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Space- and resource-related decomposition of growth for understanding mechanisms of competitive success

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Results of this dissertation have been published and submitted in peer-reviewed international journals. The following publications are included as individual chapters:

Chapter 2: **Daigo Schulte MJ**, Matyssek R, Gayler S, Priesack E, Grams TEE (2013) Mode of competition for light and water amongst juvenile beech and spruce trees under ambient and elevated levels of O_3 and CO_2. Trees 27: 1763-1773

Chapter 3: Grams TEE, **Daigo Schulte MJ**, Winkler J, Gayler S, Matyssek R (2012) Growth and space use in competitive interactions between juvenile trees. Growth and defence in plants. Springer, pp 273-286

Chapter 4: **Daigo Schulte MJ,** Matyssek R, Gayler S. Grams TEE (2015) Decomposition of Relative Growth Rate in competing *Fagus sylvatica* and *Picea abies*. Perspectives in Plant Ecology, Evolution and Sytematics, submitted for publication

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

Summary

The present study investigated the competitive growth strategies of juvenile European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.]Karst), in response to biotic limitation imposed by competition and abiotic stress caused by elevated CO_2 ($+CO_2$) and twice ambient O_3 ($+O_3$). Deciduous beech and coniferous spruce are considered the two economically and ecologically most important tree species growing in central Europe. Both exhibit complementary and contrasting strategies during their life span. Under constraints by resource competition and changing climatic conditions, such as associated with $+CO_2$ and $+O_3$ regimes, growth and functional responses may be modified, especially at the juvenile stage.

This work comprised three separate sub-studies carried out using theoretical concepts and empirical data obtained from experiments and a simulation model. The datasets utilized in this dissertation originated from a series of phytotron experiments conducted during the integrated research program Sonderforschungsbereich 607 of the Deutsche Forschungsgemeinschaft (DFG) entitled "Growth and Parasite Defence - Competition for Resources in Economic Plants from Agronomy and Forestry".

Initially, the concept of plant competition was presented in detail. This approach was then applied in the first study using empirical data, along with simulated data which were generated using the plant growth simulation model PLATHO (**P**lants as **T**rees and **H**erbs **O**bjects). Simulating resource allocation in the soil-plant system enabled the analysis of competition at the single-tree level and deriving long-term predictions beyond the experimental time scale. The second integrative study was carried out to clarify the functional relationship between Relative Growth Rate (*RGR*) and spatial efficiency indices of competitive success for juvenile beech and spruce trees grown in isolation, or in mono-and mixed culture while being exposed to $+CO_2$ and $+O_3$. Competitive success was analyzed in the third study using the concept of mathematical growth decomposition for delineating morphological and physiological plasticity of beech and spruce saplings under the biotic limitation of competition and the abiotic $+CO_2$ and $+O_3$ stress.

Three modes of competition were distinguished depending on whether larger tree saplings capture more (positive asymmetric), similar (symmetric) or less (negative symmetric) of above- (i.e. light) or belowground resources (i.e. water) per unit biomass than their smaller neighbors. The hypotheses tested in the first study were: the positive asymmetric competition for the aboveground resource light diminishes under $+CO_2$ but increases at $+O_3$ among juvenile beech and spruce individuals. Conversely, the symmetric belowground competition for water remains unchanged under $+CO_2$ and $+O_3$.

The rate of resource uptake of an individual plant (*S*) was considered as the product of three factors namely: (1) resource availability *R* (i.e. amount of light or water availability per unit crown or root volume), (2) allometry of space occupation *A* (i. e. crown or root volume per unit above- or belowground biomass) and (3) resource-capture efficiency *C* (i.e. light or water capture in relation to above-or belowground light or water availability). The mode of competition was assessed as the difference of log-transformed *S* (*ln S*) between large and small plants weighted by the inverse of the distance between them. This concept was applied to empirical data on intra-specific juvenile beech and spruce trees spanning two growing seasons under $+CO_2$ (ambient + 300 ppm) and $+O_3$ (restricted to < 150 ppb). Statistical analysis was carried out using ordinary least squares regression of the Johnson-Neyman procedure. The analysis was extrapolated for another five years using the PLATHO model, which was parameterized using a combination of experimental and literature data. An optimization of selected model parameters was conducted using a non-linear fitting model (PLAFIT) implemented in Matlab. This re-calibration of the model was performed using an independent dataset not previously used in model parameterization.

Results confirmed the mode of competition for above- (i.e. light) and belowground resource (i.e. water) as positive asymmetric and symmetric respectively. Neither $+CO_2$ nor $+O_3$ affected this outcome as simulation results predicted stability for another five years. Overall, the outcome of this sub-study affirms that the mode of competition among individuals in a mono-specific stand is determined by resource characteristics rather than abiotic stress (i.e. of $+CO_2$ and $+O_3$).

The analysis performed in the second study quantified competitiveness by space-related efficiencies of resource investment into standing biomass (space occupation) and resource gain (space exploitation). Specifically, the question was put forward i.e. whether the competitive success of plants is related to an efficient space use (i.e. optimization strategy), or conversely on the maximization of resource gain (i.e. maximization strategy). Further analysis examined whether the effects of $+CO_2$ and/or $+O_3$ were modified by different competitive settings, i.e. growth in isolation, mono- and mixed culture. The synthesis of this study required comparison of competitive success in terms of relative growth rate (*RGR*) and space-related efficiencies of resource use. As such, whole-tree *RGR* was calculated using the classical approach of comparing log-transformed whole-tree biomass development over two harvest intervals. On the other hand, space occupation efficiency was estimated aboveground as the space occupied by the crown per unit of biomass investment into stem, branches, and foliage. Belowground, this was assessed using the soil volume around the roots and calculated from the total fine root length and the radius of the depletion zone of water. Moreover, space exploitation efficiency was calculated as the resources acquired from the occupied space, i.e. per unit volume. In this sub-study, aboveground space exploitation efficiency was assessed as the annual carbon gain retrieved per unit of occupied crown space. Space exploitation efficiency was calculated belowground using water uptake from the soil, assessed as annual transpiration per unit of the occupied root space. The data utilized in this work were obtained from four consecutive phytotron experiments conducted on beech and spruce saplings and performed under similar climate conditions.

As an outcome, beech whole-tree *RGR* suffered from $+O_3$ being more pronounced in mixture with spruce and at high planting densities. Analysis of isolated plants showed that $+CO_2$ did not increase beech *RGR* but diminished the adverse $+O_3$ impact. Meanwhile, experiments using 20 trees per container (i.e. intense competition) revealed a diminished *RGR* of beech growing in monoculture. This effect was more intensified in mixture with spruce. Thus, results should be considered with caution when plant responses to $+CO_2$ and $+O_3$ are scaled from different competitive settings. Under the specific study conditions, spruce appeared to be a stronger competitor than beech, especially when competition became intense at increasing plant biomass. But such superiority may depend on soil properties and environmental condition in the phytotrons, i.e. soil moisture, pH and light availability.

The focus of this study is on the mechanistic grounds of competitive interaction between neighbors. In this study, *RGR* of juvenile beech and spruce trees was significantly correlated with aboveground space occupation. For both species,

neither above- nor belowground resource gain was correlated with *RGR*, indicating minor importance of this parameter for interactive interaction between neighbors. Beech showed a larger range of aboveground space occupation than spruce under $+CO_2$ and $+O_3$ regimes, with crown volumes between 50 and 1,100 cm^3 per g of invested above-ground biomass. Such phenotypic plasticity enabled beech to avoid intense competition with spruce at the expense of less efficient aboveground space occupation. Nevertheless, optimizing space use may be a winning strategy where competing for or occupying of space may pay-back over time through reduction of resource availability of neighbors. This situation holds true for uni-directional resources such as light where pre-emptable mechanism such as shading effect through successful space occupation may significantly reduce the resource availability to the neighbor. In such a case, the resources gained by a plant may not be raised in absolute terms but may be increased relative to a neighbor. Thus, resources gained relative to its neighbor (i.e. the marginal advantage) is maximized through optimization of space occupation.

The decomposition analysis of *RGR* performed in the third study aimed to clarify above- and belowground mechanisms responsible for morphological and physiological plasticity in the face of biotic limitation (i.e. competition) and abiotic stress (i.e. $+CO_2$, $+O_3$). Under the biotic stress of competition (mono vs mixed), the hypothesis was that the morphological plasticity would enhance *RGR* of beech and spruce saplings. Moreover, under $+CO_2$ and $+O_3$ levels, physiological plasticity would gain in significance in driving *RGR*. The analysis was first presented as a theoretical concept and then its application was demonstrated using the phytotron data obtained under similar environmental conditions and enhanced gaseous regimes.

By decomposition of *RGR*, above- and belowground factors were identified that describe morphological or physiological plasticity: space occupation (*A*), biomass ratio (*B*), space exploitation (*X*) and resource-to-biomass conversion efficiency (*E*). While *A* was calculated as crown or root volume per unit of above-or belowground biomass, respectively, *B* was assessed as above- or belowground biomass per unit total biomass. Both factors (*A* and *B*) describe plasticity in morphological response. Conversely, *X* was estimated as the rate of light uptake per unit crown volume (aboveground) or the rate of water uptake per unit root volume (belowground). Factor *E* was assessed as the instantaneous rate of increase in biomass per rate of light uptake

(aboveground) or as instantaneous rate of increase in biomass per rate of water uptake (belowground). Above- and belowground *E* was referred to as light-use (*LUE*) and water-use efficiency (*WUE*), respectively. Components comprising *X* and *E* contributed to physiological plasticity.

Results confirmed that morphological plasticity determined *RGR* of beech and spruce saplings under the biotic limitation of competition. Mean *RGR* of beech was higher in mono than mixed culture, whereas the reverse was true for spruce. Relationship comparing *RGR* and its factors revealed that aboveground space occupation positively enhanced *RGR* of beech in mono compared to mixed culture, whereas belowground space occupation favored *RGR* of spruce in mixture than in pure stands. Under +CO_2, mean *RGR* of both species remained unchanged. Notably, below-ground space occupation significantly enhanced *RGR*, although only in beech which suggested possible *RGR* stimulation in this species. Significant mean *RGR* reduction occurred under +O_3 in beech through lowered *LUE*. Mean *RGR* of spruce was not affected by +O_3, despite reduced *WUE*, suggesting the ability of this species to acclimatize to O_3 stress.

Overall, results obtained from this dissertation show that different responses to climate change and/or resource availability have to be expected for different species with different planting patterns. Therefore, interactions between environmental factors such as increasing concentrations of +CO_2 and +O_3 regimes and competitive settings in plants grown in isolation, mono-and mixed culture have to be considered when analyzing tree responses especially during early stage of development. This dissertation lays down the foundation for early developmental strategies that may influence responses in later stages. Such study is indispensable as it traces the variability that characterizes plant life history. This work has unveiled principles of mechanisms related to competition and growth under controlled phytotron conditions with scenarios of relevance for current and expected future CO_2 and O_3 regimes, now claiming empirical validation under the actual site conditions of forest ecosystems.

Zusammenfassung

In der vorliegenden Arbeit wurden die kompetitiven Wachstumsstrategien junger Buchen (F*agus sylvatica* L.) und Fichten (*Picea abies* [L.] Karst) und deren Reaktionen auf biotische Limitierung durch Konkurrenz sowie auf abiotischen Stress durch erhöhte CO_2- (+CO_2) und verdoppelte Ozon (O_3) - Konzentrationen (+O_3) untersucht. Buche und Fichte gelten als ökonomisch und ökologisch wichtigsten Baumarten in Mitteleuropa. Beide weisen gegensätzliche, sich ergänzende Wuchsstrategien auf. Beschränkungen durch Konkurrenz um Ressourcen und sich ändernde klimatische Bedingungen, wie beispielsweise erhöhte CO_2- und O_3 Konzentrationen, können zu Änderungen im Wachstum und in den physiologischen Reaktionen führen, insbesondere während in der Jugendphase.

Die vorliegende Arbeit gliedert sich in drei Teilstudien und verwendet theoretische Konzepte sowie empirische Daten aus Experimenten und einem Simulationsmodell. Die verwendeten Datensätze stammen aus einer Reihe von Phytotron-Experimenten, welche im Rahmen des Sonderforschungsbereichs SFB 607 der Deutschen Forschungsgemeinschaft (DFG) "Wachstum und Parasitenabwehr - Wettbewerb um Ressourcen in Nutzpflanzen aus Land- und Forstwirtschaft" durchgeführt wurden.

Zunächst wurde das Konzept zur Untersuchung der Konkurrenz bei Pflanzen detailliert beschrieben. Dieser Ansatz wurde in der ersten Studie unter Verwendung empirischer und simulierter Daten, die mit Hilfe des Wachstumsmodells PLATHO („**P**lants as **T**rees and **H**erbs **O**bjects“) erzeugt wurden, angewendet. Die Simulation der Ressourcenverteilung im Boden-Pflanzen-System ermöglicht die Analyse des Ressourcen-Wettbewerbs auf der Ebene einzelner Bäume und das Erstellen längerfristiger Prognosen über die Dauer der Versuche hinaus. Die zweite, integrative Studie untersuchte die funktionale Beziehung zwischen relativer Wachstumsrate (*RGR*) und raumbezogenen Effizienz-Indizes zur Beschreibung des Wettbewerbserfolgs junger Buchen und Fichten, die in unterschiedlichen Konkurrenzszenarien, d.h. in Isolation, Mono- und Mischkultur sowie unter dem Einfluss von +CO_2 und +O_3 gewachsen sind. Der Konkurrenzerfolg der beiden Baumarten wurde in der dritten Studie mit dem Konzept der mathematischen

Zerlegung der relativen Wachstumsrate hinsichtlich der Bedeutung von morphologischer und physiologischer Plastizität junger Buchen- und Fichten unter dem Einfluss von biotischem und abiotischem Stress analysiert.

Drei Arten von Konkurrenz wurden unterschieden, je nachdem ob größere Bäumchen pro Einheit Biomasse mehr (positiv asymmetrisch), gleich viel (symmetrisch) oder weniger (negativ symmetrisch) von den oberirdischen (d.h. Licht) oder unterirdischen (d.h. Wasser) Ressourcen aufnehmen können als ihre kleineren Nachbarn. Getestet wurden hierbei folgende Hypothesen: der positiv asymmetrische Wettbewerb um die Ressource Licht wird unter $+CO_2$ vermindert, jedoch unter $+O_3$ verstärkt. Im Gegensatz dazu bleibt die symmetrische Konkurrenz um Wasser unter $+CO_2$ und $+O_3$ unverändert.

Die Rate der Ressourcenaufnahme einer einzelnen Pflanze (*S*) wurde als das Produkt folgender Faktoren betrachtet: (1) die Verfügbarkeit von Ressourcen *R* (d.h. Lichtmenge oder Wasserverfügbarkeit pro Einheit an Kronen- oder Wurzelvolumen), (2) die Allometrie der Raumbesetzung *A* (d.h. Kronen- oder Wurzelvolumen pro Einheit ober- bzw. unterirdischer Biomasse) und (3) die Effizienz der Ressourcenaufnahme *C* (d.h. Licht- oder Wasseraufnahme in Bezug zur Verfügbarkeit). Die Art der Konkurrenz wurde bestimmt als die Differenz der log-transformierten *S* (ln *S*) zwischen großen und kleinen Pflanzen, gewichtet mit dem Kehrwert der Distanz zwischen ihnen. Dieses Konzept wurde auf empirische Daten zur intra-spezifischen Konkurrenz von jungen Buchen und Fichten angewendet, die über zwei Vegetationsperioden unter $+CO_2$ (Umgebungswert +300 ppm) und $+O_3$ (auf <150 ppb beschränkt) gewachsen sind. Die statistische Analyse wurde unter Verwendung von OLS-Regression mittels des Johnson-Neyman Verfahrens durchgeführt. Die Analyse wurde um weitere fünf Jahre mithilfe von PLATHO extrapoliert, welches ursprünglich mittels eine Kombination aus experimentellen und Literaturdaten parametrisiert wurde. Eine Optimierung ausgewählter Modellparameter wurde mit einem nicht-linearen Fitting Programm (PLAFIT) durchgeführt, welches in Matlab implementiert wurde. Für diese erneute Kalibrierung des Modells wurde ein unabhängiger Datensatz benutzt, welcher zuvor nicht in der Modellparametrierung verwendet wurde.

Die Ergebnisse bestätigten, dass die Art der Konkurrenz für die oberirdische Ressource Licht positiv asymmetrisch und für die unterirdische Ressource Wasser symmetrisch ist. Weder +CO_2 noch +O_3 beeinflussten dieses Konkurrenzverhalten, das auch in der Simulation über weitere fünf Jahre stabil blieb. Das Ergebnis dieser Teilstudie bestätigt, dass die Art der Konkurrenz zwischen Individuen in Monokultur von der Charakteristik der Ressourcen und nicht von abiotischem Stress (+CO_2 und +O_3) bestimmt wird.

In der zweiten Studie wurde die Konkurrenzfähigkeit durch raumbezogene Effizienz der Ressourceninvestitionen in die stehende Biomasse (Raumbesetzung) und des Ressourcengewinns (Raumausbeutung) analysiert. Es wurde untersucht, ob die Konkurrenzfähigkeit von Pflanzen im Zusammenhang mit einer effizienten Raumnutzung (d.h. Optimierungsstrategie) oder einer Maximierung des Ressourcengewinnes (d.h. Maximierungsstrategie) steht. Die Auswirkungen von +CO_2 und/oder +O_3 in unterschiedlichen Konkurrenzszenarien, d.h. Wachstum in Isolation, Mono- und Mischkultur, wurden analysiert. Dafür wurde der Konkurrenzerfolg in Bezug auf die relative Wachstumsrate (*RGR*) und Effizienz der Raumnutzung verglichen. Die *RGR* der Bäume wurde mit dem klassischen Ansatz der log-transformierten Biomasseentwicklung über zwei Ernteintervalle berechnet. Die oberirdische Effizienz der Raumbesetzung wurde durch das Kronenvolumen pro Einheit Biomasse, d.h. Investition in Stamm, Äste und Laub quantifiziert. Unterirdisch wurde diese über das Bodenvolumen um die Wurzeln sowie über die spezifische Feinwurzellänge und den Radius der Wasserverarmungszone berechnet. Die oberirdische Effizienz der Raumausbeutung (volumenbezogene Rate der Ressourcenaufnahme) wurde als der jährliche Kohlenstoffgewinn pro Kronenvolumen berechnet. Die unterirdische Effizienz der Raumausbeutung wurde anhand der Jahressumme der Transpiration pro besetztem Wurzelraum abgeschätzt. Die in dieser Arbeit verwendeten Daten entstammen aus vier aufeinander folgenden Phytotron-Experimenten, welche unter ähnlichen klimatischen Bedingungen durchgeführt wurden.

Als ein Ergebnis der Analyse hat sich gezeigt, dass die *RGR* der Buche durch +O_3 beeinträchtigt wurde, wobei dieser Effekt in Mischpflanzung mit Fichte und bei hohen Pflanzdichten stärker ausgeprägt ist. Bei isoliert wachsenden Pflanzen zeigte sich, dass +CO_2 die *RGR* der Buchen zwar nicht erhöhte, jedoch die negativen +O_3 Auswirkungen verminderte. In Experimenten mit 20 Bäumen pro Container (d.h. starke Konkurrenz) wiesen Buchen in Monokultur eine verminderte *RGR* auf. Dieser

Effekt wurde in Mischkultur mit Fichte verstärkt. Daher sind Ergebnisse mit Vorsicht zu betrachten, wenn Pflanzenreaktionen auf +CO_2 und +O_3 aus unterschiedlichen Konkurrenzsituationen skaliert wurden. Unter den spezifischen experimentellen Bedingungen schien Fichte der stärkere Konkurrent verglichen mit Buche zu sein, insbesondere bei Konkurrenzintensität in Folge von zunehmender Biomasse. Die Überlegenheit kann jedoch von den Bodeneigenschaften und Umweltbedingungen in den Phytotronen, d.h. Bodenfeuchte, pH und Lichteinfall abhängen.

Der Schwerpunkt dieser Studie liegt auf dem mechanistischen Verständnis des Konkurrenzverhaltens zwischen benachbarten Baumindividuen. Die *RGR* der jungen Buchen und Fichten war hier signifikant mit der oberirdischen Raumbesetzung korreliert. Für beide Arten war weder die ober- noch die unterirdische Raumausbeutung mit der *RGR* korreliert, was auf eine geringe Bedeutung dieses Parameters für die Interaktion zwischen benachbarten Individuen hindeutet. Buche zeigte eine größere Variabilität oberirdischer Raumbesetzung als Fichte unter +CO_2- und +O_3 bei Kronenvolumina zwischen 50 und 1100 cm^3 pro g investierter oberirdischer Biomasse. Diese phänotypische Plastiziät erlaubt der Buche eine intensive Konkurrenz mit Fichte zu vermeiden, allerdings auf Kosten einer weniger effizienten oberirdischen Raumbesetzung. Dennoch kann die Optimierung der Raumnutzung eine erfolgreiche Strategie sein, um in Konkurrenz die Ressourcenverfügbarkeit der Nachbarn langfristig zu reduzieren. Diese Situation gilt für unidirektionale Ressourcen wie Licht, wo Beschattung die Verfügbarkeit von Ressourcen für Nachbarn im Zuge einer erfolgreichen Raumbesetzung deutlich senken kann. In einem solchen Fall können die von der Pflanze gewonnenen Ressourcen zwar nicht absolut, jedoch relativ zu einem Nachbarn erhöht werden. Auf diese Weise wird der Zugewinn an Ressourcen relativ zum benachbarten Individuum (d.h. der marginale Vorteil) durch Optimierung der Raumbesetzung maximiert.

Die Zerlegungsanalyse der *RGR* wurde in der dritten Studie durchgeführt, um ober- und unterirdische Mechanismen für die morphologische und physiologische Plastizität hinsichtlich biotischer Limitierung (d.h. Konkurrenz) und bei abiotischem Stress (d.h. +CO_2 und +O_3) zu klären. Die Hypothese, dass unter biotischem Konkurrenzstress (Mono- vs. Mischkultur) morphologische Plastizität die *RGR* von jungen Buchen- und Fichten verbessern würde. Darüber hinaus wurde getestet, ob unter +CO_2- und +O_3 die Bedeutung physiologischer Plastizität für die *RGR* erhöht würde. Die Analyse wurde zunächst als theoretisches Konzept vorgestellt und dann dessen Anwendung anhand von Phytotron-Daten demonstriert, die unter ähnlichen Versuchsbedingungen und Gas-Regimen erhoben wurden.

Durch Zerlegung der *RGR* wurden ober- und unterirdische Faktoren identifiziert, die morphologische oder physiologische Plastizität beschreiben: Raumbesetzung *A*, Biomasse-Verhältnis *B*, Raumausbeutung *X* und Ressourcen-zu-Biomasse-Umwandlungseffizienz *E*. Während *A* durch das Kronen- oder Wurzelvolumen pro Einheit ober- oder unterirdischer Biomasse berechnet wurde, wurde *B* durch die ober- oder unterirdische Biomasse pro Gesamtbiomasse quantifiziert. Beide Faktoren (*A* und *B*) beschreiben die morphologische Plastizität. Umgekehrt wurde *X* als die Rate der Lichtaufnahme pro Einheit Kronenvolumen (oberirdisch) oder die Rate der Wasseraufnahme pro Einheit Wurzelvolumen (unterirdisch) bestimmt. Der Faktor *E* wurde aus dem Biomassezuwachs pro Lichtaufnahme (oberirdisch) oder als Biomassezuwachs pro Wasseraufnahmerate (unterirdisch) berechnet. Das oberirdische *E* bezeichnet die Lichtnutzungseffizient (*LUE*), das unterirdische *E* die Wassernutzungseffizienz (*WUE*). Die Komponenten *X* und *E* tragen zur physiologischen Plastizität bei.

Die Ergebnisse bestätigten, dass die morphologische Plastizität die *RGR* von jungen Buchen und Fichten unter der biotischen Einschränkung der Konkurrenz bestimmt. Die durchschnittliche *RGR* bei Buche war sowohl in der Mono- wie auch in der Mischkultur höher, während sich die Fichte umgekehrt verhielt. Das Verhältnis zwischen *RGR* und ihren Faktoren ergab, dass die Buche von einer effizienten oberirdischen Raumbesetzung in Monokulturen profitierte, während die Fichte durch eine effiziente unterirdische Raumbesetzung in Mischkulturen begünstigt wurde. Die mittlere *RGR* beider Arten blieb unter +CO_2 unverändert. Bemerkenswert ist, dass eine effizientere unterirdische Raumbesetzung die *RGR* deutlich verbesserte, wenn auch nur für die Buche, was auf eine mögliche *RGR*-Stimulation in dieser Spezies hindeutet. Für die Buche erfolgte eine signifikante Reduktion der durchschnittlichen *RGR* unter +O_3 mit Abnahme des *LUEs*. Die mittlere *RGR* bei Fichte war dagegen nicht von +O_3 beeinflusst obwohl die *WUE* abnahm, was auf die Fähigkeit zur Akklimation gegenüber O_3-Stress hindeutet.

Insgesamt zeigt diese Arbeit, dass man bei unterschiedlichen Baumarten

unterschiedliche Reaktionen auf den Klimawandel und/oder die Ressourcenverfügbarkeit erwarten muss. Daher müssen, insbesondere in der frühen Entwicklungsphase, bei der Analyse von Baumreaktionen die Wechselwirkungen zwischen Umweltfaktoren wie steigende Konzentrationen von CO_2 und O_3, und dem Konkurrenzverhalten von Baumindividuen in Isolation, Mono- und Mischkultur, berücksichtigt werden. Diese Dissertation schafft die Voraussetzungen für frühe Entwicklungsstrategien, welche die Stressreaktionen in späteren Stadien beeinflussen können. Eine solche Untersuchung ist unerlässlich, da sie die Variabilität aufzeigt, welche die Ontogenie von Pflanzen charakterisiert. In dieser Arbeit wurden Prinzipien in den Mechanismen von Konkurrenz und Wachstum unter kontrollierten Bedingungen in Phytotronen aufgeklärt, wobei Szenarien ausgewählt wurden, die für gegenwärtige und zu erwartende zukünftige CO_2- und O_3-Regim von Bedeutung sind. Eine empirische Validierung der Ergebnisse sollte nun unter den tatsächlichen Standortbedingungen in Waldökosystemen erfolgen.

1. General Introduction

Plants in the field hardly live in isolation but typically compete with neighbors for limited resources (Körner 2003a) to grow and co-exist (Silvertown 2004; Chesson 2000; Schwinning & Fox 1995). However, competition bears the risk of facing extinction (Begon & Wall 1987) through inability to tolerate limited resource supply (Tilman 1982) or at least, becoming suppressed by neighbors due to stress intolerance (Grime 1977). If competition is considered an important factor in determining the distribution and abundance of plant species and communities (Berger et al. 2008), then it should hold the key in understanding growth processes (Gomez et al. 2011). This generalization may be valid, but competition alone does not determine the growth rate of plants (Schwinning & Weiner 1998). There are alternative explanations, such as partitioning of biomass between plant organs that influence growth that are independent of competition (Schwinning 1996). Studies on competitiveness as arising from growth activity are prevalent (Kozovits et al. 2005 a & b; Poorter & Navas 2003; Grams et al. 2002). Nevertheless, there is still a long way to bridge the functional gap between growth vigor and competitiveness. Such study demands a challenge, especially for woody species, a key structural element of terrestrial ecosystem, facing risks of changing climatic conditions, spatial heterogeneity and temporal variations. The mechanistic clarification of competition and growth, especially under juvenile phase requires novel empirical and theoretical evidence to enable integration into concepts that foster functional understanding of plant competitive success.

The mode of competition between two individuals of different size can be distinguished by the way plants acquire resources in proportion to biomass: if the large plant captures (i) more (positive asymmetric), (ii) the same (symmetric) or (iii) less (negative asymmetric) resource per unit of biomass involved in the capturing process than the smaller neighbor (Schwinning 1996). The mechanisms that determine the mode of competition appear to relate to the characteristics of resource (Schwinning & Weiner 1998). Aboveground competition, being pre-emptable (e.g. for light) is described in most cases as asymmetric since larger plants mono-directionally shade shorter neighbors (Weiner & Thomas 1986). However, it can be symmetric in a slow-growing mono-specific stand due to similarities between light capture and light-use efficiencies of competing individuals (van Kuijk et al. 2008). Furthermore, the mode of competition belowground (e.g. for water) being multi-directional is assumed to be generally symmetric (von Wettberg & Weiner 2003; Cahill & Casper 1999). But such view has been disputed, since soil heterogeneity (Rajaniemi 2003) and differences in root proliferation between species (Fitter et al. 1991) could favor size-asymmetry (Caldwell et al. 1991).

Changing environmental conditions such as increasing concentrations of CO_2 and/or O_3 may complicate plant interaction, growth patterns and underlying interrelationships (Karnosky et al. 2003; Norby et al. 1999; Pye 1988). In general, elevated CO_2 (hereinafter referred to as $+CO_2$) tends to increase photosynthesis and reduce stomatal conductance (for review, see Ainsworth & Rogers 2007; Nowak et al. 2004). However, these responses could vary between species. For example, under $+CO_2$, growth appears to be more pronounced in angiosperm than gymnosperm (Poorter & Navas 2003; Ceulemans & Mousseau 1994). In woody saplings, growth under $+CO_2$ may be stimulated in species that are relatively shade-tolerant (Kerstiens 2001). Others confirmed that growth enhancement under $+CO_2$ decreases and increases with increasing shade-tolerance for seedlings of broad-leaved and conifer species, respectively (Bazzaz & Catovsky 2002). Moreover, $+CO_2$ may reduce the overall size-difference between dominant and subordinate plants (Stöcklin & Körner 1999) as the former may experience down-regulation or strong acclimation response that could inhibit growth (Bazzaz & Catovsky 2002). Photosynthetic acclimation of dominant trees under $+CO_2$ can be associated with adjustment in leaf structure and chemistry (Tjoelker et al. 1998). For example, over-production of assimilates relative to sink demand may lead to carbohydrate accumulation in leaves (Stitt 1991) that can inhibit photosynthesis (Signora et al. 1998). This dilemma of leaf photosynthesis suggests that sink (tissue growth) rather than source activity (photosynthesis) controls plant growth, therefore $+CO_2$ enrichment does not necessarily contribute to further growth enhancement as often claimed (Körner 2015).

