

The role of different modes of interactions among neighbouring plants in driving population dynamics

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Submitted by
M.Sc. Yue Lin

Supervisor:

Mrs. Prof. Dr. Uta Berger
Dresden University of Technology

Mr. Prof. Dr. Volker Grimm
Helmholtz Centre for Environmental Research – UFZ
University of Potsdam

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Explanation of the doctoral candidate

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Place, Date

Lin, Yue

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To my doctoral advisors

Prof. Dr. Uta Berger

and Prof. Dr. Volker Grimm

*whose wisdoms furnish the best of sounding boards,
whose reliance and optimisms dispel all my misgivings,
whose enthusiasms and professionalisms are contagious,
who welcomed me from China to Germany with open arms,
and who are my mentors forever.*

To my dear and loving wife

Qian-Ru Ji

who has made numerous sacrifices to support my studies.

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Summary

The general aim of my dissertation was to investigate the role of plant interactions in driving population dynamics. Both theoretical and empirical approaches were employed. All my studies were conducted on the basis of metabolic scaling theory (MST), because the complex, spatially and temporally varying structures and dynamics of ecological systems are considered to be largely consequences of biological metabolism. However, MST did not consider the important role of plant interactions and was found to be invalid in some environmental conditions. Integrating the effects of plant interactions and environmental conditions into MST may be essential for reconciling MST with observed variations in nature. Such integration will improve the development of theory, and will help us to understand the relationship between individual level process and system level dynamics.

As a first step, I derived a general ontogenetic growth model for plants which is based on energy conservation and physiological processes of individual plant. Taking the mechanistic growth model as basis, I developed three individual-based models (IBMs) to investigate different topics related to plant population dynamics:

1. I investigated the role of different modes of competition in altering the prediction of MST on plant self-thinning trajectories. A spatially-explicit individual-based zone-of-influence (ZOI) model was developed to investigate the hypothesis that MST may be compatible with the observed variation in plant self-thinning trajectories if different modes of competition and different resource availabilities are considered. The simulation results supported my hypothesis that (i) symmetric competition (e.g. belowground competition) will lead to significantly shallower self-thinning trajectories than asymmetric competition as predicted by MST; and (ii) individual-level metabolic processes can predict population-level patterns when surviving plants are barely affected by local competition, which is more likely to be in the case of asymmetric competition.

2. Recent studies implied that not only plant interactions but also the plastic biomass allocation to roots or shoots of plants may affect mass-density relationship. To investigate the relative roles of competition and plastic biomass allocation in altering the mass-density relationship of plant population, a two-layer ZOI model was used which

considers allometric biomass allocation to shoots or roots and represents both above- and belowground competition simultaneously via independent ZOIs. In addition, I also performed greenhouse experiment to evaluate the model predictions. Both theoretical model and experiment demonstrated that: plants are able to adjust their biomass allocation in response to environmental factors, and such adaptive behaviours of individual plants, however, can alter the relative importance of above- or belowground competition, thereby affecting plant mass-density relationships at the population level. Invalid predictions of MST are likely to occur where competition occurs belowground (symmetric) rather than aboveground (asymmetric).

3. I introduced the new concept of modes of facilitation, i.e. symmetric versus asymmetric facilitation, and developed an individual-based model to explore how the interplay between different modes of competition and facilitation changes spatial pattern formation in plant populations. The study shows that facilitation by itself can play an important role in promoting plant aggregation independent of other ecological factors (e.g. seed dispersal, recruitment, and environmental heterogeneity).

In the last part of my study, I went from population level to community level and explored the possibility of combining MST and unified neutral theory of biodiversity (UNT). The analysis of extensive data confirms that most plant populations examined are nearly neutral in the sense of demographic trade-offs, which can mostly be explained by a simple allometric scaling rule based on MST. This demographic equivalence regarding birth-death trade-offs between different species and functional groups is consistent with the assumptions of neutral theory but allows functional differences between species. My initial study reconciles the debate about whether niche or neutral mechanisms structure natural communities: the real question should be when and why one of these factors dominates.

A synthesis of existing theories will strengthen future ecology in theory and application. All the studies presented in my dissertation showed that the approaches of individual-based and pattern-oriented modelling are promising to achieve the synthesis.

Zusammenfassung

Das primäre Ziel meiner Dissertation umfasste die Erforschung der Rolle von Wechselwirkungen zwischen Pflanzen für die Populationsdynamik. Dazu wurden sowohl theoretische als auch empirische Ansätze angewendet. Alle meine Untersuchungen wurden auf Basis der Metabolic Scaling Theory (MST) durchgeführt, da angenommen wird, dass die komplexen räumlich und zeitlich variierenden Strukturen ökologischer Systeme weitgehend die Konsequenzen von biologischem Metabolismus sind. Allerdings berücksichtigt die MST nicht die wichtige Rolle der Wechselwirkungen zwischen Pflanzen und wurde für einige Umweltbedingungen als unzutreffend befunden. Die Integration dieser Wechselwirkungen und Umweltbedingungen in die MST hingegen ist essenziell, um die MST mit den beobachteten Abweichungen in der Natur abzustimmen. Diese Integration wird die Entwicklung von Theorien verbessern und trägt zum Verständnis der Zusammenhänge zwischen Prozessen auf Individual- und Systemebene bei.

In einem ersten Schritt leitete ich ein generelles ontogenetisches Wachstumsmodell für Pflanzen ab, welches auf Energieersparnis und physiologischen Prozessen der individuellen Pflanzen basiert. Auf dieser Grundlage entwickelte ich drei individuenbasierte Modelle (IBM), um verschiedene Fragestellungen in Bezug auf die Populationsdynamik der Pflanzen zu analysieren.

In **Kapitel 2** untersuchte ich den Einfluss verschiedener Arten von Konkurrenz auf die Prognosen der MST in Bezug auf Trajektorien der Selbstausdünnung. Ein räumlich explizites, individuenbasiertes zone-of-influence (ZOI) Modell wurde entwickelt, um die Hypothese zu eruieren, dass die MST kompatibel zu den Abweichungen in Selbstausdünnungstrajektorien ist, wenn verschiedene Arten der Konkurrenz und unterschiedliche Ressourcenverfügbarkeiten in Betracht gezogen werden. Die Ergebnisse der Simulationen bestätigen meine Hypothese, dass (i) symmetrische Konkurrenz (z.B.: unterirdisch – Wurzeln) zu signifikant flacheren Selbstausdünnungstrajektorien führt als bei asymmetrischer Konkurrenz durch die MST vorhergesagt wird; und (ii) metabolische Prozesse auf Individualebene Muster auf Systemebene vorhersagen können, wenn die überlebenden Pflanzen kaum durch lokale Konkurrenz beeinflusst werden, was bei asymmetrischer Konkurrenz meist der Fall ist.

Aktuelle Studien unterstellen, dass nicht nur die Interaktion zwischen Pflanzen, sondern auch die Biomasseallokation zu Wurzeln oder Trieben der Pflanzen das Masse-Dichte Verhältnis beeinflussen kann. In **Kapitel 3** untersuchte ich die Rolle der Konkurrenz und Biomasseallokation im Hinblick auf Veränderung des Masse-Dichte Verhältnisses der Pflanzenpopulation. Dazu wurde ein ZOI Modell mit zwei Ebenen entwickelt, welches die allometrische Biomasseallokation zu Wurzeln oder Trieben berücksichtigt und sowohl

die unter- wie überirdische Konkurrenz durch zwei unabhängige ZOI simultan darstellt. Zusätzlich führte ich ein Gewächshausexperiment durch, um die Modellprognosen zu evaluieren. Sowohl das theoretische Modell und das Experiment zeigen, dass Pflanzen in der Lage sind, ihre Biomasseallokation je nach Umweltfaktoren anzupassen. Diese individuellen Anpassungsstrategien jedoch verändern die relative Bedeutung der ober- wie unterirdischen Konkurrenz und damit das Masse-Dichte Verhältnis auf Populationsebene. Falsche Vorhersagen der MST treten mit höherer Wahrscheinlichkeit auf, wenn unterirdische Konkurrenz (symmetrisch) vorliegt.

In **Kapitel 4** führte ich ein neues Konzept verschiedener Arten der Förderung ein, z.B.: symmetrische versus asymmetrische Förderung und entwickelte ein individuenbasiertes Modell um zu ergründen, wie das Zusammenspiel zwischen verschiedenen Arten der Konkurrenz und Förderung die räumlichen Muster in Pflanzenpopulationen verändert. Diese Studie zeigt, dass die Förderung allein die Aggregation von Pflanzen maßgeblich begünstigen kann, unabhängig von anderen ökologischen Faktoren (z.B.: Samenausbreitung, Mortalität, Heterogenität).

In **Kapitel 5** betrachte ich die Ebene der Pflanzengesellschaften und prüfe die Möglichkeit, die MST mit der Unified Neutral Theory of Biodiversity (UNT) zu kombinieren. Die Analyse umfangreicher Daten bestätigt, dass die meisten untersuchten Pflanzenpopulationen nahezu neutral im Sinne des demographischen Trade-off (Geburt/Sterberate) sind, was durch eine simple Skalierung basierend auf der MST erklärt werden kann. Dieses demographische Gleichgewicht von Geburt und Mortalität zwischen verschiedenen Arten und funktionalen Gruppen steht im Einklang mit der Annahme der Neutral Theory, gestattet jedoch funktionale Abweichungen für manche Arten. Meine Untersuchung bringt die Debatte darüber, ob Nischen oder neutrale Mechanismen natürliche Pflanzengesellschaften strukturieren, in Einklang: die eigentlich Frage sollte lauten, wann und warum einer dieser Faktoren dominiert.

Das abschließende **Kapitel 6** beinhaltet eine generelle Diskussion meiner Untersuchungen und Fragestellungen. Die Synthese bestehender Theorien wird die Ökologie in Theorie und Anwendung zukünftig stärken. Alle in meiner Dissertation durchgeführten Untersuchungen zeigten, dass der Ansatz der individuenbasierten und musterorientierten Modellierung vielversprechend scheint, diese Synthese zu erreichen.

Chapter 1

General introduction

In the mid-19th century, the word 'ecology' (Ökologie) was first coined by Ernst Haeckel in *Morphology of Organisms* (1866), and was originally defined as the study of the relationship of organisms with their environment. The environment of an organism is comprised of all the external factors that could influence it, including physical and chemical factors (abiotic) or/and other organisms (biotic). Despite how precise ecology is defined to date (Table 1.1), it is no doubt that the interactions with those abiotic and biotic factors are fundamental on the elaboration of ecological theories.

However, some new ecological theories such as the metabolic scaling theory (MST) attempts at scaling up from the individuals to the ecosystem, which is based on simple physical rules but overlooks (consciously or unconsciously) the important role of such interactions. Although claimed to be a 'universal' theory, the validity and universality of MST are still under debate because some empirical observations in plant populations and communities are inconsistent with the predictions of MST.

The major goal of my dissertation is to investigate the effects of different modes of interactions in driving plant population dynamics. All my studies are under a context of MST, because I am attempted to integrate the effects of plant interactions and environmental conditions into metabolic scaling theory,

in order to reconcile metabolic scaling theory with observed variations in nature.

In the following, I will first introduce the field of plant interactions and then to the overall approach chosen in this thesis, individual-based and pattern-oriented modelling. Third, I will discuss two ‘unifying’ theories for which plant interactions play a key role: the Metabolic Scaling Theory and the Unified Neutral Theory. Finally, I will outline the structure and content of my thesis.

Table 1.1 Textbook definitions of Ecology (after Scheiner and Willig 2008)

Definition	Source
The study of the structure and function of nature	Odum (1971)
The scientific study of the relationships between organisms and their environments	McNaughton and Wolf (1973)
The study of the natural environment, particularly the interrelationships between organisms and their surroundings	Ricklefs (1979)
The study of animals and plants in relation to their habits and habitats	Colinvaux (1986)
The study of the relationship between organisms and their physical and biological environments	Ehrlich and Roughgarden (1987)
The study of interactions between organisms and between organisms and their environments	Stiling (1992)
The study of the relationships, distribution, and abundance of organisms, or groups of organisms, in an environment	Dodson et al. (1998)
The scientific study of the interactions that determine the distribution and abundance of organisms	Krebs (2001)
The scientific study of the interactions between organisms and their environment	Begon et al. (2006)
The study of the relationships between living organisms and their environments, the interactions of organisms with one another, and the patterns and causes of the abundance and distribution of organisms in nature	Gurevitch et al. (2006)

1.1 Ecology and interactions

1.1.1 *Plant competition*

In natural situations, the limitation of resources is the crucial issue that links organisms with their environment. Resource limitation can be caused by both abiotic and biotic factors. Competition, which per definition is about limiting resources, is considered perhaps the most important but not the only form of biotic interactions, which occurs naturally among living organisms that coexist in same environment. The importance of crop-weed competition was expound in the ancient Chinese encyclopedia of agriculture *The Valuable Techniques for The Welfare of People* (齊民要術, Qí Mín Yào Shù), which had been completed between A.D. 533 and 544. Although farmers (and agronomists) were already aware of the importance of competition in managing their agro-ecosystems long before, the first academic report about competition was published in the 14th century (Grace and Tilman 1990). Since Darwin (1859), competition has been established as the conceptual basis for his concept of 'struggle for life'. Henceforth, most evolutionary biologists view competition as the main driving force of 'natural selection' and, in turn, of evolution. In plant ecology, the competition is one of the most important topics: it is believed to be the main force in driving plant phenotype plasticity, life history evolution, population dynamics, and community assembly (Tilman 1988, Grace and Tilman 1990).

However, as Grace and Tilman (1990) emphasized in *Perspectives on Plant Competition*, although a great deal of research was focused on the topics of competition for a long time, it is still not well understood. Even the definition of competition is not consistent. Many ecologists attempted to give an accurate and unified definition of competition (Milne 1961, Harper 1977, Grime 1979, Tilman 1988, Begon et al. 2005), but so far, none of them has been generally accepted. This terminological confusion indicates the complexity of competition. Begon et al. (2005) defined competition in a very precise way:

“competition is an interaction between individuals, brought about by a shared requirement for a resource, and leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned”. I advocate using this definition because it gives both the cause and the consequence of competition, especially when applying in plant population ecology.

In plant ecology, competition is usually categorized as asymmetric- or symmetric competition according to the competitive effects (Weiner 1990, Schwinning and Weiner 1998, Freckleton and Watkinson 2001, Berger et al. 2008). Asymmetric competition is an unequal or disproportional division of resources amongst competing plants which can be either inter- or intraspecific. Therefore, competition may be asymmetric in the sense that some species or individuals have a competitive advantage over others in taking a disproportionately large amount of resource. The mechanisms determining the degree of inter- and intraspecific asymmetry are similar: they are size-dependent and, related to the nature of the limiting resources (Schwinning and Weiner 1998, Freckleton and Watkinson 2001). For example, taller plants will have a disproportionate advantage over smaller individuals when competing for light, because the limiting resource, light, is ‘pre-emptable’. This can lead to a growth depression of the latter, which has also been referred to as ‘dominance and suppression’ and ‘one-sided competition’ (Weiner 1990, Schwinning and Weiner 1998, Stoll et al. 2002, Berger et al. 2008). In contrast, when the limiting resources are not ‘pre-emptable’ such as water and nutrient, plants will share resources equally or proportionally to their size (Schwinning and Weiner 1998, Berger et al. 2008). It is therefore assumed that competition for light (aboveground competition) is more size asymmetric whereas competition for water and nutrient (belowground competition) is more size symmetric (Schwinning and Weiner 1998, Stoll et al. 2002, Berger et al. 2008).

The particular mode of interactions seems to vary depending on environmental conditions, and whether the interactions occur above- or

belowground. The latter strongly depends on the type of the shared resources and their availability. However, due to logistic and technical difficulties, so far only few studies exist where belowground competition was explored (Morris 2003, Deng et al. 2006, Berger et al. 2008). Most of the empirical experiments as well as theoretical models only consider light competition as the crucial process (but see Casper et al. 2003, May et al. 2009, Schiffers et al. 2011). In heterogeneous or stressful environments, including intra- and interspecific competition, the relative effect and importance of above- versus belowground interactions and how they control the structure and function of populations and communities are still poorly understood (Berger et al. 2008).

In view of its complexity, ecologists have intensely debated the relevance of different aspects of competition to particular theories. There is one debate on the prevalence and importance of competition along environmental gradient which is commonly mentioned as two opposite theories of competition, and is usually associated with two of its main protagonists, Grime and Tilman (for a summary, see e.g. Goldberg et al. 1999, Brooker et al. 2005). One view point suggested that plant competition is more dominant within plant systems in productive and mild environments, but the role of competition played within plant systems will decrease when productivity decreases and environmental gradient increases (Grime 1979, Huston 1979, Keddy 1989). The opposite view point is that competition is predominant within plant systems irrespective of system productivity or environmental stress, while the mechanisms by which plants compete can vary, namely, plants compete strongly for light or space in productive and mild environments, while in unproductive and harsh environments plants compete mainly for water or soil nutrients (Newman 1973, Tilman 1982, 1987, 1988, Grubb 1985). Both points of view have been supported by empirical evidences, and were considered to be irreconcilable at their fundamental assumptions.

Grace (1991) pointed out that this debate was primarily aggravated by a failure of distinguishing between two components of competition, the

‘importance’ and ‘intensity’ of competition. The differences between those two concepts are explicitly (Welden and Slauson 1986): The intensity of competition is the absolute impact, which relates directly to the physiological aspects of individuals, but indirectly and conditionally to their fitness, as well as the dynamics of populations and the structure of communities. The importance of competition is also not necessarily correlated with the intensities of other ecological processes. In contrast, the importance of competition is its impact relative to the environmental factors that influence individual success, which relates indirectly to their physiological aspects but directly to the ecology and fitness of individuals. The importance of competition is necessarily relative to the importance of other ecological processes. Furthermore, intensity refers to the impact of present competition on individuals, whereas importance refers to the products and consequences of past competition on individuals and possibly the systems.

Although it has been argued that Tilman’s theory concerns intensity whereas Grime’s theory more emphasize importance (see e.g. Grace 1991), the concept of importance is still frequently neglected. Such widespread confusion between intensity and importance also arise within studies of plant positive interactions (Brooker et al. 2005, Brooker and Kikvidze 2008), and becomes a barrier to our understandings about the role of interactions may play in plant populations and communities.

1.1.2 *Plant facilitation*

Over the last decade or so, the role of plant positive interactions has received increasing attention and is now widely recognized in both empirical and theoretical ecology (Bertness and Callaway 1994, Brooker et al. 2008, Bronstein 2009, Maestre et al. 2009). In plant ecology, positive interactions are usually referred to as facilitation, which I define here as: the interaction between individual plants via moderation of biotic and abiotic stress,

enrichment of resource or increased access to resource, which leads to an increase in the survivorship, growth and/or reproduction of at least some of the interacting individuals involved. This definition of facilitation is complementary to the definition of competition given by Begon et al. (2005; see above).

Facilitation seems to be particularly important under harsh environmental conditions, i.e. abiotic stress. The 'stress gradient hypothesis' (SGH) proposes that competition and facilitation may act simultaneously, but the relative importance of facilitation and competition will vary inversely along gradients of physical stress. Under high stress conditions, facilitation should be dominant over competition in shaping of community structures (Bertness and Callaway 1994, Brooker et al. 2008, Maestre et al. 2009). The SGH has been supported by many studies: the interplay between facilitation and competition can drive population dynamics (Chu et al. 2008, 2009, 2010, McIntire and Fajardo 2011), community structure (Gross 2008, Xiao et al. 2009), community diversity (Cavieres and Badano 2009), ecosystem functions (Callaway et al. 2002, Kikvidze et al. 2005), and evolutionary consequences (Bronstein 2009, McIntire and Fajardo 2011). However, there are also studies which do not support SGH predictions, as facilitative effects have not been detected in some extreme stress situations (Tielbörger and Kadmon 2000, Maestre et al. 2005, 2009). The mechanistic explanations for SGH as well as facilitation are not well presented. This indicates that the conceptual framework underlying the SGH might need further refinement (Maestre et al. 2009). And in fact, whereas numerous studies exist that explore the consequences of different modes of competition, i.e. symmetric versus asymmetric competition (Schwinning and Weiner 1998, Weiner et al. 2001, Stoll and Bergius 2005, Berger et al. 2008), so far different modes of facilitation have not been well explored. Inconsistent definitions of facilitation and the lack of differentiation between the impacts of plant-plant interactions on beneficiary and benefactor individuals have recently been identified as important gaps in current research (Brooker et al. 2008, Bronstein 2009, Brooker and Callaway 2009, Pakeman et al. 2009). Refining

and clarifying the concept of facilitation is crucial for understanding how facilitation arises, persists and evolves.

1.1.3 *The interplay between negative and positive interactions*

Theoretically, there are three fundamental forms of interaction between two individuals (species): neutral (0), positive (+) and negative (-). According to different definitions, modes of facilitation can be mutualistic (+/+), commensal (+/0) or even antagonistic (+/-) among plants (Brooker et al. 2008, Bronstein 2009). If competition and facilitation occur at the same time, there are six possible combinations: -/-, 0/0, +/+, -/0, +/0 and -/+. Considering the facts that when individuals are together or apart show different modes of interaction, the possible combinations could increase to 10 (Table 1.2). However, an approach which incorporates the existing definitions of both competition and facilitation as special cases might be more useful. Thus, it is efficient to completely transfer, albeit conversely, the concept of modes of competition to the new concept of modes of facilitation (Table 1.2). This new conceptual model has three advantages: first, it is analogous, and therefore directly comparable to the widely used and important concept of symmetric and asymmetric interaction (Schwinning and Weiner 1998, Weiner et al. 2001, Stoll and Bergius 2005, Berger et al. 2008); second, it offers a quantitative and operational means of evaluating both competitive and facilitative impacts; and last, it can help us to integrate the facilitation with competition theories (Callaway et al. 2002, Berger et al. 2008, Brooker et al. 2008, Bronstein 2009, Maestre et al. 2009).

Table 1.2 Modes of interactions among two individuals (or species) (A and B). Defined according to the effect of this interaction for each organism (positive +, negative –, or no effect 0). A: asymmetric; S: symmetric; C: competition; F: facilitation.

Forms of interaction	Together		Apart		Possible combinations of the modes of interaction
	A	B	A	B	
Neutralism	0	0	0	0	Neutrality or SC + SF
Competition	–	–	0	0	SC
Amensalism	0	–	0	0	AC
Parasitism	+	–	–	0	AC + AF
Commensalism	+	0	–	0	AF
Mutualism	+	+	–	–	SF
Unnamed	+	+	0	–	SF or AF
Proto-cooperation	+	+	0	0	SF
Unnamed	+	–	0	0	AC + AF
Unnamed	+	0	0	0	AF

1.2 Ecology, individual-based models and pattern-oriented modelling

A main goal of ecology as a science is to understand the interactions of organisms among themselves and their environment. Individual-based models (IBMs, or also known as agent-based models ABMs in social science) are thus a natural tool for ecology because IBMs are capable of taking into account local interactions, individual variability, adaptive behaviour, environmental heterogeneous, abiotic stress, disturbance and other ecological factors (DeAngelis and Gross 1992, Grimm 1999, Grimm and Railsback 2005, Grimm et al. 2005, Berger et al. 2008).

A model is a simplified version of the real world only dealing with a limited number of factors which are considered most relevant. Ecological models attempt to capture the essences of ecological system for addressing specific questions about the given system (Grimm and Railsback 2005). The systems of interest in ecology are usually made up of myriad interacting organisms. Organisms are so different from each other, interacting with others and physical environment in their unique ways. Grimm and Railsback (2005) argued that ecology and biology are still lacking in strong mathematical tools to understand and predict such individual-based complex systems.

With the development of computer science, bottom-up simulation modelling approaches have been developed a lot in ecology. Using bottom-up approaches, ecologists compile relevant information at a lower level of the system, formulate and implement rules about individual's behaviour in a computer simulation, and then observe and understand the emergence of properties related to particular questions at a higher level of integration (Grimm et al. 2005). In particular, individual-based modelling follows the bottom-up framework and helped in understanding emergent properties of complex systems such as population dynamics or community assembly out of the ecological traits, behaviours and interactions of individual organisms

(DeAngelis and Gross 1992, Breckling et al. 2005, Grimm and Railsback 2005).

In plant ecology, individual-based approaches are widely used for modelling plant interactions (Czárán 1997, Berger et al. 2008). In a recent review, Berger et al. (2008) comprehensively compared different approaches. Based on Berger et al.'s classification, there are three important approaches which I think are most advisable: cellular automaton (CA, or the so called grid-based models), zone-of-influence (ZOI), and field-of-neighbourhood (FON) (Berger and Hildenbrandt 2000, 2003, Berger et al. 2004). These approaches, from simple to more sophisticated, have their advantages and limitations and should be applied to different research questions accordingly (see Berger et al. 2008 for details). However, existing modelling approaches for investigating plant interactions show three major gaps. New approaches are needed that: (i) help understanding the mechanisms of plants' development and response to their local environment, (ii) consider plants' adaptations to changing environmental conditions, and (iii) simultaneously consider positive and negative interactions among neighbouring plants as well as above- and belowground interactions.

Modelers greatly rely on the principle of parsimony in developing models, known as the 'Occam's razor'. However, the Occam's razor should be use appropriately in individual-based modelling, because the relationship between a model's complexity and payoff is no longer monotonically negative (as assumed for classical models), but really a hump-shape (Fig 1.1). John Holland (1995) had formulated this as "Model building is the art of selecting those aspects of a process that are relevant to the question being asked". His interpretation not only highlights the principle of parsimony, but also highlights that the question being asked is the element of the scientific problem that should be referenced to determine the components of a model.

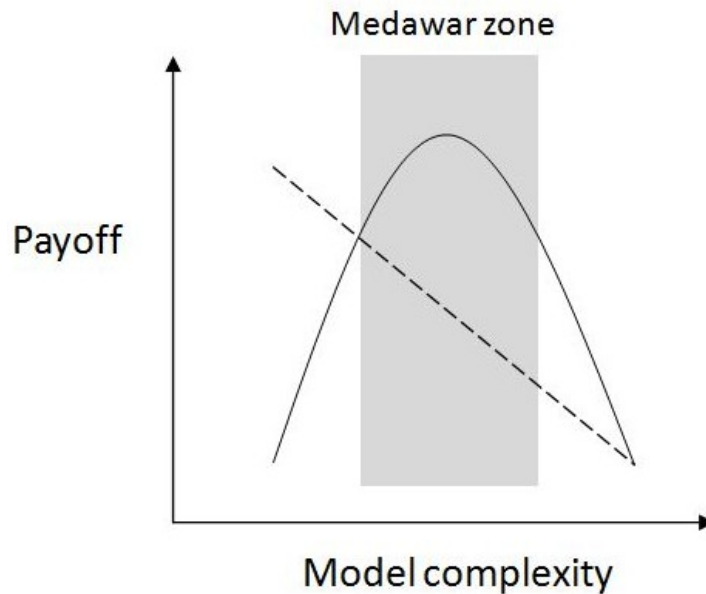


Fig. 1.1 A model's payoff (in terms of how much we can learn from it) versus its complexity (after Grimm and Railsback 2005). In contrast to analytical models of classical theoretical ecology (dashed line), where payoff is high only for very simple models and then declines continuously with complexity, IBMs and other bottom-up simulation models (humped curve) have a “Medawar zone” at intermediate complexity where payoff is maximized.

IBMs should be neither too simple nor too complex if they are to be useful (Grimm and Railsback 2005). To make the bottom-up modelling and individual-based modelling more rigorous and comprehensive, a strategy named pattern oriented modelling (POM) was developed (Grimm et al. 1996, 2005, Wiegand et al. 2003, Grimm and Railsback 2005). Because patterns are the observations of any kind showing specialized, sustained, repeated and nonrandom characteristics of the system, which contain information on the mechanisms how they emerge from lower level and the essential structures and processes, therefore could be used to guide model design (Grimm et al. 1996, 2005, Wiegand et al. 2003, Grimm and Railsback 2005).

The protocol of POM includes four steps (Wiegand et al. 2003, Grimm and Railsback 2005, Piou 2007): (1) “aggregation of individual based biological information” for model construction, (2) “determination of parameter values”, (3)

“systematic comparison between the observed pattern and the simulated pattern produced by the model” for model evaluation, and (4) “secondary predictions”. The steps (1) and (2) ensure that properties or patterns at higher levels emerge from lower-level information incorporated in IBMs. The steps (3) and (4) leading to the increase in reliability of the IBMs. In this sense, POM is useful not just for individual-based modelling, but for any kind of modelling. In addition, POM can also be used to test and refine theory, and can help to advance a synthesis of diverse theories across scales (Fig 1.2).

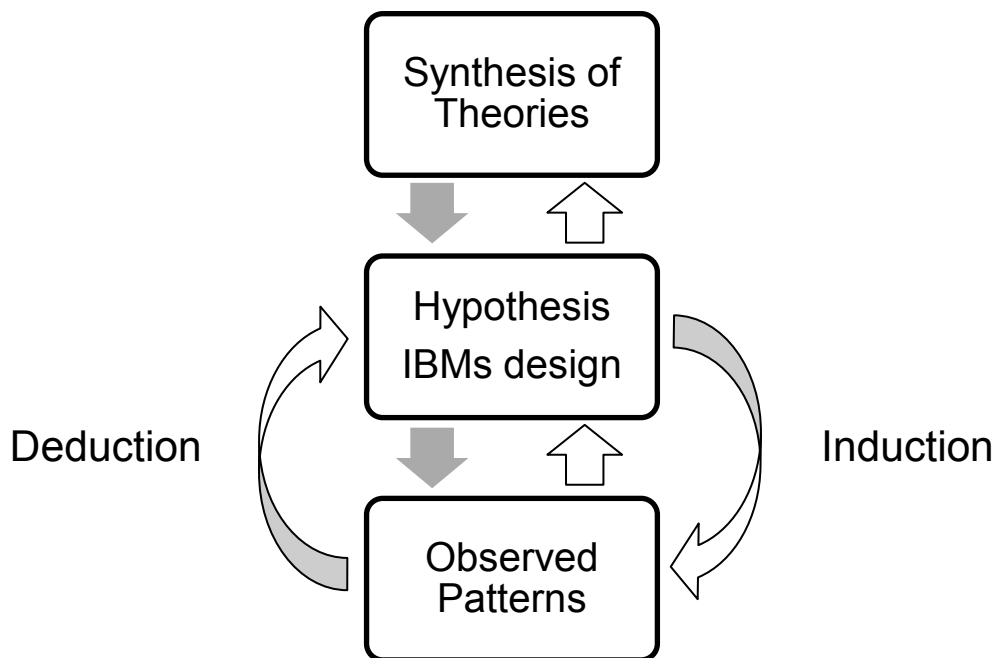


Fig. 1.2 Synthesis of theories based on pattern oriented modelling approach.

1.3 Are there universal laws or unified theories in ecology?

More than a decade ago, John Lawton (1999) wrote that, “Parts of science, areas of physics for instance, have deep universal laws, and ecology is deeply envious because it does not”. This kind of discontent is perhaps driven by a fact that use of the laws and models in ecology are usually very local and highly contingent, and the system studied in ecology are too complex and contingent to apply the general laws and models.

However, this pessimism regarding a theoretical foundation of ecology represents a misplaced ‘physical envy’ (Cohen 1971). It is misplaced on at least two aspects: first, in ecology, the building blocks of systems are living organisms not particles (Grimm and Railsback 2005). Open a bottle of perfume in a closed room, the liquid of perfume will become a smelly cloud and fills up the room eventually, which is state by the second law of thermodynamics. However, organisms try their best to avoid this smelly cloud of equilibrium, they can reproduce, interacting with others and environment, seeking fitness, acquiring resources to maintain internal order and build complexity by exporting entropy. Erwin Schrödinger (1944) also pondered these questions and described the negative entropy among organisms: “The essential thing in metabolism is that the organism succeeds in freeing itself from all the entropy it cannot help producing while alive”. It is metabolism that makes living organisms to be unique creatures. Second, the laws of physics are all ‘ceteris paribus’ laws assumed in ideal vacuums, but the actual governance of, for instance, particle movement is much more complicated than these general laws would imply (Cartwright 1983, Simberloff 2004). Therefore, ecology cannot and should not just try and copy physics.

Over the last decade, several new theories emerged which address the core principles of ecology, such as Metabolic scaling theory (Brown et al. 2004), Neutral theory in ecology (Hubbell 2001), Ecological stoichiometry (Sterner and Elser 2002), Maximum entropy of ecology (Harte 2011), Dynamic

energy budget theory (Kooijman 2009), etc., all having their advantages and shortages but claiming to be the 'general', 'universal' or 'unified' theory. There are two striking theories (Gaston and Chown 2005), which attract me most among all those theories. The first one is Metabolic Scaling Theory (MST) (also named as Metabolic theory of ecology, Brown et al. 2004), which is an attempt to link physiological processes of individual organisms with macroecology. Based on a fractal model of circulatory networks, such as the vascular system in animals and plants, MST predicts how metabolic rate increases with body size and temperature following a quarter-power scaling law. This simple scaling law has been observed from intracellular levels to individual levels of mammals, covering 27 orders of magnitude (West and Brown 2005), this even more than the span between earth and whole galaxy (18 orders of magnitude). Consequently, a large numbers of studies have explored the ecological consequences of scaling relationships between organism body size and developmental time, reproduction, population energy use, abundance, population demographic rate, community structure and species diversity. Many of these studies were published in high-profile journals which reflect the promise and potential significance of such a general theory.

However, like any other claim for a 'universal' theory, MST has also generated controversy. For instance, MST predicts a ' $-4/3$ universal scaling law' for plant mean mass-density relationships (Enquist et al. 1998), but empirical observations are more variable. Empirical evidences from harsh areas or from plantation experiments with low resource levels often deviate from these predictions and show significantly less negative exponents, i.e. shallower slopes of the self-thinning trajectory or log mass-log density relationship, respectively (Morris 2003, Deng et al. 2006, Liu et al. 2006). Consequently, both the validity and universality of scaling exponents and MST are still unclear and require further analyses of the underlying mechanisms (Coomes 2006, Deng et al. 2006, Coomes et al. 2011).

A core assumption of MST is that the processes internal to individuals determine mass-density relationships, whereas interactions among individuals are largely ignored. Therefore, population dynamic and community assembly in MST are just a spatial packing process (Reynolds and Ford 2005). An alternative view is that internal mechanism may play an important role and set limits on mass-density relationships, but that ecological interactions can be more important in determining the relationships in the field. Thus, variation in the ecological conditions and the interactions among individuals can explain the observed variation in scaling exponents. Specifically, it has been argued that competition among plants will change mass-density relationships from those predicted by MST (Coomes et al. 2011).

The second significant theory recently development in ecology is the Unified Neutral Theory of biodiversity and biogeography (UNT) (Hubbell 2001). UNT is based on a seemingly unrealistic assumption of ecological equivalence, that all individuals are functionally equivalent on a per capita basis, i.e. with respect to their birth, death, dispersal and speciation. Even so, it successfully explains many patterns about the relative species abundance across different communities (Hubbell 2001, Chave 2004, Gaston and Chown 2005). UNT emphasizes ecological drift, dispersal and speciation as the main drivers of community assembly, thus the abundance of individuals of all species should be a 'martingale' in communities. It severely bucks the basis of ecology by leaving niche differences and, hence, selection out.

