LIGHT COMPETITION AND PARTITIONING IN HERBACEOUS VEGETATION – A TEST OF THEORY

DISSERTATION

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GENERAL INTRODUCTION

The last decade has seen a burst of research activity aimed at understanding the mechanisms behind biodiversity loss. However, this research has been largely phenomenological in identifying patterns. While there have been some attempts to understand the causal mechanisms, much of the underlying biology remains unclear and a new generation of mechanistic experiments that reveal more about the workings of competition and resource partitioning are needed. This thesis focuses on the mechanisms of competition and partitioning of light in grassland communities. Using measurements of plant traits and their impact on light availability, we tried to predict the competitive outcomes in mixtures and test mechanistic theory of competition for light, partitioning of light and founder control in eutrophied grassland communities.

Background

One of the widely observed results of global change is that in many different types of ecosystems, eutrophication leads to diversity loss (Stevens et al., 2004; Silvertown et al., 2006; Stevens et al., 2006). In eutrophied terrestrial plant communities, such as many European grasslands, competition for light is thought to be a mechanism for this diversity loss (Tilman, 1982; Berendse & Elberse, 1990; Roem & Berendse, 2000; Stevens & Carson, 2002). In terrestrial systems, where plants establish three-dimensional canopies, species in the uppermost layer can pre-empt light and shade those beneath. A small advantage in height therefore allows much more of the light to be intercepted, conferring a disproportionately large competitive advantage. This mode of competition, which is disproportionate to some measure of size, is called relative-size asymmetric (Begon, 1984; Weiner, 1990; Schwinning & Weiner, 1998). Asymmetric competition acts to increase the variation in relative growth rates as smaller plants suffer more and therefore to exaggerate relative size differences (Begon, 1984; Weiner, 1990; Schwinning & Weiner, 1998). Therefore, a small initial
advantage in height allows much more of the light to be intercepted and confers a
disproportionately large competitive advantage. This increases relative size differences
between species even further (Weiner, 1990; Swinning & Weiner, 1998), enables species
intercepting more of the incident light to maintain an initial dominant position during the
whole growing season and can lead to an outcome which supports only low plant diversity
(Huston & DeAngelis, 1994; Schwinning & Fox, 1995; Lepš, 1999).

The best developed mechanistic theory of resource-competition is Tilman’s
$R^*$ (Tilman, 1982; Tilman, 1988). If species in a system are limited by a single resource, the
species that can reduce this resource to the lowest equilibrial level ($R^*$) is the best competitor
and should displace other species. However, in terrestrial plant communities $R^*$ theory has
been mainly applied to belowground resources, specifically soil nitrogen, and almost
exclusively at a single site (Miller et al., 2005; Harpole & Tilman, 2006), namely the well-
known nitrogen-limited prairie at Cedar Creek, Minnesota, USA. Studies there support the
ability of $R^*$ to predict species’ relative abundances and the outcome of competition during
secondary succession in old fields (Tilman, 1991; Tilman & Wedin, 1991; Harpole & Tilman,
2006; Fargione & Tilman, 2006).

Huisman & Weissing (1994) and Huisman et al. (1999) are some of the few
researchers to apply the $R^*$ approach to light. They performed competition experiments with
phytoplankton in continuous, well-mixed cultures that were nutrient-rich and light-limited.
They found that the critical light intensity (the minimal light requirement) at the bottom of a
water column in monoculture ($I^*_{out}$), was a good predictor of competitive outcomes in species
mixtures: the species with the lowest $I^*_{out}$ was the strongest competitor and displaced all other
species. However, their cultures of phytoplankton were constantly mixed to prevent the
organisms from forming layers, meaning that $I^*_{out}$ was directly analogous to $R^*$. So far, apart
from Dybzinski & Tilman (2007) there have been no experiments that would try to transfer the $R^*$ for light approach to terrestrial systems and to predict competitive outcomes in mixtures with measurements of minimal light requirements of monoculture. They have shown that $I^*$ can be used to successfully predict longer-term (11 years) competitive exclusion in a nitrogen gradient at Cedar Creek.

As an alternative to resource-based measures like $I_{\text{out}}^*$ or $I^*$, species’ minimal light requirements could be also obtained directly from measurements of CO$_2$ net gas exchange along light gradients. Such curves give information about the maximal potential of a species’ photosynthetic apparatus, about dark respiration but also about instantaneous light compensation point and the apparent quantum yield. The instantaneous light compensation point is the amount of light at which photosynthetic CO$_2$ consumption and respiratory CO$_2$ production are in equilibrium (e.g. Larcher, 2003) and denotes thus the minimal instantaneous light requirement of a plant to maintain itself without growth or any losses. The apparent quantum yield is the linear increase of CO$_2$ uptake with incident photons at low light intensities above the light compensation point and can be regarded as the photosynthetic efficiency at low light (e.g. Larcher, 2003).

On the other hand, increased fertilization must not necessarily lead to diversity loss. Fridley (2002, 2003) showed that plant mixtures of grassland species on highly fertile soils overyielded (were more productive than expected based on monoculture yields). Because overyielding disappeared when high fertility plots were shaded, Fridley (2002, 2003) concluded that soil fertility promotes light partitioning by emphasising size differences in species’ heights and growth forms. Therefore, aboveground niche separation could increase productivity of mixtures as compared to monocultures (Naeem et al., 1994; Spehn et al., 2000, 2005). Furthermore, aboveground niche separation and thus a more optimal use of canopy space and increased light interception in mixtures could also promote species
coexistence. Anten & Hirose (1999) have found different aboveground growth patterns in species of a tall-grass meadow that allow the species to use different positions in time and space, to absorb light efficiently, which may allow species to coexist. In other studies (Hirose & Werger 1995; Anten & Hirose 1999; Werger et al., 2002; Anten & Hirose, 2003), it has been shown that subordinate species were able to capture at least similar amounts of light per unit biomass as dominant species and thus species of different stature were equally efficient in capturing light. This could help explain why they were able to coexist (Anten 2005). However, direct experimental evidence for niche complementarity is scarce in scientific literature (Silvertown, 2004; Kahmen et al., 2006), especially related to light.

Additionally, it has been hypothesized that the asymmetric nature of competition for light also bears the potential to create opportunities for local coexistence in light-limited habitats (Pacala & Rees 1998), especially in spatially structured habitats and thus lead to an increase in species diversity (Levin, 1974; Reynolds & Pacala, 1993; Rees & Bergelson, 1997). When outcomes of competition are determined by the timing of establishment, succession can become arrested and not proceed to the best competitor for light but allow local dominance of a competitively poorer founder species (“founder control”; Reynolds & Pacala, 1993; Rees & Bergelson, 1997; Perry 2003). In this case, when this poorer competitor for light has had time to establish and reach a disproportionate advantage over an invading better light competitor, the ranking can reverse and the poor competitor can maintain its initial dominant position and prevent the better competitor from establishing. In contrast, when competition is symmetric, as for example competition for soil resources is thought to be, initial conditions should not play a role but succession should proceed to the best competitor, irrespective of initial conditions (Tilman, 1982; Tilman, 1988; Wedin & Tilman, 1993). However, most work on founder control has been purely theoretical and there are no experimental tests of this theory.
This thesis

This thesis uses an experimental approach to investigate about light competition and partitioning in experimental grassland communities. The core of our study was an experiment running over the course of three years in which species were grown under fertilized and irrigated conditions in monoculture, all pairwise mixtures and the full five-species mix set to investigate about the longer-term outcome of competition for light (Chapter 2). To be able to better explain the observed patterns, we set up three additional short-term experiments that focus specifically on the prediction of competitive outcomes using a resource-based predictor (Chapter 1), on the occurrence of possible founder effects (Chapter 3) and on the physiological and morphological changes connected to reduced light levels (Chapter 4). In all experiments, we have used a model system of five perennial grass species (Poaceae) (cf. Wedin & Tilman, 1993) selected from those found in European fertile meadows to differ in their canopy heights and light competition abilities: *Alopecurus pratensis* L., *Anthoxanthum odoratum* L., *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Festuca rubra* ssp. *commutata* Gaud. (= *Festuca nigrescens* Lam.), *Holcus lanatus* L. (Lauber & Wagner, 1996). We choose a limited set of five species so that we could include all possible pairwise combinations in our experimental design while at the same time being able to replicate each species combination five times. All experiments were conducted in the experimental garden of the Institute of Environmental Sciences, Zurich (47° 23’ N, 8° 33’ E, and 546 m height a.s.l.).

In Chapter 1, we present the results of one of the few mechanistic experiments investigating the outcome of short-term competition using measurements of light interception from monocultures of five perennial grass species grown under fertilized and irrigated conditions.
General Introduction

In Chapter 2, we present the results of an experiment where species were grown under fertilized and irrigated conditions in monoculture, all pairwise mixtures and the full five-species mix. We investigated whether species partition light and whether this lead to increased mixture biomass as compared to monoculture biomass and tried to explain the observed patterns with characteristics of monocultures and of mixtures. Further, we present the first application of a new model of light competition in plant communities.

In Chapter 3, we describe a founder experiment and we test the hypotheses that (1) with an increasing time interval between the sowing of the founder and the invader species, the dominance patterns of dominant species will decrease, and poor light competitors will be increasingly able to prevent better light competitors from establishing that therefore the correlation between founder control and traits connected to competition for light will decrease; and (2) that on a less nutrient-rich soil, competitive ability will not be connected to traits important for competition for light even on short interval.

In Chapter 4, we aimed to (1) record physiological and morphological changes of traits relevant in competition for light in response to shade and thus obtain estimates for our grass species and to (2) investigate if our species differed in shade tolerance.

References


Chapter 1

Differences in Light Interception in Grass Monocultures Predict Short-Term Competitive Outcomes under Productive Conditions

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Chapter 1: Light Competition among Grasses

Abstract

Due to its inherent asymmetry, competition for light is thought to cause loss of diversity from eutrophied systems. However, most of the work on this topic in grasslands has been phenomenological and has not measured light directly. We present the results of one of the few mechanistic experiments investigating the outcome of short-term competition using measurements of light interception from monocultures of five perennial grass species grown under fertilized and irrigated conditions. We found that the level of incident light intercepted by each species in monoculture, a direct measure of resource-reduction ability, was an excellent predictor of the relative competitive effect in pairwise mixtures. Competition for light was asymmetric in relation to differences in light intercepting ability. Our results are consistent with the idea that when light is a limiting resource, competition between species for this resource can be asymmetric, contributing to high dominance and low diversity.
**Introduction**

One of the most widely observed results of global change is that in many different types of ecosystems eutrophication leads to diversity loss [1-3]. In eutrophied terrestrial plant communities, such as many European grasslands, competition for light is thought to be a mechanism for this diversity loss [4-7] and the asymmetric nature of this competition can lead to an outcome which supports only low plant diversity [8-10]. But the details of exactly how this loss of diversity comes about are not well understood, because most studies that have been conducted so far were phenomenological.

The best developed mechanistic theory of resource-competition is Tilman’s $R^*$ [7,11]. If species in a system are limited by a single resource, the species that can reduce this resource to the lowest equilibrial level ($R^*$) is the best competitor and should displace other species. However, in terrestrial plant communities $R^*$ theory has only been applied to belowground resources, specifically soil nitrogen, and almost exclusively at a single site [12, 13], namely the well-known nitrogen-limited prairie at Cedar Creek, Minnesota, USA. Studies there support the ability of $R^*$ to predict species’ relative abundances and the outcome of competition during secondary succession in old fields [13-17].

Huisman & Weissing [18] and Huisman et al. [19] are some of the few researchers to apply the $R^*$ approach to light. They performed competition experiments with phytoplankton in continuous, well-mixed cultures that were nutrient-rich and light-limited. They found that the critical light intensity at the bottom of a water column in monoculture ($I_{out}^*$), was a good predictor of competitive outcomes in species mixtures: the species with the lowest $I_{out}^*$ was the strongest competitor and displaced all other species. However, their cultures of phytoplankton were constantly mixed to prevent the organisms from forming layers, meaning that $I_{out}^*$ was directly analogous to $R^*$. 
By contrast, in terrestrial systems, where plants establish three-dimensional canopies, species in the uppermost layer can pre-empt light and shade those beneath. A small advantage in height therefore allows much more of the light to be intercepted, conferring a disproportionately large competitive advantage. This mode of competition, which is disproportionate to some measure of size, is called relative-size asymmetric [20-22]. In contrast, when competition is relative-size symmetric, plants obtain a share of the resource proportionate to their size, as is often assumed to be the case when competition is for soil nutrients. With symmetric competition, growth of all plants is slowed down, whereas asymmetric competition acts to increase the variation in relative growth rates as smaller plants suffer more and therefore to exaggerate relative size differences [20-22]. Thus, when competition is for light, the outcome of the interaction should be quickly seen. In addition, resource utilization patterns (such as the percentage of incident light intercepted) measured during the growing season should be good mechanistic predictors of competitive outcomes. However, though some studies have shown that under conditions where competition for light is assumed to be important, competition is relative-size asymmetric [21,23], few have included estimates of actual light interception in terrestrial habitats [21].

Here we describe a competition experiment with five perennial grass species found in European fertile meadows which were selected to differ in height (and therefore their ability to compete for light). We test the hypothesis that under productive conditions there is strong asymmetric competition for light and that the relative ability of species to intercept light predicts the outcome of competition. Although we cannot identify light as the only limiting resource, we show that this resource-based approach using light interception levels in monoculture (a measure of resource reduction) predicted short-term competitive outcomes, and confirm that competition for light was asymmetric.
Results

OUTCOME OF SHORT-TERM COMPETITION FOR LIGHT

The observed competitive hierarchies averaged over all target-neighbour species combinations were: \textit{H. lanatus} > \textit{A. pratensis} >> \textit{A. elatius} >>> \textit{A. odoratum} > \textit{F. rubra} (where “>” means “had an overall higher relative competitive effect than”). Our species had highly unequal abilities to suppress target plant growth of the other species. Target plant biomass of \textit{F. rubra} and \textit{A. odoratum} decreased strongly when they were surrounded by the taller \textit{A. pratensis} and \textit{H. lanatus}, in comparison to their biomass when growing surrounded by conspecifics (Fig. 1). In contrast, target biomass of \textit{A. pratensis} and \textit{H. lanatus} increased strongly when they were surrounded by the shorter \textit{F. rubra} and \textit{A. odoratum} in comparison to their biomass when they were surrounded by conspecifics (Fig. 1).

The relative competitive effect was significantly positively related to relative differences in light interception in monoculture – measured 10, 15 and 18 weeks after sowing (linear regression with 95% confidence intervals, Fig. 2). This shows that species intercepting a greater percentage of incident light – and thus reducing the light available to species with lower canopies – had a competitive advantage. The later in the season the light interception measurement was taken, the smaller the relative differences in light interception levels between species and the less variation in the relative competitive effect was explained (Fig. 2).

The relative competitive effect was also significantly positively related to relative differences in species’ sizes (linear regression on monoculture biomass with 95% CIs: Fig. 3A; maximum monoculture canopy height: Fig. 3B).
Chapter 1: Light Competition among Grasses

Figure 1: Mean relative target biomass of all species in the control treatment. Mean target biomass (± SE) of each species in all pairwise combinations, standardized by the target biomass with conspecific neighbours. Grey bars indicate target biomass with conspecific neighbours, white bars target biomass with their respective interspecific neighbours. Target species are: (A) *A. pratensis*, (B) *A. odoratum*, (C) *A. elatius*, (D) *F. rubra* and (E) *H. lanatus*.
Figure 2: Relationship between the relative competitive effect and relative differences in light interception.

