

# Mixed Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.]) stands under drought: from reaction pattern to mechanism

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## Abstract

**Key message** We review causes of synergies in mixed-species stands, develop guiding hypotheses for revealing their mechanisms and present a rainfall exclusion experiment along with a transect (KROOF) for exploring drought effects.

**Abstract** While monocultures have dominated forest research and practice in the past, in face of growing resource scarcity and climate change, mixed-species stands are on the advance. Long-term observations show that mixed-species stands frequently over-yield monocultures, and they further suggest that the over-yielding is often higher on poor than on fertile sites and in low-growth than

in high-growth years. However, the underlying causes have not yet been clarified. We start with a review of, among others, hydraulic redistribution, complementary eco-physiological traits, and ectomycorrhizal networks as possible causes behind the observed productivity gains in mixed-species stands. Then, we develop guiding hypotheses for further exploration of synergies in mixed-species stands. Finally, we introduce into the concept and model approach of the rainfall exclusion experiment for examining the role of water supply in mixed versus pure forest stands of spruce and beech. At the Kranzberg site, six plots are equipped with water retention roofs, which only close during rain events. The remaining six plots serve as non-roofed control. Together with the rainfall exclusion experiment, an ecological gradient with five sites extending through SE-Germany forms the “Kranzberg Roof Experiment” (in short KROOF). Kranzberg Forest is a part of this gradient from moist to dry conditions, with each site providing mixed and pure associations each of spruce and beech. The ecophysiological approach will be complemented by tree ring analysis and modelling of productivity of the tree associations under intense drought.

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## Introduction

A series of recently published papers provides growing evidence for frequent over-yielding of mixed-species versus mono-specific forest stands (Morin et al. 2011; Piotta 2007; Pretzsch 2013). The mechanisms underlying such mixing effects are largely unknown, but essential for

mechanistic understanding, modelling, and management of mixed forests. In view of climate change, the dependence of species-mixing effects on water supply raises attention. Climate change with progressive drought challenges the cultivation of Norway spruce monocultures (*Picea abies* [L.] Karst.). However, species interaction in mixture may reduce drought impact and allow spruce cultivation at least within species mixture (Lebourgeois et al. 2013; Rio et al. 2014). For developing a water-use efficient, stable, and resilient production system in future, further knowledge about species interaction and its dependence on environmental conditions is indispensable.

While differences and complementarities of species traits when cultivated in mono-specific stands were subject of manifold empirical research (e.g. Zang et al. 2011), the shift of traits in inter- versus intra-specific settings and trait modification by site conditions are hardly known (Richards et al. 2010). Hence, the knowledge actually available is to be emphasized by this review. The stress-gradient hypothesis (SGH) states facilitation to dominate species interactions under high-stress levels (as, e.g., by resource limitation), whereas competition is claimed to prevail in the absence of limitation (Callaway and Walker 1997; Holmgren et al. 1997). Benefits of species-mixing are predicted in harsh and neutral, but negative effects in favourable environments (Callaway and Walker 1997). However, the underlying empirical studies consider herbaceous or solitary plants, growing on sites too poor for trees to establish or persist.

Advancing SGH towards applicability to forest ecosystems is under work (Forrester 2013), although the empirical basis for quantitative validation still is scarce. The Kranzberg Forest water exclusion experiment combined with a transect study along a gradient from dry-to-moist sites in Southern Germany forms the “Kranzberg Roof Experiment” (in short KROOF) that will counteract the deficit of empirical evidence.

The concept presented here is to trace species interaction at different spatio-temporal scales from tree organ towards stand level while considering impact by acute and chronic stress. Stands of each of the two tree species Norway spruce and European beech are consistently available as monocultures, which will allow differential analysis to identify synergism of species-mixing while distinguishing the effects of species selection from such of species interaction. Our review and experimental set-up will focus on interaction effects, i.e. “true mixing effects”, as an inter-specific phenomenon that emerges beyond species performance in monoculture. Hence, synergism emerging as multiplicative effects is of interest.

We first review over-yielding of mixed- versus mono-specific stands, exploring underlying mechanisms. Second, guiding hypotheses and set-up of KROOF that includes

sample plots along an ecological gradient will be introduced. Third, we will explore on how the integrated concept may consolidate mechanistic knowledge on effects of water supply on species-mixing. The expected outcome is envisaged to both promote process-based understanding in community ecology and management strategies for tending mixed forest stands in view of future climate conditions.

### Species-mixing effects and their modification by site conditions

While forest science and practice have focused mainly on mono-specific stands since the beginnings at more than 200 years ago, mixed-species stands have received attention only recently (Kelty et al. 1992; Scherer-Lorenzen et al. 2005). Besides providing ecological and sociocultural goods and services similar or superior to monocultures (Gamfeldt et al. 2013; Hector and Bagchi 2007), the pivotal point for propagating mixed stands is their productivity in relation to monocultures. Considerable over-yielding of 20–30 % of the yield of mixed versus pure stands has been observed in a broad range of temperate and boreal forests (Griess and Knoke 2011; Morin et al. 2011; Paquette and Messier 2011; Zhang et al. 2012; Pretzsch et al. 2010, 2012a, b, 2013), at different developmental stages, of various tree species combinations, and especially under resource-limited site conditions. Under-yielding occurs when stand density is low (Amorosos and Turnblom 2006), tree species are ecologically similar (Morin et al. 2011), or site conditions are non-limiting in resource supply (Pretzsch 2013; Stultz et al. 2007). Most studies addressed two-species mixtures which were more or less even-aged. Species interactions in multi-species and unevenly aged mixtures are even more complex, so that experiments to reveal them are more expensive and thus evidence of mixing effects in complex forests is hardly available. However, the few existing studies on multi-species forests (Pretzsch 2013) and grasslands (Hector et al. 1999) suggest that the transition from monoculture to two-species mixture probably causes the strongest increase of productivity, whereas with each additional species, the marginal benefit in terms of over-yielding decreases (Körner 2002, pp. 984–986). The benefit of multiple-species mixtures may further increase in a fluctuating environment, where species diversity may serve as insurance against productivity losses or even against drop out of low-resilient species (Yachi and Loreau 1999). Species in a polyculture that well acclimate to stress including climate change may replace declining species or compensate for growth losses of underperforming ones.

The benefit of species-mixing is often higher on resource poor compared with rich sites (Pretzsch 2013) and

during growth periods with limited rather than ample resource supply (Lebourgeois et al. 2013). Pretzsch et al. (2012a, b) provide evidence that species-mixing can mitigate limitation by drought as became evident during the extremely dry years of 1976 and 2003 in Central Europe. Rio et al. (2014) revealed the general tendency that dry years with low-growth rates enhance the benefit of growing in mixture, whereas humid years with high-growth rates reduce the over-yielding in mixed versus pure stands. Such results are relevant for advancing both SGH and forest ecosystem management in view of climate change (Griess and Knoke 2011). The prevailing benefit by tree species-mixing supports the conversion of monocultures to multi-species stands under current conditions. The high resilience of mixed stands on poor sites and in dry years suggests acclimation capacities to future environmental conditions. Attaining high mixed stand performance requires solid knowledge of underlying processes and reliable modelling of stand dynamics, productivity, and persistence compared with monocultures (Olsthoorn et al. 1999).

However, consistency in functionally explaining over-yielding of mixed versus mono-specific forest systems is missing (Richards et al. 2010). Concepts of ecological niche complementarity and facilitation comprehend mechanisms that synergistically promote species interaction, whereas concepts of interference in resource exploitation address competitive mechanisms with limitation on growth (Larocque et al. 2013). Irrespective of the outcome of stand-level productivity, supply, capture, and/or efficiency in resource use are claimed to be the drivers of differential mixed stand performance (Binkley et al. 2004; Rötzer 2013).

