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Autor: Edelkraut, Kirsten / Ramseier, Dieter / Güsewell, Sabine
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RESEARCH PROJECT

Competition of wetland plants as affected by shade and nutrient supply

KIRSTEN EDELKRAUT, DIETER RAMSEIER & SABINE
GÜSEWELL

Geobotanisches Institut ETH, Zürichbergstrasse 38, 8044 Zürich, Switzerland;
edelkraut@geobot.umnw.ethz.ch

Summary

1 Many competition experiments have shown that plant species interactions are influenced by nutrient supply. In contrast, the effect of light supply on competitive interactions has received little attention. The question whether competitive interactions depend more on the absolute or on the relative supply of above- and below-ground resources has not been investigated for herbaceous vegetation.

2 In this project we examine the influence of total light supply on interspecific competition between perennial wetland plants at different levels of nutrient supply. Total light supply is defined as the amount of light received by a vegetation stand as a whole, and can be varied independently of nutrient supply. Our main hypothesis is that light supply will influence interspecific competition in a way similar to nutrient supply, but that the two resources will interact.

3 Five *Carex* species from wetlands are being grown with and without competitors at a range of light and nutrient levels in two competition experiments. The designs enable us to measure both competitive response and competitive effect, and to distinguish between above- and below-ground competition.

4 A third experiment investigates the role of temporal variation in light availability. Mixtures of nine wetland graminoids have been established in an experimental field. All mixtures will receive a similar average light intensity during the main growing season, but periods of light and shade will differ.

5 These experiments are relevant for nature conservation. Eutrophicated fen meadows are susceptible to invasion by tall plant species, e.g. *Phragmites australis* or *Solidago serotina*, which create two-layered vegetation by overtopping all other species. Our experiments will investigate whether or not the shade cast by such invaders is likely to affect species abundance and interspecific competition of the original fen vegetation.

Keywords: *Carex*, competitive ability, light, nutrients, resource ratio hypothesis, seasonal variation

Nomenclature: Hess *et al.* (1991)

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Introduction

The question how interspecific competition is affected by the relative supply of two or more resources has raised much debate among ecologists during the last twenty years. The central point of controversy has been whether the abilities of plant species to compete for different limiting resources are positively (Grime 1977, 1979) or negatively (Tilman 1982, 1987) correlated with each other, and whether the intensity of competition for a limiting resource increases (Grime 1977) or decreases (Tilman 1982) with increasing supply of that specific resource.

Given this debate, it is striking that most studies on competition between species from herbaceous plant communities have only involved variation in the supply of one limiting resource, typically nitrogen. Rather few studies on competition have independently varied the supply of different resources (e.g. Wetzel & van der Valk 1998). Very few studies have addressed the effects of light supply on competition among herbaceous species (e.g. Weihe & Neely 1997), and none, to our knowledge, has done so at several levels of nutrient supply. The reason for this focus on nutrients is probably that the availability of nutrients can vary considerably in space or in time, both naturally and due to human activity. In natural or semi-natural herbaceous vegetation, this variation is typically associated with marked differences in species composition, which suggests that nutrient availability regulates species interactions to a significant extent. In contrast, light supply to stands of one-layered herbaceous vegetation is normally only determined by the geographic and topographic position of a site. It is therefore a constant site factor and cannot account for the differences in spe-

cies composition often found along gradients of nutrient supply within sites.

This statement may at first seem to contradict the common understanding that increasing nutrient availability, and therefore increasing biomass production, causes light to increasingly limit plant growth, especially for the subordinate plant species. Changes in species composition along gradients of nutrient supply have often been explained with reference to decreasing light supply to the smaller growing plants (e.g. Berendse & Aerts 1984; Wilson & Tilman 1991; Boeye & Verheyen 1994; Zelesny 1994). We must, therefore, define "light supply" more precisely. In the above statement, we considered the *total* amount of light received by the vegetation as a whole. This amount is independent of nutrient availability or biomass production. In contrast, when light supply was said to decrease with increasing nutrient availability, it was defined as the amount of light received by individual leaves or shoots. For a given total supply, the amount of light received per unit biomass will be negatively related to biomass production. In this view, decreasing light supply is an indirect effect of increasing nutrient supply, due to the shading effect of tall plant species on the smaller ones.