On the other hand, elevated O_3 (hereinafter referred to as $+O_3$) often significantly reduced photosynthesis of trees (Reich & Amundson 1985) as it enters the stomata from the leaves (Reich 1987). This flux of O_3 through stomata constitutes the effective dose (Emberson et al. 2000) which can account for analyzing influences of O_3 uptake on trees through analysis of stomatal regulation (Matyssek et al. 2007; Matyssek & Sandermann 2003). Moreover, factors such as heterogeneous irradiance (Fredericksen et al. 1995) and amount of anti-oxidants in leaves (Wieser et al. 2002) may affect plant response to O_3 stress. For example, foliar ozone injury is shown to be related to O_3 uptake to net photosynthesis ratio since available assimilate is essential for defence and repair of O_3 injured tissues (Tjoelker et al. 1993). At higher irradiance, net photosynthesis and growth rates among tree species were significantly related to mean stomatal conductance and estimated O_3 uptake rate (Reich 1987). This is not the case under low light with high O_3 uptake to net photosynthesis ratio (Fredericksen et al. 1996). Stomatal conductance and photosynthesis are not obligatory coupled and can be controlled by light regardless of internal CO_2 concentration (Zieger & Field 1982). Therefore, foliar O_3 injury may be higher in shaded than sun-lit foliage since stomatal conductance and photosynthesis are less coupled at low light (Tjoelker et al. 1995). Moreover, small plants exposed to low light can be vulnerable to $+O_3$ as detoxification competes with carbon availability for growth (Matyssek & Sandermann 2003). Since defence, repair and detoxification processes require energy, small plants with a high proportion of shade foliage tend to reduce biomass production proportionally more than do large plants with sun-lit foliage (van Oijen et al. 2004; Matyssek & Sandermann 2003). As a consequence, competitiveness may be favored in dominant rather than subordinate individuals. Moreover, $+CO_2$ may be expected to increase and $+O_3$ to decrease root biomass. For example, root-shoot ratio is known to increase and decrease under $+CO_2$ and $+O_3$, respectively (Oksanen & Saalem 1999; Curtis & Wang 1998). Indeed, variability became apparent in competitive ability and growth rate when scaling $+CO_2$ and/or $+O_3$ effects from individual to stand level (Matyssek et al. 2004; Kolb & Matyssek 2001), or within and between species (Poorter & Navas 2003).

Competition analysis using juvenile trees has been widely based on empirical approaches using chamber experiments (Luedemann et al. 2009; 2005; Kozovits et al. 2005a & b; Grams et al. 2002). Theoretical progress has also been made in predicting responses through ontogeny (Boyden et al. 2009). However, considering competition at the population-level is not adequate (Berger et al. 2008) since plant individuals differ in its local interaction and adaptation to changing environmental condition (Dieckmann et al. 2000). These consequences are usually explored using individual-based models (IBM) where one can control independently the strategies of plant individuals. One concept widely used in IBM is the zone of influence (ZOI), an area in which plants interact, alter their environment and capture resources (Wyszomirski et al. 1999; Silander & Pacala 1985). Other methods have also been put forward to understand the mechanistic strategies of plant competitive success (Berger et al. 2008; Schwinning 1996). For example, an approach to assess spaced-related efficiencies of resource use as important parameters in evaluating competitive success in woody species has been introduced by Grams et al. (2002). In this approach, the efficiency of space occupation is calculated from space occupied by crown volume and root volume per unit of biomass investments into above- and belowground structures, respectively. Moreover, the efficiency of space exploitation can be calculated aboveground as the annual C gain (Kozovits et al. 2005b; Falge et al. 1996) retrieved per unit of occupied crown space. Likewise, the efficiency of space exploitation belowground is estimated as water uptake from the soil per unit of the occupied root space, where the latter can be estimated through a photosynthesis model as annual transpiration. This method has been subsequently employed and promoted for evaluating competitive strategies in deciduous and coniferous species (Grams & Matyssek 2010; Luedemann et al. 2009; Kozovits et al. 2005a).

Differences in plant competition are often implicitly set as proportional to the differences in the growth rate of plants (Schwinning 1996). Moreover, there is confusion on which plant traits are greatly responsible for growth. In this case, growth analysis based on plastic responses could provide an integrative approach to understand plant form and functions (Hunt 2003). Physiological optimization may shape the growth rate of plants (Hunt & Cornelissen 1997), although morphological features may dominate (Poorter et al. 2012). Poorter (1999) proposed that interspecific variation in *RGR* is due to morphology and physiology under high and low light environment, respectively. This leads to the notion that growth plasticity could shift along environmental gradients. Thus, it is likely that biotic (i.e competition) and abiotic stress (i.e. +CO_2 and +O_3) may add to the complexity in evaluating growth. For example, +CO_2 is shown to enhance growth of individual plants through increased photosynthetic activity and decreased specific leaf area (Poorter & Nagel 2000), given absence of other resource limitations (Körner 2003a). Conversely, +O_3 is known to impact physiological traits, e.g. decreasing light-saturated photosynthesis and increasing respiration (Matyssek et al. 2010). Hence, growth lies in the area of conflict between several opposing drivers, resulting in conflicting outcome and conclusions of *RGR* (Rees et al. 2010).

At the plant level, mechanistic understanding on how these gases affect competition and associated growth is still scarce. Competition involves processes that influences tree individuals, thus stand scale analyses should be complemented by single tree analysis (Bolte et al. 2013). Few investigations if any have quantified above- and belowground mode of competition at the individual level of juvenile trees exposed to $+CO_2$ and/or $+O_3$. On the other hand, understanding growth using volume-related changes at the whole tree level as proxies of underlying mechanisms remain unclear. In woody species, quantifying competitive success as an optimization process in space use rather than as a function of maximizing resource gain poses a challenge and requires data integration of several experimental evidences for robust analysis. It has been proposed that morphological factors influence competitive success (Grams et al. 2002) and ultimately growth of plants but under changing climatic condition, physiological factors (Poorter et al. 2012) may be more important. Overall, the integration of competition and growth in plant-plant interaction forms the core of this dissertation. Thus, an appropriate model is called for, using empirical evidence of plant interaction to decomposition into functional sub-modules. Such theoretical method can be considered as an explicit description of plant processes as governing size-dependence or independence of competition (Silander & Pacala 1990) or plasticity of growth (Poorter 1999).

Along this line, Schwinning (1996) decomposed the relative rate of resource uptake of an individual plant into simpler terms. The rate of resource uptake of an individual plant depends on the amount of resource in the environment, the amount of space occupied by the plant and the fraction of available resource taken from that space (See Eqn 1.1).

$$S = R \cdot A \cdot \mathrm{C} \qquad \text{Eqn 1.1}$$

The first term on the right side of the equation is called the 'resource availability factor' *R*; whereas, the second and last term is called the allometry of 'space occupation' *A* and 'resource capture efficiency factor' C, respectively (Schwinning 1996). The product of these three terms defines the relative rate of resource uptake *S* of an individual plant. Using this analysis, it is possible to determine *S* between large and small individuals in a stand considering distance with neighbors. Using log-transformed data, the mode of competition βs denotes the relationship between the size-difference in relative rate of resource uptake $ln\ s$ between large and small plants.

In this dissertation, a plant growth simulation model called PLATHO (**P**lant as **T**rees and **H**erbs **O**bject) was utilized to supplement results obtained from experiments and extrapolate effects beyond the time span of experimental data. PLATHO is a module of a general-purpose model EXPERT-N (for details, see Stenger et al. 1999; Engel & Priesack 1993). It is a generic-based process-oriented plant simulation model that simulates individual plant growth in mono- and mixed culture, considering phenology, photosynthesis, water and nitrogen uptake by roots, biomass growth, respiration, senescence and distribution of leaf area and root length (Gayler et al. 2006). PLATHO analyzes the mechanisms of competition by considering spatial properties and species-specific parameters of individual plants (Gayler & Priesack 2006). It is able to predict responses of $+CO_2$ and/or $+O_3$ on growth processes (Gayler et al. 2009). Specifically, PLATHO calculates O_3 effects on plant growth by estimating effective O_3 influx; assimilate partitioning and overall rates of costs for detoxification and repair (Gayler et al. 2009; van Oijen et al. 2004). On the other hand, effects of $+CO_2$ is estimated using the photosynthesis model of Farquhar and von Caemmerer (Farquhar et al. 1980).

In parallel, the ability of plants to compete is highly correlated with maximum relative growth rate (*RGR*) (Grime 2006). Growth analysis provides an integrative approach to understand plant form and functions (Hunt 2003). *RGR*, a conventional index of growth (Hunt 1979) is considered an appropriate method to calculate growth since it eradicates size biases (Hunt & Cornelissen 1997). *RGR* is usually defined as the increase in biomass per unit of biomass per unit of time. Instantaneously, it is defined as Eqn. 1.2.

$$RGR = \left(\frac{1}{B}\right)\left(\frac{\partial B}{dt}\right) = \partial(\ln B)/\partial t \qquad \text{Eqn. 1.2}$$

where *B* is the total biomass of the whole plant at time *t*. In calculus, this formula is equivalent to the slope of the curve of *ln B* against time and provides a mathematical accurate specification of *RGR* (Hunt 2003). However, this calculation is difficult to determine since it represents a value at a single point in time (South 1995) and usually derived from curve fitting of mathematical functions (Hunt 2003). Thus, a mean-harvest formula known as the ‘classical approach was initiated for calculating *RGR* over discrete time points, t_1 to t_2 (Eqn. 1.3). In this method, *RGR* is derived mathematically by assuming that *B* increases at a constant or exponential rate (Blackmann 1919).

$$RGR = \left(\frac{1}{t2 - t1}\right) \int_{B1}^{B2} \partial(\ln B) = \left(\frac{\ln B2 - \ln B1}{t2 - t1}\right) \qquad \text{Eqn. 1.3}$$

Thus, *RGR* represents the mean difference of log-transformed *B* across two harvest-intervals by the time difference between those harvests. It is known that logarithmic transformation makes variability nearly homogeneous with time. In this method, the harvest-interval means of *ln B* pertains to the period of time between two successive harvests (Hunt et al. 2002) which means that at least two observations are required. Moreover, the classical method can be obtained without pairing and without using fitted functions (Hunt et al. 2002; Causton & Venus 1981; Venus & Causton 1979). Expected mean values of *RGR* and their variances over harvest interval can be estimated from replicated plant biomass and showed similar results from random pairing method (Venus & Causton 1979). This approach is considered the simplest, less complicated and straight-forward method for obtaining *RGR*.

Nevertheless, this method has been criticized as unsatisfactory, since *RGR* can be obscured by the time course between harvest intervals (Causton & Venus 1981). The need to know the trend of growth with time using derived values gives rise to the development of functional approach in calculating *RGR*. This method involves curve-fitting and the derived growth rates can take any appropriate functions. With the advances in computer programs, curve fitting to complex experimental data using fitted functions have been widely used. Generally, the advantage of functional approach is that the instantaneous term can be obtained directly from the fitted curve (Hunt 2003). However, the functional approach is not recommended when only very few harvests are available (Venus & Causton 1979). Correspondingly, one could define *RGR* as factors in the decomposition of the rate of resource utilization (Schwinning 1996; Grams & Andersen 2007) as shown in Eqn. 1.4.

$$RGR = A \cdot B \cdot X \cdot E \qquad \text{Eqn. 1.4}$$

The first term on the right side is the 'space occupation factor' *A*, calculated as the amount of space (i.e. crown or root volume) occupied by above- or belowground biomass. The second term, the 'biomass ratio' *B* characterizes the structural fractionation of above- or belowground biomass relative to whole-plant biomass. The third term is the 'space exploitation factor' *X* which describes the amount of resource capture (e.g. light or water) within occupied space. The right-most term, the 'resource-to-biomass conversion efficiency' *E* refers to the instantaneous rate of change in total biomass per time per unit resource capture (e.g. light use efficiency *LUE* or water-use efficiency *WUE*). Hence, *RGR* can be defined as the product of these four factors which can be further classified according to plastic responses in morphology (*A* and *B*) and physiology (*X* and *E*).

Overall, a conceptual model based on decomposition technique, (i.e. the mathematical expansion of a complex process into simple components) was initiated in this dissertation to understand a possible shift in the mode of competition under changing CO_2 and/or O_3 regimes. This analysis was complimented by the plant growth model, PLATHO to fit the experimental data and provide predictions for prolonged period beyond experimental time scale. Empirical data originated from a series of chamber experiments (Grams et al. 1999; Jungermann 1998) and those conducted under the project 'Sonderforschungsbereich 607 (Ritter et al. 2015; Luedemann 2009; 2005; Kozovits et al. 2005a & b; Grams 2002) of the Deutsche Forschungsgemeinschaft, DFG) entitled "Growth and Parasite Defence - Competition for Resources in Economic Plants from Agronomy and Forestry" (Matyssek et al. 2005). PLATHO was parameterized using data from experiments, literature and curve fitting estimates and validated using independent data not used in the parameterization. The decomposition technique of competition compared experimental and modelled evidence, as focusing on competition for light and water. Species studied were juvenile European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] Karst), two ecologically and economically important tree species in Central Europe.

Thereafter, *RGR* at the stand level was also analyzed in this dissertation by integrating dataset with common parameter values as inputs for calculation. This integrated analysis was explored in this work by assessing whether *RGR* of beech and spruce in mono- and mixed stand is influenced by its ability to optimize occupied space or maximize resource gain. Using basic growth parameters, this kind of analysis offers an integrative framework in assessing plant responses at the stand level. Understanding competitiveness of plants as an optimization process in space use has been challenging the conventional consideration of competitive success as a function of maximization of resource gain. Moreover, analysis of growth using the decomposition technique classifies tree plastic responses into morphological and physiological aspects. Results are presented as three individual papers within this dissertation.

The first paper (Daigo et al. 2013) addresses the mode of aboveground competition (i.e. for light) and belowground competition (i.e. for water) under $+CO_2$ and/or $+O_3$ regimes. Empirical and modeling results were integrated towards understanding size-related competition between juvenile trees of beech and spruce planted in monoculture. Using experimental data and simulation analysis, this chapter investigated whether the positive asymmetric competition aboveground would diminish under $+CO_2$ and whether $+O_3$ would enhance this outcome. Conversely, the hypothesis was tested whether the symmetric competition belowground would remain unchanged under $+CO_2$ and $+O_3$. The study was published in Trees – Structure and Function Volume 27 pp 1763-1773. 2013. (Chapter 2 of this dissertation).

The second paper is a peer-reviewed book chapter (Grams et al. 2012) consisting of integrative data analysis from a series of phytotron experiments conducted on juvenile beech and spruce and exposed to ambient, $+CO_2$ and/or +O3 regimes. Firstly, the functional relationship between whole-tree *RGR* and efficiency of space use was established as an indicator of competitive success. Thereafter, analysis is conducted on the mechanisms that modulate the effects of intra and inter-specific competition and how these competitive interactions differ under $+CO_2$ and $+O_3$. This study investigated whether the ability to optimize space (i.e. efficiency of space occupation) rather than maximization of space (i.e. efficiency of space exploitation) determine the competitive success of these two competing species. Dataset used in this work consisted of a series of phytotron experiments conducted on beech and spruce planted in isolation, or either in mono- or mixed culture, This paper is part of the book volume Matyssek et al. (2012b), 'Growth and Defence in Plants: Resource Allocation at Multiple Scales'. Ecological Studies Vol 220, pp. 273-285; (Chapter 3 of dissertation).

The third paper addresses the mode of competition for growth under biotic (i.e. competition) and abiotic stress (i.e. $+CO_2$, $+O_3$), covering the need for *RGR* as integrating above- and belowground plant processes and how these vary under competition and at $+CO_2$ and $+O_3$ concentrations. Exemplified are beech and spruce saplings. Analysis was based on the mathematical decomposition of *RGR* applied on a dataset from a phytotron study that had been conducted on mono-and mixed culture of beech and spruce saplings exposed to ambient and $+CO_2$ and $+O_3$ regimes. The analysis focused on the morphological and physiological plasticity of *RGR* in terms of above- and belowground competition for light and water, respectively, in addition to effects of elevated gaseous regimes. This paper is currently submitted to Perspectives in Plant Ecology, Evolution and Sytematics (Chapter 4 of this dissertation).

The concluding part comprises the general discussion (Chapter 5) and general conclusion (Chapter 6) comparing the methods used in the investigation such as discussing the advantages and disadvantages of experimental dataset and simulation model, the approaches in calculating *RGR* and the growth strategies of beech and spruce saplings under the biotic limitation of competition and abiotic stress of $+CO_2$ and $+O_3$. Study that extends understanding of tree growth-processes from laboratory and field experimentations to simulation models still remains a daunting challenge. The aim of this work is to reconcile the differences in integrating theory from empirical data to explain the complexity in growth analysis. Overall, the combined analyses in this dissertation can be used as a tool to enhance conceptual understanding and predictive capacity of juvenile tree responses under the biotic limitation of competition and abiotic stress of increasing atmospheric climate.

2. Mode of competition for light and water amongst juvenile beech and spruce trees under ambient and elevated levels of O_3 and CO_2

Summary

Despite numerous studies conducted on plant responses to increasing CO_2 and + O_3 concentrations, there is still a gap in understanding how these gases would affect the mode of competition (e.g., the ability by which larger and smaller plants capture resources) at the individual level of intra-specific beech and spruce saplings. Using empirical data and simulations from the plant growth model PLATHO, we analyzed underlying mechanisms of competition and extrapolated effects beyond the time span of the experiment. We hypothesized that among juvenile beech and spruce trees planted in monoculture, $+CO_2$ would diminish the positive asymmetric competition for light. Conversely, $+O_3$ would enhance this outcome. In addition, we hypothesized that the symmetric mode of competition belowground for water would remain unchanged, irrespective of $+CO_2$ and/or $+O_3$ treatments.

Our results showed that $+CO_2$ and/or $+O_3$ treatments did not alter the mode of competition above- ground for light. Conversely, we accepted our hypothesis that the mode of competition for water would remain unchanged under both treatments. Overall, we conclude that neither $+CO_2$ nor $+O_3$ alters the positive asymmetric competition for light and the symmetric competition for water among beech and spruce individuals grown in monoculture. We further conclude that competitive mechanism above- (e.g., shading or overtopping effect) and belowground (e.g., non-preemption or foraging) rather than abiotic treatments, such as elevated CO_2, O_3 and CO_2/O_3 regimes, play a dominant role for ensuring competitive success among tree sapling.

Daigo Schulte MJ, Matyssek R, Gayler S, Priesack E, Grams TEE (2013) Mode of competition for light and water amongst juvenile beech and spruce trees under ambient and elevated levels of O_3 and CO_2. Trees 27: 1763-1773

Introduction

Predictions for rising atmospheric CO_2 and O_3 concentrations have led to research efforts that used enrichment experiments (Matyssek et al. 2005; Karnosky et al. 2003) and theoretical simulations (Grote & Pretzsch 2002; Gayler & Priesack 2005) to better understand plant responses under abiotic stress and its implications on ecosystem dynamics and functions. In woody species, elevated CO_2 or O_3 have shown to influence resource availability (Hättenschwiler & Körner 2000; Andersen 2003); susceptibility to root pathogens (Luedemann et al. 2005; 2009), photosynthetic performance (Grams et al. 1999), resource allocation (Kozovits et al. 2005a), resource partitioning (Liu et al. 2004), growth response (Poorter & Perez-Soba 2001; Grams et al. 2012) and competition (Mc Donald et al. 2002; Kozovits et al. 2005b). Results have shown high variability when scaled from individual to stand level (Kolb & Matyssek 2001; Matyssek et al. 2004) or between and among species (Poorter & Navas 2003). Consequently, at the individual plant level, mechanistic understanding on how these gases would affect competitive interaction is still lacking.

Size-differences may influence the way resources are taken up by plants in a stand. When comparing the resource uptake rate between two individuals of different sizes, three modes of competition can be distinguished, depending on whether larger plants capture more (positive asymmetric), the same (symmetric) or less (negative asymmetric) resource per total biomass involved in resource capture than their smaller neighbours (Schwinning 1996). Moreover, the mode of competition may be influenced by the characteristics of the limiting resource (Schwinning & Weiner 1998). For example, above- competition (e.g. for light) is often positively asymmetric since bigger plants can pre-empt light from smaller individuals (Weiner 1986). Conversely, self-shading in taller plants could result in less shading of neighbours and may result in a negative asymmetric outcome (Schwinning & Fox 1995). On the other hand, the mode of competition belowground (e.g. for water) is apparently more size-symmetric due to the non-pre-emptable characteristic, uniform distribution of belowground resources (Casper & Jackson 1997), in addition to foraging trade-off between large and small plants (Campbell et al. 1991). Specifically, dominant and subordinate plants have high scale (i.e. extensive root system) and high precision (i.e.

fine adjustment of root distribution) foraging advantage (Campbell et al. 1991), which could result in a comparative performance between sizes.

Under increasing atmospheric concentrations, we ask to what extent elevated CO_2 or O_3 (hereafter: $+CO_2$; $+O_3$) alter the mode of competition above- and belowground for light and water, respectively, at the individual level of juvenile beech and spruce saplings planted in monoculture. It has been suggested that $+CO_2$ reduced the overall size-difference between light exposed dominant & shaded subordinate plants (Catovsky & Bazzaz 2002; Wayne & Bazzaz 1997) as the latter experience less photosynthetic acclimation that could inhibit carbon limitation (Bazzaz & Catovsky 2002). Among dominant plants, acclimation of photosynthetic rates under $+CO_2$ could be associated with adjustment in leaf structure and chemistry (Tjoelker et al. 1998). For example, over-production of assimilates relative to sink demand may lead to carbohydrate accumulation in leaves (Stitt 1991) that could inhibit photosynthesis (Signora et al. 1998). Subordinate or low-light plants under $+CO_2$ may experience less photosynthetic down-regulation since their carbon assimilation is low and thus, less likely to show imbalance in sucrose synthesis and export (Signora et al. 1998).

Conversely, small plants exposed to low light were discussed to be vulnerable to $+O_3$ as detoxification competes with carbon availability for growth (Matyssek & Sandermann 2003). For example, in shaded environment, O_3 uptake rate per net photosynthesis of foliage is higher than in sun-lit foliage because of lower coupling of photosynthesis and stomatal conductance at low light (Fredericksen et al. 1996). This results in greater O_3 injury in shade than sun-lit foliage (Tjoelker et al. 1993, Volin et al. 1993). Since defense, repair and detoxification processes require energy, smaller size plants with a higher proportion of shade foliage tend to reduce biomass more than larger size plants (e.g. with sun foliage; Matyssek & Sandermann 2003; van Oijen et al. 2004). Conversely, this translates to favorable competitive performance of dominant rather than subordinate individuals.

In view of such considerations, we hypothesize that among juvenile beech and spruce trees planted in monoculture, $+CO_2$ diminishes but $+O_3$ enhances the positive asymmetric competition for light. Meanwhile, we expect $+CO_2$ to increase and $+O_3$ to decrease root biomass. For example, root-shoot ratio (R: S) is known to increase and decrease under elevated $+CO_2$ and $+O_3$, respectively (Curtis & Wang 1998; Oksanen

& Saalem 1999). This may be attributed to expansion of root system under +CO_2 (Luo et al. 1994) and decreased storage reserves under +O_3 (Andersen 2003). However, lack of pre-emptable mechanisms belowground (i.e. shading or overtopping) suggests a proportionate resource uptake irrespective of size. In addition, trade-off between high-scale foraging in dominant plants and high-precision foraging in subordinates (Campbell et al. 1991) suggest equal competitive ability between sizes for belowground resources. Therefore, we hypothesize that the symmetric nature of belowground competition for water would remain unchanged.

Using data gathered from experiments, we analyzed the mode of competition above- and belowground at the individual level of beech (*Fagus sylvatica* L.) and spruce (*Picea abies* [L.] Karst) saplings grown in monoculture under ambient CO_2 and/or +O_3. Additionally, we applied a plant growth simulation model (PLATHO, Gayler et al. 2006), which allows for mechanistic analyses of competition over a prolonged period, extending beyond the experimental time scale.

Methods

Experimental Data

Data analyzed for this work originated from a phytotron study conducted on juvenile beech and spruce trees exposed to elevated CO_2 (ambient + 300 ppm) and elevated O_3 (restricted to < 150 ppb). Measurements spanned throughout two growing seasons. In the phytotrons, four regimes were established: ambient CO_2 / ambient O_3 (control); elevated CO_2 / ambient O_3 (+CO_2); ambient CO_2 / elevated O_3 (+O_3) and elevated O_3 / elevated CO_2 (+O_3/CO_2). Climate conditions were reproduced similar to a forest site with fluctuating ambient or twice-ambient O_3 levels (Matyssek et al. 2007). Ambient O_3 levels, irradiance, relative humidity, air and soil temperature was reproduced on an hourly basis. Canopy closure observed during the first growing season indicated that plant growth in the phytotron, particularly in the second year, is limited by light. This is not the case for water, as continuous monitoring and automatic maintenance of soil moisture ensured continuous water supply. For details, see (Kozovits et al. 2005a & b; Grams & Matyssek 2010). Our analysis utilized monoculture datasets of juvenile beech and spruce saplings planted in containers (Fig 2.1). Twenty trees were arranged in rows of 4 x 5 individuals with a plant density of 96 trees per m^2. For aboveground analysis, we gathered datasets that included crown volume (m^3), photosynthetic photon flux density (PPFD $mol\ m^{-2}\ d^{-1}$) for sun and shade leaves, and biomass of stem + axes + leaves (*g*). Light uptake value is estimated based on PPFD which attenuates exponentially within the canopy and the leaf area index (LAI) using Beer-Lambert law (Bossel 1996). For belowground analysis, data gathered included resource supply (i.e. amount of irrigated water), fine root biomass (*g*) and fine root volume (m^3). The latter was estimated from specific fine root length

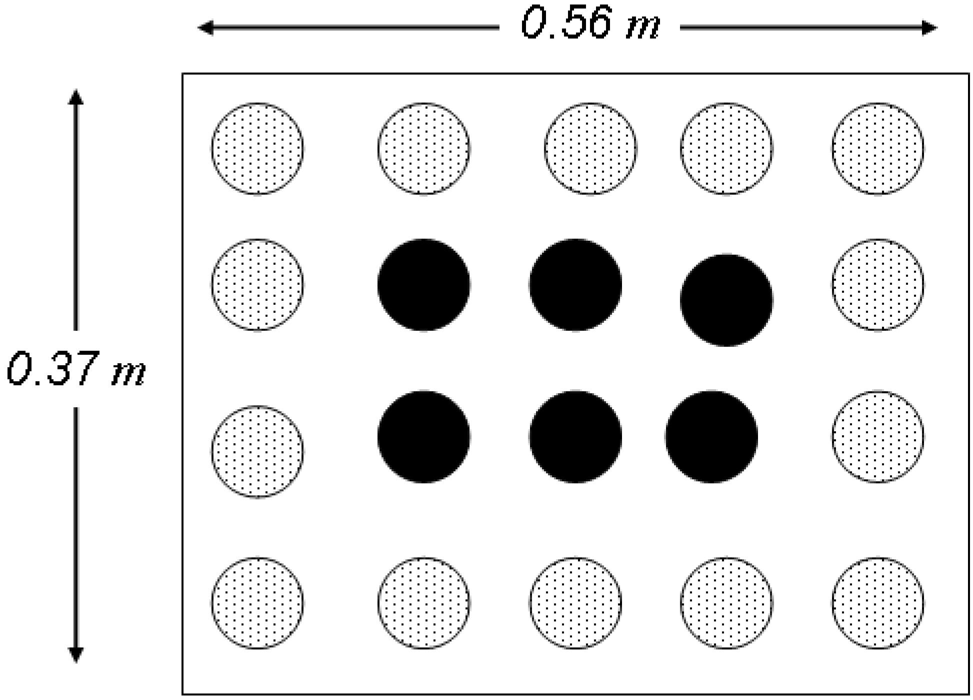


Fig. 2.1: Planting Design of trees in a container (0.56 x 0.37 x 0.30 *m*; length x width x soil depth) containing 20 juvenile trees, either beech or spruce. Sampling was focused on six central individuals (black) to diminish edge effects.

SFRL ($m\ g^{-1}$), fine root biomass Bx (*g*) and the radius of depletion zone *r (m*) where water is extracted. A value of .02 *m* for *r* is considered an appropriate approximate (Garrigues et al. 2006). Water uptake value is assumed from transpiration data (*mol* H_2O).

In addition to the empirical data, we utilized a simulation model called PLATHO (Gayler & Priesack 2005) to analyze underlying mechanisms of competition and to extrapolate effects beyond the time span of the experiment. PLATHO simulates the growth of individual plants within canopies taking into consideration phenology, photosynthesis, water uptake by roots, biomass growth, respiration, senescence and distribution of leaf area and root length. Every simulation day, light and water competition coefficients between a target plant and its four nearest neighbours were estimated from the overlap of zones of influence. Morphology of each individual tree is represented by a cylinder with flexible height to diameter ratio, which considered the occupied crown and soil volumes. The diameter of the cylinder was uniform above- and belowground and restricted by the distance between neighboring plants. The vertical distribution of leaf area and root length within these volumes depended on the respective competitive situation of the individual trees. Beech and spruce trees were characterized in the model by different phenological, morphological and physiological parameters. In PLATHO, the response of plants to irradiance and CO_2 concentrations is simulated following the approaches that were proposed by Farquhar et al. (1980) for photosynthesis and by Falge et al. (1996) for stomatal conductance. O_3 impacts on plant growth were simulated with the approach developed by van Oijen et al. (2004). The model was calibrated for juvenile beech using independent experimental datasets (Gayler et al. 2006, 2009) and the optimization toolbox in MATLAB (The Mathworks Inc., 2005).