### Norway spruce and European beech as main players in Central European Forests

Starting with the gradual warming at the end of the last glacial period around 12,000 years ago, the development of Central European forests has been dominated less by climatic fluctuations as formerly thought (Firbas 1949) rather than species-specific migration rates from the refugial areas and increasing human influence during recent 7,000 years (Küster 1998). During the first 5,000 years of the postglacial period, initial pioneer species such as pines and birches were followed by species-rich mixed stands of mainly angiosperms comprising *Corylus*, *Quercus*, *Tilia*, *Ulmus*, and *Fraxinus* species. Both European beech and Norway spruce re-arrived late in Central Europe (Ellenberg and Leuschner 2010).

Beech proceeded from the refugium on the Balkan Peninsula on an eastern and from southern Italy on a western route to Central Europe (Felbermeier and Mosandl

2006). Upon arrival, it became dominant for the first time in the quarternary period but not before some centuries B.C., when the landscape already became massively modified by agricultural activities. Although being present, beech had never gained dominance during preceding interglacial phases. The question is of whether this was due to unfavourable conditions for beech in the Eem and Holstein interglacial (e.g. mega-herbivore theory, climatic differences to the recent warm period) or special beech-promoting factors only arising during the past 5,000 years. In particular, it has been speculated that beech was favoured by neolithic human settlements leading to gaps and more open landscapes (Küster 1997). But why beech, the seeds of which are spread mainly by mice living in forests, would have profited remains unclear (Ellenberg and Leuschner 2010). Spruce began to conquer its huge area from refugia in the southern Ural Mountains, again on the Balkan Peninsula and presumably in southern alpine regions (Firbas 1949) with a migration rate of 60–500 m a<sup>-1</sup> (Ellenberg and Leuschner 2010). In beech, propagation rates of seeds ranged between 175 and 300 m a<sup>-1</sup> (Lang 1994).

European beech prefers a mild oceanic climate extending from Sicily in the south to the southern edge of Sweden in the north and from the Atlantic coast in the west to the Black Sea coast in the east. Conversely, Norway spruce is extending to the continental and cold north-eastern part of Europe and the arctic treeline in Fennoscandia and Siberia, whereas the Atlantic coast in the west is not reached. In addition, the Southern Alps are hardly occupied (with the exception of a small belt along the Dinaric coast). Both species are overlapping in a relatively small part of their ranges in Central Europe and southern Sweden as well as towards the Mediterranean Sea (Walter and Straka 1970).

The occurrence of frost events after bud break is limiting the distribution of beech to the north and east, whereas it is drought and pathogens in the case of spruce towards Southern and Western Europe, respectively (Ellenberg and Leuschner 2010). It seems that mild temperatures increase the susceptibility of spruce especially to *Heterobasidium annosum* explaining the paradox situation that spruce is missing in warm-dry climates in spite of their xeromorphic evergreen foliage type.

Kölling and Zimmermann (2007) prognosticate the shift in species distribution by means of modelled envelope functions encircling occurrence within temperature–precipitation based ecograms. Regarding Germany, in 2100, a loss of area by 65 % is estimated for spruce relative to 13 % in beech.

Currently, Norway spruce and European beech dominate in Central Europe's forests with 30 % of the forested area, being 14 × 10<sup>6</sup> ha in absolute terms (Deutsches Bundesministerium für Ernährung, Landwirtschaft und

Verbraucherschutz 2005; FAO 2010). The natural core area of European beech ranges from the colline through the submountainous to the mountainous zone, here co-occurring with Norway spruce. The latter is naturally centred in the Alps and European midlands between 800 m up to the alpine treeline (Ellenberg and Leuschner 2010). In the mixed mountainous forests (600–1,400 m a.s.l.), both species coexist successfully, often associated additionally with silver fir. The common feature and reason for stable coexistence is the high shade tolerance of all three species (Otto 1994). Being difficult to access for harvest mixed mountain forests was often managed much more extensively and left in a more natural state. Forests in the lowlands were exploited much more intensively and mostly converted to age-class systems, often cultivating Norway spruce in pure stands outside of its natural range at the expense of European beech throughout the past 200 years (Küster 1998). In the lowlands, Norway spruce out-yields most other species as long as water supply is abundant and occurrence of bark beetle, windthrow, and ice-breakage is rare (Pretzsch 2005).

However, severe losses of pure Norway spruce stands by drought, storm, and various biotic damages recalls its susceptibility to risk when cultivated outside its natural range (Kölling 2007). In order to benefit from its superior productivity but to reduce the risk in view of climate change, Norway spruce presently is mostly mixed with good success with beech or other natural and presumably stabilizing species (Pretzsch et al. 2010).

The productivity of Norway spruce and European beech in mixed versus pure stands was exhaustively analysed in regional studies (Assmann 1961; Burger 1941; Kennel 1965; Pretzsch et al. 2010; Wiedemann 1942). However, although the mixture of spruce and beech is frequently naturally occurring and artificially cultivated, the mechanistic behind the reported over-yielding of 10–30 % of both species in mixture compared with pure stands is hardly understood. They represent a mixture with many complementary traits. Hence, over-yielding might be anchored in canopy architectures favourable to light penetration and/or in enhanced complementarity of rooting systems in belowground resource use, both mediated through the combined species-specific space exploration versus exploitation strategies (Pretzsch and Schütze 2005; Schmid and Kazda 2001; Wiedemann 1942). Plasticity in crown and root architecture (Pretzsch 2014) appears to be key to understanding synergistic or antagonistic stand-level effects of mixed-systems productivity (Dieler and Pretzsch 2013; Matyssek et al. 2012). In view of drought, phenomena of hydraulic lift or redistribution of soil water resources between the associated species might become crucial (Dawson 1993). The stand-level combination of structurally and chemically contrasting litter types may, on

the long term, improve fertility and resource storage of soils (carbon, water, and nutrients), perhaps mediated through stimulated bioturbation (Heinsdorf 1999; Rothe and Binkley 2001). Enhanced use efficiency has been reported with respect to light and water resources (Pretzsch et al. 2010, 2012a).

### State of knowledge on underlying mechanisms

Species-specific structural and functional traits of Norway spruce and European beech have been well investigated in mono-specific environments each (Kennel 1965; Pretzsch et al. 2010) so that resource consumption and productivity caused by species selection are foreseeable. However, over-yielding of mixed versus pure stands suggests synergetic effects introduced by one or both species when growing in combination. Evidence exists that mixing effects emerge that overrule mere selection effects, originating from particular interactions in resource capture and use efficiency. In the following, we will focus on species interaction related to water supply, its use, and use efficiency. We will not repeat the extensive reports on species-specific traits in pure stands but introduce interactions arising from species cultivation in mixture that trigger change in resource consumption and productivity. In such cases, however, when productivity of mixed stands merely reflects the weighted average of that of the respective monocultures, species selection instead of interaction represents the causality.

Inter-specific settings may foster humus formation and water storage of soils (Augusto et al. 2002; Heinsdorf 1999). Given the highlighted beech/spruce combination, beech might be responsible for accelerating decomposition of litter, and reducing the thickness of the humus layer on top of the mineral soil. Accumulation of litter, building thick humus layers as typical for Norway spruce, can store a significant amount of precipitation which evaporates easily back to the atmosphere instead of being available to the fine roots in the mineral soil (Rothe 1997). Given cases that mixing increases stand density (Pretzsch et al. 2010), foliage area will enhance interception capacity while mitigating water availability to associated species and seepage to groundwater.