Not surprisingly, criticism in this theory has been predominantly directed at the fundamental assumption of neutrality. Hubbell (Hubbell 2001, 2005, 2006, 2008) argue that even though the equivalence assumption is not apposite, the neutral model heavily relies on the principle of parsimony and predicts real patterns in nature, therefore should not be misjudged. However, in a POM view, the neutral model is located apparently on left side of the 'Medawar zone'. It is too simple hence fails in reality and justification that species are apparently different in varied aspects, and some details on the

assumption are needed. Indeed, the neutral model stimulated ecologists to revise the equivalence assumption. Some researchers relaxed the strict neutrality assumption by considering fitness equivalence via ecological trade-offs (K. Lin et al. 2009). Their modified neutral models clearly showed that birth-death trade-offs can lead to a similar result as strict neutral model did. However, the mechanisms underlying this demographic trade-off are still unknown.

As Simon Levin (2000) laid out, “the most important challenge for ecologists remains to understand the linkages between what is going on at the level of the physiology and behaviour of individual organisms and emergent properties such as the productivity and resiliency of ecosystems”. Both MST and UNT or similar theories that are based on simple physical rules attempt to scale up from the individual to the system. Predictions made by those theories sometimes become invalid in nature because macroscopic features of the system can emerge from the large numbers of interacting individual organisms. Individual-based ecology, with IBM and POM (Grimm and Railsback 2005, Grimm et al. 2005), I believe, can help us to ultimately achieve a synthesis of theories in ecology which focus on different processes, organization levels, or scales.

1.4 Objectives and content of the dissertation

My major goal in this dissertation is to investigate the effects of different modes of interactions in driving plant population dynamics. Specifically, I explored the relative role of asymmetric- versus symmetric competition, above- versus belowground competition, and negative versus positive interactions in shaping plant population along the environmental gradients by using spatially-explicit individual-based models. The pattern-oriented modelling approach is applied in my individual-based modelling studies. Some of the model predictions are tested with greenhouse experiments and field studies. Although my studies in this dissertation are mostly on mono-population dynamics, the models and theories presented are general, so that in principle they can be extended to communities. All my studies are under a context of metabolic scaling theory (MST), because I am attempted to integrate the effects of plant interactions and environmental conditions into metabolic scaling theory, in order to reconcile metabolic scaling theory with observed variations in nature.

First of all, I derived a general ontogenetic growth model for vascular plants which is based on energy conservation and physiological process of individual plant (see Appendix A in Chapter 2). This new mechanistic model is thus different from the phenomenological growth models which are generally used in individual-based models of plant interactions. Some extensions and predictions based on the new growth model are tested by empirical data. My individual-based simulation models are developed on the basis of this general growth model.

In **Chapter 2**, I present a generic spatially-explicit individual-based model, which I named as *pi* (plant interaction) model. The *pi* model implements different modes of competition (from completely asymmetric to completely symmetric) among individual plants via their overlapping zone-of-influence (ZOI). I used the ZOI approach because it is easy to implement and to combine with metabolic scaling theory. The *pi* model was used here to

investigate the hypothesis that MST may be compatible with the observed variation in plant self-thinning trajectories if different modes of competition and different resource availabilities are considered. Specifically, two hypotheses were investigated by using a one-layer ZOI model: (1) if surviving plants are not highly affected by local interactions, then individual-level metabolic processes can predict population-level mass-density relationships; and (2) size-symmetric competition (e.g. belowground competition) will lead to shallower self-thinning trajectories.

Recent studies on plant competition and MST imply that not only plant interactions (Coomes et al. 2011, Rüger and Condit 2012) but also the plastic biomass allocation to roots or shoots of plant can affect mass-density relationship (Morris 2003, Deng et al. 2006, Zhang et al. 2011). However, the relative roles of those two factors, competition and plastic biomass allocation, are still unknown. In **Chapter 3**, both a theoretical model and an experiment are used to answer this question. Since the one-layer ρ_i model is too simple, though, to explore the relative role of plasticity of biomass allocation and below- versus aboveground competition, I developed a new two-layer model which represents both above- and belowground competition simultaneously via independent ZOIs. In the two-layer ρ_i model, plant growth and biomass allocation are represented by the growth function based on MST (Enquist 2002, Niklas 2005, Lin et al. 2012), which tries to mechanistically capture the plastic responses of plants to changing environmental conditions. In addition, a greenhouse experiment with tree seedlings is employed to evaluate the behaviour of the simulated plants related to the allocation patterns and to validate our model predictions regarding the mass-density relationship. Specifically, I focus on the following research questions: (1) how does plant phenotype plasticity (root/shoot biomass allocation in heterogeneous environments) affect emergent patterns observed at the system level (e.g., variation of plant mass-density relationship)? (2) What are the resulting effects

of above- and belowground competition modified by plants' morphological adaptations to environmental severity on population dynamics?

In **Chapter 4**, the effects of both negative and positive plant interactions on population spatial dynamics are investigated. I introduce a new concept of symmetric vs. asymmetric facilitation and present the modified *pi* model. This new model is able to simultaneously implements different modes of both facilitation and competition among individual plants. Because different modes of facilitation are considered as a continuum related to the environment, I explored this concept within the context of the stress gradient hypothesis (Bertness and Callaway 1994, Brooker et al. 2008). Specifically, I address the following questions at both the plant population and individual levels: (1) How does the interplay of different modes of competition and facilitation change spatial pattern formation during self-thinning in conspecific cohorts that initially have a random or aggregated distribution; and (2) How do combinations of modes of competition and facilitation alter the intensity of local plant interactions along a stress gradient?

In **Chapter 5**, I attempt to combine neutral theory and metabolic scaling theory. Demographic equivalence regarding birth-death trade-offs between different species is consistent with the assumption of neutral theory but allows differences between species as suggested by niche theory (Lin et al. 2009). Based on MST, I deduced an allometric scaling rule which can explain observed demographic trade-offs. In this preliminary study, I tested the validity of deduced demographic trade-off by a broad array of plant species. The ultimately aim of my study is the synthesis of existing theories to strengthen future ecology in theory and application.

The concluding **Chapter 6** offers the general discussion and outlook related to my study topics. An opinionated review about the development of theories in ecology is also presented.

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Chapter 2

Plant competition and metabolic scaling theory *

Abstract

Metabolic scaling theory (MST) is an attempt to link physiological processes of individual organisms with macroecology. It predicts a power law relationship with an exponent of $-4/3$ between mean individual biomass and density during density-dependent mortality (self-thinning). Empirical tests have produced variable results, and the validity of MST is intensely debated. MST focuses on organisms' internal physiological mechanisms but we hypothesize that ecological interactions may be more important in determining plant mass-density relationships induced by density. We employ an individual-based model of plant stand development that includes three elements: a model of individual plant growth based on MST, different modes of local competition (size-symmetric vs. -asymmetric), and different resource levels. Our model is consistent with the observed variation in the slopes of self-thinning trajectories. Slopes were significantly shallower than $-4/3$ if competition was size-symmetric. We conclude that when the size of survivors is influenced by strong ecological interactions, these can override predictions of MST, whereas

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¹ Institute of Forest Growth and Computer Science, Dresden University of Technology, P.O. 1117, 01735 Tharandt, Germany; ² Helmholtz Centre for Environmental Research – UFZ, Department of Ecological Modelling, 04318 Leipzig, Germany; ³ Institute for Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, 14469 Potsdam, Germany; ⁴ Institute of Silviculture and Forest Protection, Dresden University of Technology, 01735 Tharandt, Germany; ⁵ Department of Plant and Environmental Sciences, University of Copenhagen, DK-1958 Frederiksberg, Denmark

when surviving plants are less affected by interactions, individual-level metabolic processes can scale up to the population level. MST, like thermodynamics or biomechanics, sets limits within which organisms can live and function, but there may be stronger limits determined by ecological interactions. In such cases MST will not be predictive.

Keywords: mass-density relationships, plant competition, self-thinning, size-symmetric competition, zone-of-Influence model

2.1 Introduction

Metabolic Scaling Theory (MST) offers a quantitative framework for linking physiological processes of individual organisms with higher-level dynamics of populations and communities. It predicts that an individual's metabolic rate, B , scales with body mass, m , as $m^{3/4}$ (West et al. 1999). For plants, it is assumed that B is proportional to their rate of resource use, Q , and increases with body mass, m , as $B \propto Q \propto m^{3/4}$ (Enquist et al. 1998). When the rate of resource supply, R , per unit area is held constant, the relationship between maximum population density, N , and mean body mass is predicted to be $m \propto N^{-4/3}$. Thus, if mass-density relationships during self-thinning reflect MST, the relation between m and N is predicted to be a power law with a mass–density scaling exponent of $-4/3$.

While some empirical observations seem to be consistent with this prediction (Enquist et al. 1998, Enquist 2002), data from self-thinning populations are more variable (Morris 2003, Deng et al. 2006, Dai et al. 2009, Zhang et al. 2011). Especially the data from arid regions or areas with low resource levels often deviate from the predictions of MST and show significantly shallower trajectories, i.e. less negative exponents (Morris 2003, Deng et al. 2006). While some researchers assume that the mass–density scaling exponent is universal but disagree about the correct value, others argue that there is real biological variation in the exponent, thus questioning the generality of MST (Deng et al. 2006, Coomes and Allen 2007, Coomes et al. 2011, Rüger and Condit 2012).

A core assumption of MST is that processes internal to individuals determine mass-density relationships. An alternative view is that internal mechanism may play an important role and set limits on mass-density relationships, but that ecological interactions can be more important in determining the relationships in the field. Thus, variation in the ecological conditions can explain the observed variation in scaling exponents. Specifically, it has been argued that competition among plants will change mass-density relationships from those predicted by MST (Morris 2003, Coomes et al. 2011). The well-documented plasticity of plant form in response to competition (Weiner and Thomas 1992, Dai et al. 2009) suggests that competitive interactions could affect mass-density relationships.

Many empirical studies on plant mass-density relationships have based on data where competition for light dominates (Enquist et al. 1998, Enquist and Niklas 2001, Deng et al. 2006), but in areas where belowground resources such as nutrients and water are more limiting canopies can remain unclosed. In such areas belowground competition may affect growth and mortality much more than aboveground competition (Morris 2003, Deng et al. 2006, Allen et al. 2008).

Below- and aboveground competition are qualitatively different. Aboveground, the limiting resource, light, is directional and therefore “pre-emptable”, i.e. taller plants will have a disproportionate advantage over smaller individuals when competing for light, which has also been referred to as “size-asymmetric competition”, “dominance and suppression” or “one-sided competition” (Schwinning and Weiner 1998, Stoll et al. 2002, Berger et al. 2008). In contrast, belowground resources such as water and nutrients are not generally pre-emptable so that competing plants tend to share belowground resources in proportion to their sizes. There is much evidence that aboveground competition tends to be size-asymmetric, while belowground competition is more size-symmetric (Schwinning and Weiner 1998, Stoll et al. 2002, Berger et al. 2008). This could influence mass-density relationships.

There is evidence to support this claim. For example, for the desert shrub *Larrea tridentata*, the individuals’ allometric growth and root-shoot biomass allocation patterns are consistent with MST, but the log mass - log density relationship is shallower than predicted by MST with a substantial variation

(Allen et al. 2008). This suggests that belowground competition, which is more size-symmetric, may lead to shallower self-thinning trajectories. Results from an individual-based Zone-of-Influence plant population model indicate that the size-symmetry or asymmetry of competition will affect self-thinning trajectories (Stoll et al. 2002, Chu et al. 2010). These studies used a phenomenological model for individual plant growth (Weiner et al. 2001) that does not accommodate the physical and biological principles of MST. And indeed, the range of slopes produced by Chu *et al.*'s model (Chu et al. 2010), from -0.820 to 1.609, is larger than the range observed in the field. For example, in 1266 plots within six biomes and 17 forest types across China, the estimated log mass - log density slopes ranged from -1.103 to -1.441 (Li et al. 2006).

We hypothesize that MST may be compatible with the observed variation in self-thinning trajectories if different modes of competition and different resource availabilities are considered. We investigate two hypotheses: 1, size-symmetric competition (e.g. belowground competition) will lead to shallower self-thinning trajectories. 2, Individual-level metabolic processes can predict population-level mass-density relationships if surviving plants are not highly affected by local interactions.

To investigate our hypothesis, we modify a widely used individual-based Zone-of-Influence model of individual growth and competition, in which competition can be size-symmetric or -asymmetric (Weiner et al. 2001). To make our model compatible with the assumptions of MST, we use an individual growth model and allometric relationships derived from MST (Appendix A, Lin et al. 2012).

2.2 Methods

2.2.1 *The model*

The individual plant growth model used here is consistent with MST (see Appendix A for details, Lin et al. 2012), which was based on an energy conservation equation (Enquist and Niklas 2001, West et al. 2001, Hou et al. 2008). It takes into consideration three basic processes that require energy: maintenance of biomass, ion transport and biosynthesis (Lambers et al. 2008).

Using empirical measurements and theoretical assumptions, MST predicts quantitative relationships among these processes (Enquist 2002, Enquist et al. 2009), and we use these as the basis of our individual growth model for plants:

$$dm/dt = am^{3/4} - bm = am^{3/4} [1 - (m / M_0)^{1/4}] \quad (2-1)$$

where m is the plant's total biomass and a and b species-specific constants (Appendix A). Our derivation of this model is similar to the derivation of growth models for animals (West et al. 2001, Hou et al. 2008). The value of $M_0 = (a/b)^4$ is the asymptotic maximum body mass of plant (calculated for $dm/dt = 0$), which depends on species-specific traits and is determined by the systematic variation of the *in vivo* metabolic rate within different taxa (West et al. 2001). The gain term ($am^{3/4}$) in equation (2-1) dominates early in plant growth, and has some empirical support (Brown et al. 2004, Enquist et al. 2009). Equation (2-1) is similar to the “von Bertalanffy growth model”, but its derivation here is based on physical and biological principles of MST (West et al. 2001, Hou et al. 2008).

In our spatially explicit, individual-based model [17], plants are modelled as circles growing in 2-dimensional space (Weiner et al. 2001). The area of the circle, A , represents the resources available to the plant, and this area is allometrically related to the plant's body mass, m , as $m^{3/4} = c_0 A$ (Enquist and Niklas 2001), where c_0 is a normalization constant. Plants compete for resources in areas in which they overlap, and the mode of competition is reflected in the rules for dividing up the overlapping areas. Resource competition is incorporated by using a dimensionless competition index, f_p , which value is determined by the overlap with neighbors (can be reduced from 1 to 0). With these assumptions, equation (2-1) becomes:

$$dm/dt = f_p f_r am^{3/4} - bm = f_p f_r cA [1 - (m / M)^{1/4}] \quad (2-2)$$

where $M = (f_p f_r)^4 M_0$ represents maximum achievable biomass under resource limitation and competition, and where $c = ac_0$ is the initial growth rates in units of mass per area and time interval. We represent resource limitation with a dimensionless efficiency factor, f_r , as different levels of resource availability. For simplicity, we use a linear form here, i.e. $f_r = 1 - RL$, where RL indicates the level of resource limitation, and ranges from 0 (no resource limitation) to 1

(maximum resource limitation; Table A1). The mode of resource-mediated competition among plants can be defined anywhere along a continuum from completely size-asymmetric competition (all the contested resources are obtained by largest plants) to completely symmetric competition (resources in areas of overlap are divided equally among all overlapping individuals, independent of their relative sizes) (Schwinning and Weiner 1998). To represent the different modes of competition explicitly, we define the effect of competition, f_p , as

$$f_p = (A_{no} + \sum_{k=1}^{n_o} A_{o,k} \frac{m_i^p}{\sum_{j=1}^{n_j} m_j^p}) / A \quad (2-3)$$

This index refers to the fraction of resources available in the ZOI which the plant i could obtain after a loss of potential resources due to areas overlapped by n_j individuals of sizes m_j (Schwinning and Weiner 1998). A_{no} is the area not overlapping with any neighbors, and $A_{o,k}$ indicates the area overlapped by neighbors. Parameter p determines the mode of competition, ranging from complete symmetry ($p = 0$) to complete asymmetry ($p = \infty$).

In MST, individuals' mortality rate is assumed to be proportional to their mass-specific metabolism (Brown et al. 2004). Based on this, we assume that individuals die if their actual growth rate (realistic metabolic rate) falls below a threshold fraction of their basal metabolic rate (scaled by current biomass, i.e. 2% of $m^{3/4}$). Therefore, individual plants may die due to metabolic inactivation driven by resource limitation, competition, senescence (when m approaches M) or combinations thereof. The model follows ODD protocol (Overview, Design concepts, Details) for describing individual- and agent-based models (Grimm et al. 2006, 2010) (Appendix A) and implemented in NetLogo 3.1.4 (Wilensky 1999).

2.2.2 Simulations and Analysis

In our simulations, we investigated 4 resource limitation levels (RL equal to 0, 0.1, 0.5 and 0.9), 4 modes of competition ($p=\infty$: completely asymmetric; $p=10$: highly size-asymmetric; $p=1$: perfectly size-symmetric; $p=0$: completely symmetric) and one initial density (8100 individuals per total area). We also investigated other initial densities and the results were very similar to those

presented below. Simulations for the resulting 16 scenarios were repeated five times using different random initializations.

We used the relative interaction index RII (Armas et al. 2004) to evaluate the effects of local competition on shaping plant mass-density relationship:

$$RII = (m_x - m_{nc}) / (m_x + m_{nc}) \quad (2-4)$$

where m_x and m_{nc} are the performance (mean biomass) of surviving plants at the same resource level with and without local competition (i.e., isolated plants), respectively. Values of RII from -1 to 1 indicate the intensity of interactions as competition (from -1 to 0), neutral interaction (equal to 0) and facilitation (from 0 to 1). To estimate m_{nc} , we use the growth equation (2-2) without the competitive factor f_p .

For linear fits of the self-thinning trajectories obtained with our model, we selected data points on the basis of mortality (Westoby 1984): After density-dependent mortality starts, data points with surviving plants no less than 10% of the initial density (not less than 800 surviving plants here) and with the relative mortality larger than a threshold (the mean value of relative mortality at each time step through self-thinning process) were selected to fit the self-thinning trajectories. The thinning trajectories (log-log transformed data of mean biomass vs. density of survivors) were fitted by reduced major axis (type II model) regression, which assumes error in both variables and is widely used to investigate mass-density relationships. All statistical analyses were conducted using R 2.11.1.

2.3 Results

Variation in the mode of competition, the level of resource limitation and their interaction produced significant variation in the self-thinning trajectory (Fig. 2.1, Table S1). The mode of competition had a greater effect on the slope of self-thinning trajectories than did the level of resource limitation. For given resource limitation, RL , symmetric competition made self-thinning trajectories significantly shallower (ninety-five percent confidence intervals for the four

modes of competition did not overlap), but within same mode of competition the level of resource limitation did not change slopes much (Fig. 2.2).

In scenarios with more symmetric competition, the relative interaction index RII is close to -1 and thus the effect of competition on surviving individuals is quite strong (Fig. 2.3). In contrast, in scenarios with more asymmetric competition, surviving plants are less affected by interactions with other plants (RII close to 0). The growth curves of plants also showed same results (Fig. 2.4). Both resource limitation and asymmetric competition lowered the position of self-thinning trajectories: less biomass can be accumulated at a given density under resource limitation or with more asymmetric competition (Fig. 2.1). Resource limitation decreased intercepts within the same mode of competition (Fig. 2.2), which means that the maximum biomass of plants is smaller in harsh conditions.

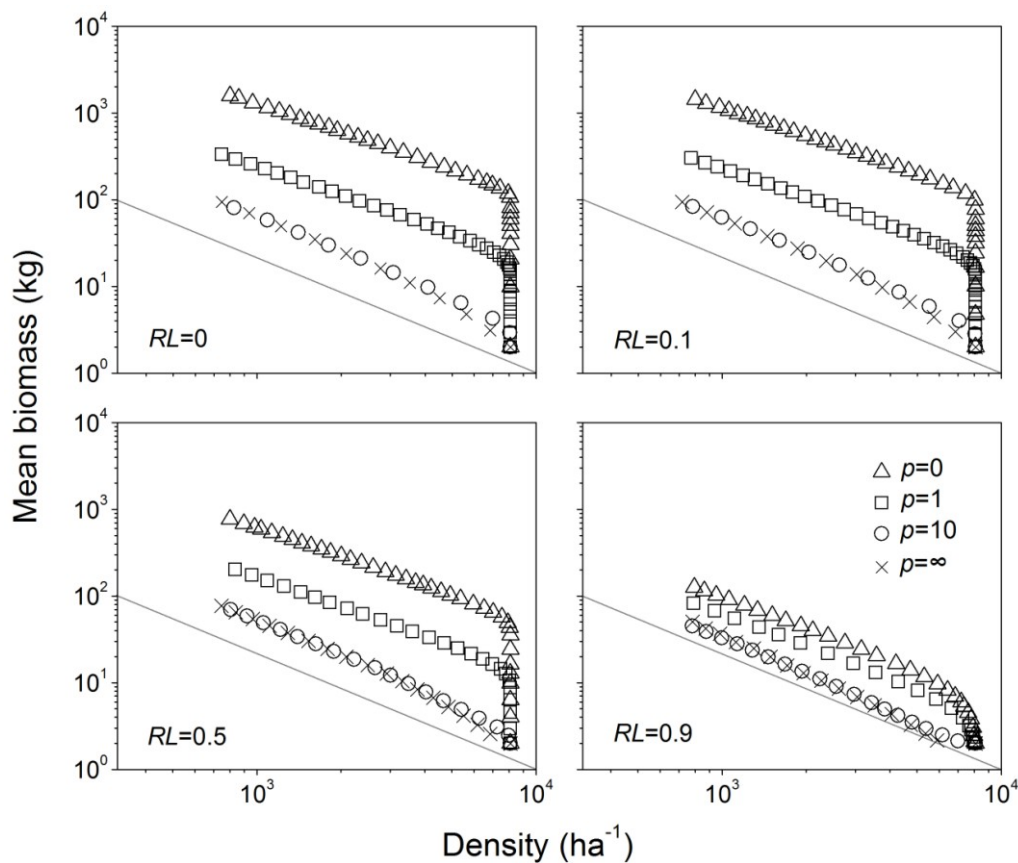


Fig. 2.1 Self-thinning trajectories for different levels of resource limitation and modes of competition. RL indicates the level of resource limitation (from 0 to 1 indicating no limitation to extreme limitation), p indicates the modes of competition (∞ : completely asymmetric; 10: highly size-asymmetric; 1: perfectly size-symmetric; 0: completely symmetric). For comparison, the solid lines in figures have same intercepts and with slopes equal to $-4/3$.

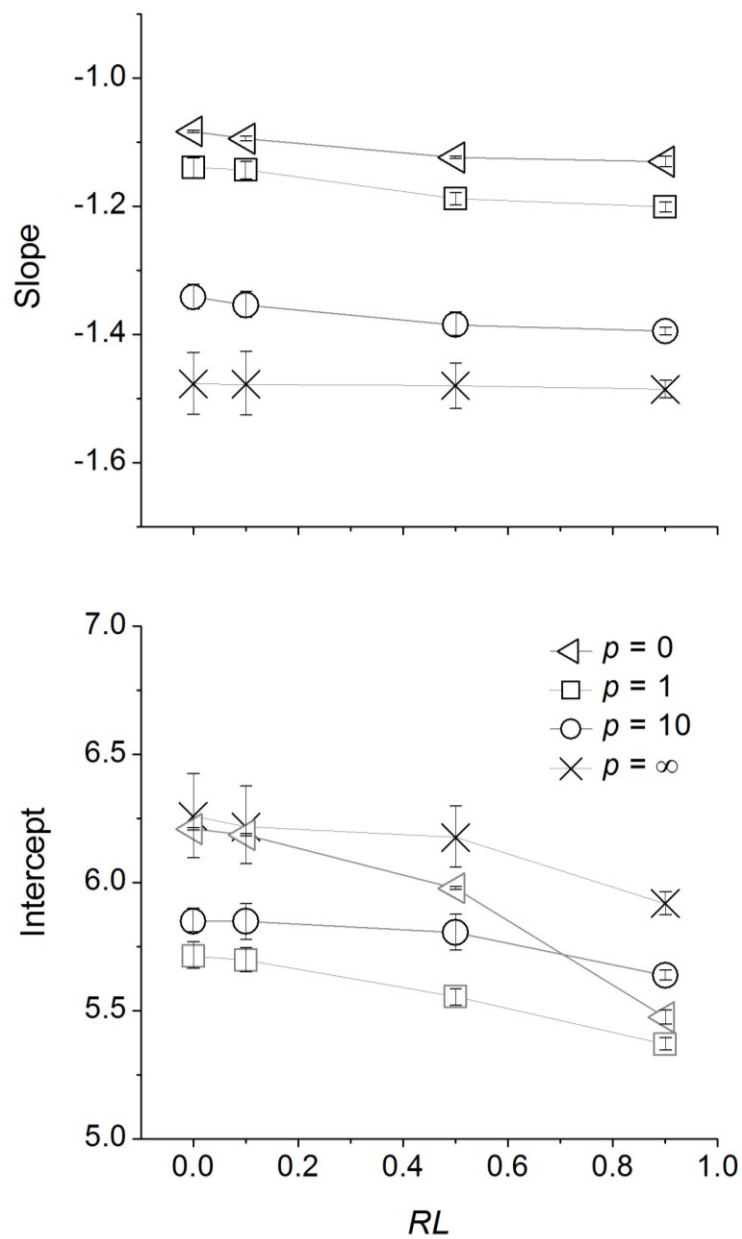


Fig. 2.2 Slopes and intercepts of self-thinning trajectories of mean individual biomass versus survivor density under different levels of resource limitation and modes of competition. *RL* indicates the level of resource limitation (from 0 to 1 indicating no limitation to extreme limitation), *p* indicates the modes of competition (∞ : completely asymmetric; 10: highly size-asymmetric; 1: perfectly size-symmetric; 0: completely symmetric). Bars indicate 95% confidence intervals.

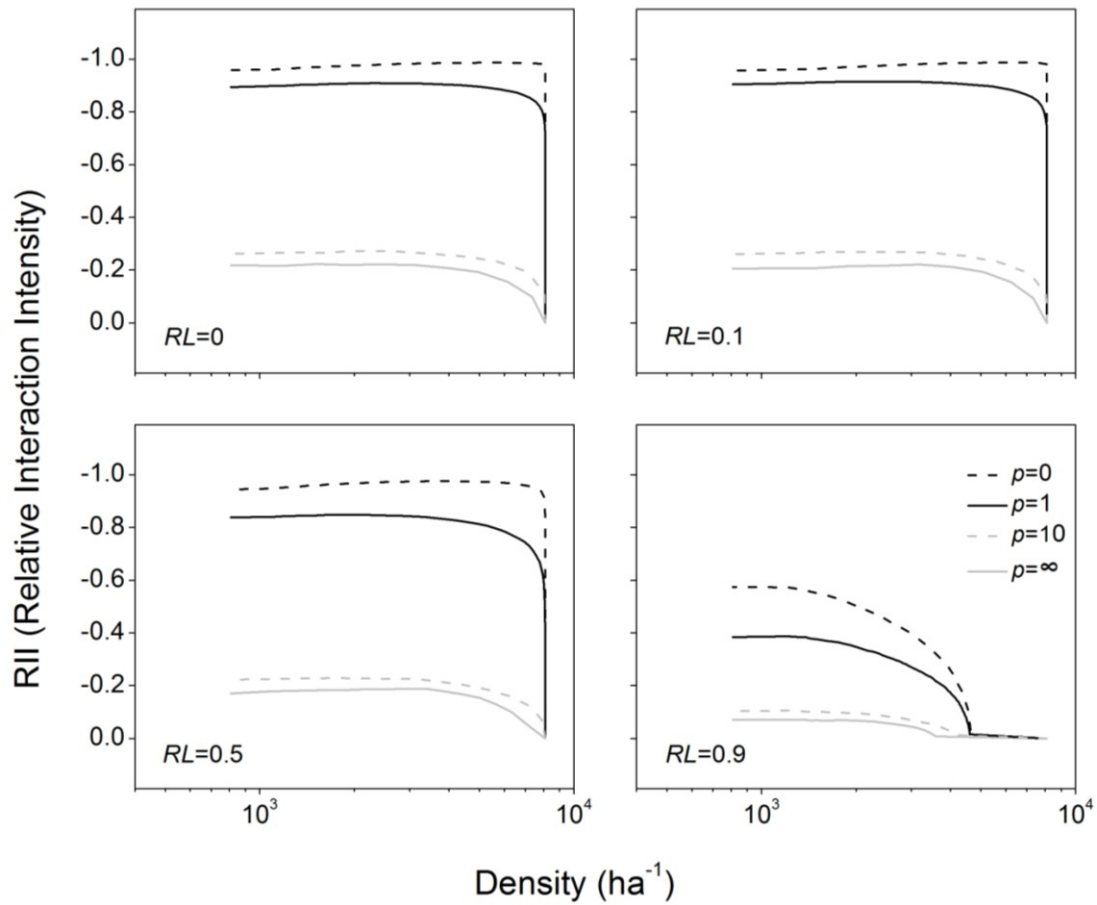


Fig. 2.3 Relationship between relative interaction intensity (RII) and density of surviving plants at different levels of resource limitation and modes of competition. RL indicates the level of resource limitation (from 0 to 1 indicating no limitation to extreme limitation), p indicates the modes of competition (0: completely symmetric; 1: perfectly size-symmetric; 10: highly size-asymmetric; ∞ : completely asymmetric). Values of RII indicate the intensity of interactions as competition (from -1 to 0), neutral interaction (equal to 0) and facilitation (from 0 to 1).

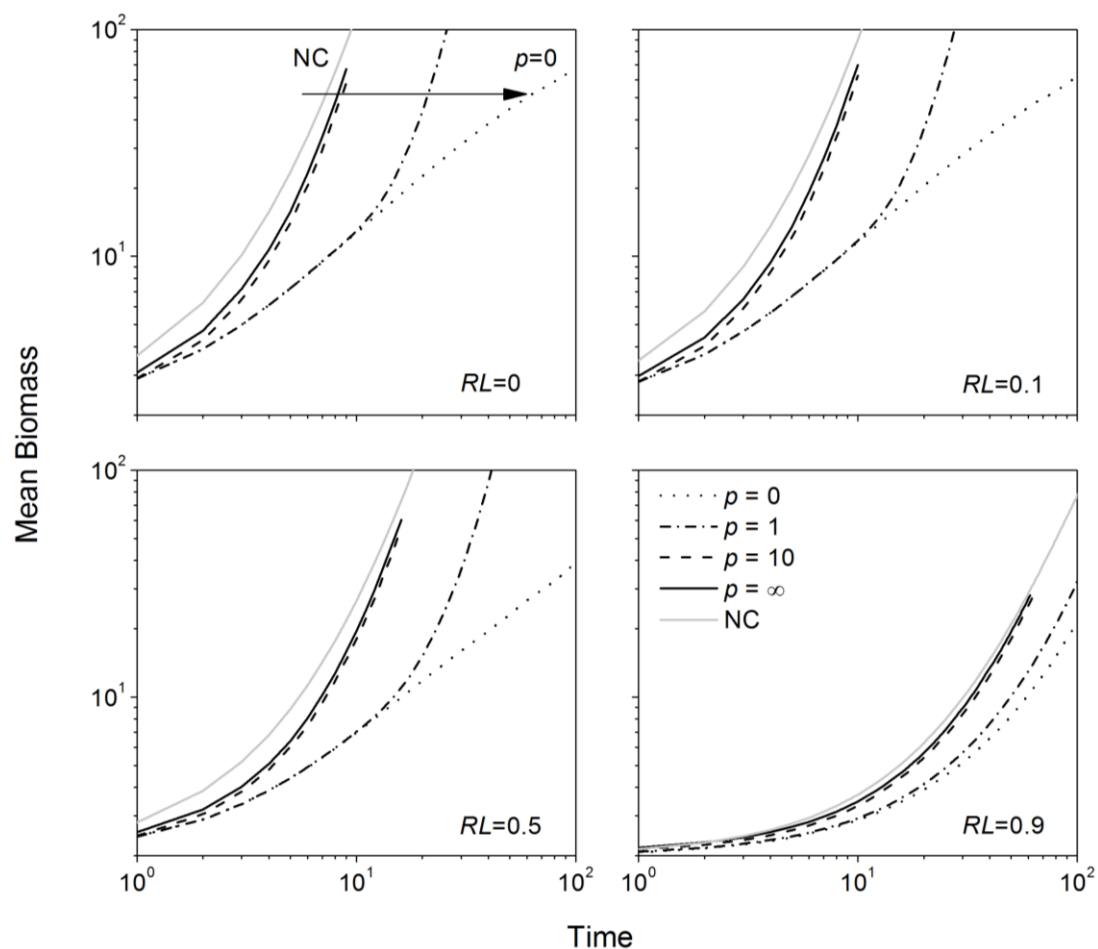


Fig. 2.4 Growth curves of surviving plants at different levels of resource limitation and modes of competition. *RL* indicates the level of resource limitation (from 0 to 1 indicating no limitation to extreme limitation), *p* indicates the modes of competition (0: completely symmetric; 1: perfectly size-symmetric; 10: highly size-asymmetric; ∞ : completely asymmetric; NC: isolated growth without competition). Values of *RL* indicate the intensity of interactions as competition (from -1 to 0), neutral interaction (equal to 0) and facilitation (from 0 to 1).

2.4 Discussion

Our results and those of previous studies (Stoll et al. 2002, Chu et al. 2010) are consistent with our first hypothesis that symmetric competition can lead to shallower self-thinning trajectories than asymmetric competition. This suggests that deviations from the slope predicted by MST are likely to occur when competition below ground is stronger than above ground because the former is size-symmetric (Weiner et al. 1997, Schwinning and Weiner 1998). Indeed, several empirical studies show that slopes of self-thinning trajectories are significantly flatter under severe water stress (Deng et al. 2006) and low nutrient levels (Morris 2003), conditions in which competition below ground is thought to be more important than above ground (Schwinning and Weiner 1998, Deng et al. 2006, Berger et al. 2008). Furthermore, boreal coniferous forests tend to have steeper slopes than deciduous broadleaved forests because the canopy of conifers is denser (with lower light transmittance) suggesting that asymmetric competition for light is more intense (Westoby 1984, Stoll et al. 2002, Li et al. 2006).

Why does symmetric competition lead to flatter trajectories in our model even though it makes surviving plants larger on average at a given density (Fig. 2.1)? With symmetric competition, the growth of all individuals is significantly reduced but the onset of mortality is delayed (Weiner et al. 2001 p. 20). Plants can survive and grow even at relatively high densities, meaning that more biomass can be maintained at a given density when competition is size-symmetric (Stoll et al. 2002).

When competition is highly size asymmetric, surviving plants are less affected by their neighbors and thus individual-level metabolic processes of MST predict plant mass-density relationship at the population level: the slope of the self-thinning trajectories are close to $-4/3$. This is consistent with our second hypothesis that MST's predictions of population-level mass-density relationships are successful when surviving plants are barely affected by local interactions. In stands of *Nothofagus solandri* (mountain beech), taller trees are relatively unhindered by competition for light and show the scaling of diameter growth which is consistent with prediction of MST, whereas small trees affected by asymmetric competition do not follow the growth trajectory of

prediction (Coomes and Allen 2007, Coomes et al. 2011). In a tropical rainforest, the trees under high-light conditions, i.e. being barely affected by neighboring trees, their diameter growth was not significantly different from the predictions of MST (Rüger and Condit 2012), which we also find in our model (Fig. S1) and support our second hypothesis.

