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Establishing *Fagus sylvatica* under annually recurring summer drought – experimental forest restoration upon wind-throw of *Picea abies* in view of climate change

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Appendix 2: Zang, U., Goisser, M., Grams, T.E.E., Häberle, K.-H., Matyssek, R., Matzner, E., Borken, W., 2014. Fate of recently fixed carbon in European beech (*Fagus sylvatica*) saplings during drought and subsequent recovery. Tree Physiol. 34, 29–38.

Appendix 3: Zang, U., Goisser, M., Häberle, K.-H., Matyssek, R., Matzner, E., Borken, W., 2013. Effects of drought stress on photosynthesis, rhizosphere respiration, and fine-root characteristics of beech saplings: A rhizotron field study. J. Plant Nutr. Soil Sci., doi: 10.1002/jpln.201300196

The candidate's individual contribution to the included publications is specified at the end of the thesis.

Zusammenfassung

In Deutschland spielt der Voranbau von Rotbuche (*Fagus sylvatica* L.) im Rahmen des klimagerechten Waldumbaus trockenheitsanfälliger Nadelholz-Reinbestände eine entscheidende Rolle. Allerdings erweist sich auch Buche, insbesondere im Jugendstadium, als trockenheitssensible Baumart. Darüber hinaus muss aufgrund des Pflanzschocks, vor allem im frühen Etablierungsstadium, von einer erhöhten Anfälligkeit gegenüber Trockenstress ausgegangen werden. Die vorliegende Arbeit untersucht daher die Reaktion sowie das Akklimatisierungspotential von Jungbuchen gegenüber Trockenheit während der ersten Jahre nach der Auspflanzung. Im Zentrum der Studie steht dabei ein dreijähriges Niederschlagsmanipulationsexperiment auf einer Fichten-Sturmwurffläche (*Picea abies*) in dessen Rahmen vorangebaute Buche jährlich wiederkehrender Sommertrockenheit ausgesetzt wurde. Grundlegende Trockenstressmechanismen in Wurzelwachstum und Kohlenstoffallokation der Pflanzen wurden in Rhizotronen und mittels $^{13}CO_2$-Pulsmarkierung untersucht. Alle Experimente wurden auf der Forschungsfläche „Coulissenhieb II" im Fichtelgebirge durchgeführt. Finanziert wurde das Forschungsprojekt vom Bayerischen Staatsministerium für Ernährung, Landwirtschaft und Forsten.

Nach einem Sturmwurfereignis im Januar 2007, wurde der aufgelichtete Fichtenbestand der Forschungsfläche im Herbst 2008 mit zweijähriger Buche unterpflanzt. Die ungleichmäßige Verteilung der verbliebenen konkurrierenden Altfichten, sowie die aufkommende Bodenvegetation bewirkte eine hohe Heterogenität in der kleinräumigen Verfügbarkeit von Wasser und Licht. Der natürliche Gradient der Bodenwasserverfügbarkeit wurde durch Niederschlagsmanipulation in den Vegetationsperioden der Jahre 2009 bis 2011 experimentell erweitert. Wasser- und Lichtverfügbarkeiten der Buchenpflanzen wurden individuell erfasst und jährliche individuelle Trockenstress- (DSD) und Lichtdosen (LD) berechnet. Blattgaswechsel wurde im Verlauf, Durchmesserwachstum, Pflanzenbiomasse und morphologische Parameter an den geernteten Pflanzen am Ende der Vegetationsperioden erfasst.

Trockenstress wirkte sich negativ, hohe Lichtverfügbarkeit positiv auf stomatäre Leitfähigkeit, CO_2-Assimilationsrate und Wachstum aus. Die Pflanzen reagierten auf erhöhte DSD mit einer Erhöhung

des Wurzel/Spross-Verhältnisses, einer gesteigerten Durchwurzlungstiefe und zeigten darüber hinaus Anpassungen der Feinwurzelmorphologie in Richtung einer effizienteren Wasseraufnahme. Eine schrittweise Akklimatisierung an die schattigen Bedingungen im Bestand zeigte sich auf Ebene der Blattmorphologie. Im Zuge der fortschreitenden Akklimatisierung an Wasser- und Lichtlimitierung im Verlauf des Untersuchungszeitraumes, zeigte sich eine Reduktion der Trockenstress- und Schattensensitivität des Durchmesserzuwachses. Die vorliegenden Ergebnisse weisen darauf hin, dass eine ausgeprägte Lichtakklimatisierung der Belaubung durch die Anzuchtsbedingungen in der Baumschule zu einem verstärkten Produktivitätsverlust bei gleichzeitiger Wasser- und Lichtlimitierung nach der Auspflanzung führt.

Kontrollierte Bewässerung der Rhizotron-, beziehungsweise der Topfpflanzen des $^{13}CO_2$-Markierungsexperiments, erzeugte drei Behandlungen unterschiedlicher Bodenwasserverfügbarkeit. Die Jungbuchen wurden dabei keinem, moderatem oder starkem Trockenstress ausgesetzt. Die individuelle Bodenwasserverfügbarkeit der Pflanzen wurde kontinuierlich erfasst und die jeweilige DSD berechnet. Die drei Behandlungen deckten dabei die Spanne des im Niederschlagsmanipulationsexperiment beobachteten Trockenstressgradienten ab.

Die zeitliche Dynamik des Feinwurzelwachstums sowie der Rhizospärenrespiration wurde im Verlauf der Vegetationsperiode 2010 erfasst. Am Ende der Vegetationsperiode wurden die Pflanzen geerntet und Feinwurzelmorphologie sowie Biomassenpartitionierung analysiert.

Die kumulierte Rhizosphärenrespiration korrelierte negativ mit DSD. Das Feinwurzelwachstum war angeregt unter moderatem, jedoch gehemmt unter starkem Trockenstress. Die Pflanzen reagierten auf Wasserlimitierung mit einer gesteigerten Produktion von sehr dünnen Feinwurzeln (<0.2mm) und einer Erhöhung des Wurzel/Spross-Verhältnisses. Das lebend/tot-Verhältnis der Feinwurzeln korrelierte negativ mit DSD. Scheinbar kann unter moderatem Trockenstress die trockenheitsbedingt erhöhte Feinwurzelmortalität teilweise durch ein stimuliertes Feinwurzelwachstum kompensiert werden. Offensichtlich ist das Feinwurzelwachstum jedoch unter starkem Trockenstress gehemmt. In Übereinstimmung mit dem Niederschlagsmanipulations-

experiment, weist die durch Trockenstress induzierte Änderung der Feinwurzelmorphologie auf eine Anpassung in Richtung einer effizienteren Wasseraufnahme hin.

Zur Durchführung der ^{13}C-Markierung im August 2011, wurden die Pflanzen des Markierungsexperiments von der Forschungsfläche in eine Klimakammer verfrachtet. Der erste Puls mit ^{13}C abgereichertem CO_2 (δ^{13}C von -47 ‰) wurde unter vorherrschendem Trockenstress appliziert. Fünf Tage nach Wiederbewässerung wurde eine zweite Pulsmarkierung mit ^{13}C angereichertem CO_2 (99 atom-% $^{13}CO_2$) appliziert, um mögliche Nachwirkungen des Trockenstresses zu untersuchen. Wiederholte Messung der ^{13}C-Signatur in Blatt und Wurzelatmung nach der jeweiligen Pulsmarkierung gab Aufschluss über den Transport rezenter Assimilate. Zwölf Tage nach der zweiten Markierung wurden die Pflanzen geerntet und eine individuelle ^{13}C Massenbilanz für jede Buchenpflanze berechnet.

Die mittlere Verweildauer von rezenten Assimilaten in der Blattatmung korrelierte positiv mit der Trockenstressdosis. Dementsprechend zeigte sich unter starkem Trockenstress auch ein verzögertes Erscheinen des Markierungssignals in der Bodenatmung. Nach Wiederbewässerung konnten weder in der mittleren Verweildauer von rezenten Assimilaten in der Blattatmung noch im Erscheinen des Markierungssignals in der Bodenatmung signifikante Unterschiede zwischen den Behandlungen festgestellt werden. Die Ergebnisse der ^{13}C-Massenbilanz zeigen im Gegensatz dazu jedoch, dass im Fall der ehemals trockengestressten Pflanzen, weniger Assimilate in die Wurzel verlagert wurden. Es wird geschlussfolgert, dass der Transport von Assimilaten in ehemals trockengestressten Jungbuchen nach Wiederbewässerung schnell wiederhergestellt werden kann. Die auch nach Wiederbewässerung beobachteten Nachwirkungen des Trockenstresses auf die Allokation des markierten Kohlenstoffes sind daher wahrscheinlich nur von begrenzter Dauer.

Die vorliegende Studie liefert neue Erkenntnisse bezüglich der Verknüpfung von Trockenstress- und Lichtreaktion bei Jungbuchen während der kritischen Phase nach der Auspflanzung von der Baumschule in das konkurrenzgeprägte Scenario eines aufgelichteten

Fichtenbestandes. Es wurde dabei für die waldbauliche Praxis relevantes Wissen im Angesicht des Klimawandels gewonnen:

Während die Ressourcen Verfügbarkeit im Boden durch die konkurrierenden Altfichten bestimmt wurde, wirkte sich die Bodenvegetation entscheidend auf die Lichtverfügbarkeit aus. Die unpassende Lichtakklimatisierung in der Baumschule verstärkte die Wachstumseinbußen durch Trockenheit unter den schattigen Bedingungen im Bestand. Die Fähigkeit zur Steigerung des Sprosswachstums als Akklimatisierung gegenüber Lichtmangel scheint in den ersten Jahren nach der Auspflanzung aufgrund des Pflanzschocks eingeschränkt zu sein. Allerdings profitierten die Jungbuchen entscheidend von ihrer ausgeprägten Fähigkeit zur Schattenakklimatisierung des Laubes. Gemeinsam betrachtet weisen die Ergebnisse des Rhizoron- und des Markierungsexperiments darauf hin, dass es unter starkem Trockenstress zu einem gehemmten Feinwurzelwachstum infolge einer gehemmten Assimilatversorgung der Wurzel kommen kann. Dies erlaubt die Schlussfolgerung, dass es während eines ausgedehnten Trockenereignisses, zu einem zeitlichen Versatz in der Abstimmung von wasserabsorbierender und transpirierender Oberfläche kommt. Besonders im Fall von kürzlich Ausgepflanzten Setzlingen ist davon auszugehen, dass unter Trockenheit eine Beeinträchtigung der Regeneration des Wurzelsystems zu entscheidenden Wachstumseinbußen im frühen Stadium der Etablierung am Standort führt.

Summary

Underplanting of European beech (*Fagus sylvatica* L.) plays an important role in the ongoing conversion of drought susceptible coniferous monocultures to mixed broadleaf-coniferous forests in Germany. However, also beech is considered to be drought sensitive, in particular during the juvenile stage of growth. Especially during the early stage of establishment, drought susceptibility may be exacerbated due to the transplant shock.

The present thesis investigates drought response and acclimation capacity of juvenile beech during the early stage of establishment upon transplant from the nursery to the competitive conditions at the forest site. The central experiment of the study was thereby a three-year precipitation manipulation experiment, subjecting recently transplanted beech saplings to annually recurring summer drought under conditions of a spruce stand (*Picea abies*) restoration upon wind-throw. Underlying drought response mechanisms of root growth and whole-plant carbon allocation were investigated in rhizotrons and through $^{13}CO_2$ pulse labeling. All experiments were conducted at the research site "Coulissenhieb II" in the Fichtelgebirge. The present study was funded by the Bavarian State Ministry of Food, Agriculture and Forestry.

After severe damage of the mature spruce stand by wind-throw in Jan. 2007, the study site was restored in autumn 2008 with two-year-old beech derived from a local nursery. Competition imposed by heterogeneously distributed spruce remnants and upcoming ground vegetation induced a pronounced patchiness of light and water availability. In the growing seasons of 2009 through 2011, the natural gradient of soil water availability was experimentally reinforced via precipitation manipulation. Water and light availability was assessed individually for each beech sapling. Individual drought stress (DSD) and light doses (LD) were calculated for each of the three years study. Leaf gas exchange was measured throughout the vegetation periods. Diameter growth, biomass and morphological parameters were assessed upon harvest at the end of the each growing period.

Stomatal conductance, CO_2-assimilation rate and growth were reduced with increasing drought stress, but facilitated by increasing light availability. Root/shoot ratio and rooting depth were increased with increasing DSD. Adjustments of fine root morphology (e.g. decreased mean fine root

diameter) towards more efficient water uptake were indicated under drought. Proceeding acclimation to the shady conditions at the forest site was indicated by morphological adjustments at the leaf level. In parallel to the progressive acclimation to water and light limitation, drought and shade sensitivity of diameter growth was reduced in the course of the study period. Results suggest that high-light acclimation in the nursery exacerbates productivity decline under co-occurring water and light limitation.