Which definition is more appropriate? – Clearly, this depends on the aim of the study. If the aim is to explain differences in species composition along gradients of nutrient supply, the second definition is needed. But if the aim is to compare the effects of light and/or nutrient supply on interspecific competition, the first definition is more adequate. With the first definition light supply and nutrient supply are defined in the same way, and the relative effects of both factors and their interactions can be examined.

Research questions and hypotheses

In the new project we will investigate how competition between plant species is affected by light supply, and how this interacts with nutrient supply. Our research will focus on three questions, and each of them will be addressed in a separate experiment.

Experiment 1: How do the competitive abilities of perennial wetland species change along gradients of nutrient and light supply?

Both the ranking of competing species and the intensity of competition (amount of growth reduction caused by the presence of competitors) have generally been found to change along gradients in the availability of limiting resources. In most cases, competition was intensified at high resource supply (Twolan-Strutt & Keddy 1996; Weihe & Neely 1997), although no difference in overall competition intensity was found in some experiments (Wilson & Tilman 1991; Keddy *et al.* 1994). As to the outcome of competition, some studies suggested a reversal in competitive rankings along resource supply gradients, i.e. species that were superior at low supply were inferior at high supply (e.g. Tilman 1987; McGraw & Chapin 1989). Other studies suggested similar rankings, but a change in competitive asymmetry: the advantage of stronger competitors over weaker ones was greater at higher resource supply (e.g. Keddy *et al.* 1994). Basically, these effects of resource supply seem to hold for both nutrient and light gradients. However, since light and nutrient supply have hardly been manipulated independently in the same competition experiment, little is known on the relative effects of the two resources.

To this end we will vary both total light supply and nutrient supply in a factorial design and study the competitive response of slow-growing *Carex* species to competition by tall

forbs (*Lythrum salicaria* and *Solidago serotina*). Because these forbs used are characteristic of nutrient-rich sites (e.g. Oberdorfer 1990), we assume them to be strong competitors for the graminoids, and we expect that their competitive effect will be positively related to nutrient supply. As regards light, the two competition models discussed above lead to opposite predictions: According to the CSR model (Grime 1977) the competitive ability of our forbs should also be positively related to light supply. In contrast, Tilman argues that often “species (are) ranked in competitive ability for one resource in reverse order of their competitive ability for the second resource” (Tilman 1987, p. 304). Thus, according to this theory, if the competitive effect of the forbs is enhanced by high nutrient supply, it will be reduced by high light supply. A more complex relationship between resource supply and competition has been proposed by Weiner *et al.* (1997). Based on studies of intraspecific competition, they suggest that increased resource supply (either nutrients or light) may enhance the competitive effect of tall plants on small ones by increasing competitive asymmetry, but only if the density and size of plants is sufficient for light competition to occur, i.e. only above a minimum level of resource supply.

Our experiments will enable us to examine these various hypotheses by addressing the following questions: (1) Does shading have a qualitatively similar effect on competition as does low nutrient supply, or are effects opposite? (2) Does a 50% light reduction affect interspecific competition to the same degree as a 50% reduction in nutrient supply, or is one effect stronger than the other? (3) Do the effects of light and nutrients interact, i.e. does strong shading prevent high nutrient supply from enhancing the competitive effect of forbs, and *viceversa*? (4) Are these effects consistent

across the light gradient, or different for slight and strong shading? (5) Are there differences among target species, and if so, can they be related to traits of these species?

Experiment 2: How is the relative intensity of above- and below-ground competition affected by light supply?

Since plants need both above- and below-ground resources, plant species will normally compete for both resource types in mixed communities. However, the relative intensity of above- and below-ground competition may depend on the absolute and/or relative supplies of above- and below-ground resources. Such dependence has, indeed, been found in studies where growth reduction due to either above-ground or below-ground competition was compared at different levels of nutrient availability. With increasing nutrient availability, above-ground competition increasingly affected plant growth compared to below-ground competition (Wilson & Tilman 1991; Twolan-Strutt & Keddy 1996; Eek & Zobel 1997; Wetzel & van der Valk 1998). Indirect evidence for changes in the relative intensity of above- and below-ground competition is also provided by changes in biomass allocation. For example, Rebele (1996) found that the shoot:root ratio of the inferior competitors increased along a gradient of nutrient availability. This was interpreted as a result of stronger above-ground competition (Rebele 1996).

