



Light partitioning in experimental grass communities

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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.

Competition for light in plant communities is thought to be asymmetric, leading to strong competition and rapid competitive exclusion (Huston and DeAngelis 1994, Schwinning and Fox 1995, Lepš 1999, Vojtech et al. 2007). 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 and Werger 1995, Anten and Hirose 1999, 2003, Werger et al. 2002), 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 and Hirose (1999) argue that species may coexist by exhibiting different aboveground growth patterns that enables 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 (Anten and Hirose 1999, Kahmen et al. 2006). 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, 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 and 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 and 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 and 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.

Material 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*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Festuca rubra* ssp. *commutata* (= *Festuca nigrescens*), *Holcus lanatus* (Lauber and Wagner 1996). The experiment described here was conducted in the experimental garden of the Inst. of Environmental Sciences, Zurich (47°23'N, 8°33'E, and 546 m 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 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 year⁻¹ 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 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 × 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 three of five replicates each with a leaf area meter.

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 and 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 \bar{D} (Loreau 1998a) as:

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

where YO_i is the biomass of species i in a given mixture and M_i the biomass in monoculture. A $\bar{D} > 0 \approx RYT > 1$ 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 $\bar{D} > 0$ (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 and Loreau 2007). To apply the model by Yachi and 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 Eq. 4 in Yachi and Loreau (2007), we calculated the increase in total biomass (δB , in g per harvested area) as:

$$\delta B = B_{\text{mix}} - \frac{1}{N} \sum_{i=1}^N B_{\text{mono}-i} \quad (2)$$

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

$$\delta E = L_{0\text{mix}} \times g(\bar{q}, LAI_{\text{mix}}) \times (LC + UG) \quad (3)$$

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

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

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

$L_{0\text{mix}}$ is the light intensity above mixture canopies, g (q , LAI) is an increasing function of q and of LAI (cf. Eq. 12 in Yachi and 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 $\text{LAI}_{\text{mono}-i}$ 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 Eq. 8a and 8b in Yachi and Loreau (2007) as:

$$e_i = \frac{\Delta E_i}{\Delta E_{i-\text{max}}} \quad (6a)$$

$$e_i = \frac{\Delta E_{\text{mix}}}{\Delta E_{\text{mix}-\text{max}}} \quad (6b)$$

ΔE_i and ΔE_{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 $\Delta E_{\text{mix}-\text{max}}$ stand for the theoretical maximum light energy of the given cultures and are calculated following Eq. 11a and 11b in Yachi and 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 Eq. 14 in Yachi and Loreau (2007) with Eq. 5) where we removed a mistake in the published version of the paper by Yachi and Loreau (2007). Further, because the Yachi and 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: $L_G = L_{G-\text{measured}}/L_{0-\text{measured}} \times 1725$. The species-specific light absorption rate (q_i) was calculated from light reflection and light transmission rates between 380 and 740 nm measured on five sun leaves and five shade leaves per species (high resolution miniature fibre optic spectrometer with a leaf probe). For an overview of parameters from the Yachi and Loreau (2007) method see Table A1 in Appendix 1.

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. All other analyses were performed with the statistical software R. Because we measured leaf area only in three of five replicates of each species combination, in the analysis of the model by Yachi and Loreau (2007)

combination means are based only on three 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 $\text{RY} \approx 0.5$ for both species. In the other pairs, RY was $\gg 0.5$ for one species while $\ll 0.5$ 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 (Appendix 1 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 \pm standard error (SEM): 2004: $454 \pm 19 \text{ g m}^{-2}$; 2005: $1420 \pm 23 \text{ g m}^{-2}$; 2006: $1463 \pm 28 \text{ g m}^{-2}$; Appendix 1 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 (Appendix 1 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, $R^2 = 0.31$; 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.

