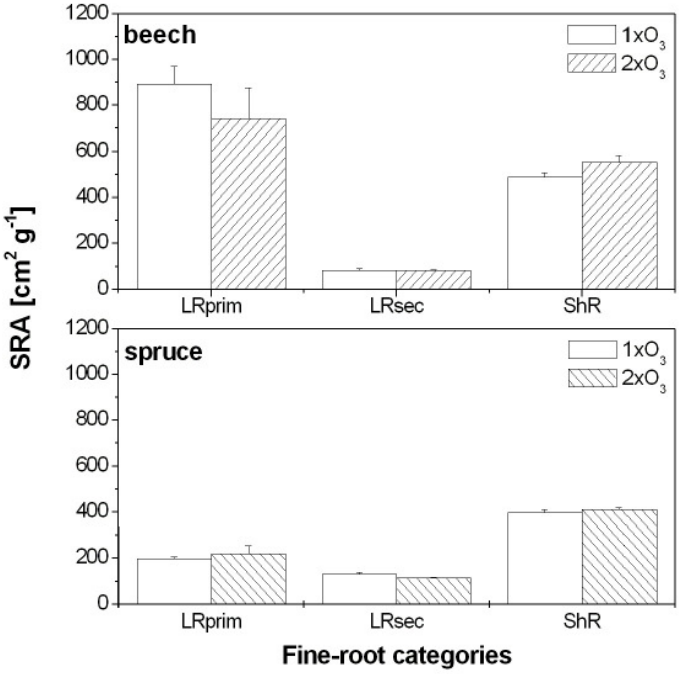

Figure 40: Specific fine root area (SRA) assessed in August 2002 under $1xO_3$ and $2xO_3$ in the fine-root categories of beech and spruce. Data represent mean $\pm$ standard error (n = 5).

Table 11A: Morphological parameters of fine roots SRA (specific fine-root surface area), D (fine-root diameter), STD (specific root tip density), RD (fine-root density) and root mortality rate (RM) assessed in beech and spruce in mono and mixed sub-plots under different ozone regimes. Roots were sampled during August of 2002 by means of soil coring within the uppermost 20 cm of the soil. Data represent means ± SE (n = 5 to 10).

Tree species	O_3 regime	SRA [$cm^2 g^{-1}$]	D [mm]	STD [$N\ cm^{-1}$]	RD [$mg\ l^{-1}$]	RM [%]
Beech, mono sub-plots	1xO_3	433 ± 68	0.70 ± 0.02	3.25 ± 0.10	1152 ± 257	34.6 ± 5.5
	2xO_3	412 ± 69	0.67 ± 0.02	3.12 ± 0.15	2178 ± 452	33.6 ± 7.1
Beech, mixed sub-plots	1xO_3	400 ± 49	0.71 ± 0.03	3.27 ± 0.10	650 ± 111	30.3 ± 6.4
	2xO_3	350 ± 53	0.72 ± 0.03	2.94 ± 0.10	1314 ± 254	30.3 ± 5.9
Spruce, mono sub-plots	1xO_3	212 ± 12	0.92 ± 0.03	2.94 ± 0.07	2495 ± 539	20.0 ± 5.4
	2xO_3	298 ± 37	0.92 ± 0.03	2.75 ± 0.10	2198 ± 705	19.9 + 5.2
Spruce, mixed sub-plots	1xO_3	291 ± 31	0.93 ± 0.04	2.54 ± 0.15	733 ± 160	4.4 ± 1.5
	2xO_3	331 ± 55	1.00 ± 0.06	2.68 ± 0.12	1336 ± 313	6.5 ± 2.0

Table 11B: Statistical analysis of the impact of the factors "treatment" (i.e. 1xO_3 and 2xO_3), "type of competition" (i.e. mono-culture and mixed culture) on RD and on fine-root morphological parameters SRA and STD (assessed mean values are shown on Table 11A) in beech and spruce. *P* value gives the levels of significance of the multivariate analysis (GLM, SPSS; with "root mortality rate" as covariate).

Factor	Root parameter	*p* value	
		beech	spruce
treatment	SRA	0.554	0.110
	STD	0.032	0.765
	RD	0.001	0.660
type of competition	SRA	0.556	0.561
	STD	0.564	0.039
	RD	0.002	<0.001
treatment x type of competition	SRA	0.727	0.722
	STD	0.305	0.047
	RD	0.469	0.238

3.7 Ectomycorrhizal colonisation rate

In both species, beech and spruce, ectomycorrhizal colonisation rate (EMycR, %) of short fine roots showed seasonal dynamics with lowest levels in May of 2003 (i.e. near 60 % of the total root tips) and highest EMycR in December of 2002 and 2003 (i.e. 96 % to 98 % of the total root tips; **Fig. 41**). During the moist August of 2002 EMycR was significantly higher in beech than in spruce ShR (86% and 72% of the total root tips for beech and spruce, respectively). During August of 2003 EMycR of spruce ShR was significantly enhanced by drought compared to August of 2002, reaching levels which are typical for beech (i.e. near 90 %). In beech, EMycR only differed significantly between November of 2002 and 2003. In December 2002 and 2003, when root growth ceased, short fine roots were nearly completely mycorrhized in both tree species.

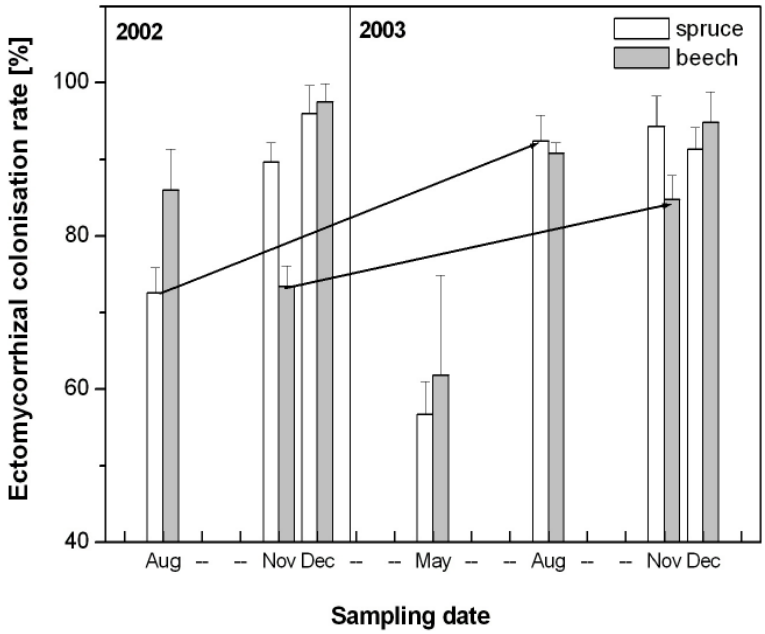

Figure 41*:* Ectomycorrhizal colonisation rate of short roots (ShR) in beech and spruce during 2002 and 2003. Arrows indicate significant differences between years at $p < 0.05$. Data represent means $\pm$ standard errors (n = 5).

The specific root tip density (STD, N cm^{-1}; **Fig. 42**, white columns) multiplied by the EMycR gives the number of mycorrhized root tips per unit root length (MycTD, N cm^{-1}; Fig.42, grey columns) for each sampling date. In both species MycTD was lowest in May of 2003 and highest in December of 2002 and 2003. In spruce, however, SDT and MycTD varied less between samplings indicating less plasticity in spruce root tip morphology and related symbiotic associations relative to beech.

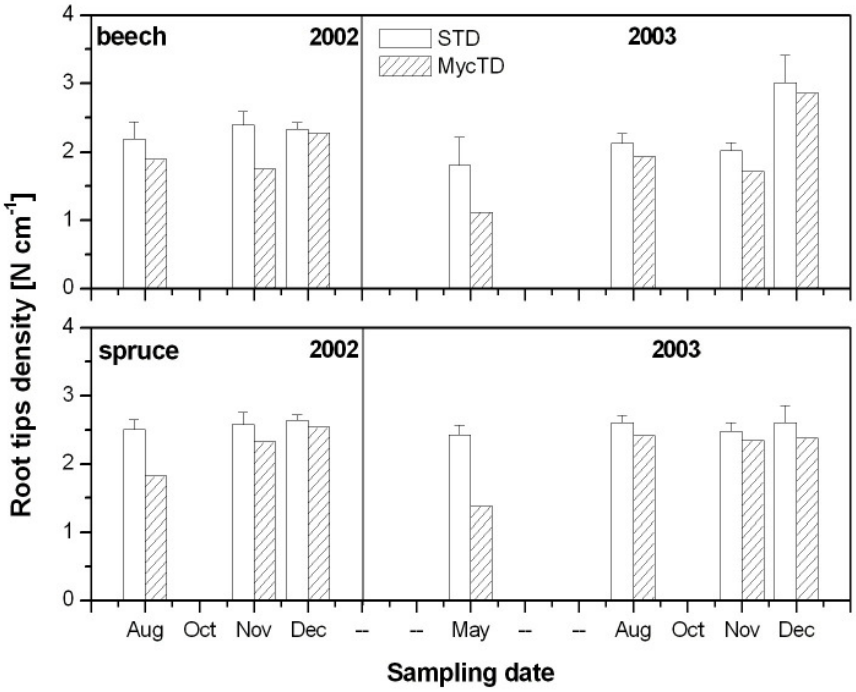

Figure 42*:* Specific root tip density (STD) and mycorrhized root tip density (MycTD) of short roots (ShR) in beech and spruce during 2002 and 2003. STD are represented as means ± standard errors (n = 5). MycTD is calculated from the mean of STD and the mean of ectomycorrhizal colonisation rate EMycR (MycTD = STD x EMycR).

3.8 Non-structural carbohydrates of fine roots

3.8.1 Ozone impact on sugar and starch concentration

As in the cases of fine-root respiration rate (**Fig. 36**) and specific fine-root area (**Fig. 40**), no differences were found in non-structural carbohydrate fractions (NSC: sucrose, glucose, fructose, pinitol and starch; mg g^{-1}) between $1xO_3$ and $2xO_3$ within each fine-root category of either tree species (**Fig. 43**). During August of 2002, starch and pinitol were detected only in the fine-root categories of spruce. In general, the total sugar concentration (TSC, integrating sucrose, glucose, fructose and pinitol) was two to three times higher (in LR_{sec} and ShR, respectively) in spruce than in beech fine-roots.

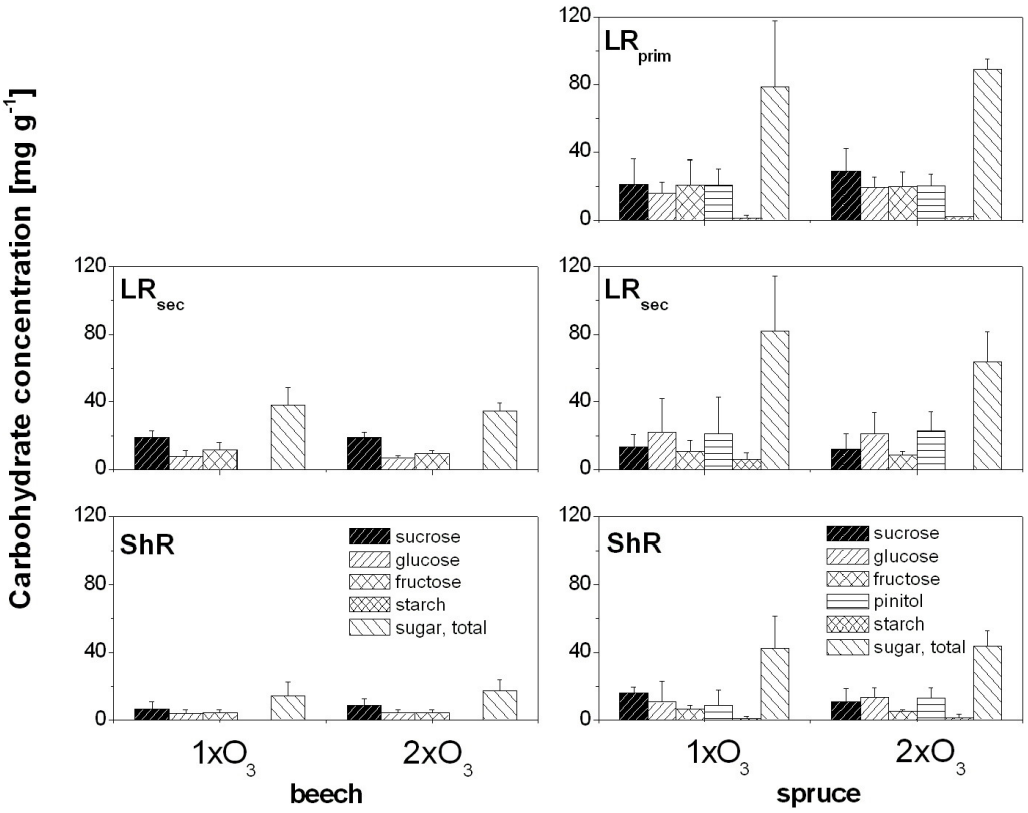

Figure 43: Carbohydrate fractions (sucrose, glucose, fructose, pinitol, starch) for long lateral roots with primary xylem (LR_{prim}), long lateral roots with secondary xylem (LR_{sec}) and short roots (ShR) in beech and spruce under $1xO_3$ and $2xO_3$. The total content of sugar is calculated as the sum of sucrose, glucose, fructose and pinitol concentrations. Fine-roots were sampled in August of 2002 (data shown as means $\pm$ 95% confidence interval, n = 4 to 6). LR_{prim} was not sampled in beech.

3.8.2 Seasonal course of non-structural carbohydrates

3.8.2.1 Starch

The three fine-root categories of beech showed different pattern of starch allocation during the study period (**Fig. 44A**). The highest levels of starch concentration were detected in LR_{prim} with maximum in May and minimum in November (**Tab. 12**). LR_{sec} showed high seasonal variability in starch concentration with maximal levels during August of 2003, whereas ShR of beech contained minimal levels starch during spring and summer months, but accumulated starch during fall (e.g. in November of 2003). Comparing starch concentrations in August of 2002 with August of 2003, beech fine roots reacted to drought by enhancing starch accumulation in LR_{sec}, whereas no changes were displayed in ShR. When calculated for individual rootlets (**Fig. 45**; c.f. Eq.1) starch concentration in beech rootlets did not show seasonal dynamics (staying around 1 mg g^{-1}) indicating that in time the starch pool of fine roots was stabil but varies across the different functional parts of the fine root system.

All fine-root categories of spruce showed during the study period a similar pattern of starch allocation with maxima in May (**Fig. 44** & **Tab. 12**) which declined during the remainder of the growing season. Slight increase of starch concentration in LR_{sec} and LR_{prim} was displayed in November. All fine-root categories of spruce showed a similar drought response, reflecting lowered starch concentration under the water limitation of August 2003 relative to the moist conditions of the same month in 2002; however, differences were significant only in the case of LR_{prim} ($p < 0.05$). In contrast to beech, starch concentration in spruce rootlets was 8 mg g^{-1} during late spring but decreased during the growing season to levels which were comparable to those of beech rootlets.

3.8.2.2 Sugars

During May and July of 2003, LR_{prim} of beech displayed similar total sugar concentration (TSC integrating sucrose, glucose, fructose, and, in case of spruce, pinitol; **Fig. 44** & **Tab. 12**) which increased in August of 2003 as a result of enhanced sucrose ($p<0.05$) and fructose (n.s.) concentration, and in November of 2003 as a result of enhanced glucose ($p<0.05$) concentration. LR_{sec} of beech had the lowest TSC in May (i.e. before leaf flush) which increased during the remainder of the growing season as a consequence of enhanced fructose ($p<0.05$) and glucose (n.s.) concentrations. In the dry August of 2003, the increase of fructose ($p<0.05$) and sucrose (n.s.) levels in LR_{sec} resulted in 30% higher TSC compared to August of 2002. Similarly as found in LR_{prim}, ShR of beech had comparable TSC during May and July of 2003, however TSC of ShR during these months was two times lower than TSC of LR_{prim}. During August and November of 2003 total sugar content of ShR was doubled compared to the levels of May and July as a result of a significantly higher (near three times, $p<0.05$) sucrose level in this fine-root category. During the drought of August 2003, TSC of ShR was more than two times higher than found in August of the previous year, with sucrose and fructose showing the highest increase in 2003 (four and two times, respectively each; $p<0.05$). In summary, sucrose was the largest carbohydrate fraction in all beech fine-root categories (40 to 65% of TSC), followed by fructose (20 to 35% of TSC) and glucose (10 to 25% of TSC). During August of 2003, enhanced sucrose (in ShR) and fructose levels (in LR_{sec}) were detected in the fine roots of beech as a response to drought.

When calculated at the individual rootlet level (**Fig. 45**; cf. Eq.1), TSC of the beech rootlets was about 30 mg g^{-1} in May and July, and increased to 45 mg g^{-1} in August and November. Hence, the seasonal course of TSC during the study year of 2003 was caused by the seasonal course of the sucrose fraction.

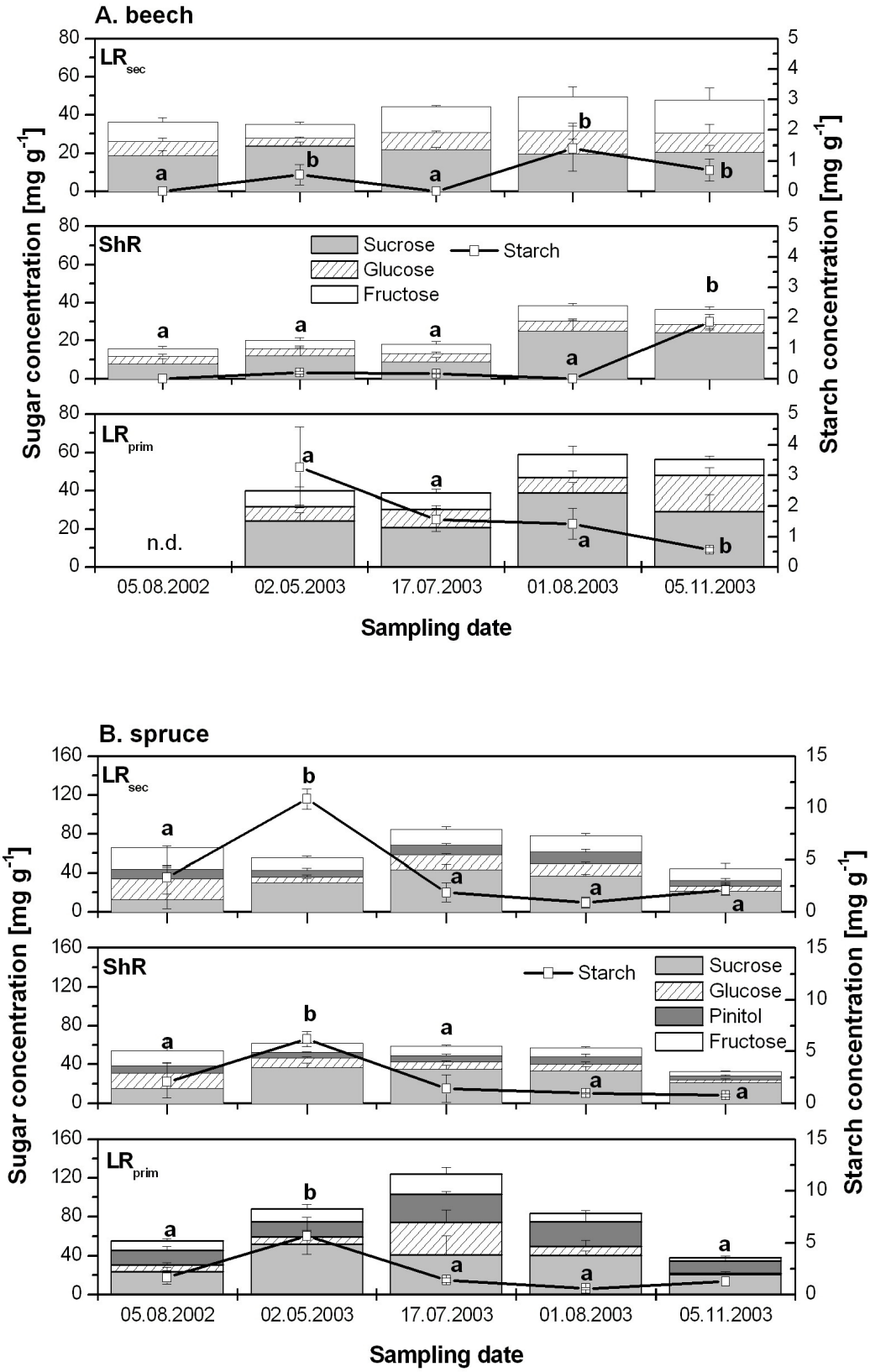

Figure 44: Seasonal course of carbohydrate fractions (sucrose, glucose, fructose, pinitol, starch) in the fine-root categories of long lateral roots with primary xylem (LR_{prim}), long lateral roots with secondary xylem (LR_{sec}) and short roots (ShR) in A, beech and B, spruce. In August of 2002, data of both O_3 regimes were pooled (no differences were found in non-structural carbohydrate fractions between $1xO_3$ and $2xO_3$ within each fine-root category of either tree species; cf. 3.6.1). Letters show statistically significant differences in starch concentration ($p < 0.05$). Data shown as means $\pm$ 95% confidence interval (n = 4 to 10).

Spruce showed a different pattern of the carbohydrate fractions in TSC compared to beech (**Fig. 44** & **Tab. 12**). LR_{prim} had the highest sucrose concentration during May, which decreased during the remainder of the growing season and reached a minimum in November. Sucrose remained the largest fraction of TSC in LR_{prim} of spruce (35 to 55% of TSC), followed by pinitol contributing between 15% (in May of 2003) and 30-35% to TSC (in August and November of 2003). Glucose and fructose reached their seasonal maximum in LR_{prim} during July of 2003 and occurred at minimum levels during November of 2003. When comparing carbohydrate fractions of LR_{prim} between August of 2002 and 2003, sucrose ($p<0.01$) and pinitol ($p<0.05$) concentrations were twice as high under the drought of 2003. TSC in LR_{sec} of spruce displayed minimum levels in May and November of 2003. During the summer months of 2002 and 2003 TSC was enhanced by 30 to 40% compared to May and November of 2003 as a result of a significant increase of glucose ($p<0.05$) and of an increases of other carbohydrates (n.s.). In 2003, changes in sucrose concentration defined the seasonal dynamics of TSC in ShR of spruce with highest levels, in contrast to beech, in May, and lowest in November. Similar seasonal dynamics also occurred in the case of the other TSC fractions. In August of 2002 and 2003, TSC in ShR and LR_{sec} was similar, although during the drought of 2003 the sucrose fraction in both fine-root categories increased by a factor of two ($p<0.05$), whereas glucose and fructose fractions decreased (n.s.). Pinitol concentration of the resent fine-root categories was not affected by the contrasting water availability. In summary, sucrose was the largest carbohydrate fraction in all spruce fine-root categories (35 to 55% of TSC), except for LR_{sec} and ShR as sampled in August of 2002 when the contribution of sucrose to TSC was comparable with those of glucose and fructose (i.e. 20 % of TSC). In the LR_{prim}, pinitol was the second largest fraction in spruce fine roots, contributing 15 to 35% to TSC, whereas across the other fine-root categories the concentrations of glucose, pinitol and fructose were found to be similar (i.e. 10 to 25% of TSC). In response to drought, spruce enhanced the sucrose level in all fine-root categories.

Spruce rootlets had two times higher TSC relative to beech at the beginning of the growing season. During summer, TSC increased in spruce (n.s.) compared to May, and decreased significantly in November to about 40 mg g^{-1}. As in the case of beech, the seasonal dynamics of TSC was caused in spruce by the seasonal dynamics of the sucrose fraction which contributed 60 to 65% to TSC in both tree species. In general, the higher sucrose level and the existence of a pinitol fraction in the fine-roots of spruce accounted for the higher TSC as compared to that of the rootlets in beech.