Linear regression slopes and 95% confidence intervals for the relationships between the relative competitive effect ($RCE_i$) and the log ratio of neighbour/target light interception levels (A) 10 weeks, (B) 15 weeks and (C) 18 weeks after sowing. The black dashed line is the expected regression line with perfect symmetry which has a

$R^2 = 0.77$

$R^2 = 0.72$

$R^2 = 0.63$
COMPETITIVE ASYMMETRY

We tested for symmetry by checking whether the 95% confidence intervals for the linear regression slopes contained the predicted value of +1. All slopes were greater than +1 with no confidence interval containing that value: 10 weeks (Fig. 2A, slope = 2.0 (1.46 – 2.54)), 15 weeks (Fig. 2B, slope = 3.0 (2.07 – 3.90)) and 18 weeks (Fig. 2C, slope = 6.7 (4.19 – 9.29)). The relationship was more symmetric when the values from later measurements of light interception levels were used, due to the decreasing differences in the light interception levels between species as they approached maximum canopy height.

Tests for relative size-asymmetry depended on the measurement of size used. The confidence intervals for the relationship between the relative competitive effect and relative difference in aboveground monoculture biomass did contain +1, consistent with relative size-symmetric competition (Fig. 3A, slope = 1.7 (0.49 – 2.86)). By contrast, the confidence intervals for the relationship between the relative competitive effect and relative difference in maximum monoculture canopy height did not contain +1, indicating an asymmetric advantage (Fig. 3B, slope = 3.2 (1.50 – 4.91)). Taken together, this implies that greater maximum canopy height and increased ability to intercept incident light confer a disproportionately large competitive advantage. This confirms that competition for light was asymmetric under the productive conditions of our experiment as predicted.
Chapter 1: Light Competition among Grasses

Figure 3: Relationship between the relative competitive effect and relative differences in sizes. Linear regression slopes and 95% confidence intervals for the relationships between the relative competitive effect (RCE$_{ij}$) and the log ratio of neighbour/target values for (A) monoculture biomass, (B) maximum monoculture canopy height. The black dashed line is as in Fig. 2.

MANIPULATION OF COMPETITION FOR LIGHT

As the light interception level measured 10 weeks after sowing was the best single predictor for the relative competitive effect, we used this variable to investigate the relative competitive release (i.e. the response of target plant biomass and height to netting away neighbours, corrected for the performance of target individuals with conspecific neighbours). As expected there was a significant positive relationship between the relative competitive release based on target plant biomass and the difference in light interception levels measured in monoculture (Fig. 4A; linear regression slope = 0.9 (0.38 – 1.44)). This shows that the magnitude to which species were released from competition depended on the relative light interception capabilities between each species pair. By contrast, the slope of the relationship between the relative competitive release based on target plant height and differences in light interception levels measured in monoculture was negative (Fig. 4B; slope = -0.3 (-0.15 – -0.39)). Thus, the
The greatest increase in biomass was seen when the best light competitor (species intercepting the most light) was netted away from the poorest light competitor (the species intercepting least light) and this was accompanied by the greatest decrease in height. The change in height presumably reflects a plastic response to the reduction of competition which removes the need to grow tall.

Figure 4: Relationship between the relative competitive release and relative differences in light interception. Linear regression slopes and 95% confidence intervals for the relationships between the relative competitive release ($RCR_{ij}$) based on (A) target plant biomass and (B) height and the log ratios of neighbour/target light interception levels 10 weeks after the sowing. Letters denote the target plant species; subscripts denote the corresponding surrounding species of each respective species pair, as given in Fig. 1.

Discussion
The aim of this experiment was to test how well the differences in the light-intercepting abilities of our deliberately selected species could mechanistically explain the short-term outcome of competition under conditions where there was strong competition for light. While we cannot exclude additional competition for other resources, we found that there was strong asymmetric competition for light and that short-term competitive outcomes could be well
Chapter 1: Light Competition among Grasses

predicted by differences in the percentage of intercepted incident light of each species in monoculture. The species that intercepted the greatest percentage of light had the greatest relative competitive effect (Fig. 2). Species differences in light interception also determined the relative response of species to the netting treatment, in which aboveground competition was reduced (Fig. 4), and confirmed that our species were highly unequal competitors. Compared with the full competition treatment, target plant biomass of *A. odoratum* and *F. rubra* (poorest light competitors) increased by an average of 47% in the netting treatment when either *A. pratensis* or *H. lanatus* (best light competitors) were neighbours. On the other hand, *A. pratensis* and *H. lanatus* showed very little change in biomass following netting when *A. odoratum* or *F. rubra* were neighbours.

Although some studies have shown that under conditions where competition for light is important, competition is relative-size asymmetric [21,23], few have included estimates of the actual light interception in terrestrial habitats [21]. By investigating the slopes of the relationship between the relative competitive effect and relative differences in light interception, we were able to show that competition was asymmetric in regard to light interception (Fig. 2). Additionally, we have also found relative-size asymmetry in the relationship between the relative competitive effect and relative differences in maximum canopy height (Fig. 3B). This implies, that a species with greater maximum canopy height which therefore intercepted more incident light, would have a disproportionate competitive advantage. Our study agrees with the following two studies that also included estimates of actual light interception. A study of intraspecific competition between birch seedlings showed that the tallest individuals within a population intercept the majority of light at the expense of shorter individuals [24]. Schwinning [25] found a positive slope in the relationship between the log ratio of light interception differences and the differences in biomass of two individuals in the high density treatment of millet plants, a positive slope in the relationship between light interception per unit leaf area and dry shoot biomass and concluded that at high density,
competition for light can be asymmetric. More recently, Dybzinski & Tilman [26] have demonstrated that $I^*$ can be used to successfully predict longer-term (11 years) competitive exclusion in a nitrogen gradient at Cedar Creek.

According to the $R^*$ theory for soil nutrients, equilibrial resource levels are required to explain competitive outcomes, because growth of all competitors is equally limited by the lack of resource and the strength of a competitor shows in its ability to persist at a resource level that is lower than that of other competitors. However, asymmetric competition increases relative size differences between species [21,22] and enables species intercepting more of the incident light to maintain their initial dominant position during the whole growing season. Under such circumstances, dominance and even competitive exclusion can develop very quickly. This implies that measurements of intercepted light taken at early stages of vegetation growth should be good predictors of competitive outcomes. All of our three light measurements (10, 15 and 18 weeks after the sowing of the experiment) gave good qualitative predictions of the relative competitive effect. However, in accordance with a recent study by Violle et al. [27], differences in light interception in monocultures at the earliest measurement (after 10 weeks) best explained competitive outcomes at harvest (18 weeks). Both studies therefore agree that instantaneous measurements of light interception can be very useful predictors, as long as they are obtained during a critical time when light becomes limiting for plant growth [27].

Because competition for light acts essentially instantaneously on quickly developing communities such as grasslands, short-term experiments can give valuable insight into underlying mechanisms. In the long-term, other factors and trade-offs might of course modify the outcomes of competition and reduce the predictive power of intercepted light in our system. For example, founder effects may play an important role when competition is for light [28-30]. Litter accumulation over long time intervals can also lead to reduced light intensities.
and have thus important effects on seedling recruitment and plant biodiversity [31,32]. However, for the reasons outlined above, we expect little scope for transient effects to occur when competition for light is as considerable as in our experiment, and thus also little potential for a mis-match between short- and long-term competitive outcomes. Our study could not test for limitation by all potential resources and so we cannot exclude an additional role of other forms of competition. Nevertheless, we have shown that under productive conditions the short-term outcome of competition in our experiment could be well predicted from a resource-based predictor: light interception (resource reduction) in monoculture. Our study is therefore consistent with competition for light as an important component of mechanisms of competitive exclusions in productive and eutrophied grasslands.

Materials and Methods

EXPERIMENTAL DESIGN

The competition experiment reported here is part of a wider project about light competition and partitioning in grasslands which uses a model system of five perennial grass species (Poaceae) [cf. 17] parsimoniously selected from those found in European fertile meadows to differ in their canopy heights and light competition abilities. The species are: *Alopecurus pratensis* L., *Anthoxanthum odoratum* L., *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Festuca rubra* ssp. *commutata* Gaud. (= *Festuca nigrescens* Lam.), *Holcus lanatus* L. [33]. The experiment was conducted in the experimental garden of the Institute of Environmental Sciences, Zurich (47° 23’ N, 8° 33’ E, and 546 m height a.s.l.).

One central target plant was grown surrounded by a ring of neighbours of each of the species including itself (i.e. in all possible intraspecific and interspecific pairwise combinations), in plots defined by PVC rings of 30 cm diameter and filled to a depth of 15 cm with a highly-fertile soil. The neighbour species were sown at a density of 1000 seeds m⁻² (corrected based on the results of prior germination trials). Aboveground competition between
the neighbours and the target species was successfully reduced by tying back the neighbouring vegetation with fine tree netting. Plants were watered with an automatic irrigation system on a daily basis. The 25 target-neighbour species combinations crossed with the control and reduced aboveground competition treatments produced 50 combinations which were repeated five times in a randomised block design giving a total sample size of 250 plots. The neighbouring species were sown in April. Target seedlings were transplanted to the experimental plots one month later. At this time the targets had approximately the same size as the neighbour plants. At the end of August (approximately 18 weeks after the sowing), aboveground parts of target plants were harvested, dried at 80°C and weighed.

ANALYSIS OF COMPETITION AND COMPETITIVE ASYMMETRY

For the control (full competition) treatments, we calculated the relative competitive effect of each neighbour species on each target species and related these competitive effects to differences in light-depletion levels and to species’ sizes [cf. 34,35]. The relative competitive effect ($RCE_{ij}$) of each neighbour species, $j$, on each target species, $i$, was calculated as the log ratio:

$$RCE_{ij} = \ln \left( \frac{B_{ij}}{B_{ii}} \right)$$  Eqn 1

where $B_{ii}$ is the biomass of target species $i$ surrounded by conspecific neighbours, and $B_{ij}$ is the biomass of target species $i$ surrounded by neighbours of species $j$. A positive value of the relative competitive effect means that the target biomass was lower when growing with species $j$ neighbours than with conspecific neighbours, i.e. neighbours of species $j$ have a stronger negative effect on the target biomass than conspecific neighbours, and vice versa. Competitive hierarchies were established by averaging over the ability of species to competitively suppress the other four species.
Light interception in monocultures (measured during the first growth season 10, 15 and 18 weeks after the sowing), and measures of species’ sizes (aboveground monoculture biomass and maximum canopy height in monoculture, measured from ground to the highest leaf) were obtained from a companion experiment started in spring 2004. It consists of 80 1 m² plots where the same five grass species as in the competition experiment described here are grown on highly fertile soil in monocultures, pairwise mixtures and the five-species mix. Light levels were measured above and below monoculture canopies (approximately at ground level) with a photosynthetically active radiation probe (SunScan System - SS1, Delta-T Devices Ltd, Cambridge, UK) and the percentage of incident light intercepted in each canopy was calculated. The relative difference in light intercepted in monoculture between species $i$ and $j$ was calculated using the log ratio:

$$L_{ij} = \ln\left(\frac{L_j}{L_i}\right).$$  
Eqn 2

A positive value of $L_{ij}$ means that the neighbouring species $j$ intercepted more light in monoculture than the target species $i$ and vice versa. Similarly, the relative difference in species’ sizes was calculated as $S_{ij}$, the log ratio of $S_j$ (aboveground monoculture biomass or maximum monoculture canopy height of the neighbouring species) and $S_i$ (aboveground monoculture biomass or maximum monoculture canopy height of the target species).

We can quantify the relationship between the relative competitive effect and relative differences in light interception and test for symmetry. If competition is symmetric and $L_{ij} = N$ we expect $RCE_{ij} = N$. However, under asymmetric competition, when $L_{ij} = N$ we expect $RCE_{ij} > N$, i.e. the difference in trait values has conferred a disproportionate competitive advantage. Thus, plotting $RCE_{ij}$ against $L_{ij}$ should reveal a slope of +1 if competition is symmetric, or $>+1$ if competition is asymmetric. We chose the percentage of incident light intercepted in monoculture ($L = 100-I^*$) instead of the absolute light level below the monoculture ($I^*$) for two reasons (see Text S1).
MANIPULATION OF COMPETITION FOR LIGHT

The netting treatment was used to confirm that there was competition for light. When there is competition for light, we expect a poor light competitor surrounded by a good light competitor to respond to the netting with a large increase of biomass, because in this case tying back the neighbour should reduce shading. In the opposite case, when a good light competitor is surrounded by a poor light competitor, we would expect no or only a small increase of biomass, because there is little shading. Thus, the magnitude of release from competition due to the netting should depend on the relative light interception capabilities between each species pair. To assess the response of target plant biomass to the reduction of aboveground competition we calculated the relative competitive release ($RCR_{ij}$) which is the log ratio of the inverse of the relative competitive effects in the control and netting treatments:

$$
RCR_{ij} = \ln \left( \frac{\frac{B_i(\text{netting})}{B_i(\text{control})}}{\frac{B_j(\text{netting})}{B_j(\text{control})}} \right).
$$

Eqn 3

The relative competitive release is positive when the target biomass (B) of species $i$ increases more when neighbours of species $j$ are netted away than when conspecific neighbours are netted away. This occurs when the relative competitive effect of species $j$ on target species $i$ is large and positive and vice versa.

In addition we also calculated the relative competitive release using target plant height instead of biomass. Plants can respond plastically to shading by increasing their height (but not their biomass) in an attempt to escape shading. Thus, we expect to find that target plants experiencing substantial shading by a neighbouring species $j$ will decrease in height in the netting treatment, whereas target plants experiencing no or only slight shading by a neighbouring species $j$ should show no decrease in height. In this case, the relative competitive release calculated using height rather than biomass is expected to be negative when the relative competitive effect of an interspecific neighbour is large and positive; that is...
when the target plant height decreases more when species $j$ neighbours are netted away than when conspecific neighbours are netted away and vice versa.

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Text S1: Additional information on the analysis of competition

Reasons why we chose the percentage of incident light intercepted in monoculture instead of the absolute light level below the monoculture:

We chose the percentage of incident light intercepted in monoculture ($L = 100 - I^*$) instead of the absolute light level below the monoculture ($I^*$) for two reasons. First, because intercepted light can be directly converted into growth by the plant and is no longer available to plant competitors, whereas $I^*$ provides information about the level of unused resource. Second, using the percentage of intercepted light also has advantages for investigating symmetry. Consider two species where one intercepts 90% of the incoming light while the other intercepts 45% (i.e. the first intercepts twice as much light). Then using Eqn 2 from the text, $L_{ij} = Ln(90/45) = Ln(2) = 0.69$. If competition is symmetric with regard to light interception, we expect $RCE_{ij}$ to be also $Ln(90/45)$, because when species $j$ intercepts twice as much light as species $i$, it should also have twice the competitive effect. In contrast, using $I^*$ directly gives a value of $Ln(10/55) = -1.7$. The same test can be performed to test for relative-size symmetry in the relationship between $RCE_{ij}$ and $S_{ij}$. 
Chapter 1: Light Competition among Grasses

References


Chapter 2

Light Partitioning in Experimental Grass Communities

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Abstract

Through complementary use of canopy space in mixtures, aboveground niche separation has the potential to promote species coexistence and increase productivity of mixtures as compared to monocultures. We set up an experiment with five perennial grass species which differed in height and their ability to compete for light to test whether plants partition light under conditions where it is a limiting resource, and if this resource partitioning leads to increased biomass production in mixtures (using relative yield-based methods). Further, we present the first application of a new model of light competition in plant communities. We show that under conditions where biomass production was high and light a limiting resource, only a minority of mixtures outperformed monocultures and overyielding was slight. The observed overyielding could not be explained by species differences in canopy structure and height in monoculture and was also not related to changes in the canopy traits of species when grown in mixture rather than monoculture. However, where overyielding occurred, it was associated with higher biomass density and light interception. In the new model of competition for light, greater light use complementarity was related to increased total energy absorption. Future work should address whether greater canopy space-filling is a cause or consequence of overyielding.
Chapter 2: Light Partitioning in Experimental Grass Communities

Introduction

Competition for light in plant communities is thought to be asymmetric, leading to strong competition and rapid competitive exclusion (Huston & DeAngelis 1994; Schwinning & Fox 1995; Lepš 1999; Vojtech et al. 2007 (chapter 1 of this thesis)). Does this mean that there is little or no possibility for partitioning of this aboveground resource and that competition for light will always lead to competitive exclusion? A recent theoretical model of light competition among tree species (Adams et al. 2007) predicts that competition for light can lead to competitive exclusion, founder control or coexistence. In several studies (Hirose & Werger 1995; Anten & Hirose 1999; Werger et al. 2002; Anten & Hirose 2003), it has been shown that subordinate species were able to capture similar amounts of light per unit biomass as dominant species and this equal efficiency in capturing light by species of different stature could also help explain why they were able to coexist (Anten 2005). Further, Anten & Hirose (1999) argue that species may coexist by exhibiting different aboveground growth patterns that enable them to use different positions in time and space and to absorb light efficiently.