Spatio-temporal complementarity in resource use in beech/spruce mixtures may be expected. In spring, before the leaf flush of beech, irradiance can penetrate the stand and break the winter dormancy of spruce, thus prolonging the growing season of the latter species in relation to beech (Schober 1950/51). Given such “ecophysiological job-sharing”, spruce in mixture with beech may profit in resource utilization (Mitscherlich 1952). Beneficial interaction effects may increase with mixture homogeneity of the system (Ellenberg et al. 1986; Rötzer 2013). In the

following, hydraulic redistribution, isohydric versus anisohydric features of spruce and beech, as well as effects of ectomycorrhizal networks will be discussed in view of water supply.

### Hydraulic lift

When thinking of tree interaction under drought, it is conducive to imagine competition for water. However, outcomes under drought may turn into benefits for some of the associates. One such phenomenon is the well-described “hydraulic lift” of water in woody plants, in particular observable under arid conditions, through deeply extending root systems, which release water at night into surface-near soil horizons of low water potential (Caldwell et al. 1998). Once released, such water represents an external storage capacitance for the deep-rooting plant, but concomitantly enables survival of neighbouring shallow-rooting plants as the profiteers. The resulting benefit is not an active support provided by the deep-rooting plant, but occurs indirectly as an emergent feature of the specific species association under a specific site scenario. In such a case, competition turns into facilitation, which denotes an indirectly mediated, functional emergence between neighbouring plants to the benefit of one or several of the associates.

### Species-specific ecophysiological traits

Facilitation, although probably mediated through mechanisms other than aforementioned, is imaginable also between neighbouring spruce and beech trees under exacerbating soil drought. The functional basis is reflected by an ongoing debate, as to whether tree species pursue different principles in attaining their water balance if approaching die-off under severe drought (Hartmann 2011; McDowell et al. 2008; McDowell and Sevanto 2010; Sala et al. 2010). One question discussed is whether carbon limitation by drought can be observed in trees (Sala 2009). Such an effect may result from depletion of carbon reserves upon drought-induced stomatal closure and associated disruption of photosynthesis, eventually leading to carbon starvation. As an alternative, it is discussed that xylem dysfunction and disrupted water transport upon spreading embolism primarily cause drought-induced growth reductions and mortality in such trees, which tend to delay stomatal closure and, hence, photosynthetic limitation. Hydraulic collapse may be exacerbated by impeded long-distance phloem transport, which relies on tree-internal water availability (Hartmann 2011). If such differential pathways to die-off actually exist, tree species may either represent the isohydric (former case) or anisohydric type (latter case) in balancing their water relations under drought (McDowell et al. 2008).

McDowell et al. (2008) stated that theoretically isohydric species are endangered by carbon starvation during moderate but long-lasting drought, as such species are expected to sensitively close stomata already during early stages of water limitation. Such species would reflect a “sit-and-wait” strategy, with the capacity of withstanding drought through a dormancy-like reduction of metabolism. Conversely, anisohydric species adapted to endure progressive water tension may be at risk by xylem dysfunction as a consequence of severe drought, while tending to keep carbon gain high. Hence, different strategies in drought response may govern the interaction between tree species, so that anisohydric species may profit belowground from lowered water sequestration by isohydric species. Consequently, competition for water may turn, under drought, into facilitation of the anisohydric tree type, i.e. enabling the latter for extending its endurance of drought. If so, then redistribution of belowground water flux should become observable between neighbouring isohydric and anisohydric trees. Most importantly, however, redistribution of soil water between isohydric versus anisohydric tree species may become a crucial mechanism enabling over-yielding in mixed forests, in particular, under situations of water limitation.

Spruce has proven to be more drought-susceptible than beech (Kölling 2007), although spruce foliage is xeromorphic. Spruce appears to reflect an isohydric strategy (Lyr et al. 1992), reducing stomatal conductance at early stages of soil drought. Xeromorphism of needles may, hence, be a feature to preserve water in the tree, once the stomata have closed. Under non-limiting water supply, the lower leaf-level transpiration rate of spruce is counteracted by higher leaf biomass and leaf area index at the stand level relative to beech (Ellenberg et al. 1986; Lyr et al. 1992). By contrast, beech appears to display an anisohydric strategy, with the stomata being less sensitive to soil drought, allowing for less limited carbon gain and stem and root growth during prolonged time spans under drought than in spruce (Leuschner 2009; Nikolova et al. 2011). Both strategies apparently lead to similar twig water potentials, as observed during the recent years at the study site of Kranzberg Forest, and were evident, in particular, during the exceptionally hot and dry summer of 2003 (Ciais et al. 2005). Operating at water potentials below  $-2$  MPa, however, beech bears a higher risk of embolism than spruce (threshold of 50 % loss of conductivity in beech at  $-2.5$  MPa, spruce at  $-3.5$  MPa; Czajkowski et al. 2009). Altogether, the different traits in water uptake, transport, and storage in beech and spruce do not convincingly explain the higher drought susceptibility of spruce, unless drought-induced carbon limitation is taken into account. Such a pathway to die-off may also explicate the increasing risk to insect attack and fungal infestations in spruce on dry

sites (Schmidt-Vogt 1989) and conforms with the growth-differentiation balance theory which claims declining defence under severe carbon limitation (Matyssek et al. 2012).

#### Ectomycorrhizal community functions

Water uptake of Norway spruce and European beech is realized by an ectomycorrhizal root system each, which acquires soil water and nutrients from finer soil pores than can be achieved by fine roots with their root hairs. Such systems are therefore important also in the redistribution of water, e.g. from deep soil to the surface via hydraulic lift (Allen 2009).

Correlations between tree growth as revealed by year ring analyses and the extent of ectomycorrhizal colonization and diversity along a gradient of drought revealed lowest species diversity under extreme limitation and highest diversity at intermediate stress conditions (Swaty et al. 2003). Under extreme drought with 50 % tree mortality, mycorrhization of the surviving trees was reduced (Swaty et al. 2003), whereas less severe conditions altered the ectomycorrhizal community composition (Shi et al. 2002; Sthultz et al. 2009; Richard et al. 2011).

Norway spruce and European beech are associated with over 100 ectomycorrhizal (ECM) fungal species each with partial overlap in their fungal associates (Agerer 1987–95; Grebenc and Kraigher 2007). If carbon starvation of isohydric Norway spruce occurs under drought, shifts in ectomycorrhizal communities should reflect reduced carbon allocation. In contrast, European beech with anisohydric strategy should maintain its carbon allocation to the ectomycorrhizal fungal partners during periods of prolonged and moderate drought. At least, shifts in community composition caused by drought should be more pronounced in spruce than in beech.

Under increasing drought stress, soil conditions change dramatically for ectomycorrhizae by increasing osmotic disparity. Under controlled conditions in mycelia cultures, several mechanisms of drought protection were identified related to osmotic regulation, protection from water loss and oxidative stress, and maintenance of cell integrity (Kerner et al. 2012). Such mechanisms have not yet been seen in ectomycorrhizal systems under site conditions.

Coping with altered carbon supply and nutrient relations in soils under drought also affects physiological traits of ectomycorrhizae. Reduced carbon allocation via their tree host may have negative impacts on fungi with high demand for carbon from photosynthesis and instead favour such fungi with enhanced saprotrophic potential (Koide et al. 2008). Compared to beech, spruce ectomycorrhizae would be affected more by drought as the communities would shift towards fungi with saprotrophic potential.