In contrast to our findings, Coomes and coworkers concluded that deviations from predictions of MST in forests are caused by size-asymmetric competition (Coomes and Allen 2007, Coomes et al. 2011). On closer inspection, our results are not inconsistent with those of Coomes and coworkers'. Coomes's studies focused on diameter growth of individuals, including small suppressed individuals that are experiencing size-asymmetric competition for light, whereas we focus here on the mass-density relationship of populations during self-thinning, i.e. on plants surviving competition. When competition is highly size-asymmetric, total biomass is primarily due to the largest individuals, which are not highly affected by neighbors. If one looks, however, at smaller individuals suffering from asymmetric competition before they die, they will be highly affected by their larger neighbors, and this will be more important for their growth and density than the internal relationships that form the basis for MST. It would be worthwhile to analyze individual-level diameter growth in our model to compare the patterns with those from empirical studies (Coomes and Allen 2007, Coomes et al. 2011, Rüger and Condit 2012) to see if the conclusions are consistent. Nevertheless, we agree with Coomes and coworkers on the central point: interactions among individuals can overrule the predictions of MST.

Both size-asymmetric competition and resource limitation lowered self-thinning trajectories (Fig. 2.2). Resource limitation reduces the growth of individual plants, leading to smaller individuals. Size-asymmetric competition results in faster mortality. The reduction of biomass due to mortality is not immediately compensated by the growth of survivors, so there is less total biomass at a given density.

Using a similar model, Chu et al. (2010) found the same effect of the mode of competition (size symmetric vs. asymmetric) on the slope of self-thinning trajectories. The most important difference between Chu *et al.*'s model and ours is that we used an individual growth model that is derived from MST,

whereas they used the phenomenological growth equation of Weiner et al. (2001). Chu et al. (2010) focused on the effects of mode of competition, resource levels, and facilitation on self-thinning *per se*, so they do not refer to MST or focus on their choice of their individual growth model. This may be why the range of scaling exponent predicted with our model (-1.083 to -1.486) is closer to the observed range of exponents (-1.103 to -1.441 for 1266 plots of six biomes and 17 forest types across China) (Li et al. 2006) than models using phenomenological growth functions (-0.8204 to -1.6095) (Chu et al. 2010). This suggests that the consideration of both neighborhood interactions and constraints provided by MST are necessary to explain the biomass-density relationships observed in the field.

Our results point to the scope and limits of MST at the population and community level. MST applies to individual organisms, not always and necessarily to populations or ecosystems. In some cases, for example where resources are not limiting and competition is highly size-asymmetric, the mass-density scaling exponent predicted by MST matches observations very well. This is because individual acquisition of resources and accumulation of biomass is driven primarily by what the individual itself does rather than by interactions with other individuals (Fig. 2.3). On the other hand, when individual behaviour is determined more by interactions with their neighbors rather than processes that are the bases of MST, the population-level behaviour will deviate from the predictions of MST.

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Chapter 2 – Appendix A

A general ontogenetic growth model for plants

The essential basis for modelling the ontogeny of individual plants starts with an energy conservation equation (Enquist and Niklas 2001; West et al. 2001; Hou et al. 2008):

$$B_p = B_r + B_s = B_r + E_s dm/dt \quad (2-A1)$$

where B_p is defined as total energy intake rate (i.e. gross photosynthetic rate). A fraction of this assimilated energy is consumed by respiration, B_r , the remainder is stored as reserves and B_s is used for synthesizing new tissues (and for reproducing) (Figure A1). E_s is the metabolic energy stored in one unit of biomass and dm/dt is the change in biomass (m) per unit time (t).

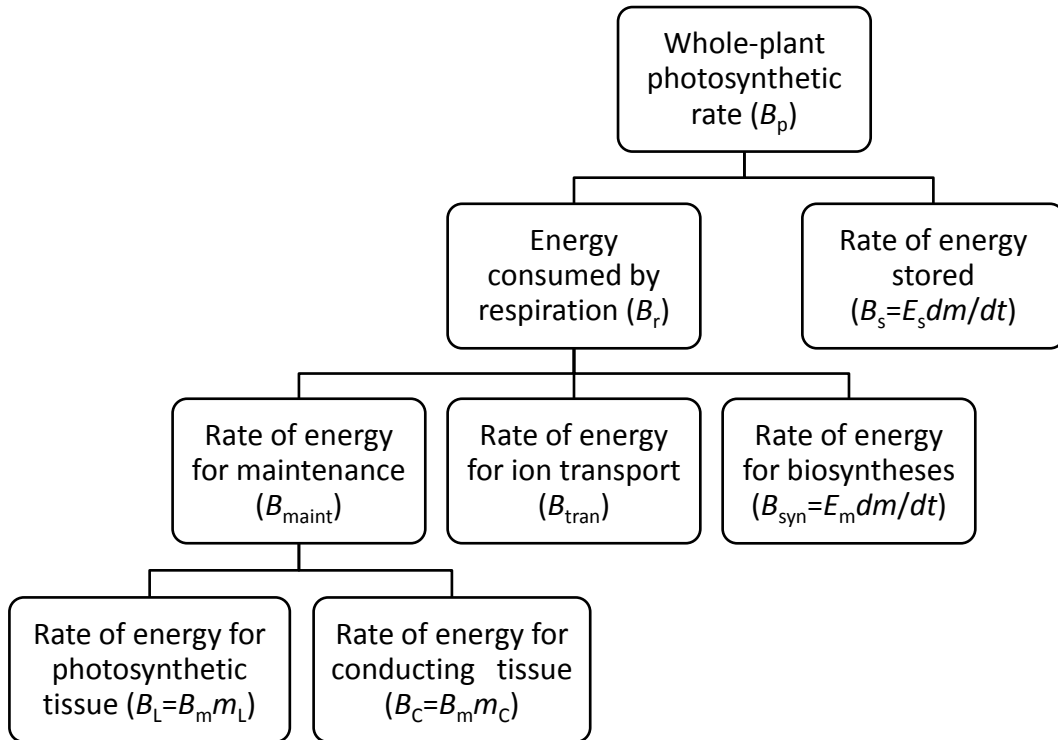


Figure A1 Assimilated energy partition of plants during ontogenetic growth.

The rate of energy consumed by respiration, B_r , depends on three major processes that require energy (Figure A1): maintenance of biomass (B_{maint}), ion transport (B_{tran}) and biosynthesis (B_{syn}), which can be summarized as (Lambers et al. 2008):

$$B_r = B_{maint} + B_{tran} + B_{syn} = \sum B_m m_{living} + B_{tran} + E_c dm/dt \quad (2-A2)$$

where B_m denotes average mass-specific maintenance metabolic rate, m_{living} stands for the biomass of living tissues, and E_c designates the energy required to synthesize a unit of biomass.

Typical average biological parameters of plant cells (tissue) are taken as a fundamental unit here, and possible differences between tissues are ignored (West et al. 2001). Note that the terms $B_s = E_s dm/dt$ in Eqn (2-A1) and $B_{\text{syn}} = E_c dm/dt$ in Eqn (2-A2) are quite different: S stands for the rate of cumulative energy content of new biomass, whereas B_{syn} refers to the metabolic energy expended on biosynthesis which is dissipated as heat instead of obtained as stored biomass (Hou et al. 2008). Combining Eqns (2-A1) and (2-A2), we get

$$B_p = B_{\text{maint}} + B_{\text{tran}} + B_{\text{syn}} + B_s = \sum B_m m_{\text{living}} + B_{\text{tran}} + E_0 dm/dt \quad (2-A3)$$

where $E_0 = E_c + E_s$, is constant for a given taxon and stands for the sum of energy stored in a unit of biomass plus the energy used to synthesize this biomass, i.e. the synthesis costs of a unit of biomass.

Equation (2-A3) is quite general, but B_{maint} may vary between woody and non-woody plants, as woody plants contain nonliving tissues (e.g. heartwood in stem and root) which do not need energy for their maintenance (Enquist et al. 2009). Also large trees with a large amount of heartwood, contain much less living tissues (m_{living}) in comparison to the total biomass (m). We assume that during ontogeny, woody plants mainly expend energy for maintaining their photosynthetic tissues (leaves), m_L , and conducting tissues (standing sapwood of stem and root), m_C , and suppose

$$B_{\text{maint}} = \sum B_m m_{\text{living}} = B_m m_L + B_m m_C = B_L + B_C \quad (2-A4)$$

for woody plants, where B_L and B_C specify the metabolic rate for maintaining photosynthetic and conducting tissues, respectively (Figure A1). Combining Eqns (2-A3) and (2-A4) we can get the energy conservation equation for woody plants:

$$B_p = B_m m_L + B_m m_C + B_{\text{tran}} + E_0 dm/dt \quad (2-A5)$$

Based on empirical measurements and theoretical assumptions linking biomass and metabolism, MST (West et al. 1999; Enquist 2002; Price et al. 2007; Enquist et al. 2009; West et al. 2009) predicts that whole-plant, or gross, photosynthesis rate, B_p , and ion transport metabolic rate B_{tran} allometrically scale with the total biomass of a plant, m , as $B_p \propto B_{\text{tran}} \propto m^\theta$, where $\theta \equiv 1/(2\alpha + \beta)$ and α and β representing the geometry and biomechanics of the vascular network. Their values may vary across different taxa (Price et al. 2007).

Although the Eqn (2-A5) can be easily recast by using empirical values of α and β , we use $\alpha = 1/2$ and $\beta = 1/3$ as common and idealized cases here (Price et al. 2007; West et al. 2009), so that $\theta = 3/4$. Models based on these

scaling relationships predict that the standing leaf biomass, m_L , scales with respect to total biomass as $m_L \propto m^{-3/4}$ across woody plants which was confirmed by empirical data (Sack et al. 2002; Niklas 2005).

The relationship between standing sapwood biomass (m_C) and total biomass m is largely unknown, therefore here we assume that the tissue- or species-specific wood density of conducting tissues, d_C , is constant for a given plant. Its total volume of conducting tissues, v_C , can be formulated as $v_C \propto A_S h$, where A_S is the mean cross-sectional area of sapwood and h is the height of plant. Because $A_S \propto m^{3/4}$ and $h \propto m^{1/4}$ (Enquist 2002; Savage et al. 2010), we therefore derive the allometric relationship $m_C = d_C v_C \propto A_S h \propto m^{3/4} m^{1/4} \propto m$ for woody plants. Substituting the allometric relationship on biomass for all related terms in Eqn (2-A5) gives

$$B_0 m^{3/4} = B_m a_L m^{3/4} + B_m a_S m + a_{\text{tran}} m^{3/4} + E_0 dm/dt \quad (2-A6)$$

where $B_p = B_0 m^{3/4}$ reflects the total energy intake rate (i.e. gross photosynthetic rate) under optimal situation, B_0 is constant for a given taxon (West et al. 1999), a_L , a_S and a_{tran} are normalization constants. Eqn (2-A6) can therefore be rewritten as

$$dm/dt = a_1 m^{3/4} - b_1 m = a_1 m^{3/4} [1 - (m / M_1)^{1/4}] \quad (2-A7)$$

with $a_1 = (B_0 - B_m a_L - a_{\text{tran}})/E_0$ and $b_1 = B_m a_S/E_0$. The value $M_1 = (a_1/b_1)^4$ is asymptotic maximum body size of the woody plant (calculated for $dm/dt = 0$), which depends on species-specific traits and is determined by the systematic variation of the *in vivo* metabolic rate within different taxa (West et al. 2001). The gain term ($a_1 m^{3/4}$) in Eqn (2-A7) dominates while plants grow to a moderate size, which has been shown to be a good quantitative description of plant growth (Niklas and Enquist 2001; Enquist et al. 2009).

Across non-woody plants which lack secondary tissues (or juveniles of woody plant which have not accumulated much secondary tissue), the total biomass of living tissues (as leaves, m_L , stem, m_S , and roots, m_R is approximately equal to the whole plant mass, $m_{\text{living}} = m_L + m_S + m_R \approx m$ (Enquist et al. 2007). Combining Eqn (2-A3) with those scaling relationship leads to

$$B_0 m^{3/4} = B_m m + a_{\text{tran}} m + E_0 dm/dt \quad (2-A8)$$

for non-woody plants.

Taking the parameters in Eqn (2-A8) in the same sense as before, Eqn (2-A8) can be re-expressed as

$$dm/dt = a_2 m^{3/4} - b_2 m = a_2 m^{3/4} [1 - (m / M_2)^{1/4}] \quad (2-A9)$$

with $a_2 = B_0/E_0$, $b_2 = (B_m + a_{\text{tran}})/E_0$, and $M_2 = (a_2/b_2)^4$, which is the asymptotic maximum body size of a non-woody plant.

Eqns (2-A7) and (2-A9) have same form, and we use a general form of the growth function for both woody and non-woody plants:

$$dm/dt = am^{3/4} - bm = am^{3/4} [1 - (m / M_0)^{1/4}] \quad (2-A10)$$

where a is a general constant and M_0 is the generally asymptotic maximum body size of plant.

Equation (2-A10) has similar form as the “von Bertalanffy growth function” (von Bertalanffy 1941, 1957) and other phenomenological logistic functions used for describing plant growth (Hunt 1982; Weiner et al. 2001; Stoll et al. 2002; Stoll and Bergius 2005; Chu et al. 2008; Chu et al. 2010). However, the ontogenetic functions derived here are based on more fundamental principles, in which all parameters determining plant growth are directly linked to physical and biological processes.

Plant growth under abiotic stress

Because ‘stress’ is not a precise concept, the characteristics of abiotic stress factors are different and can be resource-independent or dependent (Maestre et al. 2009). We assume simply that abiotic stress factors act in two ways: restricting the energy intake rate or burdening the maintenance of plant or even concurrently, this is presumably always true for plants (Lambers *et al.* 2008). Since the plant growth rate is negatively and linearly related to the degree of abiotic stress (Chu *et al.* 2008, 2010), incorporating abiotic stress in Eqn (2-A10), we have

$$dm/dt = am^{3/4} - bm - Sam^{3/4} = (1 - S)am^{3/4} [1 - (m / M_s)^{1/4}] \quad (2-A11)$$

where S is a dimensionless efficiency factor that indicates the level of stress ranges from 0 (no stress) to 1 (extreme stress), $Sam^{3/4}$ is the energy restricted or burdened by abiotic stress which is proportional to total energy intake rate and increasing with the degree of stress level, and $M_s = (1-S)^4 M_0$ is the maximum achievable biomass of plant under stress. This also implies that a plant’s final size is usually smaller than its asymptotic maximum size (optimal body size, M_0) under the environmental stress and/or resource competition, but can increase by the beneficial effects of neighbour plants via the amelioration of habitat.

Extensions and predictions based on the general growth model of plant

A general stem diameter growth model of plants

Sometimes, to get the whole biomass of plants is difficulty, especially when we are going to measure trees. It is therefore flexible to use stem diameter (D) instead of biomass (m). Since $D \propto m^{3/8}$, which is equivalent to $f(D)=dD/dm \propto m^{-5/8}$, then $dD/dt=f(D)(dm/dt)$ combine with Eqs. (2-A7), (2-A9) and (2-A10), we have

$$dD/dt = a_d D^{1/3} - b_d D^{4/3} = a_d D^{1/3} [1 - (D / D_{max})] \quad (2-A12)$$

where a_d and b_d are constants, $D_{max}=a_d/b_d$ is the asymptotic maximum stem diameter.

The sigmoid growth curve of plants

A general sigmoid growth model for plants can be obtained from integrating Equation (2-A10):

$$\begin{aligned} \left(\frac{m}{M_0} \right)^{1/4} &= 1 - \left[1 - \left(\frac{m_0}{M_0} \right)^{1/4} \right] e^{-at/4M^{1/4}} \\ \text{or } m &= \left\{ \frac{a}{b} \left[1 - \left[1 - \left(\frac{m_0}{M_0} \right)^{1/4} \right] e^{-at/4M^{1/4}} \right] \right\}^4 \end{aligned} \quad (2-A13)$$

where m_0 is the initial biomass of the plant (biomass at birth, $t=0$).

In the expression related to stem diameter,

$$\left(\frac{D}{D_{max}} \right)^{1/3} = 1 - \left[1 - \left(\frac{D_0}{D_{max}} \right)^{1/3} \right] e^{-a_d t/3D_{max}^{1/3}} \quad (2-A14)$$

where D_0 is the initial diameter of the plant ($t=0$).

Currently, we are not able to combine the data sets that are precise enough and also cover a broad plant species to test our model. However, based on a recent publishes work (Deng et al. 2012), we tested our model with three non-woody plants, the mechanistic model are proved to be reliable (Figure A2). How well of our model in capturing the fundamental features of growth in woody and non-woody plants are remains to be seen.

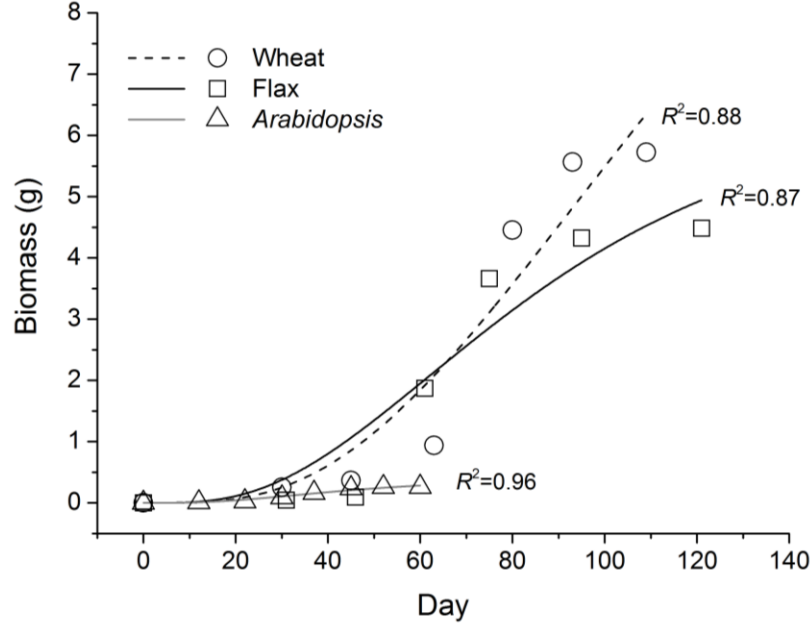


Figure A2 Growth curves for wheat, flax, and Arabidopsis. The curves are the predictions of the general growth model (Equation. 2-E2). Growth data are estimated from Deng et al. (2012).

A general model for respiratory metabolism of plant

Overall, the respiratory metabolism of plant can be generally summarized in equation (2-A2). For woody plant, because of the growth rate $dm/dt \approx a_c m^{3/4}$, where a_c is a constant, hence the respiration rate of woody plants is:

$$B_r = B_m a_L m^{3/4} + B_m a_S m + a_{\text{tran}} m^{3/4} + E_c dm/dt = a_r m^{3/4} + b_r m \quad (2-A15)$$

where $a_r = B_m a_L + a_{\text{tran}} + E_c a_c$ and $b_r = B_m a_S$.

Equation (2-A15) indicates a mixed scaling relationship of rate of energy consumed by respiration for woody and non-woody plants, i.e. the theoretical scaling exponent between whole respiration rate of plant and its whole biomass, B_r vs. m , can range from 0.75 to 1 which depends on the values of a_r and b_r , and is related to the productive biomass partitioning among different compartments (e.g. leaf, branch, stem, root, and seed reproduction). However, for woody plants with much of secondary tissues, the scaling should approach 0.75, but for non-woody plants or juveniles of woody plant which haven't accumulated much of secondary tissues, the scaling exponent between respiratory metabolism and biomass will approach to 1. These variations were perceived in empirical researches (Reich et al. 2006; Enquist et al. 2007; Mori et al. 2010; Cheng et al. 2010).

Scaling relationship between reproductive biomass and mean body mass of seed plants

Based on MST and equation (2-A10), the plant reproductive biomass should be proportional to its metabolic rate, and then we predict a simple scaling relationship between reproductive biomass ($m_{\text{rep.}}$) and plant body mass (m) as

$$m_{\text{rep.}} \propto m^{3/4} \quad (2-A16)$$

using a broad data set (Niklas and Enquist 2004) of seed plants, we proved the validity of this prediction (Figure A3).

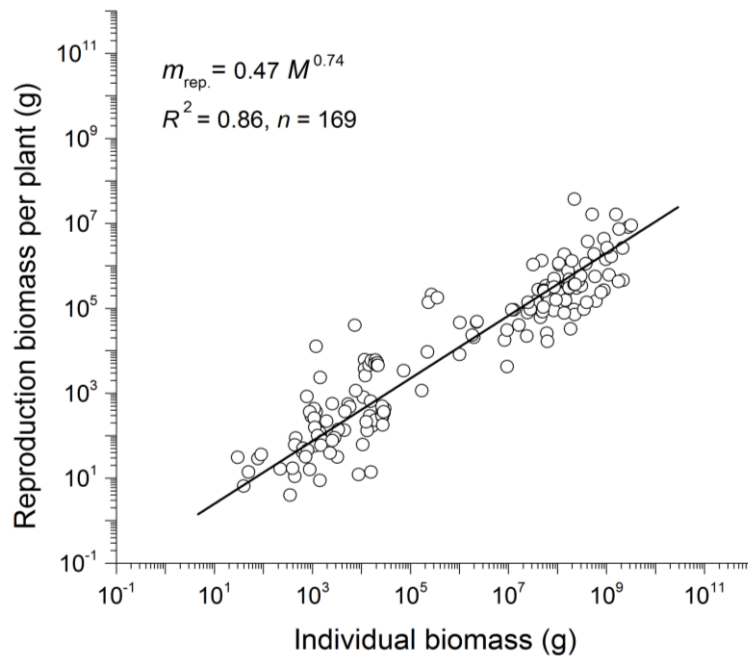


Figure A3 The scaling relationship between mean plant mass (m) and mean reproduction mass ($m_{\text{rep.}}$) across different species of seed plants. The solid line shows the fitted Reduced Major Axis (RMA, type II model) regression of equation (95% C.I. of the exponent 0.70–0.77).

ODD protocol – model description of one-layer *pi* model

The following model description follows the ODD protocol (Overview, Design concepts, Details) for describing individual- and agent-based models (Grimm *et al.* 2006; Grimm *et al.* 2010),

Purpose

The aim of this model is to evaluate the multiple effects of the mode of competition and resource limitation on regulating plant population dynamics, specifically on self-thinning trajectories and density-dependent mortality. In particular, we investigate whether interactions on individual plant level can alter the slope and intercept of the self-thinning line. The model does not represent specific species, but generic ones.

Entities, state variables, and scales

The entities in the model are plants and square habitat units, or patches (Table A1). Plants are characterized by the following state variables: initial growth rate, initial biomass, maximum biomass (asymptotic biomass), current biomass and their position, i.e. coordinates of the stem. Each individual plant has its own circular zone-of-influence (ZOI). The ZOI stands for the physical space occupied by a plant, and represents the energy and resources potentially available to this plant, which is allometrically related to its body mass. Neighboring plants only compete for the resources when their ZOIs are overlapping.

In order to make the spatial calculations of resource competition easier, ZOIs are projected onto a grid of patches. To avoid edge effects, we use a torus world with a size of 200×200 patches (Grimm & Railsback 2005). Each patch represents 0.25 m^2 or 0.25 cm^2 for woody- and non-woody plants, respectively. The state of each patch is characterized by its resource availability. We use a homogeneous environment here as all patches have the same, and constant, degree of resource limitation. One time step in the model represents approximately one year for woody plants and one day for non-woody plants.

Table A1. State variables and initialization in the individual-based model. Actual values are drawn from the given intervals to introduce a certain degree of heterogeneity among individuals.

Variable	Description	Initial Value [unit] (woody/non-woody)
Plants		
c	Initial growth rate	1 ± 0.1 [kg m ⁻² time step ⁻¹] / [mg cm ⁻² time step ⁻¹]
m_0	Initial body mass	2 ± 0.2 [kg] / [mg]
M	Maximal biomass	$2 \times 10^6 \pm 2 \times 10^5$ [kg] / [mg]
m	Current biomass	[kg] / [mg]
A	Zone of influence	[m ²] / [cm ²]
Patches		
RL	Level of resource limitation	[0, 1]
Initialization		
Mortality	Threshold of death	2% of $m^{3/4}$
Density	Number of plants	8100 ha ⁻¹ / m ⁻²

Process overview and scheduling

After initialization, all individual plants with a given density are randomly distributed in the world. The processes of resource competition, growth and mortality of each plant are fulfilled within each time step. In each step, individual plants first sense the resource qualities of patches within their ZOIs, the area (radius) of an individual plant's ZOI is determined by its current biomass. When their ZOIs are overlapping, individuals compete within the overlapping area. Thus, the overlapping area reflecting resources is divided according to the competition mode. Considering the outcome of the competition process, all individual plants grow according to the growth function. Plants with growth rates falling below a threshold die and are removed immediately. The state variables of the plants are synchronously updated within the subroutines, i.e. changes to state variables are updated only after all individuals have been processed (Grimm and Railsback 2005).

Design concepts

Basic principles: From "Metabolic Scaling Theory", we derived a general ontogenetic growth model for individual plants. We combine this model, via the ZOI approach, with the effects of different modes of competition and resource limitation.

Emergence: All features observed at the population level, e.g. mass-density relationship or self-thinning trajectories (i.e. size distribution and spatial distribution, respectively), emerge from the interaction of individual plants with their neighbors and the resource level of their abiotic environment.

Interaction: Individual plants interact via competition for resources in the overlapping area of their ZOIs.

Stochasticity: Initial growth rate, initial biomass, maximum biomass and initial position of plants are randomly taken from the intervals given in Table 1. This introduces a certain level of heterogeneity among individual characteristics to take into account that real plants are never exactly identical.

Observation: Population size, biomass of each plant, and mean biomass of all living plants are the main observations.

Initialization

Initially, individual plants are randomly distributed according to the chosen initial density. Resources are spatially and temporally constant. Each plant has an initial biomass (m_0), maximal biomass (M) and initial growth rate (c_1 or c_2) drawn from truncated normal distributions with average and intervals given in Table 1.

Input

After initialization, the model does not include any external inputs, i.e. the abiotic environment is constant.

Submodels

Plant growth

In our individual-based model the plant's ZOI stands for the physical space occupied by a plant and represents the energy and resources potentially available to this plant. This space is allometrically related to the plant's body mass, m , as $c_0 A = m^{3/4}$ (Enquist & Niklas 2001), where c_0 is a normalization constant. Accordingly, based on equation (2-A1) we have:

$$dm/dt = cA[1 - (m / M_0)^{1/4}] \quad (2-M1)$$

where $c = ac_0$ is initial growth rates in units of mass per area and time interval. For simplicity, we choose 1 ± 0.1 in our model. We also simulate the model with different c values. As expected, the results from different values were qualitatively similar (the slopes didn't change).

Resource competition and limitation

Resource limitation and competition usually cause a reduction of resource availability for plants. We therefore represent resource limitation via a dimensionless efficiency factor or index, f_R , for different levels of resource availability. Resource competition is incorporated by using a dimensionless competition factor or index, f_p , leading to

$$dm/dt = f_R f_p cA[1 - (m / M)^{1/4}] \quad (2-M2)$$

where $M = (f_R f_p)^4 M_0$, the maximum body size with resource limitation and competition.

The efficiency factor f_R , can take different forms depending on the characteristics and level of the limiting resource. For simplification, we use a linear form here, i.e. $f_R = 1 - RL$, where RL indicates the level of resource limitation, with its value ranging from 0 (no resource limitation) to 1 (maximum resource limitation; Table A1).

As for competition, the mode of resource-mediated competition among plants can be located somewhere along a continuum between completely asymmetric competition (largest plants obtain all the contested resources) and completely symmetric competition (resource uptake is equal for all plants, independent of their relative sizes; Schwinning & Weiner 1998). To represent different modes of competition explicitly, we describe the competitive factor f_p as

$$f_p = (A_{no} + \sum_{k=1}^{n_o} A_{o,k} \frac{m_i^p}{\sum_{j=1}^{n_j} m_j^p}) / A \quad (2-M3)$$

This factor thus refers to the percentage of realized resource plant i could uptake from the amount of resources available (the entire resource that plant could potentially occupy) among n_j competitors with sizes m_j (Schwinning & Weiner 1998). A_{no} is the area not overlapping with neighbors, $A_{o,k}$ denotes the area overlapping with neighbors. Parameter p determines the mode of competition, ranging from complete symmetry ($p = 0$) to complete asymmetry (p approaching infinity; for details and examples see Figure A4).

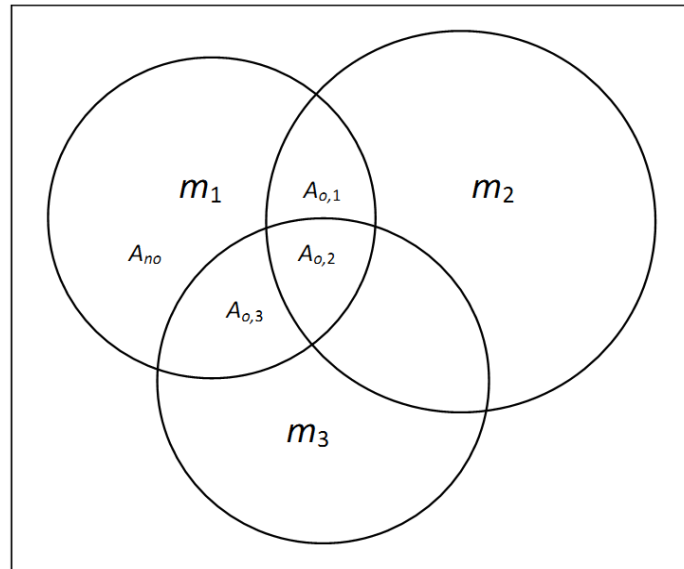


Figure A4. An example of calculating the competitive index (equation 2-M3) with different modes of resource competition in an individual-based model as a

way of dividing plants' ZOI (zone-of-influence). Three plants with sizes m_1 , m_2 and m_3 are competing in this example. For plant 1, its ZOI (A) was divided into four parts: A_{no} , the area not overlapping with the other two plants; $A_{o,1}$, the area overlapping with plant 2; $A_{o,2}$, the area overlapping with plants 2 and 3; $A_{o,3}$, the area overlapping with plant 3.

Then the actual area that plant 1 can take from $A_{o,1}$ is

$$A_{o,1} \frac{m_1^p}{\sum_{j=1}^2 m_j^p} = A_{o,1} \frac{m_1^p}{m_1^p + m_2^p}$$

For $A_{o,2}$,

$$A_{o,2} \frac{m_1^p}{\sum_{j=1}^3 m_j^p} = A_{o,2} \frac{m_1^p}{m_1^p + m_2^p + m_3^p}$$

And for $A_{o,3}$,

$$A_{o,3} \frac{m_1^p}{\sum_{j=1}^2 m_j^p} = A_{o,3} \frac{m_1^p}{m_1^p + m_3^p}$$

Therefore, the competitive index for plant 1 is:

$$f_p = \frac{A_{no} + A_{o,1} \frac{m_1^p}{m_1^p + m_2^p} + A_{o,2} \frac{m_1^p}{m_1^p + m_2^p + m_3^p} + A_{o,3} \frac{m_1^p}{m_1^p + m_3^p}}{A}$$

Where $A = m_1^{3/4} / c_0$

In total, equation (2-M2) clearly shows how a plant's growth rate is jointly determined by resource availability, f_R , and competition, f_p . This also implies that a plant's final size is usually smaller than its asymptotic maximum size (M) during resource limitation and local competition.

Mortality

An individual's mortality rate is proportional to its mass-specific metabolism (Brown *et al.* 2004). Based on this, we assume that individuals die if their actual growth rate (dm/dt) falls below a threshold of their current scaled body mass, i.e. 2% of $m^{3/4}$. Therefore, individual plants may die due to metabolic inactivation driven by resource limitation, competition, senescence (when m approaches M) or combinations thereof. This provides a more realistic representation of relevant ecological process than in previous models (Stoll *et al.* 2002; Chu *et al.* 2010).

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Slopes and intercepts of self-thinning trajectories produced by the model

Table S1. Slope and intercept (log-log transformed) of self-thinning trajectories for simulated plants under different levels of resource limitation and modes of competition*.

<i>RL</i>	<i>p</i>	Slope			Intercept			<i>R</i> ²
		Mean	95% C.I.		Mean	95% C.I.		
0	∞	-1.478	-1.525	-1.429	6.258	6.096	6.424	0.994
0	10	-1.342	-1.361	-1.322	5.848	5.808	5.898	0.999
0	1	-1.140	-1.156	-1.125	5.714	5.664	5.769	0.997
0	0	-1.083	-1.085	-1.082	6.208	6.204	6.212	0.999
0.1	∞	-1.478	-1.526	-1.427	6.217	6.074	6.377	0.994
0.1	10	-1.354	-1.374	-1.333	5.848	5.778	5.918	0.998
0.1	1	-1.144	-1.158	-1.130	5.697	5.650	5.744	0.997
0.1	0	-1.094	-1.098	-1.091	6.185	6.180	6.190	0.999
0.5	∞	-1.480	-1.516	-1.445	6.176	6.060	6.297	0.995
0.5	10	-1.385	-1.402	-1.365	5.805	5.736	5.875	0.997
0.5	1	-1.188	-1.198	-1.179	5.554	5.519	5.585	0.998
0.5	0	-1.124	-1.126	-1.122	5.978	5.972	5.984	0.999
0.9	∞	-1.486	-1.499	-1.472	5.918	5.873	5.963	0.996
0.9	10	-1.395	-1.401	-1.389	5.637	5.619	5.657	0.999
0.9	1	-1.201	-1.209	-1.194	5.370	5.345	5.395	0.998
0.9	0	-1.130	-1.139	-1.122	5.474	5.446	5.502	0.997

**RL* indicates the level of resource limitation (0–1), *p* indicates the modes of competition (with 0: completely symmetric; 1: perfectly size-symmetric; 10: highly size-asymmetric; ∞: completely asymmetric). C.I. is confidence intervals.

Chapter 3

Mechanisms mediating plant mass-density relationships: the role of biomass allocation, above- and belowground competition *

Abstract

Metabolic scaling theory (MST) predicts a ‘universal scaling law’ for plant mass-density relationships, but empirical observations are more variable. Possible explanations of this deviation include plasticity in biomass allocation between the above- and belowground compartment and the mode of competition, which can be asymmetric or symmetric. Although complex interactions of these factors are reasonable, the majority of modelling and empirical studies have been focusing on mono-factorial explanations so far. We present a generic individual-based model, which allows exploring MST predictions in realistic settings by representing plasticity of biomass allocation and different modes of competition in the above- and belowground compartment simultaneously. To evaluate the behaviour of the simulated plants related to the allocation patterns and to validate model predictions

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¹ Institute of Forest Growth and Computer Science, Dresden University of Technology, P.O. 1117, 01735 Tharandt, Germany; ² Helmholtz Centre for Environmental Research – UFZ, Department of Ecological Modelling, 04318 Leipzig, Germany; ³ Institute of Silviculture and Forest Protection, Dresden University of Technology, 01735 Tharandt, Germany; ⁴ Institute for Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, 14469 Potsdam, Germany

regarding the mass-density relationship, we conducted greenhouse experiments with tree seedlings. The simulated model well captured empirical patterns both at plant individual and population level. Without belowground resource limitation, aboveground processes dominated and the slopes of mass-density relationships followed the predictions of MST. In contrast, resource limitation resulted to an increased allocation of biomass to belowground parts of the plants. The subsequent dominance of symmetric belowground competition led to significantly shallower slopes of the mass-density relationship. We conclude that changes in biomass allocation patterns control the constraints at different levels of biological organization and explain the deviations from the mass-density relationship predicted by MST. Taking into account the plasticity of biomass allocation and its linkage to the visible aboveground competition and the invisible belowground competition is critical for fully representing many forests and eco-regions, in particular for correctly predicting the response of carbon storage and sequestration to changing environmental conditions.