If species occupy different positions in the canopy space, they might use the space in a more complementary way with some species specializing on upper canopy layers and others on the understory, which could result in canopy structures which can capture more light than monoculture stands. Generally, niche separation reduces competition between co-occurring species via complementary use of resources (Kahmen et al. 2006, Anten & Hirose 1999). Aboveground niche separation and increased light interception could therefore not only lead to species coexistence, but also increase productivity of mixtures as compared to monocultures (Naeem et al. 1994; Spehn et al. 2000, 2005). Fridley (2002, 2003) showed that plant mixtures of grassland species on highly fertile soils overyielded (were more productive than expected based on monoculture yields). Because overyielding disappeared when high fertility plots were shaded, Fridley (2002, 2003) concluded that soil fertility promotes light partitioning by emphasising differences in species’ heights and growth forms. However,
Chapter 2: Light Partitioning in Experimental Grass Communities

direct experimental evidence for local niche complementarity in plants is still scarce in the scientific literature (Silvertown 2004; Kahmen et al. 2006), especially related to light.

In a recent paper, Yachi & Loreau (2007) present a simple dynamical model for a light-limited terrestrial ecosystem that can be used to assess the effect of species diversity on light competition and biomass production and to test if it is complementary light use that leads to increased biomass production in mixtures as compared to monocultures. Their model shows that reduction in light competition intensity due to differences in canopy architecture among species increases total biomass of mixtures, but that competitive imbalance can reduce mixture biomass.

Here we describe an experiment with five perennial grass species found in European fertile meadows which were selected to differ in height as indicated by a local standard flora (Lauber & Wagner 1996) and therefore their ability to compete for light (Vojtech et al. 2007). We ask whether plants partition light under conditions where it is a limiting resource, and if this resource partitioning leads to increased biomass production in mixtures (overyielding) as compared to monocultures. Further, we present the first application of the model of light competition in plant communities by Yachi & Loreau (2007).

We show that under highly fertilized conditions, where light was a limiting resource and biomass production very high, only some mixtures outperformed monocultures and overyielding was slight. The observed overyielding could not be explained by differences between species in canopy structure and height and was also not related to changes in the canopy traits of species when grown in mixture rather than monoculture. However, where overyielding occurred, it was associated with higher biomass density and light interception. This result was confirmed by the new model of competition for light which showed that greater complementarity in light use was related to increased total energy absorption. Even though we cannot conclude from this observation that denser canopies were a consequence of
increased light interception, our results show that overyielding mixtures were able to achieve a denser filling of the aboveground space.

Materials and Methods

EXPERIMENTAL DESIGN

The experiment reported here is part of a wider project (Vojtech et al. 2007) about light competition and partitioning in grasslands which uses a model system of five perennial grass species (Poaceae): *Alopecurus pratensis* L., *Anthoxanthum odoratum* L., *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Festuca rubra* ssp. *commutata* Gaud. (= *Festuca nigrescens* Lam.), *Holcus lanatus* L. (Lauber & Wagner 1996). The experiment described here was conducted in the experimental garden of the Institute of Environmental Sciences, Zurich (47° 23’ N, 8° 33’ E, and 546 m height a.s.l.) and was set up in April 2004 and ran until autumn 2006. It consisted of 1 m² plots where species were grown on highly fertile soil (Garden humus, Ricoter, Aarb erg, Switzerland) in all monocultures (n = 5), all pairwise mixtures (n = 10) and the full five-species mix (n = 1) in a fully randomized design. Each species combination was replicated five times, yielding a total of 80 plots. Species were sown at a target density of 1000 seeds m⁻² (corrected based on the results of prior germination trials). Plants were watered daily to assure ample water. To assure continuously high nutrient amounts, plots were fertilized in 2005 and 2006 with a NPK fertilizer corresponding to 15 g m⁻² yr of nitrogen in five applications during the growth season. Plots were weeded on a regular basis.

Light levels were measured above and below canopies (approximately at ground level) with a photosynthetically active radiation probe (SunScan System - SS1, Delta-T Devices Ltd, Cambridge, UK) at the beginning of each growth season and before the harvest and the percentage of incident light intercepted in each canopy was calculated. The aboveground parts of plants growing in the inner 50 x 50 cm of each plot were harvested to a height of 3 cm at
the end of the growing season in August/September in all three years, sorted into species, dried at 80°C and weighed. In 2005 and 2006, biomass was also harvested at the beginning of June. The June harvest in 2005 was conducted as a layered harvest, i.e. after sorting to species, plants were cut every 10 cm to separate the canopies into 11 layers. Additionally, leaf tissue was separated from stem tissue and leaf area of each species in each layer was measured in 3 of 5 replicates each with a leaf area meter (LI-3100C Area Meter, LI-COR, Nebraska, USA).

ANALYSIS OF YEARLY PATTERNS
As our species all reached similarly high monoculture aboveground biomass yields in 2005 and 2006, we did not apply the additive partitioning methods (Loreau & Hector 2001; Fox 2005), because when there is no variation in monoculture biomass there can be no covariance with mixture performance and per definition selection effect = dominance effect = 0. In this case, all biomass increase in mixture as compared to monoculture can be regarded as caused by complementarity. To assess performance of mixtures relative to performance of monocultures, we calculated $D$ (Loreau, 1998a) as:

$$D = \sum_i RY_i - 1 = \sum_i \left( \frac{YO_i}{M_i} \right) - 1$$

Eqn 1

where $YO_i$ is the biomass of species $i$ in a given mixture and $M_i$ the biomass in monoculture. A $D > 0 \approx RYT > 1$ indicates that the mixture performed better than the included monocultures and therefore overyielded. When we talk about overyielding in this paper, we always refer to $D > 0$ (or, equivalently, $RYT > 1$).

DETAILED ANALYSIS OF THE JUNE HARVEST IN 2005
Because the harvest in June 2005 provided detailed information about canopy structure, we used only these data in the analyses of canopy characteristics and in the model of light
competition in plant communities (Yachi & Loreau 2007). To apply the model by Yachi & Loreau (2007), using the measured leaf area, light interception data before the harvest and the harvested biomass, we calculated for the pairwise mixtures and the full five-species mixture the increase in total biomass the following indices: According to equation (4) in Yachi & Loreau (2007), we calculated the increase in total biomass ($\delta B$, in g per harvested area) as:

$$\delta B = B_{mix} - \frac{1}{N} \sum_{i=1}^{N} B_{mono-i}$$  \hspace{1cm} \text{Eqn 2}$$

where $B_{mix}$ and $B_{mono-i}$ are the biomass of the mixture and corresponding monocultures at harvest. Following the equation (14) in Yachi & Loreau (2007), we calculated the increase in total light energy absorption ($\delta E$, in µmol photons m$^{-2}$ s$^{-1}$) as:

$$\delta E = L_{0, mix} \cdot g(\bar{q}, LAI_{mix}) \cdot (LC + UG)$$ \hspace{1cm} \text{Eqn 3}$$

the light complementarity index ($LC$, see equation (7) in Yachi & Loreau (2007)) and the unbalanced growth term ($UG$, see equation (14)) as:

$$LC = e_{mix} - \left( \frac{1}{N} \sum_{i=1}^{N} e_i \right)$$  \hspace{1cm} \text{Eqn 4}$$

$$UG = \frac{1}{N} \sum_{i=1}^{N} e_i \left[ 1 - \frac{g(q_i, LAI_{mono-i})}{g(\bar{q}, LAI_{mix})} \right]$$  \hspace{1cm} \text{Eqn 5}$$

$L_{0, mix}$ is the light intensity above mixture canopies, $g (q, LAI)$ is an increasing function of $q$ and of $LAI$ (cf. equation (12) in Yachi & Loreau (2007)), where $q_i$ is the species-specific light absorption rate per unit leaf area, $\bar{q}$ the average of all $q_i$ among the species present in a mixture and $LAI_{mono-i}$ and $LAI_{mix}$ the leaf area indices of monocultures and mixtures. $e_i$ and $e_{mix}$ are the light absorption efficiencies of monocultures and mixtures and are calculated following equation (8a) and (8b) in Yachi & Loreau (2007) as:

$$e_i = \frac{\Delta E_i}{\Delta E_{i\text{-max}}},$$  \hspace{1cm} \text{Eqn 6a}$$
\[ \frac{\Delta E_{\text{mix}}}{\Delta E_{\text{mix-max}}} \]

Eqn 6b

\( \Delta E_i \) and \( \Delta E_{\text{mix}} \) are the light energies absorbed by monocultures and mixtures respectively (calculated as a simple difference between \( L_0 \), the light above a canopy and \( L_G \), the light below the canopy). \( \Delta E_{i-\text{max}} \) and \( \Delta E_{\text{mix-max}} \) stand for the theoretical maximum light energy of the given cultures and are calculated following equation (11a) and (11b) in Yachi & Loreau (2007) from \( L_0 \) and \( g (q, LAI) \). Being the difference between the light absorption efficiencies of a mixture and the corresponding monocultures, the light complementarity index provides a measure of complementary light absorption. We used a revised equation to calculate \( UG \) (compare equation (14) in Yachi & Loreau (2007) with Eqn 5) where we removed a mistake in the published version of the paper. Further, because the Yachi & Loreau (2007) method assumes a homogeneous environment (equal light intensities above all canopies), we had to standardize our heterogeneous above canopy light measurements. We determined the average light intensity above the experiment from measurements taken above all plots as 1725 \( \mu \text{mol photons m}^{-2} \text{ s}^{-1} \) and used this average value for \( L_0 \) instead of the individual light intensities above each plot \( (L_0\text{-measured}) \) and calculated light intensities at ground \( (L_G) \) as: \( L_G = \frac{L_G\text{-measured}}{L_0\text{-measured}} \times 1725 \). The species-specific light absorption rate \( (q_i) \) was calculated from light reflection and light transmission rates between 380 and 740 nm on five sun leaves and five shade leaves per species (high resolution miniature fibre optic spectrometer (HR2000, Ocean Optics Florida, USA) with a CI-700LP leaf probe (CID Inc., Washington, USA)). For an overview of parameters from the Yachi & Loreau (2007) method see Table A1.

We calculated means for each species combination and because this generated variation along the x-axis as well as the y-axis, we performed a reduced major axis analysis (= model II regression) using the program developed by Legendre (2001), after checking that the correlation coefficient \( (r) \) of the respective relationship was significantly different from 0.
other analyses were performed with the statistical software R (R Development Core Team 2007). Because we measured leaf area only in 3 of 5 replicates of each species combination, in the analysis of the model by Yachi & Loreau (2007) combination means are based only on 3 replicates. This might have led to a low statistical power to detect significant differences and therefore our analyses are rather conservative. Unless otherwise stated, all given intervals are 95% confidence intervals (CI).

Results

ANALYSIS OF YEARLY PATTERNS

Types of pairwise mixtures, productivity and overyielding

Based on the relative yield ($RY$), we could classify the pairwise mixtures *Alopecurus-Arrhenatherum*, *Alopecurus-Holcus* and *Anthoxanthum-Festuca* as consisting of relatively equal partners, where $RY \approx 0.5$ for both species. In the other pairs, $RY$ was $>> 0.5$ for one species while $<< 0.5$ for the other in at least one year, indicating that one species was strongly dominating the mixture (Fig. 1). Generally, there were no substantial changes of dominance through the experimental period. Apart from the *Alopecurus-Holcus* mixture where a shift in dominance occurred, the initial position of the species was well preserved. In the full mix, species exhibited similar relative abundances as in the pairs (Fig. A1).

Apart from the establishment year 2004, all species combinations (mixtures as well as monocultures) yielded high amounts of biomass (mean of dry biomass per year ± standard error (SEM): 2004: 454 ± 19 g m$^2$; 2005: 1420 ± 23 g m$^2$; 2006: 1463 ± 28 g m$^2$; Fig A2). Especially in 2005, all five species produced similar biomass in monoculture. Overyielding was slight (Fig. 2), the average overyielding over all mixtures (“Average” in Fig. 2) was 4 % in 2004, 10 % in 2005 and 2 % in 2006 and only in 2005 significantly $> 0$. This shows that in our productive system consisting of only one functional group, there was little scope for complementarity and overyielding.
Outcome of competition for light and light interception

To investigate the importance of competition for light (cf. Vojtech et al. 2007), we related the whole-year biomass ratio of each pairwise mixture to the relative difference in light interception of respective species in monoculture at the beginning of the growing season. Both the biomass ratio and the relative difference in light interception were calculated as log-ratios of relative yield or monoculture light interception of the dominant species to the respective value of the subordinate species. In all three years the slope was > 0 with no 95% CI containing that value, showing that competition for light was a strong force in our experiment and competitive dominance was strongly related to the ability to intercept incident light (Fig. A3; 2004: slope = 1.7 (0.6 – 2.7); 2005: slope = 3.6 (0.7 – 6.5); 2006: slope = 2.2 (1.1 – 3.3)). Relative differences in light interception measured before the harvest were not significantly related to competitive dominance in 2004 and 2006 (data not shown) but significantly related to competitive dominance in 2005 (data not shown, R² = 0.31; slope = 18.9 (3.8 – 34.0), even though this relationship was weaker than the one with relative differences in light interception measured at the begin of the growing season. This is in line with the observation by Violle et al. (2007) that instantaneous measurements of light interception can be very useful predictors of competitive outcomes, as long as they are obtained during a critical time when light becomes limiting for plant growth. In fact, probably due to different environmental conditions, canopies intercepted generally less light in 2005 (on average 94% on 26.5.05) than in 2006 (on average 98% on 19.5.06) which might explain why in this year also a later measurement could be used for predicting competitive dominance.
Figure 1: Development of relative biomass in all replicates of the pairwise mixtures over three years (all five harvests). "Al": *Alopecurus pratensis*; "An": *Anthoxantum odoratum*; "Ar": *Arrhenatherum elatius*; "F": *Festuca rubra*; "H": *Holcus lanatus*. Each point represents the relative biomass of a species in a plot, the solid lines connect the average relative biomass of a species in a given pairwise mixture.
Figure 2: Mean overyielding ($\bar{D}$) values (± 95 % confidence intervals) based on the annual net primary biomass production of each pairwise mixture (species abbreviations see Fig. 1; names of pairwise mixtures are composed of the abbreviated species names, „AlAn“ is the pairwise mixture of “Al” and “An” etc.), the full five species mixture (“Mix”) and the average of all mixture means (“Average”) in (a) 2004, (b) 2005 and (c) 2006.
DETAILED ANALYSIS OF THE JUNE HARVEST 2005

Prediction of overyielding based on monoculture canopy differences

For a visual comparison of canopy structures, we constructed for each species canopy profiles of leaf biomass density by plotting the proportion of a species’ leaf biomass density in each layer to the total leaf biomass density of a given plot against canopy height (Fig. 3). Biomass density is calculated to correct for differing layer heights by dividing the biomass in each layer by the respective volume of the layer. The volume of each layer is calculated by multiplying the length of the harvested area with the width of the harvested area and the height of the layer (our lowest layer was only 7 cm high, the other layers 10 cm). As expected, species had different monoculture canopy structures with *Anthoxanthum* and *Festuca* having most of their biomass low in the canopy, *Alopecurus* and *Holcus* in intermediate canopy layers and *Arrhenatherum* in the upper part of the canopy (solid lines in Fig. 3).