Table 12: Non-structural carbohydrate concentrations (as presented in **Fig. 43**) in the fine-root categories of A, beech and B, spruce (means ± 95% confidence interval, n = 4 to 10).

A. beech

Sampling date	Fine-root category	Sucrose [mg g^{-1}]	Glucose [mg g^{-1}]	Fructose [mg g^{-1}]	Sugar, total [mg g^{-1}]	Starch [mg g^{-1}]
August 5 of 2002	LR_{prim}	n.d.	n.d.	n.d.	n.d.	n.d.
	LR_{sec}	18.8 ± 2.4	7.1 ± 1.7	10.1 ± 2.5	36.7 ± 5.9	0
	ShR	7.7 ± 2.9	3.9 ± 1.4	4.2 ± 1.2	16.2 ± 5.3	0
	rootlet	n.d.	n.d.	n.d.	n.d.	n.d.
May 2 of 2003	LR_{prim}	24.4 ± 4.1	7.3 ± 1.1	8.2 ± 2.1	38.2 ± 4.9	3.36 ± 1.29
	LR_{sec}	23.8 ± 2.0	3.8 ± 0.6	7.4 ± 1.2	35.2 ± 3.4	0.55 ± 0.41
	ShR	12.1 ± 4.5	3.7 ± 1.4	4.4 ± 1.6	20.1 ± 7.4	0.21 ± 0.05
	rootlet	**19.6 ± 0.8**	**4.5 ± 0.3**	**6.4 ± 0.2**	**30.6 ± 1.3**	**1.02 ± 0.27**
July 17 of 2003	LR_{prim}	20.7 ± 6.4	9.5 ± 2.2	8.5 ± 2.0	38.8 ± 10.2	1.56 ± 0.47
	LR_{sec}	21.9 ± 1.8	8.7 ± 0.8	13.6 ± 0.7	44.2 ± 2.9	0
	ShR	8.8 ± 2.3	4.4 ± 0.8	4.9 ± 1.6	18.1 ± 4.5	1.17 ± 0.02
	rootlet	**15.8 + 0.8**	**7.0 ± 0.4**	**8.3 ± 0.4**	**31.1 ± 1.4**	**0.94 ± 0.10**
August 1 of 2003	LR_{prim}	38.6 ± 5.6	8.3 ± 3.4	12.1 ± 4.3	60.1 ± 7.5	1.42 ± 0.64
	LR_{sec}	19.4 ± 7.8	12.0 ± 4.0	17.9 ± 5.2	47.5 ± 16.8	1.40 ± 0.29
	ShR	24.9 ± 5.8	5.3 ± 1.1	8.2 ± 1.2	38.7 ± 5.9	0
	rootlet	**28.3 ± 1.7**	**7.9 ± 0.7**	**10.6 ± 1.4**	**46.9 ± 1.5**	**0.82 ± 1.14**
November 5 of 2003	LR_{prim}	29.1 ± 8.9	18.9 ± 4.1	8.4 ± 1.6	52.6 ± 12.7	0.60 ± 0.02
	LR_{sec}	24.1 ± 2.5	4.5 ± 0.9	7.9 ± 1.4	37.0 ± 4.0	0.70 ± 0.44
	ShR	20.5 ± 3.4	9.8 ± 4.7	17.5 ± 6.3	48.1 ± 10.6	1.86 ± 0.36
	rootlet	**23.3 ± 0.5**	**9.1 ± 0.7**	**12.1 ± 0.7**	**44.5 ± 1.0**	**1.18 ± 0.09**

B. spruce

Harvesting date	Fine-root category	Sucrose [mg g^{-1}]	Glucose [mg g^{-1}]	Fructose [mg g^{-1}]	Pinitol [mg g^{-1}]	Sugar, total [mg g^{-1}]	Starch [mg g^{-1}]
August 5 of 2002	LR_{prim}	23.9 ± 4.5	6.9 ± 2.2	10.1 ± 2.3	14.8 ± 4.4	55.6 ± 10.3	1.66 ± 0.64
	LR_{sec}	12.7 ± 5.7	21.4 ± 1.1	21.9 ± 1.2	9.6 ± 3.5	65.4 ± 15.8	3.30 ± 3.00
	ShR	15.3 ± 6.7	15.9 ± 0.9	15.5 ± 1.6	7.5 ± 3.2	54.1 ± 2.3	2.01 + 1.46
	rootlet	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
May 2 of 2003	LR_{prim}	51.9 ± 14.3	7.4 ± 5.2	13.6 ± 4.7	15.1 ± 4.9	88.1 ± 28.3	5.67 ± 2.18
	LR_{sec}	30.1 ± 4.6	5.9 ± 2.1	12.7 ± 1.6	6.8 ± 2.1	55.5 ± 7.9	10.85 ± 1.50
	ShR	37.1 ± 4.0	9.6 ± 1.1	9.3 ± 1.1	5.7 ± 0.6	61.8 ± 5.8	6.20 ± 0.92
	rootlet	**35.3 ± 0.7**	**8.0 ± 0.2**	**10.9 ± 0.2**	**6.7 ± 0.3**	**60.9 ± 1.0**	**7.99 + 0.31**
July 17 of 2003	LR_{prim}	41.0 ± 19.7	32.8 ± 12	20.8 ± 6.9	29.2 ± 2.7	123.9 ± 34.7	1.40 ± 0.57
	LR_{sec}	43.5 ± 9.0	14.7 ± 2.8	10.1 ± 5.7	9.8 ± 3.0	84.1 ± 17.1	1.88 ± 1.50
	ShR	35.3 ± 4.1	7.4 ± 1.0	9.9 ± 0.7	6.5 ± 1.4	59.1 ± 5.6	1.40 ± 1.33
	rootlet	**38.9 ± 0.5**	**11.1 ± 1.2**	**10.3 ± 0.3**	**8.5 ± 0.8**	**68.8 ± 3.3**	**1.59 ± 0.04**
August 1 of 2003	LR_{prim}	40.7 ± 4.5	9.0 ± 6.1	8.5 ± 3.1	24.8 ± 11	83.0 ± 20.9	0.58 ± 0.21
	LR_{sec}	36.7 ± 1.8	12.4 ± 1.8	17.0 ± 2.9	2.1 ± 3.2	78.3 ± 3.8	0.90 ± 0.54
	ShR	33.1 ± 4.8	7.4 ± 2.0	9.0 ± 1.3	7.3 ± 3.0	56.9 ± 7.3	0.96 ± 0.08
	rootlet	**35.3 ± 0.4**	**9.7 ± 0.5**	**12.5 ± 0.8**	**6.5 ± 1.2**	**64.1 ± 1.3**	**0.90 ± 0.02**
November 5 of 2003	LR_{prim}	20.6 ± 3.3	1.2 ± 0.7	3.5 ± 1.3	13.0 ± 3.9	38.4 ± 3.3	1.27 ± 0.63
	LR_{sec}	21.4 ± 9.1	5.4 ± 2.1	12.0 ± 5.0	5.6 ± 2.1	44.4 ± 16.7	2.10 ± 1.72
	ShR	21.1 ± 4.1	3.2 ± 0.8	4.6 ± 0.6	4.0 ± 1.1	32.8 ± 5.8	0.76 ± 1.17
	rootlet	**21.2 ± 0.1**	**4.4 ± 0.3**	**8.9 + 0.7**	**5.4 ± 0.3**	**39.8 ± 0.9**	**1.56 ± 0.11**

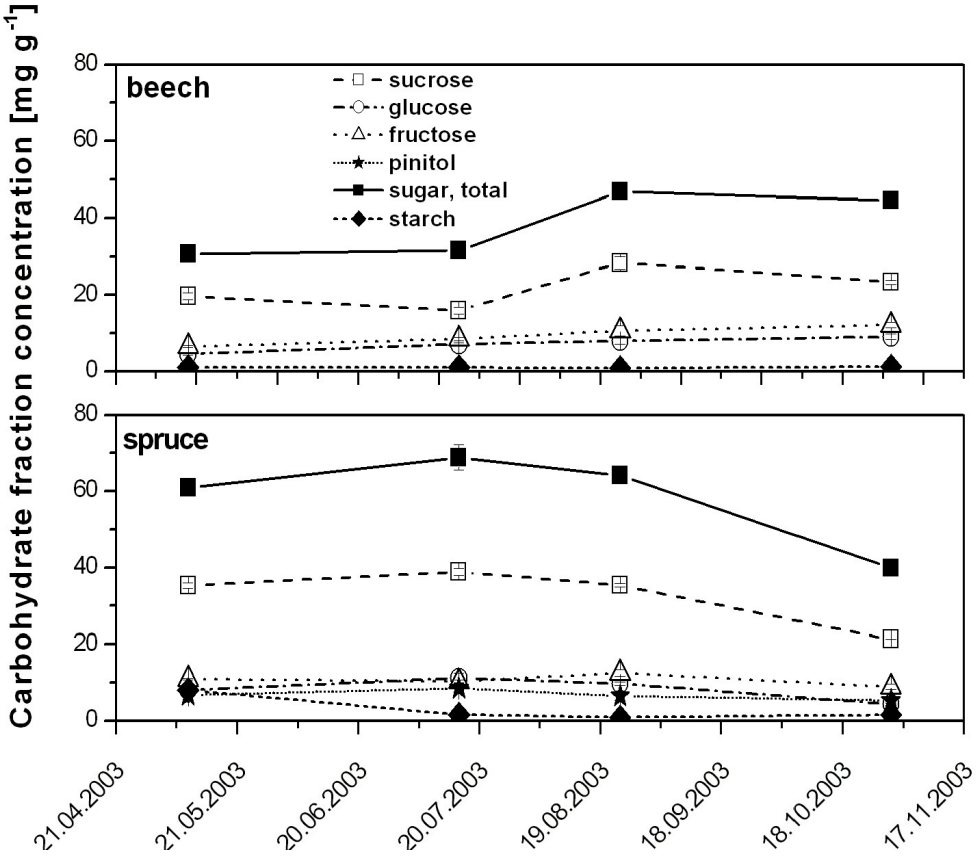

Figure 45: Concentrations of the carbohydrate fractions and the total sugar concentration (i.e. integral of sucrose, glucose, fructose and, in case of spruce, pinitol) of individual rootlets of beech and spruce during 2003 (means $\pm$ 95% confidence interval, n = 4 to 10).

3.9 Nutritional analyses

3.9.1 Nutritional status of the fine-root categories

Six essential elements - N, P, Na, K, Ca and Mg - were compared between fine-root categories and sampling dates (two each in May and August of 2003; **Fig. 46**) because of their importance to a range of plant-physiological activities (Gordon and Jackson 2000). In all fine-root categories of beech, N, P and K concentrations [mg g^{-1}] were higher in August than in May (**Tab. 13**). In contrast, the concentration of the other nutrients (except of Mn in LR_{sec}) was significantly lower in August than in May in all fine-root categories. However, C:N ratio of all fine-root categories did not differ between May and August of 2003. At both sampling dates, highest concentrations of these elements were found in LR_{prim} (except of Ca with highest concentrations in ShR during May of 2003), followed by ShR and lowest levels in LR_{sec}. Conversely, LR_{sec} of beech had the highest C investment into structure per unit of acquired N and P, followed by ShR (see averaged ratios of C:N and C:N:P in living fine roots in **Tab. 13**). Apparently, LR_{prim} had the lowest C investment per unit of acquired N and P relative to the other fine-root categories of beech.

When calculated on an individual rootlet basis (**Tab. 13** & **Fig. 47**), N, P and K contents were enhanced, and the contents of the other elements were lowered in August relative to May. As a consequence, C:N and C:N:P ratios of beech rootlets changed in August (cf. **Tab. 13**), indicating lower construction costs per unit of nutrient acquisition (i.e. of N and P) compared to May of 2003.

Compared to beech, spruce showed different nutrient status of their fine-root categories in the absence of distinct dynamics in the element levels between the sampling dates (**Tab. 13**). In August of 2003, K concentration was strongly enhanced in LR_{prim} and LR_{sec}, and lowered in ShR (**Tab. 13** & **Fig. 46**). At the same time, Ca concentration declined in LR_{prim}, but increased in LR_{sec} and ShR. Na concentration of all fine-root categories was two to three times lower in August than in May. In general, the lowest element concentrations were detected in LR_{sec}, as already described for beech. In August, the C:N ratio was slightly enhanced in ShR but stayed unchanged in LR_{prim} and LR_{sec} compared to respective levels in May. Within the fine-root categories of spruce, the highest C investment into structure per unit of acquired N and P was detected in LR_{sec}, followed by ShR, while the lowest C investment per unit of acquired N and P was found, similarly as for beech fine root categories, in LR_{prim}.

When calculated on an individual rootlet basis (**Fig. 47**), Ca and Mg contents were enhanced in August compared to May 2003, and K content did not change, whereas N, P and Na content decreased. In contrast to beech, the changes of C:N and C:N:P ratios in spruce rootlets indicated enhanced C investment per unit of N and P acquisition in August compared to May of 2003.

Table 13: Nutrient concentrations [mg g^{-1} or (*) µg g^{-1}] in fine-root categories "long lateral roots with primary xylem" (LR_{prim}), "long lateral roots with secondary xylem" (LR_{sec}), "short roots" (ShR), and in individual rootlets of beech and spruce; root sampling in May and August of 2003 (cf. section 2.14). Bold letters represent significantly higher ($p<0.05$) concentrations between sampling dates. Data shown as means (n = 4 to 10) and 95% confidence interval (in brackets).

	Fine-root categories						Rootlet	
	LR_{prim}		LR_{sec}		ShR			
Elements	May	August	May	August	May	August	May	August
beech								
C	427 (2.5)	**446 (4.1)**	467 (1.5)	**473 (0.5)**	420 (5.5)	**457 (1.5)**	441 (1.4)	**456 (1.2)**
N	27.1 (0.7)	**27.5 (0.6)**	9.6 (0.3)	**9.4 (0.5)**	16.4 (0.5)	**18.5 (0.5)**	15.7 (0.6)	**19.4 (0.1)**
P	1.66 (0.05)	**2.16 (0.08)**	0.47 (0.01)	**0.66 (0.04)**	0.94 (0.01)	**1.31 (0.02)**	0.89 (0.04)	**1.45 (0.06)**
Ca	**6.30 (0.60)**	4.72 (0.63)	**4.11 (0.14)**	2.92 (0.23)	**6.55 (0.37)**	5.28 (0.39)	**5.46 (0.08)**	4.52 (0.12)
K	6.33 (0.34)	6.54 (0.53)	2.84 (0.06)	2.98 (0.18)	3.49 (0.11)	3.62 (0.09)	3.81 (0.13)	**4.47 (0.12)**
Mg	**1.62 (0.06)**	1.38 (0.06)	**0.93 (0.01)**	0.65 (0.04)	**1.62 (0.04)**	0.65 (0.08)	**1.32 (0.02)**	0.90 (0.02)
Fe	**2.88 (0.29)**	1.36 (0.27)	1.14 (0.16)	0.59 (0.02)	3.52 (0.23)	1.94 (0.08)	**2.37 (0.07)**	1.42 (0.06)
Mn	**0.55 (0.03)**	0.28 (0.02)	0.40 (0.01)	**0.57 (0.03)**	**0.66 (0.03)**	0.42 (0.04)	**0.52 (0.01)**	0.43 (0.01)
Al	**4.22 (0.80)**	1.81 (0.41)	**1.77 (0.11)**	0.87 (0.16)	**6.12 (0.41)**	2.78 (0.12)	**3.87 (0.11)**	1.99 (0.09)
Zn*	**711 (104)**	426 (53)	**79 (2)**	66 (8)	**451 (143)**	262 (40)	**348 (21)**	272 (15)
Cu*	**149 (44)**	53 (9)	**17 (3)**	9 (1)	**59 (23)**	42 (6)	**60 (5)**	38 (2)
Na*	**557 (98)**	275 (29)	**115 (7)**	64 (7)	**481 (36)**	200 (4)	**339 (15)**	190 (10)
C:N	16 : 1	16 : 1	48 : 1	50 : 1	26 : 1	25 : 1	28 : 1	24 : 1
C:N :P	257 : 16 : 1	206 : 13 : 1	993 : 20 : 1	716 : 14 : 1	447 : 17 : 1	349 : 14 : 1	496 : 18 : 1	315 : 13 : 1
spruce								
C	447 (2.6)	**460 (1.7)**	443 (1.0)	**462 (0.8)**	463 (1.5)	**467 (0.2)**	454 (0.5)	**464** (0.2)
N	12.7 (0.3)	**14.0 (0.3)**	12.0 (0.5)	11.8 (0.6)	22.0 (0.7)	19.2 (0.3)	**17.5** (0.3)	15.6 (0.2)
P	2.20 (0.20)	1.94 (0.10)	0.90 (0.07)	**1.06 (0.03)**	**1.69 (0.07)**	1.31 (0.05)	**1.41** (0.03)	1.26 (0.01)
Ca	**5.87 (0.28)**	4.89 (0.51)	3.86 (0.19)	**4.68 (0.10)**	5.68 (0.09)	**6.37 (0.52)**	4.97 (0.05)	**5.60** (0.05)
K	6.62 (0.33)	**9.60 (0.93)**	3.28 (0.49)	**4.74 (0.20)**	**5.10 (0.57)**	3.03 (0.16)	4.47 (0.06)	4.34 (0.12)
Mg	0.90 (0.33)	1.25 (0.67)	0.86 (0.34)	0.99 (0.45)	1.23 (0.51)	1.26 (0.38)	1.06 (0.01)	**1.15** (0.01)
Fe	**0.31 (0.06)**	0.17 (0.04)	0.12 (0.02)	**0.25 (0.01)**	**0.50 (0.11)**	0.36 (0.04)	**0.34** (0.01)	0.29 (0.01)
Mn	0.64 (0.05)	0.69 (0.18)	1.05 (0.07)	1.02 (0.06)	1.01 (0.03)	0.93 (0.03)	**1.05** (0.01)	0.96 (0.01)
Al	0.39 (0.12)	0.21 (0.04)	0.15 (0.01)	**0.30 (0.03)**	0.33 (0.05)	**0.54 (0.08)**	0.26 (0.01)	**0.40** (0.01)
Zn*	**145 (9)**	84 (11)	**76 (4)**	65 (2)	**338 (10)**	192 (14)	**223** (7)	128 (4)
Cu*	11 (2)	**18 (2)**	8 (0.2)	**9 (0.5)**	20 (1)	**28 (3)**	15 (0.3)	**19** (0.6)
Na*	**661 (25)**	145 (14)	**114 (3)**	78 (4)	**356 (57)**	170 (8)	**280 (8)**	129 (3)
C:N	35 : 1	33 : 1	37 : 1	38 : 1	21 : 1	24 : 1	26 : 1	30 : 1
C:N:P	203 : 6 : 1	237 : 7 : 1	492 : 13 : 1	436 : 11 : 1	272 : 13 : 1	356 : 17 : 1	321 : 12 : 1	368 : 12 : 1

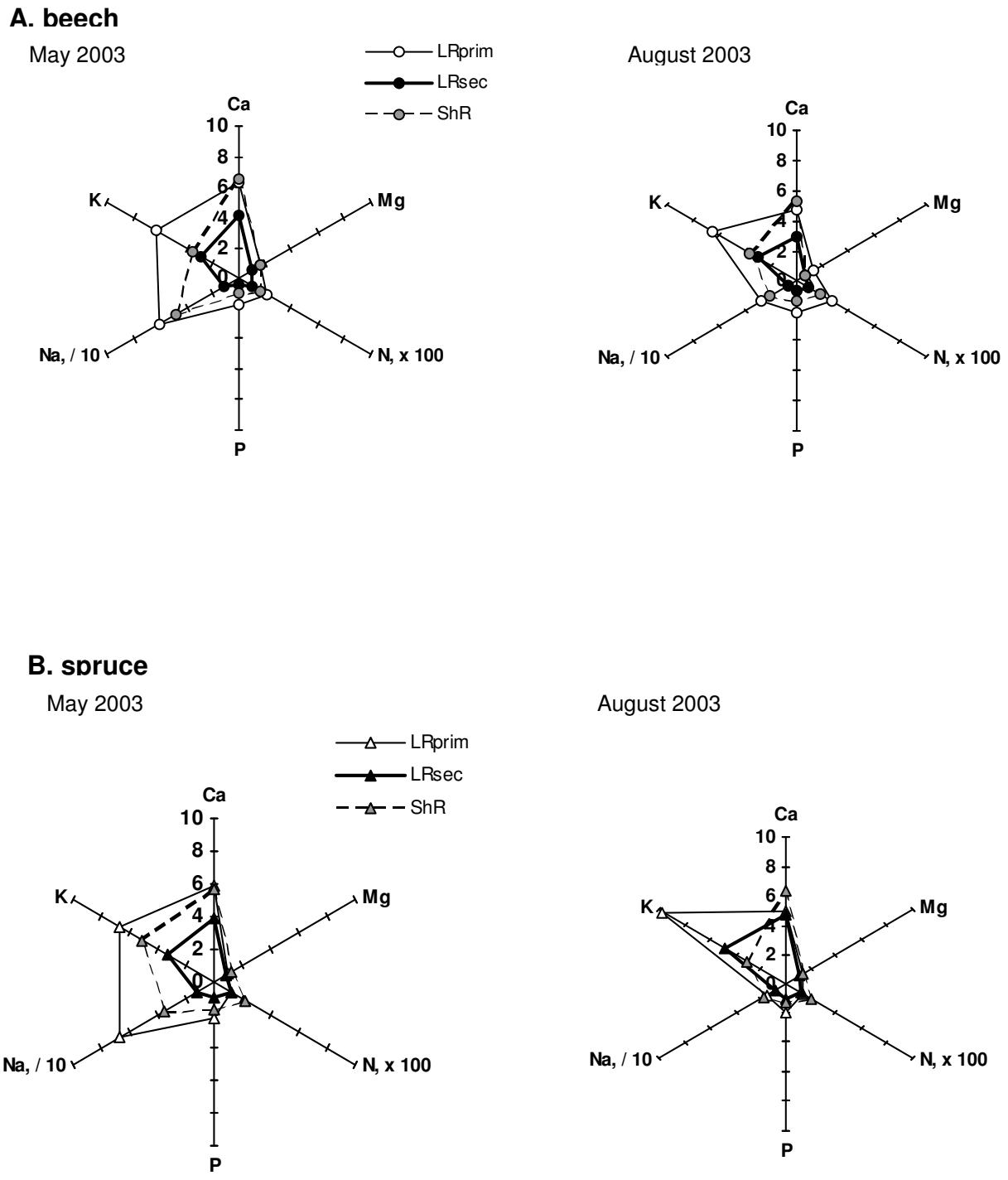

Figure 46: Concentrations [mg g^{-1}] of the elements N (nitrogen), Na (sodium), K (potassium), Ca (calcium) and Mg (magnesium) in the fine root categories of, A, beech and B, spruce. Data represent as means (n = 4 to 6; from **Tab. 13**).