Via controlled irrigation of rhizoton and potted plants of the labeling experiment, three treatments of soil water availability were induced. Beech saplings were thereby subjected to no, moderate and severe drought stress during the growing seasons in 2010 and 2011 respectively. Soil water availability was continuously measured and the individual DSD was calculated for each plant. The range of DSD between the three treatments was comparable with the observed gradient of DSD in the precipitation manipulation experiment.

The dynamic of fine root growth and rhizospheric respiration of the rhizotron plants was assessed during the course of the growing season in 2010. Fine root morphology and biomass partitioning were analyzed upon harvest at the end of the growing season.
Cumulative rhizosphere respiration was negatively correlated with DSD. Fine root growth was promoted under moderate, but impeded under severe soil drought. The proportion of very thin fine roots (<0.2 mm) and the root/shoot-ratio increased. Live/dead-ratio of fine roots decreased with increasing DSD. Apparently, stimulation of fine root growth can partly compensate for the drought related increase of fine root mortality under moderate drought. However, fine root growth is evidently constrained under severe drought. The response of fine root morphology implies increased water uptake efficiency under drought.

In August 2011, plants of the labeling experiment were transferred from the study site to a climate chamber for ^{13}C labeling. The first pulse labeling with ^{13}C-depleted CO_2 (δ^{13}C of -47 ‰) was applied under prevailing drought. Five days after soil rewetting, a second label with 99 atom-% $^{13}CO_2$

was applied to examine possible after-effects of drought stress. Repeated measurements of the isotopic signatures in leaf and soil respiration after each pulse labeling provided information on the transport of recent assimilates. Plants were harvested twelve days after the second labeling and their tissue analyzed, to calculate individual ^{13}C mass balances.

Mean residence time of recent assimilates in leaf respiration correlated positively with DSD. Consistently, the appearance of label in soil respiration was delayed under severe drought. After rewetting, no significant differences in mean residence time and appearance of label in soil respiration were found across the different treatments. In contrast, the ^{13}C mass balance revealed after-effects in C allocation for the previously drought-stressed plants. In conclusion, long-distance assimilate transport is quickly recovered upon rewetting in previously drought-stressed beech saplings, although transitional after-effects of drought stress in C allocation prevailed.

The study provides novel insights into the concerted drought and light response of juvenile beech during the critical period upon transplantation from the nursery to the competitive scenario of an opened spruce stand. Hence, knowledge relevant for silvicultural practice is acquired in the face of climate change:

While below-ground resource availability was mainly driven by root competition of the spruce remnants, substantial light competition was imposed by upcoming ground vegetation. Inadequate high-light acclimation in the nursery was found to exacerbate drought-related decline in growth performance upon transplant to the shady stand conditions. While shade acclimation by means of promoted shoot growth seemed to be overridden by the effect of the transplant shock, juvenile beech particularly benefited from its pronounced capacity for shade acclimation of the foliage. In combination, results from the rhizotron and the labeling experiment suggest that under severe and persisting drought, fine root growth may be limited through curtailed leaf-to-root assimilate transport, leading to temporary decoupling of the adjustment between water-absorptive and transpiring plant surface areas. Especially in recently transplanted plants, the negative impact of drought on the recovery of the root system can crucially lower growth performance during early establishment.

1   Background of the study

1.1   Motivation and aim of the study

Throughout the past two centuries, German silviculture promoted pure plantations of Norway spruce (*Picea abies* [L.] KARST.) outside of the natural distribution range of the species (Löf & Oleskog, 2005a). Especially in the context of climate change research on future temperature increase and frequency, intensity and duration of drought (IPCC, 2007, 2013), such spruce monocultures are considered to be highly susceptible to biotic and abiotic stress (Albrecht et al., 2010; Jönsson et al., 2009; Rouault et al., 2006; Schütz et al., 2006). As preventive countermeasure, German silviculture currently re-orients towards converting susceptible spruce monocultures to mixed broadleaf-coniferous forests, which promise increased stability and reduced risk of future decline in productivity (Knoke et al., 2007).

Given the potential dominance in Central Europe's natural sub-mountainous forest ecosystems (Ellenberg, 1996), European beech (*Fagus sylvatica* L.) plays an eminent role for forest conversion in Germany (Löf & Oleskog, 2005b).

However, beech is evidently sensitive to drought (Backes & Leuschner, 2000; Gessler et al., 2004, 2007; Michelot et al., 2012), in particular during the juvenile stage of growth (Fotelli et al., 2001; Lendzion & Leuschner, 2008; Löf & Welander, 2000; Löf et al., 2005; van Hees, 1997).

For converting and restoring already damaged spruce stands, commonly, bare-rooted nursery-derived plant material is employed. Root damage and poor root-to-soil connectivity are typical consequences of transplanting, exacerbating limitation in water and nutrient uptake during the subsequent years (Burdett, 1990; Grossnickle, 2005).

Despite the prominent importance for silvicultural practice, however, no studies have been conducted to investigate the drought response of *Fagus sylvatica* L. during the early phase of forest restoration. In view of climate change, the aim of the present study was therefore to clarify response and acclimation capacity of juvenile *Fagus sylvatica* L. to severe and annually recurring summer drought during the early phase of establishment in a spruce stand upon wind-throw.

1.2   Drought stress in juvenile *Fagus sylvatica* - an overview

The drought response of plants is a syndrome of high complexity, triggered by hundreds of genes (Chaves et al., 2003). Patterns of drought response are therefore related to genetic disposition, hence underlying inter- and intra-specific variation. Patterns may be additionally modulated by other co-occurring stressors such as high irradiance and air temperature, low nutrient uptake and potential interactions of those (Chaves et al., 2003; Niinemets, 2010). The impact of and the response to water limitation depends on the quality of the drought event, namely the combination of intensity and duration as well as preceding frequency (McDowell et al., 2008) and timing (Coll et al., 2004; Löf & Welander, 2000; Meier & Leuschner, 2008a). Interactions with co-occurring species (e.g. competition, facilitation and mutualism) can modulate drought effects and drought response (Fotelli et al., 2001; Pretzsch & Schütze, 2008; Pretzsch et al., 2013). Niinemets, (2010) highlights stress sensibility and resilience to vary with ontogeny, indicating higher susceptibility for juvenile than mature trees. Considering the outlined complexity of the topic, an overview of the drought response in *F. sylvatica* will be given in the following with focus on the juvenile stage of growth.

Impact on the hydraulic system

Along with progressive desiccation, the declining soil water potential (Ψ_{soil}) gradually limits the water uptake of the plant. Consequently, during soil desiccation the stage will be reached of transpirational demand exceeding water uptake. At that stage, drought stress overrides the plant´s capability to maintain noncritical xylem water potential in order to prevent embolism within the hydraulic system (McDowell et al., 2008). Extensive embolism of xylem vessels cause the disruption of water transport, leading to lethal tissue desiccation upon ceasing water supply to affected organs. The xylem water potential inducing a loss of 50% of xylem conductivity due to embolism (Ψ_{50}) is the most common index for xylem vulnerability to embolism (Choat et al., 2012). In *F. sylvatica*, the mean Ψ_{50} across different populations in Europe is reached at -2.8 to -3.2 MPa, depending on the genetic disposition of the local population (Wortemann et al., 2011). Globally, *F. sylvatica* ranges within the most vulnerable third of angiosperm tree species (Choat et al., 2012). Focusing on the most abundant and economically most important tree species in Central Europe, the literature overview by Czajkowski et

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al. (2009) resulted in a Ψ_{50} ranking of *Fagus sylvatica* (-2.6 MPa) > *Quercus robur* -(3.0 MPa) > *Pinus sylvestris* (-3.2 MPa) > *Quercus petrea* (-3.3 MPa) > *Picea abies* (-3.5 MPa).

In *F. sylvatica*, critical xylem water potentials inducing a loss of over 88% of xylem conductivity range between -4.0 and -4.5 MPa (Barigah et al., 2013; Czajkowski et al., 2009; Urli et al., 2013). Cochard et al., (1999) show for *F. sylvatica* that given similar branch diameters, xylem vulnerability to embolism does not significantly differ between juvenile and mature trees. This result corroborates the conclusion of Weitz et al. (2006), suggesting an ontogenetically stable hydraulic design in woody plants.

However, rooted soil volume, root surface area, density of fine root ramification and rooting depth are important characteristics of the root architecture that determine water uptake (Bréda et al., 2006). Small root systems may hence limit the capability of juvenile trees to prevent internal water deficits under drought (McDowell et al., 2008).

Impact on photosynthesis, respiration and carbon balance

The reduction of transpiration and increase of water-use-efficiency of carbon assimilation via stomatal control are crucial under water limitation (Chaves, 1991). According to Flexas & Medrano, (2002), stomatal closure is one of the earliest responses to water limitation, occurring already at mild and moderate levels of drought. This implies direct signaling between root and shoot (Davies & Zhang, 1991). Medrano et al. (2002) suggest stomatal conductance as a reference parameter for drought stress. However, McDowell et al. (2008) indicate that different drought response strategies beyond the stomatal control of transpiration have to be taken into account (cf. section below: Lethal drought stress), suggesting that stomatal conductance *per se* cannot serve as an exclusive indicator for varying levels of drought stress.

Decreased stomatal conductance (g_s) impedes H_2O and CO_2 exchange between leaf and atmosphere. Under the CO_2 demand of photosynthesis, a decreased CO_2 influx results in decreased leaf internal CO_2 concentrations (ci) and CO_2 limitation at the sites of carboxylation (Cowan & Farquhar, 1977; Farquhar & Sharkey, 1982; Flexas & Medrano, 2002; Flexas et al., 2006). Transpiration control consequently reduces carbon assimilation under drought.

Aranda et al. (2012) show that in juvenile *F. sylvatica* even mild drought (predawn leaf water potentials, $\Psi_{leaf\,PD}$ between -0.2 to -0.5 MPa) can result in a reduction of g_s and net carbon assimilation rate (A_{net}). However, results of Tognetti et al. (1994, 1995) suggest g_s and A_{net} to be relatively unresponsive for $\Psi_{leaf\,PD}$ above -0.6 MPa. Applying different treatments of vapor pressure deficit (VPD_{air}) under non-limiting soil water availability, Lendzion & Leuschner, (2008) found a significant positive correlation between g_s and $\Psi_{leaf\,PD}$ within the range of -0.4 to -0.9 MPa. The direct effect of VPD_{air} on stomatal regulation may account for such contrasting results under mild and moderate levels of water limitation. Consistency exists under conditions of severe drought, showing significant stomatal closure and reduction of A_{net} at $\Psi_{leaf\,PD}$ below -1.0 Mpa, and with g_s and A_{net} near zero at $\Psi_{leaf\,PD}$ below -2.0 Mpa (Aranda et al., 2002; Gallé & Feller, 2007; Leuschner et al., 2001; Tognetti et al., 1994, 1995).

Under concurrent exposure to high solar irradiation, the drought related decrease in c_i exacerbates photoinhibition (Foyer et al., 1994a, 1994b). Under such conditions, CO_2 limitation of the Calvin-Cycle impedes the photosynthetic use of the captured solar energy. Energy oversaturation of the photosynthetic apparatus induces photo-oxidative destruction of photopigments and thylakoid membranes in the chloroplasts. Photoinhibition severely reduces efficiency of photosynthesis (Foyer et al., 1994a, 1994b). Especially for shade-acclimated juvenile *F.sylvatica*, an abrupt increase in solar radiation (e.g. upon thinning of the overstorey) can induce photoinhibition and intensify the negative impact of co-occurring water limitation on carbon assimilation (Aranda et al., 2004; Robson et al., 2009; Tognetti et al., 1997, 1998).

In woody species, respiration consumes some large part (commonly more than 50%) of the assimilated carbon (Kozlowski, 1992). Additionally to the decrease in carbon assimilation, respiratory carbon loss can be increased under severe drought, resulting in a lower total net carbon gain of the plant (McDowell et al., 2008). Flexas et al. (2005) conclude that leaf respiration (R_{leaf}) follows a biphasic pattern, as R_{leaf} is reduced under moderate drought and increased under severe drought. However, the direct effect of drought on mitochondrial respiration is considered to be of minor importance for the overall carbon balance when compared to the much stronger drought impact on photosynthetic carbon fixation (Atkin & Macherel, 2009). Nevertheless, drought events are typically associated with high air

temperatures which significantly increase temperature driven dark respiration (R) (Atkin et al., 2005). Consistently, Rodríguez-Calcerrada et al. (2010) reports on such a drought and temperature-related response of leaf respiration in juvenile *F. sylvatica*.

Besides direct physical effects on R, energy-expensive repair processes such as refilling of embolized xylem vessels (Holbrook & Zwieniecki, 1999; Secchi & Zwieniecki, 2011; Tyree et al., 1999; Zwieniecki & Holbrook, 2009), which is also reported to occur in *F. sylvatica* (Cochard et al., 2001; Magnani & Borghetti, 1995) and maintenance of cell structure and function in defending against oxidative stress on the photosynthetic apparatus (Foyer et al., 1994a, 1994b) can increase respiratory carbon demand.