Following the hypothesis that overyielding should occur in mixtures that are composed of species differing in their monoculture canopy traits, we calculated, for each pairwise mixture, firstly the absolute difference in maximal monoculture canopy height of the respective species and secondly, following Schoener (1970), the percentage of potential spatial overlap of both monocultures canopy profiles (based on leaf biomass) as:

\[
\text{Spatial overlap} = 100 \times \left[ 1 - \frac{1}{2} \left( \sum_{i=1}^{11} |L_{Ai} - L_{Aj}| \right) \right]
\]

Eqn 7

where *LA*<sub>i</sub> and *LA*<sub>j</sub> are the average leaf biomass densities of species *i* and *j* in the 11 layers of the monoculture canopies. Overyielding was not related to either differences in monoculture height (data not shown, slope: 0.002 (-0.0016 – 0.0062)) or differences in spatial monoculture overlap (data not shown, slope: -0.015 (-0.069 – 0.038)). This shows that differences in canopy structure could not predict a better use of vertical canopy space and thus lead to overyielding.
Figure 3: Proportion of leaf biomass density in each layer to the total leaf biomass density in a plot for each species in each pairwise mixture and in corresponding monocultures as recorded at the June harvest in 2005. Shown are mean values of all five replicates, standard errors were left out for clarity. Solid lines denote monocultures, dashed lines pairwise mixtures. Additionally, each panel shows the corresponding overyielding ($D$) value ($\pm 95\%$ confidence interval) of the respective pairwise mixture. Species abbreviations see Fig. 1.
Canopy structure of mixtures and overyielding

As differences between the tested monoculture traits did not predict overyielding, we looked at changes in canopy traits of species when grown in mixture rather than monoculture. Apart from *Anthoxanthum* that visibly shifted its biomass upwards, especially when growing with *Alopecurus* or *Holcus*, vertical canopy structures of our species changed little in response to interspecific neighbours (compare solid lines with dashed lines in Fig. 3). To assess if this change in canopy structure was still meaningful and a decrease in canopy similarity between two species lead to increased overyielding, we calculated the difference between the realized spatial overlap of species’ canopies in a mixture and the potential overlap of both species’ monocultures. The realized spatial overlap was calculated according to Eqn 7 but using species’ leaf biomass densities in each replicate of a respective pairwise mixture and calculating averages for each species mixture. The difference between potential and realized spatial overlap was calculated either as a simple difference between the two values. However, there was no correlation between the difference in potential and realized overlap and the observed overyielding (data not shown; r: 0.10 (-0.56 – 0.69)) indicating that a decrease in canopy similarity was not connected to better mixture performance.

As several grassland experiments (Spehn 2000, 2005; Lorentzen 2008) showed that aboveground space use increased in mixtures due to taller canopies and higher biomass density, we investigated whether overyielding was associated with taller or denser canopies in our experiment. None of the pairwise mixtures constructed significantly higher canopies than the monoculture of the highest included species (average maximal canopy height (± 95 % confidence interval), maximal average canopy height of highest included species: *Alopecurus-Anthoxanthum*: 98 cm (88 – 108), vs. 102 cm; *Alopecurus-Arrhenatherum*: 108 cm (102 – 114), vs. 104 cm; *Alopecurus-Festuca*: 102 cm (96 – 108), vs. 102 cm; *Alopecurus-Holcus*: 102 cm (96 – 108), vs. 102 cm; *Anthoxanthum-Arrhenatherum*: 106 cm (99 – 113), vs. 104 cm; *Anthoxanthum-Festuca*: 94 cm (80 – 108), vs. 86 cm; *Anthoxanthum-Holcus*: 94 cm (83
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– 105), vs. 100 cm; *Arrhenatherum–Festuca*: 98 cm (88 – 108), vs. 104 cm; *Arrhenatherum-Holcus*: 104 cm (97 – 111), vs. 104 cm; *Festuca-Holcus*: 96 cm (82 – 110), vs. 100 cm).

Relative biomass density was calculated (according to the calculation of overyielding; see Eqn 1) as the ratio of biomass density (plot biomass divided by the volume in which the biomass was distributed, g m$^{-3}$) of species $i$ in mixture to biomass density of species $i$ in monoculture. Total relative biomass density is the sum of relative biomass densities (minus 1 to obtain the same scale as in overyielding, i.e. comparable to $D$). Because we did not have information about light interception of individual species in mixtures, we calculated relative light interception as the ratio of light interception in a mixture to the average monoculture light interception of all respective species. Overyielding was significantly positively correlated to relative biomass density (Fig. 4a; r: 0.95 (0.81 – 0.99); slope: 1.01 (0.803 – 1.279) and also to relative light interception early in the season (Fig. 4b; r: 0.71 (0.20 – 0.92); slope: 1.07 (0.644 – 1.779)). These results show that overyielding mixtures filled aboveground space more densely without enlarging the available canopy space by an increase in height. Although it seems likely that an increase in biomass density, i.e. a denser filling of the available canopy space by complementary mixtures (cf. Spehn et al. 2000, 2005) lead to higher light interception which in turn lead to overyielding, we cannot rule out some other form of complementarity increasing both.

*The Yachi & Loreau model of light competition in plant communities*

The net biodiversity effect on biomass ($\delta B$) was mainly positive; mixtures produced on average up to 70 g more biomass per harvested area. The increase in total energy absorption ($\delta E$) was on average positive in six out of the eleven mixtures; assuming an incident light level of 1725 µmol photons m$^{-2}$ s$^{-1}$, mixtures intercepted on average between 70 µmol photons m$^{-2}$ s$^{-1}$ less and 56 µmol photons m$^{-2}$ s$^{-1}$ more (corresponding to roughly 3-4%) than the involved monocultures (Fig. 5a). The relationship between the net biodiversity effect on
biomass and the increase in total energy absorption was not significant (Fig. 5a; r: 0.33 (-0.34 – 0.77)), however it is obvious from the figure that only mixtures with increased light interception produced more biomass than the involved monocultures. The increase in total energy absorption was strongly positively related to the light complementarity index (Fig. 5b; r: 0.97 (0.90 – 0.99); slope: 1673 (1409 – 1987)), showing that complementary light partitioning between species explained variation of the increase in total energy absorption. The increase in total energy absorption was not significantly related to the unbalanced growth term (Fig. 5c; r: 0.02 (0.59 – 0.61)).

Figure 4: The relationship of mean overyielding (\(\bar{D}\)) values (± SEM) of all 10 pairwise and the full five species mixture from the June harvest in 2005 with mean values (± SEM) of mixture (a) relative biomass density and (b) relative light interception early in the growing season of 2005.
Figure 5: Application of the model of light competition in plant communities (Yachi & Loreau, 2007) to data from the June harvest in 2005 (mean ± SEM of all ten pairwise and the full five species mixture). The regression line was fitted using reduced major axis analysis. (a) relationship between increase in total biomass ($\delta B$) and increase in total energy absorption ($\delta E$), (b) relationship between increase in total energy absorption ($\delta E$) and the light complementarity index ($LC$) and (c) relationship between increase in total energy absorption ($\delta E$) and the unbalanced growth term ($UG$).
Discussion

The aim of this experiment was to investigate whether plants partition light under conditions where light is a limiting resource, and if this resource partitioning leads to increased biomass production. In our productive system where competition for light was important and competitive outcomes could be well predicted with light interception in monoculture early in the growth season, we observed strong dominance patterns and only slight overyielding in some mixtures. The observed overyielding could not be explained by differences between species in canopy structure and height in monoculture and was also not related to changes in the canopy traits of species when grown in mixture rather than monoculture. However, where overyielding occurred, it was connected to increased biomass density and light interception, but not to increased canopy height. In the new model of competition for light, greater light use complementarity was related to increased total energy absorption. Even though we cannot exclude the possibility that denser canopies and increased light interception were both a consequence of some other form of complementarity, our results show that overyielding mixtures were able to achieve a denser filling of the aboveground space. In this regard, our results are in line with other studies showing that aboveground use space can increase in mixtures as compared to monocultures (Spehn et al. 2000; Lorentzen 2008), although in our study this effect was limited.

How might species in mixtures partition resources in a complementary way which leads to a more complete resource use? Our study considered the importance of complementary canopy architecture in light competition. However, in our experiment neither complementary heights nor complementary canopies were related to overyielding. Further, species in our experiment changed little in their vertical canopy structure when they were growing in mixture as compared to monoculture (low phenotypic plasticity in mixtures) and the small differences also were not related to overyielding.
Alternatively, resources can also be partitioned in time: Temporal aboveground niche differentiation may explain coexistence in some cases (Anten & Hirose 1999). However this is not likely to be the case in our experiment, because the two pairs that tended to overyield (Alopecurus-Anthoxanthum and Arrhenatherum-Holcus) have a rather similar phenology (Alopecurus and Anthoxanthum grow and flower early in the season, Arrhenatherum and Holcus flower late). Additionally, we cannot exclude the explanation that there was also some partitioning of soil resources. Even though competition for light was very strong, belowground effects could have still played a role. This could have increased aboveground biomass production and light interception and indirectly lead to overyielding. Loreau (1998b) showed with a mechanistic model that when species occupy complementary space belowground, biomass production can increase. Additionally, belowground niche separation in rooting depth, timing and form of resource uptake or along gradients of changing soil conditions has been observed (e.g. Parrish & Bazzaz 1976; Silvertown et al. 1999; McKane et al. 2002) but rarely related to overyielding (but see Berendse 1982, 1983). Alternatively, Von Felten & Schmid (in press) suggested that belowground partitioning of soil resources due to horizontal root segregation between roots of different plant species could lead to overyielding.

Resource partitioning and overyielding are predicted to be smaller when species are not functionally different, as increasing diversity of functional groups has been shown to decrease niche-overlap (Fargione et al. 2003; Turnbull et al. 2005; Mwangi et al. 2007). Complementarity in plant architecture between grasses and herbs was shown to be particularly important for increased light absorption, better three dimensional space filling and greater biomass density in mixture, whereas mixtures with only grasses showed no increase in biomass, cover or LAI (Spehn et al. 2000). Also, we did not include understorey species which accounted for changes in relative yields between high fertility and shade treatments in the experiments of Fridely (2002, 2003). In a recent study with six grass species, Gross et al. (2007) showed that overyielding can occur between grasses of different shade-tolerance levels
without the presence of other functional groups. In our experiment, we had species from only one functional group (grasses) and they did not differ in the shade level they could tolerate (Vojtech & Hector unpublished data (chapter 4 of this thesis)). This narrow range of functional diversity could have limited the scope of the complementarity between our species and thus resource partitioning and overyielding. Further studies would be necessary to investigate whether the scope for light partitioning will increase when species from different functional groups, e.g. grasses and forbs or species distinctively differing in their shade-tolerance levels are included, or whether the limited the scope of light complementarity is caused only by the high nutrient- and thus resulting low light levels.

The application of the model for light-limited terrestrial ecosystems (Yachi & Loreau 2007) showed that there is a very strong relationship between competitive relaxation due to differences in canopy architecture in mixtures as compared to monoculture and the increase in total light energy absorption (Fig. 5b). This shows that this method is a very useful tool to test for the presence of complementarity in plant communities. Even though the relationship between increase in total light interception (\(\delta E\)) and the increase in total biomass (\(\delta B\)) was not significant (which might be due to the small number of replicates and low statistical power), it is important to see that only mixtures with increased light interception produced more biomass than the involved monocultures. However, in our case the magnitude of the effects was very small: the mixture that increased its energy absorption most did so by only 3%. This confirms our previous results, that the scope for complementarity in our experiment was only very limited.

We have shown that under highly fertilized conditions where biomass production was high and light a limiting resource, overyielding was limited. The observed overyielding could not be explained with differences between species in canopy structure and height and was also not related to changes in the canopy traits of species when grown in mixture rather than monoculture. However, where overyielding occurred, it was associated with higher biomass
density and light interception. The new model of competition for light similarly showed that
greater complementarity in light use was related to increased total energy absorption. Even
though we cannot exclude the possibility that denser canopies and increased light interception
were both a consequence of some other form of complementarity, our results show that
overyielding mixtures were able to achieve a denser filling of the aboveground space.

Acknowledgements

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Chapter 2: Light Partitioning in Experimental Grass Communities


Figure A1: Development of relative biomass in all replicates of the full five species mixture over all three years (all five harvests). „Al“: Alopecurus pratensis; „An“: Anthoxanthum odoratum; „Ar“: Arrhenatherum elatius; „F“: Festuca rubra; „H“: Holcus lanatus.
Figure A2: Mean whole-year biomass (g m\(^{-2}\); ± SEM) of each combination in the experiment in (a) 2004, (b) 2005 and (c) 2006. White bars denote monocultures, light grey bars pairwise and dark grey the full five-species mixture. „Al“: *Alopecurus pratensis*; „An“: *Anthoxanthum odoratum*; „Ar“: *Arrhenatherum elatius*; „F“: *Festuca rubra*; „H“: *Holcus lanatus*. Names of pairwise mixtures are composed of the abbreviated species names, „AlAn“ is the pairwise mixture of Al and An etc. “Mix” refers to the full five-species mixture.
Figure A3: Linear regression slopes and 95% confidence intervals for the relationships between the biomass ratio and the log ratio of relative difference in light interception as measured at the begin of the growing season in (a) 2004, (b) 2005 and (c) 2006.
Table A1: Parameters used in the Yachi & Loreau (2007) method. For details see text.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Method of determination</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\delta B$</td>
<td>Increase in total biomass</td>
<td>Calculated from biomass at harvest</td>
</tr>
<tr>
<td>$L_0 (L_0, L_{0\text{mix}})$</td>
<td>Light intensity above canopy</td>
<td>Measured in the experiment</td>
</tr>
<tr>
<td>$L_G (L_G, L_{G\text{mix}})$</td>
<td>Light intensity below canopy</td>
<td>Measured in the experiment</td>
</tr>
<tr>
<td>$\Delta E (\Delta E_i, \Delta E_{i\text{-mix}})$</td>
<td>Light energy absorbed</td>
<td>Calculated from $L_0$ and $L_G$</td>
</tr>
<tr>
<td>$LAI (\text{LAI}<em>{\text{mono-i}}, \text{LAI}</em>{\text{mix}})$</td>
<td>Leaf area index</td>
<td>Calculated from measured leaf area</td>
</tr>
<tr>
<td>$q_i$</td>
<td>Species-specific light absorption rate per unit leaf area</td>
<td>Measured in the experiment</td>
</tr>
<tr>
<td>$\bar{q}$</td>
<td>Average of all $q_i$ among species in a mixture</td>
<td>Calculated from $q_i$</td>
</tr>
<tr>
<td>$g (q, LAI)$</td>
<td>Increasing function of $q$ and of LAI</td>
<td>Calculated from $q$ and of $LAI$</td>
</tr>
<tr>
<td>$\Delta E_{\text{max}} (\Delta E_{i\text{-max}}, \Delta E_{\text{mix-max}})$</td>
<td>Theoretical maximum light energy</td>
<td>Calculated from $L_0$ and $g (q, LAI)$</td>
</tr>
<tr>
<td>$E (e_i, e_{\text{mix}})$</td>
<td>Light absorption efficiency</td>
<td>Calculated from $\Delta E$ and $\Delta E_{\text{max}}$</td>
</tr>
<tr>
<td>$LC$</td>
<td>Light complementarity index</td>
<td>Calculated from $e_i$ and $e_{\text{mix}}$</td>
</tr>
<tr>
<td>$UG$</td>
<td>Unbalanced growth term</td>
<td>Calculated from $e_i$ and $g (q, LAI)$</td>
</tr>
<tr>
<td>$\delta E$</td>
<td>Increase in total light energy absorption</td>
<td>Calculated from $L_{0\text{mix}}, g (q, LAI), LC$ and $UG$</td>
</tr>
</tbody>
</table>
Chapter 3

Tests for Founder Control by Experimental Invasion of Grass Monocultures

Eva Vojtech and Andy Hector
Abstract

The asymmetric nature of competition for light between plant species can lead to dominance and rapid competitive exclusion and leave few opportunities for local coexistence in light-limited habitats. However, when outcomes of competition are determined by the timing of establishment, succession may not proceed to the best competitor for light but allow local dominance of a competitively poorer founder species (“founder control”). Here we describe an experiment with five perennial grass species which differ in their ability to compete for light. We test the hypotheses that (1) with an increasing time interval between the sowing of the founder and the invader species, poor light competitors will be increasingly able to prevent better light competitors from establishing and that therefore the correlation between founder control and traits connected to competition for light will decrease; and (2) that on a poorer soil, competitive ability will not be connected to traits important for competition for light even with a short time interval. In spite of the limitations of our study, our experiment shows that at least in the short term, founder control increases with increasing time interval between the sowing of the founder and the invader and bears thus the potential for species coexistence in spatially structured habitats.
Introduction

Asymmetric competition for light can lead to dominance and rapid competitive exclusion (Huston & DeAngelis, 1994; Lepš, 1999; Schwining & Fox, 1995; Vojtech et al., 2007 (Chapter 1 of this thesis)). Because a species in the uppermost layer can pre-empt light and shade those beneath, a small advantage in height allows much more of the light to be intercepted and confers a disproportionately large competitive advantage. This increases relative size differences between species even further (Swinning & Weiner 1998; Weiner, 1990) and enables species intercepting more of the incident light to maintain an initial dominant position during the whole growing season.