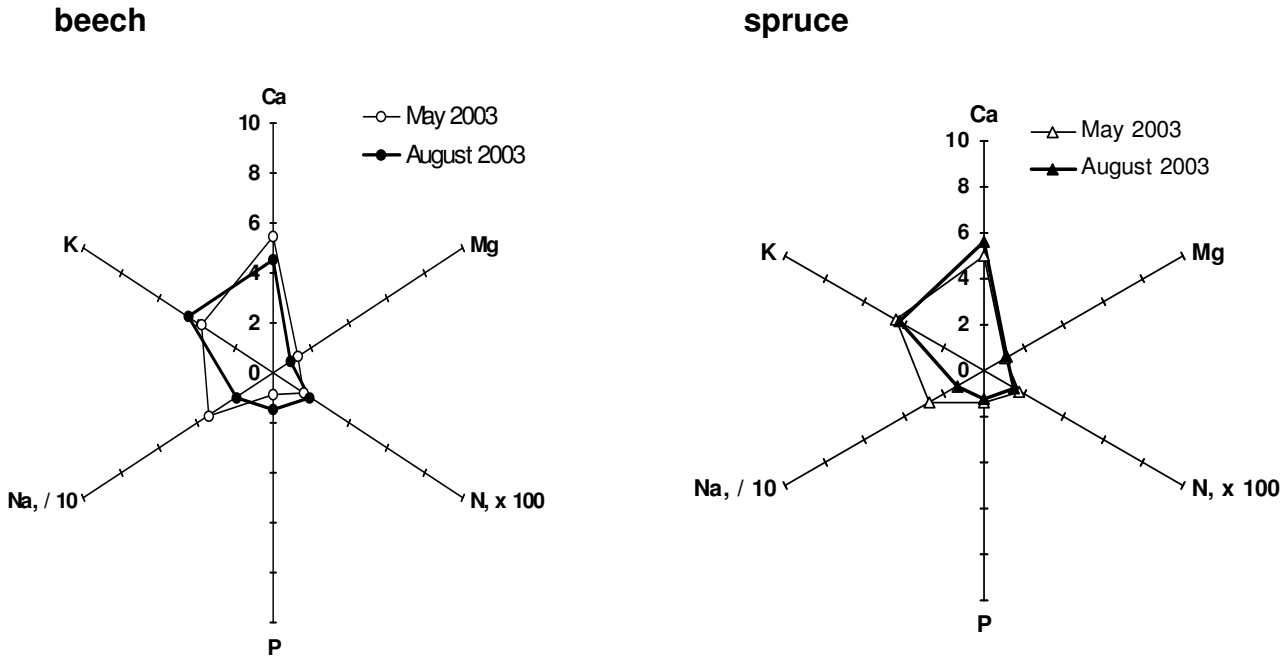

Figure 47: Contents [mg g^{-1}] of the elements N (nitrogen), P (phosphorus), Na (sodium), K (potassium), Ca (calcium) and Mg (magnesium) in the individual rootlets of beech and spruce as present in May and August of 2003 (cf. **Tab. 13**). Data given as means (n = 7 to 10).

3.9.2 Drought impact on C and N concentration

In beech, during the dry August of 2003, C and N concentrations were significantly enhanced in all fine-root categories (**Tab. 14**) compared to August of 2002. The proportional to the levels in August 2002 increase of N was higher than the proportional increase of C which leads to significant decrease of the C:N ratio in LR_{prim} and LR_{sec} during August 2003.

Spruce fine-root categories showed different response pattern in C and N concentration to drought compared to beech. In August of 2003, C:N ratio of LR_{prim} was enhanced relative to August of 2002 as a consequence of enhanced C and lowered N concentrations. C concentration in LR_{sec} was not altered by drought, but was enhanced in ShR, whereas both fine-root categories displayed higher N concentrations as compared to August of 2002.This leads to lowered C:N ratios in both fine-root categories.

3.9.3 Seasonal dynamics of C and N concentration in rootlets

Based on the sampling campaigns during 2003 and 2004 (after measurement of root respiration in same fine-roots as described in 2.18) seasonal dynamics showed higher levels of C and N concentration (with the exception of June and August in 2003) in spruce than

beech rootlets (**Fig. 48**). Seasonal mean C concentration (cf. section 2.14) was 451 mg g^{-1} in beech and 465 mg g^{-1} in spruce rootlets, and mean N concentration was 16.1 mg g^{-1} and 16.6 mg g^{-1}, respectively, so that the annual mean C:N ratio was 28 in both tree species (**Tab. 14**).

Table 14: Concentration of carbon (C, mg g^{-1}) and nitrogen (N, mg g^{-1}), and the C:N ratio in the fine-root categories "long lateral roots with primary xylem" (LR_{prim}), "long lateral roots with secondary xylem" (LR_{sec}) and "short roots" (ShR) of beech and spruce as assessed at the sampling dates during 2002, 2003 and 2004. Data shown as means (n = 4 to 6) and 95% confidence interval (in brackets).

Sampling date	Fine-root categories									Rootlet		
	LR_{prim}			LR_{sec}			ShR					
	C	N	C:N	C	N	C:N	C	N	C:N	C	N	C:N
beech												
20.08.2002	436 (4.8)	22.8 (1.1)	19.3 (0.7)	468 (2.4)	8.4 (0.3)	56.2 (1.5)	439 (0.7)	17.4 (0.6)	25.4 (1.2)	n.d.	n.d.	n.d.
24.04.2003	428 (2.6)	27.1 (0.7)	15.8 (0.4)	467 (2.1)	9.6 (0.3)	49.0 (1.5)	420 (0.6)	16.4 (0.5)	25.6 (0.6)	442 (2.9)	15.8 (1.5)	28.3 (2.8)
27.06.2003	446 (4.1)	23.0 (0.9)	19.5 (0.8)	473 (1.1)	6.8 (0.3)	69.5 (2.8)	458 (1.2)	14.2 (0.5)	32.5 (1.3)	459 (2.2)	14.5 (1.2)	31.8 (2.6)
22.08.2003	447 (3.1)	27.5 (0.6)	16.3 (0.4)	473 (1.4)	9.4 (0.5)	50.9 (2.6)	458 (2.0)	18.4 (0.5)	24.8 (0.7)	458 (2.7)	19.4 (1.8)	23.8 (2.3)
30.10.2003	431 (1.4)	19.2 (0.4)	22.5 (1.0)	476 (4.2)	10.1 (0.2)	47.2 (1.4)	447 (1.0)	19.7 (1.3)	23.0 (1.2)	446 (2.4)	15.7 (0.6)	29.2 (1.1)
16.09.2004	444 (4.4)	18.0 (0.6)	24.7 (0.8)	460 (2.3)	8.7 (0.2)	52.8 (1.2)	425 (5.2)	19.1 (0.9)	22.5 (1.2)	442 (2.4)	15.0 (0.6)	29.6 (1.4)
annual mean										451 (11.0)	16.1 (2.4)	28.5 (3.6)
spruce												
20.08.2002	422 (4.1)	17.5 (1.1)	24.5 (1.6)	463 (1.2)	10.2 (0.1)	46.4 (3.4)	453 (1.8)	18.0 (0.3)	25.1 (0.3)	n.d.	n.d.	n.d.
15.04.2003	448 (2.9)	12.7 (0.3)	35.2 (0.7)	463 (0.8)	12.0 (0.5)	38.9 (1.5)	463 (2.2)	22.2 (0.7)	20.9 (0.7)	462 (0.5)	17.6 (0.6)	26.3 (0.9)
26.06.2003	450 (1.4)	16.5 (0.4)	27.4 (0.8)	462 (3.3)	10.4 (0.4)	44.9 (1.9)	466 (1.4)	14.7 (0.5)	31.9 (0.9)	464 (0.8)	13.0 (0.4)	35.8 (1.0)
21.08.2003	460 (1.7)	14.0 (0.3)	32.9 (0.7)	462 (1.0)	11.8 (0.6)	39.6 (2.3)	467 (2.0)	19.2 (0.3)	24.3 (0.3)	464 (0.5)	15.5 (0.7)	30.1 (1.3)
28.10.2003	467 (1.2)	16.6 (1.0)	28.7 (1.9)	470 (3.2)	14.5 (0.4)	32.7 (0.9)	482 (2.4)	20.5 (0.5)	23.6 (0.6)	474 (0.8)	16.8 (0.4)	28.2 (0.7)
16.09.2004	450 (7.6)	21.8 (1.1)	20.8 (0.6)	456 (1.9)	11.1 (0.6)	41.5 (2.3)	470 (9.0)	20.5 (0.8)	23.1 (0.9)	460 (2.0)	20.3 (0.6)	22.7 (0.7)
annual mean										465 (7.1)	16.6 (3.3)	28.6 (6.0)

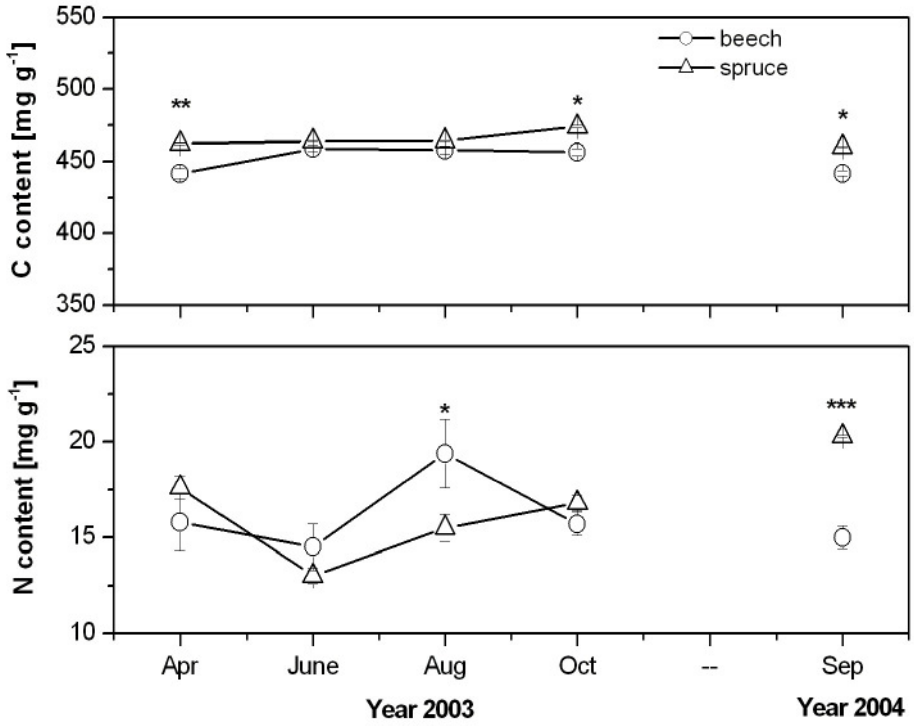

Figure 48: Carbon (C; mg g^{-1}) and nitrogen (N; mg g^{-1}) content in the individual rootlets of beech and spruce as assessed at the sampling dates during 2003 and 2004. Asterisks represent significant differences (*t*-test) between beech and spruce at (*) $p<0.05$, (**) $p<0.01$ and (***) $p<0.001$. Data shown as means (n = 7 to 10) and 95% confidence interval.

3.9.4 Relationship between root respiration rate and N concentration of the rootlets

In both tree species, the root respiration rate of individual rootlets assessed at a standard temperature of 10°C in April, June and August of 2003 (RR^{10}_{I}; nmol CO_2 $g^{-1}s^{-1}$) was positively related to the corresponding N concentration of the rootlets (**Fig. 49** & **Tab. 15**). In beech, the highest responsiveness of RR^{10}_{I} to N content was detected in April of 2003, whereas spruce showed maximum responsiveness in June of the same year (see coefficient β in **Tab. 15**). Although the response of RR^{10}_{I} to the N content was high in beech at all sampling dates during 2003 (coefficient β ranged between 4.97 and 5.83 mg g^{-1}), spruce displayed weak responsiveness during August and October of 2003 (coefficient β was 0.52 and 0.98; mg g^{-1}). This latter observation in spruce appeared to be related in 2003 to the harsh drought in August and to the autumnal dormancy of fine-roots at the end of October.

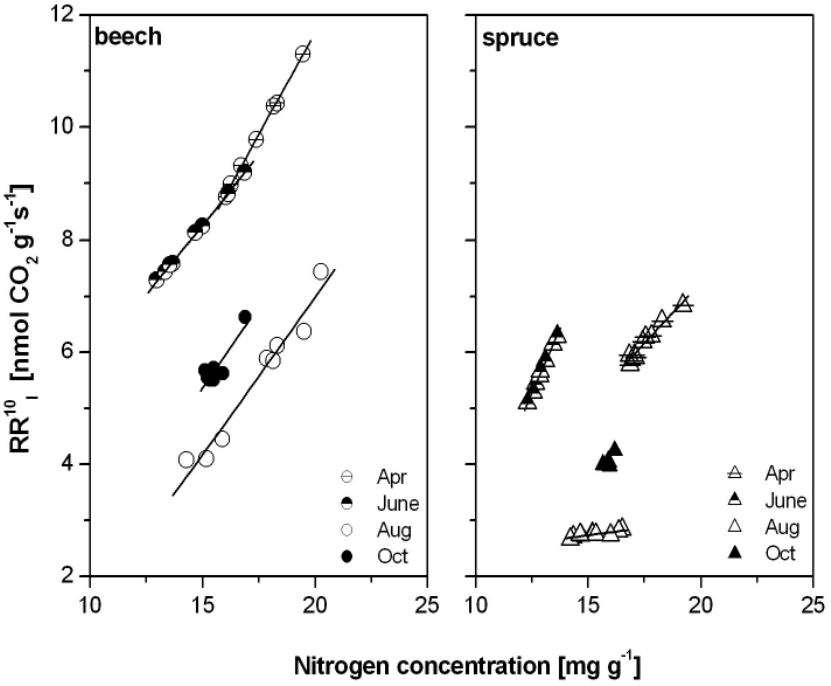

Figure 49: Relationship between root respiration rate at a standard temperature of 10 °C (RR^{10}_{l}; nmol CO_2 $g^{-1}s^{-1}$; cf. section 3.6.3) and nitrogen content (N; mg g^{-1}) in individual beech and spruce rootlets. Lines represent linear fit (regression statistics provided in **Tab. 15**).

Table 15: Statistical treatment of the data shown in **Fig. 49**. Linear fit ($RR^{10}_{l} = \alpha + \beta * N$) describes the relationship between root respiration rate at a standard temperature of 10 °C (RR^{10}_{l}; nmol CO_2 g^{-1} s^{-1}) and nitrogen content (N, mg g^{-1}) in individual rootlets of beech and spruce, with α and β being regression coefficients, n is the number of the analysed individual rootlets, R^2 representing measure of determination, and *p* giving levels of significance of the regression equations (ANOVA). Standard errors of α and β are shown in brackets.

Sampling date	Intercept, α [nmol CO_2 g^{-1} s^{-1}]	Slope, β [N; mg g^{-1}]	n	R^2	*p*
beech					
April 24	-2.86 (0.15)	7.27 (0.08)	7	0.99	<0.0001
June 27	0.81 (0.09)	4.97 (0.06)	8	0.99	<0.0001
August 22	-4.28 (0.81)	5.63 (0.46)	8	0.96	<0.0001
October 30	-3.39 (1.89)	5.83 (1.21)	8	0.79	0.003
spruce					
April 15	-1.48 (0.64)	4.36 (0.37)	9	0.95	<0.0001
June 26	-6.24 (0.33)	9.21 (0.25)	8	0.99	<0.0001
August 21	1.94 (0.17)	0.52 (0.11)	10	0.74	0.001
October 28	2.45 (2.10)	0.98 (1.31)	9	0.04	0.479

3.10 Water uptake by fine roots

3.10.1 Morphological and growth parameters of the rootlets

Beech rootlets growing from June 1 through October 29 of 2003 in the rhizotrones (cf. 2.19) had near 1.5 times higher initial (L_0), final (L_N) and mean standing fine-root length (L_{mean}) and were characterized by 2.3 times higher specific fine-root length (SRL; cm g^{-1}) relative to spruce rootlets (**Tab. 16**). The total number of assessed white root tips (N_{WRTi}) in beech was also 1.5 times higher than in spruce. Nevertheless, the mean standing biomass of the beech rootlets (M_{mean}) was 80% of the mean standing biomass of the spruce rootlets, and the newly produced fine-root biomass (RP) in beech during the recorded period of water consumption was nearly 70% of that in spruce. Although the relative root length increment (RLI), calculated as (L_N-L_0) / L_0, varied between the individual rootlets, means of beech and spruce were rather similar.

Table 16: Morphological and growth parameters of the individual rootlets in beech and spruce: initial total rootlet length L_0 [cm], total rootlet length at the end of the experimental period L_N [cm], specific fine-root length SRL [cm g^{-1}], total number of white root tips N_{WRTi}, mean standing fine-root length L_{mean}, mean standing biomass of the rootlets (M_{mean}), fine-root production RP [g] and relative length increment RLI [calculated as (L_N-L_0) / L_0)]. Bold numbers represent means ± standard error.

rootlets	L_0 ,cm	L_N, cm	SRL, cm g^{-1}	$\sum_{i=1}^{6} N_{WRTi}$	L_{mean}, cm	M_{mean}, g	RP, g	RLI
be1	160.6	1384.9	2398.1	133	1079.0	0.45	0.34	7.6
be2	354.9	1103.3	1236.2	239	818.5	0.66	0.53	2.1
be3	75.1	1788.9	1178.6	112	1400.1	1.19	1.17	22.8
be4	154.4	638.2	1490.0	658	424.6	0.28	0.28	3.1
beech mean	**186 ± 59**	**1228 ± 241**	**1575 ± 282**	**285 ± 127**	**930 ± 206**	**0.65 ± 0.2**	**0.58 ± 0.2**	**8.9 ± 4.8**
sp1	52.0	94.9	328.7	6	92.3	0.28	0.02	0.8
sp2	69.0	1663.5	791.0	488	1233.8	1.56	1.92	23.0
sp3	82.5	900.0	891.1	134	689.4	0.77	0.91	9.9
sp4	306.9	712.6	789.1	106	525.9	0.67	0.50	1.3
spruce mean	**127 ± 60**	**842 ± 323**	**699 ± 125**	**183 ± 105**	**635 ± 235**	**0.82 + 0.4**	**0.87 ± 0.4**	**8.8 ± 5.2**

3.10.2 Seasonality of the water uptake by rootlets

Focusing on the individual rootlets (**Fig. 50**), and given the basis of section 2.18, two periods of rapid growth were identified in beech during 2003, i.e. one in June, and another one during the second half of August (cf. r_i and L_i levels in **Fig. 50**). A break in root length increment occurred between mid-July and mid-August, when r_i (%), which reflects the proportion of white root tips at this time in the total number of white root tips determined across the whole experimental period, dropped to minimal 2 to 5%. Growth of the beech rootlets ceased at the end of the experimental period (i.e. during October).

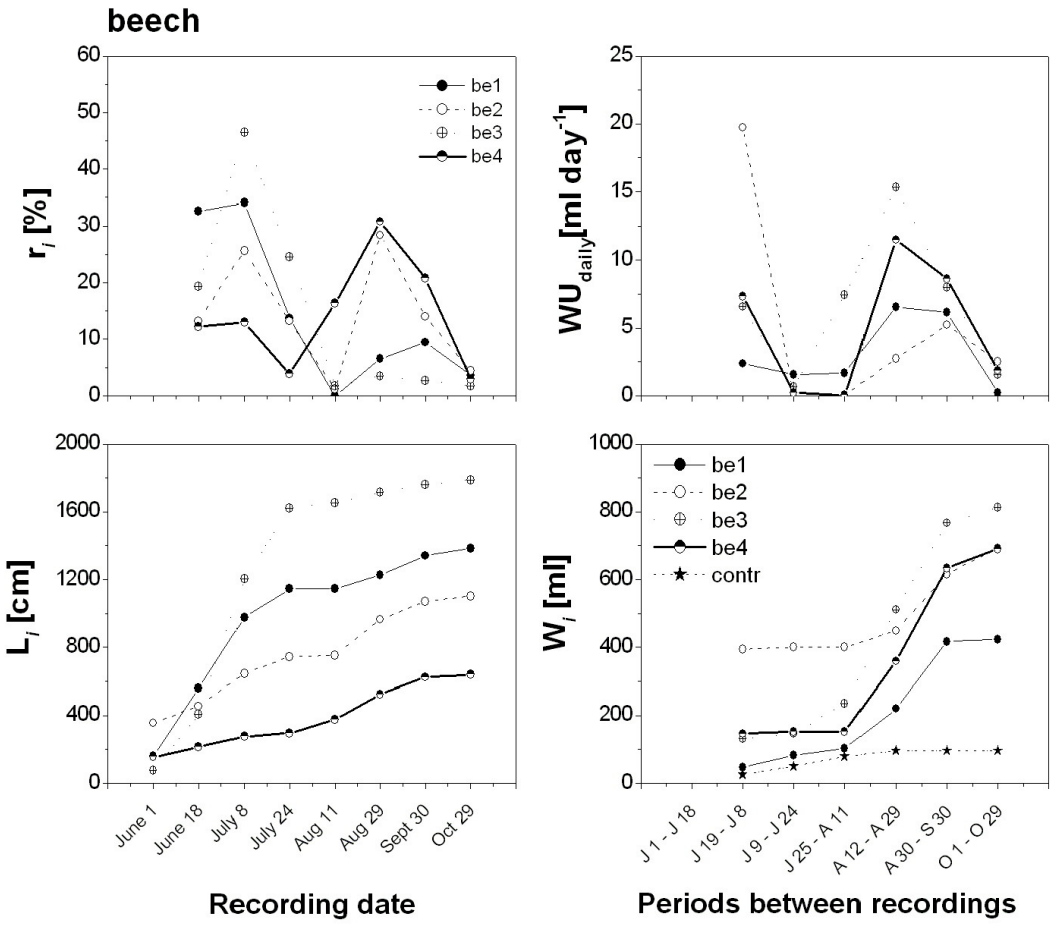

Figure 50: Seasonal course (2003) of r_i (the proportion of white root tips at the recording date *i* in the total number of white root tips determined across the whole experimental period), L_i (the total rootlet length at recording date *I*; cm), WU_{daily} (daily water uptake rate; ml day^{-1}) and W_i (water consumption of the rootlet and of the control rhizotrones during the recording period *i*) in individual beech rootlets. Data for control rhizotrones (control = rhizotrone without roots) are shown as means (n=3).

During the experimental period of 2003, daily water uptake rate WU_{daily} [ml day^{-1}] in beech was characterized by two peaks which, in general, coincided with the periods of rapid rootlet growth (**Fig. 50**). The rootlet be3 displayed the lowest specific fine-root length (SRL; cm g^{-1}) and highest levels of mean standing fine-root length L_{mean} [cm], mean rootlet standing biomass M_{mean} [g], fine-root production RP [g] and relative root length increment RLI. In parallel, highest cumulative water uptake W [ml] occurred within this rootlet. However, be3 had the lowest daily specific water uptake rate (SWU_M or SWU_{PR}; ml g^{-1} day^{-1}) of the studied beech rootlets. Rootlet be4, in contrast, displayed average levels of SRL and W but SWU_M and SWU_{PR} of 18.4 ml g^{-1} day^{-1} each, which was two to three times higher than in the other rootlet samples of beech (**Tab. 17**).