#### Hypotheses of the KROOF project

Over-yielding and under-yielding of mixed-species stands compared to their respective mono-specific stands are often reported (cf. “Species-mixing effects and their modification by site conditions” section). Their underlying mechanisms, however, are still hardly known (Richards et al. 2010), although these would advance the stress gradient hypotheses for woody plants (Callaway and Walker 1997; Callaway 2013) and improve forest ecosystem management in view of climate change (Griess and Knoke 2011). Level and direction of the effect of species-mixing strongly depend on the resource supply of the site (e.g. Pretzsch 2013; Lebourgeois et al. 2013) and meteorological conditions within the growing season (Rio et al. 2014). Fostering humus formation and water storage of soils (e.g. Augusto et al. 2002), enhancing stand density (e.g. Pretzsch et al. 2010), increasing light efficiency and water resources (e.g. Pretzsch et al. 2012a), and improving soil fertility and resource storage (e.g. Rothe and Binkley 2001) along with structural advantages such as different crown plasticities and root architecture (e.g. Dieler and Pretzsch 2013; Matyssek et al. 2012) may contribute to over- or under-yielding of mixed-species stands in comparison with mono-specific stands.

Here, we focus on species interaction related to water supply and water consumption as well as its efficiency. Species interactions at different spatio-temporal scales from organ over tree to stand level will be analysed for chronic and acute drought. Thereby, the ectomycorrhizal root system is essential because water is redistributed from the deep soil to the surface via hydraulic lift (Allen 2009). Drought, on the other hand, diminishes mycorrhization (Swaty et al. 2003) and could change ectomycorrhizal community composition (Shi et al. 2002; Sthultz et al. 2009; Richard et al. 2011) and thus water uptake.

We will scrutinize whether carbon limitation can be observed in trees under drought stress (Sala 2009). Isohydric tree species are threatened by carbon starvation because they close stomata already during early stages of drought, while anisohydric species are adapted to tolerate progressive water tension jeopardizing xylem dysfunction as a consequence of severe drought, however, still gaining carbon. These responses to drought may govern facilitation, respectively, competition for water between tree species. Anisohydric species for example may profit belowground from lowered water sequestration by isohydric species. These different strategies of the two species Norway spruce and European beech along with their different characteristics in terms of space exploitation, resource capture, and consumption make them an ideal couple to examine mixing effects of species. Because these two species are associated with over 100 ectomycorrhizal

fungal species (e.g. Grebenc and Kraigher 2007), these species are highly suitable for analysing species-mixing effects under drought.

The KROOF project strives for clarifying the underlying mechanisms of presumed over-yielding, while accounting for the role of site conditions and stress resilience under water limitation. Based on the above outline on mixing effects of species, their potential underlying mechanisms, and modifications by site conditions as well as in the view of field observations during the drought years of 1976 and 2003, the following hypotheses are posed for the KROOF project:

1. Spruce follows an isohydric strategy so that upon stomatal closure under incipient drought, growth is limited by reduced carbon uptake, and the proportion of ectomycorrhizae with high carbon demand is diminished.
2. Beech follows an anisohydric strategy so that intensive drought limits growth by hydraulic failure and/or impeded long-distant carbon transport.
3. Moderate drought limits the water consumption of Norway spruce more severely than that of European beech which, under inter-specific competition, benefits from soil water re-partitioning.
4. Increasing water limitation within a precipitation gradient drives the competitive strength of European beech relative to Norway spruce.
5. Incipient drought affects diversity and function of ectomycorrhizal communities more strongly through carbon limitation in isohydric spruce than in anisohydric beech.
6. Increasing drought stress enhances saprotrophic behaviour of spruce mycorrhizae, capacities for osmotic protection, and water supply to beech mycorrhizae.

### Envisioning a research concept

In view of the above given account on the state of knowledge related to this review, and in view of the derived hypotheses, what are the requirements to be considered in shaping a research concept? Three dimensions appear to emerge from the above analysis, demanding for clarification: (i) How to gain certainty about the regional relevance of interaction between beech and spruce for water? (ii) How does water availability drives beech–spruce interaction? (iii) Which is the mechanistic basis of the interaction, spanned between high water availability and severe drought?

#### Regional requirements

Regarding (i), investigations should be conducted within geographical boundaries that cover a representative portion

of the area, in which beech and spruce co-occur, either in monoculture each, or forming mixed stands. Given the silvicultural relevance, the area should comprise locations, at which beech and spruce plantations typically prevail. In Central Europe, such locations range across colline and sub-mountainous altitudes (i.e. from about 300 through 700 m a.s.l.). Such altitudes lie outside the natural occurrence of spruce, whereas beech does not naturally develop climax character at colline sites (Ellenberg and Leuschner 2010). With respect to evaluating the derived hypotheses, triplets of the stand types of beech and spruce (i.e. monocultures each and mixed stands) should be available at same locations (or, at least, within close proximities).

In view of (ii), investigations should make use of geographically prevalent gradients in water availability. Transects across the natural climatic and/or edaphic variation within the focused geographical boundaries should be identified. Being aware of the crucial impact of soil conditions on tree and stand performance, climatic rather than edaphic variation might be preferred. Hence, a transect, in view of water availability, might be defined within the natural variation in annual precipitation, while forest sites should be selected accordingly at similar edaphic site conditions, to the extent possible. In view of balancing statistical requirements versus logistic feasibility, five locations of stand triplets might represent the naturally occurring precipitation transect from high to low water supply within the focused geographical boundaries. In such a way, the selected locations would comprise and define the regional scale of the research concept.

#### Integrated empirical approach

The research, however, should not exhaust itself by assessing and distinguishing intra- and inter-specific interaction patterns in water acquisition of beech and spruce across the stand triplets at each location of the transect. Rather, the challenge is to be adopted by the research concept towards (iii) clarifying mechanistic grounds—not only for the sake of gaining basic knowledge per se, but in particular, for consolidating the experiential basis of silvicultural management and for fostering numeric modelling in providing decision tools (see below). Mechanistic clarification might be performed on one of the selected locations along the regional transect. What are the arguments for doing so? One is to render observations along the transect components of exploratory rationale at the experimental site, and another one to evaluate experimental outcome for its regional representativeness. To this end, the experimental site may be selected at about medium position within the transect. Such an integrated approach promotes hypothesis development best in guiding the strategy of knowledge acquisition.

## Shaping the experimental design

Mechanistic clarification, however, implies controlled experimentation at the forest site. In view of understanding water availability in driving tree interaction, drought stress must be induced experimentally and compared with the unchanged site conditions as control. However, how to induce experimental drought? Rain exclusion roofs appear to be the ultimate tool. However, the ambition must be to study maturing trees, about which knowledge is scarce on interactions for water in mixed stands. As such trees should still pass—in support of the experimental analysis—through the logarithmic stage of annual stem growth, tree dimensions will prevent roof installation above stand canopies. Apart from logistic restrictions, micro-climatic bias would be undesirable. As a consequence, exclusion roofs are to be installed underneath the canopy, perhaps at about 3 m aboveground for easing operation. Also, in such a case, micro-climatic bias needs to be prevented, regarding belowground processes. The latter criterion, however, has been a crucial weakness of previous rain exclusion experiments in forests, being based on permanently closed roofs, apart from being operated in the temperate zone of Europe mostly in mono-specific stands of Norway spruce (Gaul et al. 2008; Gundersen et al. 1998; Jyske et al. 2010; Lammersdorf et al. 1998; Lu et al. 1995; Ozolincius et al. 2009; Persson et al. 1995; Rothe 2005). Hence, as a novelty in experimentation, automated roofs are postulated, which only close upon trigger by rainfall, and then stay closed during the rain event. Hence, roof shielding advantageously becomes active only under the overcast conditions during rainfall, when greenhouse effects (i.e. warming) are negligible. In addition, lateral shielding should be omitted (Gundersen et al. 1998), which is justifiable underneath closed-canopy stand conditions, where angular rainfall is unlikely to occur. One drawback nevertheless will be left, as roofs underneath the canopy will decouple soil drought from air humidity which stays unchanged. This is the compromise to be accepted, as any experiment in the field represents a trade-off with ecological authenticity in terms of science theory. In the given case, this kind of trade-off appears to be tolerable in the absence of alternatives, perhaps requiring an extended time span for drought to build up (being aware, though, that dose effects are co-determined by stress duration).