Impact on carbon allocation, biomass partitioning and plant growth

Plant response to resource limitation is characterized by a selective investment of stored resources into structures and processes that are responsible for the acquisition of the limited resource (Bloom, 1985). The evidence for such balancing between resource uptake and use has long been recognized in plant science and was implemented into various conceptual models, which can be summarized as `functional equilibrium´ models (Matyssek et al., 2005; Poorter et al., 2012; Wilson, 1988).

In accordance with the concept of a functional equilibrium, widespread evidence can be found in literature that belowground limitation (e.g. water and/or nutrients) causes an increase in biomass allocation to the root (Kozlowski & Pallardy, 2002; Mooney & Winner, 1991; Poorter et al., 2012; Wilson, 1988)

However, the drought-induced strain on carbon balance (cf. section above) exacerbates the trade-off between maintenance of essential structures and metabolic processes, growth and carbon storage (cf. Körner, 2003). As a consequence of the limited carbon pool, increased biomass allocation to the root compartment can only be realized at the expense of the other demands. Dobbertin, (2005) suggests that reduced carbon allocation to stem growth may be one of the most stress-sensitive responses, as it is not of immediate importance for the tree´s survival under prevailing drought. Results of the meta-analysis by Poorter et al. (2012) corroborate such general assumption for a wide range of plant species. Regarding *F. sylvatica* in particular, several studies report on drought-related increases in root-shoot

biomass ratio (R/S-ratio) of juvenile trees (Fotelli et al., 2001; Löf et al., 2005; Rose et al., 2009; Schall et al., 2012; Tognetti et al., 1995; van Hees, 1997). Increased belowground biomass allocation is also indicated at the fine root level for mature *F. sylvatica* (Hertel et al., 2013). However, also contradicting results exist, indicating a minor, no or even negative response of root biomass allocation to drought (Leuschner et al., 2004; Löf et al., 2005; Mainiero & Kazda, 2006; Meier & Leuschner, 2008b) in *F. sylvatica*. Important for interpreting variations in R/S is its dependency on ontogeny (Ammer et al., 2008; Gedroc et al., 1996; McConnaughay & Coleman, 1999; Poorter et al., 2012), genetic constitution (Meier & Leuschner, 2008c; Peuke & Rennenberg, 2004; Rose et al., 2009; Tognetti et al., 1995) and interaction effects of above ground limitations, e.g. light, (Curt et al., 2005; Jarcuska & Barna, 2011; Jarcuska, 2009; Löf et al., 2005; Madsen, 1994; van Hees, 1997).

Fine roots account for the mayor part of absorptive root surface area and are hence crucial for water and nutrient uptake. Thereby, fine root growth is characterized by a perpetual process of production and dieback (Joslin et al., 2000). As a consequence, carbon costs of fine root growth represent a substantial part of the total belowground carbon allocation (Hendricks et al., 2006). Investigations of fine root growth dynamics reveal especially under drought fine root dieback to be increased (Joslin et al., 2000), hence implying that a substantial part of carbon investment in root growth is not assessable at the instant of biomass determination (Hodge, 2004). Regarding juvenile as well as mature *F. sylvatica*, several studies give evidence of high investment in fine root growth and increased fine root turnover under drought (Hertel et al., 2013; Meier & Leuschner, 2008b, 2008c; Schall et al., 2012; van Hees, 1997). Given mature *F. sylvatica*, however, results on fine root turnover under drought are not consistent. Mainiero & Kazda, (2006) suggest a conservative fine root response, as they did not find a significant correlation between drought and fine root turnover. In contrast, Leuschner et al. (2001) and Meier & Leuschner, (2008b) found high fine root growth rates under drought, while Hertel et al. (2013) highlights the high degree of plasticity in allocation of *F. sylvatica*. Genetic disposition (Meier & Leuschner, 2008c) and varying frequency, duration and intensity of drought may account for the conflicting results across diverse studies.

Apart from altered patterns of carbon allocation into structural biomass, also the formation and accumulation of osmotically effective sugars in leaf and root tissues is known as a prevalent drought

response in plants (Hare et al., 1998). Evidence under water limitation shows high cellular concentrations of osmolytes to facilitate the maintenance of cell turgor (Morgan, 1984), ameliorate photoinhibition (Hare et al., 1998), stabilize photosynthesis (Chaves, 1991; Downton, 1983), enable for further root elongation growth in dry soil (Kozlowski & Pallardy, 2002; Morgan, 1984), and may enhance water extraction from soil of low water potentials (Geiger & Servaites, 1991). However, capability for osmotic adjustment varies considerably among woody species (Kozlowski & Pallardy, 2002). In the case of *F. sylvatica*, drought induced osmoregulation is evident (Aranda et al., 1996, 2001, 2002; Backes & Leuschner, 2000; Climent et al., 2006; Robson et al., 2009). However, the capacity for osmotic adjustment depends on light supply of photosynthesis (various woody species: Aranda et al., 2005; Augé et al., 1990; Huang et al., 2009; Niinemets & Kull, 1998; Uemura et al., 2000; *F. sylvatica:* Aranda et al., 2001; Robson et al., 2009). According to Marshall & Waring, (1985), Sala et al. (2010) suggests that besides positive implications of osmotic adjustment on desiccation tolerance, the carbon pool in form of osmolytes to become temporarily unavailable.

Carbon export to soil microbes and mycorrhizae represents additional expenditure in the plant´s carbon balance (Matyssek et al., 2005). Estimates result in a 25% share of the total rhizospere respiration to be caused by the fungal partner in mycorrizal roots (Kozlowski, 1992). Mycorrhization is known to improve the overall performance of nursery trees upon transplanting (Perry et al., 1987). While the positive effect of mycorrhizal colonization of the roots on nutrient acquisition is widely proved, uncertainty remains about effects on water uptake, regarding magnitude and involved mechanisms (Lehto & Zwiazek, 2011). Nevertheless, evidence exists about positive effects of mycorrhization on plant water status under drought (Beniwal et al., 2011; in juvenile *F. sylvatica*: Davies et al., 1996; Pena et al., 2013).

Impact on plant morphology

In parallel to alterations in biomass allocation, morphological acclimation towards reduced water loss and increased water uptake is crucial for plant growth and survival under drought. Poorter et al., (2012) suggest higher capacities for morphological modification than adjustments in resource allocation as a means of acclimation to stress. The quintessence of the varying morphological drought

responses is the maintenance of a functional equilibrium between transpiring and water absorbing interfaces. Effective means are reduction in foliage area (reduced leaf number and/or size, decreased specific leaf area (SLA), shedding: Bréda et al., 2006; Chaves et al., 2003; Kozlowski & Pallardy, 2002; Poorter et al., 2009), constitutive reduction of leaf conductance (reduced number and/or size of stomata: Hamanishi et al., 2012), increase in root-system surface area (increased rooting density, specific root length (SRL), decreased fine root diameter: Montagnoli et al., 2012; Ostonen et al., 2007; Tabata et al., 2010) and improvement of water accessibility (increased rooted soil volume, rooting depth, selective forwarding: Hodge, 2004; Reader et al., 1993). Regarding *F. sylvatica*, such drought responses are only partly confirmed in literature.

Results from Löf & Welander, (2000) and van Hees, (1997) confirm drought related decrease in foliage area, whereas the drought effect seems to be increased under high light conditions (Löf et al., 2005). SLA response is found to both water and light availability (Löf et al., 2005), however, the drought effect on SLA depends on the extend of water limitation during leaf expansion growth (Coll et al., 2004; Löf & Welander, 2000; Meier & Leuschner, 2008a). The study of Löf & Welander, (2000) on carry-over effects of drought do not corroborate the presumption of a constitutive reduction in leaf stomatal conductance in *F. sylvatica*. Results about morphological root traits, indicating enhancement in absorptive root surface area are ambiguous. While the observations of Hertel et al. (2013) and Meier & Leuschner, (2008b) fit to the above-mentioned reactions, Meier & Leuschner, (2008a) and van Hees, (1997) found SRL to be reduced under drought. According to Hodge, (2004), increased mechanical resistance of dry soil can impede root elongation and hence account for decreased SRL. Additionally, effects of interspecific competition (Bolte & Villanueva, 2006), differing light exposition (Čater & Simončič, 2010) and soil quality (Richter et al., 2011) may superimpose drought related response in SRL. The conclusion of Schall et al. (2012) that juvenile *F. sylvatica* responds with increased rooting depth under drought, is not corroborated by Löf, (2000) and Meier & Leuschner, (2008c).

Lethal drought stress

Apart from biotic agents (insect calamities or pathogen infection) that can attack trees in association with drought stress, hydraulic failure and carbon starvation are suggested to be the two main mechanisms leading to plant mortality and up to large scale forest decline (Adams et al., 2009; Anderegg et al., 2012; McDowell, 2011; McDowell et al., 2008, 2013; Sala et al., 2010). McDowell et al., (2008) discuss different strategies of plants to deal with the trade-off between water loss and carbon gain: On the one hand the isohydric strategy, characterized by early stomatal closure that maintains plant water status at the expense of carbon gain. Carbon starvation under prolonged drought may be a consequence. On the other hand the anisohydric strategy which sustains high rates of carbon assimilation at concurrently high transpiration under water limitation, risking excessive xylem embolism and hydraulic failure.

Evidence indicates that angiosperm woody species generally operate at higher risk of hydraulic failure than gymnosperm woody species (Choat et al., 2012). Comparisons between and *P. abies* and *F. sylvatica* follow this general pattern, indicating higher risk of hydraulic failure for *F. sylvatica* (Häberle, unpublished). Urli et al. (2013) reports that below a threshold for xylem water potential of -4.5MPa and the resulting conductivity loss of 88%, juvenile *F. sylvatica* is unable to recover from embolism. Risk of the occurrence of critical xylem water potentials and hydraulic failure may be high in general in juvenile plants, given their small and shallow growing root systems (McDowell et al., 2008).

The process of carbon starvation can be defined `as any situation in which carbon supply from photosynthesis and the mobilization of nonstructural carbohydrates (NSC) and autophagy (vacuolar proteolysis) is less than carbon use by respiration, growth, and defense´ (McDowell, 2011). Regarding *F. sylvatica*, no studies on drought related carbon starvation can be found in literature. However, the recent study from Hartmann et al. (2013) gives evidence that carbon starvation plays a role in drought-related mortality of juvenile *Picea abies*. The latter study also highlights that impeded transport of recent assimilates and hence carbon starvation of the root, rather than the depletion of overall carbon reserves, may be the key factor under prolonged water limitation. With reference to the results of Ruehr et al. (2009), showing transport of recent assimilates to be impeded under drought, such a latter

pathway of starvation is imaginable also in juvenile *F. sylvatica.* Especially in small plants, impeded carbon assimilation in parallel with increased carbon expenses for maintenance and repair processes may rapidly lead to a depletion of the small pool of carbon reserves (Niinemets, 2010) under drought.

1.3   The effect of breeding conditions and transplanting on field growth performance

Effect of breeding conditions and harvest on plant material

Breeding conditions in the nursery are decisive for the performance of the plants upon transplanting to the field (Duryea, 1985; Grossnickle, 2012). However in silvicultural practice, soil, water and light conditions in the nursery may substantially differ from those at the designated forest sites. In such cases, nursery conditions may therefore result in suboptimal acclimated plant material. High water and nutrient availability and root pruning during the harvest, commonly result in reduced R/S-ratios of nursery plants (Davis & Jacobs, 2005; Grossnickle, 2012; Kozlowski & Davies, 1975; Struve, 1990). During lifting, cutting of core roots and severing of fine roots is inevitable, hence crucially restricting root surface for water and nutrient uptake (Burdett, 1990). Such carry-over effects of the treatment in the nursery have to be considered as important constraints on developing stress tolerance during the early stage after transplanting

Impact of the transplant

According to Kozlowski & Davies, (1975), "The most important cause of death of transplanted seedlings is desiccation". Due to the reduced R/S-ratio and root surface area, in combination with the negative impact of the transplant on root-to-soil connectivity (Burdett, 1990; Grossnickle, 2005), the potential for water and nutrient uptake is critically lowered. Directly upon transplanting, the rooting space is usually limited to the upper soil horizons. In this soil depth, the transplanted seedlings face intense competition with mature trees and ground vegetation. Hence, the risk of desiccation becomes substantial. Coinciding drought during plant establishment has therefore to be considered as an extremely critical scenario for the success of forest plantations.

1.4   Forest stands upon wind-throw - environments of heterogeneous resource supply -

Wind-throw commonly results in a highly heterogeneous distribution of the remnants of the old stand, hence inducing pronounced patchiness of different combinations of light, water and nutrient availability (Wagner et al., 2011). Upon wind-throw, patches with high resource availability are rapidly colonized by early-successional herbaceous and woody pioneer species. In the upper soil horizons, intense competition with mature spruce (Schmid et al., 2005) and/or the upcoming ground vegetation (Coll et al., 2004; Fotelli et al., 2002) for water can become crucial for under-planted juvenile *F. sylvatica*. According to Holmgren et al. (2012), shade may alleviate the effect of drought stress in shade-tolerant species. However, evidence exists that despite high shade tolerance, growth performance of juvenile *F. sylvatica* increases with increasing light exposure, even under dry conditions (Aranda et al., 2004; Robson et al., 2009).