On the other hand, it is hypothesized that the asymmetric nature of competition for light also may create opportunities for local coexistence in light-limited habitats (Pacala & Rees, 1998), especially in spatially structured habitats where it may lead to an increase in species diversity (Levin, 1974; Reynolds & Pacala; 1993; Rees & Bergelson 1997). When outcomes of competition are determined by the timing of establishment, succession can become arrested and not proceed to the best competitor for light, but allow local dominance of a competitively poorer founder species (“founder control”; Reynolds & Pacala, 1993; Rees & Bergelson, 1997; Perry et al., 2003). In this case, when this poorer competitor for light has had time to establish and reach a disproportionate advantage in height and light interception over an invading better light competitor, the ranking can reverse and the poor competitor can maintain its initial dominant position and prevent the better competitor from establishing. In contrast, when competition is symmetric, as for example competition for soil resources is thought to be, initial conditions should not play a role but succession should proceed to the best competitor for the limiting resource, irrespective of initial conditions (Tilman, 1982; Tilman, 1988; Wedin & Tilman, 1993).

We have recently shown (Vojtech et al., 2007) that measurements of light interception in monocultures taken early in the season were good predictors of short-term competitive
outcomes among grasses under productive conditions. Similarly, in a companion experiment started in spring 2004 (see Chapter 2 of this thesis) where the same five grass species were grown in pairwise mixtures sown at a ratio 50:50, light measurements taken early in the season were good predictors of competitive outcomes and strong dominances of good light competitors were observed. However, as plants of all species were established concurrently, we did not assess the effect of differing establishment times on competitive outcomes and on the predictive power of monoculture light interception.

Here we describe an experiment to test for founder effects between five perennial grass species which differ in their ability to compete for light (Vojtech et al., 2007; Chapter 2). We test the hypotheses that (1) with an increasing time interval between the sowing of the founder and the invader species, poor light competitors will be increasingly able to prevent best light competitors from establishing (i.e. founder control will increase) and that therefore the correlation between founder control and traits connected to competition for light will decrease; and (2) that on a poorer soil, competitive ability will be less strongly connected to traits important for competition for light, even with a short time interval. Our experiment shows that, at least in the short term, founder control increases with increasing time interval between the sowing of the founder and the invader, and bears thus the potential for species coexistence in spatially structured habitats.

**Materials and Methods**

**EXPERIMENTAL DESIGN**

The experiment reported here is part of a wider project (Vojtech et al., 2007; Chapter 2) about light competition and partitioning in grasslands. It uses a model system of five perennial grass species (*Alopecurus pratensis* L., *Anthoxanthum odoratum* L., *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Festuca rubra* ssp. *commutata* Gaud. (= *Festuca nigrescens* Lam.), *Holcus lanatus* L. (Lauber & Wagner, 1996)) (cf. Wedin & Tilman, 1993) selected
from those found in European fertile meadows and which differ in canopy heights and light competition abilities. Seeds were obtained from Rieger-Hofmann GmbH (Blaufelden-Raboldshausen, Germany). The experiment was conducted in the experimental garden of the Institute of Environmental Sciences, Zurich (47° 23’ N, 8° 33’ E, and 546 m height a.s.l.) in 12 litre plastic containers.

The experiment investigated whether founder control developed in competition between the five selected grass species. The experiment included the following four different treatments, differing in soil nutrient levels (highly nutrient-rich and poorer soil) and in the time interval between the sowing of the “Founder” and the “Invader” species (two, four or nine weeks): (I) rich soil, interval of two weeks; (II) rich soil, interval of four weeks; (III) rich soil, interval of nine weeks; (VI) poorer soil, interval of two weeks. Time intervals of two and four weeks can be seen as representing the difference in germination between two species, whereas the interval of nine weeks corresponds to the head start of a species establishing in spring before the incoming seed rain from species flowering in early summer. The treatment with nutrient-rich soil and nine weeks interval was set up in 2005 and the other three in 2006. For the treatment with two weeks on poorer soil, the highly fertile soil (Garden humus, Ricoter, Aarberg, Switzerland) used in all other experiments was mixed with sand in a ratio of 1:1 to reduce nutrient amounts.

Each species was sown as a founder and was invaded by each of the other species. Each founder-invader combination was replicated five times, giving a total of 100 pots for each duration/soil treatment. The founder as well as the invader species were sown at a target density of germinated 500 seeds/m² (based on the results of prior germination trials) to achieve the same total target density of 1000 seeds/m² as in the other experiments of this project (Vojtech et al., 2007; Chapter 2). The founder species were sown in late April /early May and the invaders two, four or nine weeks later, depending on the treatment. The treatment with two weeks on poorer soil was watered only for the first few weeks to assure
seed germination, and after this time period, only the other three treatments were watered daily to assure ample water amounts. To avoid nutrient limitation in the second growth season, the treatment with nine weeks interval on rich soil was fertilized with a NPK fertilizer corresponding to 15 g m\(^{-2}\) yr of nitrogen in five applications in 2006. All plots were harvested at the end of August 2006, sorted into species, dried at 80°C and weighed. The treatment on rich soil with nine weeks intervals was also harvested in August 2005 and in June 2006.

DATA ANALYSIS

General growth patterns

Biomass was analysed with general linear models and summarized in ANOVA tables with sequential sum of squares. To meet the assumptions of the analysis, data were transformed with the natural logarithm. In the case of invader biomass, a value of 0.001 was added to each data point because there were many zeros. In the models, founder and invader species identity were fitted first as well as their interaction (equivalent to a species combination term). After the factor “Nutrient level”, the continuous variable “Interval” (indicating the time interval between the sowing of the founder and the invader) was fitted in the model (thus indicating time differences between the three rich soil treatments), followed by the remaining deviance from linearity (“Experiment”). According to the experimental design, the different treatment terms were tested against appropriate error terms as indicated in Table 1-4 (Schmid et al., 2002).

Founder control and its correlation to species traits

We calculated the founder control of each founder species towards each invader species as the log ratio of biomass of the founder species by the biomass of the invader species (+ 0.001). A value of 0 would mean that the invader reached the same biomass as the founder. Positive
values indicate that there was less invader biomass as compared to the founder biomass and that the founder species was able to exert stronger founder control.

To explain variation in the founder control, we related founder control to differences in species traits (Freckleton & Watkinson, 2001; Turnbull et al., 2004; Vojtech et al., 2007) that are connected to competition for light, such as light interception in monoculture, seedling relative growth rate and maximal canopy height. Relative differences in species traits between the founder and the invader species were calculated as natural log ratios of the founder trait values divided by the trait values of the invader species. A positive value of these log ratios means that the founder species had a higher trait value (i.e. intercepted more light, had a higher seedling RGR or reached a higher maximum monoculture canopy height) than the invader species and vice versa. Light interception in monocultures (measured during the first growing season 10 weeks after the sowing), and aboveground maximum canopy height in monoculture (measured from ground to the highest leaf), were obtained from a companion experiment started in spring 2004 (Chapter 2). It consists of 80 1 m\(^2\) plots where the same five grass species as in the experiment described here were grown on highly fertile soil in monocultures, pairwise mixtures and the five-species mix. Light levels were measured above and below monoculture canopies (approximately at ground level) with a photosynthetically active radiation probe (SunScan System - SS1, Delta-T Devices Ltd, Cambridge, UK) and the percentage of incident light intercepted in each canopy was calculated. Seedling mean relative growth rate (RGR) was obtained from the literature (Grime & Hunt, 1975). We considered the relationship between founder control and a given species trait to be significant when the 95% confidence intervals (CI) for the linear regression slopes did not contain the value of 0. All analyses and calculations were performed with the statistical software R (R Development Core Team, 2007).
Chapter 3: Founder Control

Results

General growth patterns

Overall, total plot biomass was higher on rich soil than under poorer conditions (“Nutrient level”), decreased with increasing time between the sowing of the founder and the invader under rich conditions (“Interval”) and was also determined by the different competitive and growth abilities of the species (“Founder” and “Invader” main effects) as well as by the interaction of those main effects (see total plot biomass in the first season (Fig. 1; Table 1), founder biomass in the first season (Table 2) and invader biomass in 2006 (Fig. 2-3; Table 3)). Invader biomass in the first season was above all determined by the time between sowing of the founder and the invader (Table 4). In the treatment with two weeks time interval on rich soil, invasion could be substantial (Figs. 2; 3), whereas in the treatment with nine weeks time interval on rich soil, none of the invaders was able to produce any noticeable amount of biomass (data not shown). There must have been seedlings of the invaders, because in the second season we observed invasion (Figs. 2; 3). However, because the invader seedlings were too tiny to distinguish them from the founder species, we recorded them as with zero biomass. Therefore, in Fig. 2-4, there are no panels for the first season (2005) of the treatment on rich soil with nine weeks interval, but only data from 2006.
Table 1: Analysis of variance of total plot biomass in the first season.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Error term</th>
</tr>
</thead>
<tbody>
<tr>
<td>a Founder</td>
<td>4</td>
<td>23.279</td>
<td>5.820</td>
<td>69.79</td>
<td>&lt; 0.001</td>
<td>c</td>
</tr>
<tr>
<td>b Invader</td>
<td>4</td>
<td>0.267</td>
<td>0.067</td>
<td>0.80</td>
<td>0.548</td>
<td>c</td>
</tr>
<tr>
<td>c Founder x Invader</td>
<td>12</td>
<td>1.001</td>
<td>0.083</td>
<td>2.76</td>
<td>0.052</td>
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<td>25.322</td>
<td>502.75</td>
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<tr>
<td>e Interval</td>
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<td>6.610</td>
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<tr>
<td>f Experiment</td>
<td>1</td>
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<td>0.131</td>
<td>4.32</td>
<td>0.062</td>
<td>p</td>
</tr>
<tr>
<td>g Founder x Nutrient level</td>
<td>4</td>
<td>1.305</td>
<td>0.326</td>
<td>6.48</td>
<td>0.006</td>
<td>n</td>
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<td>h Founder x Interval</td>
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<td>0.619</td>
<td>10.02</td>
<td>0.001</td>
<td>o</td>
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<tr>
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<td>0.542</td>
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<td>0.167</td>
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<td>0.136</td>
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<td>0.050</td>
<td>0.88</td>
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<td>q</td>
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<td>0.062</td>
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<td>0.884</td>
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Table 2: Analysis of variance of founder species biomass in the first season.

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<th>Source of variation</th>
<th>Df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Error term</th>
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<tr>
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<td>27.275</td>
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<td>0.054</td>
<td>0.014</td>
<td>0.18</td>
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</tr>
<tr>
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<td>0.075</td>
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<td>22.002</td>
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<tr>
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<td>3.275</td>
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<td>0.060</td>
<td>1.64</td>
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<tr>
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<td>0.298</td>
<td>5.35</td>
<td>0.012</td>
<td>n</td>
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<td>0.015</td>
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<td>0.100</td>
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<tr>
<td>n Founder x Invader x Nutrient level</td>
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<td>0.89</td>
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<td>0.085</td>
<td>1.36</td>
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</table>
Table 3: Analysis of variance of invader species biomass in 2006 (second season for the treatment on rich soil with nine weeks interval, first season for the others).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Df</th>
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<th>MS</th>
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<td>366.480</td>
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<td>0.231</td>
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</tr>
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<td>1.22</td>
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Table 4: Analysis of variance of invader species biomass in the first season (2005 for the treatment on rich soil with nine weeks interval, 2006 for the others).

<table>
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<th>Source of variation</th>
<th>Df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
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</table>
Figure 1: Mean total plot biomass (g per plot ± SE) as a function of the founder species identity in the different treatments. „Al“: Alopecurus pratensis; „An“: Anthoxanthum odoratum; „Ar“: Arrhenatherum elatius; „F“: Festuca rubra; „H“: Holcus lanatus.
Figure 2: Mean invader biomass (g per plot ± SE) in 2006 as a function of invader species identity in the different treatments. „Al“: Alopecurus pratensis; „An“: Anthoxanthum odoratum; „Ar“: Arrhenatherum elatius; „F“: Festuca rubra; „H“: Holcus lanatus.
Conclusion

Chapter 3: Founder Control

Figure 3: Mean invader biomass (g per plot ± SE) in 2006 as a function of founder species identity in the different treatments. „Al“: Alopecurus pratensis; „An“: Anthoxanthum odoratum; „Ar“: Arrhenatherum elatius; „F“: Festuca rubra; „H“: Holcus lanatus.

**Founder control and its correlation to species traits**

Generally, founder control increased with a longer time interval between the sowing of the founder and the invader. Founder control was also higher on poorer soil (Fig. 4). With a two-week interval between the founder and the invader, Anthoxanthum and Festuca were not able to exert much founder control, especially not towards Alopecurus and Holcus which as invaders reached almost the same biomass as the founders (founder control = 0; Fig. 4). When the time interval on rich soil was extended to four weeks or plants were grown on poorer soil, founder control generally increased and became more similar between the combinations (Fig. 4). In the second year with nine weeks interval on rich soil, Holcus was invaded considerably, all other species exerted strong founder control (Fig. 4).
Figure 4: Founder control (± 95% CI) in 2006 of all species in all species combinations (invader species in brackets after the founder species) in the different treatments. „Al“: Alopecurus pratensis; „An“: Anthoxanthum odoratum; „Ar“: Arrhenatherum elatius; „F“: Festuca rubra; „H“: Holcus lanatus.

The ability to intercept more light early in the season than an invader was the most important trait enabling species to exert founder control (expressed as the relative biomass of the founder to the invader) on rich soil with a short time interval (Fig. 5, \(R^2 = 0.80\), slope with 95% confidence interval = 3.10 (2.33 – 3.86)). The importance of the ability to intercept light decreased slightly with a longer time interval (Fig. 5, \(R^2 = 0.61\), slope = 2.50 (1.50 – 3.45)) and more on poorer soil (Fig. 5, \(R^2 = 0.20\), slope = 1.322 (0.002 – 2.643)). In the second season on rich soil with an interval of nine weeks, founder control was not related to the ability to intercept light (Fig. 5, \(R^2 = 0.05\), slope = -0.98 (-3.05 – 1.09)).
Figure 5: Linear regression slopes and 95% confidence intervals for the relationships between the log-ratio of founder/invader biomass and the log ratio of the founder/invader light interception in the different treatments.

Seedling RGR was an important factor for early light interception. Founder control was related to differences in seedling RGR on rich soil with a short time interval (Fig. 6a, $R^2 = 0.66$, slope = 6.01 (3.87 – 8.14)), but the effect decreased with a longer time interval (Fig. 6b, $R^2 = 0.54$, slope = 4.98 (2.71 – 7.24)) and poorer soil (Fig. 6c, $R^2 = 0.27$, slope = 3.29 (0.59 – 50.99)). There was no relationship between seedling RGR and light interception in the second season on rich soil with an interval of nine weeks (Fig. 6d, $R^2 = 0.10$, slope = -2.85 (-7.17 – 1.46)). Further, founder control was related to differences in maximal canopy height on rich soil with both a short time interval (Fig. 7a, $R^2 = 0.51$, slope = 5.07 (2.59 – 7.55)) and a longer time interval (Fig. 7b, $R^2 = 0.54$, slope = 4.79 (2.60 – 6.98)). The relationship was
weaker on poorer soil (Fig. 7c, $R^2 = 0.33$, slope = 3.53 (1.05 – 6.02)) and there was no effect in the second season on rich soil with an interval of nine weeks (Fig. 7d, $R^2 < 0.01$, slope = 0.18 (-4.21 – 4.56)).