Theoretical Concept of Competition Analysis

This study utilized the decomposition analysis of resource uptake rate of an individual plant which is decomposed on three terms (Eqn 2.1) namely: amount of resource available in the environment, amount of space occupied by the plant and fraction of the available resource take up from that space (Schwinning 1996).

$$\frac{1}{B_x}\cdot\frac{\partial U_x}{\partial t}=\frac{1}{V_x}\cdot\frac{\partial I_x}{\partial t}\cdot\frac{V_x}{B_x}\cdot\left(\frac{\partial Ux/\partial t}{\partial Ix/\partial t}\right) \qquad \text{Eqn 2.1}$$

where *Bx* is the amount of above (stem +axes + leaves) or belowground (fine and coarse root) biomass, V_x (crown or root volume) is the space occupied by B_x, time derivative of ∂I_x is the rate of resource availability (e.g. PPFD or irrigated water) and the time derivative of ∂U_x is the rate of resource uptake (e.g. light or water uptake). As formulated by Schwinning (1996), the first term in the equation is called the resource availability factor (*R*); the second term is referred to as the allometry factor (*A*) and the last term the resource capture efficiency factor (*C*). Multiplying the three terms gives the relative rate of resource uptake (*S*) of an individual plant.

To compare *S* between individuals of different sizes, data were log-transformed and difference in $ln\ S$ between a large (S_1) and small individual (S_2) was weighted by the inverse of distance between them (Eqn 2.2). Thus, closer pairs have more weight than those further away. This means that the competitive effect of a tree is weighted not only through its size but also by proximity to its neighbor in the plot

$$ln\ s = (ln\ S_1 - ln\ S_2) * 1/Distance \qquad \text{Eqn 2.2}$$

(Kühlmann et al. 2005). In Eqn 2.2, $ln\ s$ denoted the size-difference in relative rate of resource uptake. Likewise, size-differences between individual pairs in resource availability factor ($ln\ r$), allometry factor ($ln\ a$), resource capture efficiency factor ($ln\ c$) and biomass ($ln\ Bx$) between large and small pairs are weighed by the inverse of distance between them.

Statistical Analysis

Experimental data were pooled (Levene Test = $P > 0.05$) and a single linear regression was fitted to the data with a common slope for all groups and treatment designations ignored. In this study, the slope of the regression between size-difference in biomass ($ln\ Bx$) and size-difference in relative rate of resource uptake ($ln\ s$) denoted the mode of competition (β_s) (Fig 2.2). Likewise β_r, β_a and β_c represented the size-dependence of resource availability, allometry and resource capture, respectively. For five-year simulated data, we employed ordinary least squares (OLS) regression of the Johnson-Neyman (J-N) procedure using Modprove (Hayes & Matthes 2009). The J-N analysis identified the level of significant or insignificant effects of a treatment group

(+O_3, +CO_2, +CO_2/O_3) on the outcome variable (*ln s*) within the range of covariate (*ln Bx*). To test the replicability of the PLATHO model, we compared regression slopes of measured and simulated data and reported significant differences at $P < 0.05$. All statistical analysis used SPSS statistical package Ver. 20 (IBM 2012).

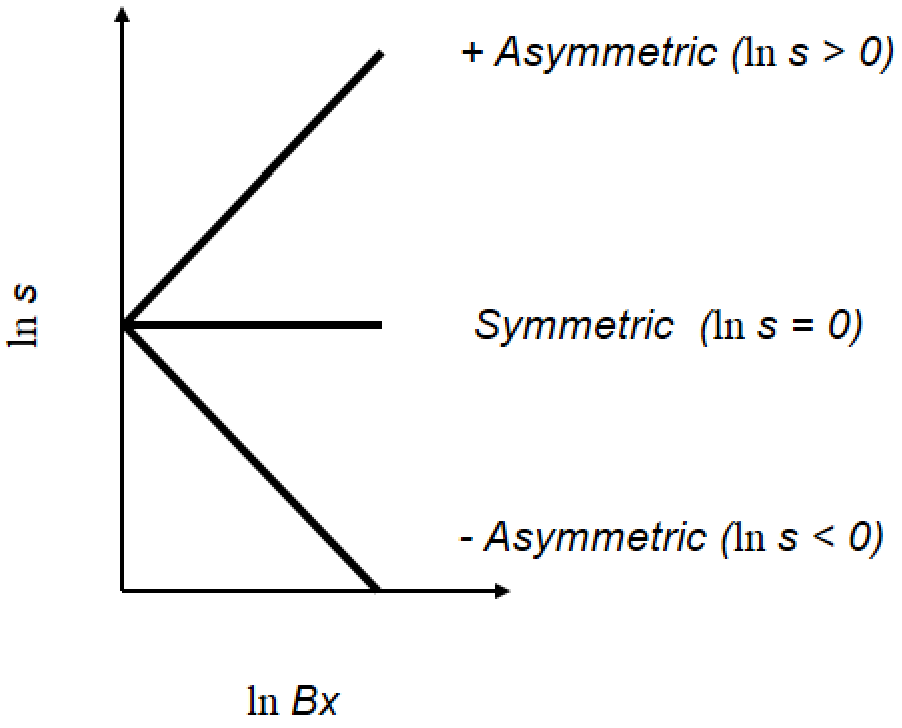


Fig. 2.2: Data analysis using linear regression showing relationship between size-difference between trees ($ln B_x$) and size-difference in relative rate of resource uptake ($ln s$). Regression slope $\beta_s = \partial(ln\ s) / \partial(ln\ B_x)$ determines whether the mode of competition is: (i) positive asymmetric ($\beta_s > 0$), with larger plants capturing proportionally more resources per unit biomass than smaller plants; (ii) negative asymmetric ($\beta_s < 0$), with smaller plants capturing proportionally more resources per unit biomass than larger plants; and (iii) symmetric ($\beta_s = 0$), with large and small plants capturing the same amount of resources per unit biomass. Data were log-transformed prior to analysis

Results

Experiment and simulation

Using data from two growing seasons, the mode of competition for light and water among intra-specific beech and spruce saplings were compared between experiment and simulation. In all cases, data from the plant growth model PLATHO was consistent with the results from experiments (Fig 2.3 & Fig 2.4). In beech monocultures, the mode of competition for light, depicted by the relationship between size-difference in biomass (*ln Bx*) and size-difference in resource uptake (*ln s*), was size-symmetric ($\beta_s = 0$) (Fig 2.3a). Conversely, the mode of competition for light in spruce was positive size-asymmetric ($\beta_s > 0$; Fig 2.4a). Irrespective of species, smaller saplings had higher resource availability ($\beta_r < 0$; Fig 2.3b & 2.4b) but larger individuals compensated by a more efficient resource capture per unit of biomass ($\beta_c > 0$ Fig 2.3d & 2.4d). Among beech saplings, smaller individuals had relatively higher allometry relative to its size than larger ones ($\beta_a < 0$; Fig 2.3c) but this was equal between sizes among spruce saplings ($\beta_a = 0$; Fig 2.4c).

Belowground competition for water, however, was consistently symmetric for both species (Fig 2.3e & Fig 2.4e). The components of competition, followed similar regression patterns as above- (Fig 2.3 & 2.4) except that the allometric factor belowground favored larger saplings ($\beta_a > 0$; Fig 2.3g & 2.4g).

Five-year prediction of the mode of competition

For both species, the extrapolation by simulation to up to five years gave evidence that the mode of competition (β_s) increased. In cases with initial symmetric competition ($\beta_s = 0$) during the first growing seasons, the mode of competition above- for light became increasingly positive asymmetric with time (Fig 2.5a-d & Fig 2.6 a-d). Belowground, the mode of competition for water (β_s) followed an increasing trend from being significantly negative asymmetric during the first year until it stabilized to symmetry towards the end of the simulation period (Fig 2.5 e-h & Fig 2.6 e-h). No treatment effects were found on the mode of competition for light and water among intra-specific beech and spruce saplings in the experimental data (Fig. 2.3 and 2.4; P >

0.05). Extrapolation by simulation for up to five years using the PLATHO model confirmed that neither $+CO_2$ nor $+O_3$ altered the mode of competition irrespective of resources (i.e. for light and water) among intra-specific beech and spruce saplings (Table 2.1).

Discussion

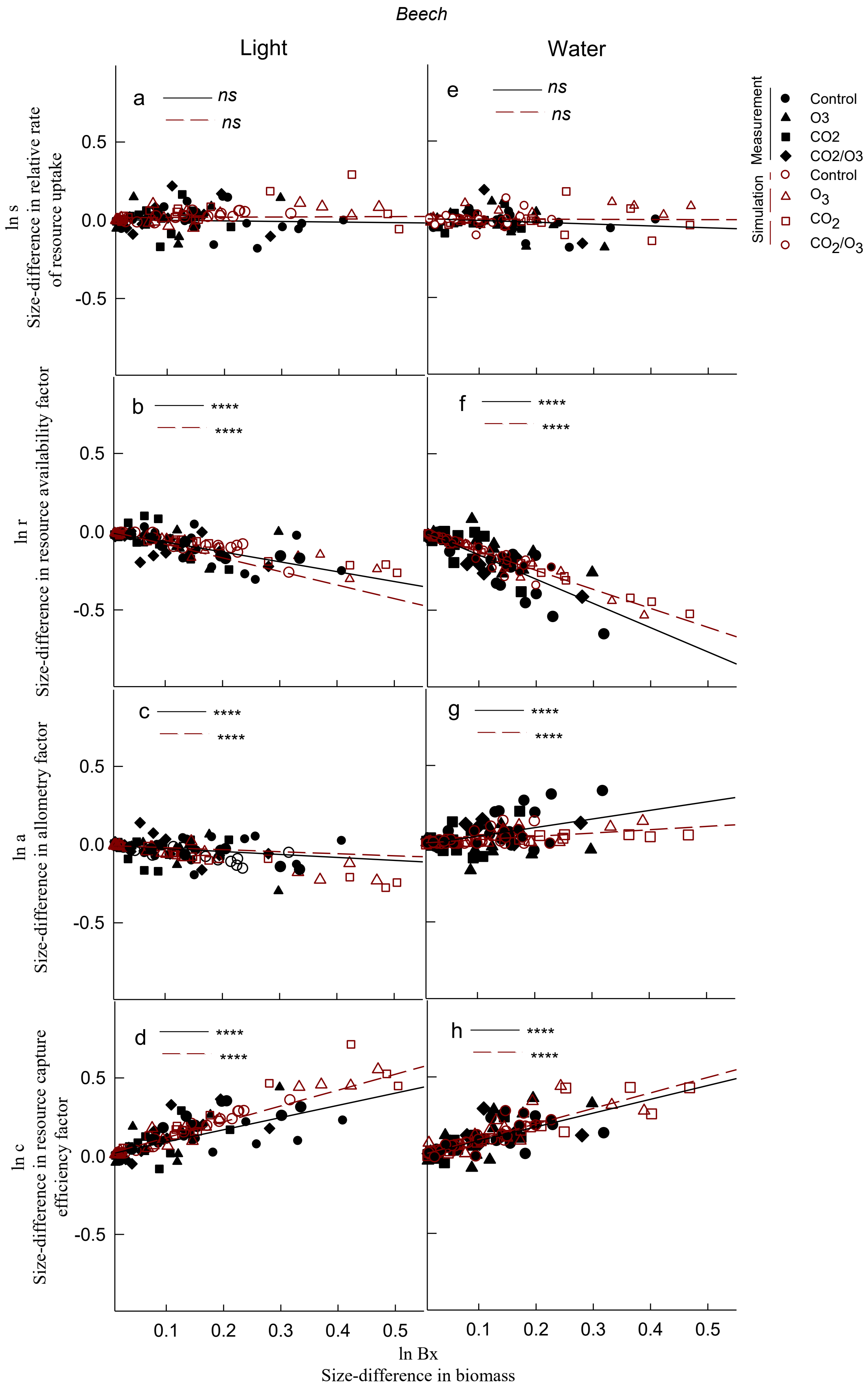
Resource competition amongst juvenile beech and spruce saplings in a two-year phytotron experiment was analyzed using the decomposition technique of Schwinning (1996) and simulated using the plant-growth model PLATHO (Gayler and Priesack 2005). We hypothesized that among juvenile beech and spruce trees planted in monoculture, $+CO_2$ diminishes the positive asymmetric competition for light (H1). Conversely, $+O_3$ was hypothesized to enhance this outcome (H2). Additionally, we hypothesized that the symmetric mode of competition belowground for water remained unchanged, irrespective of $+CO_2$ and/or $+O_3$ treatments (H3).

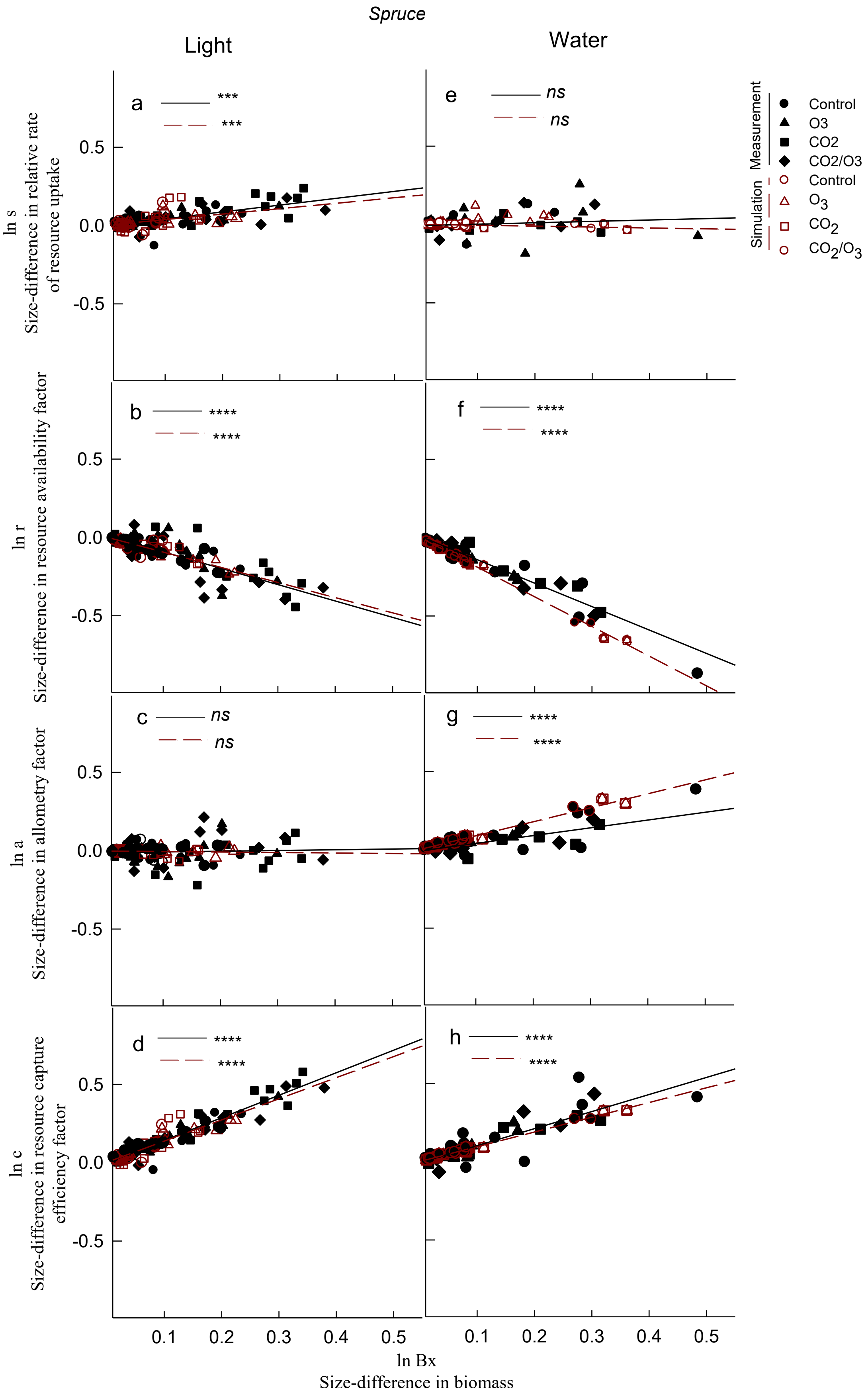
The Mode of Competition for Light

We found no evidence that the mode of competition for light among intra-specific beech and spruce saplings would decrease or increase under $+CO_2$ and/or $+O_3$, respectively, rejecting H1 and H2 (Table 2.1). In the gaseous control, the mode of competition during two growing seasons among beech and spruce individuals showed a symmetric and positive asymmetric pattern, respectively (Fig 2.3a & 2.4a). These contrasting results may indicate species-specific plasticity to occupy space, which is an important mechanism to avoid shading effects in a competitive stand (Gayler et al. 2006; Grams et al. 2012). However, outcomes may be influenced by initial condition (Weiner 1990; Pacala & Weiner 1991; Schwinning & Fox 1995, Gayler et al. 2009). Additionally, lack of independence between sampling variables might have biased our results as we analyzed six trees per container in two subsequent years. Nonetheless, the absence of significant container effects and the fair distribution of tree growth within the planting containers allowed for the use of individual plants as experimental units (Kozovits et al 2005b). Significant differences between the two growing seasons further support data independency.

Fig. 2.3: Mode of Competition for light among beech saplings in monoculture using data from experiment (closed symbols & continuous line) and simulation (open symbols & dashed line). Regression lines between size-difference in biomass (*ln Bx*) and size-difference in relative rate of resource uptake (*ln s*) depicted the mode of competition (β_s) (see Fig 2.2). Likewise, relationships between *ln Bx* and its three factors indicate the size-dependence of resource availability (β_r; b & f), allometry (β_a; c & g) and resource capture efficiency *ln c* (β_c; c & h). Data represent pooled values for two consecutive years (1999-2000) and across treatments as the slopes were not different for individual years. Circles represent control, $+O_3$ is given by triangles, $+CO_2$ by squares and $+CO_2/O_3$ by rhomboids.

Fig. 2.4: Mode of competition for light among spruce saplings in monoculture using data from experiment (closed symbols & continuous line) and simulation (open symbols & dashed line). Regression lines between size-difference in biomass (*ln Bx*) and size-difference in relative rate of resource uptake (*ln s*) depicted the mode of competition (β_s) (see Fig 2.2). Likewise, relationships between *ln Bx* and its three factors indicate the size-dependence of resource availability (β_r; b & f), allometry (β_a; c & g) and resource capture efficiency *ln c* (β_c; c & h). Data represent pooled values for two consecutive years (1999-2000) and across treatments as the slopes were not different for individual years. Circles represent control, $+O_3$ is given by triangles, $+CO_2$ by squares and $+CO_2/O_3$ by rhomboids.


Beech
Light
Water
a
e
b
f
c
g
d
h
ns
****
ln s
Size-difference in relative rate of resource uptake
ln r
Size-difference in resource availability factor
ln a
Size-difference in allometry factor
ln c
Size-difference in resource capture efficiency factor
0.5
0.0
-0.5
0.1
0.2
0.3
0.4
0.5
ln Bx
Size-difference in biomass
Measurement
Simulation
Control
O3
CO2
CO2/O3
Control
O_3
CO_2
CO_2/O_3


Spruce
Light
Water
a *** ***
e ns ns
b **** ****
f **** ****
c ns ns
g **** ****
d **** ****
h **** ****
ln s
Size-difference in relative rate of resource uptake
ln r
Size-difference in resource availability factor
ln a
Size-difference in allometry factor
ln c
Size-difference in resource capture efficiency factor
0.5
0.0
-0.5
0.1
0.2
0.3
0.4
0.5
ln Bx
Size-difference in biomass
Measurement
● Control
▲ O3
■ CO2
◆ CO2/O3
Simulation
○ Control
△ O_3
□ CO_2
○ CO_2/O_3

Extrapolations to a total of five years using the PLATHO model suggests that through time, the mode of competition for light becomes positive asymmetric irrespective of species (Fig 2.6a-d & 2.7a-d). Both experiments and simulation confirm that this outcome is altered neither by $+CO_2$ and/or $+O_3$. In our first hypothesis, we assume that $+CO_2$ reduces the size-difference between larger and smaller plants as previously mentioned (Wayne & Bazzaz 1997; Curtis & Wang 1998; Catovsky & Bazzaz 2002). Such a $+CO_2$ response could be attributed to less photosynthetic down-regulation in subordinate than dominant plants (Bazzaz & Catovsky 2002), since the carbon assimilation of shaded plants is lower. As a consequence, sucrose synthesis of subordinate plants under $+CO_2$ is less likely to exceed their sink capacity and therefore photosynthesis will not be feedback-inhibited (Signora et al. 1998).

However, in the present study, $+CO_2$ had no effect whatsoever on the mode of competition for light, rejecting H1(Table 2.1). In a meta-analysis study, Poorter & Navas (2003) reported that biomass development of dominant and subordinate plants respond exactly in the same way under $+CO_2$ confirming unchanged competition under $+CO_2$. The plant growth model PLATHO calculates CO_2 response on photosynthetic capacity based on leaf internal CO_2 concentrations. Simulations suggest that the ratio between leaf external atmospheric and leaf internal CO_2 concentration does not deviate significantly between plant sizes (data not shown). This implies that at this early developmental stage, the light use efficiency does not differ between large and small individuals under ambient and increased atmospheric CO_2 concentration.

Table 2.1: Ordinary Least Squares Regression (OLS) estimating effect of treatment ($+O_3$, $+CO_2$, $+CO_2/O_3$) on the mode of competition (β_s) + and – signs represent whether treatment increases and decreases, respectively, the mode of competition

β_s	$+O_3$	$+CO_2$	$+CO_2/O_3$
Beech Light	*(+) P* 0.630	*(-) P* 0.355	*(-) P* 0.709
Beech Water	*(-) P* 0.687	*(+) P* 0.283	*(+) P* 0.353
Spruce Light	*(+) P* 0.305	*(-) P* 0.108	*(-) P* 0.980
Spruce Water	*(+) P* 0.998	*(+) P* 0.760	*(+) P* 0.557

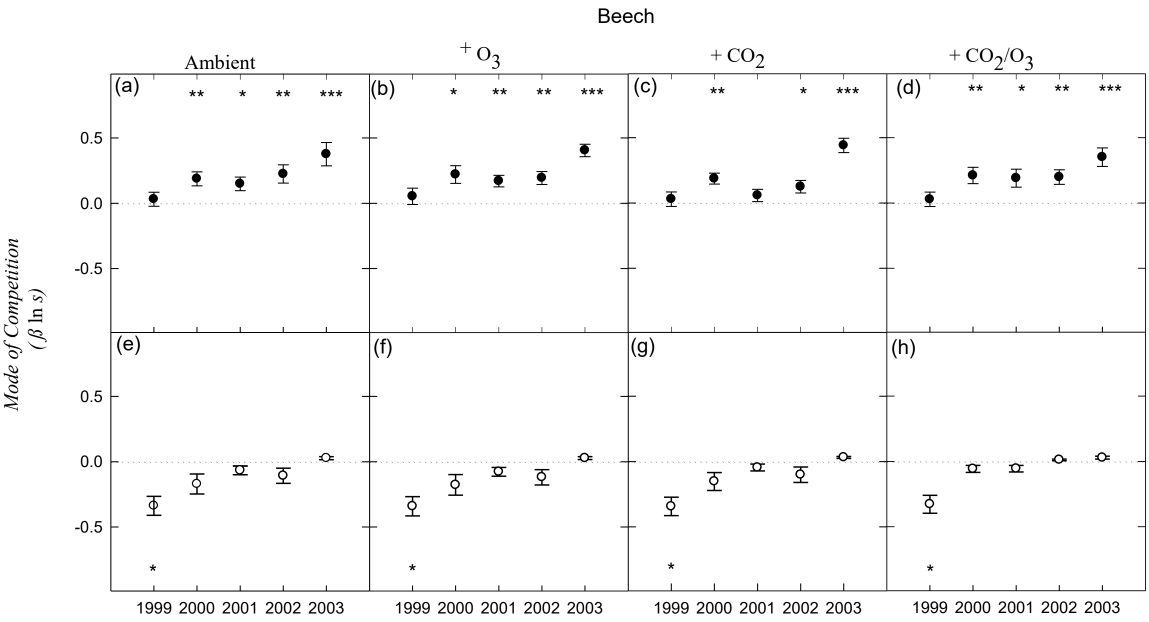


Fig. 2.5: Five-year Simulation of the mode of competition for light (a-d) and water (e-h) among beech saplings in monoculture. Each data point (n = 12) represents the slope coefficient of *ln s*, i.e. the mode of competition (*βs*), calculated from simple linear regression between size-difference in biomass (*ln Bx*) and size-difference in relative rate of resource uptake (*ln s*) between larger and smaller saplings during considered simulation times (1999-2003). Error bars indicate standard error of the coefficient. Asterisks denote statistical significance whether *βs* is positive (+ asymmetric), negative (-asymmetric) or does not differ from zero (symmetric)

Our second hypothesis states that under +O_3, the mode of competition for light favored large rather than small saplings. Injury due to O_3 is found to be higher in shade than sun-lit foliage (Tjoelker et al. 1993; Volin et al. 1993). Since defense, repair and detoxification processes require energy, smaller size plants with a higher proportion of shade foliage tend to reduce biomass more than larger size plants (e.g. with sun foliage; Matyssek & Sandermann 2003; van Oijen et al. 2004). Conversely, this would translate to favorable competitive performance of dominant as opposed to subordinate individuals. Our findings do not support such a trend for +O_3 which had no significant effect on the mode of competition for light irrespective of species. PLATHO calculates O_3 effects based on the amount of Rubisco damaged per unit of O_3 uptake rate, rate and cost of O_3 detoxification and repair (van Oijen et al. 2004;

Matyssek et al. 2008). Hence, any reduction on plant growth caused by +O3 may be related to a decrease in Rubisco and C availability. However, we could not detect any change in the positive asymmetric mode of competition for light. Our simulation confirmed that irrespective of species, leaf Rubisco concentration did not deviate across treatments and size (P > 0.05; not shown), suggesting that Rubisco content may be replenished by repair processes.

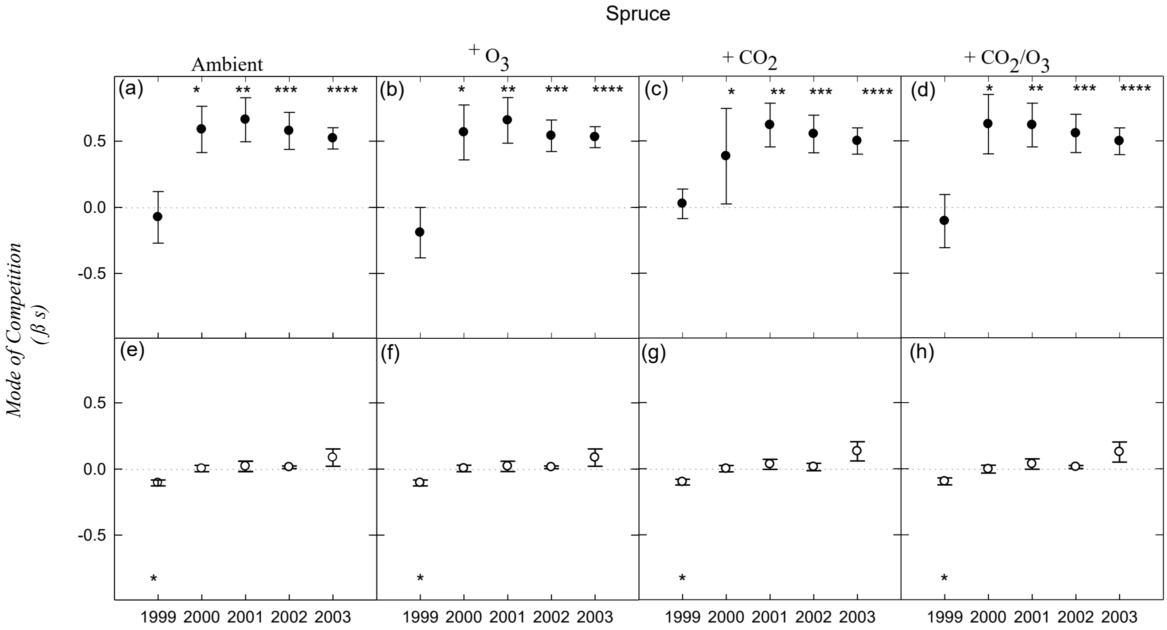


Fig. 2.6: Five-year simulation of the mode of competition for light (a-d) and water (e-h) among spruce saplings in monoculture. Each data point (n = 12) represents the coefficient of *ln s*, i.e. the mode of competition (*βs*), calculated from simple linear regression between size-difference in biomass (*ln Bx*) and size-difference in relative rate of resource uptake (*ln s*) between larger and smaller saplings during considered simulation times (1999-2003). Error bars indicate standard error of the coefficient. Asterisks denote statistical significance whether *βs* is positive (+ asymmetric), negative (-asymmetric) or does not differ from zero (symmetric)

The Mode of Competition for Water

We found no evidence that $+CO_2$ and $+O_3$ alter the size-symmetric competition for water accepting our hypothesis (H3). We assume that although $+CO_2$ and $+O_3$ may increase or decrease, respectively, belowground carbon allocation, the absence of resource pre-emption mechanism belowground (i.e. shading or overtopping) prevents bias in competition for mobile resources such as water or nitrate (Schwinning and Weiner 1998, Hodge 2004). Our simulation confirmed that at the stand-level, $+CO_2$ and $+O_3$, increased and decreased, respectively carbon availability ($P< 0.05$; not shown). Nevertheless, on an individual level, the mode of competition for water did not divert between sizes ($\beta s = 0$; Fig 2.5 & 2.6). This means that the mode of competition belowground is independent of root size, growth rate or root/shoot allocation (Rajaniemi 2007). Therefore, competitive performance of small and large individuals are size-symmetric, despite increasing $+CO_2$ and/or $+O_3$ treatments. This indicates that mobile characteristics of resource and absence of a pre-emptable mechanism, maintain the size-symmetry of competition for water under elevated CO_2 and/or O_3 regimes.