Keywords: plasticity, biomass allocation, optimization theory, symmetric competition, asymmetric competition, ontogenetic growth of plant, individual-based model, allometric exponent, power law

3.1 Introduction

The relationship between plant performance and density is one of the central topics in plant ecology (Stoll et al. 2002, Deng et al. 2006, Chu et al. 2010, Weiner and Freckleton 2010). It is widely accepted that resource competition among plants is the main force in determining plant mass-density relationships induced by density-dependent mortality. In self-thinning stands of plants, the general relationship between density (N) and mean biomass (M_y) of surviving plants can be described by a power function, $M_y = kN^\gamma$, where k and γ are referred to as the thinning coefficient and exponent, respectively. Based on Euclidean geometry, it was proposed that the value of γ is approximately equal to $-3/2$, which is well-known as the “ $-3/2$ power rule” of self-thinning (Yoda et al.

1963). More recently, based on a fractal model metabolic scaling theory (MST) predicted a 'universal scaling law' with γ equal to $-4/3$ (Enquist et al. 1998, West et al. 1999, Enquist and Niklas 2001, Enquist 2002, Brown et al. 2004, Savage et al. 2010).

The exponent predicted by MST is generally confirmed in studies addressing aboveground biomass across different types of ecological communities in environments without major resource limitation or physical stress (Deng et al. 2006). However, findings from arid areas or from plantation experiments with low resource levels often deviate from these predictions and show significantly less negative exponents, i.e. shallower slopes of the self-thinning trajectory or log mass-log density relationship, respectively (Morris 2003, Deng et al. 2006, Liu et al. 2006). Consequently, both the validity and universality of scaling exponent and MST are still unclear and require further analyses of the underlying mechanisms (Coomes 2006, Deng et al. 2006, Coomes et al. 2011).

On sites where belowground resources such as nutrients and water are limited, plants tend to allocate more biomass to their belowground parts and develop extended root systems for acquiring limited resources while canopies remain unclosed (Deng et al. 2006). In such situations belowground competition is believed to affect plant growth and mortality more than aboveground competition (Deng et al. 2006, Berger et al. 2008). Nevertheless, only few studies have explored the role of belowground process for plant mass-density relationships (Morris 2003, Deng et al. 2006, Berger et al. 2008). This is because observations of the root systems are hampered by logistic difficulties (Cahill and Casper 2000, Casper et al. 2003, Berger et al. 2008, Rewald and Leuschner 2009, Schiffrers et al. 2011).

Deng et al. (2006) found that the mass-density relationship of natural vegetation was altered by changing root versus shoot biomass allocation along a precipitation gradient. The root:shoot ratio (RSR) of biomass increased with aridity but for the belowground compartment the slope of the plant mass-density trajectory was still consistent with MST predictions. In contrast, the slopes of the aboveground compartment became less negative. This study suggested that plant mass-density relationships are altered by the well-documented plasticity of biomass allocation in response to resource

limitation (McConnaughay and Coleman 1999, Weiner 2004, Deng et al. 2006, Berger et al. 2008, May et al. 2009, Schiffers et al. 2011).

Apart from this, the mode of competition (asymmetry vs. symmetry) has also been discussed to affect plant mass-density relationships (Schwinning and Weiner 1998, Stoll et al. 2002, Coomes and Allen 2009, Berger et al. 2008, Chu et al. 2010, Coomes et al. 2011). Aboveground competition for light is considered to be asymmetric, whereas belowground competition is considered to be rather symmetric (Schwinning and Weiner 1998). In various studies with belowground resource limitation, belowground competition was shown to alter the plant mass-density relationship, i.e. the exponents became less negative than predicted by MST (Morris 2003, Deng et al. 2006, Chu et al. 2010, Lin et al., *in revision*). Nevertheless, there also seem to be cases where belowground competition can be asymmetric (Fransen et al. 2001, Rajaniemi 2003, Rewald and Leuschner 2009).

Although plant ecologists agree that the biomass allocation patterns and the relative importance of above- and belowground competition change along environmental gradients (Tilman 1988, Deng et al. 2006, Berger et al. 2008), it remains unknown which factor or which combination of them dominates the alteration of the mass-density relationship in plant populations and communities.

In a previous one-layer individual-based model (IBM), which uses the zone of influence (ZOI) approach (Wyszomirski 1983, Wyszomirski et al. 1999, Weiner et al. 2001, May et al. 2009) but does not distinguish the above- and belowground compartments, we found that symmetric competition can alter the predictions of MST (Lin et al., *in revision*). This model is too simple, though, to explore the role of resource allocation and below- versus aboveground competition. Therefore, based on recent modelling studies (May et al. 2009, Lin et al., 2012, Lin et al., *in revision*), we developed a new two-layer IBM which represents both above- and belowground competition simultaneously via independent ZOIs. In the presented model, plant growth and biomass allocation are represented by the growth function based on MST (Enquist 2002, Niklas 2005, Lin et al., 2012), which tries to mechanistically capture the plastic responses of plants to changing environmental conditions.

To validate our new model, a greenhouse experiment was also employed.

We determined root and shoot biomass allocation and relative mass-density relationships of birch seedlings grown under severe root competition at different resource levels. The combination of modelling and experiment enabled us to identify the relative role of two key factors (above- vs. belowground biomass allocation and asymmetric vs. symmetric competition) and effects on plant mass-density relationships.

3.2 Methods

3.2.1. *Individual-based model*

To explicitly assess the interplay between biomass allocation patterns and the different modes of subsequent shoot competition and root competition, we extended an established one-layer zone-of-influence (ZOI) model (Lin et al. 2012, Lin et al. *in revision*) to a two-layer model, which describes the above- and belowground part of a single plant by separate ZOIs.

A detailed description of the whole model, which follows the ODD protocol (Overview, Design concepts, Details) for describing individual-based models (Grimm et al. 2006, 2010), is provided in the supplementary material (Appendix A) as well as the model implementation in NetLogo 4.1.3 (Wilensky 1999). Here, we only describe the core elements of the model.

The fundamental function representing the ontogenetic growth of an individual plant is based on MST and does not differ from the one-layer model (Lin et al. 2012):

$$\Delta m / \Delta t = am^{3/4} - bm = am^{3/4} [1 - (m / M_0)^{1/4}] \quad (3-1)$$

where m is the current biomass of whole plant, a and b the species-specific constants, and $M_0 = (a/b)^4$ refers to the asymptotic maximum body size of a plant (calculated for $\Delta m / \Delta t = 0$).

The general description of the mode of operation of the zone-of-influence (ZOI; Weiner et al. 2001) is the same above- and belowground: the particular circular ZOI with area A stands for the physical space occupied by a plant, which also represents the potential energy and resources that are available to

this plant and is proportional to the plant's metabolic rate (B). Each ZOI is allometrically related to the respective biomass, m , as $m^{3/4}=c_0A$ (Enquist and Niklas 2001), where c_0 is a normalization constant. Resource limitation and competition usually cause a reduction of resource availability for plants. We therefore represent resource limitation via a dimensionless efficiency index, f_R , for different levels of resource availability. Resource competition is incorporated by using a dimensionless competition index, f_p . Equation (3-1) becomes:

$$\Delta m/\Delta t = f_R f_p c A [1 - (m/M)^{1/4}] \quad (3-2)$$

where $c=ac_0$, is the initial growth rate and $M=(f_R f_p)^4 M_0$ the maximum body size with resource limitation and competition. The efficiency index, f_R , can take different forms depending on the characteristics and level of the limiting resource. For simplification, we use a linear form, $f_R = 1-RL$, where RL indicates the level of resource limitation, with its value ranging from 0 (no resource limitation) to 1 (maximum resource limitation). As for competition, the modes of resource-mediated competition among plants can be located along a continuum between completely asymmetric competition (largest plants obtain all the contested resources) and completely symmetric competition (resource uptake is equal for all plants, independent of their relative sizes; Schwinning and Weiner 1998). Different modes of competition are incorporated in our model by using a competition index f_p as

$$f_p = (A_{no} + \sum_{k=1}^{n_o} \frac{m_i^p}{\sum_{j=1}^{n_j} m_j^p} A_{o,k}) / A \quad (3-3)$$

This index represents the fraction of resources available in the ZOI which plant i could obtain after the loss of potential resources on the areas overlapped by neighbours of sizes m_j (Schwinning and Weiner 1998). A_{no} is the area not overlapping with neighbours, $A_{o,k}$ are the n_o areas overlapping with n_j different neighbours. Parameter p adjusts the mode of competition (Schwinning and Weiner 1998). Here, we consider two theoretically important p values reflecting two modes of competition: allometric asymmetry ($p=10$, larger individuals get a disproportional share of overlapped areas) and size symmetry ($p=1$, the

overlapped areas are divided among all overlapping individuals proportional to their sizes; for detail and an example see Figure A2).

In the one-layer version of our ZOI model (Chapter 2, Lin et al. *in revision*), equation (3-2) lumps above- and belowground competition together. In the study presented, equation (3-2) is applied to both ZOIs representing the above- and belowground physical space a plant occupies and on which it has potential access to the resources light, water and nutrients, respectively (Figure A3). Through this modification, we take into account that the relative importance of shoot versus root competition and the size of the corresponding ZOIs can depend on environmental factors (Casper et al. 2003, Deng et al. 2006, O'Brien et al. 2007, May et al. 2009).

We assumed that (i) under optimal conditions without resource limitation and competition, the abilities of above- and belowground resource uptake are balanced, with relationships between metabolic rate, B , and biomass, m , being $B = c_{\text{shoot}} m_{\text{shoot}}^{3/4} = c_{\text{root}} m_{\text{root}}^{3/4}$ (Niklas 2005, Cheng and Niklas 2007; see Appendix A), where c_{shoot} and c_{root} are normalization constants (to simplify, we assume $c_{\text{shoot}} = c_{\text{root}} = 1$), and “shoot” and “root” refer to the above- and belowground compartment, respectively; (ii) the plant's above- and belowground ZOIs are proportional to the plant metabolic rate, B , and allometrically related to the plant's shoot and root biomass (Enquist and Niklas 2001, May et al. 2009), $A_a = c_a m_{\text{shoot}}^{3/4}$ and $A_b = c_b m_{\text{root}}^{3/4}$, where c_a and c_b are normalization constants (to simplify, we use $c_a = c_b = 1$); (iii) growth of the entire plant is limited by the compartment with smaller resource uptake rate (May et al. 2009). Thus, equation (3-2) is first independently applied for both the above- and belowground compartment, then growth of the entire plant is set to that of the more limited compartment, multiplied by two to account for the case where below- and aboveground growth are the same (May et al. 2009):

$$\frac{\Delta m}{\Delta t} = \begin{cases} 2 \times \Delta AGR = 2 \times f_{R,a} f_{p,a} c_a A_a [1 - (m / M_a)^{1/4}], & \Delta AGR < \Delta BGR \\ 2 \times \Delta BGR = 2 \times f_{R,b} f_{p,b} c_b A_b [1 - (m / M_b)^{1/4}], & \Delta AGR > \Delta BGR \\ \Delta AGR + \Delta BGR, & \Delta AGR = \Delta BGR \end{cases} \quad (3-4)$$

where ΔAGR and ΔBGR are above- and belowground growth rate and the subscripts a and b indicate the above- and belowground compartment,

respectively. Then, allocation of the gained biomass to the two compartments is assumed to be plastic (McConnaughay and Coleman 1999, Weiner 2004, Berger et al. 2008), with more biomass being allocated to the compartment with the smaller, and thus more limiting, growth rate. Adopting optimization theory (Johnson 1985, McConnaughay and Coleman 1999, May et al. 2009) and metabolic scaling theory (Niklas 2005), we assumed partitioning of biomass growth between shoot and root to be:

$$\left\{ \begin{array}{l} \frac{\Delta m_{shoot}}{\Delta t} = \frac{\Delta m}{\Delta t} \frac{\Delta BGR^{3/4}}{\Delta AGR^{3/4} + \Delta BGR^{3/4}} \quad (3-5a) \\ \frac{\Delta m_{root}}{\Delta t} = \frac{\Delta m}{\Delta t} \frac{\Delta AGR^{3/4}}{\Delta AGR^{3/4} + \Delta BGR^{3/4}} \quad (3-5b) \end{array} \right.$$

An allometric form (3/4) of resource allocation was used here as metabolic balance; we also tested the original exponent of 1 (Johnson 1985, May et al. 2009), which did not change our general findings.

An individual's mortality rate is proportional to its mass-specific metabolism, i.e. current total metabolic rate divided by body mass (Brown et al. 2004). Based on this, we assume that individuals die if their actual growth rate (actual metabolic rate, $\Delta m/\Delta t$) falls below a threshold fraction of their basal metabolic rate (scaled by current body mass, i.e. 3% of $m^{3/4}$). Therefore, individual plants may die due to metabolic inactivation driven by above- or/and belowground resource limitation, competition, senescence (when m approaches M), or combinations thereof. In total, Equations (3-4), (3-5a) and (3-5b) represent how growth, biomass allocation and mortality of a plant are jointly determined by above- and belowground resource levels and local competition. This provides a mechanistic and quantitative basis for linking the energetic metabolism and growth of plants to local interactions and population dynamics under different environmental conditions, i.e. to identify the compartment which mostly influences the plant growth at individual level and mass-density relationship at population level. The design of our model also allows us to explicitly ascribe the mortality of individual plants to above- or/and belowground processes in simulations.

3.2.2. Scenarios

In our simulation experiments, we tested high initial densities ($10^4 = 10,000$ individuals per total area), two modes of aboveground (shoot) competition (C^{AA} : allometric asymmetry, $p_a = 10$; C^{SS} : size symmetry, $p_a = 1$), and two modes of belowground (root) competition (C^{AA} : allometric asymmetry, $p_b = 10$; C^{SS} : size symmetry, $p_b = 1$) at three resource-limitation levels for the belowground compartment (RL_b equal to 0, 0.4 and 0.8 representing no, medium and strong limitation of belowground resources respectively). Simulations for the resulting nine scenarios were repeated five times, using different random initializations. We also tested low initial densities ($10^{3.5} \approx 3,163$ individuals per total area) and other combinations of competition parameters, which lead to similar conclusions as we presented here (Table S1).

3.2.3. Greenhouse experiment

To test the predictions of our model, we carried out a greenhouse experiment at the research station of Hetzdorf, Dresden University of Technology, Germany. A common tree species of central Europe, *Betula pendula* Roth (silver birch), was chosen because it is fast-growing. The germination percentage of birch in our controlled pre-test under climate chamber conditions was 45% (ISTA 1993). Seeds of *B. pendula* were sown in the pots at two initial densities (calculated as 0.09g and 0.27g per pot), then two initial seedling densities with approximately 250 and 750 individuals per pot have been established, which correspond to 10000 and 33000 plants m^{-2} . Each pot was filled with a natural mixed spruce forest humus substrate. The plastic pot size was 20×16.3 cm at top and 17×13.5 cm at bottom with 5 cm in depth. Consequently, root competition is expected to be very intensive in such shallow pots (Wilson 1988).

On 11 April 2010, seeds were sown into each pot and covered by a thin layer of sand against drought damages. We set two nutrient levels, as fertilized and non-fertilized groups. For the fertilized group, sustained-release fertilizer was placed uniformly over the ground substance surface in each pot (4.6 g per pot). In total, we used 40 pots, for two densities, two nutrient levels and ten replicates. All pots were arranged on benches in the greenhouse, and were

randomly rearranged once per week to avoid possible effects of environmental heterogeneity. On 28 July 2010, we terminated the planting experiment and harvested all plants. Self-thinning had largely reduced density of seedlings in all harvested pots. In order to avoid edge effects, we set up a 7×7 cm subplot in the center of each pot for measurement. Shoot and root dry biomass were measured for each individual plant after oven-drying to constant weights at 60°C. Two pots in the fertilization group were lost (one pot in each initial density), thus 38 pots were evaluated.

3.2.4. *Statistical analysis*

The mass-density relationship (log-log transformed data of mean biomass vs. live plant density) has the form $\log M_y = \log k + \gamma \log N$, where M_y (mean biomass of either total plants, shoots, or roots) and N (plant density) are the variables plotted on the ordinate and abscissa, respectively. The constant $\log k$ is the intercept and γ the slope of the regression line (the allometric or scaling exponent). We used the data of simulated population with high initial density (i.e. 10,000 individuals per total area) for analysis (the thinning trajectories of low initial densities were identical to high initial density in simulations; Fig. S1). Data points were selected *a posteriori* for linear fits in our simulation experiment (Weller 1987, Chu et al. 2010): for each scenario, after density-dependent mortality starts, the data points with surviving plants between 7,000 and 500 during self-thinning were selected, which excluded the data points that may cause a non-linearity effect on linear regression. Data points were fitted by standard major axis regression (SMA, type II model), which concerns the presence of error in both variables and is widely used to investigate mass-density relationships (Warton et al. 2006). All statistical analyses were conducted using R 2.11.1 (R Development Core Team, 2010).

3.3 Results

3.3.1 *Individual-based model*

Plants allocated more biomass to roots for acquiring belowground resources (RL_b) when these resources became limited. As expected, root : shoot ratio

(RSR) was significantly higher with belowground resource limitation (ANOVA, $F = 11.48$, $P < 0.001$; Fig. 3.1a). Consequently, belowground competition among plants became more intense leading to increased mortality (Fig. 3.1b). This suggests that the relative importance of above- and belowground competition for the population dynamics varies inversely along a gradient of belowground resource limitation.

Also, the plasticity of biomass allocation contributes to variable mass-density patterns (Fig. S1; Table S1). When the mode of competition is entirely asymmetric (C_{AA}^{AA} , for both above and below ground) and without resource limitation ($RL_b=0$), the slopes of log mass-log density relationships for mean total, above- and belowground biomass are all consistent with the prediction of MST (Fig. 3.2, Table S1). With increasing belowground resource limitation, the slopes of log mass-log density relationships for belowground biomass still supports MST but the slopes for aboveground part are significantly shallower (95% CI do not include $-4/3$; Fig. 3.2, Table S1). However, at all resource levels, entirely symmetric competition (C_{SS}^{SS}) results in slopes of the log mass-log density relationships significantly shallower than predicted by MST (95% CI do not include $-4/3$; Fig. 3.2, Table S1), for both above- and belowground biomass. This result indicates that the mode of competition contributed more to altering the mass-density relationship than biomass allocation did.

In the combination C_{SS}^{AA} without resource limitation ($RL_b=0$, Fig. 3.1b), aboveground competition had a greater effect on population mortality than belowground competition because there was no resource limitation. The allometric exponents were very close to those of the combination C_{AA}^{AA} (95% CI overlapped; Fig. 3.2, Table S1) and also compatible with prediction of MST (95% CI include $-4/3$), but significantly differ from C_{SS}^{SS} (95% CI did not overlap; Fig. 3.2, Table S1). When belowground resources were limited ($RL_b=0.4$), plant allocated more biomass to belowground parts; the aboveground mass-density relationship of C_{SS}^{AA} was significantly different from the prediction of MST (95% CI did not include $-4/3$) and C_{AA}^{AA} (95% CI did not overlap; Fig. 3.2, Table S1). However, exponents of belowground showed little variation and were still consistent with MST (also C_{AA}^{AA}) reflecting that mortality was mainly induced by asymmetric aboveground competition (Fig. 3.1b).

With further increased belowground resource limitation ($RL_b=0.8$), the mass-density relationships of C_{SS}^{AA} for mean total, above- and belowground biomass were very similar to the case of C_{SS}^{SS} (Fig. 3.2, Table S1) and thus significantly different from the predictions of MST and C_{AA}^{AA} (Fig. 3.2, Table S1). In this scenario, symmetric belowground competition was the main factor driving mortality (Fig. 3.1b). This result again demonstrated that the mass-density relationships are more affected by the mode of competition independent of which compartment is dominant in terms of growth limitation.

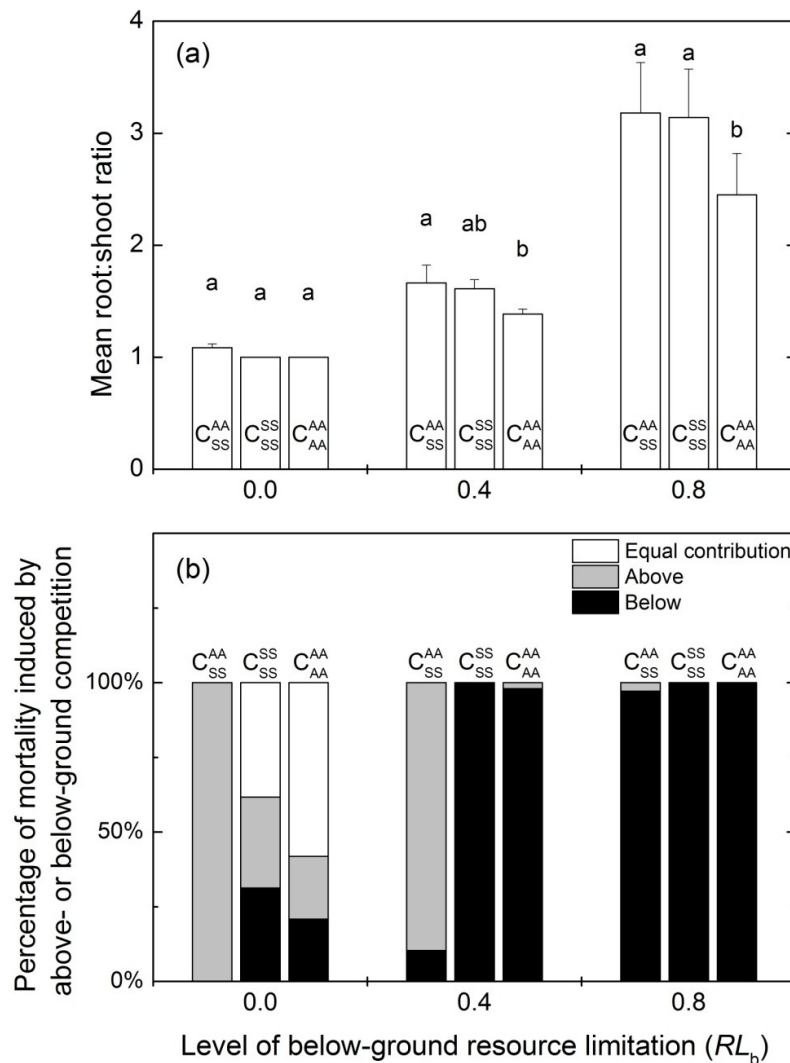


Fig. 3.1 The (a) root:shoot ratio (mean \pm 1 SD) and (b) percentage of mortality induced by above- or belowground competition in simulated plant populations at different levels of belowground resource limitation, RL_b , ranging from 0 (no resource limitation) to 1 (maximum resource limitation). C with superscript and subscript indicated the mode of competition for above- and belowground part correspondingly (AA: allometric asymmetry; SS: size symmetry). Bars in the same group that share the same letter do not differ significantly ($P > 0.05$, Holm-Sidak test).

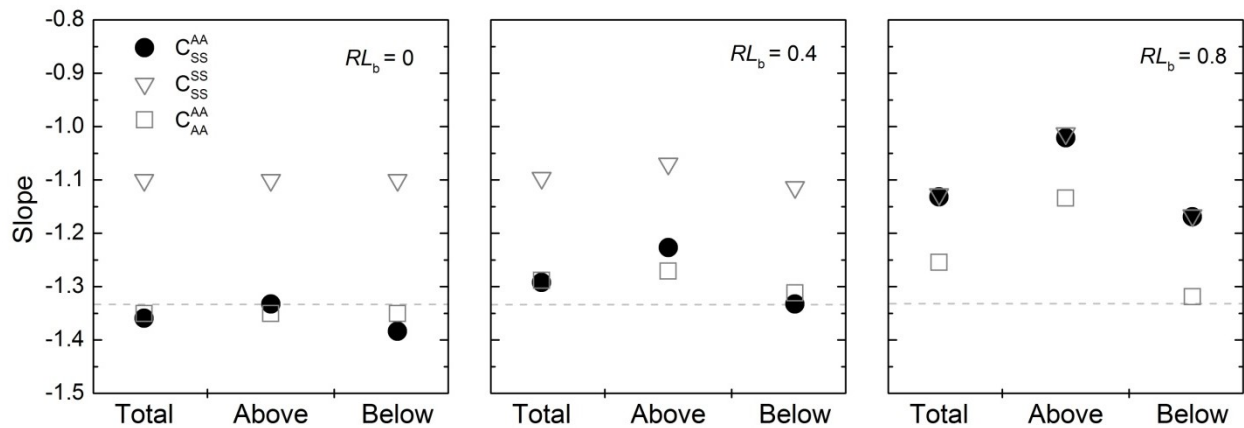


Fig. 3.2 Slopes of mass-density relationships between the mean total, above- and belowground biomass and densities in simulated plant populations (log-log transformed; as estimated by standard major axis; all regressions were significant at $P < 0.0001$). RL_b defined the level of belowground resource limitation, with its value ranging from 0 (no resource limitation) to 1 (maximum resource limitation). C with superscript and subscript indicated the mode of competition for above- and belowground part correspondingly (AA: allometric asymmetry; SS: size symmetry). The dotted lines indicate the value of exponent $(-4/3)$ predicted by MST.

3.3.2 Greenhouse experiment

Our greenhouse experiment confirmed the results of the simulation experiments. For non-fertilized plants the mean RSR of biomass was significantly higher than for fertilized plants (ANOVA, $F = 9.09$, $P < 0.001$; Fig. 3.3). The mass-density relationship varied between fertilization and non-fertilization treatment (Table S2, Fig. 3.4a). As for fertilized plants, the slopes of total, above- and belowground log mass-log density relationship were not significantly different from the prediction of MST (95% CI included $-4/3$; Table S2). However, the slopes became shallower in the group of non-fertilized plants (Fig. 3.4b) and differed significantly from the prediction of MST (95% CI do not include $-4/3$; Table S2). The overall pattern of differences in allometric exponents between fertilization and non-fertilization treatment (Fig. 3.4b) was similar to the pattern of C_{SS}^{AA} changing along the resource-limited gradient explored in the simulation experiments (Fig. 3.2)

confirming the dominance change from aboveground (asymmetric) to belowground (symmetric) competition. Therefore, the importance of belowground competition as driving force in plant population and communities is predicted to increase along gradients of decreasing belowground resource availability, whereas the importance of aboveground competition is predicted to decrease.

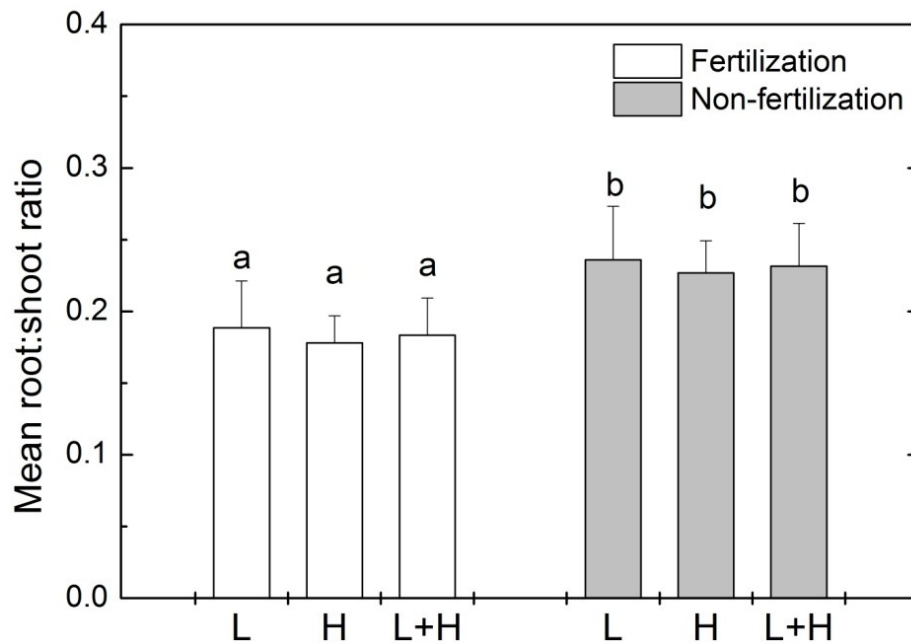


Fig. 3.3 The root:shoot ratio (mean \pm 1 SE) of *Betula pendula* seedlings in greenhouse experiment with different nutrient treatments and initial densities (L: low density, H: high density, L+H: combined data). Bars that share the same letter do not differ significantly ($P > 0.05$, Holm-Sidak test).

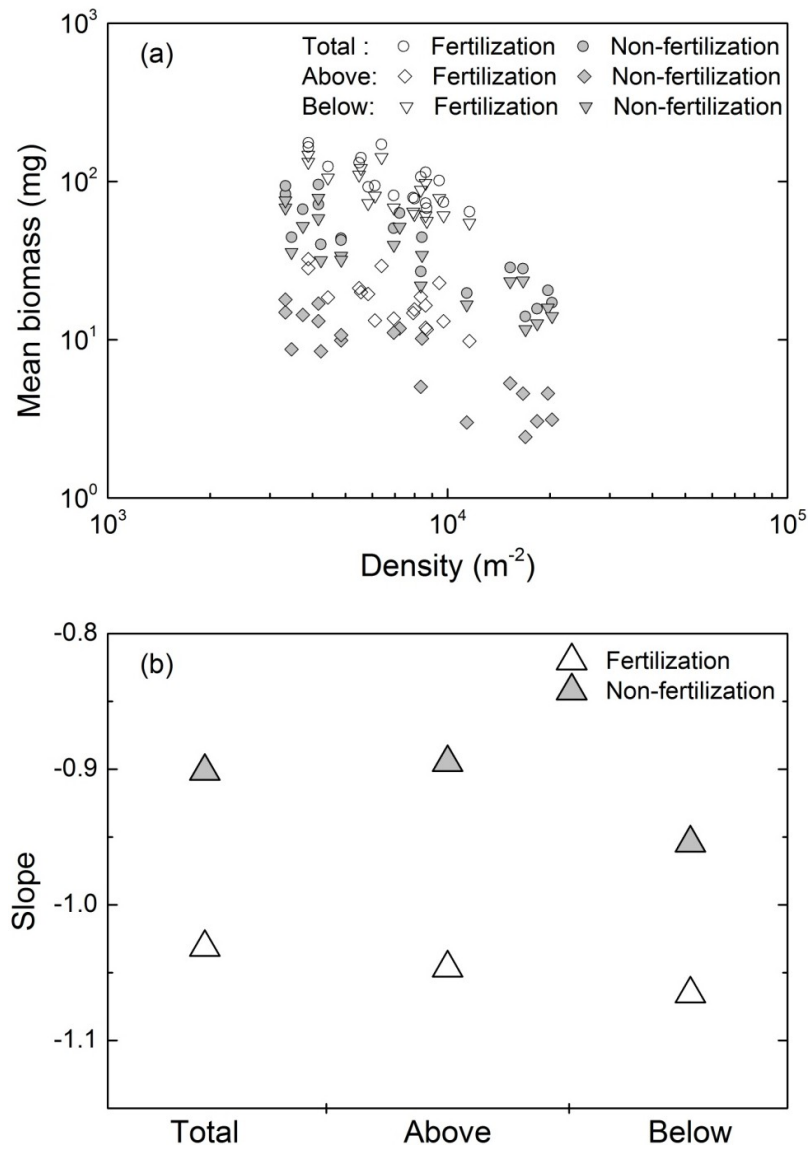


Fig. 3.4 The mass-density relationships of *Betula pendula* seedlings in greenhouse experiment with different nutrient treatments. (a) Relationships between mean total, above- and belowground biomass and densities (log-log transformed). (b) Slopes of mass-density relationships between the mean total, above- and belowground biomass and densities (log-log transformed, as estimated by standard major axis; all regressions were significant at $P < 0.001$, 95% CI of the slopes indicated that the exponents of non-fertilization treatment were statistically different from $-4/3$).

3.4 Discussion

We presented a two-layer individual-based model that is rooted in metabolic scaling theory (MST). The purpose of the model was to test whether a generic model that explicitly represents biomass allocation and different modes of

competition for both above- and belowground compartments would be able to capture observed variations and patterns in plant mass-density relationships. In addition to simulation experiments, we conducted a greenhouse experiment to verify the model's predictions.

The main finding was that changes in the allometry of plants, induced by their plasticity of biomass allocation in response to environmental factors, can alter the relative importance of above- or belowground competition on driving density-dependent mortality, which affects plant mass-density relationships. Root competition, which is assumed to be more symmetric, can have a strong effect on altering the allometric exponent, i.e. flattening plant log mass-log density relationships (also self-thinning trajectories). Deviations from the mass-density scaling exponent predicted by MST are thus likely to occur if competition occurs belowground (symmetric) rather than aboveground (asymmetric). Consequently, models or theories explaining mass-density relationships and self-thinning which are solely based on aboveground parts are unlikely to be appropriate for the cases where belowground processes predominate (Deng et al. 2006, Berger et al. 2008).

3.4.1. *The advantages of using a new mechanistic growth model*

It was important that we used a mechanistic growth model derived from MST rather than a phenomenological growth model, as usually has been done so far for analyzing biomass-density relationships (e.g., Weiner et al. 2001, Stoll et al. 2002, Chu et al. 2010). First, our generic growth model is based on the energy budget of the individuals during growth. It thus captures the salient features of energy acquisition and allocation to maintain and replace the existing tissue and the production of new tissue, and relates ontogenetic growth to metabolic energy at the cellular level (West et al. 2001). This certainly is an advantage by itself because models driven by “first principles” are more flexible and usually capture more adaptive responses of individuals to their environment than phenomenological models, which are statistically fitted to existing data (Grimm and Railsback 2005, Martin et al. 2012). Second, in contrast to previous models (Wyszomirski et al. 1999, Weiner et al. 2001, Stoll et al. 2002, Chu et al. 2010), our model is able to simultaneously explain

the observed variation in both root-shoot allocation patterns and mass-density relationships.

It is worth noting that an association of the scaling exponents with root : shoot ratios (RSR) predicted by our model matched the observed values of natural vegetations along a precipitation gradient in China very well. Deng et al. (2006) found that with drought severity increasing, the mean RSR of plant dry biomass increased approximately from 1 to 2 (RSR \pm SD: 0.92 \pm 0.31, 1.92 \pm 1.42 and 2.18 \pm 1.61) and the scaling exponent of plant total biomass-density relationship changed from -1.33 to -1.27 correspondingly (-1.33, -1.28 and -1.27). In our model, we found very similar associations between RSR and scaling exponent (Table S1; e.g., C_{SS}^{AA} : $RL_b=0$, RSR \pm SD=1.09 \pm 0.03, Slope=-1.36; $RL_b=0.4$, RSR \pm SD=1.66 \pm 0.16, Slope=-1.29), which are statistically identical to the empirical results ($P > 0.05$, Holm-Sidak test).