Figure 6: Linear regression slopes and 95% confidence intervals for the relationships between the log-ratio of founder/invader biomass and the log ratio of the founder/invader RGR in the different treatments.
Discussion

When competition was mainly for light and seeds were sown at the same time, the good light competitors *Alopecurus* and *Holcus* generally dominated over the poor light competitors *Anthoxanthum* and *Festuca* in pairwise mixtures (Vojtech et al., 2007; Chapter 2). When the founder species was given a small head start of two weeks in the present experiment, it reached a higher biomass than the invader species by the end of the growing season, except from the strongest light competitors *Alopecurus* and *Holcus* that extensively invaded the poorest light competitors *Anthoxanthum* and *Festuca*, (i.e. there was no founder effect in these species combinations Fig. 4). Light interception early in the growing season, at a time where
it becomes limiting, has been shown to be a good predictor of competitive ability (Schwinning, 1996; Berntson & Wayne, 2000; Dybzinski & Tilman, 2007; Vojtech et al., 2007). Similarly, in the present experiment, when the time interval was very short on rich soil, light interception was by far the best predictor of founder control, and traits connected to light interception, such as height and seedling RGR, also were strongly related to founder control. In recent invasion studies in grassland communities, Milbau et al. (2003, 2005) showed in a similar way that invasibility was best predicted by the percentage of light transmitted. Similarly, Thomsen & D’Antonio (2007) observed that variation among three native grass species in their effect on light availability explained much of their relative resistance to invasion by Holcus lanatus. Decreased light availability has been furthermore suggested to directly reduce weed invasions in perennial grasslands (Foster et al.; 2002; Blumenthal et al., 2005).

When the time interval between the sowing of the founder and the invader was extended to four weeks, even the strongest light competitors were not able to invade poorer light competitors to a great extent during the course of one growing season, and even the poorest light competitors exhibited founder control (Fig. 4). Accordingly, even though the relative magnitude of founder control was still related to light interception and traits connected to light interception, the relationships were less strong than in the treatment of two weeks on rich soil. Because at harvest the invader species in the treatment of four weeks looked like adult plants and no longer seedlings, we believe that their low biomass was due to the shade created by the founder and not a consequence of a shorter growth period.

Under poorer conditions, no invaders yielded high biomass, even though the time interval was only two weeks (Fig. 4). Moreover, poor light competitors exerted founder control towards strong light competitors. In contrast to our expectations, the ability to intercept light and traits connected to light competition still predicted competitive ability under these conditions, although only weakly. This significant relationship was probably
caused by the still relatively high nutrient levels in the poorer soil treatment: even though the soil contained only half of the nutrients of the rich treatment, this was still roughly 100 mg nitrate/kg soil. This is not very poor, and therefore although competition for soil resources was likely increased, competition for light was probably still playing a role.

If the invader was sown nine weeks after the founder, no species was able to observably invade in the first season. In the second year, four of the five species monocultures were still able to exert strong founder control, and (almost) no invaders were found (Fig. 4). *Holcus*, however, was visibly invaded by the other species. This is probably due to a harsh winter, which damaged *Holcus* and created open patches, and this effect was amplified by the pots in which the experiment took place. *Holcus lanatus* is known to be vulnerable to frost (Jones & Charles, 1984). This part of the experiment gives an important hint about the possible magnitude of founder control: in other experiments, where seeds were sown at the same time (Vojtech et al., 2007; Chapter 2), *Holcus* was the best light competitor. *Holcus* dominated over the poorest light competitors *Anthoxanthum* and *Festuca* already in the first season to such a large extent that even after the hard winter where *Holcus* suffered damage (second winter in that experiment) they did not have a chance to re-grow. With a time interval of nine weeks, competitive ability for light was not important anymore and therefore there was also no relationship between traits connected to light competition and competitive ability and even poor competitors for light exerted strong founder control. In the case of *Holcus*, where the growth in pots even increased the exposure to frost and magnified *Holcus’* frost damage, poor light competitors could even turn the tables and invade this strong competitor for light.

These results show that the inherent asymmetry of the competition for light, which has the potential to drive poor light competitors extinct very quickly when plant seeds germinate and establish at the same time, can also lead to arrested succession. In spatially structured habitats, where a poorer competitor for light has the possibility to establish before a stronger
light competitor, this can help to promote species coexistence and thus lead to an increase in species diversity (Levin, 1974; Reynolds & Pacala, 1993; Rees & Bergelson, 1997). This is in accordance with the spatial competition hypothesis (Tilman, 1994), which states that the spatial structure provided by individuals of different species can lead to high local diversity within a physically homogenous habitat even if all species are competing for one limiting resource. Our results are also in line with a long-term study of Wedin & Tilman (1993), where under nutrient-rich conditions with reduced light availability, seedlings of one grass species could not displace adult plants of another grass species, but the outcome of competition depended on initial conditions. Under nitrogen-limited conditions, however, seeds of a stronger competitor for nitrogen could invade an established monoculture of a poorer competitor for nitrogen and so the outcome of competition was independent of initial conditions, but depended solely on the competitive ability for the limiting resource.

We can identify four major flaws of our study: Firstly, the four treatments of the experiment were set up in two different years and thus exposed to different environmental conditions. It would have been better to conduct the complete experiment during the same time period, thus reducing additional variation above the experimental treatments. Secondly, even if we are confident that the lower plot biomass in the treatment with four weeks on rich soil as compared to the treatment with two weeks on rich soil was due to the increased shade created by the founder species and not simply caused by a growth period that was two weeks shorter, there still might be some side effects caused by the differing length in growth period between the experimental treatments. However, we cannot think of a way to separate the effect of competition from the effect of a decreased growth period. Thirdly, we do not have an appropriate control, for example a treatment where each species is sown as an invader into its own monoculture. Even if we would not have been able to distinguish the invaders from the founders, this would have enabled us to compare the relative productivities of the combinations and to calculate overyielding and complementarity and selection effects. The
biggest caveat however, is the short duration of the study. We cannot answer the question about the long-term outcomes and the question whether we observed real founder control in the nutrient-rich, light limited plots (where the initial founder would dominate its plot), whereas in the poorer plots the best competitor for soil resources would eventually win, irrespective of initial conditions.

In spite of the mentioned limitations of our study, our experiment shows that at least in the short term, founder control increases strongly with increasing time interval between the sowing of the founder and the invader species. In spatially structured habitats, this bears a potential for species coexistence even under nutrient-rich conditions.

Acknowledgements

Thanks to Ann Milbau for many helpful comments.

References


Chapter 4

Morphological and physiological changes in response to reduced light levels

Eva Vojtech and Andy Hector
Abstract

We describe an experiment with five perennial grass species differing in their ability to compete for light, and which were grown under different levels of light. The aim was to record physiological and morphological changes of traits relevant in competition for light in response to shade and to investigate if our species differed and shade tolerance. We observed pronounced changes in morphological as well as in physiological traits with the decreasing light gradient and we have obtained detailed estimates of our species’ traits under different light regimes for other parts of our project. However, even though we also observed differences between our species, we could not classify our species into different shade-tolerance classes based on the measured traits.
Introduction

In eutrophied terrestrial plant communities such as many European grasslands, competition for light is thought to be an important force for structuring plant communities, because it could lead to an outcome which supports only low plant diversity (Berendse & Elberse, 1990; Roem & Berendse, 2000; Stevens & Carson, 2002). Therefore, there is increasing activity to explain the mechanisms of species dominance and corresponding diversity loss, and to identify measures that could be used for predicting outcomes of competition for light.

So far, either trait-based approaches, where correlations of morphological plant traits with abundance are used to infer competitive dominance (Elberse & Berendse, 1993; Fynn et al., 2005; Jumpponen et al., 2005) or resource-based approaches where the level of used or unused light is taken as a substitute for species’ minimal light requirements (Dybzinski & Tilman, 2007; Vojtech et al., 2007 (Chapter 2 of this thesis)) have been applied in the attempt to predict outcomes of competition for light in grasslands. However, species’ minimal light requirements could be also obtained directly from measurements of CO$_2$ gas exchange curves. Such curves give information about the maximal potential of a species’ photosynthetic apparatus, about dark respiration but also about instantaneous light compensation point and the apparent quantum yield. The instantaneous light compensation point is the amount of light at which photosynthetic CO$_2$ consumption and respiratory CO$_2$ production are in equilibrium (e.g. Larcher, 2003) and denotes thus the minimal instantaneous light requirement of a plant to maintain itself without growth or any losses. The apparent quantum yield is the linear increase of CO$_2$ uptake with incident photons at low light intensities above the light compensation point and can be regarded as the photosynthetic efficiency at low light (e.g. Larcher, 2003).

When plants are exposed to shade, they react with changes such as increased stem elongation to escape shading by other species which is triggered by the perception of an altered red:far-red ratio under plant canopies (Smith, 2000; Vandenbussche et al., 2005).
Further they increase their leaf area to maximize photon yield (e.g. Björkman, 1981; Evans & Poorter, 2001; Niinemets, 2004), increase the apparent quantum yield and decrease the light compensation point at the expense of a lower maximal photosynthesis (Lambers et al., 1998; Givnish et al., 2004; Heschel et al., 2004; Baltzer & Thomas, 2007) to maximize their carbon gain under the reduced light levels. We have conducted other experiments (Chapter 2) using the same species as in the experiment described here, for which it would be useful to obtain estimates of plant traits connected to competition for light for plants grown under a gradient of decreasing light levels. This light gradient should be accompanied by a decrease of the red:far-red ratio which would simulate a plant canopy. This would give us plant responses that are comparable to plants grown under natural canopies. Additionally, the experiment should be designed so that we can ensure that plants of each species are experiencing an identical light level and that traits are not influenced by competition for other resources. This would additionally allow us to compare different responses to shade or shade adaptation strategies between the species in our experiments and could help us to explain patterns observed in the other experiments.

The aims of this study were therefore (1) to record physiological and morphological changes of traits relevant to competition for light in response to shade and thus obtain estimates for our grass species and to (2) investigate if our species differed in shade tolerance. We observed pronounced changes in morphological as well as in physiological traits with the decreasing light gradient and we have obtained detailed estimates of our species’ traits under different light regimes for other parts of our project. However, even though we also observed differences between our species, our species did not differ sufficiently in the measured traits to be classified into different shade-tolerance classes.
Materials and Methods

EXPERIMENTAL DESIGN

The experiment reported here is part of a wider project about light competition and partitioning in grasslands (Chapter 1; Chapter 2) which uses a model system of five perennial grass species (Poaceae) (cf. Wedin & Tilman, 1993) selected from those found in European fertile meadows to differ in their canopy heights and light competition abilities: *Alopecurus pratensis* L., *Anthoxanthum odoratum* L., *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Festuca rubra* ssp. *commutata* Gaud. (= *Festuca nigrescens* Lam.), *Holcus lanatus* L. (Lauber & Wagner, 1996).

The experiment was conducted in the experimental garden of the Institute of Environmental Sciences, Zurich (47° 23’ N, 8° 33’ E, and 546 m height a.s.l.). It was established to investigate how morphological and physiological traits connected to competition for light of the chosen grass species change in adaptations to shade as compared to full sunlight and to obtain physiological estimates of minimal light requirements based on measurements of CO$_2$ exchange. We constructed four shadehouses, each with five compartments of decreasing light level. Each compartment was 1 x 0.8 x 1.2 m (w x l x h) large and enclosed one spray nozzle of an irrigation system. The control (100% light treatment) was placed under the first spray nozzle at the southern end of each shadehouse, so that it was not shaded by the shadehouse. To obtain a gradient of decreasing light, we used combinations of green shade cloth of three intensities (37%, 27% and 16% light penetration).

In mid June 2005, the experiment was started: six weeks-old plants (on average 10 cm high), reared individually from seed in 1.1 l flower pots (11 x 11 x 12 cm) in the highly fertile soil used in all other experiments (Garden humus, Ricoter, Aarberg, Switzerland; Chapter 1, Chapter 2) were placed in the compartments of the shadehouses. One plant of each species was randomly assigned to each compartment of the four shadehouses (five shade levels plus
the control), giving a total of 120 plants. Plants were irrigated automatically on a daily basis to assure ample water amounts.

To obtain quantitative indication of the amount of photosynthetically active radiation (PAR, \( \mu \text{mol photons m}^{-2} \text{s}^{-1} \)), light levels in each compartment were measured with a photosynthetically active radiation probe (SunScan System - SS1, Delta-T Devices Ltd, Cambridge, UK) every hour from 9 am until 6 pm on a sunny day at the end of July and expressed as the percentages of light above the shadehouse. An average daily value over the ten hourly measurements was calculated for each shadehouse compartment. The light level in the full sun treatment was considered to be 100%. The daily light levels decreased with increasing shade level from 11.3-15.6% of full sun light in the first shade compartment, over 9.0-13.4% in the second, 6.6-8.5% in the third and 2.5-2.8% in the fourth down to 0.6-0.8% in the fifth, the darkest shade compartment (Fig. 1). These values were log-transformed to correct for the disproportionately large distance between the full sun treatment and the shade treatments and used in the analysis as the continuous explanatory variable light gradient (see below).

To assess the light quality, red:far-red ratios were recorded in mid August. The measured red:far-red ratio was between 0.57 and 0.71 in the first three shade compartments and decreased to 0.43 in the fourth and to 0.29 in the fifth shade, mimicking a change in light quality as observed under natural plant canopies (Lerch, 1999). The response of net photosynthesis to incident light was measured in mid August on a young, fully developed leaf from each plant with a portable photosynthesis system (LI-6400, LI-COR, Nebraska, USA), on each leaf we measured net photosynthesis at six light levels from 1000 down to 0 \( PAR \) (\( \mu \text{mol photons m}^{-2} \text{s}^{-1} \)). The length of the longest leaf was measured on first day of the experiment and then at the harvest. Aboveground plants biomass was harvested at the beginning of September 2005. Leaves were separated from stems and leaf area was measured.
with a leaf area meter (LI-3100C Area Meter, LI-COR, Nebraska, USA). Biomass was dried at 80°C and weighed.

![Graph showing light levels in each of the shadehouse compartments.](image)

Figure 1: Light levels in each of the shadehouse compartments (percent of the light above the shadehouse). Each dot represents the daily average value calculated from hourly measurements through the course of a day at the end of July between 9am – 6pm.

**DATA ANALYSIS**

We applied a two-step analysis. In the first step, we fitted curves to the photosynthesis data and in a second step, we analysed the obtained physiological response variables as well as directly measured morphological response variables with a mixed effects model (cf. Murtaugh, 2007).

We estimated the physiological parameters with the Mitscherlich model equation (Potvin *et al.*, 1990), because this function is easier to fit than a non-rectangular hyperbola or a modified Michaelis-Menten function, and often fits the data better than the other models. The Mitscherlich model is thus becoming the accepted function for light curve fitting in
physiological ecology (Peek et al., 2002; Heschel et al., 2004) using the nonlinear least-squares approach (nls-function in R, R Development Core Team 2007):

\[ A = A_{\text{max}} \left[ 1 - e^{-A_{\text{qe}}(\text{PAR} - \text{LC})} \right] \]  

Eqn 1

where \( A_{\text{max}} \) is the maximal photosynthesis per unit leaf area (\( \approx \) the asymptote of the photosynthesis at high light), \( A_{\text{qe}} \) is the apparent quantum yield (\( \approx \) the initial slope of the curve at low light levels), \( \text{PAR} \) is the incident photosynthetic light level and \( \text{LC} \) is the light compensation point (\( \approx \) the \( x \)-intercept); for more details see Peek et al. (2002). The dark respiration per unit leaf area (\( r_D \)) was calculated as: \( r_D = A_{\text{qe}} \cdot A_{\text{max}} \cdot \text{LC} \). Additionally, we calculated \( A_{\text{max,B}} \), the maximal photosynthesis per unit leaf biomass as \( A_{\text{max}} \cdot \text{SLA} \), where \( \text{SLA} \) is the specific leaf area (m\(^2\) leaf area per g of leaf biomass). The dark respiration per unit leaf biomass was accordingly calculated as \( r_{D,B} = A_{\text{qe}} \cdot A_{\text{max,B}} \cdot \text{LC} \).