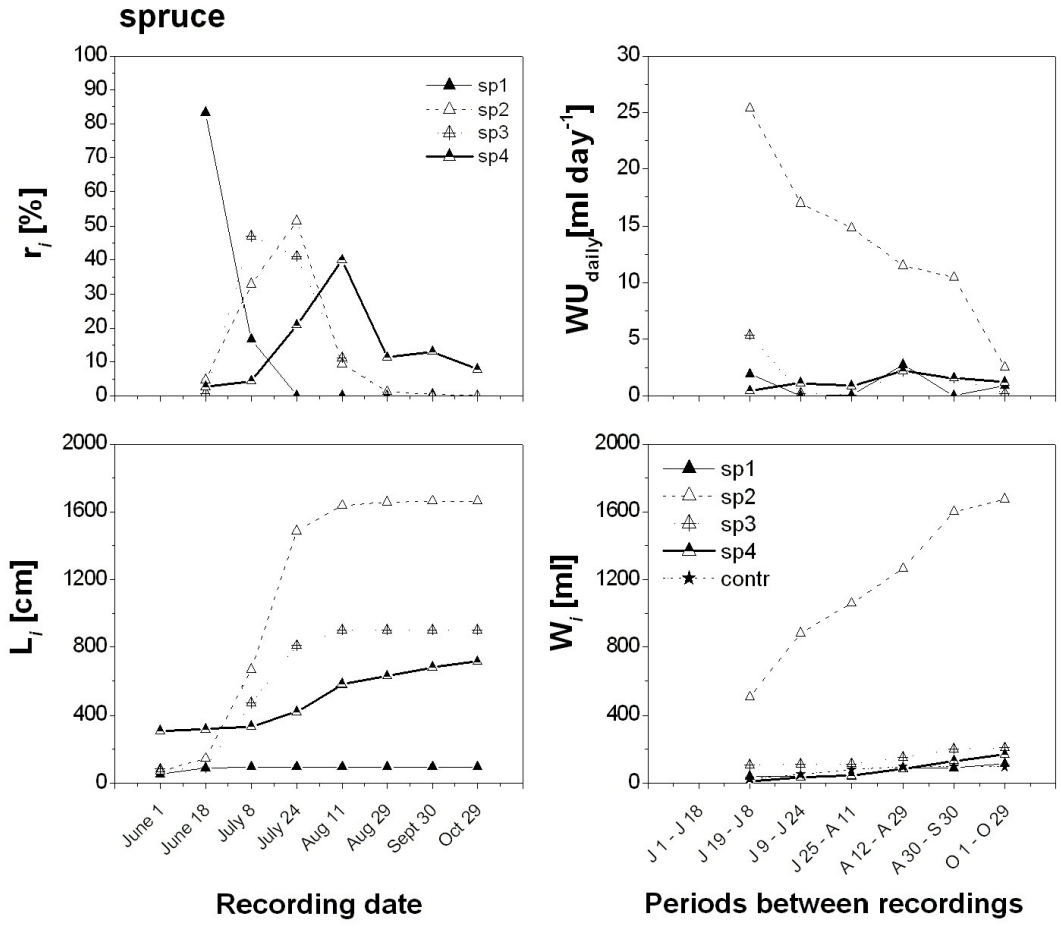

Figure 51: Seasonal course (2003) of r_i (the proportion of white root tips at the recording date *i* in the total number of white root tips determined across the whole experimental period), L_i (the total rootlet length at recording date *i*; cm), WU_{daily} (daily water uptake rate; ml day^{-1}) and W_i (water consumption of the rootlet and of the control rhizotrones for the recording period *i*) in individual spruce rootlets.
Data for control rhizotrones (control = rhizotrone without roots) are shown as means (n=3).

In contrast to beech, individual rootlets of spruce showed one period of rapid growth during 2003 (i.e. one peak of r_i was registered in June or July; **Fig. 51**) which did not correspond with WU_{daily}. In general, spruce rootlets consumed two to four times less water per day and rhizotrone than did the rootlets of beech. Only sp2 displayed WU_{daily} comparable to beech rootlets and achieved remarkable 1675 ml at the highest levels of L_{mean}, M_{mean}, RP and RLI across the spruce rootlets. Moreover, the latter structural properties were associated with higher SWU_M and SWU_{PR} relative to sp3 and sp4, but lower SWU_M similar to be4. Root development and water consumption differed in sp1, a rootlet without length increase since mid-July (cf. r_i from **Fig. 51**). Sp1 had the lowest W (119.8 ml per rhizotrone) in this analysis.

On average, beech rootlets consumed 20% more water than those of spruce (in terms of W; ml per rhizotrone) during the experimental period and showed two to three times higher SWU_M and about 30% lower SWU_{PR}. Apparently the high W of beech is related to maintaining low mean standing root biomass (M_{mean}; g) in the presence of a high number of non-suberized white root tips and high SRL (i.e. ephemeral-like structures). In contrast, the high W in spruce was achieved through intensive root elongation associated with high construction costs (i.e. high M_{mean}; cf. **Tab. 16**).

Table 17: Parameters of water uptake in beech and spruce rootlets: cumulative water uptake during the whole experimental period per rhizotrone (W; ml), SWU_M represents the daily water uptake rate of the rootlets per unit of mean standing root biomass (M_{mean}, g), and SWU_{RP} represents the daily water uptake per unit of newly produced fine roots (RP, g). Bold numbers denote means of rhizotrones with beech (n=4), spruce (n=4) or control (n=3) rhizotrones ± standard error each.
Control = rhizotrone without roots.

	Parameters of water uptake		
rootlets	W, ml	SWU_M [ml g^{-1} day^{-1}]	SWU_{PR}[ml g^{-1} day^{-1}]
be1	424	7.0	9.3
be2	692	7.8	9.7
be3	813	5.1	5.2
be4	690	18.4	18.4
beech mean	**654 ± 228**	**9.8 ± 2.9**	**10.7 ± 2.8**
sp1	120	3.2	44.7
sp2	1676	8.0	6.5
sp3	208	2.0	1.7
sp4	169	1.9	2.5
spruce mean	**543 ± 1050**	**3.8 ± 1.5**	**16.5 ± 13.0**
controls	**66 ± 19**		

3.11 Efficiency ratios of competitiveness

3.11.1 Specific fine-root length

The below-ground studies were concentrated on the uppermost 20 cm of the soil, where – because of the existing gradient in the nutrient and water supply (Schuhbäck, 2004) – two soil sub-samples were distinguished: organic sub-sample (O+Ah) and mineral sub-sample (B). Similar to other studies on below-ground competitiveness (Grams *et al.*, 2002; Kozovits *et al.*, 2005a, b), the mean specific fine-root length (SRL, cm g^{-1}; i.e. of three sampling campaigns during March, August and December of 2002; **Fig. 52**) of beech and spruce is presented within each soil sub-sample. High SRL is conceived to reflect high efficiency of below-ground space sequestration (Grams *et al.*, 2002). No significant differences in SRL were found between mono and mixed subplots of beech under both O_3 regimes, however, significant differences existed in beech between both soil sub-samples (**Tab. 19**): about two times higher SRL was found in the organic O+Ah soil sub-sample as compared to the mineral B horizon, regardless of O_3 regime or type of competition. In contrast, spruce displayed similar SRL irrespective of the tested factors "O_3 regime", "type of competition" and "soil sub-sample" (**Tab. 19**) which indicates lower morphological plasticity, and, according to Grams et al. (2002), lower efficiency in below-ground space sequestration as compared to beech.

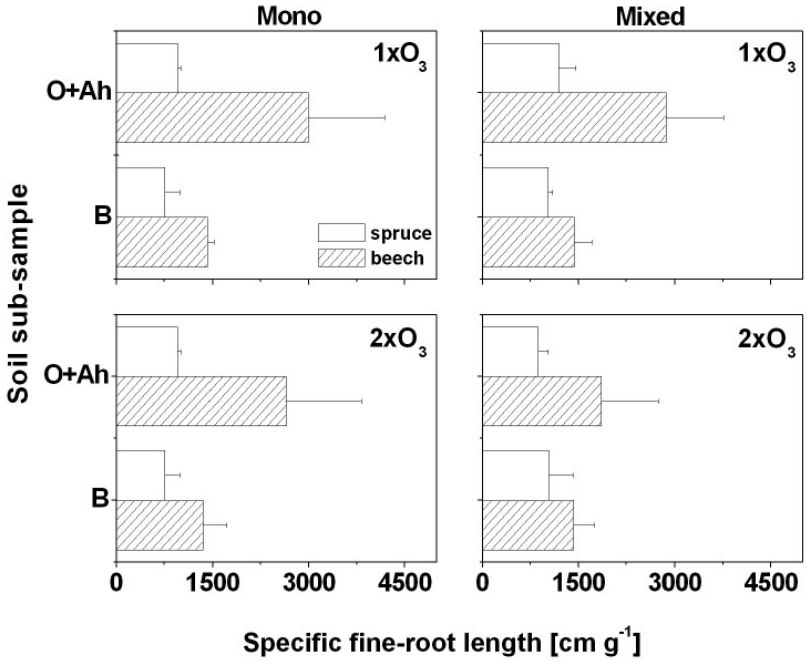

Figure 52: Specific fine-root length (SRL; cm g^{-1}): fine root length per unit of dry mass (averaged across three sampling campaigns during March, August and December of 2002) of each soil sub-sample (organic O+Ah and mineral B) of beech and spruce trees growing under $1xO_3$ or $2xO_3$. Means $\pm$ standard error (n=5-10).

3.11.2 Efficiency ratio of below-ground space occupation

In mixed subplots where below-ground space is shared by both competitors, soil volume predicted to be occupied alone by beech fine roots ($SV_{pr\ beech}$, cm^3; for methodological details see section 2.22.1) was higher than soil volume predicted to be occupied alone by spruce fine roots ($SV_{pr\ spruce}$, cm^3), regardless of the O_3 regime or soil sub-sample (significant differences at $p<0.05$ are shown in **Tab. 18**). For both (O+Ah) and (B) soil sub-samples, $SV_{pr\ beech}$ was similar under $1xO_3$ and $2xO_3$, whereas spruce was predicted to occupy more soil volume within (B) when growing under $1xO_3$, and showed similar $SV_{pr\ spruce}$ in (O+Ah) and (B) when growing under $2xO_3$ (**Tab. 18**). When $SV_{pr\ beech}$ was expressed as proportion of the total volume of the soil sub-samples (O+Ah) and (B) (i.e. of $TSV_{pr(O+Ah)}$ or $TSV_{pr(B)}$; cf. Eq. 19), beech occupied 66% and 60% of $TSV_{pr(O+Ah)}$ and $TSV_{pr(B)}$, respectively, under $1xO_3$, and 55% of $TSV_{pr(O+Ah)}$ and 65% of $TSV_{pr(B)}$ under $2xO_3$ (**Tab. 18**). Apparently, the nutrient-richest soil volume, where the strongest below-ground competition is expected in mixed sub-plots (i.e. both soil sub-samples (O+Ah) and (B); cf. section 2.7), was predominantly occupied by beech fine roots under both O_3 regimes. In addition, $SV_{pr\ beech}$ and $SV_{pr\ spruce}$ served for calculation of the efficiency ratios of below-ground space occupation (BSO; $m^3\ kmol^{-1}$) of beech and spruce within mixed subplots.

Table 18: Root volume (RV; cm^3) and factor k_c (cf. Eq. 22) used for prediction of the soil volume occupied each by fine roots of beech ($SV_{pr\ beech}$; cm^3) or spruce ($SV_{pr\ spruce}$; cm^3) when growing at mixed subplots under $1xO_3$ and $2xO_3$ during 2002. Data represent means (n=5-10); standard errors are shown in brackets. Bold numbers represent the PSV [%] of beech or spruce fine roots (Eq. 19), i.e. the proportion of $SV_{pr\ beech}$ or $SV_{pr\ spruce}$ in $TSV_{pr(O+Ah)}$ or $TSV_{pr(B)}$, respectively, for mixed subplots. Asterisks represent significant differences between beech and spruce at $p<0.05$ (*U*-test).

Treatments	Beech						Spruce					
	RV [cm^3]		k_c		$SV_{pr\ beech}$ [cm^3], **[%]**		RV [cm^3]		k_c		$SV_{pr\ spruce}$ [cm^3], **[%]**	
	O+Ah	B	O+Ah	B	O+Ah	B	O+Ah	B	O+Ah	B	O+Ah	B
$1xO_3$												
Mono	0.36 (0.06)	0.92 (0.05)	248 (26)	167 (11)			1.60 (0.2)	0.67 (0.04)	57 (6)	203 (40)		
Mixed	0.24 (0.03)	0.57 (0.05)			51 (6)* **66 (4)***	94 (7) **60 (4)**	0.49 (0.07)	0.34 (0.07)			24 (2) **34 (5)**	60 (6) **40 (7)**
$2xO_3$												
Mono	0.70 (0.14)	1.03 (0.14)					1.27 (0.30)	0.64 (0.08)				
Mixed	0.54 (0.17)	0.78 (0.08)			46 (4) **55 (8)**	86 (6)* **65 (7)**	0.98 (0.08)	0.33 (0.06)			45 (8) **45 (9)**	48 (8) **35 (7)**

The type of competition (i.e. the presence of spruce as neighbour within the mixed sub-plots) did not change the efficiency of below-ground space occupation in beech (cf. BSO; **Tab. 19**). However, under $2xO_3$, beech occupied less soil volume per unit of C investment into standing fine-root biomass at mono- and mixed subplots each compared to $1xO_3$ (**Fig. 53**). The efficiency of BSO in beech decreased with soil depth, indicating that the occupation of the mineral soil sub-sample B (being nutrient-depleted relative to O+Ah) required in beech about two times higher C investment into the fine root structure as compared to the occupation of the organic soil sub-sample (O+Ah).

"O_3 regime" and "type of competition" did not change the efficiency of BSO in spruce, however, contrary to beech, BSO in spruce increased with soil depth (**Fig. 53**). Apparently, the occupation of the organic soil sub-sample (O+Ah) which is characterized by high nutrient concentrations, but also high amplitudes in soil moisture and temperature, is more risky and expensive for spruce in terms of structural C costs as compared to the occupation of the deeper mineral soil sub-sample. Habitat partitioning in root growth between both tree species is indicated in different soil depths, which may alleviate the competition for soil resources.

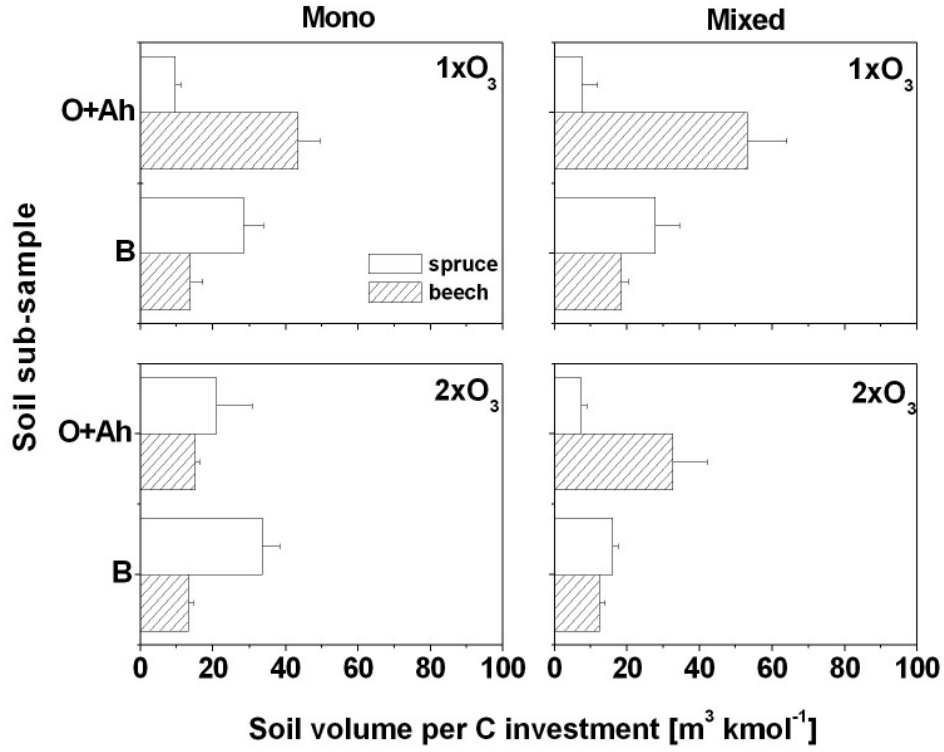

Figure 53: Below-ground space occupation (BSO): occupied soil volume per unit of C investment in the standing fine-root biomass (averaged across the three sampling campaigns during March, August and December of 2002) of each soil sub-sample (organic O+Ah and mineral B) in beech and spruce trees growing under $1xO_3$ and $2xO_3$. Means $\pm$ standard error (n=5-10).

3.11.3 Efficiency ratio of below-ground space exploitation

Based on water uptake measurements on individual rootlets under $1xO_3$ (i.e. daily specific water uptake rate SWU_M, ml g^{-1} day^{-1}; for methodological details see section 3.8) beech and spruce fine roots at mono sub-plots showed similar efficiency of below-ground space exploitation (i.e. BSE) as compared to the mixed sub-plots (**Tab. 19** & **Fig. 54**). At both mono and mixed sub-plots, beech consumed two to three times more soil water per unit of occupied soil volume within the mineral soil sub-sample B, whereas spruce was two to three times more efficient in BSE within the organic soil sub-sample (O+Ah). A decrease in competition for water is indicated between beech and spruce as an outcome of the habitat partitioning addressed in section 3.11.2.

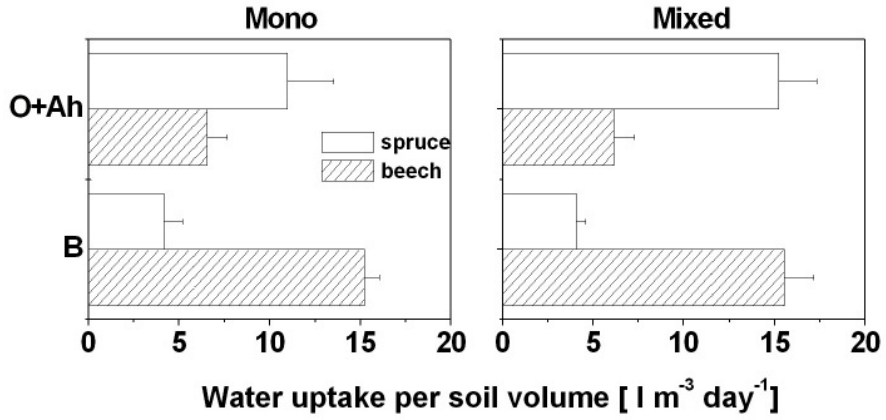

Figure 54: Efficiency in below-ground space exploitation (BSE): daily water consumption in beech and spruce fine-roots per unit of occupied soil volume of each soil sub-sample (organic O+Ah and mineral B) assessed under $1xO_3$ during 2003. Means $\pm$ standard error (n=5-10).

3.11.4 Efficiency ratio of "running costs"

Efficiency ratio of "running costs" (BRC, i.e. occupied soil volume per unit of C release in fine-root respiration) for maintenance and growth of fine roots in beech and spruce within a given soil volume under both O_3 regimes, types of competition and soil sub-samples showed patterns during 2002 similar to those of the efficiency ratio of BSO. In beech, a significantly higher efficiency ratio of BRC was detected under $1xO_3$ as compared to $2xO_3$ as well as within the organic soil sub-sample (O+Ah) as compared to the mineral B (results of the statistical evaluation shown in **Tab. 19**). "Type of competition" does not change the efficiency ratio of BRC of the fine-roots in both tree species. In spruce, only "soil sub-sample" had a significant effect on the efficiency ratio of BRC which increased with soil depth in a way similar to the efficiency ratio of BSO.

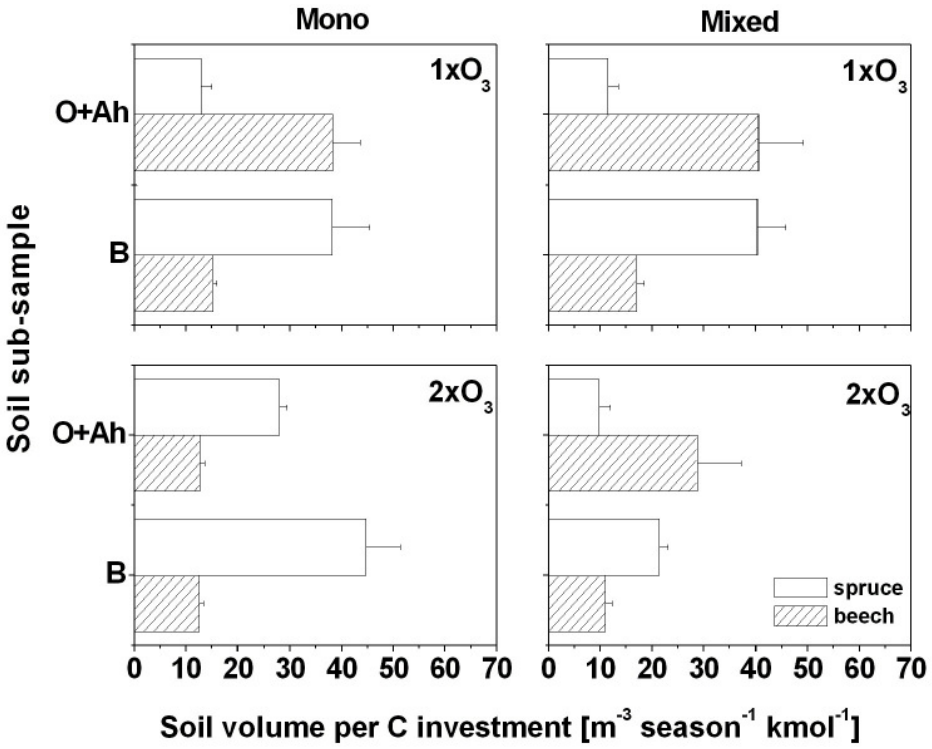

Figure 55: "Running costs" (BRC): Efficiency in occupied soil volume per unit of C investment into maintenance and growth respiration of the annual mean standing fine-root biomass assessed during 2002 for each soil sub-sample (organic O+Ah and mineral B) in beech and spruce trees growing under $1xO_3$ and $2xO_3$. Means $\pm$ standard error (n=5-10).

In summary, the efficiencies of competitiveness in beech related to C investments into standing fine-root structure and their maintenance and growth (i.e. BSO and BRC) were significantly lower under $2xO_3$ and within the nutrient-depleted B soil sub-sample (**Tab. 19**), which indicates enhanced costs for compensatory fine root production at limiting conditions. The response in BSO and BRC is supported by enhanced SRL, although only in the B soil sub-sample (shortage in nutrients) but not so under $2xO_3$ (restricted assimilation; Löw *et al.*, 2006). The third efficiency ratio of BSE which is related to the benefits in beech of the occupied and sustained space was found to be similar at mixed and mono sub-plots, but lower within the organic (O+Ah) soil sub-sample compared to the mineral B. Efficiency ratios of competitiveness BSO and BRC in spruce were lowered significantly only at the fertile soil conditions (i.e. within (O+Ah) soil sub-sample relative to B) where spruce possessed more standing fine-root biomass without any changes of SRL as compared to roots in the B soil sub-sample. The lower efficiency of spruce in BSO and BRC within the (O+Ah) soil sub-sample, however, improved the BSE of spruce contrary to beech within (O+Ah) soil sub-sample. Hence, spruce was able at mixed sub-plots to predominantly use water and nutrients from different sub-soil horizons as did beech.

Table 19: Statistical evaluation of the effect on the factors "O_3 regime ", „type of competition" and "soil sub-sample" on the efficiency ratios of competitiveness in beech and spruce. BSO = efficiency in below-ground space occupation; BSE = efficiency in below-ground space exploitation (not determined under 2xO3); BRC = efficiency in below-ground running costs. Numbers in brackets give p levels of statistical significance (tested by univariate GLM or *U*-test in case of unbalanced design); "~" denotes no difference; n.d. = not determined.