3.4.2. Above- and belowground competition

Why do the predictions of MST on plant mass-density relationship often turn out to be correct? The principal assumption of energy equivalence in MST implies that light is the limiting factor and competition is a canopy-packing process among plants (Enquist et al. 1998, Reynolds and Ford 2005, Deng et al. 2006). If then in benign environments only aboveground biomass is measured, as in most empirical studies, it is to be expected that we obtain the slope of -4/3 (scaling exponent) as shown in our model.

Our results imply the importance of adaptive behaviours of plants for system-level properties like biomass-density relationship (Grimm and Railsback 2005, Grimm et al. 2005). With “adaptive behaviour” we refer to morphological and physiological plasticity that allows plants to adapt to changing biotic and abiotic environmental conditions (Weiner 2004, Berger et al. 2008, Schiffers et al. 2011). It is recognized that features of vegetation can change in drought or oligotrophic environments (Deng et al. 2006). Based on optimization theory, plants compete primarily for limited belowground resources in those environments, which can cause an increase of RSR as well as root space, but a decrease in cover where plant canopies are not closed (Deng et al. 2006). In analogy to Liebig’s law of limiting factors, belowground

competition can overtake aboveground competition and becomes dominant in these situations. Consequently, adaptive behaviour not only alters the way plants grow but also their mode of competition.

Empirical experiments show that slopes of log mass-log density relationship are manifestly shallower under severe water stress (Deng et al. 2006, Liu et al. 2006) and low nutrient levels (reviewed in Morris 2003). Our model and greenhouse experiments confirm these results. As demonstrated, the mode of competition played a more important role for the plant mass-density relationship.

3.4.3. *Asymmetric vs. symmetric competition*

With symmetric competition, resource acquisition is more evenly distributed among interacting plants, so that competitive suppression and the corresponding onset of mortality are delayed (Stoll et al. 2002). Consequently, even at high densities plants can still survive and grow (Hautier et al. 2009, Lamb et al. 2009). This leads to the shallower self-thinning lines as has been proven in several studies (Chu et al. 2010, Lin et al. *in revision*).

Accordingly, one should also expect that slopes become shallower if aboveground competition is less asymmetric. This was indeed observed for low light conditions (Lonsdale and Watkinson 1982, Westoby 1984, Dunn and Sharitz 1990), where plants often show flexible shoot morphology and grow taller instead of wider, and competition was considered more symmetric (Schwinning and Weiner 1998, Stoll et al. 2002).

However, some researchers proposed that size-asymmetric (light) competition is more important for explaining the deviations predicted by MST in forests (Coomes and Allen 2009; Coomes *et al.* 2011). At first glance, this seems to be in contrast to our findings here, but this is not the case because those studies focused on individual's diameter growth. Asymmetric competition from larger neighbours can highly affect the growth of smaller individuals before they die. Thus, for these individuals, asymmetric competition is more important than the relationships predicted by MST. In contrast, we here focused on the biomass and density of surviving plants.

It is noteworthy to mention that it also has been surmised that

belowground competition might be rather asymmetric in heterogeneous resource conditions (Schwinning and Weiner 1998, Fransen et al. 2001, Rajaniemi 2003, Rewald and Leuschner 2009), though the experimental evidence for asymmetric belowground competition is scarce (Rajaniemi 2003, von Wettberg and Weiner 2003, Rewald and Leuschner 2009). Our model and greenhouse experiment, nevertheless, confirm the majority of empirical experiments which suggest that belowground competition is more symmetric. We conclude that an appropriate evaluation of the mode of competition should not only consider environmental heterogeneity and species-specific ecological traits of plants (Schwinning and Weiner 1998, Rajaniemi 2003, Pretzsch 2006, Rewald and Leuschner 2009), but also the interaction between above- and belowground competition (Cahill 2002).

Conclusion

It seems that Liebig's law even applies, in a generalized sense, to the debate about whether or not MST is a universally valid and relevant theory. Deviation in observed plant mass-density relationships indicates that MST is less general than originally thought. Our findings confirm that MST by itself applies to individual organisms, but not necessarily to populations or ecosystems (Lin et al. *in revision*). System-level features of ecological systems may be constrained by individual metabolism, which is taken into account in MST, or by ecological factors beyond the individual, i.e. the type of limiting resource and the mode of competition among con-specifics. The overall claim that MST provides a universal and mechanistic basis for quantitatively linking the energetic metabolism of individuals to ecological community dynamics is thus neither completely right nor wrong: the real question is when and which factors dominate in a given situation.

In addition to previous studies, which do not address the linkage between aboveground and belowground competition explicitly, the most important conclusion of our study is that changes in biomass allocation patterns can modify ecological mechanisms and subsequently the constraints which MST sets. The observed variation in mass-density relationships represents changes in the dominance of the most limiting factor in a given ecological context. This

has important implications, e.g., for using allometry-based simulation models to predict carbon storage and sequestration in plant systems. Taking into account not only the visible aboveground competition, but also the invisible belowground competition, is thus critical for many forests and eco-regions.

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Chapter 3 – Appendix A

ODD protocol – model description of two-layer *pi* model

The following model description follows the ODD protocol (Overview, Design concepts, Details) for describing individual- and agent-based models (Grimm *et al.* 2006; Grimm *et al.* 2010),

1. Purpose

The aim of this model is to evaluate the multiple effects of the mode of competition (above- and belowground part) and resource limitation on regulating plant population dynamics, specifically on mass-density relationships (self-thinning trajectories) and density-dependent mortality. In particular, we test whether interactions on individual plant level can alter the slope and intercept of the log mass-log density relationship under different environmental conditions. The model does not represent specific species, but generic ones.

2. Entities, state variables, and scales

The entities in the model are plants and square habitat units, or patches (Table A1). Plants are characterized by the following state variables: initial growth rate, initial biomass, maximum biomass (asymptotic biomass), current biomass (both shoot and root) and their position, i.e. coordinates of the stem. Each individual plant has its own circular zone-of-influence (ZOI) for both above- and belowground compartment. The pair of ZOIs stand for the physical space occupied by a plant's shoot and root respectively, and represents the energy and resources potentially available to this plant for above- and belowground part, which ZOIs are allometrically related to its shoot and root mass separately. Neighbouring plants only compete for the resources when their above- or belowground ZOIs are overlapping.

In order to make the spatial calculations of resource competition easier, ZOIs are projected onto a grid of patches. To avoid edge effects, we use a torus world with a size of 200×200 patches (Grimm & Railsback 2005), and each patch represents 0.25 cm^2 in reality. The state of each patch is characterized by its resource availability. We use a homogeneous environment here as all patches have the same, and constant, degree of resource limitation for both above- and belowground part. One time step in the model represents approximately one week for simulated plants.

Table A1. State variables and initialization in the individual-based model. Actual values are drawn from the given intervals to introduce a certain degree of heterogeneity among individuals.

Variable	Description	Initial Value [unit]
Plants		
C	Initial growth rate	1 ± 0.1 [mg cm ⁻² time step ⁻¹]
m_0	Initial total body mass	2 ± 0.2 [mg]
$m_{0, \text{shoot}}$	Initial shoot mass	50% of m_0 [mg]
$m_{0, \text{root}}$	Initial root mass	50% of m_0 [mg]
M_0	Maximal biomass	$2 \times 10^6 \pm 2 \times 10^5$ [mg]
M	Current total body mass	[mg]
m_{shoot}	Current shoot mass	[mg]
m_{root}	Current root mass	[mg]
A_a	Aboveground zone of influence	[cm ⁻²]
A_b	Belowground zone of influence	[cm ⁻²]
Patches		
RL_a	Aboveground resource limitation	0, $RL_a \in [0, 1)$
RL_b	Belowground resource limitation	0, 0.4, 0.8, $RL_b \in [0, 1)$
Initialization		
Mortality	Threshold of death	3% of $m^{3/4}$
Density	Number of plants	3163 and 10000 / total area
Random seed	Generation of random number	1, 2, 3, 4, 5

3. Process overview and scheduling

After initialization, all individual plants with a given density are randomly distributed in the world. The processes of above- and belowground resource competition, growth and mortality of each plant are fulfilled within each time step. In each step, individual plants first sense the above- and belowground resource qualities of environment (levels of resource limitation of patches) within their shoot and root ZOIs, the areas (radius) of an individual plant's ZOIs are determined from its current shoot and root biomass correspondingly. When the above- or belowground ZOIs of neighbouring plants are overlapping, plants compete only within the overlapping area. Thus, the overlapping area is divided according to the competition mode which reflecting the way of resource division. The growth rate of plant is determined by the outcome of above- and belowground process, which is restricted by the compartment with minimum

resource uptake rate according to growth function. The synthesized biomass is allocated to shoot and root optimally which follows the rule of functional balanced growth (Niklas 2005; May *et al.* 2009). Plants with growth rates falling below a threshold die and are removed immediately. The state variables of the plants are synchronously updated within the subroutines, i.e. changes to state variables are updated only after all individuals have been processed (Grimm & Railsback 2005).

4. Design concepts

Basic principles: From “Metabolic Scaling Theory”, we derived a general ontogenetic growth model for individual plants. We combine this model, via the ZOI approach, with the effects of different modes of competition for both above- and belowground compartment and resource limitation.

Emergence: All features observed at the population level, e.g. mass-density relationship or self-thinning trajectories, size distribution and spatial distribution, emerge from the interaction of individual plants with their neighbours and the resource level of their abiotic environment.

Interaction: Individual plants interact via shoot and root competition for resources in the overlapping area of their ZOIs.

Stochasticity: Initial growth rate, initial biomass (for shoot and root respectively), maximum biomass and initial position of plants are randomly taken from the intervals given in Table 1. This introduces a certain level of heterogeneity among individual characteristics to take into account that real plants are never exactly identical.

Observation: Population size, shoot and root biomass of each plant, and mean biomass of all living plants are the main observations.

5. Initialization

Initially, individual plants are randomly distributed according to the chosen initial density. Resources are spatially and temporally constant. Each plant has an initial biomass (m_0), initial shoot and root biomass ($m_{0, \text{shoot}}$ and $m_{0, \text{root}}$), maximal biomass (M) and initial growth rate (c) drawn from truncated normal distributions with average and intervals given in Table 1.

6. Input

After initialization, the model does not include any external inputs, i.e. the abiotic environment is constant.

7. Submodels

One layer model – Plant growth, resource limitation and competition

In our individual-based model the plant's ZOI, A , stands for the physical space occupied by the plant and represents the energy and resources potentially available to this plant. This space is allometrically related to the plant's body mass, m , as $c_0 A = m^{3/4}$ (Enquist & Niklas 2001), where c_0 is a normalization

constant. Since plant growth in our simulation is discrete, therefore equation (3-1) can be rewritten as

$$\Delta m / \Delta t = cA[1 - (m / M_0)^{1/4}] \quad (A1)$$

where $c=ac_0$, is the initial growth rates in units of mass per area and time interval. For simplicity, we choose 1 ± 0.1 in our model.

Resource limitation and competition usually cause a reduction of resource availability for plants. We therefore represent resource limitation via a dimensionless efficiency factor or index, f_R , for different levels of resource availability. Resource competition is incorporated by using a dimensionless competition factor or index, f_p , leading to

$$\Delta m / \Delta t = f_R f_p cA[1 - (m / M)^{1/4}] \quad (A2)$$

where $M=(f_R f_p)^4 M_0$ is the maximum body size with resource limitation and competition.

The efficiency factor f_R , can take different forms depending on the characteristics and level of the limiting resource. For simplification, we use a linear form here, i.e. $f_R = 1 - RL$, where RL indicates the level of resource limitation, with its value ranging from 0 (no resource limitation) to 1 (maximum resource limitation).

As for competition, the modes of resource-mediated competition among plants can be located somewhere along a continuum between completely asymmetric competition (largest plants obtain all the contested resources) and completely symmetric competition (resource uptake is equal for all plants, independent of their relative sizes; Schwinning & Weiner 1998). To represent different modes of competition explicitly, we describe the competitive index f_p as

$$f_p = (A_{no} + \sum_{k=1}^{n_o} \frac{m_i^p}{\sum_{j=1}^{n_j} m_j^p} \cdot A_{o,k}) / A \quad (A3)$$

This factor thus refers to the fraction of resources available in the area which plant i could obtain after a loss of potential resources due to areas overlapped by neighbours of sizes m_j (Schwinning and Weiner 1998). A_{no} is the area not overlapping with neighbours, $A_{o,k}$ denotes the n_o areas overlapping with n_j different neighbours. Parameter p determines the mode of competition, ranging from complete symmetry ($p = 0$) to complete asymmetry (p approaching infinity; for details and examples see Figure A2).

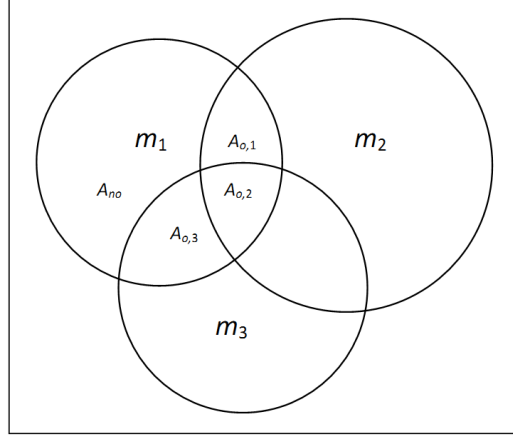


Figure A2. An example of calculating the interactive indexes (Eqns A3) with different modes of competition and facilitation in an individual-based model as a way of dividing plants' ZOI (zone-of-influence). Three plants with sizes m_1 , m_2 and m_3 are interacting in this example. For plant 1, its ZOI (A) was divided into four parts: A_{no} , the area not overlapping with the other two plants; $A_{o,1}$, the area overlapping with plant 2; $A_{o,2}$, the area overlapping with plants 2 and 3; $A_{o,3}$, the area overlapping with plant 3. Then the actual area that plant 1 can take from $A_{o,1}$ is

$$A_{o,1} \frac{m_1^p}{\sum_{j=1}^2 m_j^p} = A_{o,1} \frac{m_1^p}{m_1^p + m_2^p}$$

For $A_{o,2}$,

$$A_{o,2} \frac{m_1^p}{\sum_{j=1}^3 m_j^p} = A_{o,2} \frac{m_1^p}{m_1^p + m_2^p + m_3^p}$$

And for $A_{o,3}$,

$$A_{o,3} \frac{m_1^p}{\sum_{j=1}^2 m_j^p} = A_{o,3} \frac{m_1^p}{m_1^p + m_3^p}$$

Therefore, the competitive index for plant 1 is:

$$f_p = \frac{A_{no} + A_{o,1} \frac{m_1^p}{m_1^p + m_2^p} + A_{o,2} \frac{m_1^p}{m_1^p + m_2^p + m_3^p} + A_{o,3} \frac{m_1^p}{m_1^p + m_3^p}}{A}$$

Where $A = m_1^{3/4} / c_0$

Two layer model – Shoot versus root competition, biomass allocation and mortality

Because competition among plants can occurs at both above- and belowground simultaneously, the relative importance of shoot versus root competition and their ZOI can varies depending on the environmental factors (Deng *et al.* 2006, May *et al.* 2009). Therefore, the one layer model however cannot properly represent this property. We developed the two layer

individual-based model to represent the plant's shoot and root competition. In our two layer model, a plant has two ZOIs stand for the above- and belowground physical space occupied by the plant, which ZOIs represent the corresponding levels of energy and resources (e.g. light, water and nutrient) potentially available to this plant.

We assume that (i) under optimal conditions without resource limitation and competition, the abilities of above- and belowground resource uptake are balanced, with relationships between metabolic rate, B , and biomass, m , being $B = c_{\text{shoot}} m_{\text{shoot}}^{3/4} = c_{\text{root}} m_{\text{root}}^{3/4}$ (Niklas 2005, Cheng and Niklas 2007), where c_{shoot} and c_{root} are normalization constants (to simplify, we assume $c_{\text{shoot}} = c_{\text{root}} = 1$), and “shoot” and “root” refer to the above- and belowground compartment, respectively; (ii) the plant's above- and belowground ZOIs are proportional to the plant metabolic rate, B , and then allometrically related to the plant's shoot and root biomass (Enquist and Niklas 2001, May et al. 2009), $A_a = c_a m_{\text{shoot}}^{3/4}$ and $A_b = c_b m_{\text{root}}^{3/4}$, where c_a and c_b are normalization constants (to simplify, we use $c_a = c_b = 1$); (iii) growth of the entire plant is limited by the compartment with smaller resource uptake rate (May et al. 2009). In a view of comparability with one-layer model, the real growth rate of whole plant in two-layer model has been doubled. Accordingly, equation (A2) can be applied to above- and belowground compartment, and then we get the whole plant growth rate as

$$\frac{\Delta m}{\Delta t} = \begin{cases} 2 \times \Delta AGR = 2 \times f_{R,a} f_{p,a} c_a A_a [1 - (m / M_a)^{1/4}], & \Delta AGR < \Delta BGR \\ 2 \times \Delta BGR = 2 \times f_{R,b} f_{p,b} c_b A_b [1 - (m / M_b)^{1/4}], & \Delta AGR > \Delta BGR \\ \Delta AGR + \Delta BGR, & \Delta AGR = \Delta BGR \end{cases} \quad (\text{A4})$$

where ΔAGR and ΔBGR are above- and belowground determined growth rate. The factor of resource availability (f_R), competitive index (f_p) and ZOI (A) were applied to both two layers independently, with the corresponding subscript a and b indicate the above- and belowground compartment respectively (see Figure A3).

Adjustability of root/shoot allocation as the morphological plasticity allows plants to adapt to changing biotic and abiotic environmental conditions (Berger *et al.* 2008). We adopt the optimal allocation theory, functional balance growth hypothesis and metabolic scaling theory to quantify the partition of growth between the shoots and roots (Weiner 2004; Niklas 2005; May *et al.* 2009):

$$\begin{cases} \frac{\Delta m_{\text{shoot}}}{\Delta t} = \frac{\Delta m}{\Delta t} \frac{\Delta BGR^{3/4}}{\Delta AGR^{3/4} + \Delta BGR^{3/4}} & (\text{A5a}) \\ \frac{\Delta m_{\text{root}}}{\Delta t} = \frac{\Delta m}{\Delta t} \frac{\Delta AGR^{3/4}}{\Delta AGR^{3/4} + \Delta BGR^{3/4}} & (\text{A5b}) \end{cases}$$

which means plant allocates more biomass to the compartment that is most

limiting growth for increasing its uptake of resource. An allometric form ($3/4$) of resources allocation was used here as metabolic balance, we also tested the original allocation of linearity which only lead to a small difference on root/shoot ratio but do not change our general findings.

An individual's mortality rate is proportional to its mass-specific metabolism (as current total metabolic rate divide by body mass; Brown *et al.* 2004). Based on this, we assume that individuals die if their actual growth rate ($\Delta m/\Delta t$, represent actual metabolic rate) falls below a threshold of their basal metabolic rate (allometrically scaled with body mass), i.e. 3% of $m^{3/4}$. Therefore, individual plants may die due to metabolic inactivation driven by above- or/and belowground resource limitation, competition, senescence (when m approaches M) or combinations thereof. This provides a more realistic representation of relevant ecological process than in previous models (Stoll *et al.* 2002; Chu *et al.* 2009, 2010). In addition, we are able to ascribe the mortality of individual plants to above- or belowground process explicitly.

In total, equations (A4), (A5a) and (A5b) clearly showed how a plant's growth, biomass allocation and mortality are jointly determined by above- and belowground resource level and local competition.

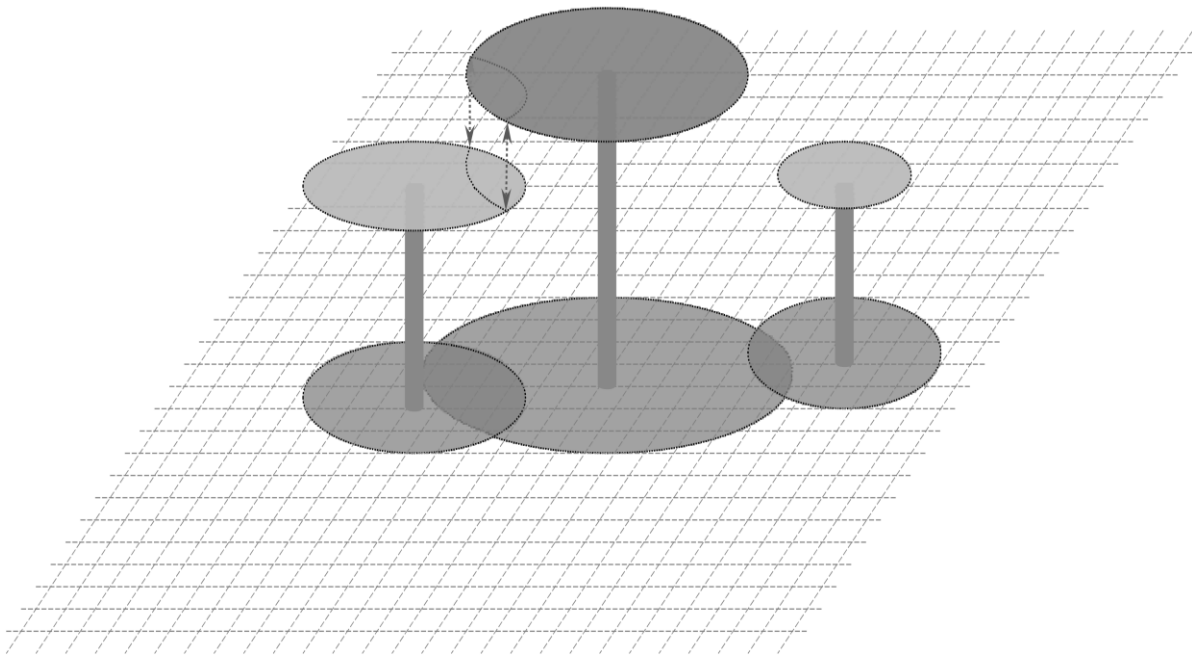


Figure A3. A visual illustration of the two-layer zone-of-influence (ZOI) approach including both above- and belowground competition. The above- and belowground ZOIs (green: aboveground, gray: belowground) are allometrically related to the plant shoot and root biomass, respectively. Plants only compete for the resources in overlapped areas with their neighbours which can occur independently at above- and belowground compartment (arrows indicate the overlapped area of aboveground competition).

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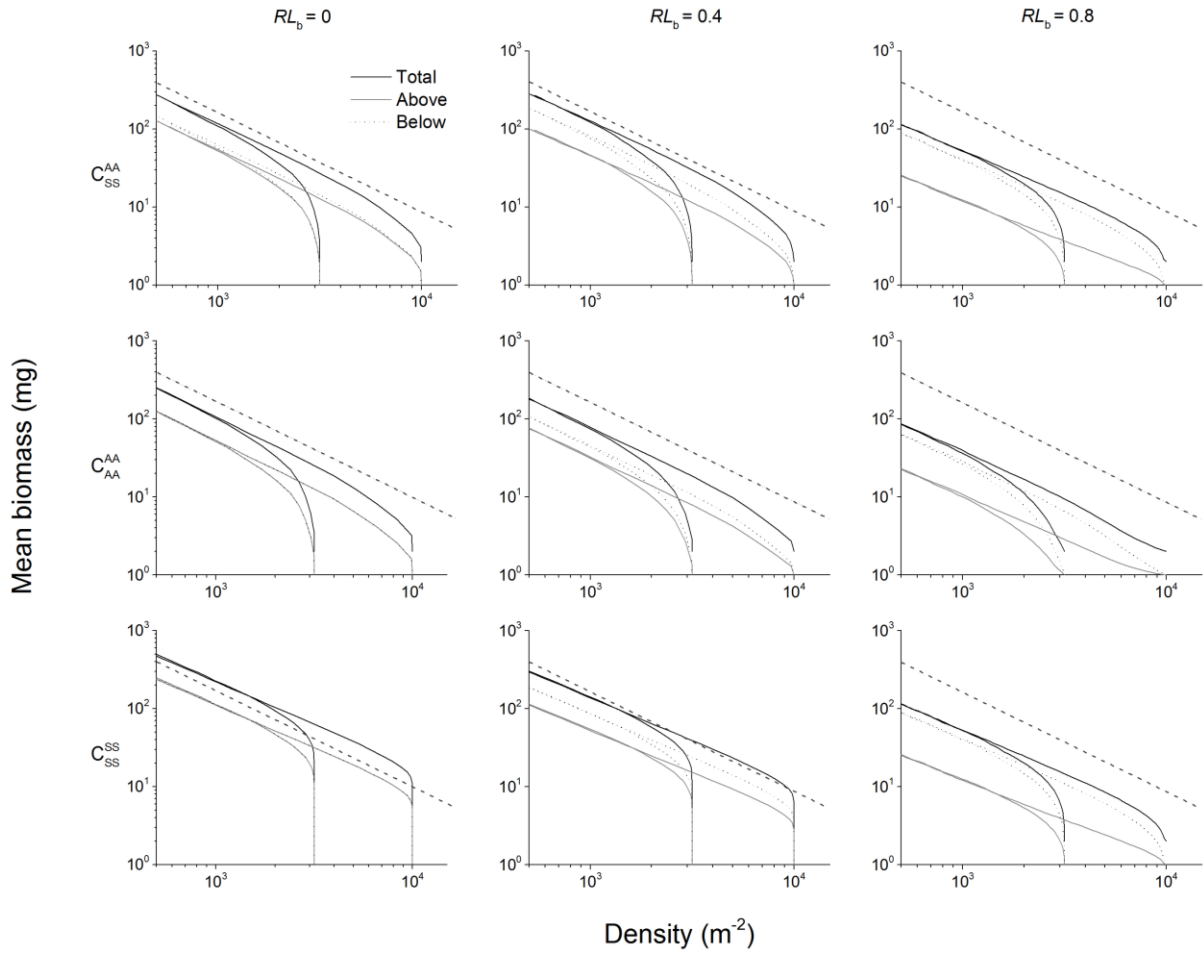


Fig. S1. Mass-density relationships between the mean total, above- and belowground biomass in simulated plant populations (log-log transformed). The gray dotted lines have a slope of $-4/3$. RL_b defined the level of below-ground resource limitation, with its value ranging from 0 (no resource limitation) to 1 (maximum resource limitation). C with superscript and subscript indicated the mode of competition for above- and below-ground part correspondingly (AA: allometric asymmetry, $p = 10$; SS: size symmetry, $p = 1$).

Table S1. Slopes and intercepts of mass-density relationships between the mean total, above- and belowground biomass in simulated plant populations (log-log transformed; as estimated by standard major axis regression). RL_b defined the level of belowground resource limitation, with its value ranging from 0 (no resource limitation) to 1 (maximum resource limitation). CA: complete asymmetry, $p = \infty$; AA: allometric asymmetry, $p = 10$; SS: size symmetry, $p = 1$; CS: complete symmetry, $p = 0$.

Resource limitation	Mode of Competition		Mean total biomass						
RL_b	Aboveground	Belowground	Slope	95% CI		Intercept	95% CI		R^2
0	CA	CA	-1.450	-1.509	-1.399	6.423	6.243	6.616	0.990
0	CA	AA	-1.475	-1.537	-1.416	6.502	6.290	6.707	0.988
0	CA	SS	-1.417	-1.461	-1.377	6.333	6.196	6.479	0.993
0	CA	CS	-1.439	-1.482	-1.401	6.420	6.289	6.563	0.993
0	AA	CA	-1.475	-1.538	-1.413	6.502	6.288	6.710	0.988
0	AA	AA	-1.351	-1.391	-1.316	6.109	5.987	6.242	0.996
0	AA	SS	-1.359	-1.394	-1.329	6.174	6.068	6.286	0.996
0	AA	CS	-1.401	-1.426	-1.379	6.348	6.273	6.430	0.998
0	SS	CA	-1.417	-1.462	-1.376	6.333	6.195	6.480	0.993
0	SS	AA	-1.359	-1.394	-1.329	6.174	6.068	6.286	0.996
0	SS	SS	-1.100	-1.110	-1.092	5.647	5.618	5.678	0.999
0	SS	CS	-1.351	-1.365	-1.342	6.764	6.728	6.805	0.994
0	CS	CA	-1.439	-1.482	-1.401	6.420	6.289	6.563	0.993
0	CS	AA	-1.401	-1.425	-1.380	6.348	6.273	6.429	0.998
0	CS	SS	-1.351	-1.363	-1.340	6.764	6.727	6.803	0.994
0	CS	CS	-1.060	-1.060	-1.059	5.868	5.866	5.870	1.000
0.4	CA	CA	-1.319	-1.344	-1.298	5.845	5.776	5.921	0.997
0.4	CA	AA	-1.319	-1.345	-1.294	5.849	5.771	5.929	0.996
0.4	CA	SS	-1.391	-1.421	-1.363	6.261	6.170	6.352	0.992
0.4	CA	CS	-1.425	-1.448	-1.403	6.405	6.337	6.474	0.994
0.4	AA	CA	-1.315	-1.340	-1.293	5.834	5.762	5.911	0.997
0.4	AA	AA	-1.288	-1.309	-1.269	5.758	5.697	5.822	0.998
0.4	AA	SS	-1.292	-1.313	-1.273	5.980	5.921	6.044	0.996
0.4	AA	CS	-1.311	-1.345	-1.279	6.286	6.190	6.387	0.957
0.4	SS	CA	-1.325	-1.352	-1.301	5.884	5.810	5.970	0.996
0.4	SS	AA	-1.281	-1.298	-1.267	5.754	5.707	5.805	0.999
0.4	SS	SS	-1.096	-1.101	-1.093	5.428	5.416	5.441	1.000
0.4	SS	CS	-1.017	-1.017	-1.016	5.391	5.390	5.393	1.000
0.4	CS	CA	-1.333	-1.361	-1.308	5.919	5.841	6.005	0.996
0.4	CS	AA	-1.285	-1.303	-1.268	5.775	5.722	5.831	0.998
0.4	CS	SS	-1.102	-1.108	-1.097	5.483	5.466	5.501	0.999
0.4	CS	CS	-1.021	-1.021	-1.020	5.398	5.397	5.400	1.000
0.8	CA	CA	-1.286	-1.303	-1.271	5.436	5.387	5.489	0.996
0.8	CA	AA	-1.263	-1.274	-1.251	5.373	5.336	5.409	0.998
0.8	CA	SS	-1.143	-1.151	-1.135	5.155	5.131	5.179	0.999
0.8	CA	CS	-1.038	-1.041	-1.035	4.889	4.880	4.898	1.000
0.8	AA	CA	-1.285	-1.301	-1.270	5.433	5.387	5.484	0.996

0.8	AA	AA	-1.256	-1.267	-1.244	5.350	5.318	5.387	0.998
0.8	AA	SS	-1.132	-1.137	-1.127	5.118	5.102	5.134	0.999
0.8	AA	CS	-1.034	-1.035	-1.032	4.874	4.870	4.878	1.000
0.8	SS	CA	-1.284	-1.301	-1.269	5.434	5.385	5.482	0.996
0.8	SS	AA	-1.257	-1.258	-1.237	5.329	5.297	5.361	0.998
0.8	SS	SS	-1.127	-1.132	-1.123	5.106	5.092	5.121	0.999
0.8	SS	CS	-1.033	-1.034	-1.032	4.870	4.867	4.873	1.000
0.8	CS	CA	-1.285	-1.302	-1.269	5.436	5.387	5.487	0.996
0.8	CS	AA	-1.248	-1.259	-1.238	5.331	5.300	5.365	0.998
0.8	CS	SS	-1.122	-1.127	-1.118	5.092	5.079	5.106	0.999
0.8	CS	CS	-1.033	-1.034	-1.032	4.871	4.867	4.874	1.000
Resource limitation	Mode of Competition		Mean aboveground biomass						
RL_b	Aboveground	Belowground	Slope	95% CI		Intercept	95% CI		R^2
0	CA	CA	-1.450	-1.507	-1.396	6.122	5.932	6.310	0.990
0	CA	AA	-1.477	-1.543	-1.417	6.204	5.991	6.423	0.988
0	CA	SS	-1.387	-1.432	-1.348	5.907	5.775	6.054	0.993
0	CA	CS	-1.392	-1.432	-1.353	5.922	5.790	6.056	0.993
0	AA	CA	-1.474	-1.533	-1.414	6.198	5.989	6.395	0.988
0	AA	AA	-1.351	-1.392	-1.315	5.807	5.685	5.943	0.996
0	AA	SS	-1.333	-1.367	-1.303	5.758	5.658	5.870	0.996
0	AA	CS	-1.359	-1.382	-1.338	5.869	5.800	5.944	0.997
0	SS	CA	-1.443	-1.491	-1.401	6.145	5.999	6.299	0.993
0	SS	AA	-1.384	-1.420	-1.350	5.977	5.861	6.091	0.996
0	SS	SS	-1.100	-1.110	-1.109	5.346	5.315	5.377	0.999
0	SS	CS	-1.308	-1.321	-1.299	6.282	6.244	6.321	0.995
0	CS	CA	-1.471	-1.516	-1.430	6.293	6.154	6.436	0.993
0	CS	AA	-1.438	-1.464	-1.414	6.203	6.124	6.290	0.997
0	CS	SS	-1.390	-1.404	-1.378	6.623	6.583	6.667	0.993
0	CS	CS	-1.060	-1.060	-1.059	5.567	5.565	5.569	1.000
0.4	CA	CA	-1.300	-1.324	-1.280	5.414	5.349	5.486	0.997
0.4	CA	AA	-1.299	-1.322	-1.278	5.409	5.343	5.478	0.997
0.4	CA	SS	-1.314	-1.340	-1.290	5.586	5.510	5.667	0.994
0.4	CA	CS	-1.318	-1.339	-1.298	5.616	5.557	5.681	0.995
0.4	AA	CA	-1.294	-1.316	-1.274	5.396	5.333	5.462	0.998
0.4	AA	AA	-1.271	-1.289	-1.253	5.327	5.273	5.383	0.999
0.4	AA	SS	-1.227	-1.242	-1.212	5.340	5.292	5.389	0.997
0.4	AA	CS	-1.138	-1.170	-1.107	5.232	5.137	5.330	0.950
0.4	SS	CA	-1.313	-1.338	-1.291	5.496	5.423	5.573	0.997
0.4	SS	AA	-1.272	-1.287	-1.258	5.368	5.325	5.416	0.999
0.4	SS	SS	-1.070	-1.073	-1.067	4.929	4.920	4.938	1.000
0.4	SS	CS	-0.888	-0.889	-0.886	4.434	4.431	4.438	1.000
0.4	CS	CA	-1.333	-1.359	-1.309	5.583	5.506	5.665	0.996
0.4	CS	AA	-1.286	-1.303	-1.270	5.436	5.385	5.488	0.998
0.4	CS	SS	-1.100	-1.105	-1.095	5.089	5.073	5.107	1.000
0.4	CS	CS	-0.899	-0.900	-0.897	4.450	4.444	4.456	0.999
0.8	CA	CA	-1.152	-1.155	-1.149	4.477	4.467	4.488	1.000
0.8	CA	AA	-1.138	-1.114	-1.136	4.438	4.432	4.444	1.000
0.8	CA	SS	-1.020	-1.022	-1.018	4.138	4.132	4.144	1.000