Given the spatial heterogeneity of wind-throw forest sites, consideration of prevailing patterns in water and light availability and their combinations is crucial when analyzing growth response and morphological acclimation.

2   Modules of the study

Focus and aim of the conducted experiments:

The conducted study consists of three complementary experiments, each focusing on a different aspect of the drought response of juvenile *F. sylvatica* (cf. Fig. 2.1).

The main experiment was focused on the response of juvenile *F. sylvatica* to annually recurring summer drought during the early stage of establishment in a Norway spruce stand, previously opened through wind-throw. To simulate recurring summer drought events in the three years upon transplanting from the nursery to the forest site, a precipitation manipulation experiment was carried out in the respective stand. Considering the characteristic spatial heterogeneity of growth conditions of such a wind-throw situation, the reactions of *F. sylvatica* was related to the individual availabilities of water and light (results of the experiment are published in Goisser et al. 2013, cf. appendix 1).

In conceptually complementary ways, two short-term experiments (one growing season) were carried out at the same study site, to investigate underlying drought response mechanisms of root growth and whole-plant carbon allocation of *F. sylvatica*:

(I) a $^{13}CO_2$ pulse labeling experiment: $^{13}CO_2$ pulse labeling is a capable experimental method to trace the pathways of recently fixed carbon. It enables for the assessment of transport velocities and mean residence times (Kuzyakov & Gavrichkova, 2010) as well as for the determination of allocation patterns of recently fixed carbon. In the present two-stage $^{13}CO_2$ pulse labeling experiment the effect of prevailing drought stress on the leaf-to-root transport of recent photosynthates and the response of transport and partitioning of recently fixed carbon to rewetting was investigated (results of the experiment are published in Zang et al. 2014, cf. appendix 2).

(II) a rhizotron experiment: Rhizotrones represent a nondestructive method to investigate the behavior of root systems and root growth dynamics (Huck & Taylor, 1982; Taylor et al., 1990). In the present rhizotron experiment the dynamic of fine root growth and rhizosphere respiration during the induced drought, as well as the drought response of fine root morphology was investigated (results of the experiment are published in Zang et al. 2013, cf. appendix 3).

Both short-term experiments were carried out on a cleared area within the stand warranting spatially homogenous light conditions. Competition was excluded in both short-term experiments. The detailed description of experimental design and methods of the respective experiment is to be found in Goisser et al. (2013), Zang et al. (2014) and Zang et al. (2013).
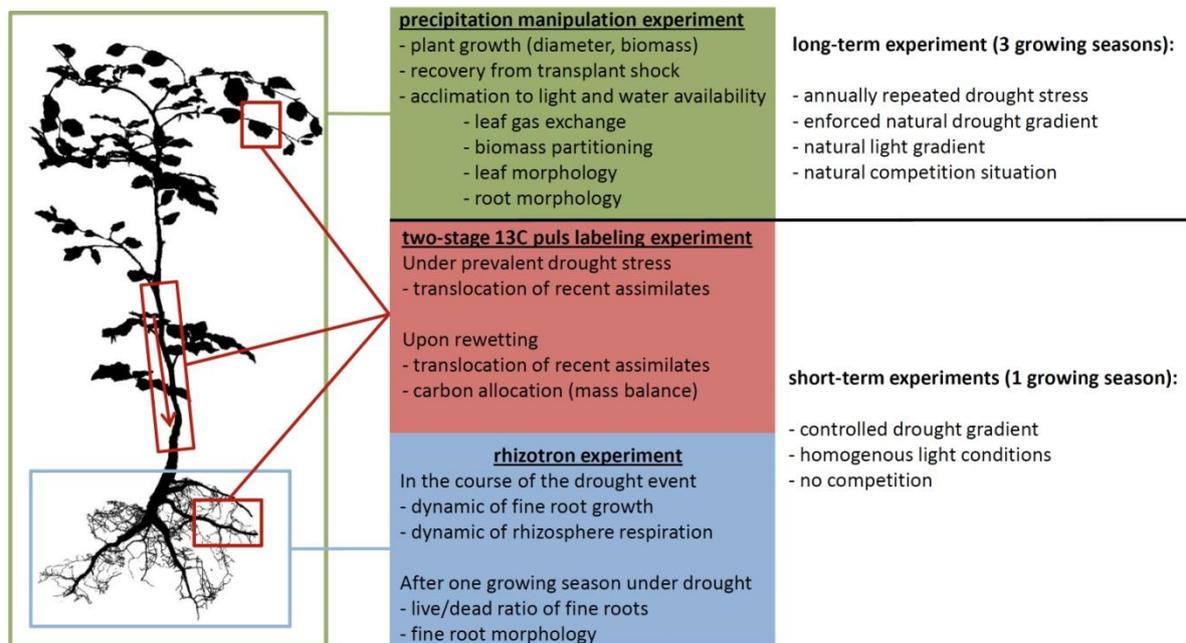
Figure 2-1: Overview on the modules of the study and the particular focus of the respective experiment

Ensuring comparability between the experiments

Comparability regarding genetic disposition and breeding conditions of the employed plant material was ensured as plants derived from the same nursery, originating from same provenance. All experiments were conducted at the same study site, ensuring the same climatic conditions. Soil from the study site was used in the rhizotron and the labeling experiment to ensure comparable edaphic conditions. In all experiments the drought treatment was conducted after complete differentiation of the leaves and lasted for 8 to 12 weeks within the growing season. According to Vicca et al. (2012) a common metric of drought stress quantification is indispensable to provide comparability of results between different drought experiments. To this end, calculation of a drought stress dose (DSD) based on the assessment of soil water potential as $DSD = \int \Psi_{soil}(t)$, was employed across the experiments. The ranges of drought stress intensity induced in the rhizotron and the labeling experiment were comparable with the drought stress gradient observed in the precipitation manipulation experiment.

3   General discussion

3.1   Approaching a generic concept of the response of juvenile *Fagus sylvatica* to light, water and nutrient limitation during the early stage of establishment

That plants respond to light limitation with decreased and to water and nutrient limitation with increased R/S-ratio has long been recognized in plant science (Brenchley, 1916; Maximov, 1929; Shirley, 1929). Different concepts describing such response of root-shoot biomass partitioning to varying resource availabilities are prevalent in literature (e.g. `balanced growth hypothesis´: Shipley & Meziane, 2002; `optimal partitioning theory´: Gedroc et al., 1996; `set-point argument´: Mooney & Winner, 1991). The underlying hypothesis of these concepts is that by adjusting R/S-ratio, carbon, water and nutrient uptake and hence the proportion of internal resource pools (e.g. C/N-ratio: Mooney & Winner, 1991; Thornley, 1972) is attuned towards the stoichiometric optimum for plant tissue formation (Chapin et al., 1987; Gleeson & Tilman, 1992; Shipley & Meziane, 2002), resulting in maximized growth (Bloom, 1985; Dewar, 1993; Mooney & Winner, 1991; Thornley, 1972).

However under field conditions, adjustments of biomass allocation are related to a multitude of interacting plant inherent and environmental factors (cf. chapter 1.2) and the momentary response in R/S-ratio may be modulated by lasting effects of prior growth conditions and treatments (e.g. Grossnickle, 2012; Kozlowski & Pallardy, 2002). In parallel with the response of R/S biomass allocation, adjustments of morphological traits of the resource absorbing organs towards increased resource uptake efficiency (Eissenstat, 1992; Poorter et al., 2006) is highly relevant for the acclimation to limited resource supply (Poorter et al., 2012).

Present results show that juvenile *F.sylvatica* adjusts both, biomass allocation and morphological traits in response to recourse limitation. Additionally, carry-over effects imposed by growing conditions in the nursery as well as the transplant became evident (cf. appendix 1 and 3). Hence, a generic concept that integrates such observed effects is needed, to provide a holistic view on the response of recently transplanted juvenile *F. sylvatica* to heterogeneous resource availabilities in the competitive scenario of an opened mature spruce stand.

In the following, the term `functional equilibrium´ will be used to describe the response to resource limitation, for two reasons: According to Wilson, (1988), `functional equilibrium´ subsumes all the above mentioned concepts in their common basic idea that the adjustment of biomass allocation to root and shoot aims towards a functional equilibrium between resource uptake and expenditure. Second, the term `functional equilibrium´ provides a higher "degree of freedom" as its meaning is not restricted to the response of biomass allocation, but also includes morphological adjustments towards a higher efficiency of resource uptake.

Implementing experimental results and boundary conditions into the framework of the functional equilibrium concept: Based on the theoretical framework of a functional equilibrium, a conceptual model of the response of *F. sylvatica* L. to varying light, water and nutrient availability during the critical period upon transplantation from nursery conditions to the competitive scenario of a spruce stand restoration has been developed (Figure A-S-2, appendix S). Considering the effect of the breeding conditions in the nursery and the impact of the transplant, the concept links between responses of biomass allocation and morphology.

Breeding conditions are decisive for initial acclimation status and hence growth performance upon transplantation (Duryea, 1985; Grossnickle, 2005, 2012). In the present study, non-limiting light availability in the nursery induced initial high-light acclimation, which was indicated by eminently low SLA values. High-light acclimated foliage was characterized by high leaf dark respiration rate and reduced efficiency of photosynthesis (cf. appendix 1). In the nursery, irrigation prevented the occurrence of drought (cf. appendix 1). Additionally, high nutrient availability is assumed. Such breeding conditions imply the absence of adjustments of R/S-ratio and root morphology towards an efficient water and nutrient uptake (Grossnickle, 2012). Typically, nursery plants loose a considerable part of absorptive root area due to severing of fine roots and root pruning during lifting (Kozlowski & Davies, 1975). Upon transplantation, root-to-soil connectivity is typically strongly reduced (Burdett, 1990; Grossnickle, 2005; Kozlowski & Davies, 1975). The above described effects of breeding conditions and transplant are implemented into the concept as negative presetting of shoot and root traits to light, water and nutrient limitation (①, Figure A-S-2).

Upon transplant to the forest site, light, water and nutrient availability was determined by competition from the spruce remnants and upcoming ground vegetation. In agree with previous observations of Ammer & Wagner, (2002) in a mature spruce stand, a significant negative correlation between size of and proximity to the mature spruce trees (here expressed as competition index, CI, after Hegyi, 1974) and soil water availability was found on the rainfall exclusion plots (Goisser et al., unpublished, cf. Figure A-S-1, appendix S). Consistent with results of Wang et al. (2001), nutrient concentrations in the fine roots of the beech plants correlated negatively with CI_{Hegyi} (Goisser et al., unpublished, cf. Table A-S-1, appendix S). In line with Lindh et al. (2003), the abundance of ground vegetation was positively correlated with the distance to mature spruce trees and, hence, decline in competition. The correlation of light availability with CI_{Hegyi} showed a non-significant negative trend. The fact that the employed competition index does not consider the cardinal direction of the competitors (spruce trees) and that upcoming ground vegetation was also substantially responsible for shading, may account for the non-significant correlation between CI_{Hegyi} and individual light availability of the beech plants. Consistently, light and water availability were found to be spatially independent (cf. appendix 1). The present concept considers therefore above and below ground competition as independent drivers for light and water/nutrient availability. In contrast to independency between light and water availability, competition by mature spruce was shown to have a significant negative effect on both, water and nutrient availability (Table A-S-1, appendix S). Evidently, water and nutrient availability were inextricably linked in the precipitation manipulation experiment. Direct interactions between water and nutrient availability in the soil (Dunham & Nye, 1974, 1976; Dyer et al., 2008) are disregarded in the present concept. Due to the negative effect of competition on resource availability, availabilities of light and water/nutrients are inversely related to the intensity of above and belowground competition (②, Figure A-S-2). How efficient resources are taken up depends on the combination of biomass (quantity) and morphology (quality) of shoot and root respectively and represents thereby the state of acclimation of these compartments to resource limitation (③, Figure A-S-2). As shown for leaf and fine root morphology (cf. appendix 1 and 3), light and water/nutrient limitation act as stimuli for morphological adjustments towards higher resource uptake efficiency of the respective organs (④, Figure A-S-2). Carbon assimilation, water and nutrient

uptake result of the combination of resource availability and resource uptake efficiency (⑤, Figure A-S-2).

Internal pools of carbon and nutrients are supplied by photosynthesis and nutrient uptake respectively (⑥, Figure A-S-2). Depending on the offset between internal carbon and nutrient availabilities and the optimum stoichiometric proportion of these resource pools (⑦, Figure A-S-2), resources are preferentially invested either into root or shoot growth (⑧, Figure A-S-2). Resource allocation to growth determines the increment of shoot and root biomass (⑨, Figure A-S-2). Present results of biomass analysis (R/S-ratio vs. DSD, cf. appendix 1 and 3) adjust to this aspect of the functional equilibrium concept.