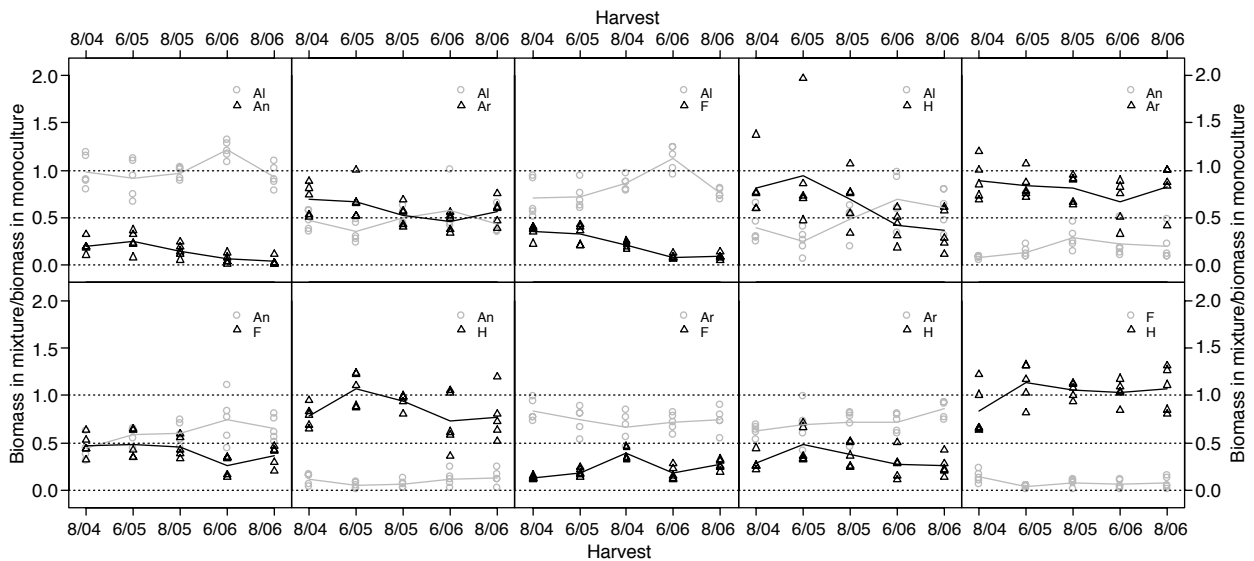


Figure 1. Development of relative biomass in all replicates of the pairwise mixtures over three years (all five harvests). Al: *Alopecurus pratensis*; An: *Anthoxanthum odoratum*; Ar: *Arrhenatherum elatius*; F: *Festuca rubra*; H: *Holcus lanatus*. Each point represents the relative biomass of a species in a plot, the solid lines connect the average relative biomass of a species in a given pairwise mixture.

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 May 2005) than in 2006 (on average 98% on 19 May 2006)