The envisaged roofs, however, require sufficiently large dimensioning to cover catchments within the forest, which mimic the stand triplet concept along the regional transect at miniaturized scale. Hence, spruce and beech individuals need to dominate each at the opposite sides within catchments (i.e. mimicking intra-specificity), while forming a boundary zone in the centre permitting inter-specific interaction. To this end, catchment and roofed area

dimensions should extend by about  $15 \times 20 \text{ m}^2$ , which would allow the catchments to harbour up to ten tree individuals each. Such a spatially confined catchment design is justified, given the tree-level focus on interaction for water.

To ensure severe drought to become experimentally effective, catchments need to be hydraulically isolated from the remainder of stands to prevent “escaping” of root systems from drought treatments. Preferable, therefore, is site selection with a soil layer at 1–2 m depth to serve as a barrier for deep-rooting (e.g. dense clay substrate) and exploration for groundwater. Laterally, soil trenching down to that impenetrable layer is required, stabilizing trenches with a durable tarp, impermeable both for water and root growth. As such preparation causes root injury, trenching should be performed several years before the actual beginning of the drought experiment, to avoid transitional injury-incited artefacts in tree response during experimentation. Drought employment should await absence of differences in key parameters such as photosynthesis and stem growth between trees inside and outside catchments. Experience proved a time period of 4 years prior to experimentation to suffice requirements (see “[Hypotheses of the KROOF project](#)” section). In view of statistical analysis, at least five catchments each, i.e. roofed and non-roofed (=control), should be envisaged as the basic experimental design.

## Postulated outcome from experimentation

The experimental design as a part of the integrated empirical approach should enable to differentially clarify, for mixed versus pure stands of both species, (1) the extents of growth responses at tree and stand level to drought, (2) species-specific drought response with respect to xylem dysfunction and carbon starvation, and (3) drought effects on ectomycorrhizal community functions and root growth. With such ambition, the experimental drought regimes should be conducted to exceed the exceptionally dry summer conditions of 2003 (Ciais et al. 2005) in terms of intensity and duration, leading the trees to the brink of, although disrupting drought prior to die-off. The disruption is to explore species-specific recovery and drought after-effects on the tree-soil system. Stable isotope labelling should be included to establish cause-effect related grounds of tree interaction at the transition to decline by tracking resource flux in the tree-soil system. Challenging the trees’ stress tolerance and survival is to foster mechanistic clarity. The combination with the extensive survey-type assessments of tree and stand-level parameters at the other locations of the regional transect (e.g. performance in relation to ectomycorrhizal dynamics) is to clarify water supply as the driving variable of tree interaction at different

spatial (organ, tree, stand) and temporal scales (diurnal, annual and retrospective decadal analysis of tree growth) within the ecologically imaginable range of moisture dependence, extending to climate change scenarios.

### Integrating empirical approaches and modelling

Both the synthesis of elaborated empirical knowledge towards theory building on the subject of the review and the development of reliable decision tools for silvicultural practice require the consolidation of numeric modelling on mechanistic, i.e. cause-effect related grounds. Evaluating the relevance of species-mixing for tree and stand growth under drought in mechanistic terms demands for combining empirical bottom-up and top-down approaches for model design and parameterization.

Within the scope of the propagated research concept, the *bottom-up approach* should comprise measurements of structure, processes, and stand-internal environmental conditions in high spatial and temporal resolution. Water supply, capture, and use efficiency should be assessed under intra- and inter-specific conditions at organ and individual tree level. Hydraulic translocation between spruce and beech must be traced within catchments, along with mycorrhizal diversity and dynamics at high temporal resolution during the experimental drought progression. Such assessments provide the mechanistic basis for understanding stand productivity and water consumption.

The *top-down approach* should provide state variables on structure, processes, and stand-internal environmental conditions as annual averages—i.e. by time resolution contrasting with that of the bottom-up perspective. Differentiation in structural data must be made (e.g. crown length, canopy layering) with respect to the prevalence of drought. Stand productivity (dry mass production) and edaphic conditions (humus conditions, soil moisture, water storage) must be assessed for concluding about long-term development. Evidently, the bottom-up oriented rationale of experimentation needs to be merged with the top-down perspective derived from transect investigations, by this strengthening the statistical basis of analysis.

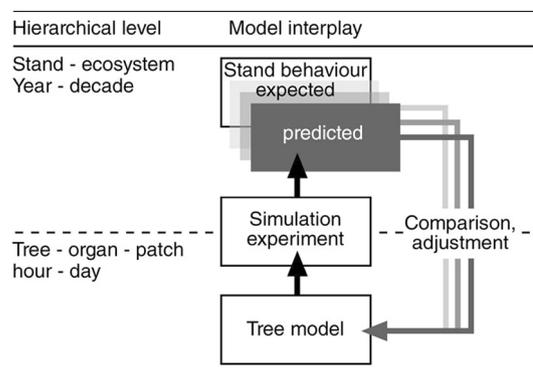
The extent of bottom-up/top-down consistencies can ascertain the mechanistic relevance across spatio-temporal scales, including stand-level long-term dynamics. In the case of low consistency, findings may be of scale-specific and/or instantaneous relevance, prone to compensation through long-term system resilience. The derived statistical information may indicate cause-effect relationships, but can hardly reveal underlying mechanisms. The latter must be acquired through synchronous tree and stand-level process assessment, response pattern analysis, and interaction scaling to be supported by mechanistic modelling as a part of the “bottom-up” perspective.

### Feedbacks between empirical approaches and modelling

Mechanistic tree-level modelling enables simulation runs (Fig. 1). As modelling comprehends state variables at stand level, validations become feasible through available knowledge on mixed stand dynamics from empirical research, validated stand models, or ecosystem theory. Comparisons between species-mixing effects found at tree versus stand level should reveal, therefore, such environmental effects, structures, and functions that are crucial for mimicking the system behaviour in silico. Re-iterating the cycle of model adjustment → simulation experiment → comparison prediction/reference → model adjustment (solid black feedback loop in Fig. 1) can identify highly resolved mixing phenomena across spatio-temporal scales in mechanistic terms (Grimm 1999). Model validation with empirical findings should be used in support of revealing such interaction mechanisms (e.g. hydraulic redistribution, spatially or temporally contrasting water demand) which define emerging properties in tree and stand-level performances (Kimmins 1997).

### Ecophysiological 3D growth models for “bottom-up”/ “top-down” integration

Eco-physiologically based growth models can integrate a wide range of spatio-temporal system knowledge derived from multi-disciplinary cooperation (Pretzsch et al. 2008). BALANCE is a model of that kind, developed and validated through preceding intense research, both locally (Rötzer et al. 2010; Häberle et al. 2012) and regionally (Grote and Pretzsch 2002; Rötzer et al. 2005, 2013). Since BALANCE is a spatially explicit tree and tree organ-level model, effects of any proportional species mixture and stand structure can be assessed (Rötzer et al. 2010; Rötzer 2013), including ecosystem responses to environmental



**Fig. 1** Towards system understanding by feedback between empirical and modelling approaches. Further explanation in the text

changes such as by drought. The use of models like BALANCE should become mandatory, as experimentation within a regional scope can provide platforms for consolidating model calibration and validation. Expected outcome is the understanding of functional emergences of stand-level functionality as originating from “interaction among its parts” (Grimm 1999), i.e. the tree individuals. Since bottom-up approaches per se, however, cannot build system-level theories, merging into the top-down perspective is indispensable (Grimm 1999), but should be backed by time series simulations of carbon, water and nutrient cycling, and regional long-term evidence. Simulations may show large-scale influences by environmental changes to be superimposed by small-scale, site-specific variables, which may have the capacity for locally reversing large-scale growth trends. It must be explored, therefore, as to whether mixing effects vary throughout forest ageing and structural development, and in particular, upon silvicultural treatment (Holmgren et al. 1997; Körner 2006).