		Efficiency ratios of competitiveness		
Factors	**SRL** (fine root length vs. fine root biomass)	**BSO** (soil volume per unit of C investment into annual mean standing fine root biomass)	**BSE** (daily mean water uptake per unit of soil volume)	**BRC** (soil volume per unit of seasonal fine root respiration)
beech				
O_3 regime ($1xO_3$; $2xO_3$)	~ (0.337)	$1xO_3 > 2xO_3$ (0.015)	n.d.	$1xO_3 > 2xO_3$ (0.029)
Type of competition (mono sub-plots; mixed sub-plots)	~ (0.511)	~ (0.150)	~ (0.871)	~ (0.423)
Soil sub-sample (O+Ah; B)	O+Ah >B (<0.001)	O+Ah > B (<0.001)	O+Ah < B (0.002)	O+Ah > B (<0.001)
spruce				
O_3 regime ($1xO_3$; $2xO_3$)	~ (0.378)	~ (0.405)	n.d.	~ (0.535)
Type of competition (mono sub-plots; mixed sub-plots)	~ (0.297)	~ (0.087)	~ (0.761)	~ (0.201)
Soil sub-sample (O+Ah; B)	~ (0.473)	O+Ah < B (<0.001)	O+Ah > B (0.002)	O+Ah < B (0.019)

In addition, efficiency ratios of competitiveness were assessed for the total length of the soil sample (0 to 20 cm soil depth) at mono and mixed subplots under both O_3 regimes to approach an integrative view on the below-ground efficiencies in beech and spruce within this densely rooted soil zone (**Fig. 56**). "Type of competition" had no impact on the efficiency ratios of BSO, BSE and BRC within the specified soil volume (levels of significance shown in **Tab. 20**). Irrespective of the "O_3 regime", beech showed a higher efficiency ratio of BSO compared to spruce, whereas BRC of both tree species were similar. Daily water uptake from the occupied soil volume (i.e. BSE) was also higher in beech relative to spruce at both mono and mixed sub-plots. "O_3 regime" showed significant effect on BSO and BRC, although $2xO_3$ decreased these efficiency ratios in beech at both mono and mixed sub-plots. In spruce, BSO and BRC were significantly affected by $2xO_3$ only under conditions of mixture.

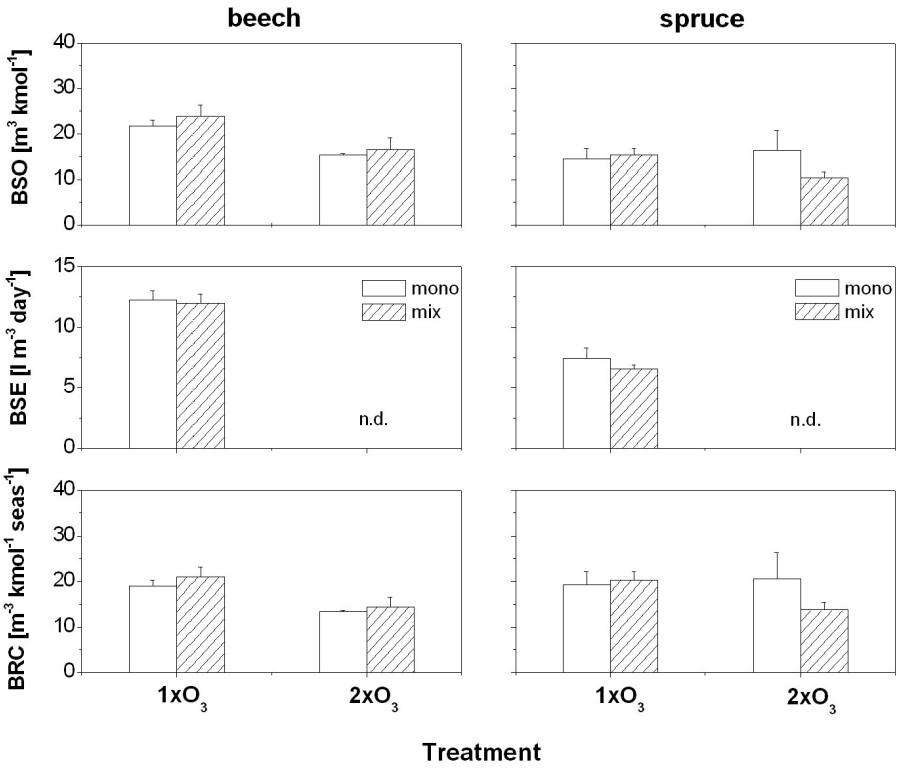

Figure 56: Efficiency ratios of below-ground space occupation (BSO), below-ground space exploitation (BSE; not determined under $2xO_3$) and running costs (BRC) as assessed within the uppermost 20 cm of the soil underneath beech and spruce trees growing at mono and mixed subplots under $1xO_3$ and $2xO_3$. Means $\pm$ standard error (n=5-10); n.d. = not determined.

Table 20: Statistical evaluation of the effect of the factors „ O_3 regime " and „tree species" on BSO (efficiency in below-ground space occupation) and BRC (efficiency in running costs), as well as "type of competition" and "tree species" on BSE (efficiency in below-ground space exploitation; not determined under $2xO_3$). Numbers in brackets give p levels of significance (tested by univariate ANOVA); "~" = no difference; n.t. = not tested; n.d. = not determined.

	Efficiency ratios of competitiveness (0-20 cm soil depth)		
Factors	**BSO** (soil volume vs. C investment into annual mean standing fine root biomass)	**BSE** (daily mean water uptake vs. soil volume)	**BRC** (soil volume vs. seasonal fine root respiration)
Type of competition (mono sub-plots; mixed sub-plots)	~ (0.637)	~ (0.737)	~ (0.241)
O_3 regime ($1xO_3$; $2xO_3$)	$1xO_3>2xO_3$ (0.013)	n.d.	$1xO_3>2xO_3$ (0.046)
Tree species (beech; spruce)	beech>spruce (0.006)	beech>spruce (<0.001)	~ (0.319)
O_3 regime x tree species	0.063	n.t.	0.224
Type of competition x tree species	n.t.	0.985	n.t.

4 DISCUSSION

Below-ground studies on competitiveness are provided in a mature *Fagus sylvatica* / *Picea abies* forest stand of high structural complexity. The high individual variability (all trees of each species of same age, but not of same size; Wipfler *et al.,* 2005; Löw *et al*., 2006) and differences in stand density (**Fig. 25**) interacted with seasonal growth dynamics which was driven by differing climatic conditions across the three study years (**Figs. 21** & **22**) and heterogenic spatial distribution of soil resources (Schuhbäck, 2004). In addition, densely packed root ramifications of adult beech and spruce trees show a high degree of aggregation in root clusters (Schmid & Kazda, 2005), often forming symphyses within or even between coarse roots of individual trees (Kutschera & Lichtenegger, 2002). In contrast to above-ground structures which form distinct branches and individual crowns (Reiter *et al*., 2005), the structural and functional distinction of the individual root systems of trees becomes hardly feasible. Here, results from below-ground studies were not quantified per individual tree, but at the stand level, as the latter level was found to reliably describe and predict species growth in relation to intra and interspecific competition (Poorter & Navas, 2003).

To determine below-ground competitive success in plants, three types of space-related cost/benefit relationships (i.e. “efficiencies”; cf. section 1.1.3) were used by combining measures from different experimental approaches. The selection of response variables can critically influence the interpretation of competition (Weigelt & Jolliffe, 2003). The explanatory power of the efficiency ratios chosen in this study was validated by comparison with conventional approaches and with the efficiency ratios defined previously for above-ground structures (Reiter *et al*., 2005). Evaluations of below-ground competitive success in plants can be confounded by methodology, when evaluating resource investments into root structure (i.e. C costs for root production; Hendricks *et al*., 2006; Hertel & Leuschner, 2002) and related maintenance (i.e. C costs for respiration; Lambers, 1979), or when assessing returns (i.e. resource uptake from a highly heterogeneous environment; Bliss *et al*., 2002). The physiological parameters assessed in this study are based on robust methods, which were adapted to field conditions as necessary. A challenging question in comparing beech and spruce was to divide the soil volume of mixed subplots into portions occupied by the fine-roots and their symbionts of each of the species. Is below-ground physical space a resource by its own which organisms compete for aside the soil function to provide nutrients and water (McConnaughay & Bazzaz, 1991)? Which are the mechanisms of the root systems of beech and spruce ensuring successful competition for soil nutrients under changing environmental conditions (i.e. under experimentally enhanced ozone concentration or naturally occurring prolonged drought)? Did the experimental design of the present study

allow to assess the profiteer in the competitive interaction for soil resources and the extent of contrasting resource exploitation strategies? The discussion will direct attention to such questions. Along with quantifying the physiological basis of below-ground competitiveness under forest stand conditions, physiological aspects will be discussed with respect to silvicultural practice and predicted “global change” scenarios, since the sustainable cultivation of mixed beech-spruce forests is of major economic interest in Central-European forestry (Rennenberg *et al.*, 2004; Ammer *et al.*, 2005).

4.1 Climatic variation during the study period 2002-2004

Climatic conditions were highly variable during the three experimental years: from moist conditions during 2002 and average rainfall in 2004 to severe drought during 2003 (Raspe *et al.*, 2004). Summer precipitation in 2003 was 30% lower during the growing season as compared to the 30-year long-term average. Schume *et al.* (2004) and Jost *et al.* (2004) reported on differences in forest hydrology between mixed and pure stands of European beech and Norway spruce which occurred during the seasonal periods when the soil water reserves were depleted. In our experiment, the *variation in time* of plant-available soil water (ASW) within both tree groups was assessed using the model LWF-BROOK90 (Hammel & Kennel, 2001; co-operation with Dr. S. Raspe, LWF). The modelled seasonal pattern in 2003 of ASW showed two periods of species-specific differences in soil hydrology: (1) during spring, when soil drying started earlier under spruce than beech, and (2) during mid-summer, when ASW was exhausted first under spruce. As a consequence, drought (i.e. the period during which water was not plant-available) was prolonged under spruce (75 days compared to 45 days in beech). At the stand level of a mixed spruce/beech forest in Lower Austria, Schume *et al.* (2003) reported the species-specific exhaustion of soil moisture to be predominantly caused by different transpiration rates. According Hietz *et al.* (2000) transpiration rates of individual beech trees were up to six times higher than those of spruce trees of comparable size. Although whole-tree transpiration was not assessed in the present study, the daily water uptake per mean standing root biomass (SWU_M) of the beech fine-root system was found to excess that of spruce by a factor of three (**Tab. 17**). Blaschke (unpubl.) reported for “Kranzberg Forest” the fine root density of beech to be twice as high (assessed within the total rooting zone of 0 to 90 cm soil depth) as in spruce. Combining the higher density of the beech fine-root system with the assessed SWU_M, the daily water uptake by fine roots within the total rooted zone in beech is concluded to exceed the corresponding parameter in spruce by the factor of six. Such a difference is consistent with that between whole-tree transpiration of individual beech and spruce trees as reported by Hietz (2000).

At “Kranzberger Forst” a *spatial heterogeneity* of volumetric soil water content (SWC) was detected under both beech and spruce monospecific sub-plots (**Fig. 26**). In a study carried out in mixed spruce-beech forests of Lower Austria, the spatial variation of soil re-wetting was interpreted in relation to the different tree architecture of the two species (Jost *et al*., 2004). The separate pathway of rain water uptake at the stand level via stem flow in beech, mediated through funnel-like upward branch inclination and smooth stem surface, caused 13 to 30% higher water input around stems relative to precipitation (Patzner, 2004; Zirlewagen & von Wilpert, 2001). In contrast, spruce displays higher interception due to the large foliage surface area (Patzner, 2004; Beier, 1998). These differences in above-ground architecture apparently have caused the spatial heterogeneity of volumetric soil water content (SWC) detected in the present study under beech and spruce monospecific sub-plots at “Kranzberger Forst”. Here, stand structure in terms of stem density was regarded as the other important factor providing patches that favour re-charging of the soil water reservoir by precipitation. In mono-subplots of beech, SWC measured at positions with high stem density exceeded SWC at low density by a factor of 2 (**Fig. 26**), possibly as a consequence of the higher water input via stem flow in the denser part of the stand. In contrast, SWC under mono-subplots of spruce increased with decreasing stem density which is ascribed to the larger crown gaps that allow precipitation to readily reach the stand floor. Consistent with the water infiltration concentrating at stem base via stem flow, beech develops high uptake capacity for water from the soil around stems due to a dense, deep-reaching and homogeneous root system (Schmid & Kazda, 2002). Spruce, in contrast, forms a shallower root system concentrated within the uppermost 30 cm of the soil (Schmid, 2002), possessing high fine-root density within a 5 m radius, and maximum horizontal root extension up to 15 m around tree trunks (Ammer & Wagner, 2002). By this spruce is restricted to exploit water mostly from the top soil; however, because of the laterally expanding root system, spruce can sequester soil recourses at higher distance from its stem base compared to beech.

As a result of the different water re-charging and exploitation patterns of both tree species, no significant relation between SWC and stem density was found in the mixed subplot (**Fig. 26**), although a slight increase in soil water was measured in less dense forest parts. The spatial distribution of soil moisture in the mixed subplot was more homogenous compared to the mono-specific subplots. These results imply mixed beech/spruce stands to be characterized by more effective re-charge (i.e. water input into the soil) and use of soil water relative to monocultures (being of relevancy for predicted “global change” scenarios; Easterling *et al*., 2000).

In summary, the extent of drought during 2003 underneath mono and mixed-species tree groups was modified by architectural as well as physiological features (i.e. transpiration rate; Heitz *et al*., 2000) of beech and spruce. Stand density was found to contribute in a contrasting way to the spatial variation of SWC within beech and spruce sub-plots, but had no significant effect within mixed plots. The species-specific difference in forest hydrology vanished during severe drought (Schume *et al*., 2003, **Fig. 31** in this study).

4.2 Comparison of beech and spruce responses to drought

The variation in the climatic conditions between study years and the extremely dry and warm summer of 2003 set the stage for evaluating the responsiveness of the two competing tree species, beech and spruce, to water limitation under the mixed-stand conditions of "Kranzberger Forst". Plant responses to drought under field conditions are complex, and can be synergistically or antagonistically modified by the superimposition of other stresses (Chaves *et al*., 2002). Based on the conventional approach of Casper and Jackson (1997), the physiological and/or morphological traits of beech and spruce fine-roots that determine below-ground competitive ability under prolonged drought are discussed in the following with respect to soil space occupation. In both species functional categories within the fine-root fraction are important to understand the different strategies of conifer and angiosperm tree species in soil exploitation (Bauhus & Messier, 1999).

4.2.1 Beech

Underneath beech growing in mono and mixed sub-plots under ambient ozone concentration ($1xO_3$), annual fine-root production (FRP) and fine-root turnover (RT) were enhanced by drought, and, respectively, fine-root longevity (RL) was reduced. Leuschner *et al*. (2001) reported from a mixed stand of *Fagus sylvatica* and *Quercus petraea* the mortality of finest roots (diameter < 1 mm) in beech to increase during summer drought, while compensatory finest-root production was stimulated, ensuring an unchanged standing biomass of this root category. Such a plant response to reduced water availability was found to raise carbohydrate partitioning to below-ground sinks while reducing C supply to other sinks in the stand (Joslin & Wolfe, 1998). Lambers *et al*., (1998) discuss a possible mechanism for sustaining the root biomass at dry soil conditions: low soil water potential sets the signal for increasing the transport of assimilates to roots, which is probably due to the reduction of the highly drought-sensitive extension growth of leaves (Smirnoff, 1995). Since photosynthesis is less affected by drought than leaf growth (Kramer & Boyer, 1995), sugar translocation to roots as well as root growth may be enhanced. This results in reduced transpiring foliage

area of the plant, relative to the sustained or even enlarged water-absorbing fine-root area. Leuzinger *et al*. (2005) detected in beech a decrease of maximum net photosynthesis and a progressively constrained sap flow under the persisting drought of 2003. Consistently, Löw *et al*. (2006) found photosynthetic electron transport rate, maximum net photosynthesis rate and stomatal conductance to be markedly lowered in beech of "Kranzberger Forst" during 2003 as compared to 2004. In accordance with this latter study, $\delta^{13}C$ of newly produced fine roots indicated enhanced WUE in beech during the CO_2 assimilation period of 2003 relative to the moist growing seasons of e.g. 2002 or 1999. The annual precipitation was found to explain only 53% from the variation in $\delta^{13}C$ of newly formed fine roots in beech ($R^2 = 0.53$; cf. **Fig. 28**). Probably, carbon sources other than currently formed assimilates, e.g. reserve C pools in stem and roots which reflect conditions of the previous growing seasons (Geßler *et al*., 2001) and were depleted in ^{13}C, were remobilised during prolonged drought and used for production of new fine roots. Such an **increase in the conversion of internal stores into new growth** is proposed by Chapin *et al*. (1987) to be a possible way by which plants increase their fitness under resource limitation (cf. section 1.1.1).

Under severe drought stress and stomatal closure the total carbon flux into the plant decreased but the proportion of sucrose and of starch reserves increased (Lawlor, 1995). Similarly in beech, total sugar content of short fine roots (ShR) and starch concentration were enhanced under drought in long lateral roots with secondary xylem (LR_{sec}) (**Tab. 21**). In addition, during the drought of 2003, long lateral roots with primary xylem (LR_{prim}) accumulated sucrose. Sucrose was found to be involved in osmo-regulation in response to drought (Peuke *et al*., 2002) and/or is consumed by root respiration and serves as a substrate for organic acid synthesis during growth (Smirnoff, 1995). Accumulation of K is another protective response to drought (Lambers *et al*., 1998); however, no seasonal accumulation of K was detected in any fine root category of beech during August of 2003 (**Fig. 47**).

Table 21: Changes in the fine-root parameters and categories of beech and spruce during the dry August of 2003 as compared to the moist August of 2002. Arrows indicate increase (↑) or decrease (↓) of each parameter in response to drought. Significance levels at: (*) $p \leq 0.1$; * $p \leq 0.05$; ** $p \leq 0.01$; n.d. = not determined; LR_{prim} = long lateral roots with primary xylem; LR_{sec} = long lateral roots with secondary xylem; ShR = short mycorrhizal roots.

Fine-root parameter	beech			spruce		
	fine-root category			fine-root category		
	LR_{prim}	LR_{sec}	ShR	LR_{prim}	LR_{sec}	ShR
Specific fine-root area	~	~	↓(*)	~	~	↓*
Specific root tip density	n.d.	n.d.	~	n.d.	n.d.	~
Ectomycorrhizal colonisation rate	n.d.	n.d.	~	n.d.	n.d.	↑*
Concentration of:						
Starch	n.d.	↑*	~	↓*	~	~
Fructose	n.d.	↑*	↑*	~	~	~
Sucrose	n.d.	~	↑**	↑**	↑*	↑*
Glucose	n.d.	~	~	~	↓(*)	↓(*)
Pinitol				↑*	~	~
Total sugars	n.d.	↑(*)	↑**	↑(*)	↑(*)	~
C	↑*	↑*	↑*	↑*	~	↑*
N	↑*	↑*	↑*	↓*	↑*	↑*
C:N	↓*	↓*	~	↑*	↓*	↓*

The sequestration of enriched nutrient/water patches in the soil offsets the expense of new organ construction (cf. Casper & Jackson, 1997; Grime *et al.*, 1991). Only LR_{prim} showed sustained temperature sensitivity of root respiration during drought (**Fig. 37** & **Tab. 10**), indicating sustained growth of this fine-root category (in August of 2003 LR_{prim} amounted to 35% of the total biomass of the individual rootlets in beech; cf. Appendix: **Tabs. 1A** & **1B**). LR_{prim} of beech displayed low structural investment relative to the other fine-root categories by forming thin roots with high SRA (**Figs. 39** & **40**). Species like beech that have very fine non-mycorrhizal lateral roots of high hydraulic conductivity tend to shed their roots in dry soil and re-construct them quickly when soil is rewetted (Anderson *et al.*, 2003). This recent finding supports the high respiration and proliferation activity of LR_{prim} assessed during August of 2003 in the present study. Apparently, the ability of beech to form and maintain such ephemeral fine-root structures and to shed them after sequestering the resources in patches represents a plastic foraging behaviour for soil nutrients and water during drought periods. However, long-lived and expensive structures such as LR_{sec} have to tolerate and survive harsh environmental periods. This need requires various protective mechanisms ranging from anatomical and morphological characteristics (Kutschera & Lichtenegger, 2002) to biochemical mechanisms as osmotic adjustment (Smirnoff, 1995). Osmotic adjustment was indeed detected in LR_{sec} as fructose concentration in this fine root category was

enhanced during the dry August of 2003. As a response to drought, ShR of beech tended to decrease SRA but maintained the ectomycorrhizal colonisation rate (EMycR). Symbiotic association with the fungal partner represents a strong carbohydrate sink in the plant: up to 30% of the total photoassimilate production was found to be transferred to the fungal partner (Nehls & Hampp, 2000). The plant, on the other hand, compensates for this carbohydrate loss by increasing its photosynthetic capacity, enlarging the volume of exploited soil (via fungal structures) and, by this, enhancing the exploration for nutrients (Agerer, 2001). In response to drought, the carbohydrate demand of ShR in beech was enhanced, as a considerable increase in sucrose concentration was detected in August of 2003 relative to August of 2002. Simultaneously, root respiration of ShR was strongly reduced indicating less growth in this fine-root category during drought (**Fig. 37A**). This finding was consistent with Tibbett (2000) who suggested that root proliferation will become obsolete when roots are colonized by ectomycorrhizal fungi (as fungal hyphae also proliferate into soil patches). Because of their small size ectomycorrhizal hyphae are less expensive in construction than fine roots in terms of C investment (Fitter, 1991) but require significant maintenance costs (Andersen, 2003). Since beech allocates starch reserves during midsummer mainly into the root system (Larcher, 1994), such a pattern of C partitioning apparently is advantageous for producing and maintaining the ephemeral and mycorrhizal fine roots and their symbionts during summer drought.

In summary, the construction of ephemeral-like fine-roots (as shown for LR_{prim}) or morphologically plastic ShR (with lowered SRA but retained EMycR) is interpreted as metabolic feedbacks in beech for “optimising” the structure in response to drought. Such a fine-root construction may allow beech to proliferate into nutrient-rich micro-sites. As a result, the nutritional status of beech fine roots in terms of concentration of nitrogen was sustained in beech during drought, perhaps indicating sustained N status of the whole plant. In addition to the **increased conversion of internal stores into new growth,** the **increased resource uptake via constructing drought-induced ephemeral fine-roots** may be another way by which beech plant increases its fitness at low resource level (cf. section 1.1.1).

4.2.2 Spruce

In spruce growing under ambient ozone levels in mono sub-plots, the strong reduction of the FRP and RT observed during 2003 compared to 2002 led to enhanced fine-root longevity of remarkable 12.5 years. However, no changes in these fine-root parameters were observed in spruce growing in mixture with beech. Nearly 80% of the fine-roots of spruce growing at “Kranzberger Forst” were localized within the uppermost 15 cm of the soil (Mainiero, pers.

comm.) where soil water was hardly available during June through September of 2003. Apparently, sustaining the root biomass at such soil conditions (e.g. by enhanced transport of assimilates to roots and stimulation of root proliferation) was not possible in the case of spruce. Raised $\delta^{13}C$ in newly formed fine roots during 2003 compared to 2002 indicate that the reduced root growth during drought in spruce was accompanied by significant stomatal limitation of photosynthetic CO_2 uptake during assimilation period of 2003. Compared to beech, spruce showed stronger correlation of $\delta^{13}C$ in newly formed fine roots with the annual precipitation (R^2 = 0.80; cf. **Fig. 28**). These results indicate FRP of spruce to depend to a larger extent on current assimilates than beech. On the other hand, during the dry summer of 2003 LR_{prim} of spruce changed colour from white to brown due to suberization of cell walls in the primary cortex (**Fig. 15**). Drought lowered the starch concentration of this fine-root category, although carbohydrates in total were enhanced due to increased sucrose and pinitol concentrations (**Tab. 12**). Both carbohydrate fractions deriving from recently fixed C are important solutes which regulate the osmotic balance, protect membranes and serve as carbohydrate depot during drought (Lambers *et al*., 1998). In addition, the K concentration of LR_{prim} was strongly enhanced in August of 2003 compared to levels in May of the same year. The solute accumulation indicates biochemical adjustment of LR_{prim} of spruce to drought. Lipp & Andersen (2003) demonstrated lower respiration rate and lower sensitivity in ponderosa pine to supply of current photosynthate in brown fine-roots compared to white (non-suberized) fine-roots. Similarly, during August of 2003, brown LR_{prim} of spruce showed strong reduction in the respiration rate (RR) compared to June of 2003 so that RR dropped to the level of LR_{sec}. Since RR strongly relates to root growth rate (Lipp & Andersen, 2003), and root growth rate defines the extent to which a plant explores soil for water and mineral nutrients (Hsiao & Xu, 2000) water uptake through roots was apparently reduced in spruce. In addition, Steudle (2000) points out the low cell hydraulic conductivity in roots to be attributed to a high degree of suberization. In this way, the suberized cell walls of LR_{prim} act as a physical barrier to the movement of water and dissolved mineral nutrients into the plant. This is consistent with the strongly reduced N concentration of LR_{prim} during drought (**Tab. 14**). At the same time, suberization which was concentrated in the root cortex should reduce water loss from the root surface to the soil (cf. Taleisnik *et al*., 1999). Such mechanism of **decreasing resource loss** (detected in the present study for spruce fine-roots) is proposed by Chapin *et al*. (1987) to be a way for increasing plant fitness in the case of limited resource supply.