The effect of variation in the total light supply on the relative importance of above- and below-ground competition has apparently not yet been studied directly, but both Tilman's (1982) resource ratio hypothesis and studies of biomass allocation at different light levels (e.g. Olff 1992) suggest that along gradients of light supply, above-ground competition will become less important relative to below-

ground competition (Cui & Caldwell 1997). To test this hypothesis we will investigate the effect of shading on inter- and intraspecific competition separately for each of four possible types of competition (above-ground, below-ground, full, none; cf. Johansson & Keddy 1991; Keddy *et al.* 1994; Keddy *et al.* 1999; Leishman 1999). Different levels of shading will again be combined with different levels of nutrient supply.

Our expectation is that the relative intensity of above-ground competition (compared to below-ground competition) will be negatively related to light supply and positively related to nutrient supply. However, with respect to the absolute intensity of above- and below-ground competition two different outcomes seem plausible: either that both competition types are intensified by enhanced light supply, or that above-ground competition is reduced, and only below-ground competition strengthened. It is also possible that the relation between light supply and competition intensity is hump-shaped, as suggested by Weiner *et al.* (1997). Additional questions are related to possible interactions between light and nutrient supply. For instance, will the relative intensity of above- and below-ground competition be affected if both light and nutrient supply increase by the same factor? Or, as an alternative, will only the *absolute* effects of competition increase, while the *relative* intensity of above- and below-ground competition remains unchanged?

Experiment 3: Do seasonal patterns of light supply affect competitive interactions?

Our interest in seasonal patterns of light supply was triggered by studies demonstrating that species coexistence and competition in plant communities are not only regulated by the amount of nutrient supply, but also by its spatial and temporal distribution. Some spe-

Table 1. Plant species selected for the experiments and ecological characteristic by indicator values (see Landolt 1977) for nutrients (N) and light (L); scale 1–5 with "1" for low resource demand and "5" for high demand

Species	N value	L value
Carex species		
<i>Carex davalliana</i>	2	5
<i>Carex elata</i>	3	4
<i>Carex flacca</i>	2	3
<i>Carex flava</i>	2	4
<i>Carex panicea</i>	2	4
Grasses		
<i>Agrostis canina</i>	2	4
<i>Anthoxanthum odoratum</i>	3	4
<i>Holcus lanatus</i>	3	4
<i>Molinia coerulea</i>	2	4
Forbs		
<i>Lythrum salicaria</i>	3	3
<i>Solidago serotina</i>	3	3

cies are better able to use patchy supply than others, and therefore gain a competitive advantage from a heterogeneous situation (Kielland & Chapin 1994; Rebele 1996; Goldberg & Novoplansky 1997; Boeye *et al.* 1999). Experiments with temporal variation in nutrient supply have shown that different plant species (or even ecotypes) may respond differently to changing availability of nutrients, and that these differences can be interpreted as adaptations to the natural sites of the species or ecotypes (Poorter & Lambers 1986; Crick & Grime 1987; Kielland & Chapin 1994). Likewise, seasonal patterns of light availability can be expected to have significant effects on the above-ground biomass, phenology and turnover of plant species (Hirose & Werger 1994), and therefore, on their competitive interactions.

To test this hypothesis we established experimental plant communities (mixtures of nine species, cf. Table 1) in an experimental field. Treatments will consist in different sea-

sonal patterns of light supply, while overall light supply will be the same for all treatments.

Based on the preceding experiments on effects of nutrient availability we expect that the various species in our mixtures will be differently affected by early shading, late shading or short-term light fluctuations, so that the rank order of abundance will differ among treatments. The phenotypic plasticity of the species is expected to determine their performance under different seasonal patterns of light availability. We assume plasticity in phenology and turnover to play a more important role than plasticity in morphological traits. Moreover, we hypothesize that shading in late summer will promote species that are abundant at sites where light conditions deteriorate severely in the course of the summer.