The physiological parameters \( A_{\text{max}}, A_{\text{max,B}}, r_D, r_{D,B}, A_{\text{qe}} \) and \( \text{LC} \) as well as plant biomass (as a measure of plant growth and survival) and the morphological response variables plant height, \( \text{SLA} \) (m\(^2\) plant leaf area per g of leaf biomass), \( \text{LAR} \) (m\(^2\) plant leaf area per g of plant biomass) and \( \text{LMR} \) (g plant leaf biomass per g of total plant biomass) were analysed with a mixed effects model using the lme-function (nlme-library in R, R Development Core Team 2007). We fitted the linear shade gradient (daily average light level in each compartment, “Light”) and because the data seemed to follow a humped-shaped curve showing highest trait values at intermediate light levels also the square of Light (\( \text{“Light}^2 \))”, as well as “Species” (factor of species identity) as fixed effects, followed by interaction between these main effects. The factor shade level nested within shadehouse (i.e. the compartment) was fitted as a random effect. \( A_{\text{max}}, A_{\text{max,B}}, r_D, r_{D,B} \) and \( \text{LC} \) were log-transformed to meet the assumption of homoscedasticity. Values of 0.01 and 0.0001 were added to each data point of \( r_D \) and \( r_{D,B} \) respectively prior to the analysis because there were zeros. Plants in Shade level 5 (all dead) were excluded from all analyses so that the fitted curves were not distorted. For
graphical presentation we plotted regression lines for each species together with 95% confidence intervals, this allows an informal comparison of differences between species (non-overlapping confidence intervals indicate differences between two respective regression lines).

Used abbreviations are summarized in Table 1.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Unit</th>
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<tbody>
<tr>
<td>PAR</td>
<td>Photosynthetically active radiation</td>
<td>µmol photons m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>SLA</td>
<td>Specific leaf area</td>
<td>m$^2$ leaf area g$^{-1}$ leaf biomass</td>
</tr>
<tr>
<td>LAR</td>
<td>Leaf area ratio</td>
<td>m$^2$ plant leaf area g$^{-1}$ plant biomass</td>
</tr>
<tr>
<td>LMR</td>
<td>Leaf mass ratio</td>
<td>g plant leaf biomass g$^{-1}$ total plant biomass</td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>Maximal photosynthesis per unit leaf area</td>
<td>µmol CO$_2$ m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$A_{\text{max,B}}$</td>
<td>Maximal photosynthesis per unit leaf biomass</td>
<td>µmol CO$_2$ g$^{-1}$ s$^{-1}$</td>
</tr>
<tr>
<td>$r_D$</td>
<td>Dark respiration per unit leaf area</td>
<td>µmol CO$_2$ m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$r_{D,B}$</td>
<td>Dark respiration per unit leaf biomass</td>
<td>µmol CO$_2$ g$^{-1}$ s$^{-1}$</td>
</tr>
<tr>
<td>$A_{\text{qe}}$</td>
<td>Apparent quantum yield</td>
<td>µmol CO$_2$ µmol photon$^{-1}$</td>
</tr>
<tr>
<td>LC</td>
<td>Light compensation point</td>
<td>µmol photons m$^{-2}$ s$^{-1}$</td>
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Results

Plant growth and survival

In the analysis of plant biomass, the Species-by-Light$^2$ interaction was significant (Fig. 2; $F_{4,68} = 4.24$, $p = 0.004$), indicating that the growth responses to reduced light differed between species. This is because the biomass of *Alopecurus* decreased from the full sun treatment and the biomass of *Holcus* was higher in the brighter shade levels than in the full sun, probably because *Alopecurus* suffered least and *Holcus* most under drought in the full sun treatment (see below). The main effects of light (Light$^2$: $F_{1,14} = 31.07$, $p = 0.0001$) and species identity ($F_{4,68} = 30.00$, $p < 0.0001$) were more significant than the interaction term. *Alopecurus* and *Holcus* were the species with the highest biomass per plant in the full sun treatment and the brighter shade levels. However, at the darker end of the shade gradient, biomass of all species was similarly close to 0.
**Morphological changes in response to shade**

In the analysis of plant height, the Species-by-Light\(^2\) interaction (Fig. 3; F\(_{4,68} = 3.54, \ p = 0.0111\)) was significant because *Alopecurus* was the species with highest plants in the full sun and in the brighter shade levels, but its height decreased disproportionately in the darker shade where *Holcus* plants were highest. However, the effect of species identity (F\(_{4,68} = 20.77, \ p < 0.0001\)) and even more pronouncedly the effect of the light level (Light\(^2\): F\(_{1,14} = 103.73, \ p < 0.0001\)) had a stronger effect on species height.

![Figure 2: Biomass at harvest in all light levels of the experiment. Thick bold lines are regression lines for each species, thin grey lines are 95% confidence intervals of the respective regression line.](image-url)
The Species-by-Light\textsuperscript{2} interaction was also significant in the analysis of all three leaf traits \textit{SLA} (F\textsubscript{4,62} = 3.49, \(p = 0.0123\); Fig. 4), \textit{LAR} (F\textsubscript{4,62} = 2.60, \(p = 0.0446\); Fig. 5) and \textit{LMR} (F\textsubscript{4,62} = 2.94, \(p = 0.0274\); Fig. 6). Species differed strongly in the two leaf-area based traits (\textit{SLA}: F\textsubscript{4,62} = 38.75, \(p < 0.0001\); \textit{LAR}: F\textsubscript{4,62} = 21.28, \(p < 0.0001\)): \textit{Festuca} was the species that in contrast to the other species showed only limited tendency to increase its leaf area with shading. \textit{Festuca} was also the species with the lowest \textit{SLA} and \textit{LAR} over large parts of the shade gradient. The four other species invested increasingly into leaf area with increasing shade, however \textit{Alopecurus} shows a strong drop in \textit{SLA} and \textit{LAR} in darkest shade levels probably because in the darkest shade it was not able to construct new leaves. Thus, the leaves for which the \textit{SLA} and \textit{LAR} was recorded, were still the sun leaves grown before the start of the experiment. \textit{Arrhenatherum}, \textit{Anthoxanthum} and \textit{Holcus} all show a drop in \textit{LAR} towards the darkest shade while still increasing their \textit{SLA}, this is probably an indication that their growth
was suboptimal and they were loosing leaves. Because of the high variation in SLA and LAR in the darkest shade, it is difficult to assess whether *Arrhenatherum*, *Anthoxanthum* and *Holcus* differ significantly or not. Regarding LMR, the effect of species identity ($F_{4,62} = 14.15$, $p < 0.0001$) was also stronger than the Species-by-Light$^2$ interaction, the latter being mainly caused by *Festuca*, the only species that continuously decreased its LMR with increasing shade level whereas the other species decreased their mass investment to leaves only under darkest shade. Under darkest shade conditions, *Anthoxanthum* seems to be the species with the highest and *Holcus* the species with the lowest mass investment into leaves, probably because *Anthoxanthum* has a high LAR with a lower SLA and *Holcus* the opposite. However, the differences between the species are marginal and difficult to interpret. The main effect of the linear shade gradient (SLA: $F_{1,14} = 33.56$, $p < 0.0001$) or the quadratic light term (LAR: $F_{1,14} = 27.28$, $p = 0.0001$; LMR: $F_{1,14} = 31.42$, $p = 0.0001$) had a stronger effect on all leaf traits than the differences in species’ reactions.

![Figure 4: Specific leaf area (SLA) at harvest in all light levels of the experiment. Thick bold lines are regression lines for each species, thin grey lines are 95% confidence intervals of the respective regression line.](image-url)
Chapter 4: Changes in Response to Reduced Light Levels

Figure 5: Leaf area ratio (LAR) at harvest in all light levels of the experiment. Thick bold lines are regression lines for each species, thin grey lines are 95% confidence intervals of the respective regression line.

Figure 6: Leaf mass ratio (LMR) at harvest in all light levels of the experiment. Thick bold lines are regression lines for each species, thin grey lines are 95% confidence intervals of the respective regression line.
Physiological changes in response to shade

A visual summary of species’ photosynthetic responses to light in the different shadehouse compartments is given in Figure 7. The obtained response variables are shown in Figure 8 (maximal photosynthesis per unit leaf area, $A_{max}$), Figure 9 (maximal photosynthesis per unit leaf biomass, $A_{max_B}$), Figure 10 (dark respiration per unit leaf area, $r_D$), Figure 11 (dark respiration per unit leaf biomass, $r_{D_B}$), Figure 12 (apparent quantum yield, $A_{qe}$) and Figure 13 (light compensation point, $LC$).

![Graph showing photosynthetic CO$_2$ assimilation against incident photosynthetic photon flux as measured on a young, fully developed leaf from each plant. Also shown are fitted curves obtained from a nonlinear model analysis. Each curve represents the average for a species grown in a given light climate: Full sun (---); Shade 1(·-·); Shade 2 (····); Shade 3 (··-·); Shade 4 (– –).](image-url)
Maximal photosynthesis per unit leaf area ($A_{max}$) decreased strongly non-linearly in all species with increasing shade, especially from the bright to the darker shade levels (Fig. 8; $F_{1,14} = 26.69, p = 0.0007$); there were no significant differences between species or their reactions to shade. In the analysis of maximal photosynthesis per unit biomass ($A_{max_B}$), the Species-by-Light$^2$ interaction was significant (Fig. 9; $F_{4,61} = 5.90, p = 0.0004$), as well as the Light$^2$ ($F_{1,14} = 36.77, p < 0.0001$) and species identity ($F_{4,61} = 22.29, p < 0.0001$). While Holcus maintained the same level of $A_{max_B}$ over the whole shade gradient, $A_{max_B}$ of the other species increased from sun to shade and then decreased again under the darkest shade level. Under these darkest shade conditions, Alopecurus and Festuca had strongly decreased photosynthetic capacity compared to the other species, probably because of their leaves with high SLA.

Figure 8: Maximal photosynthesis per unit leaf area ($A_{max}$, log-transformed) in all light levels of the experiment. Thick bold lines are regression lines for each species, thin grey lines are 95% confidence intervals of the respective regression line.
Figure 9: Maximal photosynthesis per unit leaf mass ($A_{\text{max}, B}$, log-transformed) in all light levels of the experiment. Thick bold lines are regression lines for each species, thin grey lines are 95% confidence intervals of the respective regression line.

Dark respiration per unit leaf area ($r_D$) decreased linearly (Fig. 10; $F_{1,14} = 16.93, p = 0.0011$) and dark respiration per unit biomass ($r_{D,B}$) changed slightly non-linearly with increasing shade (Fig. 11; $\text{Light}^2$: $F_{1,14} = 7.49, p = 0.0161$), and there were no significant differences between species. Apparent quantum yield ($A_{qe}$) increased linearly with shade (Fig. 12; $F_{1,14} = 22.56, p = 0.0003$). Because there was very high variation, there were no significant differences between species and in their responses, even though there is a hint that Festuca showed the slightest increase in $A_{qe}$. The light compensation point decreased linearly with decreasing light (Fig. 13; $F_{1,14} = 25.23, p = 0.0002$). The Species-by-Light$^2$ interaction was significant ($F_{4,54} = 4.69, p = 0.0025$), probably mainly because of the extremely high values of Festuca under darkest conditions.
Figure 10: Dark respiration per unit leaf area ($r_{D}$, log-transformed) in all light levels of the experiment. Thick bold lines are regression lines for each species, thin grey lines are 95% confidence intervals of the respective regression line.
Figure 11: Dark respiration per unit leaf mass ($r_{D,B}$, log-transformed) in all light levels of the experiment. Thick bold lines are regression lines for each species, thin grey lines are 95% confidence intervals of the respective regression line.
Figure 12: Apparent quantum yield ($A_{qe}$) in all light levels of the experiment. Thick bold lines are regression lines for each species, thin grey lines are 95% confidence intervals of the respective regression line.
Figure 13: Light compensation point ($LC$, log-transformed) in all light levels of the experiment. Thick bold lines are regression lines for each species, thin grey lines are 95% confidence intervals of the respective regression line.

Discussion

All plants showed the typical morphological shade adaptation strategy, i.e. they responded to shade with increased investment in height growth and leaf area (increase in specific leaf area, $SLA$ and leaf area ratio, $LAR$). The increase of $SLA$ (e.g. Björkman, 1981 and references within; Anten & Hirose, 1999; Evans & Poorter, 2001; Niinemets, 2004; Baltzer & Thomas, 2007) and of $LAR$ (e.g. Van Huylenbroeck et al., 1999; Niinemets, 2004 and references within) with increasing shade is a commonly observed strategy for plants increase light harvesting efficiency. All plants similarly showed the typical physiological responses to shade: the maximal photosynthesis per unit leaf area ($A_{max}$), dark respiration per unit leaf area ($r_D$) and the light compensation point ($LC$) decreased, while the apparent quantum yield ($A_{qe}$)
increased (Lambers et al., 1998; Givnish et al., 2004; Heschel et al., 2004; Baltzer & Thomas, 2007), showing that the plants adapted their photosynthetic apparatus to low light conditions; i.e. they increased the efficiency of photosynthesis under shade at the expense of a high photosynthetic capacity. Maximal photosynthesis per unit leaf mass ($A_{\text{max}, B}$) was highest under moderate shade levels, because of the higher SLA but probably also because of the changes of chloroplast characteristics in shade leaves (Larcher, 2003). Differences between patterns based on leaf area versus leaf biomass are driven by SLA (Reich & Walters, 1994; Givnish et al., 2004). In fact, expressing photosynthesis and respiration per unit leaf mass instead of per unit leaf area is more useful in assessing adaptation to sun and shade (Givnish, 1988). Similarly, Poorter & Evans (1998) found that with higher SLA, $A_{\text{max}, B}$ was also significantly higher. These shade adaptations enabled the species to compensate well for reduced light quantities to around 10% of average daily light, under which most of them could maintain similar biomass as under full sun. With increasing shade, plants were decreasingly able to compensate for reduced light quantities and at roughly 3% of average daily light (Shade 4; Fig. 1) biomass decreased strongly, and leaves were dying or nor even constructed (decrease in $LAR$ and $LMR$). When plants received < 1% of incident daily light (Shade 5; Fig. 1), this light amount clearly was below a threshold which they could tolerate, because all plants died before the harvest. This is consistent with previous work identifying the threshold for growth of vascular plants at 1% of incident light (Lerch, 1999).