In August 2003, osmotic adjustment such as enhanced sucrose content was detected also in LR_{sec} of spruce, however starch concentration decreased and total sugars remained at a similar level as during moist August of 2002. Decrease of starch reserves apparently resulted in low respiration rates in this fine-root category approaching levels of maintenance

respiration. In addition, the enhanced K concentration in LR_{sec} increased the drought tolerance of this expensive and long-lived structure (i.e. LR_{sec} showed the lowest SRA within all fine-root categories). As response to drought, ShR of spruce significantly reduced SRA and enhanced EMycR up to levels typical for the dormant season so that almost all root tips were mycorrhized during drought. Mycorrhizal associations may enhance root lifespan and resistance of fine-roots to drought (Eissenstat, 2002). The hyphae and rhizomorphs greatly increase the volume of exploited soil (Agerer, 2001) and are shown to enlarge effectively the phosphate-absorbing surface per unit C cost, despite the additional C demand of the fungus (Lambers *et al*., 1998). Like in the other fine-root categories of spruce, drought enhanced sucrose concentration of ShR at lowered fructose and glucose concentrations. Sucrose is shown to be hydrolyzed to glucose and fructose and the resulting mono-saccharides are taken up from the common apoplastic interface by both the fungal partner and root cortical cells (Nehls & Hampp, 2000). This demand for photo-assimilates of highly mycorrhized fine-roots in spruce apparently resulted in enhanced sucrose concentration and depleted fructose and glucose concentrations in ShR. In addition, Langley *et al*. (2002) pointed out, that mycorrhizal roots of regenerating shrub oaks tended to have a higher percentage of new C than the corresponding non-mycorrhizal roots. In a mature deciduous forest in Switzerland, Körner *et al*. (2005) found 64% of the newly fixed carbon to be allocated into mycorrhizal fungi already by the end of the first year after applying $\delta^{13}C$ labelling. If such a demand for current assimilates also holds true for mycorrhizal roots in spruce, then, during periods of restricted photosynthetic activity, spruce would allocate the new C mainly to ShR. Thereby, the non-mycorrhized root tips will be neglected and the mycorrhized root tips will be maintained, i.e. the density of mycorrhizal root tips will enhance as found in this study (MycTD, see **Fig. 42**).

In summary, suberization of LR_{prim}, shedding of non-mycorrhized root tips and maintenance of ectomycorrhizatial colonisation on ShR are interpreted as “structural optimizations” of spruce in response to drought (Pregitzer *et al*., 1993). This allows spruce to set their most desiccation-sensitive fine-root category into dormancy and to sustain simultaneously soil exploitation effectively through symbiotic associations. In spruce, nitrogen concentration decreased by drought only in LR_{prim}, whereas LR_{sec} and ShR showed enhanced N relative to the moist August of 2002. This indicates that the induced loss/reduction of metabolic activity of LR_{prim} during summer drought of 2003 was a decisive factor for the monitored strong decline of the fine-root system in spruce in terms of reduced root extension growth (i.e. low size increment).

Plant strategies to cope with drought involve stress avoidance and tolerance that vary with genotype (Jackson *et al*., 2000). In addition, tolerance at one level (e.g., of the roots) may allow drought avoidance at another (e.g., of the leaves) (Lambers *et al*., 1998). Data of the

present study support evidence that stress avoidance and tolerance varied between the different functional fine-root categories. The most drought-sensitive fine-root category of beech, i.e. LR_{prim}, showed drought-avoiding strategy via root shedding. Possibly, the advantages of drought avoidance (i.e. high growth and uptake activity under favourable conditions) are offset by the relatively low C costs of producing new ephemeral roots in nutrient-rich zones or after even small events of rain. In contrast, ShR and LR_{sec} of beech (i.e. the more expensive fine-root categories in terms of C costs for structure) showed increased tolerance to drought via physiological and biochemical adjustments. In spruce, LR_{prim} showed drought tolerance via entering into dormancy. As with ShR and LR_{sec}, LR_{prim} of spruce has relatively high C costs of producing new roots and exhibits morphological and physiological adaptations for drought tolerance or water conservation. Apparently, root increment of LR_{prim} occurs only after rains that are large enough to support growth. In addition, above-ground stand characteristics such as annual stem diameter increment (SDI; Wipfler, pers. comm.) indicated in beech a 35% decrease in SDI compared to the humid 2002, while FRP stayed unchanged relative to levels in the humid 2002. Compared with beech, reductions in SDI on spruce were more pronounced in 2003 (65%, respectively), and FRP was reduced by 70 %, relative to humid conditions in 2002 (**Fig. 57**). These results are in consistency with the hypothesis of Grace (1990) that species with rapid growth and uptake rates (i.e. beech) are more likely to be able to take advantage of nutrients when supplied in pulses (i.e. during arid periods; James & Richards, 2006) than are species with low growth and uptake rates (i.e. spruce) but tolerance of low resource levels.

4.2.3 Responses of beech and spruce to drought at the stand level

The maintenance of fine root biomass and symbiotic associations in beech, although being costly in terms of carbon use for respiration, may be beneficial for beech in capturing water upon re-wetting of the soil. This hypothesis is supported in the present study by the observed differences in spatial distribution of newly produced fine-roots: compared to 2002, beech tended to realize during dry 2003 the highest FRP at the densest and moistest parts of the mono sub-plot. Similarly, Hodge (2004) observed morphological plasticity within root systems in response to localized water and nutrient enrichment. However, Hartung (1996) noted the progressive severity of drought to turn stimulation of root growth into inhibition, as found here for less dense and dryer parts (apparently due to enhanced radiation and intense evaporation) within the beech mono sub-plot. Stand density has high importance for root functioning and, as a consequence, for whole-tree and stand performance when precipitation becomes limiting. Results support and provide a physiological context to the finding of

Pretzsch (2005) that on sites with poor water and nutrient supply beech reacts with increment reduction upon intense thinning.

During moist 2002, spruce but not beech increased fine-root production in the less dense parts of the sub-plot, where SWC was shown to be higher. In consistency with the present study, water uptake of soil underneath canopy gaps in spruce stands was found to be higher relative to crown centres and edges (Zirlewagen & von Wilpert, 2001). However, during extremely dry 2003, when water deficit underneath spruce extended through 75 days (cf. **Fig. 31**), spruce strongly reduced FRP independent of the stand density. Hence, spruce root systems responded to changes in soil water by strong decrease in FRP during drought years and by increase of FRP during moist years. Root growth dynamics of this kind are regarded as "opportunistic" (Pregitzer *et al*., 1993; Joslin & Wolfe, 1998), and result in large changes in net root production when soil conditions vary from year to year. In summary, since drought during 2003 persisted longer underneath spruce than beech (**Fig. 31**), the different extent of soil water deficit supposedly resulted in contrasting physiological root responses in beech and spruce, i.e. promotion versus inhibition of root growth, respectively. Hence, *hypothesis (i)* formulated in this study (i.e. *drought-induced limitation of C gain by the foliage results in stimulation of compensatory fine-root production*) was corroborated in case of beech, and was rejected in case of spruce, when plants were growing under $1xO_3$.

In the mixed sub-plots, beech tended to produce more fine roots during dry 2003 at the parts of the stand with lower tree dencity. During drought, spruce rather produced fine-roots at dense stand parts, where water flux via stem flow into the soil apparently was enhanced because of the close proximity to beech trees. In summary, the structure of the mixed sub-plots allowed beech and especially spruce trees to sustain fine-root production during harsh drought conditions in 2003. In this way, the below-ground response of competing plants to water limitation was shown to depend on the type of competition, thus corroborating *hypothesis (v)* for beech and spruce. In addition, the conclusion of Pretzsch (2004) is supported that mixed stands are rather tolerant to changing site conditions and resilient upon natural disturbances.

4.2.4 Drought effects on soil respiration components

4.2.4.1 Partitioning of total soil respiration (SR_t) under spruce and beech as affected by drought

During summer of 2003, when ASW was limited (75 days in spruce and 45 days in beech), both SR_t and SR_h declined under beech and spruce, despite rising soil temperature. Similar drought response of SR_t is reported from Mediterranean mixed oak forest (Rey *et al*., 2002). In the present study, the "autotrophic" soil respiration accounted for 41 to 58% of SR_t under beech, and for 25 to 60% of SR_t under spruce which falls within the range of 22 to 70% as

reported for European forests (Epron *et al*., 1999; Janssens *et al*., 2001 & 2003). Underneath beech, "autotrophic" soil respiration was reduced by drought to the same extent as was "heterotrophic" soil respiration, since in 2003 no significant changes in the partitioning of SR_t occurred as compared to humid 2002/2004. Annual FRP under beech remained unchanged by drought; however, indications of enhanced WUE during the CO_2 assimilation period of 2003 were present (**Fig. 28**; cf. section 3.3). In woody plants, conductivity for water flow from roots to leaves is approximated by the Hagen-Poiseuille law, i.e. proportionality to the fourth power of the vessel diameter in the xylem (Lambers *et al*., 1998). Near 5% of the vessels in the beech coarse roots (0.8 to 2 cm in diameter) have diameters between 50 and 100 µm, and were responsible for more than 50% of the hydraulic conductance (Nikolova, unpubl.). Such large vessels are successful for rapid water transport upon re-wetting of the soil. On the other hand, large vessels have a high cavitation risk, which needs to be counteracted by sensitivity in stomatal regulation to plant water status. At "Kranzberger Forst", pre-dawn water potential dropped in beech to extraordinarily low -1.4 MPa during 2003 (Löw *et al*., 2006), although the daily minimum water potential did not fall below -2.0 MPa (consistent with general observations in temperate forests; Larcher, 1994). This lower limit in minimum water potential suggests that stomatal closure prevents cavitation (Tyree & Zimmermann, 2002) and – as a consequence – injury to photosynthesis. Högberg *et al*. (2002) reported photosynthate to drive root respiration, which contributes to a large extent to the autotrophic soil respiration (SR_a). In addition to the sustained temperature sensitivity of root respiration (RR) during drought (cf. the temperature response of RR in LR_{prim}, **Fig. 37**), the correlation of RR^{10}_{I} (i.e. the respiration rate of individual rootlets assessed at a standard temperature of 10°C) with the N content of the rootlets was high at all sampling dates during 2003. The high correlation to N level confirmed the high metabolic activity of beech fine-roots during drought (Burton *et al*., 2002) and simultaneously assured sustained contribution of SR_a to SR_t.

Under spruce, contrary to beech, the contribution of SR_a to SR_t was significantly reduced during 2003 as compared to 2002/2004, which indicates a lower metabolic activity of roots under drought conditions relative to that of free-living soil micro-organisms (i.e. SR_h). Above-ground, pre-down water potential measured in spruce (Löw, pers. comm.) dropped to extraordinarily low -1.6 MPa during 2003, although the daily minimum water potential did not fall below -2.0 MPa (similar values were reported for beech; Löw *et al*., 2006). Other evergreen coniferous species (*Abies lasiocarpa* and *Juniperus monosperma*) were reported by Pockman *et al*. (1995) to induce cavitation only at -3.5 MPa due to their small tracheid diameters. Similarly, in spruce coarse roots more than 90% of the vessels had diameter less than 30 µm (Nikolova, unpubl.). Vessels with narrow diameters have the disadvantage of low hydraulic conductance but are less vulnerable to drought and freezing-induced cavitation (Lambers *et al*., 1998). According to the wood density of spruce (i.e. 450 kg m^{-3}; Fromm *et*

al., 2001) stem water storage of spruce is estimated to make up about 50% of the fresh biomass (Lambers *et al*., 1998). In contrast to beech, the lower limit in daily minimum water potential of -2.0 MPa suggests in spruce that stomatal closure and partial dormancy of fine-roots may serve rather to decrease water loss from tree water pool in stems and coarse roots than to prevent the vessels with relatively small diameters from cavitation. Similarly as in beech, stomatal closure in spruce can limit the photosynthesis. Since photosynthate drive root respiration (Högberg *et al*., 2002; Bond-Lamberty *et al*., 2004), the decline of SR_a underneath spruce in 2003 was probably caused by reduced belowground C allocation rather than soil properties (e.g. T_s, SWC). This is confirmed by a tree girdling experiment (Högberg *et al*., 2001) as the seasonal pattern of photosynthesis was more important than soil temperature in determining „root-mycorrhizal" respiration (i.e. SR_a). Obviously, the absence of a temperature response in SR_a during May-June 2003 may be interpreted as a decline of RR to the level of maintenance respiration, required to maintain the existing fine-root biomass. In contrast to beech, spruce fine-roots displayed weak correlation of RR^{10}_I during August of 2003 with the N level, apparently indicating dormancy during this month. In addition, prolonged drought may cause higher mortality within the shallow fine-root system in spruce, as shown for peach and grape fine roots growing closely underneath the soil surface (Wells *et al*., 2002; Anderson *et al*., 2003). Restricted root respiration and enhanced fine-root mortality were reflected during 2003 by hysteresis in the time course of the temperature response of SR_a underneath spruce (**Fig. 33**).

4.2.4.2 Parameterisation for SR_a and SR_h modelling

The exponential response function of SR_a and SR_h to T_s, and the higher temperature sensitivity of SR_a compared to SR_h (as expressed by Q_{10}) which determined modelling in both tree species corroborated *hypothesis (iv)*, i.e. *that SR_a and SR_h differ in their response to changing T_s and SWC, with higher sensitivity reflected in SR_a*. This is consistent with findings of Epron *et al*. (2001) that indicate higher Q_{10} in SR_a than SR_h, probably reflecting the seasonality in shoot and root metabolic activities (Boone *et al*., 1998; Davidson *et al*., 2006). In spruce, the relationship between T_s and SR_a changed during 2003: SR_a at 10°C (i.e. coefficient *a*) declined significantly between June and October 2003, while the T_s sensitivity of SR_a (i.e. coefficient *b*) remained unchanged in relation to 2002/2004. The reduction in SR_a at 10° C was apparently related to the reduction in standing fine-root biomass that occurred at the same time. In contrast, SR_a in beech did not differ at 10°C between humid and dry conditions, being consistent with sustained root standing biomass, while the sensitivity of SR_a to T_s decreased under drought. The difference in species-specific T_s/SR_a response relationships suggested physiological plasticity in beech fine roots compared to morphological plasticity via root loss in spruce (Hodge, 2004).

The moisture dependence of SR_a^{10} was more pronounced in spruce than beech across the entire range of ASW. However, the bimodal relationship between SR_h^{10} and ASW was species-independent, and the break-points of these relationships differed between beech and spruce. Examining the effects of moisture regimes in soils of different texture on the microbial activity, Schjønning *et al.*, (2003) showed that CO_2 evolution was stimulated by increasing SWC, reaching a plateau with the break-point being determined by soil porosity, i.e. CO_2 evolution was found to increase by high porosity. "Kranzberger Forst", porosity within the uppermost 10 cm of the soil was higher underneath beech than spruce (0.57 m^3 m^{-3} and 0.45 m^3 m^{-3}, respectively; after Schuhbäck, 2004). Hence, the species-related break-points found in the present study were consistent with differences in soil porosity.

The correction factor *L* (accounting for respiratory stimulation upon autumnal leaf litter production) enhanced modelling precision of SR_a and SR_h by 6 and 8%, respectively. As soil micro-organisms are typically C-limited, they rapidly respond to changing supply of decomposable substrate, unless limited by other factors (Zak *et al.*, 1994; Ekblad & Nordgren, 2002). Also, incorporation of soluble C and nutrients from freshly fallen leaf litter into the soil may promote the growth of fine roots and ectomycorrhizal mycelium in beech, altering SR_a (cf. Wallander *et al.*, 2001).

4.2.4.3 Intra-annual variation in SR_a and SR_h

SR_t underneath beech (789 to 945 g C m^{-2} a^{-1}) and spruce (613 to 928 g C m^{-2} a^{-1}) were within the range reported from European forests (760 $\pm$ 340 g C m^{-2} a^{-1}, Janssens *et al.*, 2001). Although broad-leaved deciduous and coniferous forests differ substantially in their nutrient-cycling characteristics, Raich & Potter (1995) did not find apparent differences with respect to CO_2 efflux. This was consistent with the findings at "Kranzberger Forst" in water non-limited 2002. The drought of 2003, however, reduced SR_t in both species, despite similar mean annual T_s throughout the three years (cf. **Tab. 9**). By this, *hypothesis (iii)* that *drought reduces the CO_2 efflux from the soil* was confirmed in both beech and spruce soils. The relation between SR_a, SR_h, and annual means of P_{an}, T_{air}, TGR (total global radiation) and stand characteristics (e.g. annual stem diameter increment = SDI; Wipfler, pers. comm.) indicated that only SR_a was dependent on tree species (**Fig. 57**). In beech, the decline of SR_a in 2003 by about 15% was paralleled by a 35% decrease in SDI, while FRP stayed unchanged relative to levels in the humid 2002. In spruce, reductions in SR_a and SDI were more pronounced in 2003 (50 and 65%, respectively), and FRP was reduced by 70 %, relative to humid conditions compared with beech. This decline in spruce supports the hypothesis of Grime (1979; after Hodge, 2004) that morphological adjustments are more costly than physiological adjustments in response to stress, such that only beech was able to recover in SR_a and SDI to pre-drought levels during 2004. The results indicate that mixed

forests are buffered against risks of climate change, if the involved species possess contrasting strategies for coping with drought.

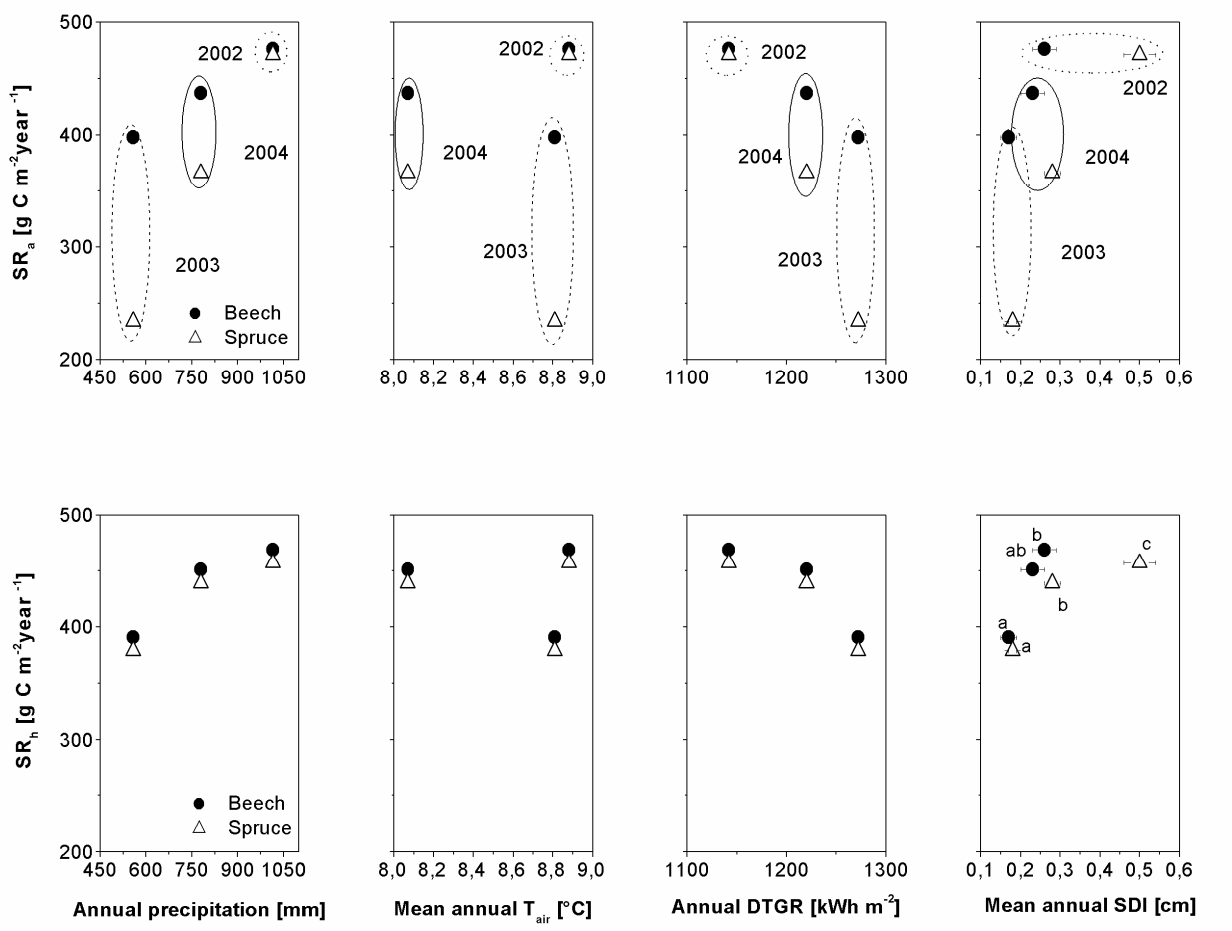

Figure 57: Relationship between annual SR_a and SR_h (assessed for each experimental year) and annual sum of precipitation (P_{an}, mm), mean annual air temperature (T_{air}, °C), annual sum of total global radiation (TGR, kWh m^{-2}) and mean annual stem diameter increment (SDI, cm) in beech (n=64) and spruce (n=54); means of SDI ± standard error, significance level at $p < 0.05$ (*t*-test).

4.3 Comparison of beech and spruce responses to enhanced ozone concentration

Given the extensive research on the O_3 effects on above-ground plant parts (Matyssek & Innes, 1999; Grulke *et al.*, 2003; Nunn *et al.*, 2005a, b; Wipfler *et al.*, 2005; Matyssek *et al.*, 2006), and, on the other hand, the scarce quantitative knowledge on below-ground changes in response to O_3 (reviewed in Andersen, 2003), the current part of the discussion analyzes the belowground responsiveness of competing adult beech and spruce trees to O_3 stress under forest stand conditions. During 2002 and 2003, a spectrum of physiological and morphological parameters of the fine root system (cf. **Fig.13**) was assessed in both tree

species under the experimentally enhanced ($2xO_3$) and ambient ozone regime ($1xO_3$ = control). In view of the exceptionally dry year of 2003 in Central Europe (Raspe *et al.*, 2004), selected parameters reflect the O_3/drought interactions in morphological and ecophysiological responses of the fine roots of adult beech and spruce trees (**Tab. 22**).