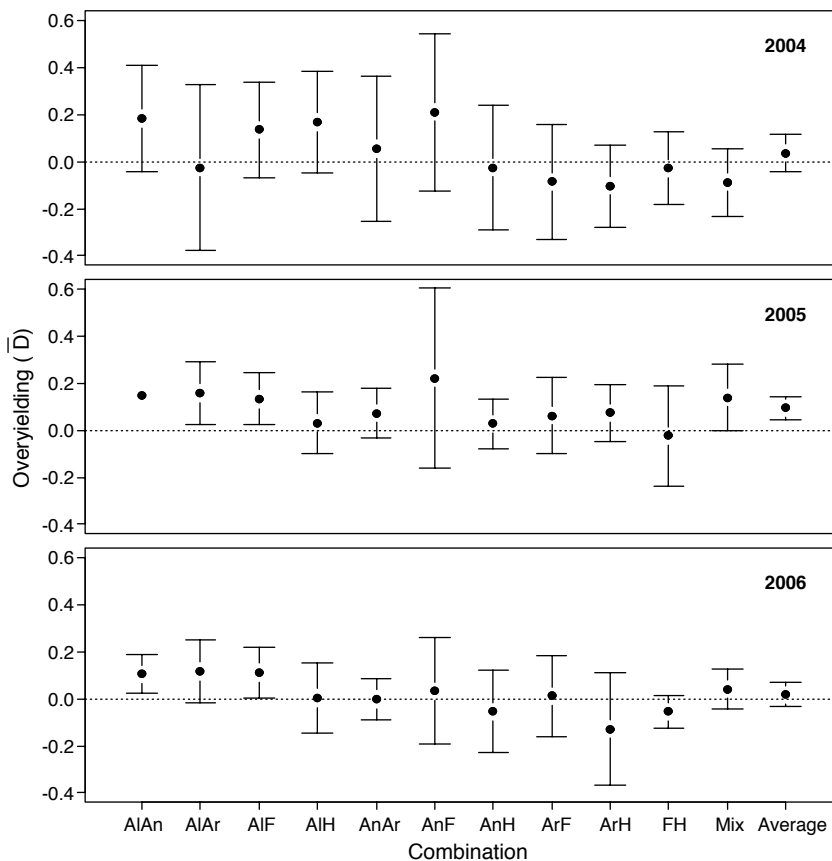


Figure 2. Meanoveryielding (\bar{D}) values ($\pm 95\%$ CI) based on the annual net primary biomass production of each pairwise mixture (species abbreviations see Fig. 1; names of pairwise mixtures are composed of the abbreviated species names, AlAn is the pairwise mixture of Al and An etc.), the full five species mixture (Mix) and the average of all mixture means (Average) in (a) 2004, (b) 2005 and (c) 2006.

which might explain why in this year also a later measurement could be used for predicting competitive dominance.

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:

$$\text{Spatial overlap} = 100 \times \left[1 - \frac{1}{2} \left(\sum_{i=1}^{11} |LA_i - LA_j| \right) \right] \quad (7)$$

where LA_i and LA_j 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.

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 Eq. 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