Experimental design

The three experiments involve different shading treatments. Shading will be effected by green horticultural shading fabric, which causes a 75% light reduction. The fabric will be cut into strips to obtain shading intensities lower than 75%, and two layers will be superposed to create higher shading intensities. In the first two experiments, shading is combined with different nutrient levels, which will be obtained by growing plants in nutrient-poor sand and supplying them with different amounts of commercial fertiliser. The test species in the experiments are common *Carex* species of fens of the Northern Swiss Plateau. The genus *Carex* occurs under a broad range of light and nutrient conditions so that it is possible to study ecologically different, but phylogenetically closely related species. Thus, in our experiments we compare species that occur naturally under differing nutrient and light conditions (Table 1).

In *Experiment 1*, we will determine how the competitive responses of five *Carex* species (Table 1) change along gradients of both light and nutrient supply. To this end an additive design will be applied, where target plants of the *Carex* species will grow either alone in a pot, or surrounded by four plants of species that can be characterised as fairly strong competitors (*Solidago serotina* and *Lythrum salicaria*). Four light levels will be combined with four levels of nutrient availability. Target plants will be harvested at the end of the first and second growing seasons, and the biomass of plants grown with or without surrounding competitors will be compared. The percentage reduction in biomass due to competition will be used to measure the competitive responses of the five *Carex* species under the different treatments. Plants grown without competitors will be used for measurements of plant traits such as height, canopy structure, shoot and leaf turnover, leaf area and specific leaf area, root length and specific root length, tissue N and P concentrations. Correlations between these traits and the competitive responses of the *Carex* species will be examined.

In *Experiment 2*, we will determine how the relative importance of above- and below-ground competition changes along gradients of both light and nutrient supply. A replacement series design will be applied. In each experimental pot one central target plant will grow in the middle of four neighbours. Only two species will be involved, as central and/or

as surrounding plants, yielding four experimental combinations, two with interspecific and two with intraspecific competition. By partitioning the rooting volume and/or the above-ground area of the experimental pots, four different competitive situations will be created (above-ground, below-ground, full, none). Six light levels will be combined with two levels of nutrient availability, and both interspecific and intraspecific competition will be considered. The relative importance of above- and below-ground competition will be assessed by comparing the percentage reduction of growth due to either competition type.

In *Experiment 3*, mixtures of five *Carex* species and four perennial grass species differing in nutrient and light demand (cf. Table 1) will be established in an experimental field near lake "Hasensee" in Kanton Thurgau, Switzerland. The field is a former fen long used for agriculture; mesotrophic conditions will be created by removing the uppermost 20 cm of soil which are nutrient-rich due to former fertilizer application. All shaded plots will receive a similar average light intensity between the end of April and the end of August, but periods of light and shade will differ; an unshaded treatment will be included as reference (Fig. 1). Shading will be performed during two consecutive growing seasons. The above-ground biomass of each species in each plot will be harvested at the end of the first, second and third growing season and taken as a measure of the species' competitive ability under the different seasonal patterns of

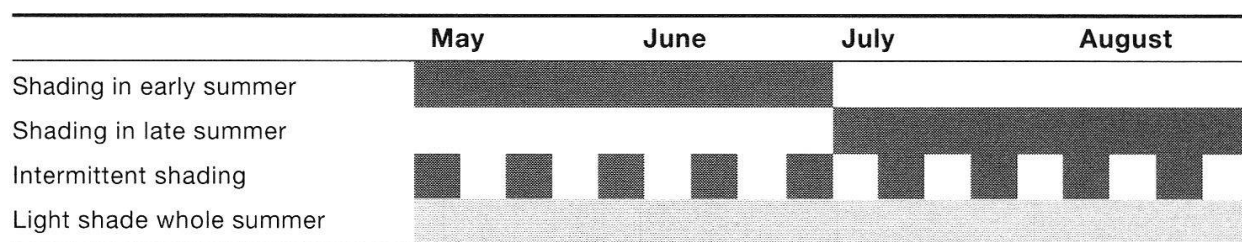


Fig. 1. Patterns of light and shade in the four treatments of Experiment 3.