0.8	CA	CS	-0.911	-0.917	-0.905	3.792	3.773	3.811	0.996
0.8	AA	CA	-1.149	-1.152	-1.146	4.469	4.459	4.479	1.000
0.8	AA	AA	-1.134	-1.136	-1.133	4.428	4.422	4.434	1.000
0.8	AA	SS	-1.021	-1.024	-1.018	4.144	4.135	4.152	1.000
0.8	AA	CS	-0.921	-0.927	-0.915	3.821	3.802	3.840	0.996
0.8	SS	CA	-1.147	-1.151	-1.143	4.469	4.457	4.481	1.000
0.8	SS	AA	-1.129	-1.131	-1.128	4.418	4.413	4.424	1.000
0.8	SS	SS	-1.013	-1.015	-1.010	4.125	4.116	4.133	1.000
0.8	SS	CS	-0.917	-0.923	-0.911	3.808	3.788	3.828	0.996
0.8	CS	CA	-1.147	-1.152	-1.143	4.473	4.461	4.487	1.000
0.8	CS	AA	-1.129	-1.131	-1.127	4.420	4.414	4.426	1.000
0.8	CS	SS	-1.011	-1.013	-1.009	4.121	4.114	4.129	1.000
0.8	CS	CS	-0.918	-0.924	-0.911	3.808	3.789	3.830	0.996
Resource limitation	Mode of Competition		Mean belowground biomass						
RL_b	Aboveground	Belowground	Slope	95% CI		Intercept	95% CI		R^2
0	CA	CA	-1.450	-1.508	-1.395	6.122	5.933	6.317	0.990
0	CA	AA	-1.474	-1.534	-1.415	6.198	5.986	6.399	0.988
0	CA	SS	-1.443	-1.491	-1.401	6.145	5.999	6.299	0.993
0	CA	CS	-1.471	-1.514	-1.429	6.293	6.154	6.436	0.993
0	AA	CA	-1.477	-1.541	-1.419	6.204	5.999	6.421	0.988
0	AA	AA	-1.351	-1.389	-1.314	5.807	5.681	5.936	0.996
0	AA	SS	-1.384	-1.419	-1.350	5.977	5.862	6.092	0.996
0	AA	CS	-1.438	-1.464	-1.414	6.203	6.124	6.289	0.997
0	SS	CA	-1.387	-1.432	-1.348	5.907	5.775	6.054	0.993
0	SS	AA	-1.333	-1.367	-1.303	5.758	5.658	5.870	0.996
0	SS	SS	-1.100	-1.109	-1.092	5.346	5.316	5.375	0.999
0	SS	CS	-1.390	-1.405	-1.378	6.623	6.581	6.666	0.993
0	CS	CA	-1.392	-1.432	-1.352	5.922	5.791	6.058	0.993
0	CS	AA	-1.359	-1.380	-1.339	5.869	5.790	5.945	0.997
0	CS	SS	-1.308	-1.319	-1.297	6.282	6.246	6.320	0.995
0	CS	CS	-1.060	-1.060	-1.059	5.567	5.565	5.569	1.000
0.4	CA	CA	-1.333	-1.361	-1.308	5.650	5.571	5.737	0.996
0.4	CA	AA	-1.334	-1.364	-1.308	5.660	5.576	5.752	0.996
0.4	CA	SS	-1.440	-1.473	-1.407	6.213	6.110	6.315	0.992
0.4	CA	CS	-1.487	-1.514	-1.462	6.411	6.334	6.494	0.993
0.4	AA	CA	-1.331	-1.359	-1.306	5.643	5.564	5.728	0.996
0.4	AA	AA	-1.312	-1.335	-1.289	5.563	5.489	5.633	0.998
0.4	AA	SS	-1.332	-1.355	-1.312	5.908	5.840	5.978	0.995
0.4	AA	CS	-1.395	-1.430	-1.364	6.387	6.291	6.491	0.958
0.4	SS	CA	-1.334	-1.361	-1.309	5.657	5.575	5.470	0.996
0.4	SS	AA	-1.289	-1.307	-1.274	5.525	5.478	5.579	0.998
0.4	SS	SS	-1.114	-1.119	-1.108	5.271	5.255	5.288	1.000
0.4	SS	CS	-1.072	-1.072	-1.071	5.418	5.415	5.421	1.000
0.4	CS	CA	-1.332	-1.360	-1.308	5.650	5.572	5.735	0.996
0.4	CS	AA	-1.284	-1.302	-1.269	5.510	5.462	5.563	0.998
0.4	CS	SS	-1.104	-1.110	-1.099	5.258	5.242	5.277	0.999
0.4	CS	CS	-1.070	-1.071	-1.069	5.414	5.411	5.417	1.000
0.8	CA	CA	-1.340	-1.365	-1.320	5.485	5.416	5.559	0.993

0.8	CA	AA	-1.320	-1.341	-1.301	5.404	5.352	5.463	0.995
0.8	CA	SS	-1.185	-1.197	-1.174	5.171	5.137	5.207	0.997
0.8	CA	CS	-1.075	-1.080	-1.070	4.905	4.889	4.920	0.999
0.8	AA	CA	-1.350	-1.373	-1.328	5.486	5.417	5.558	0.993
0.8	AA	AA	-1.319	-1.337	-1.303	5.374	5.323	5.430	0.996
0.8	AA	SS	-1.169	-1.177	-1.161	5.118	5.094	5.144	0.998
0.8	AA	CS	-1.065	-1.068	-1.062	4.876	4.867	4.884	1.000
0.8	SS	CA	-1.341	-1.365	-1.318	5.491	5.420	5.565	0.993
0.8	SS	AA	-1.321	-1.337	-1.298	5.347	5.299	5.398	0.997
0.8	SS	SS	-1.167	-1.175	-1.159	5.111	5.088	5.136	0.999
0.8	SS	CS	-1.065	-1.067	-1.062	4.874	4.867	4.882	1.000
0.8	CS	CA	-1.351	-1.375	-1.329	5.492	5.422	5.565	0.993
0.8	CS	AA	-1.301	-1.317	-1.285	5.350	5.301	5.400	0.997
0.8	CS	SS	-1.161	-1.168	-1.154	5.093	5.072	5.116	0.999
0.8	CS	CS	-1.065	-1.067	-1.062	4.874	4.866	4.882	1.000

Table S2. Slopes and intercepts of mass-density relationships between the mean total, above- and belowground biomass of *Betula pendula* seedlings in greenhouse experiment with different nutrient treatments (log-log transformed; as estimated by standard major axis regression). F: fertilization, NF: non-fertilization.

Treatment	Biomass	Slope	95% CI	Intercept	95% CI	R^2
F	Total	-1.031	-1.428 to -0.745	5.967	5.145 to 7.288	0.609
	Above	-1.047	-1.450 to -0.756	5.943	5.168 to 7.327	0.609
	Below	-1.066	-1.489 to -0.738	5.330	4.447 to 6.685	0.498
NF	Total	-0.901	-1.146 to -0.709	5.081	4.389 to 5.771	0.760
	Above	-0.895	-1.145 to -0.701	4.961	4.255 to 5.617	0.748
	Below	-0.954	-1.209 to -0.753	4.575	3.882 to 5.338	0.767

Chapter 4

Exploring the interplay between modes of positive and negative plant interactions *

Abstract

Facilitation (positive interaction) has received increasing attention in plant ecology over the last decade. Just as for competition, distinguishing different modes of facilitation (mutualistic, commensal or even antagonistic) may be crucial. We therefore introduce the new concept of symmetric vs. asymmetric facilitation and present a generic individual-based zone-of-influence model. The model simultaneously implements different modes of both facilitation and competition among individual plants via their overlapping zone of influence. Because we consider facilitation modes as a continuum related to environmental context, we integrated this concept with the stress gradient hypothesis (SGH) by exploring differences in spatial pattern formation in self-thinning plants along a stress gradient in our model. The interplay among

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¹ Institute of Forest Growth and Computer Science, Dresden University of Technology, P.O. 1117, 01735 Tharandt, Germany; ² Helmholtz Centre for Environmental Research – UFZ, Department of Ecological Modelling, 04318 Leipzig, Germany; ³ Institute for Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, 14469 Potsdam, Germany; ⁴ Institute of Hydrobiology, Dresden University of Technology, Zellescher Weg 40, 01062 Dresden, Germany

modes of interaction creates distinctly varied spatial patterns along stress gradients. When competition was symmetric, symmetric facilitation (mutualism) consistently led to plant aggregation along stress gradients. However, asymmetric facilitation (commensalism) produces plant aggregation only under more benign conditions but tends to intensify local competition and spatial segregation when conditions are harsh. When competition was completely asymmetric, different modes of facilitation contributed little to spatial aggregation. Symmetric facilitation significantly increased survival at the severe end of the stress gradient, which supports the claim of the SGH that facilitation should have generally positive net effects on plants under high stress levels. Asymmetric facilitation, however, was found to increase survival only under intermediate stress conditions, which contradicts the current predictions of the SGH. Our modelling study demonstrates that the interplay between modes of facilitation and competition affects different aspects of plant populations and communities, implying context-dependent outcomes and consequences. The explicit consideration of the modes and mechanisms of interactions (both facilitation and competition) and the nature of stress factors will help to extend the framework of the SGH and foster research on facilitation in plant ecology.

Keywords: asymmetry, competition, metabolic scaling theory, plant-plant interaction, plant population and community dynamics, self-thinning, spatial pattern, stress gradient hypothesis, symmetry

4.1 Introduction

The role of positive interactions in driving population and community dynamics has received significant attention and is now widely recognized in both empirical and theoretical ecology (Bertness & Callaway 1994; Brooker *et al.* 2008; Bronstein 2009; Maestre *et al.* 2009; Fajardo & McIntire 2011; McIntire & Fajardo 2011). In plant ecology, positive interactions are usually referred to as facilitation, which has been defined as the beneficial effects of neighbours via the amelioration of habitat (Bertness & Callaway 1994; Bronstein 2009); e.g. via moderation of stress, enrichment of nutrients, or increased access to nutrients. Facilitation has been shown particularly important when considering the performance of plants under stressful environmental conditions. ‘Stress’ is not a precise concept (Maestre *et al.* 2009), and can be biotic and abiotic (Bronstein 2009). The best-understood examples of plant facilitation were mostly carried out under abiotic stress conditions (Bronstein 2009). Moreover, the characteristics of abiotic stress factors are also different and can be resource-independent (e.g. wind, frost and salinity) or resource-dependent (e.g. water, nutrient and light; Maestre *et al.* 2009).

The “stress gradient hypothesis” (SGH) proposes that competition and facilitation may act simultaneously, but the relative importance of facilitation and competition will vary inversely along gradients of abiotic stress (Bertness & Callaway 1994). Under high stress conditions, facilitation should be dominant over competition in affecting community structures (Bertness & Callaway 1994; Brooker *et al.* 2008; Maestre *et al.* 2009). The SGH was originally formulated at the interspecific level, but recent studies revealed that SGH is also valid at the intraspecific level (Chu *et al.* 2008, 2009; Eränen & Kozlov 2008; McIntire & Fajardo 2011). The interplay between facilitation and competition can thus drive intraspecific population dynamics (Chu *et al.* 2008, 2009, 2010; Jia *et al.* 2011; McIntire & Fajardo 2011), community structure

(Gross 2008; Xiao *et al.* 2009), community diversity (Cavieres & Badano 2009), and ecosystem functions (Callaway *et al.* 2002; Kikvidze *et al.* 2005); and can even have evolutionary consequences (Bronstein 2009; McIntire & Fajardo 2011).

However, there are also studies which do not support SGH predictions, as facilitative effects have not been detected under some extreme stress conditions (Tielbörger & Kadmon 2000; Maestre *et al.* 2005, 2009). This indicates that the conceptual framework underlying the SGH might need further refinement (Maestre *et al.* 2009). Moreover, whereas numerous studies have explored the consequences of different modes of competition, i.e. symmetric versus asymmetric competition (Schwinning & Weiner 1998; Weiner *et al.* 2001; Stoll & Bergius 2005; Berger *et al.* 2008), different modes of facilitation have not yet been explored. Inconsistent definitions of facilitation and the lack of differentiation between the impacts of plant-plant interactions on beneficiary and benefactor individuals have recently been identified as important gaps in current research (Brooker *et al.* 2008; Bronstein 2009; Brooker & Callaway 2009; Pakeman *et al.* 2009). Refining and clarifying the concept of facilitation is crucial for understanding how facilitation arises, persists and evolves, and then could help extend the general SGH framework and improve plant ecology research in general (Brooker *et al.* 2008; Bronstein 2009; Maestre *et al.* 2009).

According to different definitions, modes of facilitation can be mutualistic (+/+) or commensal (+/0) amongst plants (Brooker *et al.* 2008; Bronstein 2009). However, a more continuous approach to facilitative interactions might be more accurate and useful, as has been the case for the corresponding continuous approach to exploring competitive interactions (Schwinning & Weiner 1998). We therefore suggest using a new concept of modes of facilitation: any facilitation among plants, no matter whether inter- or intra-specific, can be placed along a continuum ranging from completely symmetric facilitation (interacting plants receive the same amount of benefit

from each other, irrespective of their species or sizes) to completely asymmetric facilitation (Vellend 2008; the beneficiary plant receives all benefits but there are no positive effects on the benefactor; Table 4.1). Thus, mutualistic cases are expected to be at the symmetric end of the facilitation continuum, and commensal cases at the asymmetric end (Fig. S1).

Table 4.1 Definition and description of facilitation modes. The index q determines the mode of facilitation among plants (see equation 5-5 and Appendix A).

Mode of facilitation	Effect and definition	Index value	Expected prevalent nature of stress factor
Complete symmetry	All plants receive the same amount of benefit from each other, irrespective of their species or sizes	$q = 0$	Symmetry: temperature, moisture, nutrient, salinity, pollution, wind desiccation, altitude etc.
Partial symmetry	Benefit increases with benefactor's size, but less than proportionally	$0 < q < 1$	
Proportional symmetry	Benefit is proportional to benefactor's size (equal gain per unit size)	$q = 1$	
Partial asymmetry	Benefit increases with benefactor's size super-linearly	$q > 1$	Asymmetry: light, UV-radiation, transpiration, tide, water, nutrient fixation, pollution, wind, herbivory, etc.
Complete asymmetry	The beneficiary plant receives all benefits, with no advantage to the benefactor plants	$q = \infty$	

This new conceptual model (with its terminology) has two main advantages: it is analogous, and therefore directly comparable to the widely used and important concept of symmetric and asymmetric competition (Schwinning &

Weiner 1998; Weiner *et al.* 2001; Stoll & Bergius 2005; Berger *et al.* 2008); it also offers a quantitative and operational means of evaluating facilitative impacts.

The analogy between different modes of competition and facilitation is evident. In reality, competition and facilitation often interact: clusters of cohorts facilitate each other against cold or wind desiccation (symmetric facilitation), but they may also compete for nutrients and water (symmetric competition; Fajardo & McIntire 2011). Adult nurse plants facilitate the growth and survival of small plants of their own or other species (asymmetric facilitation), which may lead to asymmetric light competition if the crown of an adult plant is very dense or the small plants are not “stress-tolerant” (Reinhart *et al.* 2006; Maestre *et al.* 2009). In general, modes of interaction depend on both the ecological traits of the interacting plants and the nature of the stress factors themselves (Maestre *et al.* 2009).

Competition usually leads to the spatial segregation of plants, implying that distributions are more regular than aggregated (Stoll & Bergius 2005; Perry *et al.* 2006). However, spatial aggregation is ubiquitous amongst varied plant systems, especially in harsh environments (Bertness & Callaway 1994; Haase 2001; Perry *et al.* 2006). Because SGH predicts that facilitation should dominate in such harsh environments, facilitation is believed to be an important factor explaining plant aggregation in addition to other ecological factors (e.g. topography, resource availability and dispersal) (Bertness & Callaway 1994; Haase 2001; Perry *et al.* 2006). It has indeed been shown that facilitation tends to maintain the aggregation of seedling cohorts and established plants (Bertness & Callaway 1994; Fajardo & McIntire 2011; Jia *et al.* 2011; McIntire & Fajardo 2011), but we do not yet know whether this is generally true for different modes of facilitation and at different stress levels.

Consequently, we do not know how different modes of competition modify the effects of facilitation on plants and structure their populations and communities in different environmental contexts (Brooker *et al.* 2008). To

address this issue, we implemented different modes of facilitation and competition in a generic individual-based model based on the zone-of-influence (ZOI) approach of Weiner *et al.* (2001). Plant growth and density-dependent mortality are described according to a growth model as deriving from “metabolic scaling theory” (MST; Brown *et al.* 2004; Savage *et al.* 2010) to provide mechanistic representation of plant response to stress. To simplify, we restrict ourselves to intraspecific plant interactions. Specifically, we addressed the following questions at both the plant population and individual levels: (1) How does the interplay of different modes of competition and facilitation change spatial pattern formation during self-thinning in conspecific cohorts that initially have a random or aggregated distribution; and (2) How do combinations of modes of competition and facilitation alter the intensity of local plant interactions along a stress gradient?

4.2 Methods

4.2.1 The model

Metabolic scaling theory (MST) predicts quantitative relationships amongst metabolic processes using empirical measurements and theoretical assumptions (West *et al.* 2001; Enquist 2002; Enquist *et al.* 2009; Savage *et al.* 2010). We adopted these relationships as the basis of our individual growth model for plants (see Chapter 2). The model is derived from an energy conservation equation (Enquist & Niklas 2001; West *et al.* 2001; Hou *et al.* 2008) and takes into account respiration and three basic energy-demanding processes: biomass maintenance, ion transport and biosynthesis (Lambers *et al.* 2008). It provides a mechanistic and quantitative basis for linking the energy used in metabolism of plants under abiotic stress to local interactions and population dynamics. The growth model is:

$$dm/dt = am^{3/4} - bm = am^{3/4} [1 - (m / M_0)^{1/4}] \quad (4-1)$$

where m is total plant biomass, a and b are species-specific constants (Chapter 2) determined by systematic variation of the *in vivo* metabolic rate of different taxa (West *et al.* 2001), and $M_0 = (a/b)^4$ is the asymptotic maximum size of a plant (calculated for $dm/dt = 0$). The term $am^{3/4}$ in equation (4-1) dominates during early plant growth and provides a good quantitative description of plant growth (Enquist *et al.* 2009).

Because stress can be resource-independent or resource-dependent (Maestre *et al.* 2009), we assume abiotic stress factors act in one or both of two ways: by restricting the energy intake rate and burdening biomass maintenance. This assumption provides a mechanistic basis for representing the effects of stress on plant performance (Lambers *et al.* 2008). Accordingly, the growth model with stress is:

$$dm/dt = (1 - S) am^{3/4} [1 - (m / M_s)^{1/4}] \quad (4-2)$$

where S is a dimensionless efficiency factor that indicates the level of stress, ranging from 0 (no stress) to 1 (extreme stress). $M_s = (1-S)^4 M_0$ is the maximum plant biomass achievable under stress.

Our individual-based model (IBM; Grimm & Railsback 2005) is described in detail in the Supporting Information, following the ODD protocol (Overview, Design concepts, Details) for describing individual-based models (Grimm *et al.* 2006; Grimm *et al.* 2010). In the following, we describe the model's main elements. In our IBM, a plant's circular ZOI (Weiner *et al.* 2001), A , is the physical space in which a plant acquires resources and represents the energy and resources potentially available to the plant. This space is allometrically related to plant biomass, m , as $c_0 A = m^{3/4}$ (Enquist & Niklas 2001), where c_0 is a normalization constant. We represent plant interaction by calculating the overlapping areas among the plants' ZOIs (Weiner *et al.* 2001; Chu *et al.* 2008, 2009, 2010). Competition and facilitation under abiotic stress are incorporated

by using dimensionless factors or indexes, f_p and f_q , respectively. With these assumptions, equation (4-2) becomes:

$$dm/dt = f_p f_q c A [1 - (m / M)^{1/4}] \quad (4-3)$$

where f_p is the index of competition, f_q refers to the abiotic stress (S) modified by facilitation (see below), $c = ac_0$ is the initial growth rate in units of biomass per area and time, and $M = (f_p f_q)^4 M_0$ is the maximum biomass achievable under stress in the presence of competition and facilitation. Modes of competition among plants can be defined along a continuum from completely asymmetric competition (largest plants obtain all contested resources) to completely symmetric competition (resources in areas of overlap are divided equally among all overlapping individuals, irrespective of their relative sizes; Schwinning & Weiner 1998). To represent the different modes of competition, we define the index of competition, f_p , as

$$f_p = (A_{no} + \sum_{k=1}^{n_o} \frac{v_i m_i^p}{\sum_{j=1}^{n_j} v_j m_j^p} A_{o,k}) / A \quad (4-4)$$

This index refers to the fraction of resources available in a given area to a plant i after the loss of potential resources from areas overlapping neighbours with biomass m_j (Schwinning & Weiner 1998). A_{no} is the area with no overlap from neighbours, and $A_{o,k}$ denotes the n_o areas overlapping n_j different neighbours. The number of overlapping areas, n_o , can vary due to the position and number of neighbours (see Appendix A). Parameter p indicates the mode of competition, ranging from complete symmetry ($p = 0$) to complete asymmetry (p approaching infinity). In this article we restrict ourselves to intraspecific competition and facilitation, and assume, therefore, that the species-specific weighting constants of competition v_i and v_j equal 1.

Similarly, we define the index of facilitation modifying abiotic stress, f_q , as

$$f_q = 1 - \frac{S}{A_f + 1} = 1 - \frac{S}{\sum_{k=1}^{n_o} \left(1 - \frac{w_i m_i^q}{\sum_{j=1}^{n_j} w_j m_j^q}\right) A_{o,k} + 1} \quad (4-5)$$

This term is based on SGH, which reflects the facilitative effect of relieving stress, and is consistent with earlier models (Chu *et al.* 2008, 2009, 2010). Our definition includes earlier indices of facilitation as a special case, all of which only represent symmetric facilitation (Brooker *et al.* 2008; Chu *et al.* 2008, 2009, 2010; Jia *et al.* 2011; see Appendix A). Here, A_f indicates the benefits gained by a plant from all interactive neighbours under abiotic stress (S), which is calculated as the sum of the areas overlapping ZOIs of neighbour plants. Index q determines the mode of facilitation among plants, ranging from complete symmetry ($q = 0$, algorithmic equivalent to the form used in Chu *et al.* 2008, 2009) to complete asymmetry (q approaching infinity; Table 1). When there is no facilitation ($A_f = 0$), equation (4-5) becomes $1-S$, which reflects the effect of abiotic stress. As for competition, the species-specific weighting constants of facilitation, w_i and w_j , equal 1 when considering intraspecific interactions, as we do here.

Equation (4-3) describes how plants grow under local competition, abiotic stress and facilitation. Equations (4-1), (4-2) and (4-3) are similar to the von Bertalanffy growth function and other phenomenological growth functions (Weiner *et al.* 2001; Chu *et al.* 2008, 2009, 2010; Jia *et al.* 2011). However, these equations are derived from first principles and their parameters and are directly linked to physical and biological processes.

Because individual plant mortality is proportional to mass-specific metabolic rate (Brown *et al.* 2004), we assume that individuals die if their actual growth rate (realistic metabolic rate) falls below a threshold fraction of their basal metabolic rate (scaled by current biomass, i.e. 5% of $m^{3/4}$). Therefore, individual plants may die due to metabolic inactivation caused by environmental stress, local competition, senescence (when m approaches M)

or combinations thereof.

Our model was implemented in NetLogo 4.1.3 (Wilensky 1999). The source code is available in the online supporting information of the publication (<http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2745.2012.02019.x/supinfo>).

4.2.2 Scenarios and analysis

We investigated 2 modes of facilitation ($q = 0$: completely symmetric and $q = \infty$: completely asymmetric) and 2 modes of competition ($p = 0$: completely symmetric and $p = \infty$: completely asymmetric), at 3 stress levels ($S = 0.1, 0.5$ and 0.9). Two initial conditions were used: 300 initial plants distributed over space either with aggregation or randomly (Fig. 4.1). For both aggregated and random initial location scenarios, all simulations (42 scenarios in total) began with exactly the same plant locations (i.e. using the same random number seed), so that differences in results can be ascribed entirely to the interplay among modes of competition and facilitation at different stress levels. (In simulations not reported here, we used other initial densities, initial locations, and interaction combinations to confirm that our general conclusions were not artefacts of initial conditions.)

Ripley's K function is widely used to analyse the spatial point pattern of plants (Ripley 1981; Stoll & Bergius 2005; Perry *et al.* 2006). Here, we employed the variance-stabilizing K function, the so-called Ripley's L function, to evaluate spatial pattern dynamics. The L function, $L(r)$, characterizes the point pattern at certain scales (r), with an expected value of zero under the null hypothesis of complete spatial randomness (CSR). We carried out 499 Monte Carlo simulations for each scenario to determine the 95% confidence envelopes of the L function for CSR. Observed $L(r)$ values out of the envelopes indicate significant aggregation or regularity. Spatial point pattern data were collected at 6 densities (300, 250, 200, 150, 100 and 50 plants) during the self-thinning process. All statistical analyses were accomplished using R 2.11.1 (R Development Core Team, 2010).

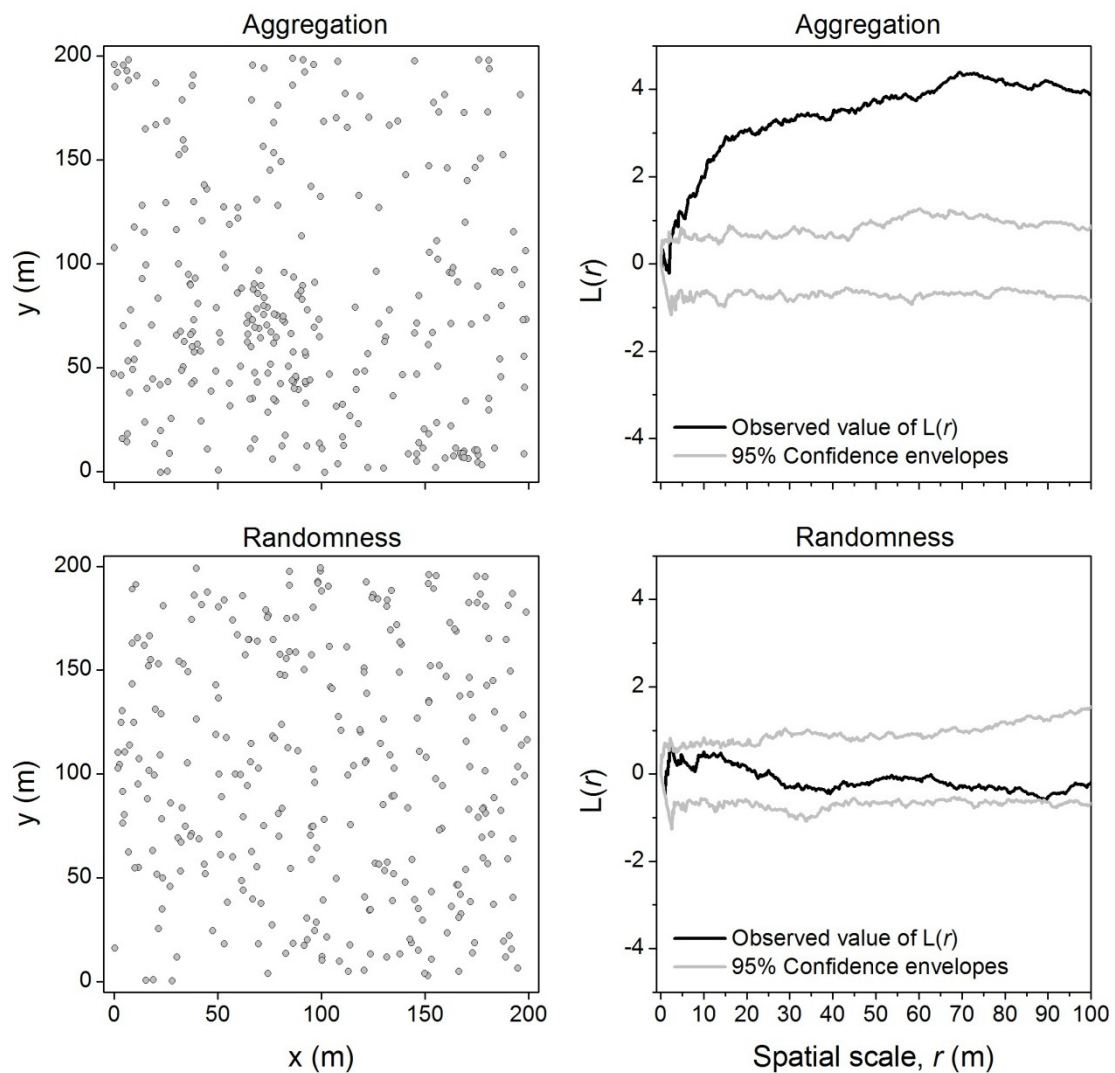


Fig. 4.1 Initial spatial pattern (left) and corresponding spatial point analysis (Ripley's L function, right) of simulated populations. The relative position of observed value of $L(r)$ in relation to 95% confidence envelopes indicates the spatial pattern at certain scales (r): above the bounds indicates aggregation, between the bounds indicates randomness, and below them indicates regularity.

To evaluate the net outcome of local interactions (interplay between competition and facilitation) on the performance of individual plants, we used the relative interaction index RII (Armas *et al.* 2004):

$$RII = (m_1 - m_0) / (m_1 + m_0) \quad (4-6)$$

where m_1 and m_0 are the performance (mean biomass) of surviving plants at the same resource level with and without local interactions (i.e. isolated plants),

respectively. Values of RII from -1 to 1 indicate the net outcome of interactions as negative (from -1 to 0), neutral (equal to 0) and positive (from 0 to 1). To estimate m_0 , we using equation (4-2) for plant growth in all scenarios.

4.3 Results

The interplay between competition and facilitation strongly influenced spatial pattern formation in the plant population along the stress gradient. Different modes of competition and facilitation also led to distinct spatial patterns. With aggregated initial locations (Fig. 4.1), facilitation was vital for maintaining aggregated patterns if competition was completely symmetric (C_{CS} , $p = 0$) (Fig. 4.2). Without facilitation (NF), aggregation was maintained only until the number of surviving plants decreased to 200 (Fig. 4.2a–c). With symmetric facilitation (F_{CS} , $q = 0$), plant aggregation patterns can be maintained (Fig. 4.2d–f) even at quite low density (100 plants), depending on the level of stress. Aggregated patterns are particularly robust at high stress levels, which is consistent with the predictions of SGH.

In contrast, with asymmetric facilitation (F_{CA} , $q = \infty$), aggregating (Figs 4.2g and 4.2h) can be maintained only at mild or intermediate stress levels ($S = 0.1$ and 0.5). Under harsh conditions ($S = 0.9$), aggregation disappears early in the self-thinning process (Fig. 4.2i), a result that deviates from predictions of SGH. However, modes of facilitation had little effect on maintaining aggregation when competition was completely asymmetric (C_{CA} , $p = \infty$; Fig. S2).

The importance of facilitation for creating aggregation became more obvious when the initial pattern was random (Fig. 4.3). Under completely symmetric competition without facilitation and under benign condition, there was some slight spatial aggregation (values of $L(r)$ were very close to the upper boundary of the 95% confidence envelopes defining lack of aggregation) at very small scales (Fig. 4.3a), but this aggregation instantly disappeared when stress

increased (Fig 4.3b and 4.3c). In contrast, more pronounced aggregation patterns emerged in the presence of facilitation: symmetric facilitation consistently forced aggregation under harsh conditions (Fig. 4.3d–f); asymmetric facilitation led to aggregation only when stress was milder (Fig. 4.3g–i). Nevertheless, asymmetric competition can largely override the effects of facilitation on spatial pattern formation at all stress levels, leading to non-aggregative (even regular) spatial distributions (Fig. S3). This is in agreement with empirical findings (Stoll & Bergius 2005).

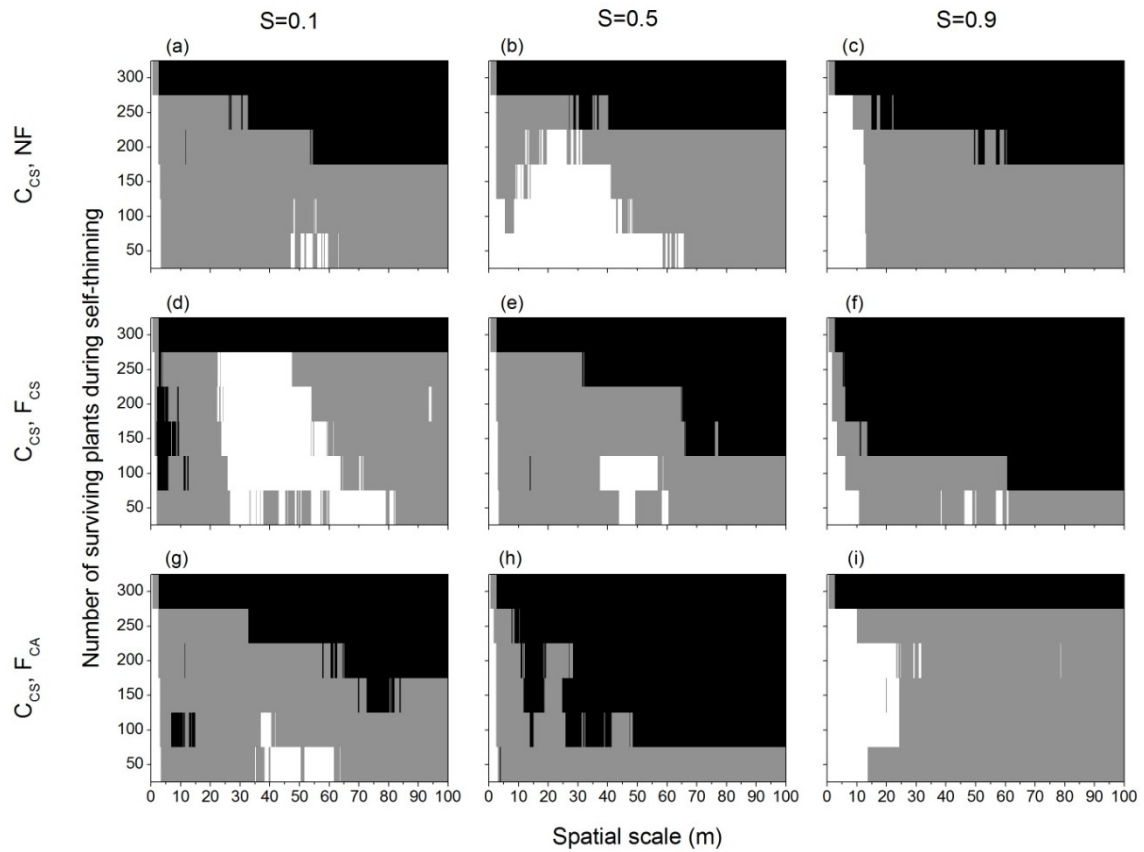


Fig. 4.2 Spatial dynamics (black, aggregation; grey, randomness; white, regularity) during self-thinning, with aggregated initial locations and completely symmetric competition (C_{CS} , $p = 0$) in the absence (NF) or presence of facilitation (F_{CS} , completely symmetric facilitation, $q = 0$; F_{CA} , completely asymmetric facilitation, $q = \infty$) at different levels of abiotic stress (S).