Conclusions

In this study, we reject our hypothesis that $+CO_2$ and/or $+O_3$ treatments alters the mode of competition above- for light (H1 & H2). Conversely, we accept our hypothesis that the mode of competition for water would remain unchanged under both treatments (H3). Overall, we conclude that neither $+CO_2$ nor $+O_3$ alter the positive asymmetric competition for light and symmetric competition for water among beech and spruce saplings grown in monoculture. These suggest that competitive mechanisms above (e.g. shading effect) or belowground (e.g. non-preemption, foraging) rather than abiotic treatments such as $+CO_2$ and/or $+O_3$ are important for ensuring the competitive success among tree saplings. This study has unveiled principles of mechanisms related to competition under controlled phytotron conditions with scenarios of relevance for current and expected future O_3/CO_2 regimes so that empirical validation is to be awaited for the actual site conditions of forest ecosystems.

3. Growth and space use in competitive interactions between juvenile trees

Summary

We review a series of growth chamber experiments on the effects of elevated carbon dioxide (CO_2) and ozone (O_3) on Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* L.), grown in isolation or under intra and inter-specific competition. Focus is on the mechanistic grounds of competitive interactions between the two tree species and on the question of whether competition affects the responses of plants to the gaseous treatments. We found competitive interactions between plants to significantly alter impacts of atmospheric CO_2 and O_3 concentrations. It appears that the more intense the competition is, the stronger the response to other stressors may be modified. Hence, responses of plants grown in isolation are of only limited relevance for plants grown in mono or mixed cultures. In situations with intense competitive interactions, the efficient occupation of space represents an effective mechanism to be competitive by increasing the resource accessibility relative to competing neighbors.

Grams TEE, **Daigo Schulte MJ**, Winkler J, Gayler S, Matyssek R (2012) Growth and space use in competitive interactions between juvenile trees. Growth and defence in plants. Springer, pp 273-286

Introduction

Plants are exposed to a plethora of environmental influences that are affecting their life cycle by either abiotic e.g. physico-chemical or biotic factors such as associations with microorganisms or interactions with animals. Those influences create a dilemma in resource allocation (Matyssek et al. 2012b; Ernst et al. 2012) as they rarely act as single impacts but are typically multi-factorial. For instance, under conditions of climate change, increase of atmospheric carbon dioxide (CO_2) concentration is paralleled by rising temperature and enhanced risk of drought events. These multi-factorial influences do not affect plants as isolated individuals but as parts of complex interactions with their neighboring plants, comprising positive and negative i.e. facilitative and competitive interactions, respectively.

This chapter discusses the effects of elevated concentrations of CO_2 and ozone (O_3, as an intrinsic component of climate change; Fowler 2008; Sitch et al. 2007) on growth and resource allocation of two ecologically and economically important tree species in Central Europe, European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] Karst). Focus is on the mechanisms of intra and inter-specific competition between the two tree species and on how competitive interactions may modulate impacts of elevated O_3 and CO_2. To this end, we review a series of growth chamber experiments where beech and spruce were grown in isolation or under intra and inter-specific competition.

Competition of plants for resources is conceived as the integral of spatio-temporal resource use (Küppers 1989; Matyssek and Schulze 1987; Schwinning 1996). Along this line, an approach to interpret competition as space-related resource investments and gains was introduced for woody plants to quantify competitiveness by space-related efficiencies of (1) resource investment into standing biomass (space occupation) and (2) resource gain (space exploitation) (Grams et al. 2002). Subsequently, this approach has been employed and promoted (Grams and Matyssek 2010; Kozovits et al. 2005b; Luedemann et al. 2009; Rodenkirchen et al. 2009). Understanding competitiveness of plants as an optimization process in space use has been challenging the conventional consideration of competitive success as a function of maximization of resource gain. Or in other terms, as expressed by Fakhri A.

Bazzaz during the first international meeting of SFB 607 in 2001 “You (i.e. the plant) don’t have to optimize, you have to maximize.” In this chapter we will (1) valuate this question, i.e. whether the competitive success of a plant is related to an efficient space use, i.e. optimization strategy, or conversely to the maximization of resource gain as such, i.e. maximization strategy. It will (2) be examined further of whether effects of elevated O_3 and CO_2 concentrations and the combination of both are modified by the different competitive settings, i.e. growth in isolation, mono or mixed culture.

Material and Methods

Plants, climate conditions and O_3/CO_2 treatments

We report on a total of four consecutive phytotron experiments which were performed under similar environmental conditions (regarding climate and O_3/CO_2 regimes) in the four walk-in phytotrons (size ca. 2.8 m x 3.4 m, Fig. 3.1a; Kozovits et al. 2005a; Payer et al. 1993; Thiel et al. 1996). The experiments were run during the years 1995 through 2005 (see Table 3.1) and are described in detail elsewhere (Grams et al. 1999; Kozovits et al. 2005a; Luedemann et al. 2005; Ritter et al. 2015). Trees were planted in forest soil (dystric cambisol, pH of about 4.5).

In the first experiment beech trees were grown individually in 10 L pots, whereas in the subsequent three experiments 20 plants were grown together in one container (soil volume of 62 L, with an area of 0.56 m × 0.37 m, soil depth of 0.30 m). The container experiments (Exp. 2 to 4, see Table 3.1) used either monocultures or “one-by-one” beech/spruce mixtures. In each case, the twenty trees were arranged in rows of 4 x 5 individuals (Fig. 3.1b). After planting, trees were kept for one growing season in a climate controlled greenhouse under outside conditions at either ambient or elevated (i.e. ambient + 300 $\mu L\ L^{-1}$) CO_2 concentrations. During the following spring, plants were transferred to the four phytotrons. We reproduced the climate conditions and O_3 regimes throughout entire growing seasons as previously recorded at forest sites with fluctuating ambient or elevated (i.e. twice-ambient but restricted to 150 $nL\ L^{-1}$) O_3 levels. In the first and second experiment (Table 3.1,

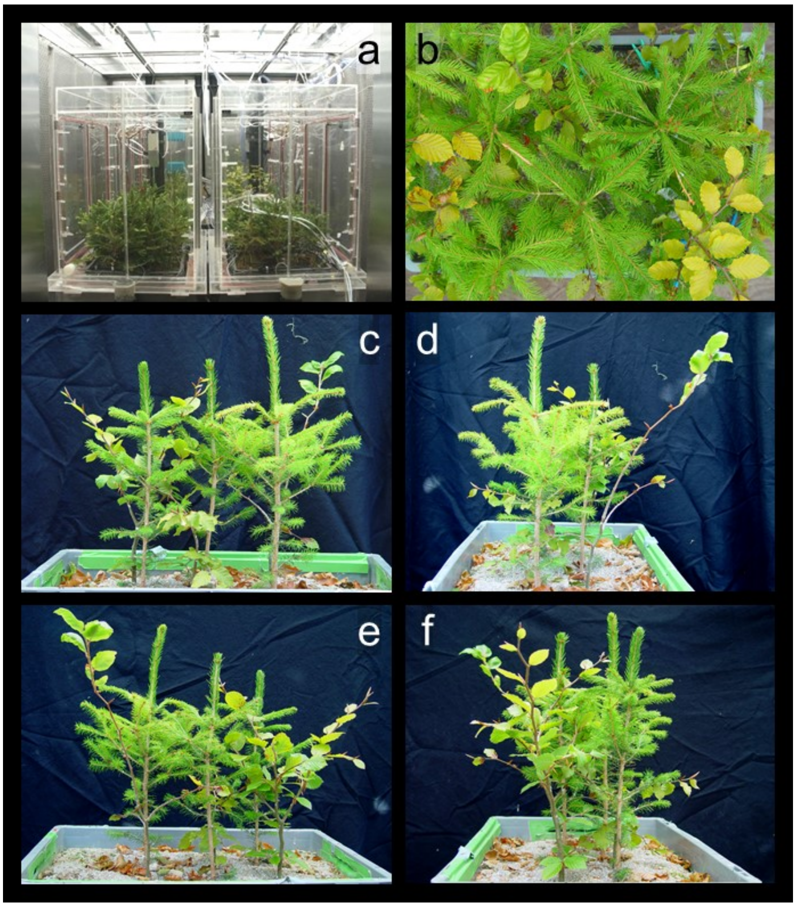


Fig. 3.1: a) One of the four walk-in phytotrons of the GSF - National Research Center for Environment and Health (present name: "Helmholtz Zentrum München – German Research Center for Environmental Health") in Munich/Germany. b) Top view on juvenile spruce and beech trees (10 each) grown in mixed culture in Experiment 3. c to f) Photographs of the six central trees of beech and spruce (3 each) grown together in mixed culture in Experiment 3. The 14 trees grown at the edge of the container have been cut away to give better view on the central six tree individuals.

Grams et al. 1999; Kozovits et al. 2005a) four gaseous treatments were established, denoted as follows: ambient CO2/ambient O3 = "gaseous control", ambient CO_2/elevated O_3 = "+O_3", elevated CO_2/ambient O_3 = "+CO_2" and elevated CO_2/elevated O_3 = "+CO_2/+O_3". In the third and fourth experiment (Table 3.1,

Table 3.1: Overview on experiments.

	Duration[a]	**Planting pattern**	**Gaseous treatments**				**Planting density**[b]		
	(years)		Ambient air (control)	$+O_3$	$+CO_2$	$+O_3/+CO_2$	Plants / m^2	DM / m^2 (g/m^2)	DM / soil volume (g/L)
Exp. 1	1 + 1 1995 - 1996	individual trees of beech	✓	✓	✓	✓	25	1640 ± 106	6.61 ± 0.48
Exp. 2	1 + 2 1998 - 2000	mono-and mixed cultures of beech and spruce	✓	✓	✓	✓	96	3947 ± 196	3.89 ± 1.55
Exp. 3	1 + 2 2001 - 2003	mixed culture of beech and spruce	✓	✓	-	-	96	2448 ± 213	8.18 ± 1.10
Exp. 4	1 + 1 2004 - 2005	mono-and mixed culture of beech and spruce	✓	✓	-	-	96	644 ± 23	2.16 ± 0.22

[a] Pre-treatment adaptation years in a climate controlled glasshouse plus experimental years in the four phytotrons of the GSF - National Research Center for Environment and Health" (present name: "Helmholtz Zentrum München – German Research Center for Environmental Health").

[b] Dry mass at the end of the experiment. Data originate from Jungermann (1996), Kozovits et al. (2005a, b), Luedemann et al. (2005, 2009) and Ritter et al. (2015).

Luedemann et al. 2005; Luedemann et al. 2009; Ritter et al. 2015), focus was on effects of ambient and elevated O_3 under ambient CO_2 concentrations ("gaseous control" and "+O_3", respectively). During winter, plants were kept outdoors in open-top chamber, where corresponding CO_2 concentrations were maintained (Exp. 1 and 2) or under a pergola as shelter against hard frost events (Exp. 3 and 4).

Whole-tree relative growth rate (RGR)

At the end of each experimental growing season, biomass of the single potted trees (Exp. 1) or of the six central trees of each container (Exp. 2 to 4) was determined through destructive harvests or allometric relations (Kozovits et al. 2005a). Together with the starting biomass of trees, the annual whole-tree RGR was calculated as (Hunt et al. 2002):

$$RGR = \frac{\ln(Biomass_{t1}) - \ln(Biomass_{t0})}{t_1 - t_0} \qquad \text{Eqn 3.1}$$

where $Biomass_{t0}$ and $Biomass_{t1}$ represent the biomass at the end of two subsequent years, i.e. the years t_0 and t_1, respectively.

Analysis of competitiveness

Above- and belowground competitiveness was quantified by two space-related efficiencies of resource use. The efficiency of space occupation above- was calculated as the space occupied by the crown per unit of biomass investments into stem, branches and foliage (for details see Grams et al. 2002; Kozovits et al. 2005b). Belowground the occupied space was assumed as the soil volume around the roots and calculated from the total fine root length and the radius of the depletion zone of water around roots (Daigo et al. 2013). A radius of 20 mm was considered as an adequate approximation (Garrigues et al. 2006; Syring and Claassen 1995; see also Agerer et al. 2012). The second parameter of competitiveness, the efficiency of space exploitation, was calculated as the resources acquired from the occupied space, i.e. per unit volume. Above- this parameter was calculated as the annual C gain retrieved per unit of occupied crown space. Annual C gain was quantified through a photosynthesis model parameterized for the study trees (Falge et al. 1996; Kozovits et al. 2005b). Belowground the uptake of water from the soil, assessed through the photosynthesis model as annual transpiration, was expressed per unit of the occupied root space.

Statistical analysis

We rely on the statistical analysis of biomass development performed in each phytotron study (Grams et al. 1999; Grams and Matyssek 1999; Kozovits et al. 2005a; Kozovits et al. 2005b; Luedemann et al. 2005; Luedemann et al. 2009; Ritter et al. 2015). In this present synthesis, coefficients of correlations between *RGR* and efficiencies of space-related competitiveness were calculated using linear regressions in SPSS (SPSS Inc., Chicago, USA).

Results

The intended synthesis requires the comparison of the key findings on the biomass development (i.e. whole-tree relative growth rate, *RGR*) and competitive efficiencies (i.e. space use). Therefore, corresponding datasets from the above mentioned experiments are presented in the following.

The whole-tree relative growth rate (*RGR*) of juvenile beech trees grown isolated (Exp. 1) was significantly reduced from 1.92 under gaseous control conditions to 1.68 under +O_3 (Table 3.2). Elevated CO_2 did not enhance *RGR* but diminished the adverse O_3 impact (*RGR* of 1.85 under +O_3/+CO_2). The overall range of *RGR* was similar for juvenile beech trees grown in mono or mixed culture (20 trees per container) during the first experimental year of Exp. 2 when biomass density was still low. In the second year with a final biomass of about 4000 g per m^2 soil surface, all three gaseous treatments resulted in reduction of *RGR* by 20 to 40% compared to the control in monoculture (Fig. 3.2). These adverse effects were intensified in mixture with spruce as the reductions in *RGR* relative to the control were about 60% under +CO_2 and +O_3/+CO_2 and about 95% under +O_3. The enhancement of adverse

O_3 effects on beech grown in competition with spruce was confirmed by Exp. 3 and 4 where *RGR* at the end of the experiment under $+O_3$ was reduced by about 70% and 50%, respectively (Fig. 3.2). Hence, adverse O_3 effects on beech were stronger when growing in mixed culture with spruce than in beech monoculture.

The range of *RGR* of beech observed under the various gaseous treatments was distinctly larger than of spruce under the same conditions (see *RGR* of spruce plotted versus *RGR* of beech in Fig. 3.3). Juvenile beech trees displayed a range from almost 0.0 to about 2.5 with the highest *RGR* in monoculture and lowest when grown in mixture with spruce. In contrast, *RGR* of juvenile spruce trees (see Y-axis in Fig. 3.3) was restricted to a much narrower range from about 0.4 to 1.3 (with the exception of one high *RGR* of 1.7). This illustrates the larger phenotypic plasticity of beech compared to spruce. In general, data on *RGR* of the two species under the different treatments in mono-and mixed culture (Exp. 2 to 4) do not follow the 1-to-1 line in Fig. 3.3, indicating different *RGR* of the two species under identical conditions, i.e. same treatments and experiments. At lower growths rates of beech, i.e. < 0.6, *RGR* of spruce was larger than that of beech. Conversely, for *RGR* of beech above 0.9, *RGR* of spruce was lower than that of beech.

RGR of juvenile beech trees was positively related to the efficiency in aboveground space occupation (see logarithmic fit in Fig. 3.4). Here *RGR* is understood as a measure of competitive success of a tree and related to its aboveground space occupation, calculated as the ratio of occupied crown space per unit of above- biomass (sum of leaf, branch and stem). The lowest *RGR* of juvenile beech (< 0.5) has been observed in mixture with spruce (open symbols) and corresponds to an occupied crown space of less than 400 cm^3 per g biomass. We did not find positive correlations of *RGR* with above- space exploitation, calculated as carbon gain per unit of occupied crown space, or with annual carbon gain in absolute terms. Likewise, neither efficiencies in belowground space occupation and exploitation (i.e. occupied root volume or water uptake per unit of biomass, respectively) nor total resource gain in absolute terms (i.e. annual water uptake) were related to *RGR* (data not shown). In a similar way in spruce, none of the above mentioned correlations was significant (data not shown), reflecting the low responsiveness and, hence, low phenotypic plasticity compared to beech.

Table 3.2: Whole-tree relative growth rate (*RGR*) of juvenile beech trees under the four gaseous treatments (means ± SE) in isolation (i.e. one tree per pot) in Exp. 1 or in mono-and mixed cultures in Exp. 2 to 4. Data originate from Jungermann (1996), Kozovits et al. (2005a, b), Luedemann et al. (2005, 2009) and Ritter et al. (2015).

	Year	**Culture**	**RGR**							
			Control		**$+O_3$**		**$+CO_2$**		**$+O_3$/$+CO_2$**	
Exp. 1	1996	Isolated plants	1.92	± 0.03	1.68	± 0.08	1.92	± 0.05	1.85	± 0.06
Exp. 2	1999	Monoculture	2.20	± 0.11	2.29	± 0.08	2.46	± 009	2.39	± 0.09
		Mixed culture	1.52	± 0.13	1.69	± 0.10	1.72	± 0.13	1.72	± 0.13
	2000	Monoculture	1.36	± 0.14	1.00	± 0.23	0.80	± 0.11	1.10	± 0.13
		Mixed culture	0.58	± 0.18	0.01	± 0.17	0.20	± 0.23	0.21	± 0.12
Exp. 3	2002	Mixed culture	1.91	± 0.25	1.91	± 0.13	-	-	-	-
	2003	Mixed culture	1.14	± 0.22	0.34	± 0.18	-	-	-	-
Exp. 4	2005	Monoculture	0.82	± 0.07	0.91	± 0.11	-	-	-	-
		Mixed culture	1.35	± 0.18	0.67	± 0.20	-	-	-	-

Discussion

In this chapter we aimed at answering two questions. First, whether effects of $+O_3$ and $+CO_2$ and the combination of both ($+O_3/+CO_2$) are modified by the different competitive settings, i.e. growth in isolation, mono or mixed culture and second, whether the competitive success of a plant is related to an efficient space use, i.e. optimization strategy, or conversely to the maximization of resource gain as such, i.e. maximization strategy.

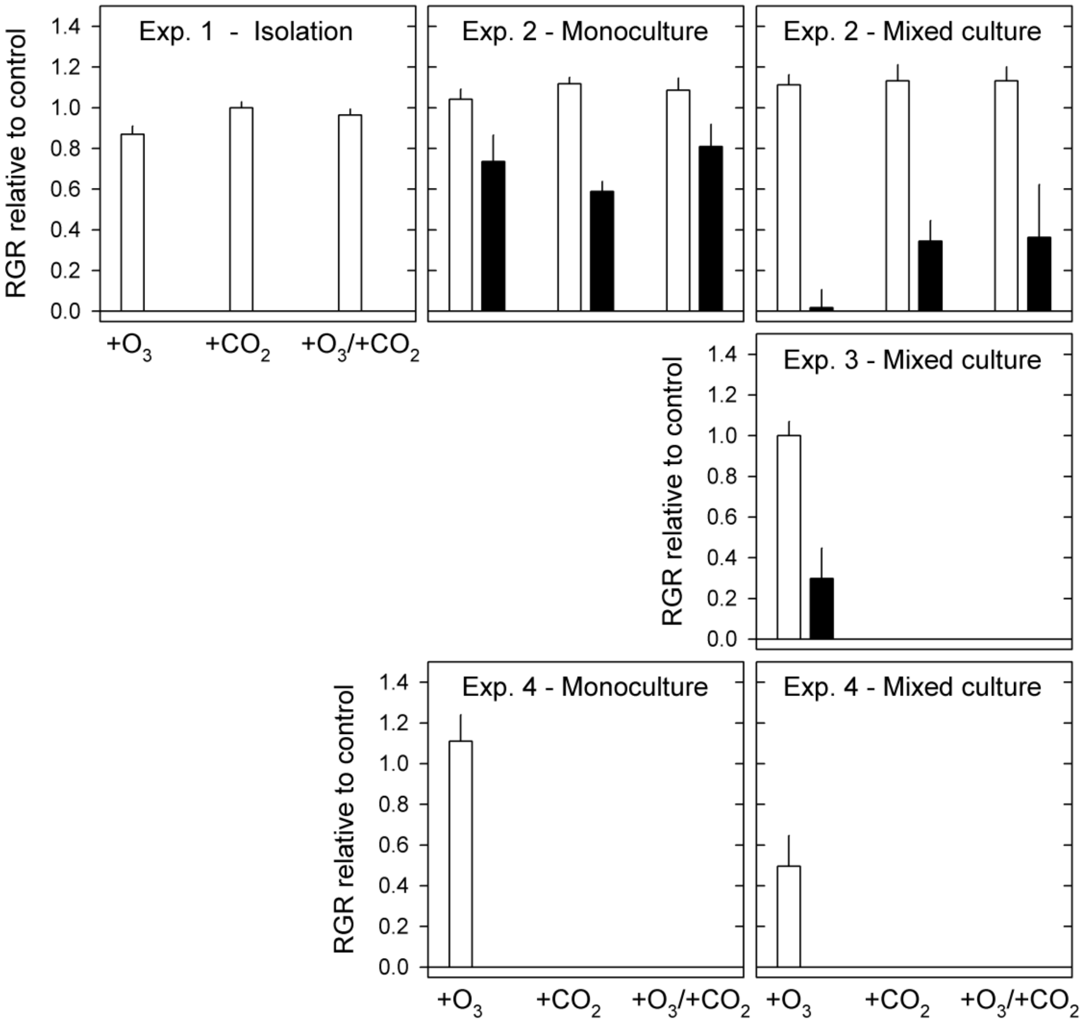


Fig. 3.2: Changes in whole-tree relative growth rate (*RGR*) of juvenile beech trees under $+O_3$, $+CO_2$ and $+O_3/+CO_2$ relative to the *RGR* under gaseous control conditions. Data are originating from experiments 1 (isolated growth in pots: Jungermann (1996), experiment 3 (growth in mixed culture: Luedemann et al. (2005, 2009)) and experiments 2 and 4 (growth in both mono-and mixed cultures: Kozovits et al. (2005a, b) and Ritter et al. (2015). Open and closed bars represent data from the

first and second experimental year (see Table 3.1) under the corresponding gaseous treatments.

In general, whole-tree *RGR* of beech was found to be negatively affected by elevated O_3 concentrations, a result consistent with preceding experiments (Langebartels et al. 1997) and recently confirmed for adult beech trees (Matyssek et al. 2010a; Matyssek et al. 2010b). However, the extent of the O_3-related have only limited ecological significance relative to corresponding responses of plant grown in monoculture and, in particular, in mixed culture. This conclusion is similar to the one by Navas et al. (1999) and Poorter and Navas (2003) for plant biomass responses under elevated CO_2 as growth enhancement in mixed communities could not be scaled from responses of isolated plants (Körner 2006; Millard et al. 2007). Our experiments support such findings on effects of elevated CO_2 as similarly *RGR* of

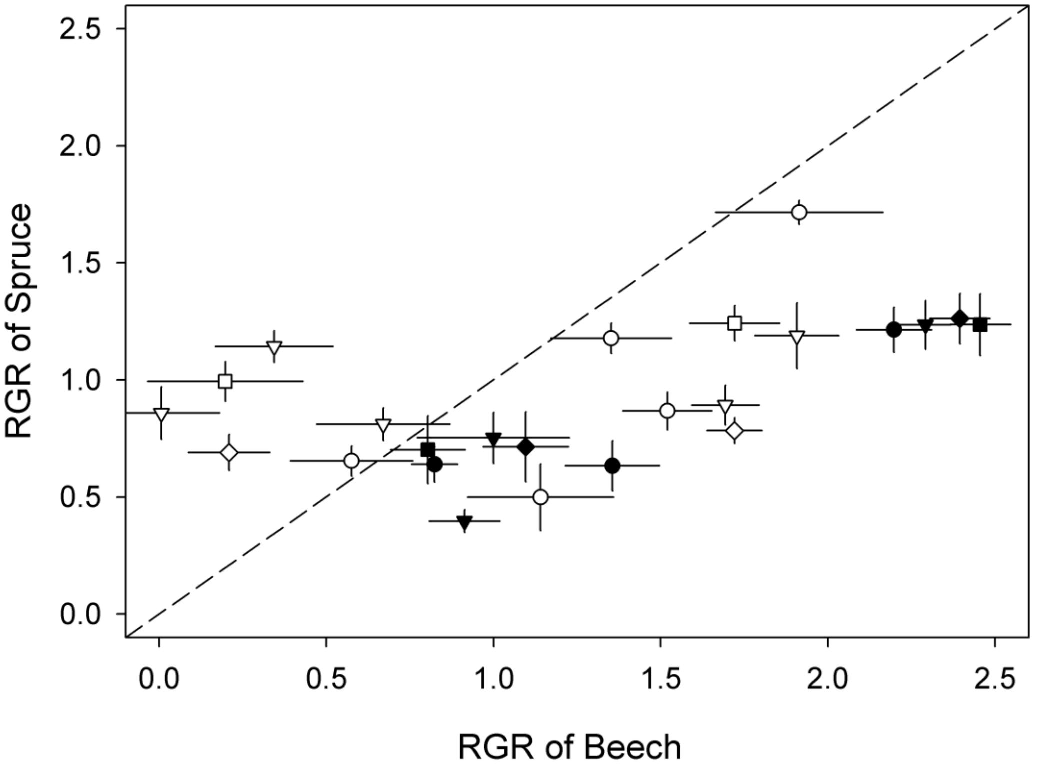


Fig. 3.3: Whole-tree relative growth rate (*RGR*) of juvenile spruce versus beech grown in mono or mixed cultures (closed and open symbols, respectively). Circles denote gaseous control, triangles $+O_3$, squares $+CO_2$ and diamonds represent the $+O_3/+CO_2$ treatment. Each symbol gives the *RGR* of spruce (y-axis) versus beech (x-axis) under the same treatment and in the same experiment. Data originate from Kozovits et al. (2005a, b), Luedemann et al. (2005, 2009) and Ritter et al. (2015)

beech was diminished under intense intra-specific and, in particular, inter-specific competition. Conversely, *RGR* of spruce benefited from elevated CO_2 concentrations, in particular when grown in mixture with beech (Kozovits et al. 2005a).

Under the specific experimental conditions of the presented phytotron experiments juvenile spruce was found to be a superior competitor compared to beech, in particular when competitive interactions became more intense with increasing plant biomass. Such an experimental outcome may depend on environmental conditions such as light intensity or soil moisture and pH. The dominance of spruce was confirmed when trees were grown in an experiment on acidic soil similar to that in the phytotrons presented here (Körner 2003b; Spinnler et al. 2002). However, growth on calcareous soils favored beech and the competitive advantage of spruce largely vanished.

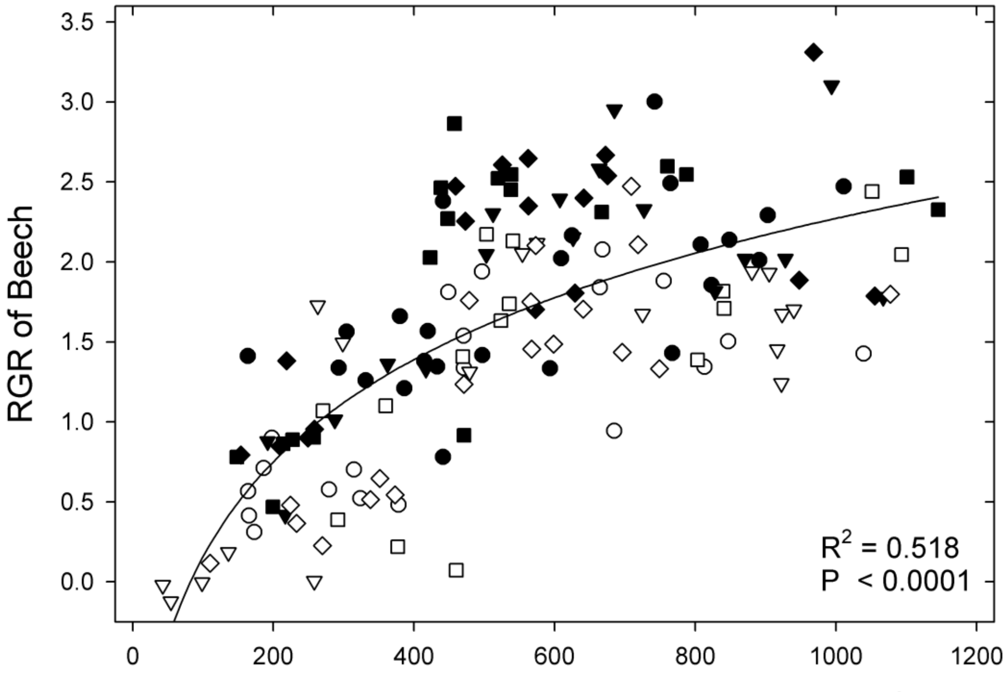


Fig. 3.4: Whole-tree relative growth rate (*RGR*) of juvenile beech trees correlated with the efficiency in aboveground space occupation, calculated as the occupied crown space per investment of above- biomass. Circles denote gaseous control, triangles $+O_3$, squares $+CO_2$ and diamonds represent the $+O_3/+CO_2$ treatment. Closed and open symbols denote growth in mono-and mixed culture, respectively. Data originate from Kozovits et al. (2005a, b).