To exemplify plant response to different combinations of resource availability, four extreme combinations of above and below ground competition and corresponding light, water and nutrient availabilities were applied to the present concept (Figure 3.2-1):
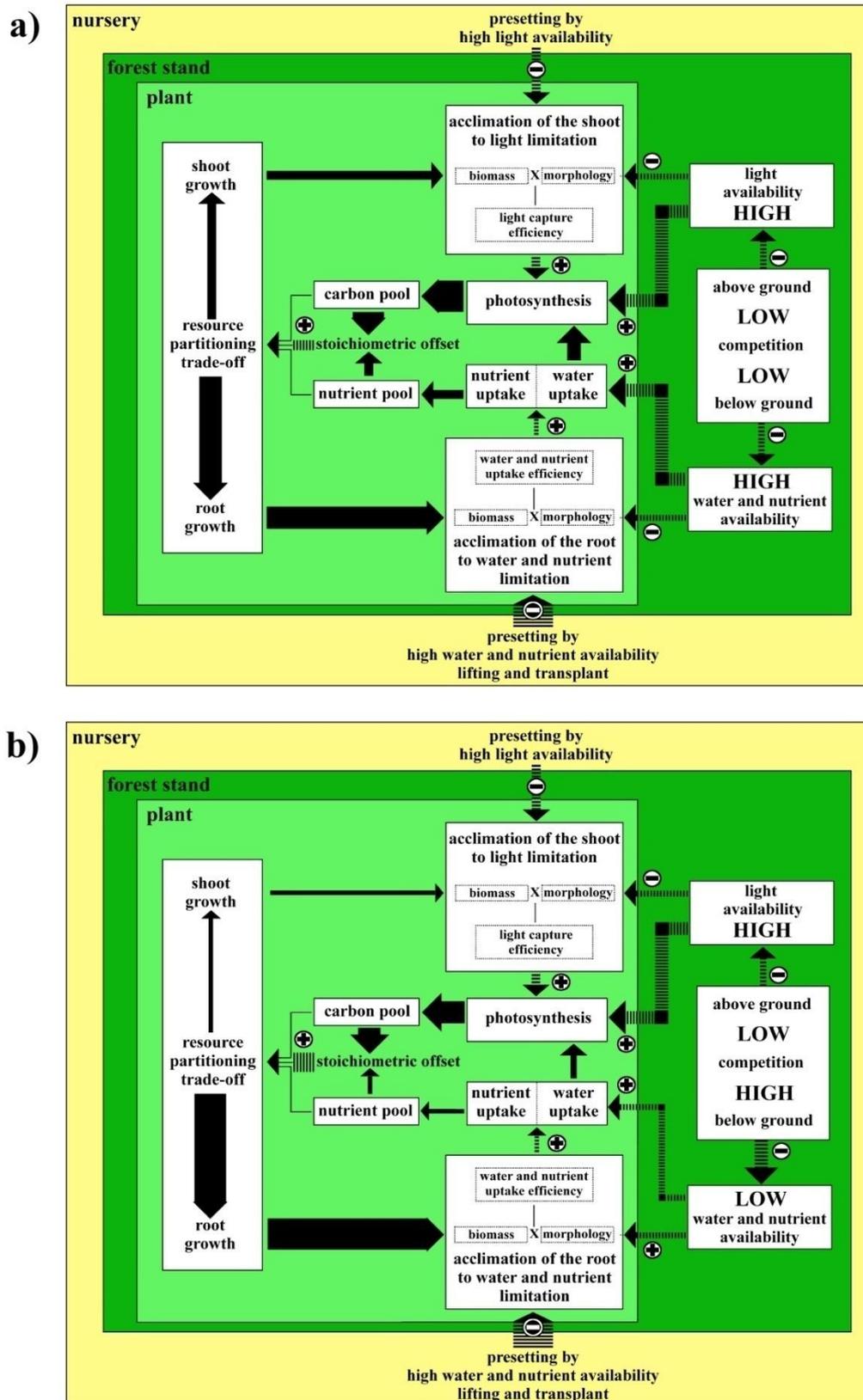
Figure 3.2-1: Schematic presentation of resource allocation and morphological adjustments in *F. sylvatica* as response to different combinations of high and low availability of light and water/nutrients during the early stage of establishment.
Shown are internal fluxes of carbon, water and nutrients (solid arrows) and prevailing dependencies (broken arrows) in their qualitative magnitude (arrow width) and effect direction (algebraic signs) for the four combinations of: (a) high light and high water/nutrient availability corresponding to low above ground and low below ground competition, (b) high light and low water/nutrient availability corresponding to low above ground

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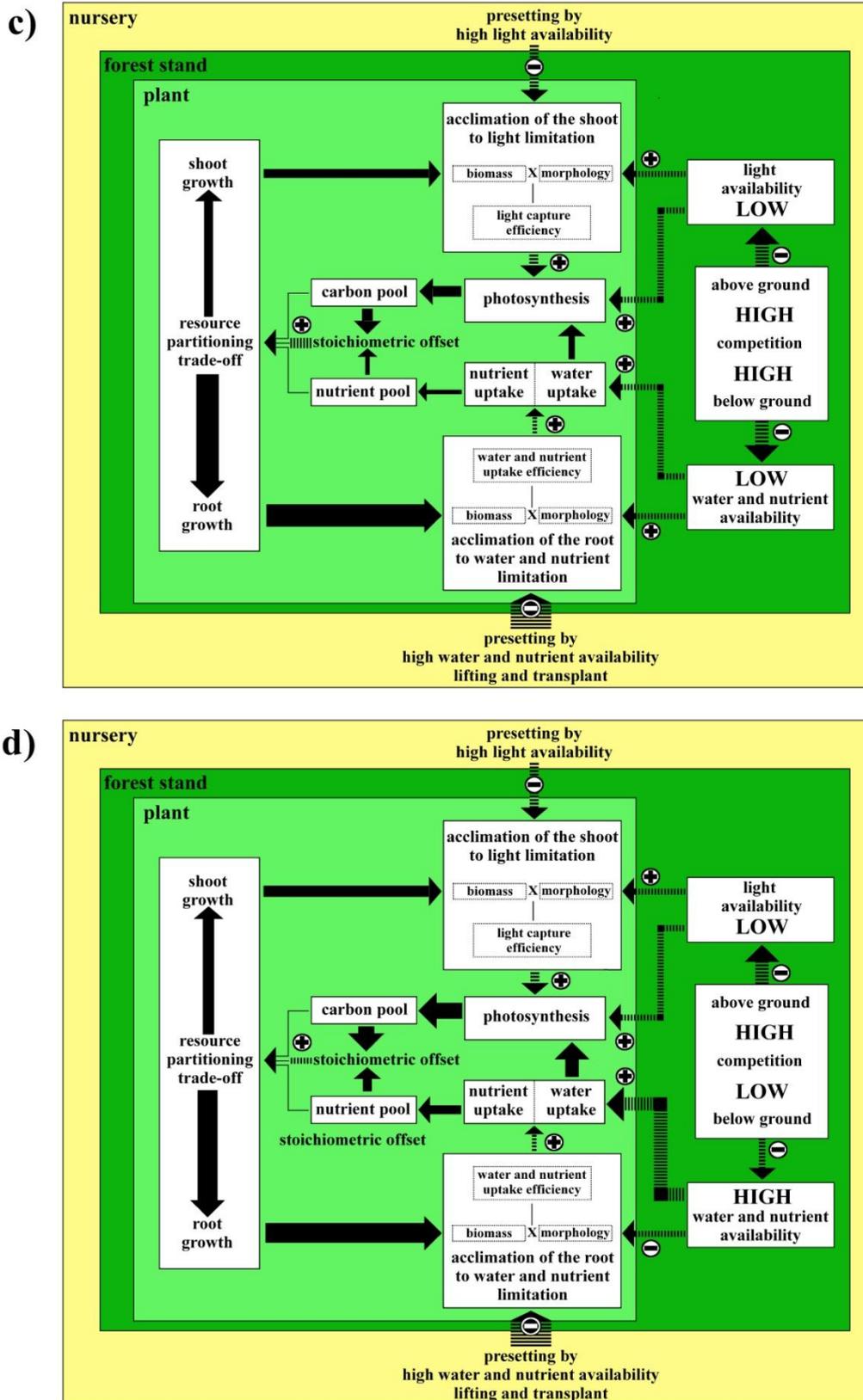
and high below ground competition, (c) low light and low water/nutrient availability corresponding to high above ground and high below ground competition, (d) low light and high water/nutrient availability corresponding to high above ground and low below ground competition; The terms `high´ and `low´ refer to the observed maximum or minimum of competition and resource availability in the present study. The magnitudes of the resource fluxes from the resource pools to resource partitioning are omitted for graphical reasons. A detailed description of the particular fluxes and dependencies is given in Figure A-S-2.

Adjustments towards a functional equilibrium in the context of the transplant shock:
According to the threefold negative effect of high water and nutrient availability in the nursery, root injury during lifting and poor root-soil connectivity upon transplanting, a predominant negative presetting of the root and hence strongly reduced water and nutrient uptake efficiency is presumed in the present concept. As consequence of the strong negative presetting of the root, the concept implies that root growth is generally promoted for all combinations of light and water/nutrient availability. This outcome adjusts to experimental results, showing root biomass to be independent of total DSD and LD (cf. appendix 1), highlighting the overriding role of root growth during recovery from transplant shock (cf. Burdett, 1990; Grossnickle, 2005). According to the underlying optimal partitioning concept and in agree with results of other studies on juvenile *F. sylvatica* (e.g. Löf et al., 2005; Schall et al., 2012), the present concept also implies that under light limitation relatively more biomass should be allocated into the shoot, hence resulting in lower R/S-ratios. However, in this aspect present results conflict with the optimal partitioning theory, as no correlation between R/S-ratio and light availability was found. Such unresponsiveness of root-shoot biomass partitioning to light is in agree with Curt et al. (2005) and with observations of Madsen, (1994) on water limited juvenile *F.sylvatica*. According to Poorter & Nagel, (2000), nutrient limitation has a stronger effect on biomass partitioning than light limitation, which may explain present results. Also the direct effect of root damage on shoot growth may be causal for the lacking light response of shoot biomass, as root pruning causes a hormonal down regulation of shoot growth at concurrently enhanced root growth (Poorter & Nagel, 2000; Saure, 2007; Wilson, 1988). The fact that in horticulture root pruning is employed in order to control shoot growth of fruit trees (Saure, 2007) illustrates the considerable effect strength of such a treatment. As described in appendix 1, the employed plant material was neither transplanted nor undercut in the nursery. According to Kozlowski & Davies, (1975), especially such non-pruned plants suffer severe root damage during the harvest in the nursery, as they normally have only few but long roots which are largely cut during lifting. Assumedly, hormonal inhibition of shoot growth may have superimposed the stimulating effect of shade on shoot growth upon transplanting and may account for the non-significant correlation between R/S-ratio and LD.

Especially in context of impeded shoot growth, juvenile *F. sylvatica* particularly benefits from its pronounced potential for shade acclimation of the foliage (cf. Curt et al., 2005), as indicated by progressively increased efficiency of photosynthesis as well as progressively reduced shade sensibility of diameter growth (cf. appendix 1).

Assimilate supply of the root under drought and its implication for growth and morphology of fine roots: In contrast to the absent response of root biomass in the precipitation manipulation experiment, results from the rhizotron experiment show fine root growth to be promoted under moderate (Ψ_{soil} around -0.4 MPa), but to be reduced under severe soil drought ($\Psi_{soil} \leq$ -1.0 MPa). Such unimodal response pattern may account for conflicting results of the drought response of fine root growth and turnover and in literature (cf. chapter 1.2).

Evidence underlines that in trees, a large part of the carbon demand of fine root production is fueled by recent photosynthates (Gaudinski et al., 2001; Joslin et al., 2006; Lynch et al., 2013; Sah et al., 2011; van den Driessche, 1987). Results of the precipitation manipulation experiment (gas exchange data of 2011, appendix 1) show that moderate drought ($\Psi_{soil} \geq$ -0.5 MPa) had only minor effect on g_s and A_{net}, whereas stomatal limitation of photosynthesis significantly increased as soon as Ψ_{soil} dropped below -0.5 MPa. This observation is in accordance with the results of gas exchange measurements in the labeling and the rhizotron experiment (appendix 2 and 3). Assuming similar values for $\Psi_{leaf\ pd}$ and corresponding Ψ_{soil} (cf. highly significant correlation between $\Psi_{leaf\ pd}$ and Ψ_{soil}, appendix 1), this result is also in accordance with previous observations from Tognetti et al. (1994, 1995) in juvenile *F. sylvatica*. Beyond reduced carbon assimilation under drought, drought-impeded shoot-root carbon translocation (Deng et al., 1990; Holtta et al., 2009; Plaut & Reinhold, 1965) may also reduce carbon supply of the root compartment and hence fine root growth. In consistency with reports of Ruehr et al. (2009) on juvenile *F. sylvatica*, present results confirm the restraint on assimilate transport to the root compartment under severe drought stress ($\Psi_{soil} \leq$ -1.2 MPa) (cf. appendix 2). Implied is that under prolonged drought, below ground C-demand for maintenance, as well as structural growth increasingly relies on C-supply from the carbon storage pool of the root compartment. In line, recent findings of

Hartmann et al. (2013) on juvenile *Picea abies* show the depletion of the root carbon pool and related mortality under continuous severe water limitation.