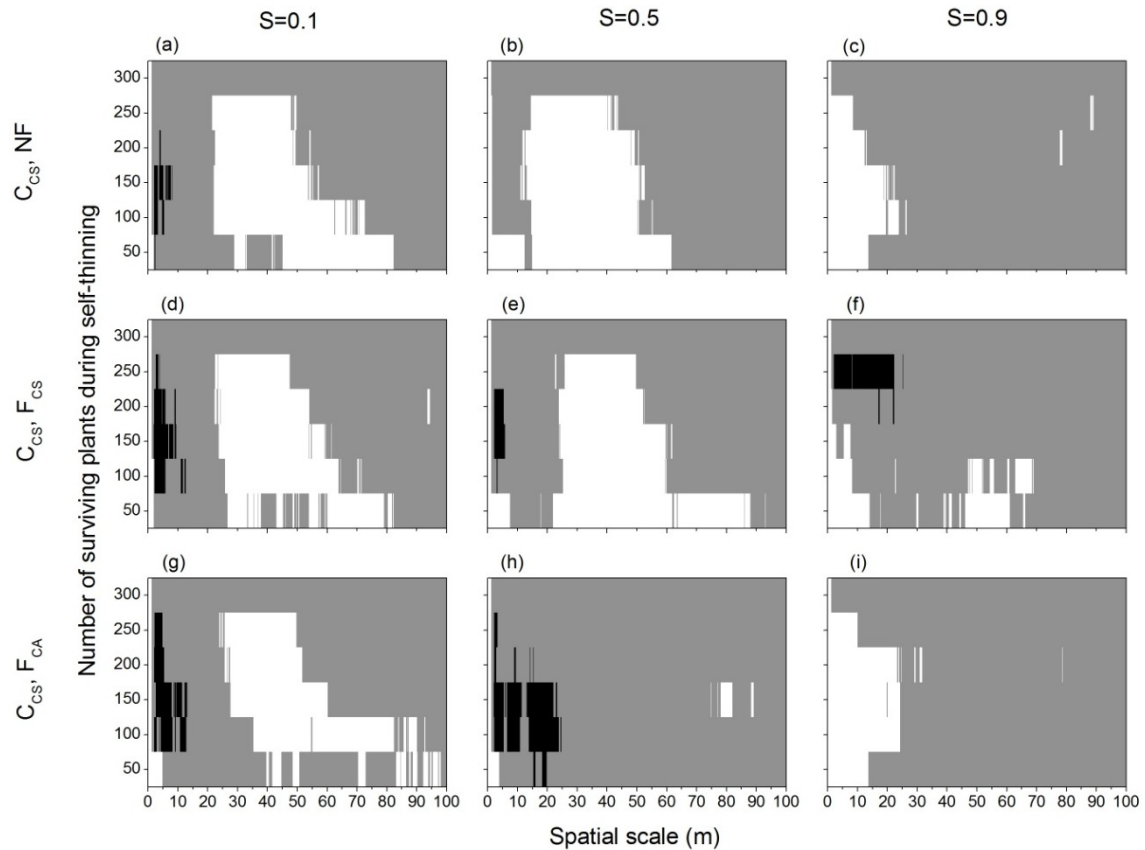


Fig. 4.3 Spatial dynamics during self-thinning with random initial locations. Symbols and abbreviations are the same as in Fig. 4.2.

The relationship between net outcome of local plant interactions (as evaluated with the RII index) and spatial pattern formation also depended on the modes of interaction and the level of abiotic stress (Fig. 4.4). In the case of symmetric competition, the net outcome of local interactions was significantly negative (RII close to -1) under mild and intermediate stress conditions independent of the mode of facilitation. RII increased with stress levels and had clearly positive values (RII close to 1) at high stress levels in the presence of symmetric facilitation. In the case of asymmetric competition, the net outcome of local interactions was slightly negative under mild conditions. RII increased monotonically with increasing abiotic stress under symmetric facilitation, but first increased then decreased with increasing abiotic stress under asymmetric facilitation.

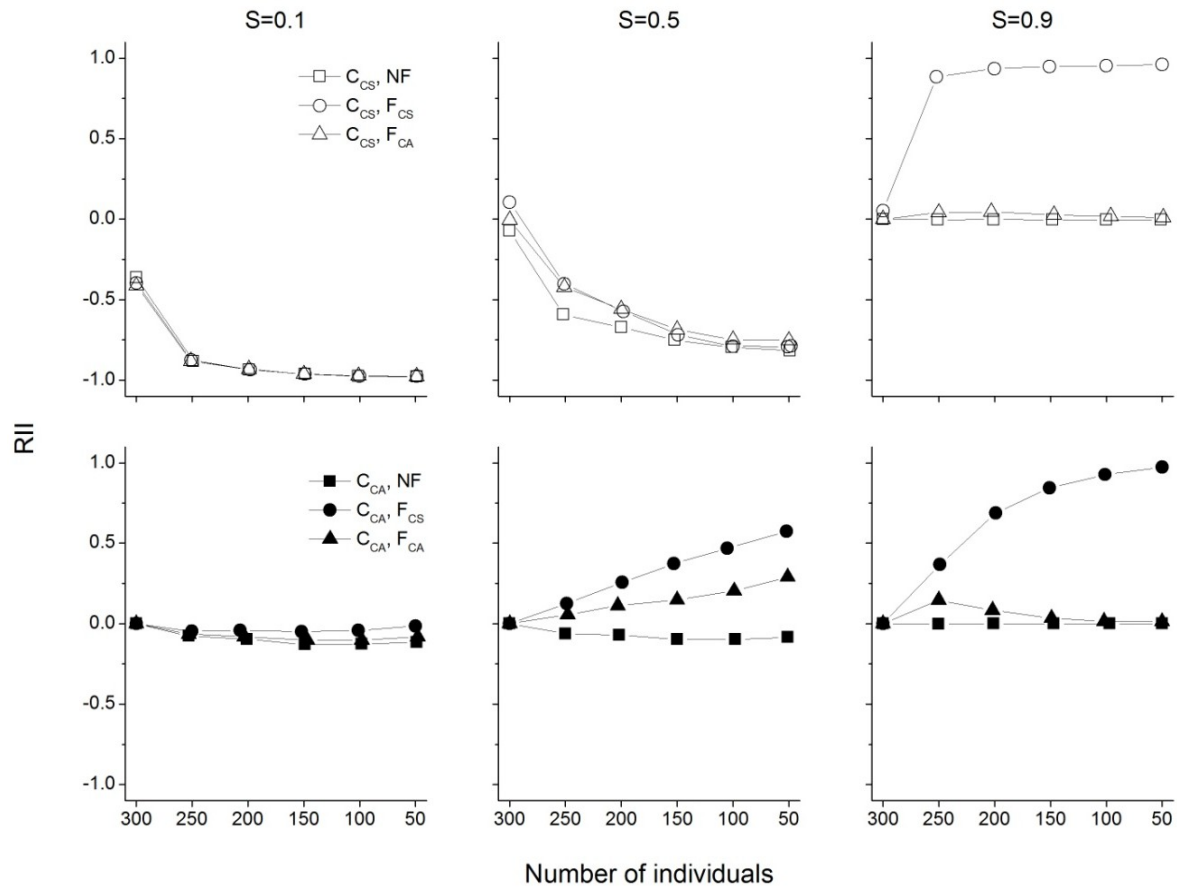


Fig. 4.4 Relative interaction intensity (RII) during self-thinning under different modes of competition (C_{CS} , completely symmetric competition, $p = 0$; C_{CA} , completely asymmetric competition, $p = \infty$) in the absence (NF) or presence of facilitation (F_{CS} , completely symmetric facilitation, $q = 0$; F_{CA} , completely asymmetric facilitation, $q = \infty$) at different levels of abiotic stress (S), and with aggregated initial locations.

Facilitation sometimes resulted in spatial aggregation (Figs 4.2 and 4.3) even though the net outcome (RII) of local interaction was negative. This spatial patterning also depended on the mode of competition. Such results indicate that even though facilitation was responsible for resulting plant aggregation, the net outcome of local interaction was not always positive under harsh conditions. In other words, modes of interaction can have different effects on different population characteristics, i.e. here individual growth (RII) and spatial pattern.

Symmetric facilitation not only mitigated abiotic stress but also delayed the onset of mortality in the case of symmetric competition, at all stress levels (Duncan's test, $P < 0.05$). Symmetric facilitation delayed the self-thinning process, as indicated by the increased survival over time (Fig. 4.5). Asymmetric facilitation had the same effect only at intermediate stress levels, not at harsh conditions (Duncan's test, $P > 0.05$). However, in the case of asymmetric competition, the effects of facilitation were relatively weak.

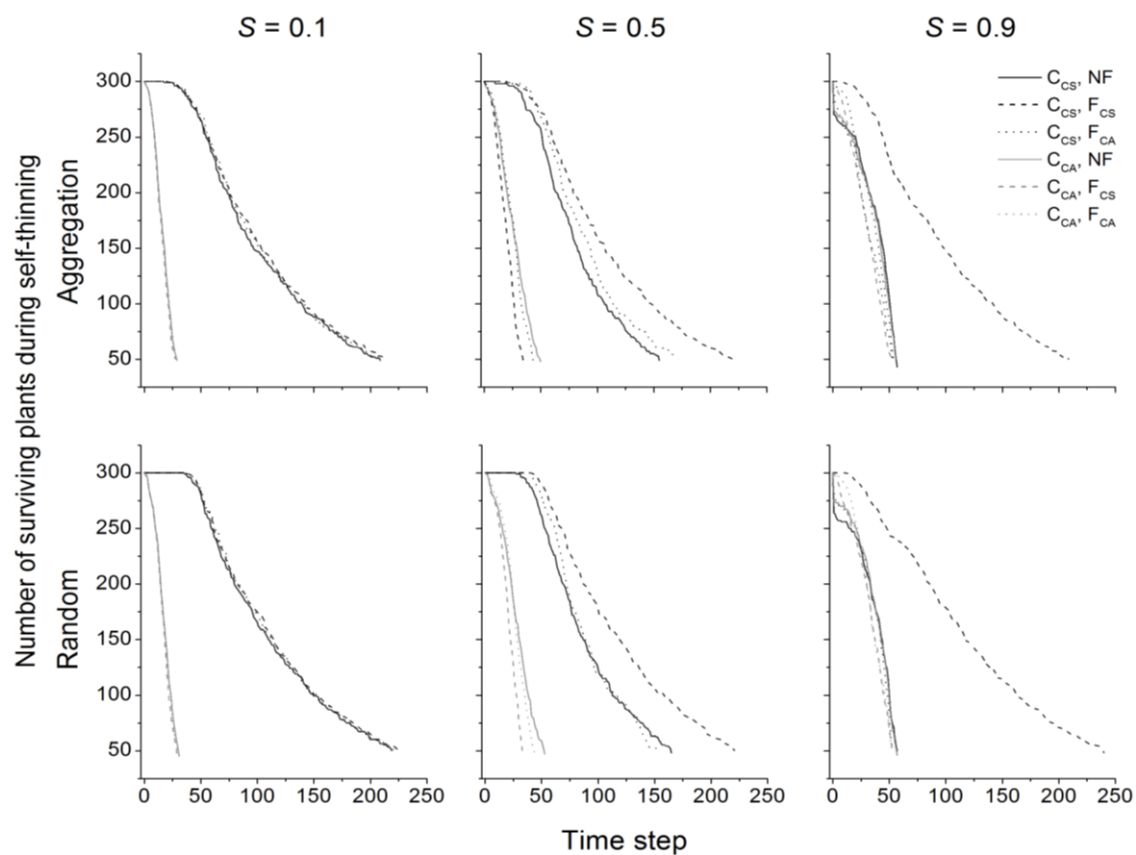


Fig. 4.5 Temporal dynamics of density-dependent mortality under different modes of competition (C_{CS} , complete symmetric competition, $p = 0$; C_{CA} , complete asymmetric competition, $p = \infty$) in the absence (NF) or presence of facilitation (F_{CS} , completely symmetric facilitation, $q = 0$; F_{CA} , completely asymmetric facilitation, $q = \infty$) at different levels of abiotic stress (S), and for both initial location scenarios.

4.4 Discussion

We have introduced the new concept of modes of facilitation, i.e. symmetric versus asymmetric facilitation, and have used an individual-based model to explore how these facilitation modes affect plant populations differently. Specifically, we explored how the interplay between different modes of competition and facilitation changes spatial pattern formation during self-thinning in populations that start with either random or aggregated distributions, and how combinations of competition and facilitation modes alter the intensity of local plant interactions along a stress gradient.

Our main finding was that the spatial aggregation of plants can be attributed to different modes of facilitation if competition is symmetric rather than asymmetric, whereas non-aggregative (regular) patterns indicate strong asymmetric competition driving density-dependent mortality (Stoll & Bergius 2005). Facilitation by itself can play an important role in promoting plant aggregation independent of other ecological factors ignored in our scenarios (e.g. seed dispersal, recruitment, and environmental heterogeneity); moreover, different modes of facilitation led to different spatial and temporal patterns.

In our simulations of harsh conditions, plants had highest biomass accumulation and survival under the combination of symmetric competition and facilitation. This result emerged from growing in association with neighbours due to facilitation and the increased importance of facilitation at higher stress levels as predicted by SGH. McIntire & Fajardo (2011) found that spatial aggregation and symmetric interactions in *Nothofagus pumilio* are essential for the species' success under harsh conditions. Seedlings growing in clustered cohorts facilitate each other and have higher survival rates than isolated individuals under stress of wind desiccation. With seedlings growing in clusters, natural grafts (physiological and physical merging of stem, branch or root) occur in later growth stages, and multi-stemmed trees survive better than single-stemmed trees. The mode of facilitation and competition among grafted

plants is considered to be symmetric because the transport of resources and assimilates is bidirectional (Silvertown & Charlesworth 2001; Lambers *et al.* 2008). The combination of symmetric facilitation and competition in these tree clusters decreases the impact of stress and the onset of competition among them (Fajardo & McIntire 2010; Tarroux & DesRochers 2011). Therefore, mortality is lower within clusters and leads to aggregation, an outcome we also found in our model.

Because we based our model of facilitation on SGH, a monotonic increase in the importance of facilitation with increasing stress should be expected due to the assumptions underlying equation (4-5). Surprisingly, this effect was outweighed by asymmetric facilitation. Our study indicated that with symmetric competition, asymmetric facilitation first promotes plant aggregation under mild and intermediate stress conditions, but then brings about spatial disaggregation at the more stressful end of the gradient (Fig. 4.2g-i). Moreover, asymmetric facilitation was found to delay the self-thinning process (indicated by increased survival over time) only under intermediate stress conditions (Fig. 4.5). This is because under very stressful conditions, plants are very sensitive to physical stress and local competition. Competition will thus aggravate the mortality of those individuals that were disadvantaged by asymmetric facilitation. Asymmetric facilitation can thus promote plant survival and aggregation only if the environment is less harsh, as we observed in our model.

Our results regarding asymmetric facilitation are consistent with recent empirical findings that the SGH is not fully supported by observations (Maestre *et al.* 2009). Reduced positive effects on plant survival have been observed in arid areas at high stress levels (Tielbörger & Kadmon 2000; Maestre *et al.* 2005; Maestre *et al.* 2009). A switch from negative to positive and back to negative effects on plant survival was found in a semi-arid steppe along a gradient of decreasing rainfall (Maestre & Cortina 2004). Similarly, Tielbörger & Kadmon (2000) found that the effect of desert shrubs on abundance and

reproductive success of understory annuals shifted from positive to neutral and to negative with decreasing annual rainfall.

Our findings suggest a mechanism explaining such exceptions to the SGH's prediction of monotonic increasing net positive effect with stress: the nature of abiotic stress factors is also important (Maestre *et al.* 2009). Abiotic stress factors not only alter the mode of competition (Schwinning & Weiner 1998; Berger *et al.* 2008), but also the mode of facilitation (Maestre *et al.* 2009). It is therefore important to ask how symmetric and asymmetric facilitation are interrelated with different kinds of stress factors. In the light of the new concept presented here, it should be expected that if the effect of stress is symmetrically mitigated by other individuals, symmetric facilitation should usually be prevalent (detected via plant aggregation or positive RII in our simulation). Using an individual-based model, Chu *et al.* (2009) found that symmetric facilitation (mutualism) among plants can increase plant biomass and size inequality in conspecific populations. Their results are consistent with empirical findings for an annual species (*Elymus nutans*) in alpine meadows (although they worked with clonal ramets, which probably confounded physiological integration with positive interactions among individuals; Fajardo & McIntire 2011). The mode of facilitation in their experiment was probably symmetric because frost is the most important stress factor in their research area (Chu *et al.* 2009): all individuals endure the same degree of low temperature stress, which is not asymmetrically mitigated by other individuals.

In contrast, when the stress factor is “pre-mitigable” and/or directional (e.g. higher ultraviolet radiation due to ozonosphere depletion or direct damage caused by wind), facilitation should be more asymmetric (Fig. S1). For example, in a conspecific plant population under strong ultraviolet radiation, taller plants (benefactor) will suffer most from radiation stress but their crowns can reduce stress in the understory microenvironment. As a result, smaller plants (beneficiary) can receive disproportionately more benefit from their neighbouring taller plants for maintenance and growth, and therefore survive

longer. Asymmetric facilitation should thus reduce size inequality in plant populations, which is in contrast to symmetric facilitation that can increase size inequality (Chu *et al.* 2009). This effect of asymmetric facilitation is observed in our model and consistent with empirical studies (Zhang *et al.* 2012). To the best of our knowledge, effects of different modes of facilitation have not been addressed systematically in empirical experiments yet, so we suggest this topic for future research.

To answer our second research question about the effect of different combinations of competition and facilitation on local interactions, we employed the index R_{II} to measure the direction and magnitude of local interactions along a stress gradient. We found a monotonically increasing strength of facilitation relative to competition for symmetric facilitation but not for asymmetric facilitation. Negative interaction was dominant under mild and less harsh conditions.

Our results indicate that even though facilitation can lead to plant aggregation at the population level, the net outcome and intensity of local interactions at the individual plant level is not necessarily positive. In particular, we found that for some scenarios (e.g. C_{CS} , F_{CA} , $S = 0.5$), competition is the dominant process when assessing plant growth (the net outcome is negative as indicated by R_{II} ; Fig. 4.4), whereas the corresponding spatial aggregation and greater survival probability indicate a dominance of facilitation (Figs 4.2, 4.3 and 4.5). In other words, the intensity of interaction (as the net outcome between competition and facilitation) is insufficient to express the relative importance of competition and facilitation on structuring plant systems (Brooker *et al.* 2005). Furthermore, our findings imply that facilitation may be more common than generally believed, but its important role in structuring populations and communities can be hidden simply because it is hard to detect. Thus, establishing whether competition or facilitation is the dominant process in plant populations or communities can be difficult, because competition and facilitation act simultaneously (Callaway 2007) but can affect different aspects

of plant populations or communities.

Nevertheless, the importance of facilitation has been clearly detected in arid, alpine and arctic habitats, which are assumed highly sensitive to global change (Callaway *et al.* 2002; Brooker *et al.* 2008). It is therefore crucial to better understand both the mode of facilitation and nature of stress factors, because the facilitative effect from key species is essential for system diversity and stability in such conditions (Brooker *et al.* 2008; Vellend 2008). Although we focused here on intraspecific interactions, our approach can easily be used to analyse communities. Our conclusions may thus also be relevant for plant communities.

To conclude, our study is the first to quantitatively define different modes of facilitation, and it is also the first attempt to integrate different modes of facilitation with different modes of competition into the SGH. We showed that facilitation can have an important influence on population structure. Moreover, different modes of facilitation and competition can affect different aspects of plant populations and communities, implying context-dependent outcomes and consequences. Explicit consideration of modes and mechanisms of interaction (both facilitation and competition) and the nature of stress factors may help us extend the SGH framework and foster research on facilitation in ecology (Brooker *et al.* 2008; Maestre *et al.* 2009).

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Chapter 4 – Appendix A

ODD protocol – model description of *pi* model with competition and facilitation

The following model description follows the ODD protocol (Overview, Design concepts, Details) for describing individual- and agent-based models (Grimm *et al.* 2006; Grimm *et al.* 2010),

Purpose

The aim of this model is to evaluate the multiple effects of the modes of competition and facilitation under abiotic stress on regulating plant population dynamics, specifically on spatial pattern formation induced by density-dependent mortality. In particular, we test whether different modes of facilitations at individual plant level can result in the spatial aggregation of the population. The model does not represent specific species, but generic ones.

Entities, state variables, and scales

The entities in the model are plants and square habitat units, or patches (Table A1). Plants are characterized by the following state variables: initial growth rate, initial biomass, maximum biomass (asymptotic biomass), current biomass and their position, i.e. coordinates of the stem. Each individual plant has its own circular zone-of-influence (ZOI). The ZOI stands for the physical space occupied by a plant, and represents the energy and resources potentially available to this plant, which is allometrically related to its body mass. Neighbouring plants only compete for the resources when their ZOIs are overlapping.

In order to make the spatial calculations of resource competition easier, ZOIs are projected onto a grid of patches. To avoid edge effects, we use a torus world with a size of 200×200 patches (Grimm & Railsback 2005). Each patch represents 1 m^2 or 1 cm^2 for woody- and non-woody plants, respectively. The state of each patch is characterized by its resource availability. We use a homogeneous environment here as all patches have the same, and constant, degree of abiotic stress. One time step in the model represents approximately one year for woody plants and one day for non-woody plants.

Table A1. State variables and initialization in the individual-based model. Actual values are drawn from the given intervals to introduce a certain degree of heterogeneity among individuals.

Variable	Description	Initial Value [unit] (woody/non-woody)
Plants		
c	Initial growth rate	1 ± 0.1 [kg m ⁻² time step ⁻¹] / [mg cm ⁻² time step ⁻¹]
m_0	Initial body mass	2 ± 0.2 [kg] / [mg]
M_0	Maximal biomass	$2 \times 10^6 \pm 2 \times 10^5$ [kg] / [mg]
m	Current biomass	[kg] / [mg]
A	Zone of influence	[m ²] / [cm ⁻²]
Patches		
S	Abiotic stress level	[0, 1]
Initialization		
Mortality	Threshold of death	5% of $m^{3/4}$
Density	Number of plants	300 [ha ⁻¹] / [m ⁻²]
Random seed	To generate random number	123456789
(Aggregation)	Number of cohort	6 (50 individuals / cohort)
(Aggregation)	Cluster scale (diameter)	50% of the world size

Process overview and scheduling

After initialization, all individual plants with a given density are randomly distributed in the world. The processes of local competition, facilitation, growth and mortality of each plant are fulfilled within each time step. In each step, individual plants first sense the environment qualities of patches within their ZOIs, the area (radius) of an individual plant's ZOI is determined by its current biomass. When their ZOIs are overlapping, individuals compete and facilitate within the overlapping area. Thus, the overlapping area reflecting resources is divided according to the mode of competition. At the same time, under abiotic stress in the presence of facilitation, the overlapping area reflecting the ameliorated habitat by neighbours is also divided according to the mode of facilitation. Considering the outcome of the interaction process, all individual plants grow according to the growth function. Plants with growth rates falling below a threshold die and are removed immediately. The state variables of the

plants are synchronously updated within the subroutines, i.e. changes to state variables are updated only after all individuals have been processed (Grimm & Railsback 2005).

Design concepts

Basic principles: From “Metabolic Scaling Theory”, we derived a general ontogenetic growth model for individual plants. We combine this model, via the ZOI approach, with the effects of different modes of competition and facilitation under abiotic stress.

Emergence: All features observed at the population level, e.g. mass-density relationship or self-thinning trajectories (i.e. size distribution and spatial distribution, respectively), population size inequality and spatial pattern, are emerged from local interactions among plants under abiotic stress of their environment.

Interaction: Individual plants interact via competition for resources and facilitation from neighbours in the overlapping area of their ZOIs.

Stochasticity: Initial growth rate, initial biomass, maximum biomass and initial position of plants are randomly taken from the intervals given in Table 1. This introduces a certain level of heterogeneity among individual characteristics to take into account that real plants are never exactly identical.

Observation: Spatial point patterns of plants, population size, biomass of each plant, and mean biomass of all living plants are the main observations.

Initialization

If the initial spatial pattern is aggregation, we randomly choose several patches (determined by the number of cohorts) as centers and to transplant groups of individual plants (initial density / number of cohorts) among the centers within a certain cluster diameter. In the case of randomness, individual plants are randomly distributed according to the chosen initial density. Resources and abiotic stress are spatially and temporally constant. Each plant has an initial biomass (m_0), maximal biomass (M_0) and initial growth rate (c) drawn from truncated normal distributions with average and intervals given in Table A1.

Input

After initialization, the model does not include any external inputs, i.e. the abiotic environment is constant.

Submodels

Plant growth

In our individual-based model the plant's ZOI stands for the physical space occupied by a plant and represents the energy and resources potentially available to this plant. This space is allometrically related to the plant's body mass, m , as $c_0 A = m^{3/4}$ (Enquist & Niklas 2001), where c_0 is a normalization constant. Accordingly, Eqn (4-1) can be rewritten as

$$dm/dt = cA [1 - (m / M_0)^{1/4}] \quad (A1)$$

and with abiotic stress, it becomes

$$dm/dt = (1 - S) cA [1 - (m / M_s)^{1/4}] \quad (A2)$$

where $c = ac_0$, is the initial growth rates in units of mass per area and time interval. For simplicity, we choose $c = 1 \pm 0.1$ in our model. In addition, we simulate the model with different c values. As expected, the results from different values were qualitatively similar (consist with our findings).

Competition and facilitation under abiotic stress

Competition and facilitation are incorporated by using dimensionless factors or indexes, f_p and f_q respectively. With the above assumptions, equation (A2) becomes:

$$dm/dt = f_p f_q cA [1 - (m / M)^{1/4}] \quad (A3)$$

where $M = (f_p f_q)^4 M_0$ is the maximum achievable biomass under stress with competition and facilitation.

As for competition, the modes of resource-mediated competition among plants can be located somewhere along a continuum between completely asymmetric competition (largest plants obtain all the contested resources) and completely symmetric competition (resource uptake is equal for all plants, independent of their relative sizes; Schwinning & Weiner 1998). To represent different modes of competition explicitly, we describe the competitive index f_p as

$$f_p = (A_{no} + \sum_{k=1}^{n_o} \frac{v_i m_i^p}{\sum_{j=1}^{n_j} v_j m_j^p} A_{o,k}) / A \quad (A4)$$

This factor thus refers to the fraction of resources available in the area which plant i could obtain after a loss of potential resources due to areas overlapped by neighbours of sizes m_j (Schwinning and Weiner 1998). A_{no} is the area not overlapping with neighbours, $A_{o,k}$ denotes the n_o areas overlapping with n_j different neighbours. Parameter p determines the mode of

competition, ranging from complete symmetry ($p=0$) to complete asymmetry (p approaching infinity; for details and examples see Figure A2). In this research, we restrict ourselves to intraspecific facilitation and competition, and assume therefore the species-specific weighting constant of competition v_i and v_j equal 1 here, as conspecific case.

Simultaneously, assuming the effect of facilitation is additive (Molofsky 2001; Molofsky & Bever 2002; Chu *et al.* 2008, 2009), we define the effect of different modes of facilitation, f_q , as

$$f_q = 1 - \frac{S}{A_f + 1} = 1 - \frac{S}{\sum_{k=1}^{n_o} \left(1 - \frac{w_i m_i^q}{\sum_{j=1}^{n_j} w_j m_j^q}\right) A_{o,k} + 1} \quad (\text{A5})$$

This factor is based on SGH, which reflects the facilitative effect of relieving stress and is consist with other model (Chu *et al.* 2008, 2009, 2010; Jia *et al.* 2011; for details and examples see Figure A2). To keep things simple, we follow the assumption of Chu *et al.* (2008, 2009) that the ZOI, A , is the same for competition and facilitation (they could be different). Where A_f refers to the benefit gained by plant from all interactive neighbours, and is calculated as the sum of the areas (ZOIs) overlapped with neighbour plants. The index q determines the mode of facilitation among plants, ranging from complete symmetry ($q = 0$, algorithmic equivalent to the form used in Chu *et al.* 2008; 2009) to complete asymmetry (q approaching infinity; see Table 1 for the complete form and definitions). Since we investigate the monopopulation here, to simplify, we assume the species-specific weighting constant w equals 1 here as the conspecific case, so the facilitation is size dependent. When there is no facilitation ($A_f = 0$), equation (A5) becomes $1-S$, which reflects the effect of abiotic stress.

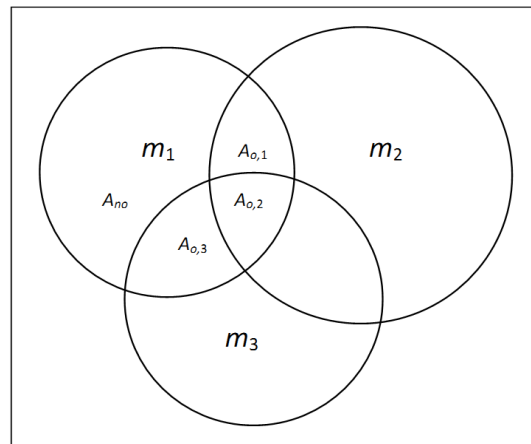


Figure A2. An example of calculating the interactive indexes (equations A4 and A5) with different modes of competition and facilitation by dividing plants'

ZOI (zone-of-influence). Three plants with sizes m_1 , m_2 and m_3 are interacting in this example. For plant 1, its ZOI (A) was divided into four parts: A_{no} , the area not overlapping with the other two plants; $A_{o,1}$, the area overlapping with plant 2; $A_{o,2}$, the area overlapping with plants 2 and 3; $A_{o,3}$, the area overlapping with plant 3.

Then the actual area that plant 1 can take from $A_{o,1}$ is

$$A_{o,1} \frac{m_1^p}{\sum_{j=1}^2 m_j^p} = A_{o,1} \frac{m_1^p}{m_1^p + m_2^p}$$

For $A_{o,2}$,

$$A_{o,2} \frac{m_1^p}{\sum_{j=1}^3 m_j^p} = A_{o,2} \frac{m_1^p}{m_1^p + m_2^p + m_3^p}$$

And for $A_{o,3}$,

$$A_{o,3} \frac{m_1^p}{\sum_{j=1}^2 m_j^p} = A_{o,3} \frac{m_1^p}{m_1^p + m_3^p}$$

therefore, the competitive index for plant 1 is:

$$f_p = \frac{A_{no} + A_{o,1} \frac{m_1^p}{m_1^p + m_2^p} + A_{o,2} \frac{m_1^p}{m_1^p + m_2^p + m_3^p} + A_{o,3} \frac{m_1^p}{m_1^p + m_3^p}}{A}$$

where $A = m_1^{3/4} / c_0$. For plant 1, the benefit received from neighbours is

$$A_f = A_{o,1} \frac{m_2^q}{m_1^q + m_2^q} + A_{o,2} \frac{m_2^q + m_3^q}{m_1^q + m_2^q + m_3^q} + A_{o,3} \frac{m_3^q}{m_1^q + m_3^q}$$

and the facilitative index for plant 1 under abiotic stress is:

$$f_q = 1 - \frac{S}{A_f + 1} = 1 - \frac{S}{A_{o,1} \frac{m_2^q}{m_1^q + m_2^q} + A_{o,2} \frac{m_2^q + m_3^q}{m_1^q + m_2^q + m_3^q} + A_{o,3} \frac{m_3^q}{m_1^q + m_3^q} + 1}$$

In total, equation (A3) clearly shows how a plant's growth rate is jointly determined by abiotic stress, S , competition, f_p , and facilitation f_q . This also implies that a plant's final size is usually smaller than its asymptotic maximum size (M_0) during environmental stress and local competition, but can increase by the beneficial effects of neighbour plants via the amelioration of habitat.

Mortality

An individual's mortality rate is proportional to its mass-specific metabolism (as current total metabolic rate divide by body mass; Brown *et al.* 2004). Based on

this, we assume that individuals die if their actual growth rate (dm/dt , realistic metabolic rate) falls below a threshold fraction of their basal metabolic rate (allometrically scaled with body mass), i.e. 5% of $m^{3/4}$. Therefore, individual plants may die due to metabolic inactivation driven by abiotic stress, competition, senescence (when m approaches M) or combinations thereof. This provides a more realistic representation of relevant ecological process than in previous models (Stoll *et al.* 2002; Chu *et al.* 2009, 2010; Jia *et al.* 2011).

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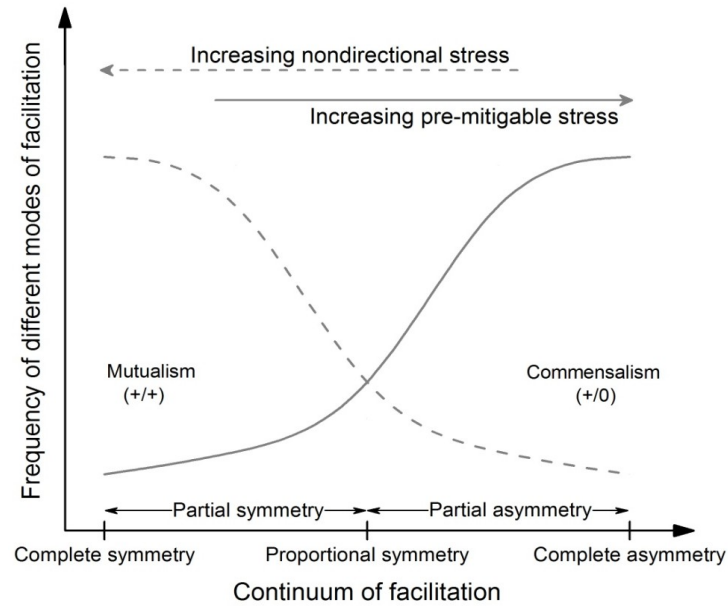


Fig. S1. Conceptual model of the occurrence of mutualism versus commensalism in a continuum of symmetric versus asymmetric facilitation.

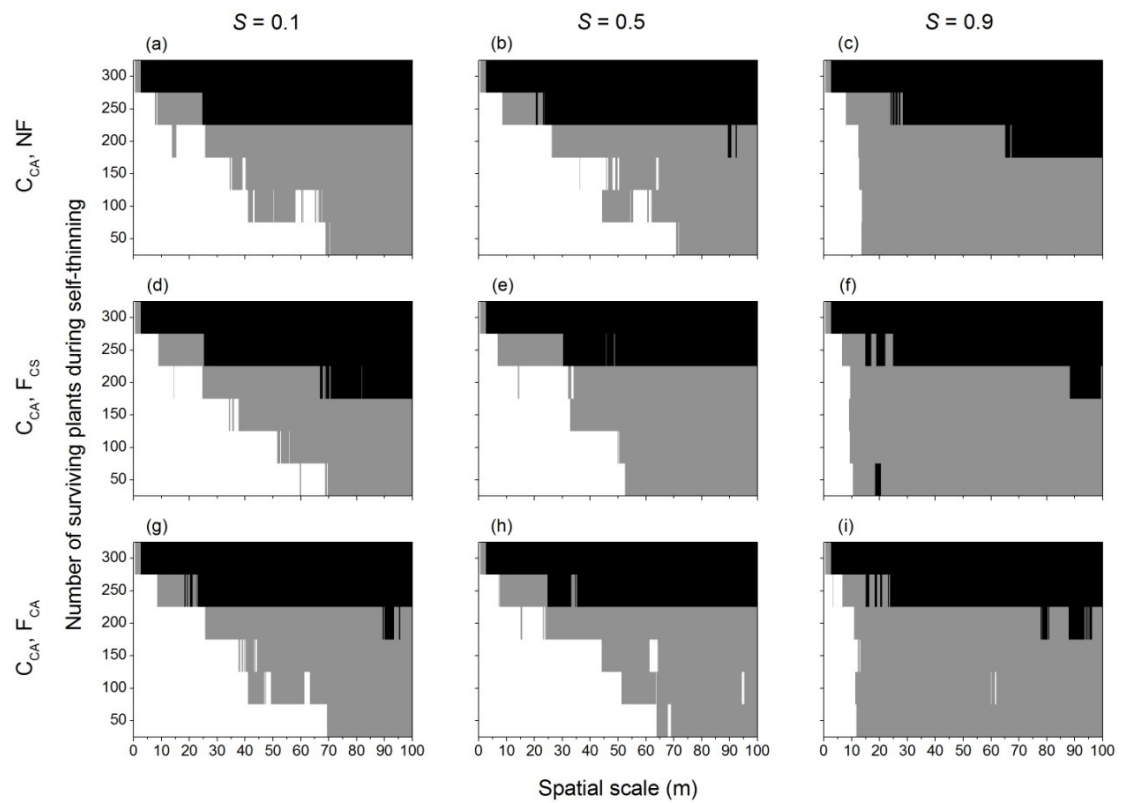


Fig. S2. Spatial dynamics (black, aggregation; grey, randomness; white, regularity) during self-thinning with aggregated initial locations and completely asymmetric competition (C_{CA} , $p = \infty$) in the absence (NF) or presence of facilitation (F_{CS} , completely symmetric facilitation, $q = 0$; F_{CA} , completely asymmetric facilitation, $q = \infty$) at different levels of abiotic stress (S).