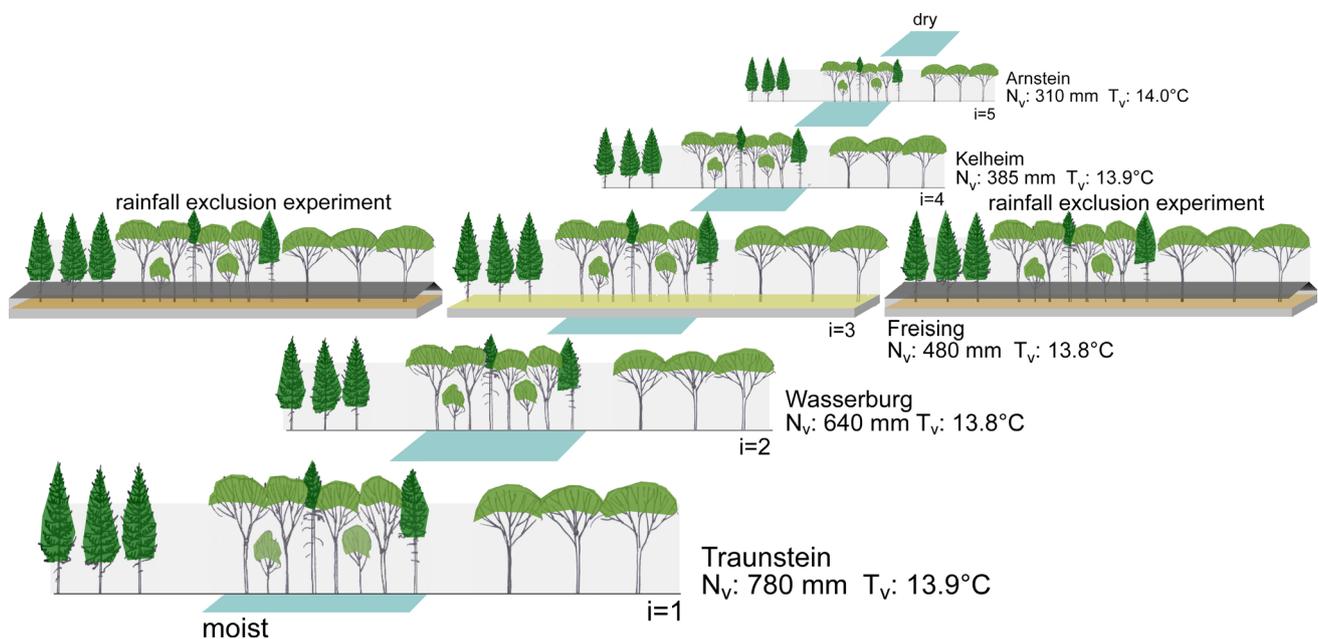
### From concept design to research realization

#### The regional transect

The considerations evolved above on a research design related to the subject of this review have in fact begun to

become realized. The geographical region of such an experiment is Bavaria/Germany, with five locations forming the ecological transect determined climatically through annual precipitation rather than edaphic site conditions (Fig. 2; Table 1). The transect extends from the humid SE part of Bavaria to its dry NW, although the latter range still cannot be viewed as arid at the global scale. Locations are spread with upper colline through sub-mountainous altitudes. At each of the five locations, stand triplets exist, representing beech and spruce monocultures and mixed stands each, established by forestry within close proximities. Bavaria located in Central Europe is a part of the natural distribution areas of beech and spruce, although spruce would prevail naturally only at mountainous to sub-alpine altitudes, in the midland ranges and the Northern Alps (only here, spruce would naturally form mixed forests with beech), beech would develop into the climax tree species only within the sub-mountainous range.

In detail, sites are situated at 330 m a.s.l. in NW-Bavaria to 600 m a.s.l. in the SE. With increasing altitude as well as decreasing latitude, mean annual precipitation and its portion within the growing season rise from 625 to 1,350 mm and from 310 to 780 mm, respectively. Simultaneously, the mean seasonal air temperature ranges between 13.8 and 14.0 °C along the entire gradient, with soil characteristics being similar across sites. The precipitation gradient provides ideal grounds for analysing the posed hypotheses in view of water availability as a driving factor.



**Fig. 2** The KROOF project: transect setup comprising a series of triples (pure spruce, pure beech, mixed spruce/beech stands) as located along a precipitation gradient from moist to dry sites across Bavaria (SE-Germany) combined with a controlled rainfall exclusion

experiment on one site in the centre of the gradient with medium water supply (N<sub>v</sub>: average (1971–2000) precipitation of the growing season, T<sub>v</sub>: average (1971–2000) temperature of the growing season)

**Table 1** Geographical and soil characteristics of the transect plots

Name	Site	Longitude	Latitude	Altitude a.s.l. (m)	Geological substrate	Soil quality	Cation exchange capacity	Water holding capacity	Species	Exposition
Arnstein	Gramschatz	9°58'37.2"E	49°54'10.8"N	330	Valley sediments	Good	High	High	Spruce Beech	South Plain
Kelheim	Parsberg	11°49'19.2"E	48°56'8.16"N	550	Loess over deteriorated limestone	Good	High	Medium	Spruce/beech Spruce Beech	Plain Northwest Northwest
Freising	Kranzberger Forst	11°39'39.6"E	48°25'8.4"N	490	Loess over tertiary sediments	Good	High	High	Spruce/beech Beech Spruce/beech	Northwest Northwest Plain
Wasserburg	Großhager Forst	12° 04' 22.8"E	48° 08' 31.2"N	620	Morains from Würm glaciation	Good	Medium	High	Spruce Beech Spruce/beech	Plain South South
Traunstein	Froschham	12° 40' 19.2"E	47° 56' 20.4"N	600	Morains from Würm glaciation	Good	High	Medium	Spruce/beech Spruce Beech Spruce/beech	South West West North

In addition to basic initial recordings at the transect locations (diameter at breast height, height, crown dimensions), sampling of leaf area, fine roots, stem growth, coarse root increment, and mycorrhizal communities is being performed. Also, tree increment boring and stable isotope analysis are conducted in the stand triplets of the transect to retrospectively analyse drought impact on species-mixing.