Present results indicate that, in spite of rapid recovery of photosynthesis and assimilate transport velocity upon rewetting, root-directed carbon allocation stayed reduced in such plants that had previously experienced drought stress (cf. appendix 2). Reduced conductivity of sieve cells after experienced drought stress (Woodruff, 2014) may account for such result.

This implies that, besides the negative effects of low soil water potentials (Joslin et al., 2000) and increased mechanical resistance of dry soil (Bengough et al., 2006) on fine root elongation growth, impeded assimilate supply of the root compartment may additionally contribute to the observed depression in fine root growth under severe drought. This assumption is corroborated by the observed reduction of rhizosphere respiration under severe drought, indicating reduced metabolic activity under severe water limitation.

Reduced fine root growth conflicts with the need for compensatory fine root growth upon increased fine root mortality under severe drought (Bréda et al., 2006; Eissenstat et al., 2000; Meier & Leuschner, 2008b). Especially in recently transplanted plants with need for root recovery and restoration of an adequate balance between transpiring and water-absorptive plant surface areas, inhibited C supply to roots can become crucial under persisting drought (Burdett, 1990; Grossnickle, 2005).

Joslin et al. (2000) and Olesinski et al. (2011) report root growth to be promoted during favorable periods for various deciduous broadleaf tree species. Still in late autumn, *F. sylvatica* exhibits the potential of relevant fine root growth (Mainiero et al., 2010). Due to the humid climate at the study site, water availability was only limited during 8 to 12 weeks in summer when the roofs were covered. Hence, compensatory root growth during autumn and spring at ample water availability may have facilitated the formation of high R/S-ratios and may account for the non-significant correlation of root biomass and DSD in the precipitation manipulation experiment.

Despite compensatory root growth during an extended period of non-limiting water availability, persisting drought may limit fine root growth through curtailed belowground C flux and temporarily decouple the adjustment between water-absorptive and transpiring plant surface areas. The generalized

conclusion that below ground carbon allocation is increased under drought (cf. Appendix 3), has therefore to be differentiated between instantaneous carbon allocation under prevailing drought stress and long-term adjustments of carbon allocation after an extended recovery period.

Root morphological data from both the rhizotron and the precipitation manipulation experiment indicate drought to favor growth of finest roots (cf. appendix 1 and 3). Such morphological response appears to reflect efficient resource investment in the formation of absorbing root surface area (Eissenstat, 1992; Grams et al., 2002), perhaps being a strategy that compensates for restrictions in C supply for fine root growth.

3.2 Remarks on the present methodological approach of drought induction and drought stress quantification.

Rainfall exclusion as a means of drought induction: Possible side effects of roof constructions are the reduction of light reaching the forest floor along with further alterations of micro-climate, interference with nutrient cycling upon impeded leaching from canopies and lowered litter input (Gundersen et al., 1998).

In the present study, roof constructions stayed uncovered during 9 to 10 months of the year. During that period, roof impact is assumed to have been negligible. In fact, no significant micro-climatic differences were found across 117 measurement positions between control and open-roof plots. (T_{air} below and beside the roof, t-test: $p = 0.44$). However, upon roof closure, light attenuation was significant as accounting for a 27 % reduction of PPFD (PPFD below and beside the roof, t-test: $p < 0.05$). This effect was accounted for by the data analysis which also considered beech tree-related differences in light availability as being dominated by shading through mature spruce trees and ground vegetation.

Rainfall exclusion enables for the induction of soil drought even under generally humid atmospheric conditions. Notwithstanding, vapor pressure deficit (VPD_{air}) is the driving factor of evaporation and transpiration and determines dynamic and intensity of water consumption from the soil and build-up of soil drought. Hence, experimental soil desiccation under climatic conditions characterized by low VPD_{air}, develops slower and drought intensity remains lower as compared with

conditions that prevail during natural drought events, which are typically characterized by high T_{air} and high VPD_{air}. Furthermore, VPD_{air} has a direct effect on stomatal conductance (Grantz, 1990; Lange et al., 1971; Oren et al., 1999), thus modulating the response to soil drought mediated through root-shoot signaling (cf. Davies & Zhang, 1991). Lendzion & Leuschner, (2008) showed that in seedlings of *F. sylvatica* stomatal conductance, total leaf area, SLA and biomass increment were significantly reduced under increasing VPD_{air} even under non-limiting soil water availability.

Present results indicate that for the severely drought stressed plants the threshold for incipient xylem embolism of -1.9 MPa in *F.sylvatica* (Hacke & Sauter, 1995) was exceeded. However low VPD_{air} at the study site apparently impeded the decline of xylem water potentials below the critical threshold for hydraulic failure at -4.0 to -4.5 MPa xylem water potential (Barigah et al., 2013; Czajkowski et al., 2009; Urli et al., 2013), so that mortality from hydraulic failure was not reached. Apparently, under the humid natural conditions of the study site, precipitation exclusion periods were too short to induce lethal drought stress. Considering the relevance of high VPD_{air} and high T_{air} for the plant water status (i.e. xylem water potential) and carbon balance (through increased respiration rates, c.f. chapter 1.2), it is concluded that given similar levels of soil water limitation, the impact of natural drought on plant performance should be stronger than observed in the present experiment.

Cumulative soil water potential (DSD) - a concept for drought stress quantification: According to McDowell et al. (2008), drought events are characterized through both intensity and duration of water limitation, so that different qualities of drought stress result.

The concept of drought stress quantification used in the present study with $DSD = \int \Psi_{soil}(t)$, integrates both, intensity and duration of water limitation. In contrast to common approaches of drought quantification (e.g. as based on means or maxima of volumetric soil water content or soil/leaf water potentials) the advantage of the DSD concept is the integration of the time course of soil desiccation, inherently covering and quantifying recurring drought events (e.g. with DSD extending over three consecutive years in this study). However theoretically, different combinations of intensity and duration of drought as well as intermittent peaks of Ψ_{soil} can result in the same value of DSD.

In the present study, precipitation exclusion resulted in monotonically decreasing time courses of Ψ_{soil}. The induction of intermittent maxima in Ψ_{soil} due to irrigation in the rhizotron and labeling experiment was restricted to short time intervals (once per one to three days). Also, only small amounts of water were applied each time through slow and homogenous infiltration into the soil (cf. chapter 3.2 and 3.3). The duration of drought treatment did not differ substantially between experiments and plant individuals, ranging consistently between 10 to 12 weeks (8 weeks during the first year). Therefore, DSD calculation as $\int\Psi_{soil}$ (t) ensures comparability across plant individuals and experiments. DSD as drought index can be regarded as a first step towards a generic method of drought quantification, needed to facilitate the transferability of results between drought stress studies (Vicca et al., 2012). Consideration of duration/intensity interactions in determining the DSD function will increase the ecological relevance of this stress index.

4   General conclusions

The present study provides novel insights into the concerted light and drought response of juvenile *F. sylvatica* during the early stage of establishment under the competitive conditions of a mature spruce stand upon wind-throw. Integration of the present results into the conceptual framework of a functional equilibrium, uncovered relevant physiological mechanisms that underlie the response to concurrent light, water and nutrient limitation during the critical stage of establishment.

Increased resource uptake efficiency by means of morphological adjustments of leaf and fine roots compensate for impeded adjustments in biomass allocation: Adjustments of biomass allocation to shoot and fine root growth in response to light and water limitation were shown to be impeded by the effect of root pruning and impeded long-distance transport of assimilates under severe drought. Beyond the response of biomass allocation, the capacity of juvenile *F. sylvatica* to adjust leaf and fine root morphology towards an increased efficiency of resource uptake was found to be decisive for the growth performance of recently transplanted *F. sylvatica* under light and water limitation.

Adequate acclimation to light limitation can increase productivity under drought: Initial high-light acclimation and progressive acclimation to the shady conditions at the forest site was indicated by a gradually increase of SLA at concurrently increased mass-based CO_2 assimilation rate and water-use-efficiency of photosynthesis. In the course of the experiment, progressive recovery from transplant shock and simultaneous acclimation to drought and shade resulted in a gradually increased diameter growth.

Drought response of leaf gas exchange indicates an anisohydric drought strategy in F. sylvatica: The results of leaf gas exchange measurements showed that g_s and A_{net} is only minor effected for Ψ_{soil} above -0.5 MPa. The marginal stomatal reaction for Ψ_{soil} above -0.5 MPa may indicate an anisohydric drought response strategy of *F. sylvatica*. Assumedly, such strategy is advantageous under moderate drought stress intensity, as it enables the plant to keep up carbon assimilation and hence provide assimilate supply for fine root growth.

5 Implications and recommendations for silvicultural practice

Forest plantations are expensive and labor-intensive. The successful establishment of such plantations is hence crucial for the economic efficiency in silviculture. Vigor and competitiveness of the employed plant material is decisive during establishment, especially under conditions of low resource availability (e.g. due to a drought incident) at concurrently high competition.

Silvicultural possibilities to influence the performance of *F. sylvatica* upon transplant are related to inherent growth potential of the plant material and particular environmental conditions at the forest site (Grossnickle, 2012). In this chapter, results of the present study will be linked with knowledge from literature to deduce possible approaches in order to increase growth performance of juvenile *F. sylvatica* during the early stage of establishment.

Breeding conditions in the nursery: In contrast to the high silvicultural effort to adapt German forests to climate change, still no recommendations for the production of drought acclimated nursery plants are specified (cf. §12 FoVG; Schlegel, 2009). This is remarkable, considering the available knowledge of possible practices of drought hardening in the nursery (Grossnickle, 2012).

Present results show that juvenile *F. sylvatica* has the potential for effective drought acclimation of the root system. A moderate drought stress treatment in the nursery could stimulate root growth in general as well as the adjustment of root morphological traits towards increased efficiency of water and nutrient uptake (cf. appendix 1 and 3). Under severe drought the R/S-ratio of juvenile *F. sylvatica* was increased to > 0.7 (cf. appendix 1). This implies that commonly recommended R/S-ratios of 0.5 for small nursery plants (15-30cm plant height) and 0.25 for larger plants (80-120 cm plant height) (Schlegel, 2009) are definitely far from being optimal under water limitation.

Root pruning in the year before lifting could stimulate root growth and ramification and furthermore reduce following damage on the root system during lifting (Kozlowski & Davies, 1975). Following the assumptions in chapter 3.1, reduced root injury during lifting could also facilitate above ground competitiveness for light upon transplant, as hormonal shoot growth repression would be mitigated.

In the present study, plants progressively acclimated foliage morphology to low light conditions at the forest site. Shade preconditioning of *F. sylvatica* in the nursery could take advantage of its high

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plasticity in leaf morphology. Adequate light acclimation of the foliage to prevailing light conditions in the designated forest site can increase the efficiency of carbon assimilation and water-use-efficiency of photosynthesis and consequently facilitate growth and the regeneration from transplant shock (cf appendix 1). According to Eschrich et al. (1989), the application of a shade stimulus between June and July induces the formation of shade-leaf primordia in developing buds in *F. sylvatica*. Such treatment in the growing season before transplant to the forest site should provide a significant shade acclimation of the foliage in the subsequent year. Unintended side effects of the shade treatment, such as reduced overall growth and reduced R/S-ratios, can be assumed to be of minor extent, as the shade stimulus can be restricted to less than two month in total.

Plantation and site preparation: During a drought event, water reserves in the upper soil horizons are depleted very soon, especially under intensive root competition by shallow rooting spruce and ground vegetation (Schmid et al., 2005). Present results indicate that seedlings of *F. sylvatica* tend to avoid severe drought stress and competition in the upper soil layer by means of increased rooting depth (cf. appendix 1). In the same manner, transplanting the seedlings deeper into the soil could help them to elude the strong competition for water and nutrients in the upper soil layer and facilitate the access to deeper soil water resources (Oliet et al., 2012). However, the increase in transplant depth may be limited by technical reasons (e.g. seedling size, planting tool, stony soil, time consumption per planted seedling).

Water and nutrient availability decreased with increasing proximity to the spruce trees (Goisser et al., unpublished, appendix S). Root trenching of overstorey spruce trees can increase water and nutrient availability and hence growth of juvenile *F. sylvatica* within the trenched area (Ammer, 2002; Petritan et al., 2011). Trenching of overstorey roots around the transplanted seedling could transitionally reduce below ground competition and hence facilitate plant establishment during the most critical stage immediately after transplant.

At the stand level, thinning reduces above and below ground competition, resulting in increased light availability as well as increased soil water availability during drought (Aussenac & Granier, 1988; Breda et al., 1995; Sohn et al., 2013). Reduced below ground competition also implies higher nutrient

availability (Wang et al., 2001). According to the present results and in line with Johnson et al. (1997), growth of underplanted *F. sylvatica* can be increased and the risk of drought related losses reduced by a lower stem density of the overstorey. However thinning intensity is crucial, as heavy thinning may also impose negative side effects such as photoinhibition due to high light exposition (Aranda et al., 2004; Robson et al., 2009; Tognetti et al., 1997, 1998), elevated VPD_{air} (Lendzion & Leuschner, 2008) at the forest floor as well as increased competition by upcoming ground vegetation (Goisser et al., unpublished, appendix S; Lindh et al., 2003; Wagner et al., 2011).