Thus, the better growth performance of spruce compared to beech in the presented study is not the key finding. Instead, focus is on the mechanistic grounds of competitive interactions between the two species. Whole-tree *RGR* of beech, used as a measure of competitive success, was positively related to the efficiency of aboveground space occupation, i.e. the relation of occupied crown space per unit of biomass investment in leaves, branches and stem (Fig. 3.4). Only at very high efficiencies of aboveground space occupation, i.e. when the logarithmic fit in Fig. 3.4 starts to saturate, *RGR* appears to be limited by other factors (e.g. carbon availability). Beech displayed a large range in aboveground space occupation with crown volumes between 50 and 1100 cm^3 per g of invested above- biomass. Apparently, this high phenotypic plasticity enables beech to escape from intense competition with spruce at the expense of less efficient aboveground space occupation. For example in Fig. 3.1d (see arrow), a small crown space is occupied by seven leaves that are supported by a relatively large branch and stem biomass, resulting in a low efficiency of aboveground space occupation. This high phenotypic plasticity of beech and its shift to rather inefficient above- space use in mixture was realized as a crucial factor in above- competition with spruce in experimental (Grams and Matyssek 2010; Kozovits et al. 2005b) and modeling studies (Gayler et al. 2006; Priesack et al. 2012; Gayler et al 2012). These findings are challenged by the question of whether optimization or maximization of resource gain is decisive in competitive interactions. In both species, above or belowground resource gain in absolute terms was not significantly related to whole-tree *RGR*, indicating minor importance of the resource gain as such. In the case of carbon, this result supports the view that biomass development of trees is not driven by their carbon availability, but that photosynthesis delivers on growth demand –at least as long as surrounding conditions allow for it (Körner 2003a, 2006)

Having identified the efficiency of space occupation as a crucial factor in the competition between juvenile beech and spruce, the question arises of whether space *per se* is a resource to plants. This has been recently debated by Grams and Lüttge (2011). Their simplest but most straightforward and illustrative example is the space provided for atmospheric bromeliads by a telephone-line wire devoid of any other resources. Hence, they come to the conclusion that indeed sheer space in itself has the function of a resource to plants. Coming back to the competitive interaction between beech and spruce, an example from adult trees may support this conclusion. At the experimental site “Kranzberg Forest” (Pretzsch 2012), studying C balances of branches of adult trees, Reiter et al. (2005) found shaded branches with negative C balances of the foliage to be sustained by the tree for at least five years. Having the paradigm of carbon autonomy in mind (Landhausser 2011; Sprugel et al. 1991; Volpe et al. 2008), one might have expected trees to abandon such branches much earlier. This behavior of trees can be interpreted as a “sit-and-wait” strategy (Falster and Westoby 2003; Reiter et al. 2005) as the value of the occupied space may increase with time, e.g. after gap formation by collapsing neighboring trees with resulting increase of irradiance. Such a temporal aspect of space occupation is supported by a belowground example where roots keep occupying soil space of low ecological value (i.e. with low resource availability). If this space is in the vicinity of belowground pathways of rodents (or other animals) the resource availability may improve by more or less frequent urination events (J. F. Cahill, University of Alberta, Canada, personal communication). Thus, competing for and keeping this soil space occupied may pay back over time. In addition to the direct effects of space occupation on the resource budget of a plant, the effects on its competing neighbor should not be overlooked. In particular in the case of unidirectional resources, such as light, that are “pre-emptable” and allow for shading effects (Schwinning and Weiner 1998) successful space occupation may significantly reduce the resource availability to the neighbor. Hence, optimization of above or belowground space occupation appears to be the mechanistic basis for competitive success – at least in the case of “pre-emptable” resources (Fig. 3.4; Grams and Andersen 2007; Kozovits et al. 2005b). In such a case, the resources gained by a plant may not be raised in absolute terms but be increased relative to a neighbor. Thus, we may conclude that the resources gained relative to its neighbor (i.e. the marginal advantage) is maximized through optimization of space occupation.

Conclusions

Competitive interactions between plants have the potential to alter abiotic impacts of atmospheric O_3 and CO_2 concentrations. It appears that the more intense the competition is for a limiting resource, the higher the potential becomes to modify the response to other stressors. Hence, responses of plants grown isolated or under low competitive pressure are of only limited relevance for plants grown in mono or mixed cultures. In particular in situations with intense competitive interactions, the efficient occupation of space represents an effective mechanism to be competitive by increasing the resource accessibility relative to competing neighbors.

4. Decomposition of Relative Growth Rate in competing *Fagus sylvatica* and *Picea abies* saplings under elevated CO_2 and O_3 regimes

Summary

Relative Growth Rate (*RGR*) provides one means for tackling complex plasticity in plant response to biotic and abiotic stress. We hypothesize that morphological rather than physiological plasticity determines *RGR* of beech (*Fagus sylvatica* L.) and spruce (*Picea abies* [L.] Karst) saplings competing for above- and belowground resources, namely light and water, respectively (H1). Under increasing atmospheric climate, priorities may shift to physiological adjustment such as increasing resource uptake of the limiting resource. Thus, under elevated CO_2 ($+CO_2$) and enhanced O_3 ($+O_3$) levels, physiological plasticity is crucial in driving *RGR* (H2). The decomposition of *RGR* into four components of morphological and/or physiological nature is demonstrated in this work under competitive conditions and enhanced gas regimes: Space occupation (*A*), biomass ratio (*B*), space exploitation (*X*) and resource-to-biomass conversion efficiency (*E*). *A* and *B* describe morphological plasticity, while *X* and *E* correspond to physiological plasticity. Above- and belowground *E* is referred to as light-use (*LUE*) and water-use efficiency (*WUE*), respectively. The decomposition analysis was based on data from a phytotron experiment conducted on intra and interspecific competition between beech and spruce saplings under ambient, $+CO_2$ and $+O_3$ regimes. H1 was confirmed in that morphological plasticity of aboveground *A* determines the competitive success, in terms of mean *RGR*, of beech in mono rather than mixed culture, whereas belowground *A* favors the competitiveness of spruce in mixture with beech. Mean *RGR* of both species remained unchanged under $+CO_2$. However morphological plasticity was enhanced under $+CO_2$, although only in beech, suggesting possible growth stimulation. Significant mean *RGR* reduction occurred under $+O_3$ in beech through decreased aboveground physiological plasticity *E*, in particular *LUE*, hence corroborating H2. Mean *RGR* of spruce was not affected by $+O_3$, despite a decrease in belowground *E*, specifically *WUE*, suggesting its ability to acclimatize to O_3 stress. The analysis provides an integrative framework for interpreting plasticity of *RGR*. We conclude that under biotic limitation, such as through competition, *RGR* is determined by morphological plasticity. Under abiotic stress (as through $+CO_2$, $+O_3$), *RGR* may be varied by physiological plasticity as specifically depending on species and stress scenario.

Daigo Schulte MJ, Matyssek R, Gayler S, Grams TEE (2015) submitted to Perspectives in Plant Ecology, Evolution and Sytematics

Introduction

Relative growth rate (*RGR*), one basic index of plant performance, is considered to intrinsically mirror resource utilization (Schwinning 1996) and efficiency in use (Hunt 2003). Calculated as rate of change in biomass per unit of total biomass present (Poorter & Nagel 2000), *RGR* typically decreases with time (West et al. 2001). Previous studies addressed various components of *RGR* (Shipley et al. 2006; Poorter et al. 1990) and their dynamics under changing climate (Grams et al. 2012). The notion has emerged that plant response is governed by appreciable phenotypic plasticity that is dependent on both biotic and abiotic scenarios (Matyssek et al. 2012b; Schlichting 1986). Phenotypic expressions can be morphological or physiological in nature, as both components are closely interdependent in mutually adjusting each other (Bradshaw 1965). Important drivers of such interrelationships, triggered by competition and anthropogenic increases of atmospheric CO_2 and O_3 could have important ramifications for plant *RGR*.

Mechanisms of plant growth and underlying theories have been studied and documented (Tilman 1987; Grime 1977). Nevertheless, uncertainty prevails about such plant traits greatly responsible for variation in *RGR*, as being the case in juvenile trees competing for above- and belowground resources. Physiological optimization may shape the growth rate of plants (Hunt & Cornelissen 1997), although morphological features may dominate (Poorter et al. 2012). Exemplifying mixed canopies, greater morphological plasticity of beech (*Fagus sylvatica* L.) than spruce (*Picea abies* [L.] Karst) was responsible for its competitive success (Gayler et al. 2006; Kozovits et al. 2005a; Grams et al. 2002). As shown through modelling, such high plasticity can be disadvantageous, especially for juvenile beech trees with homogeneous resource supply (Gayler et al. 2006). However, under heterogeneous environments, greater morphological plasticity of crown (Petritan et al. 2009) and root architecture (Bolte & Villanueva 2006) readily enables foraging on patchily distributed resources and contributes to out-competing spruce (Pretzsch & Dieler 2012). Poorter (1999) argued that interspecific variation in *RGR* is attributed to morphology and physiology under high and low light environments, respectively, proposing growth plasticity to shift along environmental gradients. Thus, it is likely that biotic (i.e competition) and abiotic stressors (i.e. $+CO_2$ and $+O_3$) may add to the complexity in analyzing *RGR*. For example, $+CO_2$ is shown to enhance growth of individual plants through increased photosynthetic activity and decreased specific leaf area (Poorter & Nagel 2000), given an absence of other resource limitations (Körner 2003a). Conversely, $+O_3$ is known to impact other physiological traits, e.g. decreasing light-saturated photosynthesis and increasing respiration (Matyssek et al. 2010). Hence, growth lies in the area of conflict between several opposing drivers, resulting in conflicting outcome and conclusions regarding *RGR* (Rees et al. 2010). In general, *RGR* can be factored into three components namely: net assimilation rate, specific leaf area and leaf mass ratio (Hunt & Cornellissen 1997; Evans 1972). However, such a view is focused on aboveground biomass only, and omits belowground drivers. We advocated an integrative *RGR* analysis, which incorporates morphological and physiological plasticities, both of above- and belowground components. Thus, the question may be put forward, for example, may interrelationships vary between juvenile trees, that compete for above- and belowground resources, while being exposed to increasing CO_2 and O_3 levels, and what is the relevance in response to climate change (Matyssek et al. 2014)?

In the present study, we decomposed *RGR* into four components: space occupation (*A*), biomass ratio (*B*), space exploitation (*X*) and resource-to-biomass conversion efficiency (*E*). Components *A* and *B* comprise morphological divisions of *RGR* whereas physiological components include *X* and *E* (see Theory in Material and Methods for details). Morphological factors are shown to influence competitive success (Grams et al. 2002) and ultimately growth of plants (Poorter et al. 2012). In the present study, we hypothesize that plasticity in morphology rather than physiology primarily determines *RGR* of juvenile beech and spruce trees (H1). However, under changing environmental condition, priorities may shift to physiological adjustments by increasing resource uptake of the limiting resource (Poorter et al. 2012). Thus, we hypothesize that under $+CO_2$ and $+O_3$, physiological plasticity dominates variations of *RGR* (H2). For hypothesis evaluation, mathematical decomposition of *RGR* was analyzed with experimental data from a phytotron study, which had been conducted on beech and spruce saplings competing in mono-and mixed culture while exposed to ambient, +CO_2 and +O_3 regimes (Kozovits et al. 2005a, 2005b).

Material and Methods

Experimental Setup

Data used in this analysis originated from a phytotron study conducted on two to five year-old beech and spruce saplings exposed to ambient, +CO_2 (ambient +300 ppm) and +O_3 (2x ambient O_3, restricted to 150 ppb) regimes (Fig. 4.1).

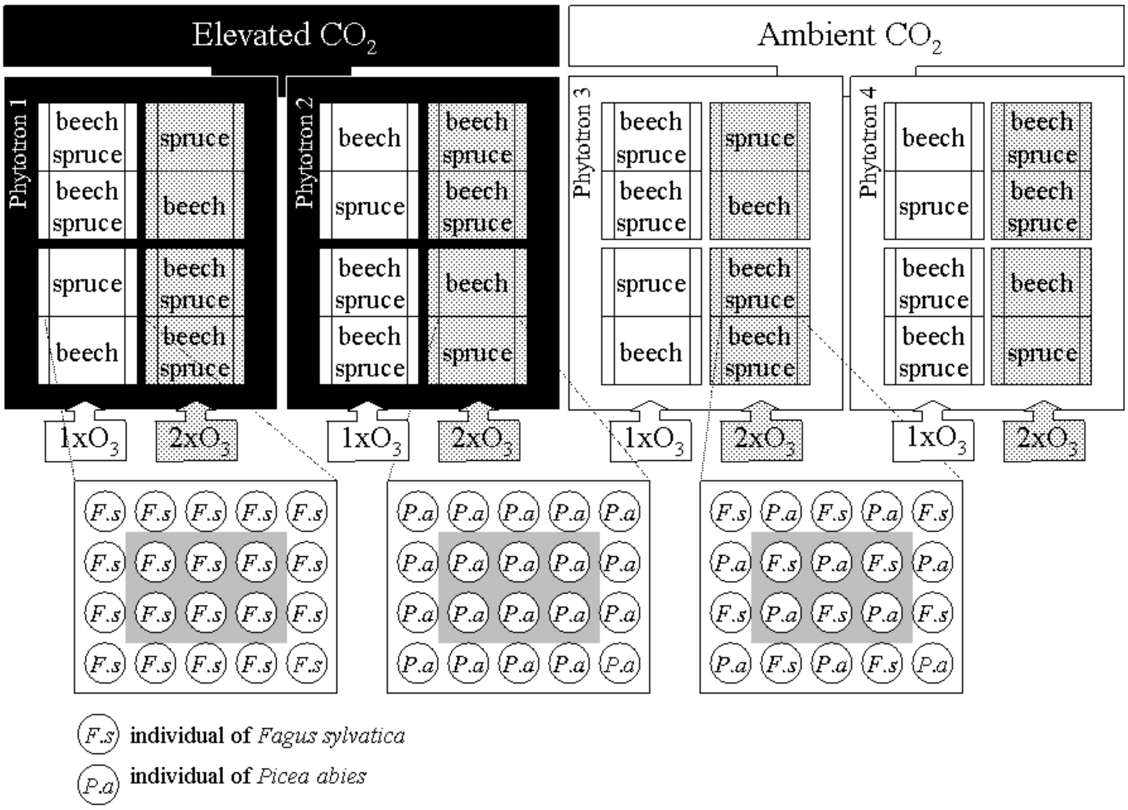


Fig. 4.1: Experimental design in the phytotrons of the National Research Center for Environmental Health (adapted from Liu et al. 2004; Kozovits et al. 2005a). Each phytotron consisted of four Plexiglas sub-chambers for individual O3 fumigation at ambient (Phytotron 3 and 4) and elevated (Phytotron 1 and 2) CO2 concentrations. Two planting container consisting of either two mixed or one monoculture of beech and spruce saplings, were placed into each of the four sub-chambers per phytotron. The position of the six target trees is highlighted.

Measurements extended through two consecutive growing seasons (1999 and 2000; see Kozovits et al. 2005a, 2005b for details). The dataset included 32 experimental containers in mono- and mixed cultures for beech and spruce exposed to ambient and $+CO_2$ and/or $+O_3$ regimes. In the present study, we grouped data according to the type of competition (mono- vs mixed culture) and atmospheric gaseous treatments (ambient vs $+CO_2$ and ambient vs $+O_3$).

Aboveground analysis included crown volume (m^3), “stem + shoot axis + foliage” biomass (g), foliage area (m^2), leaf area index ($m^2\ m^{-2}$), whole-plant biomass (g), photosynthetic photon flux density (PPFD; mol m^{-2} $year^{-1}$). Light capture (MJ $plant^{-1}$ $year^{-1}$) was derived from PPFD which attenuates exponentially within the canopy with leaf area index *LAI* (foliage area per surface area, $m^2\ m^{-2}$) according to Beer-Lambert law (Bossel 1996). Belowground analysis was based on irrigation (L day^{-1}), denoting water availability, and on fine root biomass (g) and soil volume (m^3). The latter was derived from specific fine root length SFRL (m g^{-1}), fine root biomass (g) and the radius of the rhizospheric water depletion zone r (m). The value for r was set at 0.02 m according to Garrigues et al. (2006). Water uptake was derived from transpiration data (mol of H_2O).

Theory

The *RGR* decomposition technique (Schwinning 1996; Grams and Andersen 2007) was used in this study and modified as Eqn. 4.1:

$$\frac{1}{B_i} \cdot \frac{\partial B_i}{\partial t} = \frac{Vx}{Bx} \bullet \frac{Bx}{Bi} \bullet \left(\frac{1}{Vx} \cdot \frac{\partial Ux}{dt}\right) \bullet \frac{\partial B_i / \partial t}{\partial Ux / \partial t} \qquad \text{Eqn. 4.1}$$

$$RGR = A \cdot B \cdot X \cdot E$$

where *Vx* is the space occupied by biomass (*Bx*) of an individual plant, involved in the uptake of above- or belowground resource *x*. The time derivative of *Ux* is the rate of resource uptake and ∂B_i denotes the instantaneous rate of increase of total biomass per individual plant. In Eqn. 4.1, the first term on the right side is designated as ‘space occupation' *A* (m^3 g^{-1}), calculated as the amount of space *Vx* (i.e. crown or root volume m^3) occupied by above- or belowground biomass *Bx* (g). The second term, 'Biomass Ratio' *B* (g g^{-1}), refers to the structural fractionation of *Bx* relative to whole-plant biomass B_i (g). The third term, 'space exploitation' *X* (MJ m^{-3} or Mol m^{-3}) describes the amount of resource capture (e.g. MJ light or Mol water) per occupied space (m^3). The rightmost term, 'resource-to-biomass conversion efficiency' *E* refers to the instantaneous rate of change in total biomass per time (g y^{-1}) per resource capture, representing *LUE* (g^{-1} MJ $year^{-1}$) or *WUE* (g^{-1} Mol $year^{-1}$). Hence, *RGR* (i.e. total) is the product of the four components, as representing the rate of biomass change per unit of whole-plant biomass per time (g g^{-1} $year^{-1}$).

Statistical Analysis

Data were analyzed using repeated measures ANOVA to compare average *RGR* between treatments over two years (1999 and 2000). Regression analysis was used to determine significant relationships between *RGR* and its group components (i.e. *A*, *B*, *X* and *E*). Three separate approaches were used for this study. First, we pooled data for two years and plotted *A*, *B*, *X* and *E* (independent variables) vs *RGR* (dependent variable) by competition (e.g. mono- and mixed) and gaseous regimes (e.g. ambient and +CO_2 or ambient and +O_3). For each group, we used simple linear regression to determine relationship between *A*, *B*, *X* and *E* on *RGR*. Second, we used the model ($RGR = \alpha + \beta_{component} + \beta_{time} + \beta_{component\ x\ time}$); with *A*, *B*, *X* and *E* ($\beta_{component}$) as a covariate, and harvest years (β_{time}) as fixed factors and their interaction ($\beta_{component\ x\ time}$). If time was not significant ($P > 0.05$), we compared regression coefficients between groups (e.g. mono vs mixed) using a dummy variable to test the null hypothesis that H0: $\beta_{mono} = \beta_{mixed}$ (if time interaction $P > 0.05$) or H0: $\beta_{mono\ x\ time} = \beta_{mixed\ x\ time}$ (if time interaction $P < 0.05$). Similar equations were applied to analyze slope difference between +CO_2 vs ambient or +O_3 vs ambient. All statistical analyses were calculated using SPSS Ver. 20 statistical package (IBM 2012).

Results

Competition Effect

Throughout two consecutive growing seasons, average *RGR* of beech in monoculture was significantly higher than in mixed culture (Fig. 4.2a). Spruce behaved contrarily, as growth was significantly stimulated in combination with beech (Fig 4.2d).

Slope analysis in beech showed *RGR* increased with aboveground morphological plasticity of *A* and *B* irrespective of competition type (Fig. 4.3a and b). Notably, the slope of *RGR* on *A* increased with time in mono- but not so in mixed-culture (two-way interaction Table 4.1a). A comparison of slope coefficients considering time effect indicated that mono-cultures had a significantly higher slope ($P < 0.0001$; slope difference Table 4.1a). In contrast, *B* slopes did not differ between types of competition. Time did not influence this outcome ($P > 0.05$; two-way interaction Table 4.1a). Thus, the competitive success, in terms of mean *RGR* of beech in mono- compared to mixed-culture is confirmed by the ability to occupy aboveground space (*A*). Meanwhile, *RGR* decreased and increased as *X* and *E* increased, respectively (Fig. 4.3c and d). A comparison of slopes indicated *X* to be similar across competition ($P > 0.05$; slope difference Table 4.1a), although the relationship of *RGR* on *E* (*LUE*) was significantly lower in mono- than in mixed culture ($P < 0.05$; slope difference Table 1a). Meanwhile, belowground analysis yielded slopes of *RGR* on *A* and *B* in beech to be significantly positive and negative, respectively (Fig. 4.3e and f). Conversely, belowground slopes of *X* were not significantly different from zero but positive with *E* (Fig. 4.3 g and h). Comparing regression slopes of belowground growth components did not yield significant differences between mono and mixed culture ($P > 0.05$; slope difference Table 4.1b), so that competition in beech apparently was not determined belowground.

In spruce, aboveground regressions showed *RGR* slopes on *A* and *B* to be positive and not significantly different from zero, respectively, both in mono-and mixed culture (Fig. 4.4a and b). Conversely, corresponding slopes on *X* and *E* were negative and positive, respectively (Fig. 4.4c and d). Comparing slope coefficients of aboveground *A*, *B*, *X* and *E* did not yield differences between competition types ($P >$

0.05; slope difference Table 4.2a). Thus, the competitive success of spruce in mixture over beech saplings, in terms of mean *RGR* was not determined by aboveground components. Remarkably, analysis of belowground competition for water in spruce revealed the difference in mean *RG*R between mono- and mixed culture to be attributed to belowground morphological plasticity of *A*. Specifically, the slope of *A* on *RGR* in monoculture was not different from zero but was positive in mixed culture (Fig. 4.4e). This difference was statistically significant ($P < 0.05$; slope difference Table 4.2b). Moreover, *RGR* on *B* was not different from zero (Fig. 4.4f), and no significant difference prevailed between mono- and mixed culture ($P > 0.05$; slope difference Table 4.2b). The physiological plasticity of *X* and *E* reflected positive and zero

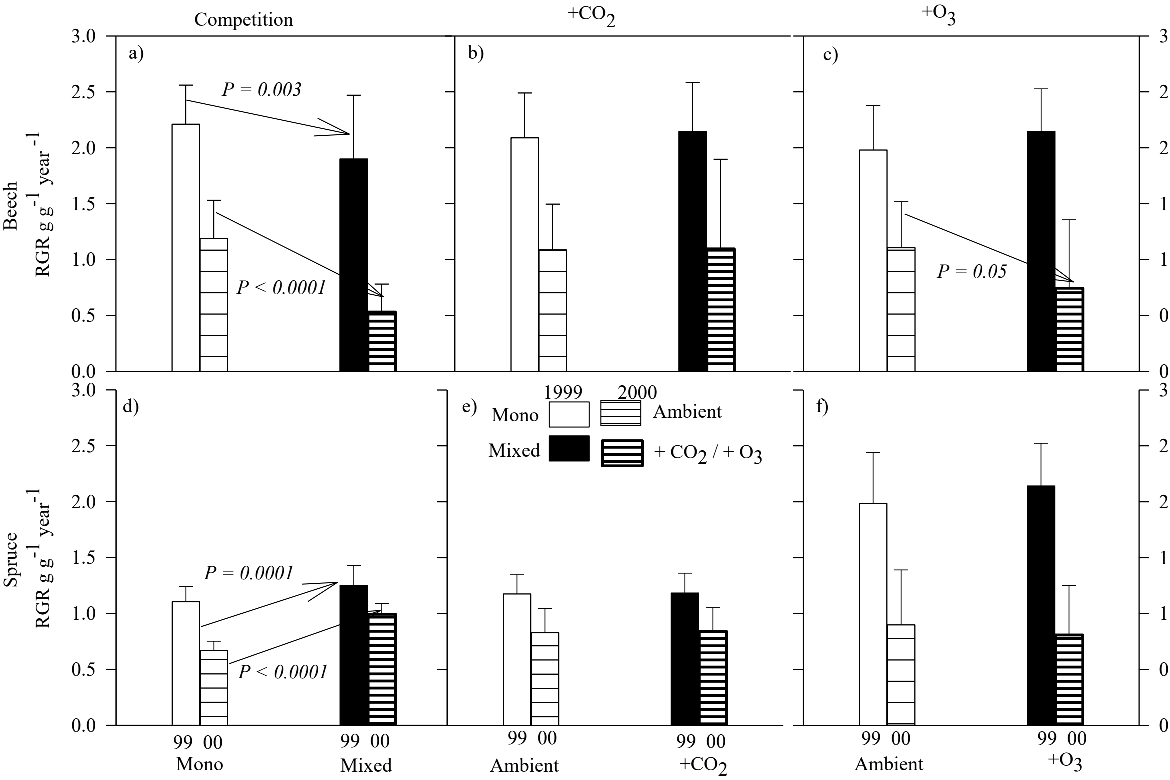


Fig. 4.2: Mean *RGR* (g $g^{-1}year^{-1}$) of beech (*F.sylvatica*) (a, b, c) and spruce (*P.abies*) (d, e, f) under competition, $+CO_2$ and + O_3 growing in 1999 and 2000. Bars without hatching represent *RGR* in 1999 while those with hatching denote *RGR* in 2000. White and black/dark bars represent mono-and mixed culture or ambient and $+CO_2$ or ambient and $+O_3$ (means ± SE, *n 20-40*). Arrows denote significant effects between means of mono vs mixed culture or between ambient vs + CO_2 or ambient vs $+O_3$ at $p < 0.05$.

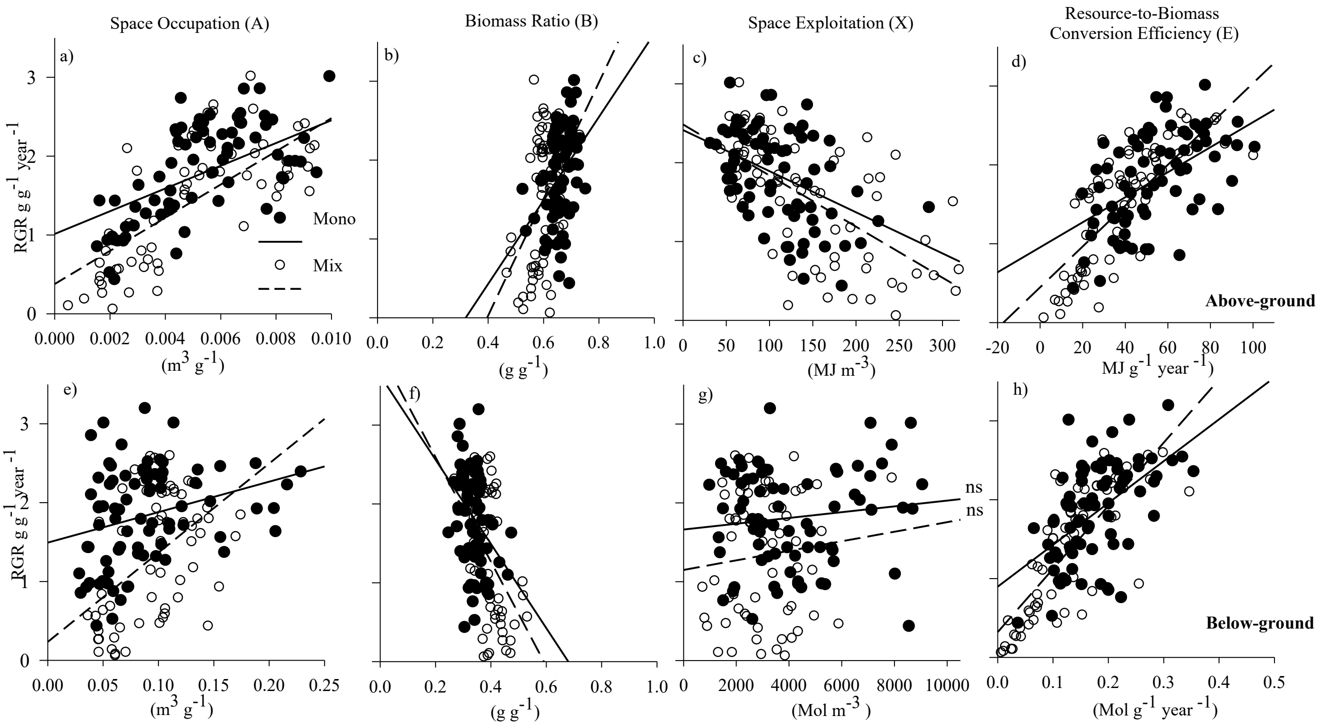


Fig. 4.3: Above- (a-d) and belowground (e-h) competition of beech (*F. sylvatica*) for light and water. Simple linear regression between RGR and space occupation (A), biomass ratio (B), space exploitation (X) and resource-to-biomass conversion efficiency (E). Non-significant relationships ($P > 0.05$) with RGR are indicated by ns. Statistics are presented in Table 4.1a & b.

slopes, respectively (Fig. 4.4g and h). Overall, *RGR* regressions of belowground growth components in spruce did not differ between types of competition, except for *A*. As a consequence, belowground *A* turned out to be crucial for the competitive success of spruce in mixture with beech.