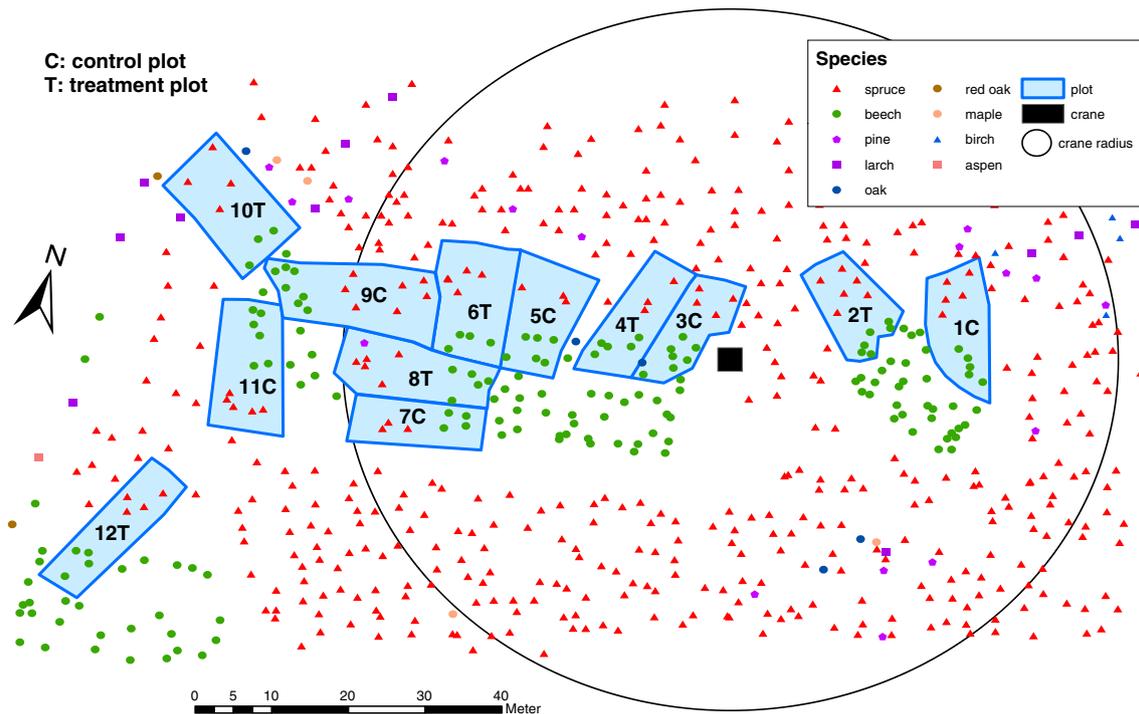
#### The experimental site

One of the five locations, Kranzberg Forest (close to the city of Freising), harbours the experimental site, positioned within the medium range of rainfall availability within the regional transect. The Kranzberg site has a size of 0.5 ha and is located at 11°39'42"E, 48°25'12"N, in the southern part of Bavaria, approximately 35 km north-east of Munich. At an altitude of 490 m a.s.l., the stand stocks on a luvisol that originated from loess over Tertiary sediments and provides high nutrient and water supply. The average precipitation (1971–2000) is 750–800 mm year<sup>-1</sup> and 460–500 mm during growing seasons, whereas the mean air temperature is around 7.8 °C on an annual average and 13.8 °C on average for the growing season. The mixed stand comprises large groups of beech surrounded by spruce. The tree ages were determined in 2010 as 59 ± 2 years in spruce, and 79 ± 4 years in beech.

The experimental plots within the site comprise the transition between intra-specific spruce and intra-specific beech, forming an inter-specific contact zone. Altogether 12 plots were installed, with six plots representing the non-roofed control (C), and another six the treatment plots with roof-induced drought (Fig. 3).

Evidently, plot characteristics such as stand density, basal area, or stem volume of mono-specific spruce, mono-specific beech, and beech/spruce mixture are similar across the six control and treatment plots each (Table 2). Plot sizes range between 110 and 200 m<sup>2</sup>, yielding total ground area of 868 and 862 m<sup>2</sup> across control and treatment plots, respectively. Each plot carries 4–6 beech trees at one side and the same number of spruce trees at the opposite side, enabling a broad contact zone in-between (Fig. 3). Edge effects are minimized as sample trees for detailed measurements will be chosen within the central area of each plot. Most tree crowns are accessible through the canopy crane.

Rainfall exclusion by roofs at about 3 m aboveground underneath the stand canopy will induce soil drought, with the first drying cycle being started in April 2014 for the remainder of the growing season. As the evaporative demand within the atmospheric canopy boundary cannot be manipulated (cf. Gaul et al. 2008; Rothe 2005), it is



**Fig. 3** Map of the plots of the controlled rainfall exclusion experiment within Kranzberg Forest

**Table 2** Characteristics of the six control and six treatment plots at Kranzberg Forest as part of the KROOF project in 2012

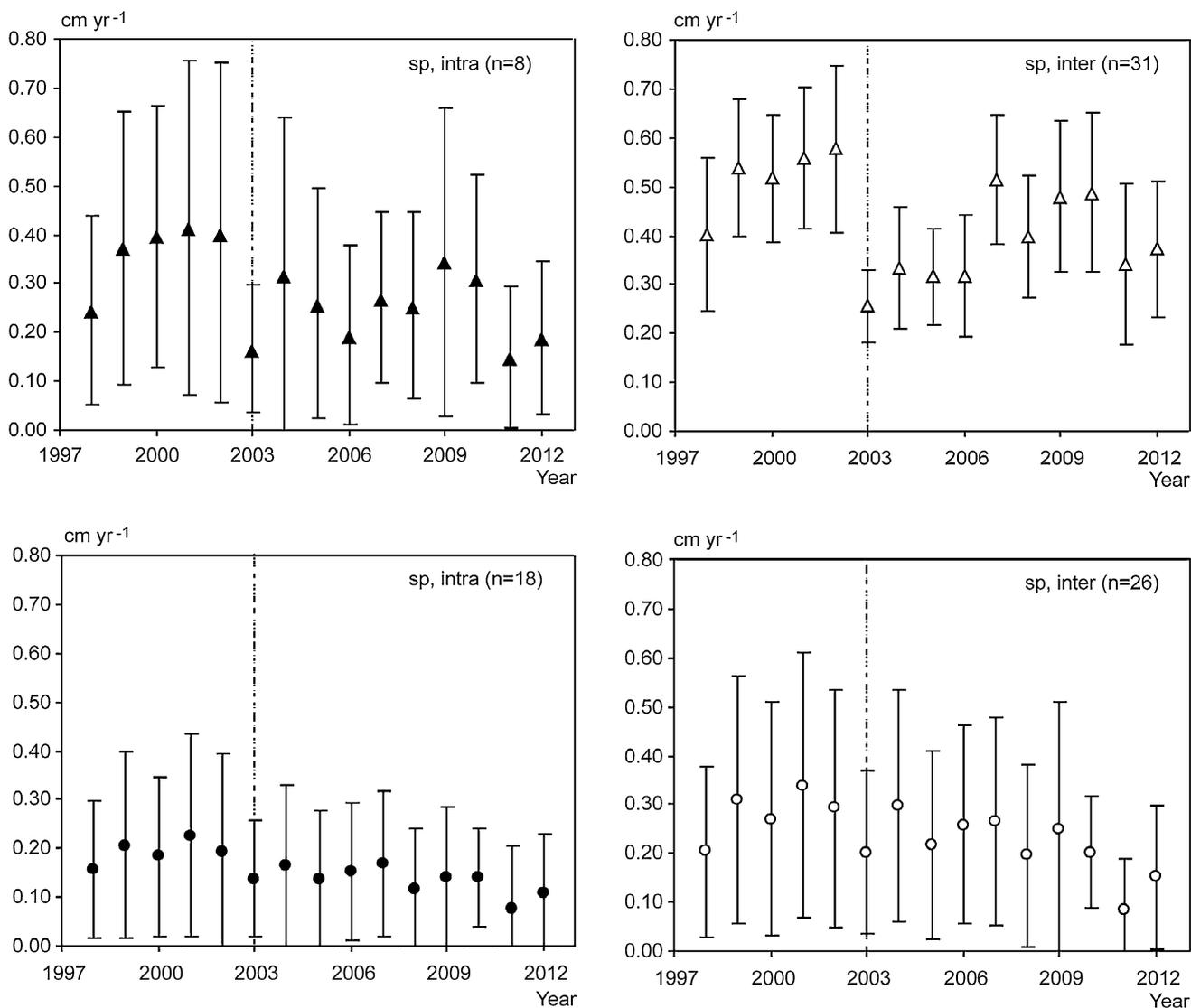
Type	Area (m <sup>2</sup> )	Species	<i>N</i> (ha <sup>-1</sup> )	<i>ba</i> (m <sup>2</sup> ha <sup>-1</sup> )	<i>V</i> (m <sup>3</sup> ha <sup>-1</sup> )	<i>KKL</i>	<i>dm</i> (cm)	<i>d100</i> (cm)	<i>hm</i> (m)	<i>h100</i> (m)
Control (6 plots)	868	Spruce	300	30.0	451	1.12	35.7	47.1	31.6	34.3
		Beech	334	21.6	326	2.21	28.7	41.0	29.2	30.3
		Total	634	51.6	777	1.69				
Treatment (6 plots)	862	Spruce	302	27.2	406	1.39	34.5	46.7	31.3	34.3
		Beech	325	21.6	328	2.14	29.1	45.4	29.3	30.6
		Total	627	48.8	734	1.79				