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§12FoVG, n.d. Forstvermehrungsgutgesetz vom 22. Mai 2002 (BGBl. I S. 1658), das zuletzt durch Artikel 37 des Gesetzes vom 9. Dezember 2010 (BGBl. I S. 1934) geändert worden ist.

Appendix 1: Growth of juvenile beech (*Fagus sylvatica* L.) upon transplant into a wind-opened spruce stand of heterogeneous light and water conditions[I]

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Abstract

Climate models predict increasing frequency and intensity of summer drought events for Central Europe. In a field experiment, we investigated the response of young beech (*Fagus sylvatica* L.) to extreme and repeated summer drought and the modulation of drought response patterns along the natural gradient of light availability at the study site. In autumn 2008, two-year-old, nursery derived beech – as used for forest conversion practices – was planted under a Norway spruce stand primarily opened through winter storm. Precipitation was manipulated in the growing seasons of 2009 through 2011, inducing a pronounced gradient of water availability. Individual drought-stress doses (DSD) and light doses (LD) were calculated for each beech sapling during the three growing seasons. Plant growth, CO_2-assimilation rate and stomatal conductance were reduced with increasing drought stress, but facilitated by increasing light availability. Progressive acclimation to water and light limitation during the three years of the experiment led to a decreased drought and shade sensitivity of diameter growth. Water-use efficiency, root/shoot ratio and rooting depth, were increased with decreasing water availability. Mean fine root diameter and specific fine root length correlated positively with both DSD and LD. Proceeding low-light acclimation was indicated by progressively increasing specific leaf area and reduced leaf dark-respiration. Present results suggest that nursery-induced high-light acclimation of the beech saplings, exacerbated light limitation upon transplant and hence productivity decline under co-occurring water limitation.

Appendix 2: Fate of recently fixed carbon in European beech (*Fagus sylvatica*) saplings during drought and subsequent recovery [II]

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Abstract

Drought reduces the carbon (C) assimilation of trees and decouples aboveground from belowground carbon fluxes but little is known about the response of drought-stressed trees to rewetting. This study aims to assess dynamics and patterns of C allocation in beech saplings under dry and rewetted soil conditions.

In October 2010, five-year-old beech saplings from a forest site were transplanted into 20 L pots. In 2011, the saplings were subjected to different levels of soil drought between non-limiting water supply (control) to severe water limitation with soil water potentials of < -1.5 MPa. As a physiologically relevant measure of drought, the cumulated soil water potential (i.e. *drought stress dose*) was calculated for the growing season. In late August, the saplings were transferred into a climate chamber and pulse-labeled with ^{13}C-depleted CO_2 (δ^{13}C of -47 ‰). Isotopic signatures in leaf and soil respiration were repeatedly measured. Five days after soil rewetting, a second label was applied using 99 atom-% $^{13}CO_2$. After another 12 days, the fate of assimilated C in each sapling was assessed by calculating the ^{13}C mass balance.

Photosynthesis decreased by 60 % in saplings under severe drought. The mean residence time of recent assimilates in leaf respiration was more than three times longer than under non-limited conditions and was positively correlated to drought stress dose. Also the appearance of label in soil respiration was delayed. Within five days after rewetting, photosynthesis, mean residence time of recent assimilates in leaf respiration and appearance of label in soil respiration recovered to full extents. Despite the fast recovery, less label was recovered in the biomass of the previously drought-stressed plants which also allocated less C to the root compartment (45 % vs. 64 % in the control).

We conclude that beech saplings quickly recover from extreme soil drought, although transitional after-effects prevail in C allocation, possibly due to repair-driven respiratory processes.

Appendix 3: Effects of drought stress on photosynthesis, rhizosphere respiration, and fine-root characteristics of beech saplings: A rhizotron field study[III]

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Abstract

Soil drought influences the carbon turnover as well as the fine root system of tree saplings. Particularly during the period of establishment, the susceptibility to drought stress of saplings is increased because of incompletely developed root systems and reduced access to soil water. Here, we subjected beech saplings (*Fagus sylvatica* L.) to different levels of drought stress.

Beech saplings were planted in rhizotrons, which were installed in the soil of a Norway spruce forest before bud burst. Soil moisture was manipulated in the following year during May to September. We measured photosynthetic net CO_2 uptake, volume production of fine roots and rhizosphere respiration during the growing season. Biometric parameters of the fine root system, biomass and non-structural carbohydrates were analyzed upon harvest in October.

Photosynthesis and rhizosphere respiration decreased with increasing drought stress dose (cumulated soil water potential) and cumulative rhizosphere respiration was significantly negatively correlated with drought stress dose. Fine root length and volume production were highest at moderate soil drought, but decreased at severe soil drought. The proportion of fine roots < 0.2 mm and the root/shoot-ratio increased whereas the live/dead-ratio of fine roots decreased with increasing drought stress dose.

We conclude that the belowground C allocation as well as the relative water uptake efficiency of beech saplings is increased under drought.

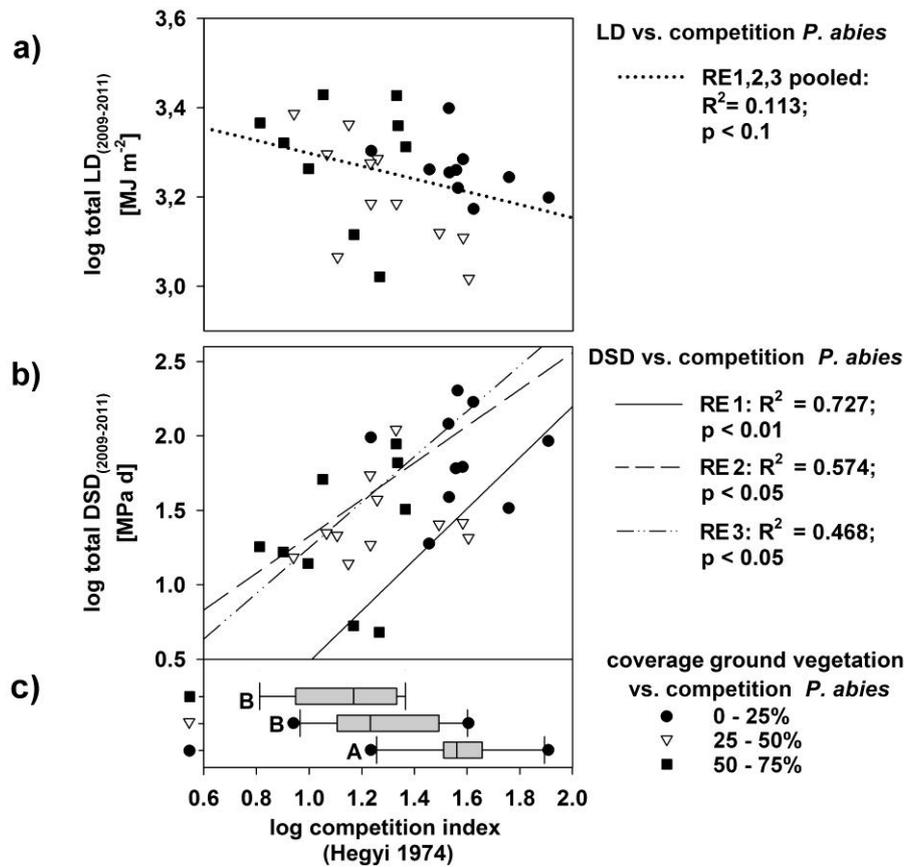## Appendix S: Supplementary data and material

Figure A-S-1: Effect of spruce competition on individual drought stress dose (DSD), light dose (LD) and on the abundance of competing ground vegetation.
Shown are the datasets of individual LD (a), DSD (b) and abundance of competing ground vegetation within 1m radius around the respective beech plant (c) from the plants of the three rainfall exclusion plots (RE 1 -3) in correlation with competition intensity (competition index, CI after Hegyi 1974) imposed by the remnants of the old spruce stand. Symbols: percentage of forest floor covered by competing ground vegetation; Lines: linear regressions of LD/DSD and CI; Boxplots: degree of coverage by ground vegetation in correlation with CI, capital letters indicate significant differences (p < 0.05, one factorial ANOVA, with Tamhane post-hoc test) in CI for the particular class of coverage (Goisser, unpublished).

Table A-S-1: Effect of competition by mature spruce on plant nutrition.
Results of the chemical analysis of leaf and fine root samples after the growing period 2011; Correlations of element concentrations and the logarithmized annual drought stress dose (DSD) or the competition index (after Hegyi 1974) respectively (Pearson´s test of correlation). Significance of the correlation is indicated with: ns for non-significant, * for p < 0.1, ** for p < 0.05 and *** for p < 0.001. Algebraic signs indicate the direction of the correlation with: - for negative correlations and + for positive correlations (Goisser, unpublished).

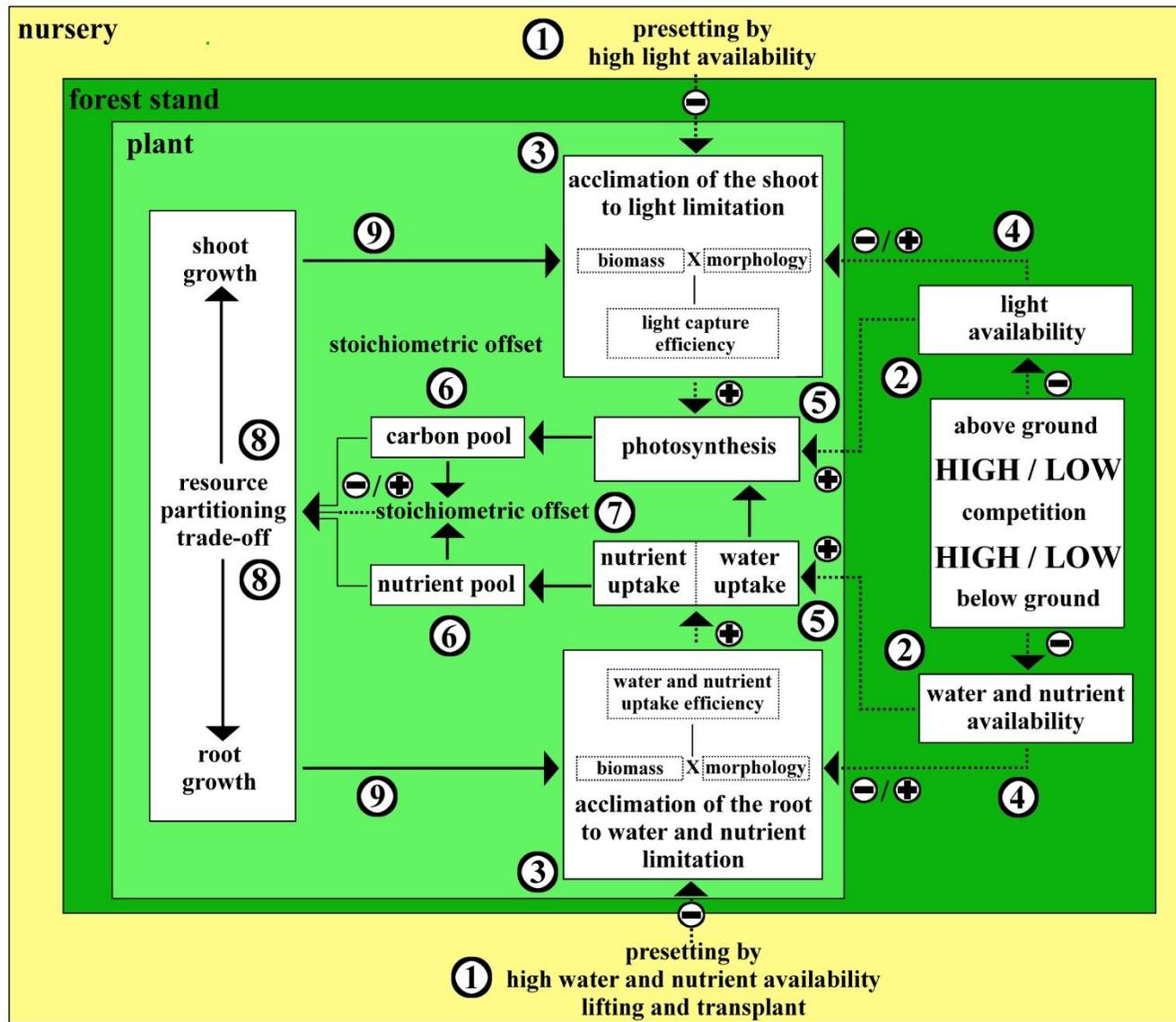|	log DSD (2011)	nutrients in leaves				nutrients in fine roots			
		K [mg/g]	Mg [mg/g]	P [mg/g]	molar C/N	K [mg/g]	Mg [mg/g]	P [mg/g]	molar C/N
mean value (+/-SD)		7.29 (2.07)	0.81 (0.44)	1.51 (0.30)	22.74 (2.38)	3.71 (0.79)	0.66 (0.20)	1.35 (0.38)	45.90 (5.21)
log DSD (2011)		ns	ns	ns	** (+)	*** (-)	* (-)	ns	ns
log CI (Hegyi)	*** (+)	** (+)	ns	ns	*** (+)	** (-)	** (-)	ns	ns

Figure A-S-2: Schematic presentation of resource allocation and morphological adjustments in *F. sylvatica* in response to varying light and water/nutrient availability during the early stage of establishment.