Effects of +CO2 and +O3

Throughout two growing seasons, +CO_2 did not affect mean *RGR* of beech and spruce saplings (Fig. 4.2b and e) so that other factors must have impeded growth enhancement. Beech regressions between all aboveground growth components and *RGR* did not differ significantly from the ambient CO_2 regime (*$P > 0.05$*; slope difference Table 4.1c). Notedly, *RGR* slope on *B* almost reached significance in being enhanced under +CO_2 (*$P = 0.06$*; not shown). Hence, potential *RGR* enhancement aboveground might have been caused by morphological plasticity under +CO_2, as represented by *B*. Regression comparisons belowground yielded no significant treatment differences in beech across the *RGR* components except for *A*, where the slope was significantly enhanced under +CO_2 in relation to the ambient CO_2 regime (*$P < 0.0001$*; slope difference Table 4.1d). Given such morphological conspicuity, mean *RGR* of beech, nevertheless, was not significantly changed under +CO_2 (Fig. 4.2b). Meanwhile in spruce, both above- and belowground analysis confirmed regressions to stay unaffected by CO_2 regime (*$P > 0.05$*; slope difference Table 4.2c and d).

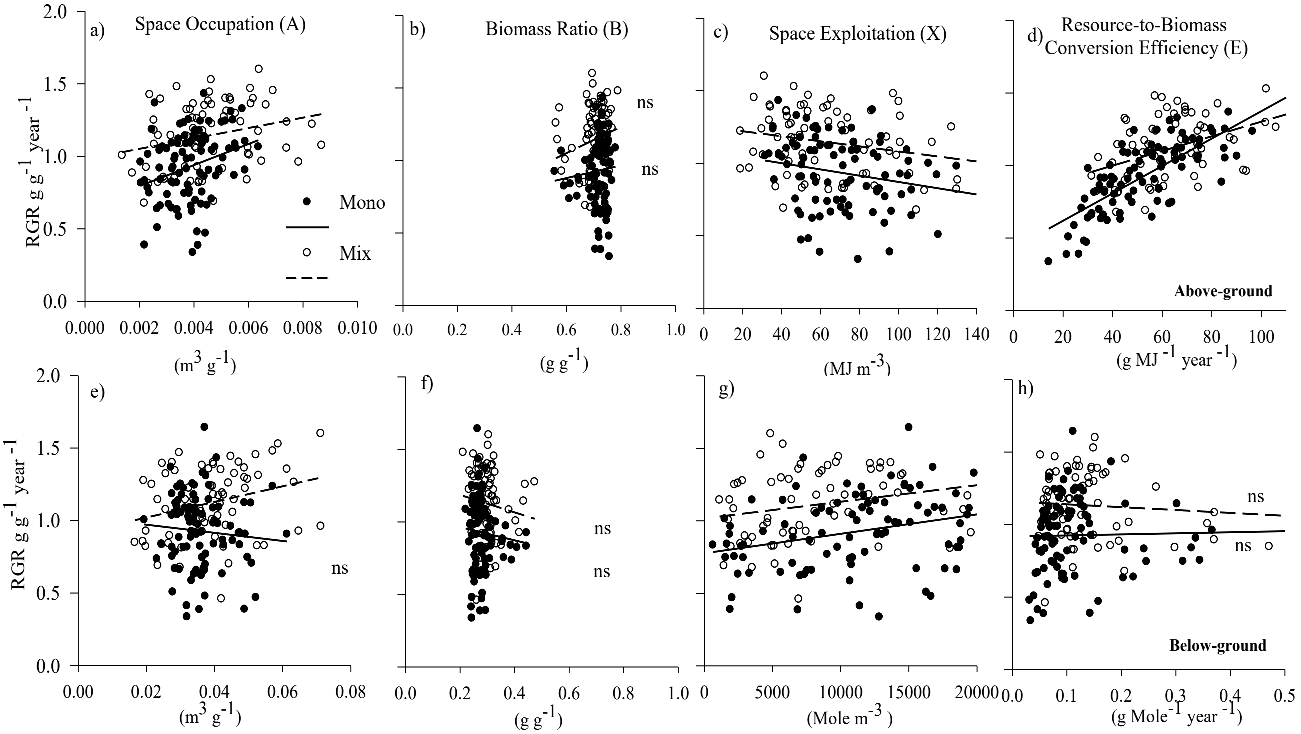


Fig. 4.4: Above- (a-d) and belowground (e-h) competition of spruce (*P. abies*) for light and water. Simple linear regression between *RGR* and space occupation (*A*), biomass ratio (*B*), space exploitation (*X*) and resource-to-biomass conversion efficiency (*E*). Non-significant relationships (*$P > 0.05$*) with *RGR* are indicated by *ns*. Statistics are presented in Table 4.2 a & b.

Mean *RGR* was significantly lower in beech under $+O_3$ compared to ambient condition, although only during the second growing season (Fig. 4.2c). Regression analysis showed that in beech, above- and belowground slopes between growth components and *RGR* did not differ across treatments ($P > 0.05$; slope difference Table 4.1e and 4.4f). Exceptionally, *RGR* on aboveground *E* or *LUE* was significantly lower under $+O_3$ than under ambient condition ($P < 0.05$; slope difference Table 4.1e). Evidently, decreased mean *RGR* in beech under $+O_3$ was attributed to lowered aboveground physiological plasticity, as mirrored by *LUE*.

In contrast, spruce mean *RGR* was not affected by $+O_3$ (Fig. 4.2f). Above-regression analysis indicated relationships between *RGR* and its growth components under $+O_3$ to be similar to such under ambient conditions ($P > 0.05$; slope difference Table 4.2e). However, belowground *E* represented by *WUE* was significantly reduced under $+O_3$ compared to that under ambient condition ($P < 0.05$; slope difference Table 4.2f). However, this had no significant effect on spruce mean *RGR* (Fig 4.2f). This meant that *WUE* does not play a significant role for spruce *RGR* under $+O_3$.

Table 4.1: a-f: Beech (*F. sylvatica*) above- and belowground estimates of regression coefficient depicting the relationship between independent variables (*A*, *B*, *X* and *E*) and dependent variable (*RGR*); its interaction with time under (a-b) competition; (c-d) +CO_2 and (e-f) +O_3. Highlighted column indicates slope difference between groups, where positive sign (+) denotes (mono > mixed); (+CO_2 > ambient); (+O_3 > ambient). A negative sign (-) depicts the reverse. ns not significant $P > 0.05$; * $P < 0.05$; ** $P < 0.001$; *** $P < .0001$

RGR	Components	simple slope		two-way interaction		**slope difference**
		mono	mixed	mono x time	mixed x time	**mono vs mixed**
a) Competition Aboveground	*A*	+ ****	+ ****	+ **	- ns	+ ***
	B	+ **	+ ****	- ns	- ns	- ns
	X	- ****	- ****	+ ns	+ ns	+ ns
	E	+ ****	+ ****	+ ns	+ ns	- *
b) Competition Belowground	*A*	+ *	+ ****	+ *	+ *	- ns
	B	- **	- ****	+ ns	+ ns	+ ns
	X	+ ns	+ ns	+ ns	+ ns	+ ns
	E	+ ****	+ ****	- ns	+ ns	+ ns
		ambient	+CO_2	ambient x time	+CO_2 x time	**+CO_2 vs ambient**
c) +CO_2 Aboveground	*A*	+ ****	+ ****	+ **	+ *	- ns
	B	+ *	+ ****	- ns	+ ns	+ ns
	X	- ***	- ****	+ ns	+ ns	- ns
	E	+ ****	+ ****	+ *	+ ns	+ ns
d) +CO_2 Belowground	*A*	+ *	+ ****	+ ns	- ns	+ ***
	B	- ***	- ****	+ ns	- ns	- ns
	X	+ *	+ ns	+ ns	+ ns	- ns
	E	+ ***	+ ****	+ ns	+ *	+ ns
RGR +O_3		ambient	+O_3	ambient x time	+O_3 x time	**+O_3 vs ambient**
e) +O_3 Aboveground	*A*	+ ****	+ ****	+ **	+ ns	- ns
	B	+ ****	+ **	- ns	+ ns	- ns
	X	- ****	+ ****	+ ns	+ ns	+ ns
	E	+ ****	+ ****	+ ns	+ ns	- *
f) +O_3 Belowground	*A*	+ **	+ **	+ ns	+ ns	- ns
	B	- ***	- ***	- ns	- ns	+ ns
	X	+ ns	+ ns	+ ns	+ ns	- ns
	E	+ ***	+ ***	+ ns	+ *	+ ns

Table 4.2: a-f: Spruce (*P.abies*) above- and belowground estimates of regression coefficient depicting the relationship between independent variables (*A*, *B*, *X* and *E*) and dependent variable (*RGR*); its interaction with time under (a-b) competition; (c-d) +CO_2 and (e-f) +O_3. Highlighted column indicates slope difference between groups, where positive sign (+) denotes (mono > mixed); (+CO_2 > ambient); (+O_3 > ambient). A negative sign (-) depicts the reverse. ns not significant *$P > 0.05$*; * *$P < 0.05$*; ** *$P < 0.001$*; *** *$P< .0001$*

RGR	Components	simple slopes		two-way interaction		**slope difference**
		mono	mixed	mono x time	mixed x time	**mono vs mixed**
a) Competition Aboveground	*A*	+ **	+ *	- ns	- ns	+ ns
	B	+ ns	+ ns	- ns	- ns	- ns
	X	- *	- *	+ ns	+ ns	+ ns
	E	+ ****	+ ****	+ *	+ *	+ ns
b) Competition Belowground	*A*	- ns	+ *	+ ns	- ns	**-** *
	B	- ns	- ns	+ ns	+ ns	+ ns
	X	+ **	+ *	+ ns	+ ns	+ ns
	E	+ ns	- ns	- ns	- ns	+ ns
		ambient	+CO_2	ambient x time	+CO_2 x time	**+CO_2 vs ambient**
c) +CO_2 Aboveground	*A*	+ *	+ **	+ ns	- ns	+ ns
	B	+ ns	- ns	- ns	- ns	- ns
	X	- *	- *	+ ns	+ *	- ns
	E	+ ****	+ ****	+ *	+ *	- ns
d) +CO_2 Belowground	*A*	+ *	+ ns	- ns	+ ns	- ns
	B	- ns	+ ns	+ ns	+ ns	- ns
	X	+ **	+ *	+ ns	+ ns	- ns
	E	+ *	+ ***	- ns	- **	+ ns
		ambient	+O_3	ambient x time	+O_3 x time	**+O_3 vs ambient**
e) +O_3 Aboveground	*A*	+ **	+ **	- ns	+ ns	+ ns
	B	- ns	+ ns	+ ns	- ns	+ ns
	X	- *	- **	+ *	+ ns	- ns
	E	+ ****	+ ****	+ ***	+ *	+ ns
f) +O_3 Belowground	*A*	+ ns	+ ns	+ ns	+ ns	- ns
	B	+ ns	- ns	+ ns	+ ns	- ns
	X	+ **	+ *	+ ns	+ ns	+ ns
	E	+ ns	- ns	- ns	- ns	**-** *

Discussion

Competition and RGR

H1 was supported as morphological rather than physiological plasticity determined *RGR* of competing juvenile trees. Specifically, space occupation *A* is the decisive factor that decides the competitive success of woody species (Grams et al. 2002; Kozovits et al. 2005b; Matyssek et al. 2005). Higher mean *RGR* of beech in mono than mixed culture was significantly enhanced by aboveground space occupation. Functionally, high biomass-related crown volume favors competitive ability and growth through effective branching architecture (Petritan et al. 2009). Conversely, the decline of aboveground space occupation of beech in mixture can be attributed to low investments in foliage per unit of shoot biomass (Kozovits et al. 2005a) in combination with the ability of neighboring spruce to cast shade effectively (Küppers 1989; Schulze et al. 1989). However, higher light availability due to canopy stratification in mixed than pure stands (Forrester et al. 2007) may lead to higher resource-use efficiency (Richards et al. 2010). The present study confirmed higher *LUE* in mixed than monoculture (Table 4.1a). However, this strategy has no direct effect on beech mean *RGR* (Fig 4.3d). In a simulation study, Pearcy et al. (2005) argued that the cost of increasing mechanical support (e.g. internode length) would outweigh the advantage provided by higher light capture efficiencies confirming a trade-off between the photosynthetic benefits and mechanical costs of light capture (Givnish 1988). Thus, the strategy of beech in monoculture to enhance the morphological plasticity of aboveground space occupation rather than the physiological plasticity of *LUE* ensured higher mean *RGR* in mono compared to mixed culture.

In spruce, higher mean *RGR* in mixed compared to monoculture was significantly enhanced by belowground space occupation. Aboveground morphological and physiological components had similar *RGR* patterns for mono-and mixed culture, confirming that belowground components play a significant role in driving spruce *RGR*. Likewise in a study on niche differentiation, Brassard et al. (2009; 2011) found belowground productivity to be higher in mixed than pure stands as a result of greater space occupation by fine roots.

Elevated CO_2 and RGR

In the case of +CO_2, H2 was not supported as mean *RGR* and both above- and belowground physiological plasticity for beech and spruce remained unaltered under +CO_2. Likewise, Poorter and Navas (2003) suggested that *RGR* is only marginally affected by elevated CO_2, whereas Körner et al. (2005) found no lasting tree growth stimulation after four years of CO_2 studies in a temperate forest. Moreover, there are studies claiming that plant insensitivity to +CO_2 may be masked by other signals (Körner et al. 2005) such as resource competition (Daigo Schulte et al. 2013; Grams and Matyssek 2010), type of soil condition (Spinnler et al. 2002) and photosynthetic acclimation (Ainsworth and Rogers 2007). Notedly, in the present study, +CO_2 enhanced belowground space occupation (*A*) in beech, suggesting possible growth stimulation by +CO_2 on this species.

Elevated O_3 and RGR

Under +O_3, H2 was accepted for beech but declined for spruce. In our study, +O_3 decreased beech mean *RGR* through lowered *LUE*. This corroborates findings that under +O_3, beech saplings are more susceptible to biomass reduction than such of spruce (Landolt et al. 2000). Ozone negatively affects tree growth (Matyssek et al. 2007) through reduction of photosynthetic capacity (Reich 1987 ; Paolletti et al. 2007) thereby affecting *LUE* (van Oijen et al. 2004). Photosynthesis is controlled by stomatal regulation (Hoshika et al. 2012, 2014), as exposure to +O_3 modifies stomatal behaviour (Reich & Amundson 1985). Through meta-analysis, Wittig et al. (2007) reported that gymnosperms, on average, have lower stomatal conductance than angiosperms and thus lower +O_3 uptake, confirming the earlier findings of Reich (1987). In our study, spruce mean *RGR* remained unperturbed by O_3 stress, despite lowered *WUE*. Ozone-induced stomatal sluggishness is observed to increase water loss (Hoshika et al. 2012), which typically is associated with decreased *WUE* (Mansfield 1998).

In beech, decreased mean *RGR* under +O_3 may not be attributed only to decreased photosynthetic capacity and reduced stomatal conductance but also to increased diversion of resources into leaves for detoxification and repair (Wieser & Matyssek 2007) as well as lowered carboxylation efficiency (Sasek & Richardson 1989). Photo-chemically induced decrease in *LUE* may occur under advanced O_3 exposure (Dizengremel 1994). Under chronic O_3 exposure, carbon gain could possibly decline with cumulative O_3 uptake attributed to enhance dark respiration (Reich et al. 1983) triggering stimulated metabolic activity (Wieser and Matyssek 2007). Van Oijen et al. (2004) developed a model that estimates the decrease in *LUE* and growth rate under O_3 stress from the metabolic costs, in terms of the amount of assimilates that are used for detoxification and repair. Our findings confirmed such tendencies in beech but not so in spruce.

Conclusion

The decomposition technique and a generic classification of defining plasticity of above- and belowground functions underlying growth, simplify the complexity inherent of *RGR*. In this work, a straight-forward approach is introduced towards understanding growth performances of juvenile woody trees facing biotic (e.g. competition) and abiotic limitations (e.g. $+CO_2$, $+O_3$). As such, this work contributes to theory building and extending more than just revisiting knowledge of plasticity. Our result shows that competitive interaction between juvenile beech and spruce appear to be governed by morphology. Abiotic stress from $+O_3$ seems to affect *RGR* by inducing physiological plasticity in beech but not in spruce. Hence, different reactions to climate change and/or resource availability can be expected for different species. Moreover, morphological and physiological plasticity depend on resource availability and gaseous regime. Therefore, interactions between environmental factors will be decisive in analyzing tree responses.

5. General Discussion

This dissertation encompasses the analysis of competition and growth of juvenile beech and spruce trees exposed to ambient, +CO_2 and/or +O_3. A novel approach is introduced using empirical and theoretical evidences to foster functional understanding of competitive success.

Experimental Data and Simulation Models

Initially, this work combined empirical data gathered from experiments and results of a theoretical simulation model to unravel the complexity of the mode of competition for above- (i.e. light) and belowground resources (i.e. water) at the individual-level of beech and spruce saplings in monoculture and exposed to +CO_2 and/or +O_3. The concept of the mode of competition (see Introduction for details) is applied and tested using experimental data and then extrapolated using a plant growth simulation model for extended periods beyond the experimental time scale.

In Chapter 2 of this dissertation, results from a two-year phytotron study are extrapolated to five vegetation periods using the generic, process-oriented plant growth simulation model PLATHO. This model was developed to simulate growth of juvenile trees and herbaceous plants depending on climatic conditions and availability of external resources such as light, water and nitrogen (Gayler & Priesack 2006). Like other process-based models, PLATHO aims to be comprehensive without being too complex. Complex models are difficult to validate, hard to communicate and difficult to analyze (Grimm et al. 1999). Thus, it is proposed that models should be parsimonious and simple (Wiegand et al. 2006), whenever mechanisms can be expressed freed from complexity in conceptual or numeric depiction (Caswell 1989). In particular, inclusion of physiological details in simulation models is often beset by lack of database to explain underlying mechanisms and process descriptions are sometimes based on effective parameters whose values are difficult to estimate. Consequently, attempts have been made to aggregate system behavior by simplifying model structures (Landsberg & Warring 1997). Simple, individual-based models (IBM) are indispensable for developing new hypotheses and identifying underlying plant processes (Berger et al. 2008). However, these models are often based on allometric relations (Weiner et al. 2001) and neglect physiological process simulation (Grote & Pretzsch 2002).

PLATHO model enables the analysis of competition mechanisms between plants considering the spatial arrangement of the competing individuals and the spatial and temporal distribution of resources without restricting the details of information needed for simulating physiological processes (Gayler et al. 2006; Gayler et al. 2004). The model combines common approaches to predict plant physiological process such as growth and photosynthesis with a "zone of influence” (ZOI) approach to simulate competition depending on the overlapping zone with neighboring plants (Gates & Wescott, 1978). Such an approach is quite common in plant models (Weiner & Daamgard 2006; Weiner et al. 2001) but criticized for considering only the area used by a tree and neglect the specific distance between competing individuals (Berger & Hildebrandt 2000). Nevertheless, ZOI models, being semi-mechanistic and conceptually simple provide theoretical insights in the spatial competition among individual plants (Weiner et al. 2001; Wyszomirski et al. 1999). For example, ZOI approach, successfully reproduced the outcome of competitive interactions between juvenile beech and spruce (Gayler et al. 2006).

In plant growth models, many processes are typically described by empirical functions depending on parameters obtained from experiments. Often, parameterization of these functions are based on laboratory studies that may not be sufficient to cover the range of values found in the field (Dang et al. 1998), resulting in a poor goodness of fit between model and observed data. Root Mean Square Error (*RMSE*) is considered the paramount measure of accuracy of a simulation model as it provides a percentage term of the difference between model predictions and observation (Willmott et al. 1985). *RMSE* at best equals zero, but there are no ‘universal goodness-of-fit’ criteria and some researchers question the *RMSE* approach (Roberts & Pashler 2000). Nonetheless, it is suggested that not only the modeler should minimize the difference between experimental data and simulated result, but also the experimentalist must elaborate data conducive to overcoming model weaknesses (Wilmott et al. 1985). In this way, the predicted outcome can be validated with accuracy and precision (Willmott & Matsuura 2005). Often, but not necessarily, model performance improves with increasing number of parameters (Reynolds & Acock 1985), although poorly known parameters may be included that only pretend goodness-of-fit, which then renders models difficult to interpret (Mohren & Burkhart 1994). Hence, a compromise must be found between a simplistic approach with only a small number of parameters and more physiology-based process descriptions based on additional parameters whose values are not known a priori and must be estimated (Bugmann 2001).

An optimization technique is therefore recommended to improve model performance. This method has an advantage that the parameter values are based on the components in the observed ecosystem (Ward et al. 2001). PLATHO model was initially parameterized and validated for the specific conditions of a phytotron experiment (Gayler et al. 2006), with beech and spruce saplings as study plants. In this work, parameters of PLATHO were re-adjusted using PLAFIT, a non-linear least squares fitting method implemented in Matlab (Mathworks 2005). Possible values of parameters were restricted to ranges that were derived either from empirical data gathered in a series of phytotron experiment (Ritter et al. 2015; Kozovits et al. 2005a & b) and lysimeter studies (Gayler et al. 2009; Pritsch et al. 2008) or from literature calculated from other plant simulation models (Penning de Vries et al. 1989; Thornley & Johnson 1990; Bossel 1996; van Oijen et al. 2004). The selected parameters relate to phenology, climatic condition (Payer et al. 1993), allometry of growth, maximum growth rate and ozone impacts. PLAFIT searches new parameter values in an iterative way, refining PLATHO by predicting a reasonable output reflecting experimental data (See Appendix 1). Generally, least squares method is a standard approach in regression analysis with the purpose of adjusting the parameters of a model. In non-linear least squares optimization, a problem is to find the value of the parameters so that the curve fits the input data in the least squares sense. In this way, the large number of square residuals or discrepancy between an estimated model (e.g. PLATHO) and experimental data is minimized.

PLAFIT used an iterative approach by searching parameter values repeatedly that best fit the input data, here, represented as aboveground and total plant biomass in the phytotron experiments in mono (Ritter et al. 2015) and mixed culture (Kozovits et al. 2005a &b). The iteration process lasted 10 – 15 hours for each run before a new set of parameter values replaced the default option. The new values were checked manually to prevent each parameter from taking values outside the range of experimental data. PLATHO was then validated using dataset not used in the parameterization which originated from phytotron studies conducted in mixed (Luedemann et al. 2009; 2005) and monoculture (Kozovits et al. 2005a & b), and also from isolated plants after adjusting for planting density (Jungermann 1998).

Parameter optimization using PLAFIT improved PLATHO performance (Chapter 2; Fig 2.3 & 2.4) and provided a possibility to explore plant responses to changing climatic condition over extended period not covered by experiments (Chapter 2; Fig. 2.5 & 2. 6). In this work, PLATHO sets a time trend on the behavior of juvenile saplings competing for above- and belowground resources under +CO_2 and/or +O_3. Specifically, analysis of the mode of competition using simulated data extended results obtained from experiments and predicted possible scenarios over time. It is important to consider that PLATHO, like any other plant growth model, is an abstract representation of reality and should not be used to substitute situation found in experiments. However, when properly parameterized through optimization using robust experimental data, PLATHO simulation can provide reliable estimation of plant responses observed under experimental condition.

Whole-tree RGR, a measure of competitive success

Substantial efforts were made to study plant functional traits especially under climate change (Nicotra et al. 2010). Experimental analyses have utilised *RGR*, the most important indicator of growth under environmental stress and disturbance regimes (Poorter & Evans 1998). In this work, *RGR* is used to analyze the competitive success of beech and spruce saplings under the biotic limitation of competition and abiotic stress of +CO_2 and/or +O_3 regimes. *RGR* is considered as a standardised measure of growth since it eradicates size biases (Hunt & Cornelissen 1997) and, hence, an adequate tool for conducting comparative studies of plant performance (Pommerenning & Muzta 2015).

There are two ways to calculate *RGR*, namely the classical and functional approach. The classical analysis is calculated by dividing the difference in *ln*-transformed biomass between two harvests by the time difference between those harvests (Hunt et al. 2002; Hoffman & Poorter 2002). This means that at least two observations are required. Expected mean values of *RGR* and their variances over harvest intervals can be estimated from replicated plant biomass (Hunt et al. 2002; Causton & Venus 1981; Venus & Causton 1979). Despite the simplicity and straight-forwardness of this approach, the classical approach has been criticized as unsatisfactory, since *RGR* can be obscured by the time course between harvest intervals (Causton & Venus 1981). The need to know the trend of growth with time using derived values gives rise to the development of functional approach in calculating *RGR*. This method involves curve-fitting and the derived growth rates can take any appropriate functions. With the advances in computer programs, curve fitting of complex experimental data utilizing fitted functions have been widely used. Generally, the advantage of the functional approach is that the instantaneous term at a specific time can be obtained directly from the fitted curve (Hunt 2003). However, the functional approach is not recommended when only few harvests are available (Venus & Causton 1979). Notedly, considering a short time period, functionally-derived instantaneous *RGR* is approximately equal to classical mean *RGR* (Pommerenning & Muzta 2015).

In Chapter 3 of this dissertation, *RGR* was estimated using the classical approach to assess the competitive success of juvenile beech and spruce trees planted in isolation, mono-and mixed culture and exposed to ambient, +CO_2 and/or +O_3 regimes (Ritter et al. 2015; Lüdemann et al. 2009; 2005; Kozovits et al. 2005a & b; Jungerman 1998). In *RGR* analysis, ontogenetic drift remains a critical issue. Decreases in *RGR* with ontogeny reflect a change in growth variables that are size-dependent (Rees et al. 2010). It is recommended that when doing comparative analysis from studies involving experimental treatments, ontogenetic drift should be accounted for (Coleman et al. 1994), since differences in growth strategy may be confounded by initial size-differences (Turnbull et al. 2008; McConnaughay & Coleman 1999). In this work, whole-tree *RGR* is calculated at a common size per individual experiment. Results showed that *RGR* of beech generally decreased under

$+O_3$, although this was dependent on competitive setting and distinctly enhanced in mixture with spruce and at high densities (Chapter 3, Table 3.2), thereby confirming the scaling problem of many comparative studies using different-sized individuals under varying competitive condition (Millard 2007; Körner 2006). Furthermore, whole tree *RGR* between beech and spruce was compared to examine the mechanisms behind the interaction of these two species under varying competitive setting and climatic condition. Functional relationship between *RGR* and space-related efficiencies of (1) resource investment into standing biomass (space occupation) and (2) resource gain (space exploitation) (Grams et al. 2002) was established to quantify competitive success of beech and spruce saplings under biotic limitation (mono- vs mixed culture) and exposure to abiotic $+CO_2$ and $+O_3$ stress. Others have used similar parameters for assessing structural and functional effectiveness in resource uptake (Grams & Matyssek 2010; Küppers 1989; Matyssek & Schulze 1987; Schulze et al. 1986; Tremmel & Bazzaz 1986).

Results displayed significant correlation between whole-tree *RGR* and efficiency of aboveground space occupation i.e. space occupied by crown volume per unit investment in stem, leaves and shoot biomass, irrespective of species (see Chapter 3, Fig 3.4). In comparison with spruce, beech demonstrated higher phenotypic plasticity by having a wider range of aboveground space occupation Neither above- nor belowground efficiency in space exploitation (defined here as annual C gain per unit crown volume or belowground water uptake per root volume) showed significant trends with *RGR*. Thus, by relating *RGR* to space-related efficiencies of resource investments (i.e. space occupation) and resource gain (i.e. space exploitation), growth performance among and between species can be readily analyzed. In this study, results affirmed that the strategy of juvenile trees to optimize efficient space use (i.e. the relation of occupied crown space per unit of biomass investment in leaves, branches and stem rather than to maximize resource gain (i.e. space exploitation) proves to be a suitable indicator of competitive success. In the case of uni-directional resources such as light, that are ‘pre-emptable’ and enable shading effect, successful space occupation may diminish the resource availability to the neighbour. Although the resources gained by the plant may not increase in absolute terms, it can be raised relative to competing neighbors. Thus, this marginal advantage is maximized through optimization of space occupation.

However, another problem in comparing responses of individuals or species to different environmental condition is how to weigh the contributions of other components of growth. This requires insight into the morphological and physiological aspects of *RGR*. Using a single dataset (Kozovits et al. 2005a & b), the functional analysis of *RGR* and its components was analyzed using the decomposition technique to determine trees species-specific response when facing the biotic stress of competition (e.g. mono, mixed culture) and abiotic $+CO_2$ and $+O_3$ stress (Chapter 4). The equation of *RGR* $\frac{1}{Bi} \bullet \frac{\partial Bi}{\partial t}$ denotes the instantaneous rate of increase in biomass per unit biomass per unit time. Instantaneous *RGR* cannot be measured in theory since it represents a single point in time, however it can be derived from functions, for example in linear regression as the slope of *ln B* over time (Perez-Harguindeguy et al. 2013).

This dissertation expands the meaning of *RGR* beyond the classical or functional approach through decomposition analysis (Chapter 4). Earlier subdivision of plant growth analysis has been initiated (Rees et al. 2010; Shipley 2006; Poorter & Nagel 2000; Schwinning 1996; Hunt 1990), but it is used here to examine the contributions of above- and belowground mechanisms in explaining growth variations of juvenile beech and spruce trees as competing for light and water and exposed to $+CO_2$ and $+O_3$ exposure.

In the growth decomposition equation (see Chapter 4; Materials & Methods for details), the morphological parameters are based on proportions (i.e. crown volume or root volume per biomass) obtained from experimental data, whereas the physiological components (i.e. light-use-efficiency, water-use-efficiency, instantaneous rate of biomass) are derived quantities obtained from functional equations. In this study, decomposition of the complexity of *RGR* into simplified components enable to delineate specific-specific strategies that determine the competitive success of juvenile species under the biotic limitation of competition and abiotic stress of $+CO_2$ and $+O_3$.