*N* number of trees per ha, *ba* basal area per ha, *V* total stem volume per ha, *KKL* competition index, *dm* mean diameter at 1.3 m breast height, *d100* dominant diameter at 1.3 m breast height, *hm* mean height, *h100* dominant height

assumed that the exhaustion of the soil water reserves through tree transpiration under rainfall exclusion may take longer than under co-occurring high-evaporative demand. On such grounds, the drought cycle is started early in the growing season to ensure threatening tree survival during the seasonal course. Prolonged drought periods during the growing season are a realistic scenario predicted for upcoming climate change in Germany (Allen et al. 2010; Leuschner 2009). The novelty of the roof construction is the automated closure during rain by means of water-impermeable, tile-composed roller blinds, which are electrically motorized, while the roof-intercepted water amounts are channelled out of the study site.

At the experimental site, additional assessments beyond those also conducted along the transect are installations in

each catchment of mini-rhizotrons and root windows for detection of fine root growth as well as of TDR probes for soil moisture assessment, including special regard to ectomycorrhizal community functions associated with root growth. Stem diameter at breast height (1.3 m height) and at 50 % tree height as well as diameter of coarse roots will continuously be measured by electronic dendrometers and permanent girth tapes. Besides basic meteorological recordings measurements of sap flow, stomatal conductance of leaves and needles in the sun crowns and of water potential will provide grounds for hypothesis evaluation. The latter is deepened by stable isotope analysis for exploring alterations in isotopic signatures in tree biomass upon drought impact and for tracing resource flux by labelling experiments.



**Fig. 4** Annual diameter increment of the spruce (*above*) and beech trees (*below*) at Kranzberg Forest as depending on their intra (*left*) or inter-specific growth conditions (*right*). Of special interest are the

growth responses to the drought year 2003 (*broken vertical line*) in inter-specific compared with intra-specific environment

#### Pilot studies and activities

Orientation for disrupting the drought treatment when reaching the brink of tree death will be provided by databases established at Kranzberg Forest during the exceptionally warm and dry summer of 2003 (Ciais et al. 2005). Databases indicate to set safety margins of pre-dawn twig water potentials to  $-1.6$  MPa and diurnal minimum potentials to  $-2.2$  MPa in the first year for both species (Löw et al. 2006). In the second year, levels will be lowered to  $-2.0$  and  $-2.5$  MPa, respectively. When the experimental drought treatment will be repeated—after a first drying and recovery cycle—soil moisture conditions will be exacerbated towards water potentials that may induce catastrophic “run-away” cavitation (below

$-2.5$  MPa, according to species-specific xylem vulnerability in beech and spruce; cf. Czajkowski et al. 2009; Lösch 2001).

During the preparatory stage, trees were classified within all catchments at Kranzberg Forest in terms of species affiliation and association with neighbouring trees by mean annual diameter increments during 1998 through 2012 (Fig. 4). Increments of both tree species were evidently higher under inter-specific than intra-specific conditions throughout the assessment period. In spruce, high inter-annual variability prevailed both under intra- and inter-specific conditions, whereas in beech, variability was smaller in mixture. Averaged over the 15-year assessment, the incremental diameter of spruce in monoculture was  $0.29$  cm year $^{-1}$ , whereas  $0.43$  cm year $^{-1}$  was reached with

beech in mixture. Similarly, in beech, the mean annual incremental stem diameter was 0.15 cm year<sup>-1</sup> in monoculture, but 0.24 cm year<sup>-1</sup> when growing in mixture with spruce.

A crucial prerequisite of the drought experiment was the hydraulic isolation of the plots (including control) from the remainder of the forest stand. To this end, the 12 plots were trenched to 1 m of soil depth (i.e. permanently disrupting the lateral hydraulic continuum). At that depth, a root-impermeable soil horizon prevents further downward-rooting (Häberle et al. 2012). In this way, catchments were created, which allow quantitative stand-level water balancing. Trenching was performed already 4 years before the beginning of the drought treatment scheduled for April 2014. The early trenching treatment warranted stabilization of soil water relations and acclimation of root systems upon trenching injury while disrupting lateral water exchange with the stand outside catchments. Assessment of eco-physiologically crucial parameters such as the soil water content or fine root development since the beginning of the second year after trenching proved absence of statistical differences in structural and functional performance between trees inside and outside catchments prior to employing the experimental drought. In addition, tree and stand growth parameters such as diameter at breast height (1.3 m), tree height, or lower canopy edge have been measured continuously since 1994 (see summary on treatment plots in Table 2).

## Modelling

The transect enables an integrated empirical and modelling-based investigation by employing the physiological growth model BALANCE (Grote and Pretzsch 2002; Rötzer et al. 2010), which sets the experimentally induced drought at one site of the transect (i.e. at Kranzberg Forest) into perspective of the naturally prevailing soil moisture regimes across the five study sites.

## Conclusions: from evidence to relevance through KROOF

KROOF will reveal tree species-mixing effects between spruce and beech as modified by chronic and acute drought. The integrated approach, based on empirical assessments (including retrospective dendro-ecological analysis of extreme drought years) and modelling, is expected to clarify both spatial and temporal variations of species-mixing, through pursuing a tree/organ to stand-level scaling concept. Linking the concept with information from existing and newly elaborated databases on system performance along the regional precipitation transect, with the drought experiment as one component, will advance

ecological evidence and silvicultural and political relevance derivable from the outlined research programme.

The particular gain in knowledge on community ecology is the understanding of differential ecological niching within tree-species mixtures in view of competitive or facilitative water use under exacerbating drought (cf. Callaway and Walker 1997; Callaway 2013). Such gain in knowledge enables advancement of SGH towards adequate coverage of woody plant, in particular, forest tree ecology. Understanding on such grounds of over-yielding in productivity and underlying mechanisms as emerging from multi-specific forest tree associations will be of paramount importance for silvicultural management. Crucial mechanisms here will refer to complementary light capture and water-use efficiency of productivity under severe drought.

The development of resource-efficient, stress-resistant, and resilient production systems in forestry requires knowledge about species interaction under prevalent environmental conditions. The results will answer the crucial question as to whether forest practice can further rely in Central Europe on its favourite species Norway spruce, and if so, whether cultivating spruce in mixture with European beech will become an ultimate requirement in facing drought under climate change or if the “worst-case scenario” is to be faced with an outcome that may signalize aggravating competition rather than facilitation between the two species, leading to under rather than over-yielding of mixtures under drought. Such latter case may eventually enforce obsolescence in the future of beech and spruce in Central European forestry.

**Author contributions statement** H.P., R.M., and J-C.M. initiated the project. K.P., H.P., T.R., and K.-H.H. compiled the review, T.R., K.-H.H., T.G., K.P., and R.K. developed and established the experimental design, H.P., T.R., and K.P. wrote the manuscript. R.M. revised the manuscript.

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**Conflict of interest** The authors declare that they have no conflict of interest.

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