Table 22: Changes in the beech and spruce fine-root parameters observed to the factors "enhanced ozone concentration" (O_3), "water limitation" (drought), and to their interaction (O_3 + drought). Arrows indicate increase (↑) or decrease (↓) of each parameter in response to the respective scenario. Significance levels at: (*) $p \leq 0.1$; * $p \leq 0.05$; ** $p \leq 0.01$; n.t. = not tested.

Root parameter	Sub-plots					
	mono			mixed		
	O_3	drought	O_3+ drought	O_3	drought	O_3+ drought
beech						
Fine-root production; mg l^{-1}	↑*	↑*	↑(*)	↑*	~	~
Root turnover	↑ (n.t.)	↑ (n.t.)	↑ (n.t.)	↑ (n.t.)	↑ (n.t.)	↓ (n.t.)
Root life span	↓ (n.t.)	↓ (n.t.)	↓ (n.t.)	↓ (n.t.)	↓ (n.t.)	↑ (n.t.)
$\delta^{13}C$ in newly formed fine-roots	↑***	↑*	~	~	~	~
spruce						
Fine-root production	~	↓*	↓*	↑*	~	~
Root turnover	↑ (n.t.)	↓ (n.t.)	↓ (n.t.)	↑ (n.t.)	~	↓ (n.t.)
Root life span	↓ (n.t.)	↑ (n.t.)	↑ (n.t.)	↓ (n.t.)	~	↑ (n.t.)
$\delta^{13}C$ in newly formed fine-roots	~	↑*	~	~	~	~

4.3.1 Beech trees under intraspecific competition

The present study shows stimulation of fine-root production in beech under $2xO_3$ during the third year of fumigation (i.e. water non-limited 2002; **Tab. 22**) without any changes in the assessed morphological (i.e. SRA; cf. **Fig. 40** & **Tab. 11A** & **11B**), physiological (i.e. RR; cf. **Fig. 36**) or biochemical (i.e. NSC concentration; cf. **Fig. 43**) parameters due to ozone. Since SWC was found to be lower at $2xO_3$ than $1xO_3$ (cf. section 3.2.3), the compensatory enhancement of FRP in beech under $2xO_3$ (**Tab. 4** & **Fig. 24**) perhaps resulted from an induced shift in allocation under O_3 stress and/or dryer soil conditions. FRP in beech under "$1xO_3$" and "$2xO_3$" was similar during the year prior to the start of the free-air O_3-fumigation (i.e. 1999) and during 2000 (the first year of fumigation; data according to Blaschke, pers. comm.). Moreover, $\delta^{13}C$ in newly produced beech fine-roots during 1999 did not differ between $1xO_3$ and $2xO_3$ (**Fig. 28**). During the third year of fumigation (i.e. 2002), $\delta^{13}C$ in fine roots produced under $2xO_3$ was increased compared to the controls which can result from

raised WUE (i.e. through lowered g_s) or increased phosphoenol pyruvate carboxylase (PEPC) activity in fumigated beech trees (Matyssek *et al*., 1992; Saurer *et al*., 1995). Another possible source of variation is that $\delta^{13}C$ is higher at the bottom than at the top of the canopy due to the contribution of ^{13}C-depleted CO_2 from soil respiration (Medina & Klinge, 1983; cf. Lambers *et al*., 1998). For beech trees growing at "Kranzberger Forst", Löw *et al*., (2006) reported the levels of g_s to be significantly reduced (under water non-limited conditions during 2004) in $2xO_3$ compared to $1xO_3$ regime, which was interpreted as a result of reduced cell wall lignification of the stomata or disturbed osmotic control of the guard cells upon membrane impairment. In addition, ozone had a negative effect on PEPC activity in sun leaves under $2xO_3$ (Löw *et al*., 2005) which should rather decrease than increase $\delta^{13}C$, as found in this study. Therefore, the elevated $\delta^{13}C$ in fine-roots rather reflected raised WUE in fumigated beech trees than alteration in the enzymatic activity of C uptake.

The stimulated FRP which was found in beech at $2xO_3$ during 2002 (i.e. the third year of fumigation) can result from nutrient or water depletion that occurs as a result of changed root biomass under O_3 stress (Andersen, 2003), or can be driven by phytohormones (Lambers *et al*., 1998). Grebenc *et al*. (2005) report from the same experimental site a doubled total cytokinin concentration in fine root samples of fumigated trees, also higher ectomycorrhizal diversity and higher total number of mycorrhizal fine root tips. All these findings correspond to the higher turnover of fine roots reported in this study. In addition, enhanced fine-root turnover and reduced longevity of fine-roots accompanied the stimulated fine-root growth in beech under $2xO_3$. Such changes can alter rhizodeposition and nutrient and soil carbon cycling under O_3-fumigated beech trees. The ozone-induced increase in fine-root turnover (near 2.5 times relative to the control sub-plot) leads to increased N release due to an increasing amount of dying roots. Based on ^{15}N-tracer experiments in forests under temperate climate, Gebauer & Ehleringer (2000) pointed out that broadleaf stands show higher nitrification rates and can utilize a greater fraction of the throughfall N deposition compared to coniferous forests. Broadleaf stands also show a considerably higher nitrate assimilation capacity and faster transport of the N to above-ground compartments. This finding indicates that the higher N release due to increase in below-ground C allocation and simultaneously enhanced fine-root turnover may result in faster internal cycling of N in O_3-exposed beech trees. Similarly, in their conceptual model for assessing both singular and combined effects on plants raised under various nutrient supplies and O_3 regimes, Greitner & Winner (1989) found a shift in optimum nutrition (i.e. N) for growth of *Salix nigra* to high supply as O_3 concentrations increased. Nitrogen can be used for growth but also for synthesis of secondary metabolites or repair processes in response to ozone (Kytoviita *et al*., 2001). In addition, greater N input into the soil may increase rates of decomposition by altering the activity of free-living soil micro-organisms (Andersen, 2003) and accelerate the

mineralization process. In summary, the capacity to ensure sufficient nutrient supply for faster internal cycling via enhanced C allocation into fine-roots may be the strategy in beech to cope with ozone stress. In support of this finding, based on the data from three experimental years (i.e. 2002, 2003 and 2004), no significant O_3 effect on stem diameter increment (considered as a stress sensitive variable; Dittmar *et al.*, 2003) was detected in beech trees (Wipfler *et al.*, 2005).

In general, ozone is known to alter the source-sink balance in plants, resulting initially in carbon retention in shoots and decreased carbon allocation below-ground (Matyssek *et al.*, 1992; Matyssek & Sandermann, 2003; Andersen, 2003). The study of Löw *et al.* (2006) conducted at the same experimental trees, detected significantly reduced net CO_2 uptake (under water non-limited conditions) under $2xO_3$, indicating limited carbon gain by the foliage, as caused by O_3 stress. Hence, *hypothesis (i)* formulated in this study (i.e. *O_3-induced limitation of C gain by the foliage results in stimulation of compensatory fine-root production;* cf. section 4.2.1) was corroborated in the case of beech when growing in monoculture under water non-limited conditions.

During 2003, drought alone or in combination with O_3 (i.e. "O_3+drought") influenced beech fine-root dynamics in a similar way as was found for the ozone impact alone (**Tab. 22**). For beech growing in monoculture, this resulted in corroboration of *hypothesis (i)* in the case of "water limitation" (i.e. *drought-induced limitation of C gain by the foliage results in stimulation of compensatory fine-root production*). However, the ozone effect on $\delta^{13}C$ of newly formed beech fine-roots disappeared under "O_3+drought" which indicated drought to overrule the ozone impact on C uptake. In support of this view, Löw *et al.* (2006) point out (for the same study trees at "Kranzberger Forst") that the difference in g_s between both O_3 regimes vanished during the dry period of 2003.

4.3.2 Spruce trees under intraspecific competition

In spruce fine-roots, no morphological (i.e. SRA; cf. **Fig. 40** & **Tab. 11A** & **11B**), physiological (i.e. RR; cf. **Fig. 36**) or biochemical (i.e. NSC concentration; cf. **Fig. 43**) responses were detected to sensitively respond to O_3. No compensatory fine-root production occurred under $2xO_3$, however RT was moderately enhanced and, respectively, RL was moderately reduced by O_3 during water non-limited 2002 (**Tab. 22**). In addition, $\delta^{13}C$ of newly-formed fine roots in spruce was not altered by O_3, reflecting responsiveness that differed from that in beech.

Since ozone mainly acts at the leaf level upon uptake through stomata into the mesophyll and only indirectly affects other tree organs, stomatal behaviour has a crucial role in regulating O_3 uptake (Matyssek *et al.*, 1995). In twigs of spruce trees fumigated with ozone the irregular and delayed stomatal closure was found to result in a quotient of water uptake to water loss of < 0.5 or lower, depending on the degree of injury (Maier-Maercker & Koch, 1991). The cited study highlights the long-term effects of O_3 pollution as a specific disturbance of plant water relations: The O_3-fumigated needles of spruce showed lower lignification in the walls of the stomatal apparatus, which results in malfunction of the stomata in response to dry air. In the present work, the unchanged $\delta^{13}C$ of newly formed fine-roots in spruce indicate unchanged WUE under $2xO_3$. However, WUE (i.e. $\delta^{13}C$) may stay unchanged, if adjustment between photosynthesis and g_s occur (Lloyd & Faraquhar, 1994), i.e. if photosynthesis in spruce declines in proportion to a decrease in g_s. In general, conifers (except for *Larix*) have lower g_s and photosynthetic rates, and thus lower O_3 uptake rates of O_3 than hardwood trees (Matyssek, 1986). However, based on the data from three experimental years (i.e. 2002, 2003 and 2004; "Kranzberg Forst" site) Wipfler *et al.* (2005) registered negative influence of ozone exposure on SDI (i.e. stem diameter increment) in spruce trees growing under $2xO_3$ (in parallel, SDI of beech trees had remained unaffected). The O_3-induced reduction of stem growth in trees (Karnosky *et al.*, 2001) was found to be mediated by reduction in CO_2 assimilation (Matyssek *et al.*, 1992; Grulke *et al.*, 2002), or lowered C allocation to roots (Grulke *et al.*, 1998) and their symbionts (Kytöviita *et al.*, 2001). At the same time, the C demand of the O_3-exposed leaves can be significantly enhanced for detoxification and repair (Matyssek & Sandermann, 2003) which may require rising N demand in the leaves (Greitner & Winner, 1989; Kytöviita *et al.*, 2001). Since nutrient "foraging" mediated through enhanced root turnover is costly in spruce (cf. section 4.2.2), the increase in N uptake may be achieved in this tree species at unchanged FRP (**Tab. 22**) but increasing uptake surface via enhanced ectomycorrhizal colonization (Smith & Read, 1997). The external mycelium of mycorrhizae was found to be the dominant pathway through which C entered the soil organic matter (SOM) pool even exceeding the input via leaf litter and fine-root turnover (Godbold *et al.*, 2006), being a significant C sink in the tree. For spruce trees growing in mono-culture the O_3-induced decrease in SDI (Wipfler *et al.*, 2005) may relate rather to the enhanced C costs for the root symbiotic partner (i.e. enhanced C investment into structure and maintenance of such structure) than to the enhanced C costs for the fine-roots itself. However, the present study was concentrated on the analysis of O_3-induced reactions in the fine-root system of trees and not in fine-root symbiotic associations. The results indicate in spruce that no compensatory fine-root production occurred under $2xO_3$, thus rejecting *hypothesis (i)* for spruce growing in mono-culture under water non-limited conditions.

During 2003, drought induced in spruce responses contrasting to those caused by ozone (**Tab. 22**). Consistent with the drought-provoked reactions described on the levels of "fine-root category" and "individual rootlet" (see section 4.2.2), parameters at the "stand level" (**Tab. 22**) indicated acclimation of the root system (dormancy) and – as a consequence - lowered nutrient cycling in the soil as during drought. Remarkably, the drought effect on $\delta^{13}C$ of newly formed fine-roots during 2003 was smaller in spruces growing under $2xO_3$ than $1xO_3$ (**Fig. 28**). Since ozone can induce defence reactions in leaves similar to those caused by drought (Matyssek *et al*., 2006), the observed marginal changes in WUE of the spruce trees growing at $2xO_3$ to drought may have resulted from "hardening" of the evergreen leaves caused by the 3-year-long chronic ozone fumigation.

4.3.3 Beech and spruce trees under interspecific competition

In comparison to fine-root reactions of beech and spruce trees from monocultures, only spruce from mixed sub-plots showed reaction to ozone under water non-limited conditions (enhanced FRP in 2002 under $2xO_3$; **Tab. 22**). Fine-root parameters of beech from mixed sub-plots to O_3 were similar to those in response to drought; however no compensatory FRP was detectable under water limitation. Remarkably, spruces growing in mixture, showed no significant response to drought in any of the studied parameters. One possible explanation may be the positive influence of beech on water and nutrient cycling in mixed stands, however the extent of this influence is strongly site-specific (Rothe *et al*., 2002; Armbruster *et al*., 2004). Apparently spruce which is more efficient in water uptake within the upper soil horizons relative to beech (see efficiency ratio of space exploitation; **Fig. 54**), gained rain water (supplied by short showers during the growing season of 2003; **Fig. 21**) before it could infiltrate into deeper horizons rooted mainly by beech. In addition, the organic layer which is thicker and more hydrophobic due to admixed needles at mixed sub-plots (Schuhbäck, 2004) may reduce water inflow into the soil due to enhanced evaporation. Such an evaporative loss is high especially after short rain events during hot summer days. Severity of drought can arise for beech trees growing in mixture with spruce; in contrast, spruce seems to profit from neighbouring beech.

Beech and spruce trees growing in mixture at "drought+O_3" conditions reacted with lower root turnover and sustained FRP (**Tab. 22**), indicating in both tree species the synergism of both factors to lower internal cycling of nutrients (i.e. N). Since N has a crucial role in detoxification and defence processes, it can be hypothesised that the prolongation of the "drought+O_3" period may result in exhaustion of stress capacity in trees of mixed sub-plots. Under predicted "global change" scenarios (i.e. regional increase of drought, enhanced

tropospheric ozone concentrations, altered precipitation pattern; Ciais *et al*., 2005) the interspecific competition of beech and spruce has the potential to arise the severity of the complex unfavourable conditions (i.e. "drought+O_3").

4.3.4 Total soil respiration

During both study years (i.e. 2002 and 2003), 2xO_3 significantly increased total soil respiration rate (SR_t) independent of the tree species or type of competition (**Fig. 29**), thus confirming *hypothesis (iii) (i.e. ozone exposure enhanced the CO_2 efflux from the soil)* and rejecting *hypothesis (v)* (*i.e. the responses of beech and spruce plants to O_3 stress depend on type of competition).* In addition, fine-root density did not appear to affect the response of SR_t to ozone in any sub-plot. In the free-air CO_2 and O_3 enrichment experiment with aspen Pregitzer *et al*. (2006) found the greatest rates of SR_t to occur in the interaction treatment (CO_2+O_3), although SR_t was lowest at elevated O_3. Similarly, O_3 exposure was found to significantly disrupt CO_2 release from soil and roots of ponderosa pine seedlings (Scagel & Andersen, 1997). In a supplementary study Andersen & Scagel (1997) reported on the nutrient availability to alter the belowground respiratory response to O_3, such that the response to O_3 was greatest at low nutrient supply. Since SR_a accounted for 41 to 58% of SR_t under beech and for 25 to 60% of SR_t under spruce (**Fig. 30**), changes in root biomass and activity (mirrored by their respiration rates and allocated assimilates; Högberg *et al*. 2002) may be expected to be reflected in SR_t. However, in the present study, root biomass was enhanced under 2xO_3 only in beech, whereas RR and NSC concentrations in fine roots of beech and spruce appeared to stay unaffected by O_3 (**Figs. 36** & **43**). The latter findings are in conflict with observations of decreased RR and NSC by O_3 (Grulke *et al*., 2001; Andersen, 2003). The positive effect of O_3 on SR_t detected in the present experiment may be explained by stimulation of the rhizospheric activity, e.g. changes in the ectomycorrhizal network (ECM; see for beech in Grebenc *et al*., 2005) and/or stimulation of free-living soil decomposers. Such organisms use root exudates or plant detritus as C source (Coleman *et al*., 2004). Since their activity is typically C-limited, they rapidly respond to changing supply of decomposable substrate, unless limited by other factors (Zak *et al*., 1994; Ekblad & Nordgren, 2002). In a short-term $^{14}CO_2$ pulse and chase experiments in wheat seedlings, McCrady & Andersen (2000) found out that the increase in soluble root exudation under O_3 resulted in enhanced microbial activity in the rhizosphere. At "Kranzberger Forst" Grebenc *et al.* (2005) reported for beech on enhanced diversity of ECM fungi and higher total number of mycorrhizal fine roots in the O_3-fumigated plots as compared to the control. This shift in the mycorrhizal community was supposed to induce shift in fine root turnover (Grebenc *et al*., 2005), which was supported in the present study for beech and spruce at mono and mixed

sub-plots under 2xO_3 (**Tab. 22**). Enhanced decomposition of dead fine roots and mycorrhizal network was found to stimulate the growth of new fine roots and ectomycorrhizal mycelium (Wallander *et al*., 2001) which apparently led to enhanced SR_t at O_3-fumigated sub-plots. In addition, ozone can cause high nutrient content in leaf litter via incomplete N remobilization from the foliage (Matyssek *et al*., 1993) which may result also in increased rates of decomposition. In summary, the pathway through which O_3 alters carbon flux to/from soil may be enhanced rhizodeposition by: (1) increased root exudation and microbial activity in the rhizosphere along active root apices (similarly found in a phytotrone experiment with beech/spruce mixed cultures; cf. Pritsch *et al*., 2005), (2) enhanced diversity of ECM, enlarged mycorrhizal network and turnover (Grebenc *et al*., 2005), and (3) enhanced fine-root production and turnover (present study). These below-ground responses may increase the supply of substrates, and, thus, the respiration activity of soil decomposers.

Statistical analysis (**Fig. 29**) showed a significant effect of the "year" (factor "year" reflects the effect of climate conditions on SR_t during the experimental years 2002, water non-limited, or 2003, dry) on SR_t only in beech at the mono sub-plot. "Year" tended to influence SR_t underneath spruce at the mono sub-plot, and showed no effect on SR_t in mixture. However, the O_3 impact on SR_t was independent of the climatic differences between both study years and remains the primary factor which determined enhanced SR_t even during the harsh drought of 2003. In the context of "global change" scenarios predicting increase of O_3 levels, the results from the case study in "Kranzberger Forst" indicate that forests with beech and spruce, independent of the type of competition, have the capacity to enhance soil C efflux into the atmosphere.

4.4 Belowground efficiency ratios of tree competitiveness

Quantitative assessments of the space-related *cost/benefit* relationships such as *space occupation, space exploitation* and *"running costs"* (cf. section 1.1.3 & Grams *et al*., 2002) were used as measures of the below-ground competitive ability of adult beech and spruce forest trees. The present study focuses on space occupation and water uptake which occurs along resource gradients within soil space (as assessed by organic and mineral soil sub-samples; cf. section 2.7). Free-air ozone fumigation at the crown level was used in the present study as an experimental tool to provoke the belowground responsiveness of both competitors in allocation to disturbance under closed stand canopy conditions.

4.4.1 Beech vs. spruce

Independent of the type of competition, the competitive below-ground advantage of beech within the uppermost 20 cm of the soil was indicated by higher efficiency of space occupation (BSO: occupied soil volume per C investment into mean standing biomass). When focusing on the efficiency ratios along resource gradients within the soil, beech was more efficient in BSO within the organic (O+Ah) soil sub-sample, whereas spruce had higher efficiency of BSO within the mineral B soil sub-sample independent of growing in mixed or mono-culture (**Fig. 53**). The efficiency in below-ground space occupation was determined by the species-specific factor k_c: beech fine roots showed a larger zone of influence (reflected in high factor k_c) within the organic soil sub-sample (O+Ah) compared to spruce, which had larger k_c within the mineral soil sub-sample B (**Tab. 18**). In beech, the difference in the factor k_c between (O+Ah) and B was found to relate to SRL assessed in fine-roots from both soil sub-samples (**Fig. 52**). Beech occupied the organic soil sub-sample by forming thinner fine roots with higher SRL (i.e. less investment into biomass per unit root length) as compared to the fine-roots from the mineral soil. This shows a morphological adjustment/plasticity in beech fine-roots along the studied resource gradient. Spruce showed differing k_c in both soil sub-samples, but contrasting with beech, displayed unchanged SRL along the soil gradient (**Fig. 52** & **Tab. 18**). Since no morphological adjustment to the resource supply was detected in spruce fine-roots, the enlargement of the “zone of influence” within B (as indicated by higher k_c within this soil sub-sample) probably profited from the higher mycorrizal biomass and its extending network within the mineral soil. This conclusion is supported by the diversity of ECM species (Agerer & Göttlein, 2003) and/or associated soil exploration types that changed from a short to medium-distance range (Baier, 2006). Similar mechanism (i.e. to sustain the occupied soil volume at lower construction costs by means of symbiotic associations) was previously described for spruce as a possible response to drought stress (for more details see section 4.2.2). In summary, the efficiency ratio of BSO indicated *habitat partitioning* in root growth between both tree species. According to Gersani *et al*. (2001) such “ownership” of space allows plants to favour efficiency rather than speed of uptake when developing its root mass, architecture, and uptake kinetics. Similarly, a high degree of segregation (i.e. clustering) was shown for coarse-root systems of beech and spruce by Schmid & Kazda (2005): Regardless of soil property, significantly higher clustering of beech roots suggested higher efficiency in below-ground space acquisition than in spruce.

Within the uppermost 20 cm of the soil, beech showed higher efficiency in space exploitation (BSE: daily mean water uptake per occupied soil volume) relative to spruce. This competitive advantage of beech was found at both mono and mixed sub-plots. Resource uptake, which is the mechanism through which plants influence soil resource availability, can be affected by

the amount and spatial distribution of resource-acquiring organs (i.e. for nutrient ions with low diffusive supply; Raynaud & Leadley 2004), but also by aboveground characteristics, such as transpiration capacity (i.e. in the case that nutrients are primary supplied by mass flow; Schulze *et al*., 1994). When focusing on the efficiency ratio of BSE along resource gradients within the soil, spatial segregation of beech and spruce fine-roots within differing soil sub-samples resulted in decreased competition for water: Spruce was more efficient within the organic (O+Ah), whereas beech was more efficient within the mineral B soil sub-sample. In addition, Bernston (1994) suggests features of root architecture, such as SRL or branching pattern, to substantially determine the exploitation capacity of roots. In beech, high SRL were accompanied by high efficiency in BSO, but low efficiency in BSE, and *vice versa.* In contrast, the conservative morphology of spruce fine-roots (reflected by similar SRL within both soil sub-samples) neither related to changes in BSO nor BSE within the soil profile (**Tab. 19**). Overall, based on the studied fine-root parameters, the present investigation provided evidence in support of the suggestion by Fitter (1991) that it is not possible to derive a simple analytical relationship between root system architecture and resource acquisition due to the complex spatial arrangement of roots within the soil.

Competitive advantage of beech over spruce is not indicated in mono and mixed sub-plots when comparing the efficiency ratios of “running costs” (BRC: occupied soil volume per seasonal fine-root respiration). The reason is the nearly 50% higher species-specific respiration rate in beech than spruce, which led to comparable maintenance costs in both competitors within the uppermost 20 cm of soil, although beech possessed a lower standing fine-root biomass as compared to spruce. This is consistent with similar annual SR_a in beech and spruce (cf. non-limited 2002/2004; **Tab. 6** & **9**). Along the soil profile, the efficiency ratio of BRC displayed a response pattern similar to BSO and contrasting with BSE: Beech occupied more soil volume per unit C invested in respiration within (O+Ah) soil sub-sample, whereas spruce was more efficient within B soil sub-sample.