Growth responses of juvenile beech and spruce

Growth is a key process that features the dynamics and functioning of plants. Stress of biotic (i.e. competition) and abiotic nature (i.e. $+CO_2$, $+O_3$) are known to influence growth processes causing complex responses that may persist in the longer term or decline after a while. Studies suggest that species dominance in mixed forest will change under $+CO_2$ enrichment (Spinnler et al. 2002; Bazzaz & Williams 1991), $+O_3$ exposure (Grams et al. 2007; Matyssek et al. 2004) and neighbor interaction (Poorter & Bartelink 2002). There has been an unresolved scientific debate on the effects of mixing tree species on productivity particularly in European forests with mixed beech and spruce plantation (Bolte et al. 2013). Whereas studies predict beech competitive ability to increase with changing atmospheric climate (Bolte et al. 2002), the competitive strength of spruce will decrease with time (Pretzsch et al. 2010). Such uncertainty generates questions on which of these two most economically important tree species in Europe would dominate given the biotic effect of competition and abiotic stress of $+CO_2$ and $+O_3$.

Biotic Limitation of Competition

Spatial structure, a distinct feature in terrestrial communities, is believed to play a significant role in plant dynamics (Dieckmann et al. 1997). In woody forest, canopy expansion and corresponding plasticity in crown (Muth & Bazzaz) or root volume (Bolte et al. 2004) may profoundly affect trees competitive ability (Stoll & Prati 2001), species composition (Küppers 1989) and stand productivity (Pretzsch 2014; Matyssek 2012). In the case of juvenile trees, beech saplings exhibited lower aboveground space occupation (i.e. crown volume per aboveground biomass) in mixed than monoculture, whereas the opposite holds true for spruce (Grams et al. 2002; Kozovits et al. 2005a). This strategy of beech during early stages of development is attributed to a size-independent change in architectural arrangement by decreasing allocation to leaves in relation to shoot biomass when mixed with spruce (Kozovits et al. 2005b). Indeed, lower mean-*RGR* of beech saplings in mixed than monoculture (Chapter 4; Fig 4.2a) was correlated with aboveground space occupation (Chapter 4; Table 4.1a). Moreover, higher mean-*RGR* of juvenile spruce in mixed than monoculture (Chapter 4; Fig 4.2d) was attributed to space occupation efficiency belowground (Chapter 4; Table 4.2b). The strategy of spruce saplings to ensure competitive success affirmed the importance of morphological plasticity during early stages of canopy development. For example, adjustment of growth by distributing biomass through shoot elongation is a rapid response and can happen before shading between neighbors can take place (Pierik et al. 2009; Ballare 1990). Conversely, beech slows its volume-related investment presumably avoiding competition in response to a declining light environment.

Plants occupying a range of micro-environment from sun to shade display a series of plastic compromises to optimize light capture (Valladares et al. 2002). For example, lowering of space occupation efficiency of beech in mixture with spruce may be related to a decrease of its foliage per shoot to avoid self-shading (Horn 1971). Spruce in contrast employs an impulsive character of volume-related shoot elongation, thereby casting shade on beech, by this ensuring its competitive ability to maximize light capture. It should be considered that beech can grow at different light intensities (Tognetti et al. 1997), more plastic than spruce (Schall et al. 2012) and displays higher morphological plasticity at low than high light (Valladares & Niinemets 2008). These suggest that although beech saplings in mixture demonstrate a lower biomass investment through decreased space occupation efficiency, it can optimize growth through shade tolerance (Pretzch & Schütze 2005; Ellenberg 1988). Thus, aboveground optimization strategy in space occupation during early stage of canopy development may pay off through time and strengthen the competitive capability of beech in mixed stands at the later stage.

However, growth does not only depend on competition for aboveground resources (i.e. light) but belowground resources (i.e. water) could also play an important function. In this dissertation, *RGR* increased with belowground space occupation for juvenile saplings irrespective of type of competition except for spruce where belowground space occupation efficiency was higher in mixed than in mono culture (Chapter 4, Table 4.2b). This confirms findings that spruce saplings had higher root biomass investment in mixed than monoculture (Kozovits et al. 2005a). Nevertheless, higher belowground space occupation could possibly enhance beech competitive ability through time as Schmid et al. (2012) claimed that fine roots of adult beech were over represented in the rooting zone of mixed stands, indicating a displacement of spruce fine roots.

Although the wait-and-see attitude of beech may slow growth, high phenotypic plasticity as shown from optimization of space occupation efficiency can ensure a long-term competitive success. Moreover, aboveground resource-to-biomass conversion efficiency in terms of light-use efficiency (*LUE*) significantly increased with *RGR* for beech and spruce irrespective of planting type, but greater enhancement was observed for beech in mixed than in monoculture (Chapter 4, Table 4.1a). This suggests a trade-off mechanism in spruce where higher space occupation strategy may weaken its neighbors (i.e. beech) at the expense of its *LUE*. Schulze et al. (1977) confirms lower photosynthetic capacity of spruce than beech as the former achieved higher photosynthesizing biomass due to the longevity of its needles.

Abiotic Stress of +CO_2 and/or +O_3

Impacts of +CO_2 and +O_3 on plants are derived from two undisputed processes: photosynthesis and stomatal conductance. Both affect plants in opposite ways. For example, leaf-photosynthesis and stomatal conductance increases and decreases, respectively under +CO_2 (Wittig et al.,2007; Medlyn et al. 2002; Long & Naidu, 2002; Eamus & Ceulemans 2001). Conversely, both processes are reduced under +O_3 with gymnosperms and tree saplings showing less response than angiosperms and adult trees (Wittig et al. 2007). However, results from growth chamber studies showed that juvenile trees to be more sensitive than adult trees (Matyssek et al. 2010). Moreover, a combination of both gases could ameliorate individual gas effects (Paoletti & Grulke 2005). The question on how these outcomes translate into changes in growth or biomass (Karnosky et al. 2003) remains a challenging task.

This study decomposed growth into morphological and physiological components to delineate effects of +CO_2 and +O_3. Results did not show any +CO_2 growth enhancement for beech and spruce saplings (Chapter 4; Fig 4.2) despite a positive correlation of *RGR* with above- and belowground space occupation for these two species (Chapter 4; Table 4.1 & 4. 2). Nonetheless, beech belowground space occupation was significantly increased under $+CO_2$ suggesting possible growth enhancement which may possibly accrue over time. Effects of $+CO_2$ on photosynthesis are similar between conifers and deciduous species (Saxe et al. 1998), but differs between mature and juvenile ones. For example, dry matter production for juvenile trees per year is 32% higher under $+CO_2$ than those in control (Wullschleger et al. 1997), whereas, Norby et al. (1999) reported a growth increment of 27%. Körner (2000) claims that this $+CO_2$ effects is much lower than those reported for photosynthesis increase at 40%, suggesting no straightforward association between photosynthesis and growth stimulation. In comparison, this study reported negative effect of $+O_3$ on beech (Chapter 4; Fig 4.2c) and was correlated with physiological plasticity in aboveground *LUE*. This supports claims that beech is more susceptible to biomass reduction than spruce under $+O_3$ exposure (Landolt et al. 2000) consequently decreasing growth performance (Matyssek et al. 2007) due to reduced photosynthetic capacity (Reich 1987; Paolletti et al. 2007) as affected by *LUE* (van Oijen et al. 2004). Conversely, $+O_3$ has no effect whatsoever on the mean *RGR* of spruce (Chapter 4; Fig 4.2f). Overall, this analysis affirms the susceptibility to $+O_3$ of juvenile beech compared to spruce. Nevertheless, beech response under $+CO_2$ through increased space occupation efficiency (Chapter 4; Table 4.2) may equalize the negative effect of O_3 on this species.

6. General Conclusion

This dissertation was initiated in order to elucidate competition and growth processes of juvenile woody saplings such as beech and spruce under exposure to $+CO_2$ and $+O_3$. It has identified the role of resources in competing for above- and belowground resources, delineated strategies that determine competitive success and identified the importance of morphological and physiological plastic responses under the biotic limitation of competition and abiotic stress caused by $+CO_2$ and $+O_3$. Despite a number of studies conducted on plant responses to $+CO_2$ and $+O_3$, a mechanistic understanding on how these gases would affect competitive interaction between tree individuals (i.e. mode of competition) and competitive success (i.e. *RGR*) at the intra- and interspecific-level and ultimately breaking down the components into plants plastic responses, especially during early stage of development are still lacking. Thus, this dissertation was sought to answer the following hypotheses.

In Chapter 2 of this dissertation, two hypotheses were tested:

- Among beech and spruce trees planted in monoculture, $+CO_2$ would diminish the positive asymmetric competition for aboveground resource such as light, whereas, $+O_3$ would enhance this outcome.
- The symmetric mode of competition belowground for water would remain unchanged irrespective of $+CO_2$ and $+O_3$ treatments.

Resource characteristics rather than $+CO_2$ or $+O_3$ determine the mode of competition: Empirical evidences from a two-year phytotron experiments and extension of predictions of the mode of competition for a five-year period revealed that neither $+CO_2$ nor $+O_3$ altered the mode of competition for light and symmetric competition for water. These results implied that mechanisms of over-topping and casting shades on neighbors for aboveground resource such as light or non-pre-emption for belowground competition for heterogeneous resource such as water could not be easily modified by increasing +CO_2 and/or +O_3 regimes, at least for beech and spruce planted in monoculture under early stage of development.

In Chapter 3 of this dissertation, two research questions were put forward:

- Whether effects of +CO_2 and/or +O_3 are modified by different competitive settings, i.e. growth in isolation, mono- or mixed culture.
- Whether the competitive success of a plant in terms of relative growth rate (*RGR*) is related to an efficient space use (i.e. optimization strategy) or conversely to the maximization of resource gains (i.e. maximization strategy).

Competitive interaction between plants have the potential to alter the abiotic impact of +CO_2 and +O_3: Indeed, analysis using a series of growth chamber experiments, where beech and spruce were grown in isolation, mono-and mixed culture confirmed that competitive interaction between plants have the potential to alter the abiotic impact of +CO_2 and +O_3. It is most likely that the more intense the competition for a limiting resources, the higher the potential to modify the response to other stressors. Therefore, responses exhibited by plants in isolation or under low competitive pressure could not be transferred for plants grown in mono or mixed culture.

Optimization of space occupation efficiency rather than maximization of resource gain determines competitive success: Analysis using dataset from four consecutive phytotron experiments performed under similar environmental condition (regarding climate and CO_2/O_3 regimes) confirmed that the strategy of juvenile trees to optimize space use (i.e. the relation of occupied crown space per unit of biomass investment in leaves, branches and stem) rather than to maximize resource gain (i.e. space exploitation) proved to play a significant role in determining competitive success. Moreover, the biotic stress caused by competition has the potential to alter abiotic impacts of +CO_2 and/or +O_3. In situation where competition is intense, the strategy to occupy space efficiently represents an appropriate mechanisms for competitive success.

In Chapter 4 of this dissertation, two hypotheses were tested:

- Morphological plasticity determines the *RGR* of beech and spruce saplings competing for above- and belowground competition for light, and water respectively.

- However, under $+CO_2$ and $+O_3$, physiological plasticity is crucial in driving *RGR*.

Morphological plasticity in space occupation serves to be an effective strategy for ensuring competitive success: Analysis using a single dataset identified the role of morphological and physiological plasticity in understanding growth performances of juvenile woody trees facing biotic (e.g. competition) and abiotic limitations (e.g. $+CO_2$, $+O_3$). Results confirmed that morphological plasticity of aboveground space occupation determined higher mean-*RGR* of beech in mono than mixed culture; whereas, belowground space occupation played a significant role for increasing mean-*RGR* of spruce in mixed than monoculture.

Physiological plastic responses become important under abiotic stress: Although $+CO_2$ had no significant effect on beech and spruce *RGR*, $+O_3$ negatively affected *RGR* of beech through physiological plasticity of *LUE*. These results implied that different reactions to climate change and/or resource availability have to be expected for different species. Since plastic responses are largely influenced by resource availability and gaseous regimes, interactions between these factors will be decisive in analyzing tree responses.

Theoretical Implication and Recommendation

Under climate change, the paradigm shift of plant growth, i.e. the shift from a carbon centric (source) to meristem (sink) oriented approach of explaining growth, (Körner 2015) supports the need to re-visit the methods used in plant growth analysis. Thus, there is a demand to come up with a novel approach that could explain plants complex mechanisms that may have been overlooked when analyzing above- and belowground plant strategies exposed to $+CO_2$ and/or $+O_3$ regimes. Such study warrants an integrative approach using theoretical concept and simulation models to identify mechanistic factors that drive competitive success. This challenge is initiated in this dissertation to investigate competition and growth at the juvenile phase of beech and spruce, the two most important economically growing tree species in Europe. There is still difficulty in reconciling tree responses as influenced by ontogeny. Thus, investigation of the competitive success of juvenile trees lays down the foundation for early developmental strategies that may influence responses in later stages. Such study is indispensable as it traces the variability that characterizes plant life history.

Firstly, this work affirmed the decisive role of resource characteristics rather than $+CO_2$ or $+O_3$ in determining the mode of competition for above-(i.e. light) and belowground resources (i.e. water). Hence, future investigation on competitive interaction should prioritize resource-based approaches rather than environmental manipulations. Notedly, the result presented here applies only to conditions found in monoculture and thus may not hold true in mixed stands. Indeed, analysis using a series of growth chamber experiments, where beech and spruce were grown in isolation, mono-and mixed culture confirmed that competitive interaction between plants have the potential to alter the abiotic impact of $+CO_2$ and $+O_3$. It is most likely that the more intense the competition for a limiting resources, the higher the potential to modify the response to other stressors. Therefore, responses exhibited by plants in isolation or under low competitive pressure could not be transferred for plants grown in mono or mixed culture. In situation where competition is intense, the strategy to occupy space efficiently represents an appropriate mechanism for competitive success. Growth decomposition analysis simplifies the complexity in understanding plant responses. In particular where plants are faced by the biotic limitation of competition (mono vs mixed), the morphological plasticity of space occupation serves to be an effective strategy for ensuring competitive success. Under the abiotic stress, physiological plastic responses become important, at least for beech under $+O_3$.

The conceptual study applied in this dissertation encompassing the mode of competition (Chapter 2), the analysis of competitiveness using space-related efficiencies of resource used (Chapter 3) and the decomposition of growth (Chapter 4) are unique in its application to woody-plant systems under ambient, $+CO_2$ and/or $+O_3$ regimes. The research questions and outcome addressed by each sub-study were developed independent of the other but complement to unravel the complexity in understanding competitive interaction and growth of juvenile trees. Generally, this dissertation seeks to provide an integrated analysis of competitive success in juvenile trees for discussion and improvement of current methods for re-analysis and therefore foster understanding and predict responses of climate change. The approaches presented here can be further investigated using novel experiments and theoretical simulations considering temporal and spatial scenarios under exposure to +CO_2 and +O_3 regimes. In this way, the conceptual understanding of competitive success presented in this dissertation supported by the predictive capability of computer model could provide a promising tool for investigating growth responses under changing climate and ontogeny.

Overall, this dissertation helps clarify the complexity in understanding competitive success of a juvenile deciduous (i.e. beech) and coniferous (i.e. spruce) trees under the biotic limitation of competition and abiotic +CO_2 and +O_3 stress. Since plastic responses are largely influenced by resource availability and gaseous regimes, interactions between these factors will be decisive in analyzing tree responses. This dissertation lays down the foundation for early developmental strategies that may influence responses in later stages. Such study is indispensable as it traces the variability that characterizes plant life history. This work has unveiled principles of mechanisms related to competition and growth under controlled phytotron conditions with scenarios of relevance for current and expected future CO_2 and O_3 regimes, now claiming empirical validation under the actual site conditions of forest ecosystems.

Appendix 1: Parameterization of PLATHO using PLAFIT: A Matlab Optimization Technique

```
    function f = plafit_costfun(x,meas,l)
    %PLATFIT_COSTFUN Cost function to minimise
    % f = plafit_costfun(x)
    % f (scalar) function value (in a least square sense)
    % x vector (4) with values to enter into platho and minimise
    global glo_l
    glo_l = glo_l+1;
    create_platho_txtfile(x);
    %system('C:\programFiles\Expert-N\expertn /autostart');
    % now read platho and calculate cost in a least squares sense:
    data = read_rfu('C:\programFiles\Expert-N\result\B1110.rfu');
    sim = data(607,[47 56 83 92 119 128]+2);
    f = sum(sum((repmat(sim,[size(meas,1) 1])-meas).^2));
    % f = 0;
    % for m=1:size(meas,1),
    % f = f + sum((sim(~isnan(meas))-meas(m,~isnan(meas))).^2);
    % end
    save(['tmp\res' num2str(l) '_' num2str(glo_l) '.mat'],'x','sim','f','meas');
    function plafit(larr)
    global glo_l
    opt = optimset('MaxFunEvals',1000,'FunValCheck','on',...
    'TolX',1d-2,'TolFun',1d-2,...
    'Display','iter');
    x0 = [0.2073 0.6737 0.8904 1.0710];
    meas{1} = [18.09 21.43 36.23 29.99 15.11 7.20];
    meas{2} = [11.05 14.97 36.74 3.34 10.38 22.87];
    meas{3} = [27.14 25.15 17.54 38.98 nan 10.18];
    meas{5} = [24.73 24.81 11.15 23.57 21.62 18.70];
    meas{6} = [24.73 24.81 11.15 23.57 21.62 18.70];
    meas{7} = [32.32 11.71 28.94 27.84 22.10 24.35];
    meas{8} = [32.32 11.71 28.94 27.84 22.10 24.35];
    %meas{9}                                                              =
[meas{1};meas{2};meas{3};meas{4};meas{5};meas{6};meas{7};meas{8};];
    fname_rfu{1} = 'C:\programFiles\Expert-N\result\B1110.rfu';
    fname_rfu{3} = 'C:\programFiles\Expert-N\result\2B12O0.rfu';
    %fname_rfu{4} = 'C:\programFiles\Expert-N\result\2B12O0.rfu';
    for l=larr,
    glo_l = 0;
    [x,fval,exitflag]                                                     =
fminsearch(@(x)plafit_costfun(x,meas{l},l,fname_rfu{l}),x0,opt)
    save(['results' num2str(l) '.mat'])end
```

References

Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. Plant, cell & environment 30: 258-270

Ainsworth EA, Yendrek CR, Sitch S, Collins WJ, Emberson LD (2012) The Effects of Tropospheric Ozone on Net Primary Productivity and Implications for Climate Change. Annual review of plant biology 63: 637-661

Agerer R, Hartmann A, Pritsch K, Raidl S, Schloter M, Verma R, Weigt R (2012) Plants and their ectomycorrhizosphere: cost and benefit of symbiotic soil organisms. Growth and Defence in Plants. Springer, pp 213-242

Andersen CP (2003) Source–sink balance and carbon allocation below ground in plants exposed to ozone. New New Phytologist, 157(2), 213-228.

Ballaré CL, Scopel AL, Sánchez RA (1990) Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. Science 247: 329

Bazzaz FA, Catovsky S (2002) Plants—from cells to ecosystems: impacts of global environmental change. Encyclopedia of global environmental change 2: 94-111

Bazzaz FA (1996) Plants in a changing environment. Cam-bridge University Press, New York, New York, USA. Plants in a changing environment

Bazzaz FA, Williams WE (1991) Atmospheric CO_2 Concentrations Within a Mixed Forest: Implications for Seedling Growth. Ecology: 12-16

Begon M, Wall R (1987) Individual variation and competitor coexistence: a model. Functional Ecology: 237-241

Berger U, Hildenbrandt H (2000). A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. Ecological Modelling 132: 287-302

Berger U, Piou C, Schiffers K, Grimm V (2008) Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. Perspectives in Plant Ecology, Evolution and Systematics 9: 121-135

Blackman VH (1919) The compound interest law and plant growth. Annals of Botany: 353-360

Bolte A, Hilbrig L, Grundmann BM, Roloff A (2014) Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest"the Siggaboda case study. Annals of forest science 71: 139-147

Bolte A, Kampf F, Hilbrig L (2013) Space sequestration below ground in old-growth spruce-beech forests: signs for facilitation? Frontiers in plant science 4

Bolte A, Rahmann T, Kuhr M, Pogoda P, Murach D, Gadow Kv (2004) Relationships between tree dimension and coarse root biomass in mixed stands of European beech (*Fagus sylvatica L.*) and Norway spruce (*Picea abies [L.] Karst.*). Plant and Soil 264: 1-11

Bolte A, Villanueva I (2006) Interspecific competition impacts on the morphology and distribution of fine roots in European beech (*Fagus sylvatica L.*) and Norway spruce (*Picea abies (L.) Karst.*). Eur J Forest Res 125: 15-26

Bossel H (1996) Deriving indicators of sustainable development. Environmental Modeling & Assessment 1: 193-218

Bossel H (1996) TREEDYN3 forest simulation model. Ecological modelling 90: 187-227
Botany 77: 47-57

Boyden SB, Reich PB, Puettmann KJ, Baker TR (2009) Effects of density and ontogeny on size and growth ranks of three competing tree species. Journal of Ecology 97: 277-288

Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. Advances in genetics 13: 115-155

Brassard BW, Chen HYH, Bergeron Y (2009) Influence of environmental variability on root dynamics in northern forests. Critical Reviews in Plant Science 28: 179-197

Briggs GE, Kidd F, West C (1920) A quantitative analysis of plant growth: part II. Annals of applied Biology 7: 202-223

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85: 1771-1789

Browne MW, Cudeck R (1992) Alternative ways of assessing model fit. Sociological Methods & Research 21: 230-258

Bugmann H (2001) A review of forest gap models. Climatic Change 51: 259-305

Cahill JR JF, Brenda C (1999) Growth consequences of soil nutrient heterogeneity for two old-field herbs, Ambrosia artemisiifolia and Phytolacca americana, grown individually and in combination. Annals of Botany: 471-478

Caldwell M, Manwaring J, Jackson R (1991) Exploitation of phosphate from fertile soil microsites by three Great Basin perennials when in competition. Functional Ecology: 757-764

Campbell BD, Grime JP, Mackey JML (1991) A trade-off between scale and precision in resource foraging . Oecologia: 87: 532-538.

Casper BB, Jackson RB (1997) Plant competition underground. Annu. Rev. Ecol. Syst 28: 545-570

Caswell H (1989) Analysis of life table response experiments I. Decomposition of effects on population growth rate. Ecological Modelling 46: 221-237

Catovsky S, Bazzaz FA (2002) Plant competition in an elevated CO_2 world. Encyclopedia of global environmental change 2: 471-481

Causton DR, Venus JC (1981) The biometry of plant growth. Edward Arnold.

Ceulemans R, Mousseau M (1994) Tansley Review No. 71. Effects of elevated atmospheric CO_2 on woody plants. New phytologist: 425-446

Chesson P (2000) Mechanisms of maintenance of species diversity. Annual review of Ecology and Systematics: 343-366

Clark AJ, Landolt W, Bucher JB, Strasser RJ (2000) Beech (Fagus sylvatica) response to ozone exposure assessed with a chlorophyll a fluorescence performance index. Environmental Pollution 109: 501-507

Coleman JS, McConnaughay KDM, Ackerly DD (1994) Interpreting phenotypic variation in plants. Trends in Ecology & Evolution 9: 187-191

Curtis PS, Wang X (1998) A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. Oecologia 113: 299-313

Daigo Schulte MJ, Matyssek R, Gayler S, Priesack E, Grams TEE (2013) Mode of competition for light and water amongst juvenile beech and spruce trees under ambient and elevated levels of O_3 and CO_2. Trees 27: 1763-1773

Dang Q-L, Margolis HA, Collatz GJ (1998) Parameterization and testing of a coupled photosynthesis-stomatal conductance model for boreal trees. Tree physiology 18: 141-153

Dieckmann U (1997) Can adaptive dynamics invade? Trends in Ecology & Evolution 12: 128-131

Dieckmann U, Law R, Metz JA (2000) The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press

Eamus D, Ceulemans R (2001) Effects of greenhouse gases on the gas exchange of forest trees. The impact of carbon dioxide and other greenhouse gases on forest ecosystems. Vienna, Austria: CABI Publishing: 17-56

Emberson L, Ashmore M, Cambridge H, Simpson D, Tuovinen J-P (2000) Modelling stomatal ozone flux across Europe. Environmental Pollution 109: 403-413

Engel T, Priesack E (1993) Expert-N-A Building Block System of Nitrogen Models as Resource for Advice, Research, Water Management and Policy. Integrated soil and sediment research: a basis for proper protection. Springer, pp 503-507

Evans GC (1972) The quantitative analysis of plant growth. Univ of California Press

Falge E, Graber W, Siegwolf R, Tenhunen J (1996) A model of the gas exchange response of Picea abies to habitat conditions. Trees 10: 277-287

Falster DS, Westoby M (2003) Plant height and evolutionary games. Trends in Ecology and Evolution 18:337-343

Farquhar GD, Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. Planta 149: 78-90

Fischer A (1921) Growth of fibroblasts and hydrogen ion concentration of the medium. The Journal of experimental medicine 34: 447-454

Fitter A (1991) Characteristics and functions of root systems. Plant roots: the hidden half 2: 1-29

Forester JD, Ives AR, Turner MG, Anderson DP, Fortin D, Beyer HL, Smith DW, Boyce MS (2007) State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecological Monographs 77: 285-299

Fowler (2008) Ground-level ozone in the 21st century: future trends, impacts and policy implications.

Fredericksen T, Joyce B, Skelly J, Steiner K, Kolb T, Kouterick K, Savage J, Snyder K (1995) Physiology, morphology, and ozone uptake of leaves of black cherry seedlings, saplings, and canopy trees. Environmental Pollution 89: 273-283

Fredericksen TS, Kolb TE, Skelly JM, Steiner KC, Joyce BJ, Savage JE (1996) Light environment alters ozone uptake per net photosynthetic rate in black cherry trees. Tree Physiology 16: 485-490

Garrigues E, Doussan C, Pierret A (2006) Water uptake by plant roots: I - formation and propagation of a water extraction front in mature root systems as evidenced by 2D light transmission imaging. Plant and Soil 283: 83-98

Garrigues S, Allard D, Baret F, Weiss M (2006) Influence of landscape spatial heterogeneity on the non-linear estimation of leaf area index from moderate spatial resolution remote sensing data. Remote Sensing of Environment 105: 286-298

Gates DJ, Westcott M (1978) Zone of influence models for competition in plantations. Advances in Applied Probability: 499-537

Gayler S, Grams TEE, Kozovits A, Winkler J, Luedemann G, Priesack E (2006) Analysis of Competition Effects in Mono-and Mixed Cultures of Juvenile Beech and Spruce by Means of the Plant Growth Simulation Model PLATHO. Plant Biology 8: 503-514

Gayler S, Klier C, Mueller C, Weis W, Winkler J, Priesack E (2009) Analysing the role of soil properties, initial biomass and ozone on observed plant growth variability in a lysimeter study. Plant and soil 323: 125-141

Gayler S, Leser C, Priesack E, Treutter D (2004) Modelling the effect of environmental factors on the trade-off between growth and defensive compounds in young apple trees. Trees 18: 363-371

Gayler S, Priesack E (2005) PLATHO Documentation- a simulation model of resource allocation in the plant-soil system http://www.sfb607.de/english/projects/c2/platho.pdf

Givnish TJ (1988) Adaptation to sun and shade: a whole-plant perspective. Functional Plant Biology 15: 63-92

Gomez-Aparicio L, Garcia Valdes R, Ruiz Benito P, Zavala MA (2011) Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. Global Change Biology 17: 2400-2414

Grams TEE, Daigo Schulte MJ, Winkler J, Gayler S, Matyssek R (2012) Growth and space use in competitive interactions between juvenile trees. Growth and defence in plants. Springer, pp 273-286

Grams TEE, Kozovits A, Reiter I, Barbro Winkler J, Sommerkorn M, Blaschke H, Häberle KH, Matyssek R (2002) Quantifying competitiveness in woody plants. Plant Biology 4: 153-158

Grams TEE, Anegg S, Häberle KH, Langebartels C, Matyssek R (1999) Interactions of chronic exposure to elevated CO_2 and O_3 levels in the photosynthetic light and dark reactions of European beech (Fagus sylvatica). New Phytologist 144: 95-107

Grams TEE, Andersen CP (2007) Competition for resources in trees: Physiological versus morphological plasticity. In: Esser K, Lüttge U, Beyschlag W, Murata J (eds) Progress in Botany, vol 68. Springer-Verlag, Berlin, Heidelberg, pp 356-381

Grams TEE, Kozovits AR, Häberle KH, Matyssek R, Dawson TE (2007) Combining δ13C and δ18O analyses to unravel competition, CO_2 and O_3 effects on the physiological performance of different-aged trees. Plant, Cell & Environment 30: 1023-1034

Grams TEE, Lüttge U (2011) Space as a resource. In: Esser K, Lüttge U, Beyschlag W, Murata J (eds) Progress in Botany, vol 72. Springer, Berlin, Heidelberg, pp 349-370.