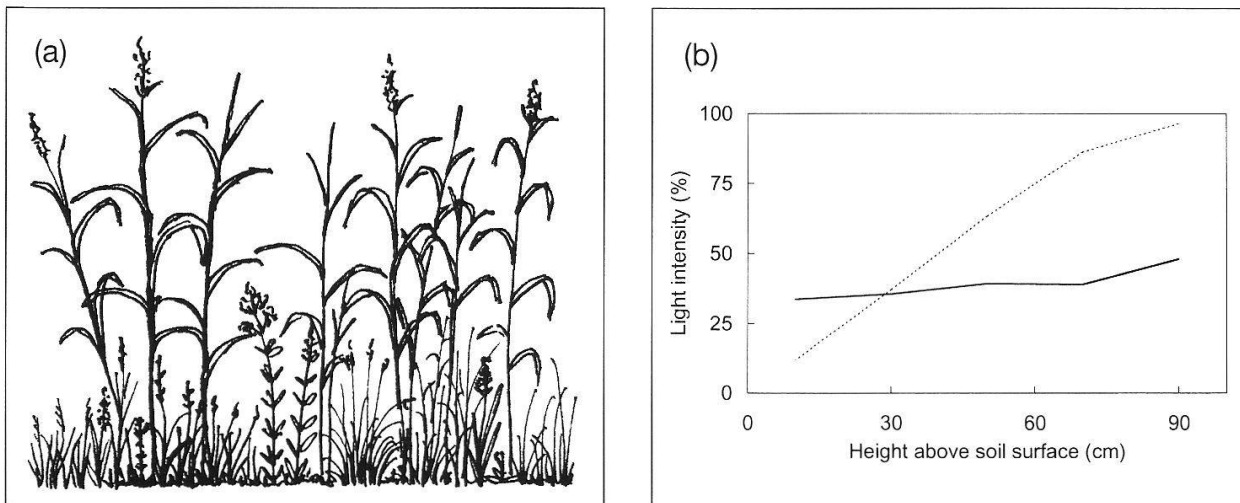


Fig. 2. (a) Two-layered vegetation structure in fen meadows overgrown by *Phragmites australis* and (b) light profiles in plots in which either *Phragmites* (dashed line) or all other species (full line) have been clipped, showing the strong vertical gradient in light intensity caused by the other species compared with the almost uniform reduction in light intensity caused by *Phragmites* (Güsewell & Edwards 1999).

shading in each of the years. Differences in performance among treatments can then be due either directly to the treatments, or to effects of the treatments on interspecific competition, or to both together. Our design will not enable us to distinguish between these possibilities, but it will show whether significant differences among treatments occur, and thus, whether it will be worthwhile to investigate in more detail the effects of seasonal patterns of shading on interspecific competition.

Relevance for nature conservation

The results of the experiments can be relevant for nature conservation and management of nature reserves. Indeed, most of our target *Carex* and grass species are characteristic of fens or wet grasslands of central Europe. Many of these sites have become increasingly invaded by tall species such *Phragmites australis*, *Phalaris arundinacea*, *Solidago serotina* or other tall forbs (Voser-Huber 1983; Rosenthal 1992; Güsewell 1997; Güsewell & Edwards 1999). *Lythrum salicaria*, one of the experimental competitors, is considered a

troublesome invader in wetlands of North America (Edwards *et al.* 1995).

Invasion by tall dominants does not affect total light supply as defined in the Introduction, but it creates a two-layered herbaceous vegetation, in which the small sedges and forbs of the lower layer are shaded because they are too small to compete for light with the tall invaders (Fig. 2). Our study will, therefore, show whether interspecific competition within the lower vegetation layer is likely to be influenced by the tall invaders, as has been suggested by field studies in fen meadows with differing abundance of *Phragmites australis* (Güsewell & Klötzli 1998; Güsewell & Edwards 1999). For the management of these fen meadows it would be of great interest to know whether shading by *Phragmites* and/or other invasive tall forbs actually triggers changes in species composition. Our investigations will contribute to answer this question and thus, to choose the appropriate management for invaded sites.

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