4.4.2 Ozone impact

Beech was more efficient in BSO and BSE than was spruce at both mono- and mixed sub-plots under $1xO_3$ (**Fig. 56** & **Tab. 20**). However, the disturbance through elevated O_3 enhanced investments of beech into fine-root structure and their maintenance, which led to lowered efficiency of beech in BSO and BRC under $2xO_3$ (BSE was determined at $1xO_3$ only). Spruce, in contrast, showed similar C costs in occupation of below-ground space under both O_3 regimes and types of competition, corroborating – for this species – *hypothesis (ii)* and rejecting *hypothesis (v)*. This indicates, within the soil depth of 20 cm, the competitive advantage of beech over spruce in terms of occupied below-ground space per

unit invested C to vanish under chronic O_3-fumigation independent of the type of competition so that *hypothesis (v)* is rejected in the case of beech. However, calculation of BRC in the present study does not account for the maintenance costs for symbiotic associations in any of both competitors. In beech growing at "Kranzberger Forst", Grebenc *et al.* (2005) found an enhanced diversity of ECM fungi and higher total number of mycorrhizal fine-roots under $2xO_3$. In addition to the stimulated fine-root production under $2xO_3$, the O_3-enhanced activity of the symbiotic associations apparently contributed to the higher CO_2 efflux from soils, which may contribute to the altered BRC of beech at O_3-fumigated sub-plots. Also in spruce, the higher CO_2 soil efflux under $2xO_3$ at unchanged standing fine-root biomass (cf. **Figs. 23** & **29**) appeared to be related to an enhanced mycorrhizal network. Perhaps, ECM associations significantly enhanced the below-ground C costs in spruce under $2xO_3$, mitigating the efficiency ratio of "running costs". In addition, Yanai *et al.* (1995) pointed out the mycorrhizal hyphae to be more efficient than fine roots in terms of expenditure of C in the nutrients uptake from the soil. Hence, the extension of the below-ground analysis of space-related efficiency ratios towards costs/benefit relationships that account for the symbiotic associations appears to be promising, as additional and profound understanding of below-ground processes can be acquired, in particular, in view of changing environmental conditions.

4.4.3 Mechanisms of below-ground competition between beech and spruce

Beech and spruce differed in their efficiencies in BSO and BSE with a significant competitive advantage of beech within the uppermost 20 cm of the soil. This soil volume represents the "biological space" richest in nutrients and water for both competitors (cf. McConnaughay & Bazzaz, 1991) being characterized, in addition, by high spatial and temporal variability (i.e. "patchy nutrient supply"; Bliss *et al.*, 2002). Resource capturing and its relation to below-ground production may influence the way of plant interaction (i.e. competition) in patchy environments (O'Brien *et al.*, 2005). Fine-roots of beech and spruce showed different structural responses to variable environment: *precision in nutrient foraging* (i.e. flexible response to local water- and nutrient-rich soil patches; cf. section 4.2.1) was detected in beech, whereas spruce showed changes *in size* (i.e. in the spatial extension of a fine root system; cf. section 4.2.2). As described by Volder *et al.* (2004), Leuschner *et al.* (2001) and Eissenstat (2002), the present study showed root foraging in beech (and thus competitive advantage in BSO) to be related to high fine-root production and turnover. The higher mortality of beech roots possibly gave belowground space free for re-occupancy (i.e. "free biological space"). At mixed sub-plots, such zones enriched in soil resources can theoretically be re-occupied by both neighbours, since the three dimensions of a nutrient

patch render the associated space less likely to be claimed exclusively by one individual only (Blair, 2001). Huang & Eissenstat (2000) found the species with greater specific fine-root length (SRL) or finer roots to have more rapid root proliferation in response to enriched nutrients than those with high SRL or thicker roots. The present study reports on higher SRL in beech compared to spruce, independent of the type of competition, resource gradients or O_3 regime (**Fig. 52**). This suggests beech to profit efficiently from the enhanced mortality of own fine-roots in terms of rapid re-occupancy of the "abandoned" space via development of ephemeral fine-roots with high SRL. In addition, beech showed nearly two times higher SRL within (O+Ah) compared to B. This morphological adjustment of beech fine-roots apparently dominates over physiological aspects (i.e. high respiration rates) in competing for soil space, and resulted in higher efficiency of space occupation in relation to the morphologically more conservative spruce. As a result, *habitat partitioning* in root growth occurs between both competitors, which apparently reduce competition for the soil resources present within below-ground space. Findings support the statement of Casper & Jackson (1997) that competition for soil resources is *symmetric* if competing plants are able to take up soil resources from different horizons (i.e. due to *habitat partitioning*). In summary, data from the present study appear to provide evidence for *symmetric* competition below-ground. At "Kranzberger Forst", a tendency of *habitat partitioning* within the whole rooted zone (0-90 cm soil depth) was denoted by Blaschke (unpubl.). He found a shift towards a more superficially distributed fine-root system of spruce in mixture with beech, which indicates a higher below-ground competitive ability of beech compared to spruce in this stand. Similarly, Schmid & Kazda (2002) found coarse and fine roots of spruce to show shifts towards the upper soil layers in mixture with beech in an ageing mixed forest in Austria. In view of such findings, spruce appears to be at higher risk than beech, regarding *hazards* such as prolonged drought or wind-throw. Probably, the *competitive exclusion* from a given "biological space" may represent the below-ground mechanism that enables beech to out-compete spruce on a long-term scale.

Explanatory power of space-related cost/benefit relationships for below-ground studies of competitiveness may be assessed by comparison with conventional approaches. Many studies have focused on a subset of size-independent root architectural and morphological features (i.e. topology, inter-root distances, root tip lengths, specific fine-root length; cf. Bernston 1994; Farley & Fitter, 1999) for examining such aspects of root architecture on root efficiency in space sequestration (cf. Kozovits *et al.*, 2005a) or soil exploitation (cf. Fitter *et al.*, 1991). Other studies examined the role of size variations in the root system such as total root length (Hodge *et al.*, 2000), root production and abundance (Leuschner *et al.*, 2001; Hodge *et al.*, 2000), root lifespan (Eissenstat 2002) on the below-ground competitive ability of plants. In addition, changes in root physiology with root age were found to strongly

influence the acquisition of water and nutrients, affecting root efficiency and competitive effectiveness of plants (Volder *et al*., 2004). Recently, a phytotron study was conducted to investigate the intra and inter-specific competitive behaviour of juvenile beech and spruce trees (Kozovits *et al*., 2005a, b) using fine-root length as a one-dimensional substitute of estimating occupied soil volume. The below-ground space sequestration (i.e. the "structural costs" assessed as the fine-root length per unit of biomass invested into fine roots) was then assessed by comparing SRL of fine-roots between beech and spruce. In contrast to the present study which found SRL to be independent of the type of competition in both tree species, beech plants from the phytotrones showed morphological adjustment below-ground in the presence of spruce, i.e. enhancement of SRL in mixed compared to monocultures. The higher SRL of beech was interpreted as compensation for its lowered biomass per unit of soil volume in mixed culture. Conversely, spruce plants from the phytotrones did not show significant differences in SRL between types of competition, which is consistent with the present study on adult forest trees. In addition, the presence of spruce in mixed culture was supposed to decrease the amount of nutrients available for beech. Overall, Kozovits *et al*. (2005a, b) concluded young beech from the phytotron study to be the weaker competitor for below-ground resources. This conclusion contrasts with the findings from the present field study, where beech turned out to be more efficient in below-ground space occupation than spruce. However, such discrepancy in both studies may be related to the different ontogenetic stage (i.e. young vs. adult trees) and/or different experimental conditions.

Explanatory power of space-related cost/benefit relationships in support of below-ground studies of competitiveness was assessed also by comparison with the efficiency ratios defined previously for above-ground structures. In the study conducted at "Kranzberger Forst" on the same experimental trees, Reiter *et al*. (2005) concluded above-ground competitiveness of both competitors to be determined by different strategies of space sequestration, whereas space exploitation and "running costs" of transpiration and respiration of the above-ground structures were similar in beech and spruce. In addition, the physical interaction of swaying tree crowns in both tree species resulted in formation of crown gaps. Since the relative annual increment of crown volume was larger in sun branches of beech than spruce, the formation of crown gaps was considered to be advantageous in beech, as trees of the latter species are able to more rapidly re-conquer abandoned canopy space. The present study demonstrated below-ground interactions between adult beech and spruce trees to be controlled by principles similar to those found above-ground so that *hypothesis (vi)* is corroborated *(i.e. below-ground competitiveness of adult beech and spruce trees is determined by similar efficiency ratios as above-ground competitiveness)*. In addition, the competitive success of beech over spruce in the present study was decided by the

efficiency and different strategies of below-ground space occupation, hence confirming the above-ground findings of Reiter *et al*. (2005) also for below-ground processes.

5 CONCLUSIONS

Under 1xO_3, beech was the more successful competitor below-ground relative to spruce. The success of beech was determined by the efficiency of space occupation (BSO), hence confirming consistency with the above-ground findings of Reiter *et al*. (2005). The spatial segregation of beech and spruce fine-roots within differing soil sub-samples (i.e. the habitat partitioning in root growth between both competitors; cf. section 3.11.2) was interpreted as a result of symmetric below-ground competition of beech and spruce trees (cf. section 1.2). Competitive advantage of beech over spruce is not indicated in mono and mixed sub-plots when comparing the efficiency ratios of "running costs" (BRC). The reason is the nearly 50% higher species-specific fine-root respiration rate in beech than spruce, which led to comparable maintenance costs in both competitors, although beech possessed a lower standing fine-root biomass as compared to spruce.

When focusing on the efficiency ratio of space exploitation (BSE) along resource gradients within the soil, the habitat partitioning in root growth between both competitors resulted in different soil exploitation strategies: Spruce was more efficient within the organic, whereas beech was more efficient within the mineral soil sub-sample. However, such a habitat partitioning may result, on a long-term scale, in a shift towards a more superficially distributed fine-root system of spruce in mixture with beech. Since the species with deeper root systems are generally better adapted to dry climatic conditions than shallow-rooted species (Caldwell & Richards, 1986), spruce growing in mixture with beech appears to be at higher risk than beech at prolonged drought or regarding hazards like wind-throw. Such a "competitive exclusion" via shifting the spruce fine-root system from mineral soil into more "risky" organic soil was supposed to represent the below-ground mechanism that enables beech to out-compete spruce in natural mixed forests on a long-term scale.

The extent of drought during 2003 persisted longer underneath mono-specific spruce sub-plots than under mono-specific beech sub-plots, which resulted in contrasting physiological root responses, i.e. promotion (in beech) versus inhibition (in spruce) of fine-root growth. When growing in mixture, beech and especially spruce trees showed sustained fine-root production during harsh drought conditions in 2003. This apparently resulted from the different above- and belowground tree architecture (Schume *et al*., 2003) and physiological properties (i.e. transpiration rates; Heitz *et al*., 2000) of the two species. It is concluded that,

on a short-term scale, beech/spruce managed forests (e.g. “Kranzberger Forst”) may be buffered against risks of drought.

The competitive advantage of beech over spruce in BSO was found to vanish under chronic enhanced O_3 stress (i.e. during water non-limited 2002) independent of the type of competition. However, no change in stem diameter increment (SDI) of beech trees was detected under $2xO_3$ (SDI data according Wipfler *et al*., 2005). The capacity of beech trees to maintain fine-root system with enhanced turnover and thus, to ensure sufficient nutrient supply for faster internal cycling, was proposed to be the strategy of beech to cope with ozone stress. In spruce, no changes in BSO occurred under $2xO_3$; however, in contrast to beech, enhanced O_3 stress induced decrease in SDI of spruce trees (Wipfler *et al*., 2005). The present study shows that such a decrease in SDI was not related to enhanced C costs of the spruce fine-roots *per se*.

Under $2xO_3$, significantly increased SR_t was detected under both tree species and types of competition. Fine-root density did not appear to affect the response of SR_t to ozone in any tree species or type of competition. The positive effect of O_3 on SR_t detected in the present experiment may be explained by stimulation of the rhizospheric activity, e.g. changes in the ectomycorrhizal network (ECM; see for beech in Grebenc *et al*., 2005) and/or stimulation of free-living soil decomposers (e.g. due to high nutrient content in leaf litter via incomplete N remobilization from the foliage; cf. Matyssek *et al*., 1993). In the context of “global change” scenarios predicting increase of O_3 levels, the results from the case study in “Kranzberger Forst” indicate that forests with beech and spruce, independent of the type of competition, have the capacity to enhance soil C efflux into the atmosphere.

The combination of factors “O_3+drought” (i.e. during 2003 at $2xO_3$) influenced fine-root dynamics in beech in a similar way as found for the O_3 impact alone. However, the ozone effect on $\delta^{13}C$ of newly formed beech fine-roots (as a measure of WUE) disappeared under “O_3+drought” which indicated in this deciduous tree species drought to overrule the ozone impact on C uptake. The combination of factors “O_3+drought” during 2003 induced in spruce responses contrasting with those caused by ozone: Results indicated acclimation of the fine-root system (i.e. via passing into dormancy) and – as a consequence - lowered nutrient cycling in the soil as during drought. The drought effect on $\delta^{13}C$ of newly formed fine-roots during 2003 was smaller in spruces growing under $2xO_3$ than $1xO_3$, which may have resulted from “hardening” of the evergreen leaves caused by the 3-year-long chronic O_3-fumigation. Beech and spruce trees growing in mixture at “drought+O_3” conditions reacted with lower root

turnover, indicating in both tree species the synergism of both factors to lower internal cycling of nutrients.

The high degree of ectomycorrhizal infection in beech and spruce and the different "exploration types" of mycorrhizae may alter the dimension of below-ground space exploitation (Agerer, 2001). The extension of the below-ground analysis of space-related efficiency ratios towards costs/benefit relationships that account for the symbiotic associations is currently being studied in the SFB research program (www.sfb607.de; cf. project B7). In addition, the biomass of the field-grown tree root system is predominantly composed of coarse woody roots (Göttsche, 1972) which are partly permeable for ions and are able to take up considerable amounts of water (Lindenmair, 2004). It appears to be promising to include space-related cost/benefit relationships in future investigations of below-ground plant competitiveness which account for the efficiency of the coarse-root system.

Analysis of below-ground plant competitiveness is provided in this case study at the stand level under closed-canopy conditions of the experimental site "Kranzberger Forst". The competitive below-ground success of beech (i.e. determined by the efficiency of space occupation) was associated with the capacity of the root system to exploit rapidly available resources from soil via constructing fine-roots with high morphological plasticity and high turnover. This finding supports the theory of Grime (1977), that *the competitive success is a reflection of the individual capacity to exploit resources rapidly* (cf. section 1.1.2). Additionally, the present study shows that beech which turned out to be the superior competitor for light (Reiter *et al.*, 2005) was superior competitor also for soil resources (i.e. soil water, determined by the efficiency of space exploitation). This result was in agreement with the statement of Grime (1977) *that superior competitors for light would be equally successful in competing for soil resources* (cf. section 1.1.2). In general, the novel approach of a quantitative, space-related assessment of cost/benefit relationships (i.e. based on space-related "efficiencies" of resource turnover) proved suitable to analyse and clarify the below-ground competitive ability of forest trees. This space-related perspective allowed comparisons of the below-ground competitive ability between species of contrasting seasonal growth dynamics (i.e. deciduous broadleaved *Fagus sylvatica* vs. evergreen coniferous *Picea abies*) under variable spatio-temporal environmental conditions (in terms of soil water availability, tropospheric O_3 regimes and gradients in soil resources across organic and mineral soil horizons). In addition, the differences in fine-root soil exploitation strategies among both tree species shown in this study might be as important as those reported aboveground (Reiter, 2004) to understand the principles of interspecific competition and coexistence of beech and spruce trees under different environments of the Central European forests.

6 APPENDIX

Table A1: Dry weights DW [g] of beech roots from each fine-root category (DW_{LRprim}, DW_{LRsec} and DW_{ShR}; cf. section 2.12), and of the proportion PTR [%] of each of the three fine-root categories in the total rootlet biomass (PTR_{LRprim}, PTR_{LRsec} and PTR_{ShR})

Sampling date	N of the individual rootlet	Weight, g				Proportion, %		
		DW_{LRprim}	DW_{ShR}	DW_{LRsec}	Rootlet	PTR_{LRprim}	PTR_{ShR}	PTR_{LRsec}
09.05.2003	b1	0,149	0,473	0,785	1,407	10,6	33,6	55,8
	b2	0,129	0,432	0,636	1,197	10,7	36,1	53,1
	b3	0,070	0,195	0,134	0,399	17,5	49,0	33,6
	b4	0,150	0,093	0,169	0,412	36,4	22,5	41,1
	b5	0,148	0,465	0,465	1,077	13,7	43,2	43,1
	b6	0,133	0,202	0,240	0,575	23,1	35,2	41,7
	b7	0,133	0,129	0,104	0,367	36,3	35,3	28,4
	mean					**21,2**	**36,4**	**42,4**
	SD					**11,2**	**8,2**	**9,8**
15.07.2003	b1	0,115	0,136	0,164	0,415	27,7	32,7	39,6
	b2	0,351	0,389	0,302	1,042	33,7	37,3	29,0
	b3	0,306	0,272	0,113	0,691	44,3	39,4	16,4
	b4	0,070	0,333	0,178	0,581	12,0	57,3	30,7
	b5	0,105	0,091	0,058	0,254	41,5	35,8	22,8
	b6	0,108	0,232	0,099	0,439	24,5	53,0	22,5
	b7	0,137	0,240	0,232	0,609	22,5	39,4	38,1
	b8	0,040	0,091	0,064	0,195	20,5	46,7	32,8
	mean					**28,4**	**44,1**	**27,5**
	SD					**11,8**	**8,4**	**7,3**
24.08.2003	b1	0,478	0,320	0,807	1,605	29,8	19,9	50,3
	b2	0,121	0,287	0,195	0,603	20,1	47,6	32,3
	b3	0,224	0,313	0,024	0,561	40,0	55,8	4,2
	b4	0,667	0,667	0,548	1,882	35,4	35,4	29,1
	b5	0,308	0,437	0,278	1,023	30,1	42,7	27,2
	b6	0,299	0,231	0,040	0,570	52,4	40,5	7,0
	b7	0,183	0,283	0,042	0,508	36,0	55,7	8,3
	b8	0,577	0,614	0,557	1,748	33,0	35,1	31,9
	mean					**35,3**	**44,7**	**20,0**
	SD					**9,8**	**8,7**	**12,8**
17.09.2003	b1	0,478	0,320	0,807	1,605	29,8	19,9	50,3
	b2	0,121	0,287	0,195	0,603	20,1	47,6	32,3
	b3	0,224	0,313	0,024	0,561	40,0	55,8	4,2
	b4	0,667	0,667	0,548	1,882	35,4	35,4	29,1
	b5	0,308	0,437	0,278	1,023	30,1	42,7	27,2
	b6	0,299	0,231	0,040	0,570	52,4	40,5	7,0
	b7	0,183	0,283	0,042	0,508	36,0	55,7	8,3
	b8	0,577	0,614	0,557	1,748	33,0	35,1	31,9
	mean					**35,3**	**44,7**	**20,0**
	SD					**9,8**	**8,7**	**12,8**
30.10.2003	b1	0,030	0,123	0,117	0,270	11,1	45,6	43,3
	b2	0,145	0,215	0,285	0,645	22,5	33,3	44,2
	b3	0,080	0,142	0,197	0,418	19,1	33,9	47,0
	b4	0,135	0,350	0,361	0,847	15,9	41,4	42,7
	b5	0,097	0,153	0,225	0,475	20,4	32,2	47,3
	b6	0,090	0,507	0,447	1,043	8,6	48,6	42,8
	b7	0,042	0,520	0,367	0,929	4,6	56,0	39,5
	b8	0,163	0,289	0,175	0,627	26,0	46,1	27,9
	mean					**16,7**	**41,6**	**41,6**
	SD					**7,7**	**9,0**	**6,6**

Table A2: Dry weights DW [g] of spruce roots from each fine-root category (DW_{LRprim}, DW_{LRsec} and DW_{ShR}; cf. section 2.12), and of the proportion PTR [%] of each of the three fine-root categories in the total rootlet biomass (PTR_{LRprim}, PTR_{LRsec} and PTR_{ShR})

Sampling date	N of the individual rootlet	Weight, g				Proportion, %		
		DW_{LRprim}	**DW_{ShR}**	**DW_{LRsec}**	**Rootlet**	**PTR_{LRprim}**	**PTR_{ShR}**	**PTR_{LRsec}**
08.05.2003	s1	0,159	0,578	1,169	1,906	8,4	30,3	61,3
	s2	0,117	0,756	1,148	2,021	5,8	37,4	56,8
	s3	0,114	1,480	3,830	5,424	2,1	27,3	70,6
	s4	0,027	0,592	0,628	1,248	2,2	47,4	50,4
	s5	0,024	0,800	0,758	1,581	1,5	50,6	47,9
	s6	0,093	0,722	0,798	1,613	5,8	44,8	49,5
	s7	0,078	0,311	0,343	0,732	10,6	42,5	46,9
	s8	0,084	0,280	0,425	0,789	10,6	35,5	53,9
	s9	0,088	0,362	0,505	0,954	9,2	37,9	52,9
	mean					**6,0**	**40,8**	**53,2**
	SD					**4,1**	**7,9**	**8,1**
17.07.2003	s1		0,522	1,329	1,852	0,0	28,2	71,8
	s2	0,050	0,831	0,865	1,746	2,9	47,6	49,5
	s3	0,124	1,262	1,485	2,871	4,3	44,0	51,7
	s4	0,000	0,457	0,808	1,265	0,0	36,1	63,9
	s5	0,000	0,310	0,443	0,753	0,0	41,2	58,8
	s6	0,123	0,758	0,569	1,450	8,5	52,3	39,3
	s7	0,087	0,862	0,559	1,508	5,8	57,2	37,0
	s8	0,018	0,282	0,849	1,149	1,6	24,6	73,8
	mean					**3,3**	**43,3**	**53,4**
	SD					**3,1**	**10,8**	**13,2**
24.08.2003	s1	0,051	0,527	0,608	1,186	4,3	44,4	51,3
	s2	0,066	0,197	0,366	0,629	10,5	31,3	58,2
	s3		0,583	0,334	0,917	0,0	63,6	36,4
	s4	0,276	0,406	0,815	1,497	18,4	27,1	54,4
	s5	0,081	0,995	0,581	1,657	4,9	60,0	35,1
	s6	0,041	0,297	0,456	0,794	5,2	37,4	57,4
	s7	0,028	0,135	0,149	0,312	9,0	43,3	47,8
	s8	0,043	0,207	0,209	0,459	9,4	45,1	45,5
	s9	0,180	0,542	0,327	1,049	17,1	51,7	31,2
	s10	0,015	0,189	0,299	0,503	3,0	37,6	59,4
	mean					**9,6**	**43,2**	**47,3**
	SD					**6,1**	**10,7**	**10,9**
30.10.2003	s1	0,050	0,323	0,274	0,648	7,8	49,9	42,3
	s2	0,047	0,642	0,401	1,090	4,3	58,9	36,8
	s3		1,303	0,954	2,257	0,0	57,7	42,3
	s4	0,038	0,967	0,538	1,543	2,4	62,7	34,9
	s5	0,063	1,023	0,744	1,829	3,4	55,9	40,7
	s6	0,081	0,965	0,676	1,721	4,7	56,0	39,3
	s7	0,024	0,784	0,627	1,435	1,7	54,6	43,7
	s8		0,881	0,182	1,063	0,0	82,9	17,1
	s9	0, 025	0,655	0,568	1,482	1,7	44,2	38,3
	mean					**2,3**	**59,1**	**36,6**
	SD					**1,9**	**11,8**	**9,1**

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Nikolova P., H. Blaschke, K.-H. Häberle, R. Matyssek: 17.-19.11.2004:
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