Grams TEE, Matyssek R (1999) Elevated CO_2 counteracts the limitation by chronic ozone exposure on photosynthesis in Fagus sylvatica L.: Comparison between chlorophyll fluorescence and leaf gas exchange. Phyton - Annales Rei Botanicae 39 (4):31-39

Grams TEE, Matyssek R (2010) Stable isotope signatures reflect competitiveness between trees under changed CO_2/O_3 regimes. Environmental Pollution 158:1036-1042

Grime J (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American naturalist: 1169-1194

Grime JP (2006) Plant strategies, vegetation processes, and ecosystem properties. John Wiley & Sons

Grimm V (1999) Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecological modelling 115: 129-148

Grote R, Pretzsch H (2002) A model for individual tree development based on physiological processes. Plant Biology 4: 167-180

Hättenschwiler S, Körner C (2000) Tree seedling responses to in situ CO_2-enrichment differ among species and depend on understorey light availability. Global Change Biology 6: 213-226

Hayes A, Matthes J (2009) Computational procedures for probing interactions in OLS and logistic regression: SPSS and SAS implementations. Behavior Research Methods 41: 924-936

Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytologist 162: 9-24

Hoffmann WA, Poorter H (2002) Avoiding bias in calculations of relative growth rate. Annals of Botany 90: 37-42

Horn HS (1971) The adaptive geometry of trees. Princeton University Press

Hoshika Y, Watanabe M, Inada N, Koike T (2012) Ozone-induced stomatal sluggishness develops progressively in Siebold's beech (Fagus crenata). Environmental Pollution 166: 152-156

Hunt R (1990) Basic growth analysis. Unwin Hyman Ltd

Hunt R (2003) Growth analysis, individual plants. Encyclopaedia of applied plant sciences. Academic Press, Londres: 579-588

Hunt R, Causton DR, Shipley B, Askew AP (2002) A modern tool for classical plant growth analysis. Annals of Botany 90 (4):485-488

Hunt R, Cornelissen J (1997) Components of relative growth rate and their interrelations in 59 temperate plant species. New Phytologist 135: 395-417

IBM (2009) PASW Version 19. Polar Engineering & Consulting

initial biomass and ozone on observed plant growth variability in a lysimeter study. Plant Soil 323:125–141

Jungermann A (1998) Photosynthese, Wasserbedarf und Allokation in Buche (Fagus sylvatica L.) unter kombinierten CO_2/O_3-Regimen. Diploma thesis, FH Weihenstephan

Karnosky D, Zak D, Pregitzer K, Awmack C, Bockheim J, Dickson R, Hendrey G, Host G, King J, Kopper B (2003) Tropospheric O_3 moderates responses of temperate hardwood forests to elevated CO_2: a synthesis of molecular to ecosystem results from the Aspen FACE project. Functional Ecology 17: 289-304

Kerstiens G (2001) Meta-analysis of the interaction between shade-tolerance, light environment and growth response of woody species to elevated CO 2. Acta Oecologica 22: 61-69

Kolb T, Matyssek R (2001) Limitations and perspectives about scaling ozone impacts in trees. Environmental Pollution 115: 373-393

Körner C (2000) Biosphere responses to CO_2 enrichment. Ecological Applications 10: 1590-1619

Körner C (2003a) Carbon limitation in trees. Journal of ecology 91: 4-17

Körner C (2003b) Ecological impacts of atmospheric CO_2 enrichment on terrestrial ecosystems. Philosophical Transactions of the Royal Society of London Series a-Mathematical Physical and Engineering Sciences 361 (1810):2023-2041

Körner C (2006) Plant CO_2 responses: an issue of definition, time and resource supply. New Phytologist 172 (3):393-411

Körner C (2015) Paradigm shift in plant growth control. Current Opinion in Plant Biology 25: 107-114

Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Pelaez-Riedl S, Pepin S, Siegwolf RTW, Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science 309: 1360-1362

Kozovits AR, Matyssek R, Blaschke H, Göttlein A, Grams TEE (2005a) Competition increasingly dominates the responsiveness of juvenile beech and spruce to elevated CO_2 and/or O_3 concentrations throughout two subsequent growing seasons. Global Change Biology 11:1387-1401

Kozovits AR, Matyssek R, Winkler JB, Gottlein A, Blaschke H, Grams TEE (2005b) Aboveground space sequestration determines competitive success in juvenile beech and spruce trees. New Phytologist 167: 181-196

Kühlmann-Berenzon S, Heikkinen J, Särkkä A (2005) An additive edge correction for the influence potential of trees. Biometrical Journal 47: 517-526

Küppers M (1985) Carbon relations and competition between woody species in a Central European hedgerow. Oecologia 66: 343-352

Küppers M (1989) Ecological significance of aboveground architectural patterns in woody plants - a question of cost-benefit relationships. Trends in Ecology & Evolution 4 (12):375-379

Landhausser SM (2011) Aspen shoots are carbon autonomous during bud break. Trees-Structure and Function 25 (3):531-536

Landolt W, Bühlmann U, Bleuler P, Bucher J (2000) Ozone exposure–response relationships for biomass and root/shoot ratio of beech (Fagus sylvatica), ash (Fraxinus excelsior), Norway spruce (*Picea abies*) and Scots pine (Pinus sylvestris). Environmental Pollution 109: 473-478

Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecology and Management 95: 209-228

Langebartels C, Ernst D, Heller W, Lütz C, Payer H-D, Sandermann H, Jr. (1997) Ozone Responses of Trees: Results from Controlled Chamber Exposures at the GSF Phytotron. In: Sandermann HJ, Wellburn AR, Heath RL (eds) Ecological Studies, vol 127. Springer-Verlag, Berlin, pp 163-200

Liu X, Kozovits AR, Grams TEE, Blaschke H, Rennenberg H, Matyssek R (2004) Competition modifies effects of enhanced ozone/carbon dioxide concentrations on carbohydrate and biomass accumulation in juvenile Norway spruce and European beech. Tree Physiology 24: 1045-1055

Long S, Naidu S (2002) Effects of oxidants at the biochemical, cell and physiological levels, with particular reference to ozone. Air pollution and Plant life 2: 69-88

Luedemann G, Matyssek R, Fleischmann F, Grams TEE (2005) Acclimation to ozone affects host/pathogen interaction and competitiveness for nitrogen in juvenile *Fagus sylvatica* and *Picea abies* trees infected with *Phytophthora citricola*. Plant Biology 7: 640-649

Luedemann G, Matyssek R, Winkler J, Grams TEE (2009) Contrasting ozone× pathogen interaction as mediated through competition between juvenile European beech (Fagus sylvatica) and Norway spruce (*Picea abies*). Plant and soil 323: 47-60

Luo Y, Field CB, Mooney HA (1994) Predicting responses of photosynthesis and root fraction to elevated CO_2: interactions among carbon, nitrogen, and growth. Plant, Cell & Environment 17: 1195-1204

Mansfield TA (1998) Stomata and plant water relations: does air pollution create problems? Environmental Pollution 101: 1-11

Mathworks Inc. (2005) Matlab Version 7.3. Natick Massachusetts

Matyssek R, Agerer R, Ernst D, Munch J, Osswald W, Pretzsch H, Priesack E, Schnyder H, Treutter D (2005) The plant's capacity in regulating resource demand. Plant Biology 7: 560-580

Matyssek R, Bytnerowicz A, Karlsson P-E, Paoletti E, Sanz M, Schaub M, Wieser G (2007) Promoting the O_3 flux concept for European forest trees. Environmental Pollution 146: 587-607

Matyssek R, Karnosky DF, Wieser G, Percy K, Oksanen E, Grams TEE, Kubiske M, Hanke D, Pretzsch H (2010a) Advances in understanding ozone impact on forest trees: Messages from novel phytotron and free-air fumigation studies. Environmental Pollution 158 (6):1990-2006

Matyssek R, Wieser G, Ceulemans R, Rennenberg H, Pretzsch H, Haberer K, Löw M, Nunn AJ, Werner H, Wipfler P, Oßwald W, Nikolova P, Hanke DE, Kraigher H, Tausz M, Bahnweg G, Kitao M, Dieler J, Sandermann H, Herbinger K, Grebenc T, Blumenröther M, Deckmyn G, Grams TEE, Heerdt C, Leuchner M, Fabian P, Häberle K-H (2010b) Enhanced ozone strongly reduces carbon sink strength of adult beech (Fagus sylvatica) – Resume from the free-air fumigation study at Kranzberg Forest. Environmental Pollution 158:2527-2532

Matyssek R, Kozovits AR, Schnitzler J-P, Pretzsch H, Dieler J, Wieser G (2014) Forest trees under air pollution as a factor of climate change. Trees in a Changing Environment. Springer, pp 117-163

Matyssek R, Sandermann H (2003) Impact of ozone on trees: An ecophysiological perspective. Progress in Botany: 349-404

Matyssek R, Sandermann H, Wieser G, Booker F, Cieslik S, Musselman R, Ernst D (2008) The challenge of making ozone risk assessment for forest trees more mechanistic. Environmental Pollution 156: 567-582

Matyssek R, Schnyder H, Oßwald W, Ernst D, Munch JC, Pretzsch H (2012) Growth and defence in plants: resource allocation at multiple scales. Springer Science & Business Media

Matyssek R, Schulze ED (1987) Heterosis in hybrid larch (Larix decidua x leptolepis). Trees 1: 225-231

Matyssek R, Wieser G, Calfapietra C, De Vries W, Dizengremel P, Ernst D, Jolivet Y, Mikkelsen TN, Mohren G, Le Thiec D (2012a) Forests under climate change and air pollution: gaps in understanding and future directions for research. Environmental Pollution 160: 57-65

Matyssek R, Schnyder H, Oßwald W, Ernst D, Munch JC, Pretzsch H (2012b) Growth and defence in plants: resource allocation at multiple scales. Springer Science & Business Media

Matyssek R, Wieser G, Nunn AJ, Kozovits AR, Reiter IM, Heerdt C, Winkler JB, Baumgarten M, Häberle KH,Grams TEE, Werner H, Fabian P, Havranek WM (2004) Comparison between AOT40 and ozone uptake in forest trees of different species, age and site conditions. Atmospheric Environment 38: 2271-2281

McConnaughay KDM, Coleman JS (1999) Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. Ecology 80: 2581-2593

McDonald EP, Kruger EL, Riemenschneider DE, Isebrands JG (2002) Competitive status influences tree-growth responses to elevated CO_2 and O_3 in aggrading aspen stands. Functional Ecology 16: 792-801

Medlyn B, Dreyer E, Ellsworth D, Forstreuter M, Harley P, Kirschbaum M, Le Roux X, Montpied P, Strassemeyer J, Walcroft A (2002) Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. Plant, Cell & Environment 25: 1167-1179

Millard P, Sommerkorn M, Grelet GA (2007) Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. New Phytologist 175 (1):11-28

Mohren G, Burkhart H (1994) Contrasts between biologically-based process models and management-oriented growth and yield models. Forest Ecology and Management

Monteith JL (1995) A reinterpretation of stomatal responses to humidity. Plant, Cell & Environment 18: 357-364

Muth CC, Bazzaz F (2002) Tree seedling canopy responses to conflicting photosensory cues. Oecologia 132: 197-204

Navas ML, Garnier E, Austin MP, Gifford RM (1999) Effect of competition on the responses of grasses and legumes to elevated atmospheric CO2 along a nitrogen gradient: differences between isolated plants, monocultures and multi- species mixtures. New Phytologist 143 (2):323-331

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F Plant phenotypic plasticity in a changing climate. Trends in plant science 15: 684-692

Norby RJ, DeLucia EH, Gielen B, Calfapietra C, Giardina CP, King JS, Ledford J, McCarthy HR, Moore DJ, Ceulemans R (2005) Forest response to elevated CO2 is conserved across a broad range of productivity. Proceedings of the National Academy of Sciences of the United States of America 102: 18052-18056

Norby RJ, Wullschleger SD, Gunderson CA, Johnson DW, Ceulemans R (1999) Tree responses to rising CO2 in field experiments: implications for the future forest. Plant, Cell & Environment 22: 683-714

Nowak RS, Ellsworth DS, Smith SD (2004) Functional responses of plants to elevated atmospheric CO2–do photosynthetic and productivity data from FACE experiments support early predictions? New Phytologist 162: 253-280

Oksanen E, Saleem A (1999) Ozone exposure results in various carry-over effects and prolonged reduction in biomass in birch (Betula pendula Roth). Plant, Cell & Environment 22: 1401-1411

Pacala S, Weiner J (1991) Effects of competitive asymmetry on a local density model of plant interference. Journal of Theoretical Biology,*149*(2), 165-179.

Pacala SW, Silander Jr J (1990) Field tests of neighborhood population dynamic models of two annual weed species. Ecological Monographs: 113-134

Paine C, Marthews TR, Vogt DR, Purves D, Rees M, Hector A, Turnbull LA (2012) How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. Methods in Ecology and Evolution 3: 245-256

Paoletti E, Grulke NE (2005) Does living in elevated CO2 ameliorate tree response to ozone? A review on stomatal responses. Environmental Pollution 137: 483-493

Paoletti E, Manning WJ (2007) Toward a biologically significant and usable standard for ozone that will also protect plants. Environmental Pollution 150: 85-95

Paoletti E, Nali C, Lorenzini G (2007) Early responses to acute ozone exposure in two Fagus sylvatica clones differing in xeromorphic adaptations: photosynthetic and stomatal processes, membrane and epicuticular characteristics. Environmental monitoring and assessment 128: 93-108

Payer HD, Blodow P, Köfferlein M, Lippert M, Schmolke W, Seckmeyer G, Seidlitz HK, Strube D, Thiel S (1993) Controlled environment chambers for experimental studies on plant responses to CO_2 and interactions with pollutants. In: Schulze ED, Mooney HA (eds) Ecosystems Research Report Nr. 6: Design and execution of experiments on CO_2 enrichment. Commission European Communities, Brussels, pp 127-145

Pearcy RW, Muraoka H, Valladares F (2005) Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. New Phytologist 166: 791-800

Penning de Vries F (1989) Simulation of ecophysiological processes of growth in several annual crops. Int. Rice Res. Inst.

Perez-Harguindeguy N, Diaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE (2013) New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61: 167-234

Petritan AM, von Lüpke B, Petritan IC (2009) Influence of light availability on growth, leaf morphology and plant architecture of beech (*Fagus sylvatica L.*), maple (Acer pseudoplatanus L.) and ash (Fraxinus excelsior L.) saplings. European Journal of Forest Research 128: 61-74

Pierik R, Djakovic-Petrovic T, Keuskamp DH, de Wit M, Voesenek LA (2009) Auxin and ethylene regulate elongation responses to neighbor proximity signals independent of gibberellin and DELLA proteins in Arabidopsis. Plant Physiology 149: 1701-1712

Pommerening A, Muszta A (2015) Methods of modelling relative growth rate. Forest Ecosystems 2:1-9

Poorter A, Bartelink HH (2002) Modelling mixed forest growth: a review of models for forest management. Ecological modelling 150: 141-188

Poorter H, Evans JR (1998) Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. Oecologia 116: 26-37

Poorter H, Garnier E (1996) Plant growth analysis: an evaluation of experimental design and computational methods. Journal of Experimental Botany 47: 1343-1351

Poorter H, Nagel O (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Functional Plant Biology 27: 1191-1191

Poorter H, Navas M-L (2003) Plant growth and competition at elevated CO_2: on winners, losers and functional groups. New Phytologist 157: 175-198

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist 193: 30-50

Poorter H, Perez-Soba M (2001) The growth response of plants to elevated CO_2 under non-optimal environmental conditions. Oecologia 129: 1-20

Poorter H, Remkes C, Lambers H (1990) Carbon and nitrogen economy of 24 wild species differing in relative growth rate. Plant Physiology 94: 621-627

Poorter L (1999) Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. Functional ecology 13: 396-410

Pretzsch H, Block J, Dieler J, Dong PH, Kohnle U, Nagel Jr, Spellmann H, Zingg A (2010) Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Annals of Forest Science 67: 712

Pretzsch H, Dieler J (2012) Evidence of variant intra-and interspecific scaling of tree crown structure and relevance for allometric theory. Oecologia 169: 637-649

Pretzsch H, Rötzer T, Matyssek R, Grams TEE, Häberle K-H, Pritsch K, Kerner R, Munch J-C (2014) Mixed Norway spruce (*Picea abies* [L.] Karst) and European beech (Fagus sylvatica [L.]) stands under drought: from reaction pattern to mechanism. Trees 28: 1305-1321

Pretzsch H, Schutze G (2005) Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica L.*) in pure and mixed stands. Plant Biology 7: 628-639

Pritsch K, Ernst D, Fleischmann F, Gayler S, Grams TEE, Göttlein A, Heller W, Koch N, Lang H, Matyssek R (2008) Plant and soil system responses to ozone after 3 years in a lysimeter study with juvenile beech (*Fagus sylvatica L.*). Water, Air, & Soil Pollution: Focus 8: 139-154

Pye JM (1988) Impact of ozone on the growth and yield of trees: a review. Journal of environmental quality 17: 347-360

Rajaniemi T (2007) Root foraging traits and competitive ability in heterogeneous soils. Oecologia 153: 145-152

Rajaniemi TK (2003) Evidence for size asymmetry of belowground competition. Basic and Applied Ecology 4: 239-247

Rees M, Osborne CP, Woodward FI, Hulme SP, Turnbull LA, Taylor SH (2010) Partitioning the components of relative growth rate: how important is plant size variation? The American Naturalist 176: E152-E161

Reich PB (1987) Quantifying plant response to ozone: a unifying theory. Tree physiology 3: 63-91

Reich PB, Amundson RG (1985) Ambient levels of ozone reduce net photosynthesis in tree and crop species. Science 230: 566-570

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB (2003) The evolution of plant functional variation: traits, spectra, and strategies. International Journal of Plant Sciences 164: S143-S164

Reiter IM, Häberle KH, Nunn AJ, Heerdt C, Reitmayer H, Grote R, Matyssek R (2005) Competitive strategies in adult beech and spruce: space-related foliar carbon investment versus carbon gain. Oecologia 146 (3):337-349

Reynolds JF, Acock B (1985) Predicting the response of plants to increasing carbon dioxide: a critique of plant growth models. Ecological Modelling 29: 107-129

Richards AE, Forrester DI, Bauhus Jr, Scherer-Lorenzen M (2010) The influence of mixed tree plantations on the nutrition of individual species: a review. Tree Physiology 30: 1192-1208

Ritter W, Lehmeier CA, Winkler JB, Matyssek R, Grams TEE (2015) Contrasting carbon allocation responses of juvenile European beech (Fagus sylvatica) and Norway spruce (*Picea abies*) to competition and ozone. Environmental Pollution 196: 534-543

Roberts S, Pashler H (2000) How persuasive is a good fit? A comment on theory testing. Psychological review 107: 358

Rodenkirchen H, Göttlein A, Kozovits AR, Matyssek R, Grams TEE (2009) Nutrient contents and efficiencies of beech and spruce saplings as influenced by competition and O_3/CO_2 regime. European Journal of Forest Research 128:117-128

Rothe A, Binkley D (2001) Nutritional interactions in mixed species forests: a synthesis. Canadian Journal of Forest Research 31: 1855-1870

Sasek TW, Richardson CJ (1989) Effects of chronic doses of ozone on loblolly pine: photosynthetic characteristics in the third growing season. Forest Science 35: 745-755

Saxe H, Ellsworth DS, Heath J (1998) Tree and forest functioning in an enriched CO_2 atmosphere. New Phytologist 139: 395-436

Schall P, Lödige C, Beck M, Ammer C (2012) Biomass allocation to roots and shoots is more sensitive to shade and drought in European beech than in Norway spruce seedlings. Forest Ecology and Management 266: 246-253

Schlichting CD (1986) The evolution of phenotypic plasticity in plants. Annual review of ecology and systematics: 667-693

Schmid I (2002) The influence of soil type and interspecific competition on the fine root system of Norway spruce and European beech. Basic and Applied Ecology 3: 339-346

Schulze ED (1986) Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. Annual Review of Plant Physiology 37: 247-274

Schulze ED (1989) Air pollution and forest decline in a spruce (*Picea abies*) forest. Science 244: 776-783

Schulze ED, Fuchs M, Fuchs M (1977) Spacial distribution of photosynthetic capacity and performance in a mountain spruce forest of Northern Germany. Oecologia 29: 43-61

Schwinning S (1996) Decomposition analysis of competitive symmetry and size structure dynamics. Annals of Botany 77:47-57

Schwinning S, Fox GA (1995) Population dynamic consequences of competitive symmetry in annual plants. Oikos: 422-432

Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113:447-455

Shipley B (2006) Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. Functional Ecology 20: 565-574

Shipley B, Lechowicz MJ, Wright I, Reich PB (2006) Fundamental trade-offs generating the worldwide leaf economics spectrum. Ecology 87: 535-541

Signora L, Galtier N, Skøt L, Lucas H, Foyer CH (1998) Over-expression of sucrose phosphate synthase in Arabidopsis thaliana results in increased foliar sucrose/starch ratios and favours decreased foliar carbohydrate accumulation in plants after prolonged growth with CO_2 enrichment. Journal of Experimental Botany 49: 669-680

Silander Jr JA, Pacala SW (1985) Neighborhood predictors of plant performance. Oecologia 66: 256-263

Silvertown J (2004) Plant coexistence and the niche. Trends in Ecology & Evolution 19: 605-611

Sitch S, Cox PM, Collins WJ, Huntingford C (2007) Indirect radiative forcing of climate change through ozone effects on the land-carbon sink. Nature 448 (7155):791-794

South DB (1995) Relative growth rates: a critique. South African Forestry Journal 173: 43-48

Spinnler D, Egli P, Körner C (2002) Four-year growth dynamics of beech-spruce model ecosystems under CO_2 enrichment on two different forest soils. Trees-Structure and Function 16 (6):423-436

Spinnler D, Egli P, Körner C (2002) Four-year growth dynamics of beech-spruce model ecosystems under CO_2 enrichment on two different forest soils. Trees 16: 423-436

Sprugel DG, Hinckley TM, Schaap W (1991) The Theory and Practice of Branch Autonomy. Annual Review of Ecology and Systematics 22:309-334

Stenger R, Priesack E, Barkle G, Sperr G (1999) A tool for simulating nitrogen and carbon dynamics in the soil-plant atmosphere system. Proceedings of the technical session, pp 19-28

Stitt M (1991) Rising CO_2 levels and their potential significance for carbon flow in photosynthetic cells. Plant, Cell & Environment 14: 741-762

Stocklin J, Korner C (1999) Interactive effects of elevated CO_2, P availability and legume presence on calcareous grassland: results of a glasshouse experiment. Functional Ecology: 200-209

Stoll P, Prati D (2001) Intraspecific aggregation alters competitive interactions in experimental plant communities. Ecology 82: 319-327

Syring KM, Claassen N (1995) Estimation of the influx and the radius of the depletion zone developing around a root during nutrient uptake. Plant and Soil 175 (1):115-123
The plants capacity in regulating resource demand. Plant Biology 7: 560-580

Thiel S, Döhring T, Köfferlein M, Kosak A, Martin P, Seidlitz HK (1996) A phytotron for plant stress research: how far can artificial lighting compare to natural sunlight? Journal of Plant Physiology 148:456-463

Thornley JHM, Johnson IR (1990) A Mathematical Approach to Plant and Crop Physiology

Tilman D (1982) Resource Competition and Community Structure. (Mpb-17). Princeton University Press Princeton, NJ

Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological monographs 57: 189-214

Tjoelker M, Oleksyn J, Reich P (1998) Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO_2 and temperature. Tree physiology 18: 715-726

Tjoelker M, Volin J, Oleksyn J, Reich P (1993) Light environment alters response to ozone stress in seedlings of Acer saccharum Marsh, and hybrid Populus L. New Phytologist 124: 627-636

Tjoelker M, Volin J, Oleksyn J, Reich P (1995) Interaction of ozone pollution and light effects on photosynthesis in a forest canopy experiment. Plant, Cell & Environment 18: 895-905

Tognetti R, Johnson JD, Michelozzi M (1997) Ecophysiological responses of Fagus sylvatica seedlings to changing light conditions. I. Interactions between photosynthetic acclimation and photoinhibition during simulated canopy gap formation. Physiologia Plantarum 101: 115-123

Tremmel DC, Bazzaz FA (1995) Plant architecture and allocation in different neighborhoods: implications for competitive success. Ecology: 262-271

Turnbull LA, Paul-Victor C, Schmid B, Purves DW (2008) Growth rates, seed size, and physiology: do small-seeded species really grow faster. Ecology 89: 1352-1363

Valladares F, Chico J, Aranda I, Balaguer L, Dizengremel P, Manrique E, Dreyer E (2002) The greater seedling high-light tolerance of Quercus robur over Fagus sylvatica is linked to a greater physiological plasticity. Trees 16: 395-403

Valladares F, Niinemets Ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. Annual Review of Ecology, Evolution, and Systematics: 237-257

Van Kuijk M, Anten N, Oomen R, Van Bentum D, Werger M (2008) The limited importance of size-asymmetric light competition and growth of pioneer species in early secondary forest succession in Vietnam. Oecologia 157: 1-12

Van Oijen M, Dreccer M, Firsching K-H, Schnieders B (2004) Simple equations for dynamic models of the effects of CO_2 and O_3 on light-use efficiency and growth of crops. Ecological Modelling 179: 39-60

Venus JC, Causton DR (1979) Plant growth analysis: a re-examination of the methods of calculation of relative growth and net assimilation rates without using fitted functions. Annals of Botany 43: 633-638

Volin JC, Tjoelker, MG, OleksynJ, & Reich P B (1993) Light environment alters response to ozone stress in seedlings of *Acer saccharum Marsh*. and hybrid *Populus L. II*. Diagnostic gas exchange and leaf chemistry.New Phytologist, 637-646.

Volpe G, Bianco LB, Rieger M (2008) Carbon autonomy of peach shoots determined by 13C photoassimilate transport. Tree Physiology 28 (12):1805-1812

von Wettberg EJ, Weiner J (2003) Larger Triticum aestivum plants do not preempt nutrient-rich patches in a glasshouse experiment. Plant Ecology 169: 85-92

Ward BA, Friedrichs MAM, Anderson TR, Oschlies A (2001) Parameter optimisation techniques and the problem of underdetermination in marine biogeochemical models. Journal of Marine Systems 81: 34-43

Wayne P, M, & Bazzaz F (1997) Light acquisition and growth by competing individuals in CO_2 enriched atmospheres: consequences for size structure in regenerating birch stands. Journal of Ecology, 29-42.

Weiner J (1990) Asymmetric competition in plant populations. Trends in Ecology & Evol 5:360 364

Weiner J, Damgaard C (2006) Size-asymmetric competition and size-asymmetric growth in a spatially explicit zone-of-influence model of plant competition. Ecological Research 21: 707-712

Weiner J, Stoll P, Muller-Landau H, Jasentuliyana A (2001) The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. The American Naturalist 158: 438-450

Weiner J, Thomas SC (1986) Size variability and competition in plant monocultures. Oikos: 211-222

West C, Briggs GE, Kidd F (1920) Methods and significant relations in the quantitative analysis of plant growth. New Phytologist 19: 200-207

West GB, Brown JH, Enquist BJ (2001) A general model for ontogenetic growth. Nature 413: 628-631

Wiegand K, Saltz D, Ward D (2006) A patch-dynamics approach to savanna dynamics and woody plant encroachment: insights from an arid savanna. Perspectives in Plant Ecology, Evolution and Systematics 7: 229-242

Wieser G, Häsler R, Götz B, Koch W, & Havranek W (2000) Role of climate, crown position, tree age and altitude in calculated ozone flux into needles of *Picea abies* and *Pinus cembra*: a synthesis. Environmental Pollution, 109(3), 415-422.

Wieser G, Hecke K, Tausz M, Haberle K, Grams TEE, Matyssek R (2002) The role of antioxidative defense in determining ozone sensitivity of Norway spruce (Picea abies (L.) Karst.) across tree age: Implications for the sun-and shade-crown. Phyton-horn- 42: 245-254

Wieser G, Matyssek R (2007) Linking ozone uptake and defense towards a mechanistic risk assessment for forest trees. New Phytologist 174: 7-9

Willmott CJ, Ackleson SG, Davis RE, Feddema JJ, Klink KM, Legates DR, O'Donnell J, Rowe CM (1985) Statistics for the evaluation and comparison of models. Journal of Geophysical Research: Oceans (1978-2012) 90: 8995-9005

Willmott CJ, Matsuura K (2005) Advantages of the mean absolute error (MAE) over the root mean square error (RMSE) in assessing average model performance. Climate research 30: 79

Wittig VE, Ainsworth EA, Long SP (2007) To what extent do current and projected increases in surface ozone affect photosynthesis and stomatal conductance of trees? A meta-analytic review of the last 3 decades of experiments. Plant, cell & environment 30: 1150-1162

Wyszomirski T, Wyszomirska I, Jarzyna I (1999) Simple mechanisms of size distribution dynamics in crowded and uncrowded virtual monocultures. Ecological Modelling 115: 253-273

Zeiger E, Field C (1982) Photocontrol of the functional coupling between photosynthesis and stomatal conductance in the intact leaf blue light and par-dependent photosystems in guard cells. Plant Physiology70:370-375.

Candidate's Individual Contribution

Daigo Schulte MJ, Matyssek R, Gayler S, Priesack E, Grams TEE (2013) Mode of competition for light and water amongst juvenile beech and spruce trees under ambient and elevated levels of O_3 and CO_2. Trees 27: 1763-1773

The candidate developed the research question and the story of this paper with the assistance of her co-authors. She integrated and re-analyzed various dataset as input for the study. She worked on the theory, statistics, parameterized, optimized PLATHO, implemented PLAFIT in Matlab, simulated the data, wrote the manuscript and worked in the suggestions and comments of her co-authors.

Grams TEE, **Daigo Schulte MJ**, Winkler J, Gayler S, Matyssek R (2012) Growth and space use in competitive interactions between juvenile trees. In: Growth and defense in plants. Springer, 273-286

The candidate gathered, integrated and analyzed data from a series of phytotron experiments as inputs for the manuscript. She initiated and assisted the statistical and methodological part of the study, analyzed, discussed and helped on the completion of the manuscript together with her co-authors.

Daigo Schulte MJ, Matyssek R, Gayler S. Grams TEE (2015). Decomposition of Relative Growth Rate in competing Fagus sylvatica and *Picea abies*. Perspectives in Plant Ecology, Evolution and Systematics, submitted for publication

The candidate developed the research question and story of this paper with the assistance of her co-authors. She worked on the theoretical and statistical application of the study. She analyzed and composed the graphs and figures; wrote the manuscript; worked in the suggestions and comments of her co-authors and submitted the manuscript for publication to Perspectives in Plant Ecology, Evolution and Systematics.

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