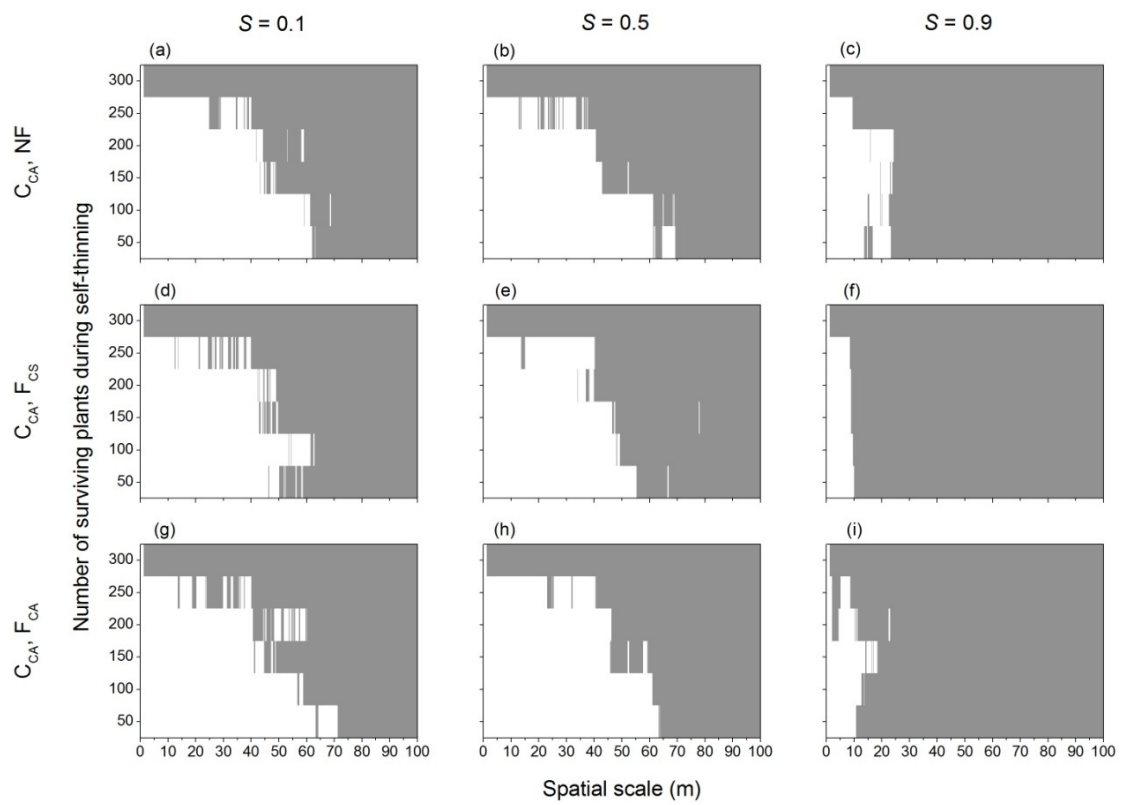


Fig. S3. Spatial dynamics during self-thinning with random initial locations. Symbols and abbreviations are the same as in Fig. S2.

Chapter 5

Metabolic scaling theory predicts near ecological equivalence in plants *

Abstract

Both niche and neutral theory aim to explain biodiversity patterns but seem incompatible: whilst niche theory is based on the differences between species, neutral models assume there are no such differences. Ecological equivalence mediated by trade-offs however, is consistent with neutral theory whilst allowing for ecological differences as suggested by niche theory. Here we show with data from 375 plant species that metabolic scaling theory predicts such trade-offs and thus supports ecological equivalence, at least as a near approximation. This highlights a potentially important role for metabolic scaling and points the way to a possible reconciliation between niche and neutral theory.

Keywords: allometric scaling, neutral theory, ecological equivalence, functional equivalence, demography, trade-offs, birth rate, death rate

* Manuscript in preparation

Yue Lin, Uta Berger, Volker Grimm, Qian-Ru Ji, James Rosindell, Jens Kattge, Helge Bruelheide, and Richard Sibly

5.1 Introduction

Ecological difference among species (niche difference) is the conceptual basis has been established since Darwin for explaining species coexistence and diversity. By contrast, neutral theory (Hubbell 2001) provides models that assume all species are ecologically identical. The idea received enormous attention due to its accurate predictions despite its surprising simplicity, and controversial assumption of ecological equivalence (Chave 2004; Rosindell *et al.* 2012) which seems to be violated by many observable species-specific characteristics.

One important aspect of neutral theory, however, has not yet been sufficiently appreciated: ecological differences do not necessarily lead to differences in net fitness (Chave 2004; Allouche & Kadmon 2009; Lin, Zhang, & He 2009). Ecological equivalence regarding trade-offs between birth and death rates among different species is still consistent with the neutral assumption but allows for functional differences as suggested by niche theory (Hubbell 2001; Chave 2004; Allouche & Kadmon 2009; Lin *et al.* 2009). It has been shown in the simulation models that these birth-death trade-offs can be incorporated into neutral theory without impairing its ability to predict biodiversity patterns (Chave 2004; Lin *et al.* 2009; Rosindell *et al.* 2012).

Although predictions of neutral model have been tested extensively (Hubbell 2001, 2005, 2006, 2008; Chave 2004; Allouche & Kadmon 2009; Lin *et al.* 2009; Rosindell, Hubbell, & Etienne 2011), the cornerstone of neutral theory which is the hypothesis of ecological equivalence has rarely been tested (Hubbell 2008). Such ecological equivalence amongst individuals (species), namely the demographic trade-offs, can be attributed to the intrinsic explanations as neutral assumption assumed and/or the extrinsic explanations as niche differences suggested. The intrinsic explanations are determined essentially by the metabolism of organisms, whereas the extrinsic

explanations are mainly related to external factors of environment such as competition, resource, disease, predation or disaster (McCoy & Gillooly 2008).

In this study, we attempt to give a mechanistic, generic explanation for these observed birth-death trade-offs, and thus provide a new and compelling explanation for the success of neutral theory in a non-neutral world. To test our predictions, we compiled data of demographic rates of 375 plant species which include different functional groups and cover 11 orders of magnitude in plant size ranging from mosses to trees.

The explanation we seek is provided by building on a base given by the metabolic scaling theory (MST). This theory of ecology predicts quantitative relationships between various functional traits of organisms and their body size based on their metabolic rates (Brown *et al.* 2004; Price *et al.* 2010). Extensions of MST yield that birth and death rates, b and d , are strongly governed by the mass-specific metabolic rate (B), and thus should show the body size (M) and temperature dependence (Brown *et al.* 2004; McCoy & Gillooly 2008; Price *et al.* 2010) as:

$$b \propto d \propto B \propto M^{-1/4} e^{-E/kT} \quad (5-1)$$

where $e^{-E/kT}$ is the Boltzmann-Arrhenius factor which describes the exponential increase in biochemical reaction rates with body temperature (Brown *et al.* 2004; Marbà *et al.* 2007; McCoy & Gillooly 2008; Price *et al.* 2010), E the average activation energy of rate-limiting biochemical metabolic reactions (≈ 0.32 eV for plants), k the Boltzmann's constant ($= 8.62 \times 10^{-5}$ eV K $^{-1}$), and T the absolute temperature (Kelvin).

Although such scaling relationships have partly been statistically validated before (Brown *et al.* 2004; Marbà, Duarte, & Agustí 2007; Price *et al.* 2010), so far they were not linked to neutral theory. A reasonable estimation of overall fitness (R_0) can be measured as the ratio of birth rate over death rate which

gives the lifetime reproductive success or intrinsic rate of increase (Hubbell 2001; Chave 2004; Niklas 2007; Allouche & Kadmon 2009) leading to

$$R_0 = b / d \propto M^{-1/4} e^{-E/kT} / M^{-1/4} e^{-E/kT} \propto M^0 \quad (5-2)$$

Thus, fitness is predicted to be invariant with respect to body size, temperature, as well as the metabolic rate across different functional groups of plant species. It is almost self-explanatory that birth-death trade-offs is strongly governed by the metabolic constraints of organisms, in other words, the intrinsic mechanisms are expected to be the primary explanations. If this is true, the overall fitness should be a constant among individuals and species, and the ecological equivalence is to be expected as $R_0 = 1$, which is also the parameter setting of neutral models (Hubbell 2001; Chave 2004; Allouche & Kadmon 2009).

5.2 Materials and Methods

Temperature dependence of metabolism. Coexisting plant species in a community can be assumed to experience the same temperature, so the Boltzmann-Arrhenius factor can be omitted among species that coexisting in a certain community. Moreover, the data set of birth and death rates analyzed in this study also shows temperature independence (Student's *t*-test, $P = 0.43$ and $P = 0.50$ respectively), which is consistent with previous studies suggesting that metabolic rates of plant are less temperature dependent than those of animals (Marbà *et al.* 2007; Niklas 2007; Allouche & Kadmon 2009). Such findings might also due to either statistical “noise” or the narrow band of temperature in the data set (Marbà *et al.* 2007; Niklas 2007).

Data Compilation. Because the predictions of MST are based on a fractal-like architecture of transporting network, so we compiled data on individual average body masses, natural birth and death rates from a broad array of higher plant species (excluding phytoplankton, algae, and macro-algae which

do not have fractal-like architectures). Our data set includes mosses, seaweeds, ferns, grasses, herbs, succulents, shrubs, lianas, mangroves as well as other tree species. Each taxonomic group is represented by a diversity of species and with plant body sizes span a very broad range (7.0×10^{-3} to 1.1×10^7 g). All these data were primarily compiled from published data sets and some are gathered from large census plots.

Measure of birth rate. We calculated the birth rates (b , in year⁻¹) from initial number of individuals (N_0) and the number of new-born individuals (N_b) during the time past between census interval (t , in year) as:

$$b = \frac{\ln (N_0 + N_b) - \ln (N_0)}{t} \quad (5-3)$$

Measure of death rate. The death rates (d , in year⁻¹) are calculated as:

$$d = \frac{\ln (N_0) - \ln (S)}{t} \quad (5-4)$$

where S indicates the number of survivors in the later census.

Estimate of tree mass. Tree mass (M , dry biomass in grams) that cannot directly get was estimated from DBH (diameter at breast height in centimeters) by using an allometric equation:

$$M = 78 \cdot DBH^{2.5} \quad (5-5)$$

this equation was fitted for a compilation of independent data set which enclosing a very broad range of size for tree flora (Marbà *et al.* 2007).

Data Analysis. Because we are intend to answer different biological questions, both Model I and II regressions are applied in our work by following the suggestions about model selection (Smith 2009). To test the relationship between body size (M) and the birth rates, death rates, and overall fitness (R_0), the allometric equations are fitted to log-transformed data by using ordinary least squares regression (OLS, Model I regression). This is because we are interested about how demographic rates change with plant body size. We use

the reduced major axis regression (RMA, Model II regression) for log-transformed data fitting between birth and death rates. Because we attempt to ascertain the actuality of ecological equivalence ($b = d$), meaning that the bivariate relationship is symmetric and regardless of which variable is dependent and which is independent.

5.3 Results and Discussion

Our analysis of data confirms that most plant populations examined here are ecologically equivalent. Death rate, d , is proportional to the birth rate, b , as $d = 1.104 b^{1.001}$ (Fig. 5.1 A). This does not differ statistically from the equivalence in vital rates ($b = d$) assumed by neutral model. Furthermore, observed distribution of the intrinsic rate of increase ($R_0 = b / d$) is unimodal with a mean of 1 (Fig. 5.1 B), implying a validity of nearly ecological equivalence (Hubbell 2008).

In agreement with theoretical predictions, the data shows that species balance high birth rates with high death rates according to mass-specific metabolic rates and scale as $-1/4$ power of body mass (Fig. 5.2, A and B). The overall fitness, R_0 , scales as $M^{0.006}$, and does not differ statistically from the predicted mass invariance (M^0) (Fig. 5.2 C). Such results imply that ecological equivalence as demographic trade-offs among different plant species are largely constrained by intrinsic mechanisms of individual metabolic rate, despite the fact that ecologically extrinsic factors exist in nature.

Nevertheless, the results also point to substantial variation (Fig. 5.1A) that cannot be explained by metabolic constraints alone. Such variation might be viewed as an indicator of non-neutral process among species from particular communities, suggesting that both intrinsic and extrinsic constraints may contribute to population and community dynamics. Therefore, it is more relevant to test the relative contributions of intrinsic and extrinsic factors in different populations and communities.

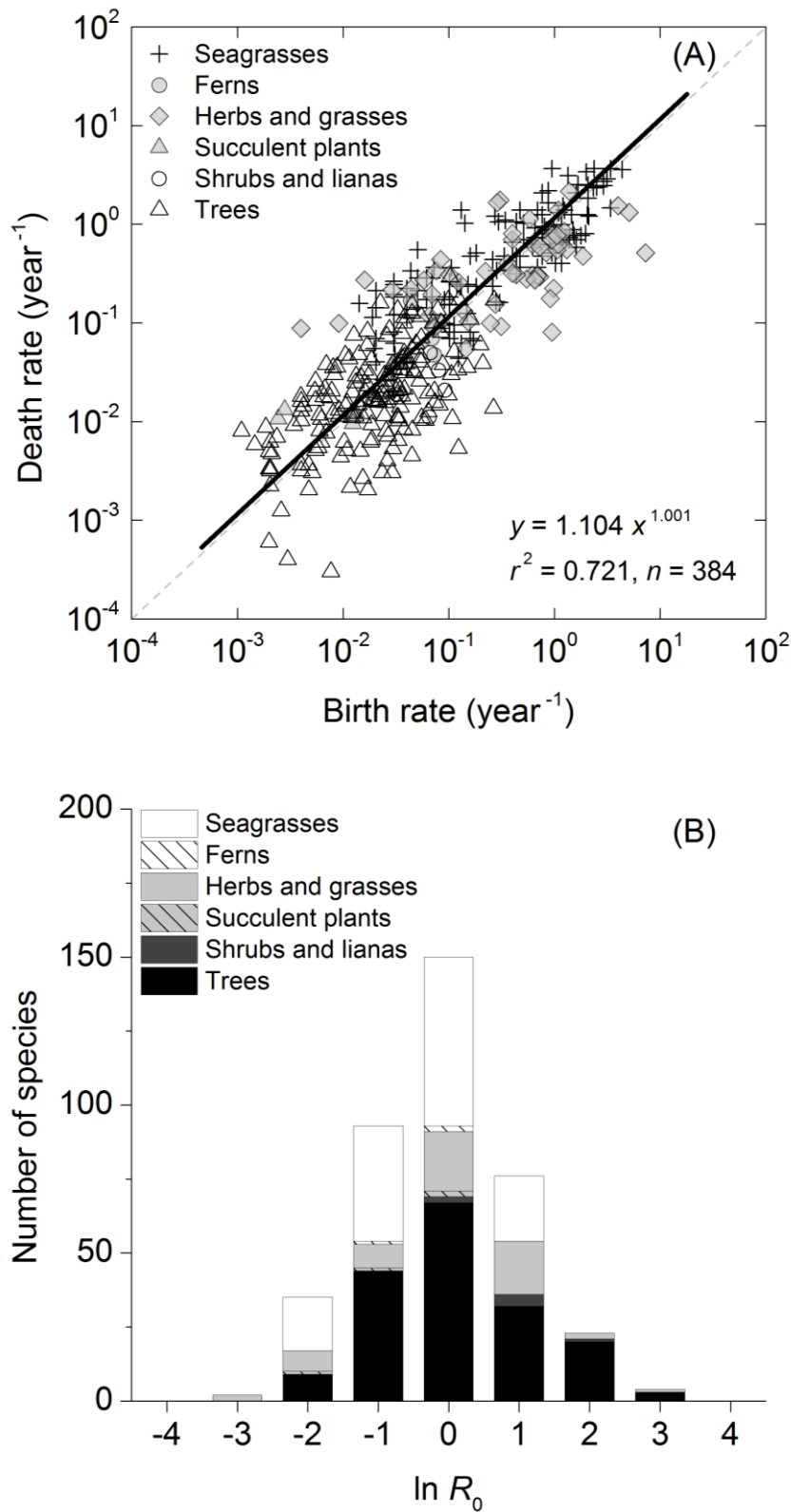


Fig. 5.1 (A) The relationship between birth rates and death rates of plants (375 species). Red line shows the fitted reduced major axis regression ($P < 0.0001$, 95% confidence intervals, exponent: 0.950 to 1.056, constant: 0.966 to 1.271). **(B)** Distribution of the intrinsic rate of increase (overall fitness, calculated as the ratio between birth rate and mortality rate, $R_0 = b / d$) of plant species.

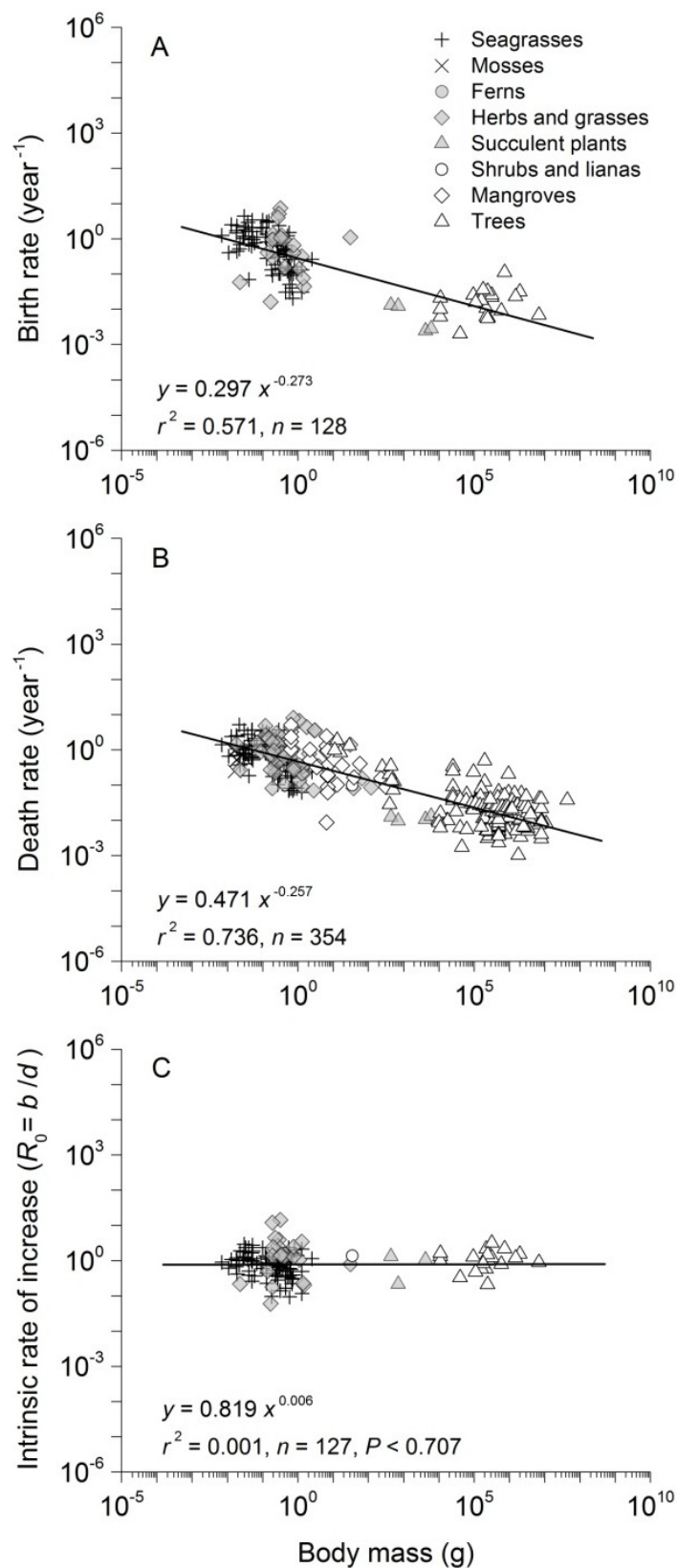


Fig. 5.2 (A) The relationship between plant body size and birth rates. Black line shows the fitted ordinary least squares regression (OLS, Model I regression; $P < 0.0001$, 95% confidence intervals, exponent: -0.315 to -0.232, constant: 0.237 to 0.372). **(B)** The relationship between plant body size and

death rates. Black line shows the fitted OLS regression ($P < 0.0001$, 95% confidence intervals, exponent: -0.273 to -0.241, constant: 0.408 to 0.545). (C) The relationship between plant body size and overall fitness (intrinsic rate of increase, calculated as the ratio between birth rate and death rate, $R_0 = b / d$). Black line shows the fitted OLS regression ($P < 0.707$, 95% confidence intervals, exponent: -0.024 to 0.036, constant: 0.697 to 0.964).

Overall, our study indicates that neutrality as assumed by neutral theory might be the consequence of scaling relationships which emerges from constraints, trade-offs, and evolved characteristics of metabolism and physiology. Meanwhile, MST also predicts different functional traits across different functional groups of species (Brown *et al.* 2004; Price *et al.* 2010). Thus, niches and neutrality are not excluding each other but might in fact have the same mechanistic root. The current debate about whether niche or neutral mechanisms structure natural communities might miss the point. The real question should be when and why one of these factors dominates. Our initiative work may provide some insights regarding the relative importance of niche vs. neutral based process on community assembly and species diversity.

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Chapter 6

General discussion

The general aim of my dissertation was to investigate the role of plant interactions in driving population dynamics. Both theoretical and empirical approaches were employed, such as individual-based models (IBMs) and greenhouse experiment. All my studies are conducted on the basis of metabolic scaling theory (MST, Brown et al. 2004, Price et al. 2010), because the complex, spatially and temporally varying structures and dynamics of ecological systems are considered to be largely consequences of biological metabolism (Brown et al. 2004). On the other hand, MST didn't consider the important role of plant interactions and was found to be invalid in some environmental conditions. Integrating the effects of plant interactions and environmental conditions into MST may be essential for reconciling MST with observed variations in nature. Such integration will improve the development of theory, and will help us to understand the relationship between individual level process and system level dynamics.

In the following, I will discuss what we in general learned from the work presented in this thesis. First, I will discuss the pros and cons of mechanistic and phenomenological models, in particular whether it paid to develop and use an ontogenetic growth model. Then I will turn to plant competition and how modelling it can be integrated with MST. Next, facilitation in combination with competition will be discussed as a framework for exploring interactions of plants with each other and their abiotic environment. The final two sections will be devoted to synthesis: first, of plant competition, MST, and Neutral Theory, and finally of the approach to addressing ecological questions used in this thesis, Individual-Based Ecology.

Mechanistic models versus Phenomenological models

In the beginning of this dissertation, we deduced a mechanistic growth model for plant. It is important that we use a mechanistic growth model derived from MST rather than a phenomenological growth model, as usually has been done so far in other plant IBMs (e.g., Weiner et al. 2001, Stoll et al. 2002, Stoll and Bergius 2005, Chu et al. 2008, 2009, 2010, May et al. 2009). First, our mechanistic growth model is based on the energy budget of the individuals during growth which captures the key features of metabolic process of organisms (West et al. 2001, Hou et al. 2008). Such mechanistic models driven by 'first principles' are more flexible and are capable of capturing adaptive responses of individuals to their environment than phenomenological models, which are statistically fitted to existing data and forego any attempt in explaining the underlying mechanisms (Hilborn and Mangel 1997, Grimm and Railsback 2005, Martin et al. 2012). Second, the mechanistic models can be easily extended to predict further patterns by deduction (e.g., the reproduction biomass of individual plant, in Appendix of Chapter 1), whereas phenomenological models are usually induced by patterns that were observed. Mechanistic models are more likely to work correctly when extrapolating beyond the current states than empirical models. Third, ecological or mathematical artifacts are easier to be prevented if using mechanistic models deduced from physical or physiological rules. For instance, in many IBMs plant growth is assumed to be negatively and linearly related to resource competition and environmental stress (Weiner et al. 2001, Stoll et al. 2002, Stoll and Bergius 2005, Chu et al. 2008, 2009, 2010, May et al. 2009, Jia et al. 2011), with maximum body size kept constant. This phenomenological assumption is both mathematical and ecological incorrect, because it implies that plants can reach their optimal size regardless environmental conditions. Fourth, in contrast to previous models used in plant IBMs (Wyszomirski 1983, Wyszomirski et al. 1999, Weiner et al. 2001, May et al. 2009), our model is not

only able to explain the observed variation in both root-shoot allocation patterns, but also simultaneously describe the mass-density relationships (in Chapter 3).

Yet, the merits of phenomenological/statistical models should not be underestimated, especially when the aim is only to describe (or predict) rather than to understand the mechanisms. Both the mechanistic models and phenomenological models are useful, it is more relevant to ask how to choose a model properly, in particular in IBMs. The POMIC (pattern-oriented modeling information criterion, Piou et al. 2009) offers a rigorous statistical approach of model selection which is in a context of POM (pattern-oriented modeling) and is more efficient and specialized for IBMs. Nevertheless, in IBMs, with all other things being equal, mechanistic models are arguably more powerful because they can explain underlying processes driving observed patterns. Meanwhile, the phenomenological models can also be used to stimulate and improve our understandings on the mechanisms underlying observed patterns. A case in point is how the ‘Kleiber’s law’ urge MST to come out (Brown et al. 2004).

Plant competition

In Chapter 2, we investigated the role of different modes of competition in altering the prediction of MST on plant self-thinning trajectories. Our spatially-explicit individual-based zone-of-influence (ZOI) model was developed to investigate the hypothesis that MST may be compatible with the observed variation in plant self-thinning trajectories if different modes of competition and different resource availabilities are considered. Our one-layer ZOI model supported our hypothesis that (i) size-symmetric competition (e.g. belowground competition) will lead to significantly shallower self-thinning trajectories than size-asymmetric competition as predicted by MST; and (ii) individual-level metabolic processes can predict population-level patterns when surviving plants are barely affected by local competition, which is more likely to be in the case of asymmetric competition. In contrast to our findings,

some researchers proposed that asymmetric competition is more important to explain the deviations predicted by MST (Coomes and Allen 2009, Coomes et al. 2011). However, this debate again is due to a failure of distinguishing between the ‘importance’ and ‘intensity’ of competition (Welden and Slauson 1986): we respect to the competitive effect on population level (mass-density relationship) which is about the importance of competition, whereas they focus on competitive response of single tree (individual tree growth) which is more related to the intensity of competition.

In Chapter 3, we go further and add a bit more complexity by considering the phenotypic plasticity and adaptive behaviour of plants in changing environments. A two-layer ZOI model was developed which considers allometric biomass allocation to shoots or roots and represents both above- and belowground competition simultaneously via independent ZOIs. In addition, we also performed greenhouse experiment to evaluate the model predictions. Both our theoretical model and experiment demonstrated that: plants are able to adjust their biomass allocation in response to environmental factors, and such adaptive behaviours of individual plants, however, can alter the relative importance of above- or belowground competition, thereby affecting plant mass-density relationships at population level. Root competition, which is assumed to be more symmetric, can strongly affect the growth of surviving plants therefore alter the mass-density relationships. Invalid predictions of MST are likely to occur where competition occurs belowground (symmetric) rather than aboveground (asymmetric). Consequently, models or theories which only consider aboveground part are not appropriate for the cases where belowground processes predominate (Deng et al. 2006, Berger et al. 2008). In addition to previous studies which do not consider the linkage between above- and belowground competition, our study implies that adaptive behaviours of plants such as allometry can modify ecological mechanisms and subsequently the constraints set by MST. This has important implications for many forests and eco-regions, e.g., for using allometry-based models to

predict carbon storage and sequestration.

Plant competitions and metabolic scaling theory

Chapter 2 and 3 jointly showed that, MST, like principles from energetics and biomechanics, sets limits on the behaviour of individuals and therefore of populations and communities. In some ecological situations these limits will dominate, and MST will predict higher-level behaviour. In many cases however, other constraints will determine the patterns observed. Our most important conclusion is that the behaviour of populations and communities may be dominated by internal physiological mechanisms addressed by MST or by ecological factors beyond the individual level, such as the type of resource limitation and the mechanisms of competition among individuals. In the latter cases MST will not be predictive, although nor will it be violated. The claim that MST provides a ‘universal law’ for quantitatively linking the energetic metabolism of individuals to ecological system dynamics is thus neither completely right nor wrong: the real question is when and which factors dominate in a given situation. However, our studies show that cross-level tests are needed to explore and develop individual-level theories. Martin et al. (2012), who used an individual-based population model of *Daphnia* based on Dynamic Energy Budget theory (Kooijman 2009), arrived at the same conclusion. Without doubts, the consideration of plant interactions is critical for understanding variation in observed patterns.

Plant competition and facilitation

In Chapter 4, we introduced the new concept of modes of facilitation, i.e. symmetric versus asymmetric facilitation, and developed an individual-based model to explore how the interplay between different modes of competition and facilitation changes spatial pattern formation in plant populations, and how combinations of competition and facilitation modes alter the intensity of local

plant interactions along a stress gradient. Our study shows that facilitation by itself can play an important role in promoting plant aggregation independent of other ecological factors (e.g. seed dispersal, recruitment, and environmental heterogeneity). Such finding identifies the origin of an important mechanism underlying self-organization: the process of local facilitation among plants that set against the background of overall control by environmental constraints.

Our results also indicate that the indices widely used to estimate intensity of local interactions is too limited to represent the relative importance of different modes of interactions in structuring plant system dynamics. Different modes of facilitation and competition can affect different aspects of plant populations and communities, leading to variously spatial and temporal patterns, and implying context-dependent outcomes and consequences. For instance, we find that the net outcome of local interactions among plants can show a dominance of competition when using the index of relative interaction intensity, in spite of the fact that local facilitation plays an important role in structuring spatial aggregation. Although the intensity of interaction as the net outcome is measurable, but the relative importance of competition and facilitation in structuring system dynamics is much more complicated. To clarify some debates in current ecological researches, it is necessary to distinguish the differences between intensity and importance of different modes of competition and facilitation, and to develop a comprehensive approach rather than only use some indices. Moreover, a moderate mixture of positive and negative interactions is demonstrated to stabilize population dynamics (Mougi and Kondoh 2012). The diversity of species and interaction types may be the essential element of biodiversity that maintains ecological communities, and may hold the key to understanding population and community dynamics (Grimm and Railsback 2005, Mougi and Kondoh 2012).

Towards a synthesis of metabolic scaling, niche, and neutral theory

In Chapter 5, we went from population level to community level and explored

the possibility of combining the MST and unified neutral theory of biodiversity (UNT, Hubbell 2001). Studies addressing UNT have largely focused on testing the predictions of neutral models, whereas the fundamental assumption of ecological equivalence has rarely been tested with empirical studies. Our analysis of extensive data confirms that most plant populations examined are nearly neutral in a sense of demographic trade-offs, which can mostly be explained by a simple allometric scaling rule that based on MST. This demographic equivalence regarding birth-death trade-offs between different species and functional groups is consistent with the assumption of neutral theory but allows functional differences between species (K. Lin et al. 2009). Both niche and neutral mechanisms may be essential processes in community assembly. In agreement with this, a new theoretical framework proposed four basic processes in a community: natural selection (niche mechanisms), ecological drift (neutral mechanisms), dispersal limitation and speciation. But the relative importance of these four processes varies among communities (Vellend 2008).

Current debate about whether niche or neutral mechanisms structure natural communities apparently missing the point. Our initial study provides some insights into this debate: the real question should be when and why one of these factors dominates. Because UNT emphasizes neutral mechanisms (ecological drift) as the main drivers of community assembly, for this reason the demographic dynamics of all species in a certain community should be a martingale. However, our results also show the variation of demographic trade-offs that cannot be explained by metabolic constraints alone. Such variation may be viewed as an indicator of non-neutral mechanisms (e.g., interactions and natural selection) among species in the communities, and the goodness of fit (the coefficient of determination) may be viewed as the contribution of neutral mechanisms. The empirical tests about the relative importance of different mechanisms in natural communities are urgently needed.

MST or similar bio-energetic theories (e.g., Dynamic energy budget theory, Kooijman 2009) have the potential to unify existing biodiversity theories, which are focused on abundances and species number, and link them to questions regarding ecosystem functioning, e.g. productivity, plasticity, stability, respiration, carbon flux etc. Such a synthesis of bio-energetic and demographic theories is needed to better understand the relationship between diversity and function of ecosystems and to unify future research in biodiversity theory and management.

The Individual-Based Ecology

Ecology as a developing science is full of fresh ideas, but most of the influential ideas still have not been mathematically well developed (Lawton 1999, Ghilarov 2003, Simberloff 2004, Grimm and Railsback 2005, Scheiner and Willig 2008, 2011, Odenbaugh 2011a). Elaborate theories of ecology which reflect ‘physics envy’ often omit the differences among organisms and their traits, which I so-called ‘the assumption of spherical trees in a vacuum’. However, since organisms are not just atoms such ‘physics envy’ theories are of little use if we are going to understand the emergent properties of complex systems such as population dynamics or community assembly out of ecological traits, behaviours and interactions of individual organisms (DeAngelis and Gross 1992, Breckling et al. 2005, Grimm and Railsback 2005). The legendary ecologist MacArthur claimed “the best ecologists had blurry vision so they could see the big patterns without being overly distracted by the contradictory details” (Odenbaugh 2010, 2011b). Yet, an approach that can ‘zoom in and zoom out’ would be more appropriate if we are going to understand the ecologically complex systems from individual levels (Grimm and Railsback 2005). Accounting for omitted details often leads to more refined theories. For instance, the van der Waals equation was derived as a more precise version of the ideal gas law by incorporating the facts that molecules have a nonzero volume and that they’re attracted to each other, for

which Johannes van der Waals received the Nobel Prize for Physics in 1910 (Fox 2011). As in all such quests, it is important to keep in mind Einstein's dictum 'seek simplicity, and distrust it'. Nevertheless, the main challenge in ecology is to understand complexity and how it emerges from the adaptive traits of individuals (Levin 2000, Grimm and Railsback 2005) which is the major goal of individual-based ecology. The approaches of individual-based and pattern-oriented modelling are promising to achieve the synthesis.

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