We could nevertheless observe differences between species’ reactions to shade. One difference in morphological response was between *Festuca* and the other four species, *Festuca* being the species investing least in increased leaf area with a decrease in light. Secondly, *Alopecurus* was obviously the only species that could not construct new leaves under the darkest shade level. This also led to very low values of photosynthesis per unit leaf mass ($A_{\text{max}, B}$) in the darkest shade in those two species. According to these findings, we would classify *Alopecurus* and *Festuca* as being shade-intolerant and put *Anthoxanthum*,
Arrhenatherum and Holcus in the more shade-tolerant group. However, in the physiological traits that are most related to shade adaptation ($A_{qe}$ and $LC$) we did not detect relevant differences between our species. Even though Festuca had a lower apparent quantum yield ($A_{qe}$) in the darkest shade, this difference was not significant and the significantly higher light compensation point ($LC$) of Festuca might be due to problems associated with our measurements (see below). Further, we need to keep in mind that most of the differences between species’ reactions are based on the darkest shade level (roughly 3% of incident light), such low values we only rarely found in the highly productive plots of our long-term experiment (Chapter 2) and if that was the case, only at the ground. Already at the height of 10 cm, the light level in densest canopies was roughly 8% of incident light (Vojtech, unpublished data). Therefore, species’ performance at this low light level, which is not naturally experienced by plants beyond the seedling stage, might not be fully relevant for the assessment of shade-tolerance of plants beyond the seedling stage, as is the case in our experiment. Seedlings might differ from older plants in leaf traits (Niinemets 2004) and in shade tolerance (Lusk, 2004; Lusk & Warton, 2007). Additionally, the above mentioned classification is not fully confirmed by our other experiments where the differences in height and light interception proved to be the main factor determining the outcome of competition (Chapter 1, Chapter 2). While Festuca was indeed suffering when grown together with the taller species Alopecurus, Arrhenatherum or Holcus, these three species suppressed the growth of Anthoxanthum, which we classified as shade-tolerant, to the same extent. Further, Alopecurus did not show any sign of impaired growth when growing together with the other tall species, even though it was shorter than Arrhenatherum. Therefore, we cannot correctly classify our species into shade-tolerant or shade-intolerant based on the measured morphological and even less on the physiological traits, because in the traits that are most related to shade adaptation (light compensation point and apparent quantum yield) we did not detect any significant or relevant differences between our species.
In the analysis of the light compensation point, the curve of *Festuca* not only has an unusual shape (high at full sun and again at the darkest shade level, low in between), but we also encountered problems with the gas exchange measurements. Out of the 100 curves, we had to exclude the value of $LC$ in 14 cases, because we obtained a negative estimate, caused by a CO$_2$ intake at 0 PAR (instead of CO$_2$ release). Therefore we were had doubts if our measurements were correct and compared our values to the values in scientific literature to assess their validity. Maximum net photosynthesis (in µmol CO$_2$ m$^{-2}$ s$^{-1}$) of our species in full sun (7.6 (0.23) - 10.0 (0.15); average and standard error of the mean) was well in the range of values in literature (5-15 for grasses and sedges in Larcher (2003), Table 2.4; summary from many original publications; 5-20 in two C$_3$ perennial grass species in Chen *et al.* (2005); 3.89 (0.43) – 15.7 (0.5) in two tussock grasses (Pugnaire & Haase, 1996)), However, our values for apparent quantum yield and light compensation points were indeed lower than those reported in the literature. While our values for the apparent quantum yield in (µmol CO$_2$ µmol photon$^{-1}$) in full sun lay between 0.007 (0.001) and 0.008 (0.001), Chen *et al.* (2005) report 0.03-0.06 for their two C$_3$ perennial grass species, Peri *et al.* (2005) report a value of 0.036 in *Dactylis glomerata* and Gemino & Wraith (2003) values between 0.036 (0.012) and 0.044 (0.014) in the C$_3$ bunchgrass *Dichanthelium lanuginosum*. For the light compensation point under full sun (in µmol photons m$^{-2}$ s$^{-1}$), we obtained an average value of 10.2 (1.44), while the values for C$_3$ plants given in literature are 20-40 (Larcher, 2003 (Tab 2.8); Lerch (1999), 30-40 (Chen *et al.*, 2005) or up to 74.9 (25.7) (Gemino & Wraith, 2003). Even though variation within our samples seems not to be much higher than the variation in other studies (where presented), our $A_{qe}$ values are roughly 5 times lower and our $LC$ values 2-8 times lower, which confirms our concern that we cannot fully trust these values (and thus necessarily dark respiration, which is calculated based on $A_{qe}$ and $LC$). The reason for our underestimation of these values is most likely that we did not allow enough time for the leaves to adapt to each measured light level, thus steady state might not have been reached, and this problem was
particularly severe when we took measurements at low incident light levels. While we usually took a measurement after two or three minutes, other studies allowed leaves to adapt during 0.5-1 h at measured light levels or in darkness (Reich et al., 1998; Van Huylenbroeck et al., 1999). Alternatively, to obtain more exact values for $LC$ and $A_{qe}$, we could have measured gas exchange not only from high to low light levels, but also the other way round. Another factor that we did not correct for is the change of photosynthetic rates during the course of the day (Lerch, 1999; Larcher, 2003). Because we always measured from the full sun treatment in the morning to the darkest shade level in the late afternoon, shade level and course of the day are confounded which might have led to underestimated values of maximal photosynthesis ($A_{max}$) in the intermediate shade levels. However, plants in the shade levels were well watered and never experienced water stress, not even during the hottest time periods, so this effect is not likely to be strongly pronounced. In fact, water limitation is the main reason for the midday-repression of photosynthesis (Lerch, 1999). On the other hand, plants in the full sun treatment suffered under water stress in the hot June and July of 2005 which might have led to an underestimation of their growth potential and showed for example in their lower biomass in spite of higher photosynthetic capacity as compared to the plants in the brighter shade levels.

We observed pronounced changes in morphological as well as in physiological traits with the decreasing light gradient and we have obtained detailed estimates of our species’ traits under different light regimes for other parts of our project. However, even though we also observed differences between our species, we could not classify our species into different shade-tolerance classes based on the measured traits.
References


Chapter 4: Changes in Response to Reduced Light Levels


Chapter 4: Changes in Response to Reduced Light Levels


GENERAL DISCUSSION

Recent theoretical work has predicted that in the general case where allometric and life-history parameters differ between species, competition for light can lead to competitive exclusion, coexistence or founder control (Adams et al., 2007). We used a model system of five perennial grass species selected from those found in European fertile meadows to differ in their canopy heights and light competition abilities and set up experiments to test for outcomes of competition for light, partitioning of light and founder effects in the case when light is a limiting resource. We have shown that strong dominance of good light competitors can develop very quickly (Vojtech et al., 2007 (Chapter 1)) and persist over at least a period of three years. Further, we have shown that only a minority of mixtures outperformed monocultures and overyielding was slight and that the observed overyielding could not be explained by complementarity in canopies or heights. The explanations for limited light partitioning and overyielding could be that our species did not show trade-offs that would enable them to partition light efficiently. For example, our species did not differ in the shade level they could tolerate (Chapter 4), whereas a recent study with six grass species (Gross et al., 2007) showed that substantial overyielding can occur between grasses of different shade-tolerance levels.

Similarly, the conditions for coexistence in the model by Adams et al. (2007) are that the more frequent one species becomes, the more favourable the environment must become to the other species, which means that each species must be a weaker competitor under its monoculture light level. Specifically this means that trade-offs that would enabling coexistence should for example involve height allometry linked with variation in canopy light interception (Adams et al., 2007). In our experiment, tall stature, high light interception and competitive dominance were coupled and it does not seem realistic that the environment would become more favourable for a smaller, shade-intolerant species casting lower shade with increasing abundance of the taller species that intercepts more light.
A consequence of the assumption that the environment becomes more favourable for a species with increasing abundance of a competitor is that to coexist, both species must be able to invade a monoculture of the other species (Adams et al., 2007). In our experiment, at least in the short-term, no species was able to invade a monoculture of another, when the interval between establishment and invasion was long enough (Chapter 3). Therefore, giving the poorer light competitor a head start prevented a better light competitor from establishing. This founder control allows the possibility for species coexistence even under nutrient-rich, light-limited conditions, especially in spatially structured habitats where it may lead to an increase in species diversity (Levin, 1974; Reynolds & Pacala; 1993; Rees & Bergelson, 1997).

References
SUMMARY

One of the widely observed results of global change is that in many different types of ecosystems eutrophication leads to diversity loss. In eutrophied terrestrial plant communities, such as many European grasslands, asymmetric competition for light is thought to be a mechanism for this diversity loss. On the other hand, complementary between species in light and canopy space use, could promote species coexistence and even lead to higher biomass production in mixtures as compared to monocultures. Additionally, it has been hypothesized that even the asymmetric nature of competition for light could result in the local coexistence in light-limited habitats (via founder control), especially in spatially structured habitats and thus lead to an increase in species diversity. The best developed mechanistic theory of resource-competition for soil nutrients is Tilman’s $R^*$, an approach which tries to predict competitive outcomes with species minimal requirements. However, very few experiments tried to transfer the $R^*$ for light approach to terrestrial systems, direct experimental evidence for niche complementarity is scarce in scientific literature and most work on founder control has been purely theoretical and there are no experimental tests. We have used a model system of five perennial grass species selected from those found in European fertile meadows to differ in their canopy heights and light competition abilities. Using measurements of plant traits and their impact on light availability, we tried to predict the competitive outcomes in mixtures and test mechanistic theory of competition for light, partitioning of light and founder control in eutrophied grassland communities and to understand the underlying biology.

In Chapter 1, we present the results of one of the few mechanistic experiments investigating the outcome of short-term competition using measurements of light interception from monocultures of our five perennial grass species. We found that the level of incident light intercepted by each species in monoculture, a direct measure of resource-reduction ability,
Summary

was an excellent predictor of the relative competitive effect in pairwise mixtures. Competition for light was asymmetric in relation to differences in light intercepting ability. Our results are consistent with the idea that when light is a limiting resource, competition between species for this resource can be asymmetric, contributing to high dominance and low diversity.

In Chapter 2, we present the results of an experiment where species were grown under fertilized and irrigated conditions in monoculture, all pairwise mixtures and the full five-species mix over the course of three years. We investigated whether species partition light, whether this resource partitioning leads to increased biomass of mixtures as compared to monocultures and tried to explain the observed patterns with characteristics of monocultures and of mixtures. We showed that under conditions where biomass production was high and light a limiting resource, only a minority of mixtures outperformed monocultures and overyielding was slight. The observed overyielding could not be explained by species differences in canopy structure and height in monoculture and was also not related to changes in the canopy traits of species when grown in mixture rather than monoculture. However, where overyielding occurred, it was associated with higher biomass density and light interception. This result agreed with the new model of competition for light which showed that greater complementarity in light use was related to increased total energy absorption. Even though we cannot exclude the possibility that denser canopies and increased light interception in overyielding mixtures were both a consequence of some other form of complementarity, our results show that overyielding mixtures were able to achieve a denser filling of the aboveground space.

In Chapter 3, we describe a founder experiment in which we test the hypotheses that (1) with an increasing time interval between the sowing of the founder and the invader species, the dominance patterns of dominant species will decrease, and poor competitors will be
increasingly able to dominate a pairwise mixture and that therefore the correlation between founder control and traits connected to competition for light will decrease; and (2) that on a less nutrient-rich soil, competitive ability will not be connected to traits important for competition for light even on short interval. Our experiment shows that at least in the short term, with increasing time interval between the sowing of the founder and the invader, founder control increases and bears the potential for species coexistence in spatially structured habitats.

In Chapter 4, we aimed to (1) record physiological and morphological changes of traits relevant in competition for light in response to shade and thus obtain estimates for our grass species and to (2) investigate if our species differed in shade tolerance. We observed pronounced changes in morphological as well as in physiological traits with the decreasing light gradient and we have obtained detailed estimates of our species’ traits under different light regimes for other parts of our project. The species we measured did not differ consistently and significantly in shade tolerance, based on the measured traits.

Conclusions

Under fertilized conditions when all species were sown at the same time, competition for light was strong and asymmetric and outcomes could be best explained with light interception in monoculture. Mixtures outperformed monocultures only very slightly, nevertheless, mixtures that did overyield, were able to fill more the available aboveground space and to intercept more light. When subordinate species were given a head start, they were able to exert founder control towards dominant species. This could alleviate the negative effects of asymmetric competition, high dominance and low diversity, and bears the potential to for species coexistence in spatially structured habitats.
ZUSAMMENFASSUNG

Zusammenfassung

In Kapitel 1 präsentieren wir die Ergebnisse eines der wenigen mechanistischen Experimente, das den Ausgang der Konkurrenz zwischen Pflanzen verschiedener Arten mithilfe von Lichtmessungen in den entsprechenden Monokulturen untersucht. Wir zeigen, dass die Fähigkeit Licht aufzufangen, asymmetrisch war, und dass die Menge des einfallenden Lichtes, die von jeder Art in Monokultur aufgenommen wird, sich hervorragend dazu eignet, die relative Konkurrenzstärke in paarweisen Mischungen vorherzusagen. Unsere Ergebnisse unterstützen die Annahme, dass wenn Licht eine begrenzende Ressource ist, die zwischenartliche Konkurrenz um diese Ressource asymmetrisch sein kann, was zu hoher Dominanz und niedriger Diversität führen kann.

In Kapitel 2 präsentieren wir die Ergebnisse eines Experiments, in dem die gewählten Pflanzenarten während drei Jahren unter gedüngten und bewässerten Bedingungen in Monokulturen, paarweisen Mischungen und der Mischung aller fünf Arten gewachsen sind. Wir fragten, ob die Arten das Licht untereinander aufteilen, ob dies dazu führt, dass Mischungen im Vergleich zu Monokulturen mehr Biomasse produzieren, und versuchten die beobachteten Muster mit Merkmalen von Monokulturen und Mischungen vorauszusagen. Wir konnten zeigen, dass wenn viel Biomasse produziert wird und Licht eine begrenzende Ressource ist, nur wenige Mischungen in der Lage waren, Monokulturen zu über treffen und die Ertragssteigerung der Mischungen sehr gering war. Die beobachtete Ertragssteigerung konnte nicht mit den in den Monokulturen gemessenen artenspezifischen Unterschieden in Bestandesstruktur und Bestandeshöhe erklärt werden und wies ebenfalls keinen Bezug zu Änderungen in den Bestandesmerkmalen auf, wenn die Arten in Mischung statt in Monokulturen gewachsen waren. In den Fällen, in denen Mischungen mehr Biomasse produzierten, als man aufgrund der Monokulturen erwartet würde, hatten diese jedoch eine höhere Biomassendichte und konnten mehr Licht auffangen. Dieses Ergebnis stimmte mit dem Model für Lichtkonkurrenz überein, welches zeigte, dass eine höhere Komplementarität in...
Zusammenfassung

Bezug auf die Lichtnutzung mit einer erhöhten Energieaufnahme zusammenhängt. Selbst wenn wir die Möglichkeit nicht ausschliessen können, dass sowohl dichtere Bestände als auch höhere Lichtaufnahme durch eine andere Art von Komplementarität verursacht wurden, zeigen unsere Ergebnisse dennoch, dass Mischungen die produktiver waren als die entsprechenden Monokulturen, den oberirdischen Raum dichter füllen konnten.


In Kapitel 4 massen wir physiologische und morphologische Anpassungen an wachsende Beschattung bei Merkmalen, die für Konkurrenz um Licht relevant sind, um Schätzwerte für die gewählten Grasarten zu erhalten und untersuchen ob sich unsere Arten in ihrer Toleranz gegenüber Lichtmangel unterscheiden. Sowohl morphologische wie physiologische Merkmale veränderten sich stark mit abnehmender Lichtmenge und wir haben für unsere Arten detaillierte Schätzwerte erhalten. Obwohl wir jedoch auch Unterschiede zwischen den
Zusammenfassung

Arten fanden, konnten wir unsere Arten anhand der gemessenen Merkmale nicht in unterschiedliche Schattentoleranz-Klassen einordnen.

Schlussfolgerungen

Unter nährstoffreichen Bedingungen und wenn alle Arten gleichzeitig angesäht worden sind, war die Konkurrenz um Licht ausgeprägt und asymmetrisch und das Ergebnis konnte am besten mit der Menge des in Monokulturen aufgefangenen Lichtes vorhergesagt werden. Mischungen produzierten nur wenig mehr Biomasse als die entsprechenden Monokulturen. Mischungen jedoch, die produktiver waren als die entsprechenden Monokulturen, konnten den oberirdischen Raum dichter füllen und mehr Licht auffangen. Wenn unterlegene Arten einen zeitlichen Vorsprung bekamen, konnten sie gegenüber dominanteren Arten Gründerkontrolle ausüben. Dies könnte die negativen Effekte der asymmetrischen Konkurrenz um Licht, der starken Dominanz einzelner Arten und geringer Diversität mildern und zur Koexistenz in räumlich strukturierten Lebensräumen beitragen.
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Veröffentlichungen