Shown are internal fluxes of carbon, water and nutrients (solid lines) as well as prevailing dependencies between parameters (broken lines); algebraic signs indicate either positive or negative dependencies. Description of fluxes and dependencies:

① presetting of shoot and root acclimation to light and water/nutrient limitation imposed by the breeding conditions and the impact of the transplant; ② effect of above and below ground competition intensity at the forest site on light and water/nutrient availability; ③ acclimation of shoot and root to resource limitation and the resulting resource uptake efficiency; ④ effect of the availability of light and water/nutrient on morphological adjustments of shoot and root to resource limitation; ⑤ photosynthetic carbon assimilation and water/nutrient uptake resulting from light, water and nutrient availability and the corresponding recourse uptake efficiency; ⑥ internal pools of carbon and nutrients; ⑦ offset from optimum stoichiometry of internal carbon and presetting of availability, root accimation on light and water/nutrient limitation imposed by the breeding conditions and the impact of the transplant; ② effect of above and below ground competition intensity at the forest site on light and water/nutrient availability; ③ acclimation of shoot and root to resource limitation and the

Candidate´s contribution to the included publications

Appendix 1

Goisser, M., Zang, U., Matzner, E., Borken, W., Häberle, K.-H., Matyssek, R., 2013. Growth of juvenile beech (Fagus sylvatica L.) upon transplant into a wind-opened spruce stand of heterogeneous light and water conditions. For. Ecol. Manage. 310, 110–119.

This publication presents the results of the three-year precipitation manipulation experiment, investigating the response of recently transplanted beech saplings to annually recurring summer drought under conditions of a spruce stand restoration upon wind-throw. The heterogeneous spatial distribution of the remnants of the old stand induced a pronounced patchiness of growth conditions (e.g. water and light availability). In the growing seasons of 2009 to 2011, the natural gradient of soil water availability was experimentally reinforced by the precipitation manipulation. Water and light availability was assessed individually for each beech sapling. Individual drought stress and light doses were calculated for each of the three years of the experiment. At the end of each growing season, randomly selected plants were harvested to assess specific leaf area (SLA) and tree ring width. Rooting depth (deepest root with a diameter > 2 mm), mean fine root diameter, specific root length (SRL) and plant biomass was assessed in 2011 on a subsample of 30 plants. Leaf gas exchange of the plants was measured once in the nursery, monthly during the growing season of 2010 and twice a month during the growing season of 2011.

The candidate developed the concept and the research question of this paper with help of his coauthors. In field and lab work, he conducted the measurements of leaf gas exchange, plant growth, shoot and leaf morphology during the three years of the experiment, as well as the measurements of specific leaf area and leaf gas exchange in the nursery. He assessed the individual light availability via hemispheric photography and assisted in the installation of the soil moisture sensors and the assessment of the individual water availability of the saplings. After each of the three growing seasons he harvested the sample plants together with his colleague Ulrich Zang and assisted in the assessment of root and shoot biomass and of root morphology. He carried out the statistical analysis of the

measurement data, interpreted and discussed the results and prepared the graphs of the paper. In close collaboration with his colleague Ulrich Zang, he wrote the first draft of this paper. He worked in the suggestions by his co-authors. He submitted the manuscript to *Forest Ecology and Management*. After review he worked in the suggestions of the referees and resubmitted the revised manuscript.

Appendix 2

Zang, U., Goisser, M., Grams, T.E.E., Häberle, K.-H., Matyssek, R., Matzner, E., Borken, W., 2014. Fate of recently fixed carbon in European beech (Fagus sylvatica) saplings during drought and subsequent recovery. Tree Physiol. 34, 29–38.

This publication presents the results of the two stage ^{13}C labeling experiment, investigating dynamics and patterns of C allocation in beech saplings under dry and rewetted soil conditions. In autumn 2010 five-year-old beech saplings were transplanted into 20 L pots. In the growing season of 2011, the saplings were subjected to three levels of soil water availability (with corresponding target soil water potentials of: -0.05 MPa, -0.6 MPa and -1.2 MPa). The dynamic of soil water availability was assessed continuously during drought treatment. Leaf gas exchange was measured to assess the impact of the induced drought stress during the drought treatment period. For the labeling procedure in late August, the saplings were transferred into a climate chamber facility. Single tree labeling chambers that were constructed for this particular purpose enabled for the individual application of the ^{13}C label. In the first step under prevalent drought stress, plants were and pulse-labeled with ^{13}C-depleted CO_2 (δ^{13}C of -47 ‰) and isotopic signatures in leaf and soil respiration were repeatedly measured. Five days after soil rewetting, a second label was applied using 99 atom-% $^{13}CO_2$. After another 12 days, the fate of assimilated C in each sapling was assessed by calculating the individual ^{13}C mass balance.

The candidate developed the experimental design, the concept and the research question of this paper with the help of his co-authors. He measured the photosynthetic carbon uptake of the plants and calculated the corresponding individual quantities of $^{13}CO_2$ that were to apply to provide the necessary labeling intensity. Together with his colleague Ulrich Zang, he carried out the labeling procedure and the extensive sampling of leaf and root respiration as well as the sampling of the different plant tissues

upon harvest. He conducted the major part of lab work in processing the tissue samples for isotopic analysis. He assisted in the statistical analysis of the measurement data and gave substantial input for interpretation and discussion of the results. In close collaboration with his colleague Ulrich Zang, he wrote the first draft of this paper and assisted in working in the suggestions of the co-authors as well as the comments of the referees during the review process after submission to *Tree Physiology.*

Appendix 3

Zang, U., Goisser, M., Häberle, K.-H., Matyssek, R., Matzner, E., Borken, W., 2013. Effects of drought stress on photosynthesis, rhizosphere respiration, and fine-root characteristics of beech saplings: A rhizotron field study. J. Plant Nutr. Soil Sci., doi: 10.1002/jpln.201300196

This publication presents the results of the rhizotron experiment. Juvenile *F. sylvatica* was subjected to three different levels of soil water availability (with corresponding target soil water potentials of: -0.03 MPa, -0.4 MPa and -1.0 MPa) and the drought response of photosynthesis, fine root growth and rhizosphere respiration was assessed in the course of the growing season. Fine root morphology, biomass partitioning and concentrations of non-structural carbohydrates in the fine roots were analyzed upon harvest in October.

The candidate conducted the leaf gas exchange measurements and assisted in the interpretation and the discussion of the experimental results. As co-author, the candidate gave input to the first draft of this paper and assisted in the implementation of the suggestions of the referees during the review process after submission to *Journal of Plant Nutrition and Soil Science*.

Danksagung

An erster Stelle möchte ich mich bei meinem Doktorvater Herrn Prof. Dr. Rainer Matyssek bedanken, der mir die Promotion am Lehrstuhl für Ökophysiologie der Pflanzen ermöglicht hat. Bei ihm fand ich zu jedem Zeitpunkt volle Unterstützung, in fachlichen sowie administrativen Problemen.

Dasselbe gilt für meinen Betreuer Dr. Karl-Heinz Häberle. Seine Betreuung war für mich die optimale Mischung aus Vertrauen in meine selbständige Arbeit und Unterstützung bei alleine nicht zu lösenden Problemen. Mit einem Schmunzeln erinnere ich mich an stundenlange fruchtbare Diskussionen, während derer nicht selten die Sonne unterging und der Alarm seiner Armbanduhr mehrmals weggedrückt wurde.

Auch Thorsten Grams möchte ich hier herzlich für seine fachliche Unterstützung danken. Seine Tür stand mir buchstäblich immer offen. Auch möchte ich ihm dafür danken, dass er mir zum Ende raus den nötigen Druck gemacht hat.

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Den besten Eindruck vom Arbeitsklima am Lehrstuhl verschafft wohl die für mich unvergessliche Aussage meines Betreuers Dr. Karl-Heinz Häberle: „ …Du musst sagen, wenn es Probleme im Projekt gibt. Wenn es nötig ist, steht der ganze Lehrstuhl auf der Matte…"

Auch den Kollegen aus Bayreuth, Prof. Dr. Egbert Matzner und Dr. Werner Borken möchte ich für die gute Zusammenarbeit herzlich danken.

Bei Gerhard Müller und Uwe Hell bedanke ich mich für ihre technische Hilfe vor Ort.

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Abschließend bedanke ich mich bei meiner Familie und meinen Freunden. Ich möchte Simon Putzhammer, Markus Kornprobst, Rainer Zierer und Felix Bierling danken, mit denen ich sowohl über meine Arbeit reden, als auch den nötigen Ausgleich dazu finden konnte. Ich bedanke mich bei meinen Eltern, die mich zu jeder Zeit unterstütz haben und dabei immer an meinen Erfolg geglaubt haben.

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Curriculum vitae

Personal Data

Name	Michael Goisser
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Professional Experience

since June 2013

Research associate at the Chair of Ecophysiology of Plants (Technische Univerität München)

Research focus: Drought as a modifier of interactions between beech and spruce

Research projekt: „Kranzberg Forest Roof Experiment ".

$\Rightarrow$ Investigations: drought effects on long-distance transport of carbo-hydrates (^{13}C-labeling approach), linking stable isotope signatures in tree rings with physiological processes (analysis of drought related patterns of ^{13}C and ^{18}O natural abundance signature in structural and non-structural carbohydrates), gas exchange measurements (LICOR 6400), C-reserve consumption under prolonged drought (analysis of the dynamics of C-storage pools), below ground water repartitioning by spruce and beech under prolonged drought (D-labeling approach)

May 2009 – July 2014

Doctorate at the Chair of Ecophysiology of Plants, Technische Univerität München, Freising, Germany.

Research focus: Response and acclimation capacity of juvenile *Fagus sylvatica* L. to extreme and repeated summer drought under conditions of a spruce stand restoration.

Research projekt: „Response of beech saplings to extreme and repeated summer droughts" (KLIP 13).

$\Rightarrow$ Investigations: effect of repeated drought on growth dynamics (biomass, digital tree ring analysis), shoot and root morphology, leaf gas exchange (LICOR 6400), effect of drought and subsequent rewetting on transport and allocation of recent photosyntathes (^{13}C-labeling), quantification of soil water availability (TDR/FDR-probes, tensiometer), quantification of light availability (hemispherical photography, WinSCANOPY).

Publications

Zang et al., 2014	"Effects of drought stress on rhizosphere respiration and fine root characteristics of beech saplings: A rhizotron field study". In: *Journal of Plant Nutrition and Soil Science*.
Zang[*], Goisser[*] et al., 2014	"Fate of recently fixed carbon in European beech (*Fagus sylvatica*) saplings during drought and subsequent recovery" In: *Tree Physiology.*
Goisser[*], Zang[*] et al., 2013	"Growth of juvenile beech (*Fagus sylvatica* L.) upon transplant into a wind-opened spruce stand of heterogeneous light and water conditions." In: *Forest Ecology and Management*.

Conferences

September 2013	Oral presentation at the GfÖ congress 2013 in Potsdam, Germany: "High-light acclimation of young afforested beech (*Fagus sylvatica* L.) exacerbates productivity decline under water limitation."
May 2012	Oral presentation at the IUFRO conference 2012 in Kaunas, Lithuania: "Response of beech saplings to extreme and repeated summer droughts of relevance for stand establishment in the future"
March 2012	Oral presentation at the Klimasymposium 2012 in Freising, Germany: „Trockenstress bei Jungbuchen"

Education

May 2009 – September 2012	PhD student at the Chair of Ecophysiology of Plants, Technische Univerität München, Freising, Germany.
	Title of PhD thesis: "Establishing *Fagus sylvatica* under annually recurring summer drought – experimental forest restoration upon wind-throw of *Picea abies* in view of climate change"
October 2003 – April 2010	Study of Forestry Sience, Technische Univerität München, Freising, Germany
	Title of diploma thesis: "Effekte von Mykorrhizierung und Düngung auf Photosynthese, Kohlenstoffallokation und Wachstum: ein Vergleich von Tabebuia chrysantha und Heliocarpus americanus bei der Forstpflanzenproduktion in Südecuador." The experiment was conducted at the „Reserva Biologica San Francisco", Loja, Ecuador.
	Degree: Forestry science engineer (Dipl.-Ing. silv. Univ.)
September1993 – June 2002	Gymnasium „Helene-Lange-Gymnasium" in Fürth, Germany
	Degree: Allgemeine Hochschulreife (Abitur)

Freising den_____   Michael Goisser_____

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[*] These authors contributed equally to this work