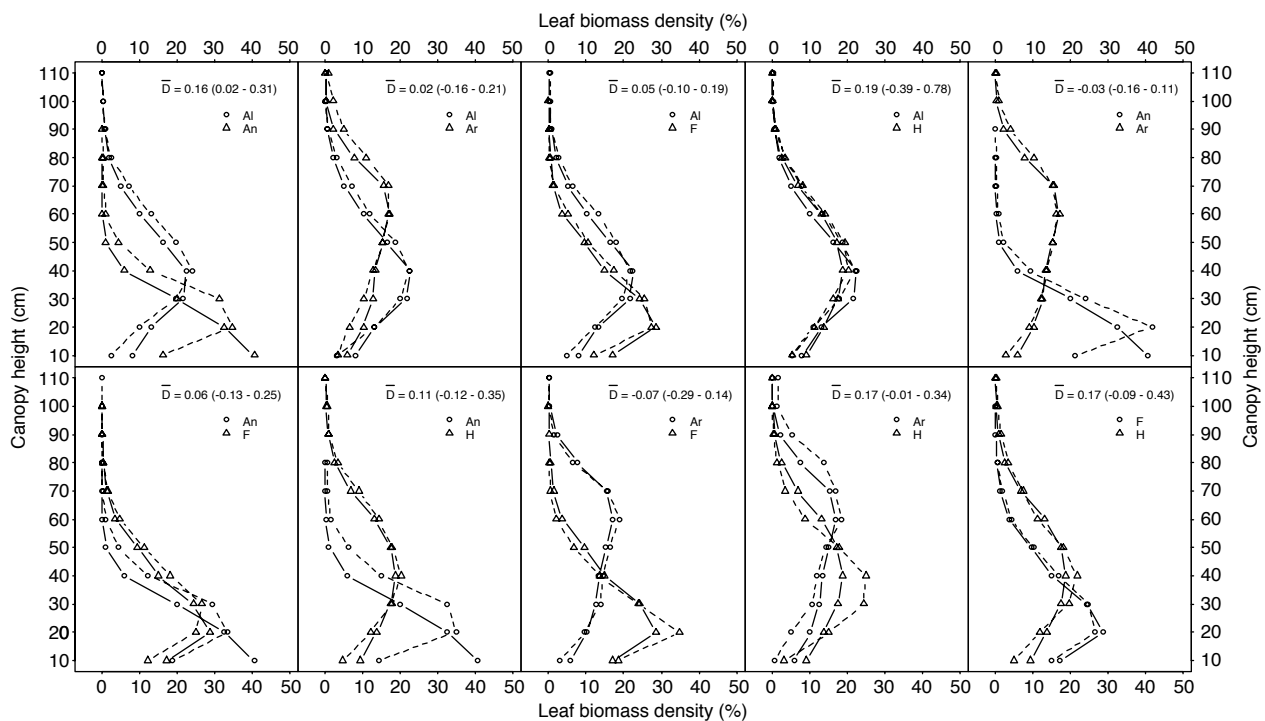


Figure 3. Proportion of leaf biomass density in each layer to the total leaf biomass density in a plot for each species in each pairwise mixture and in corresponding monocultures as recorded at the June harvest in 2005. Shown are mean values of all five replicates, standard errors were left out for clarity. Solid lines denote monocultures, dashed lines pairwise mixtures. Additionally, each panel shows the corresponding overyielding (\bar{D}) value ($\pm 95\%$ CI) of the respective pairwise mixture. Species abbreviations see Fig. 1.

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 ($\pm 95\%$ CI), 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 (83–105), 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; Eq. 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 \bar{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 and Loreau model of light competition in plant communities

The net biodiversity effect on biomass (δB) was mainly positive; mixtures produced on average up to 70 g more biomass per harvested area. The increase in total energy absorption (δB) was on average positive in six out of the eleven mixtures; assuming an incident light level of $1725 \mu \text{ mol photons m}^{-2} \text{ s}^{-1}$, mixtures intercepted on average between $70 \mu \text{ mol photons m}^{-2} \text{ s}^{-1}$ less and $56 \mu \text{ mol photons m}^{-2} \text{ s}^{-1}$ 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; $r: 0.02 (-0.59-0.61)$).

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

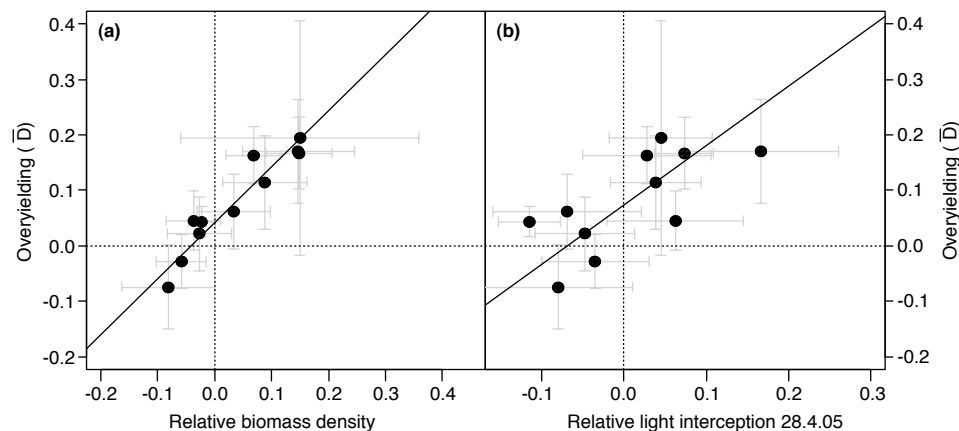


Figure 4. The relationship of mean overyielding (\bar{D}) values (\pm SEM) of all 10 pairwise and the full five species mixture from the June harvest in 2005 with mean values (\pm SEM) of mixture (a) relative biomass density and (b) relative light interception early in the growing season of 2005.

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 and 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 (Parrish and Bazzaz 1976, Silvertown et al. 1999, McKane et al. 2002) but rarely related to overyielding (but see Berendse 1982, 1983). Alternatively, Von Felten and 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

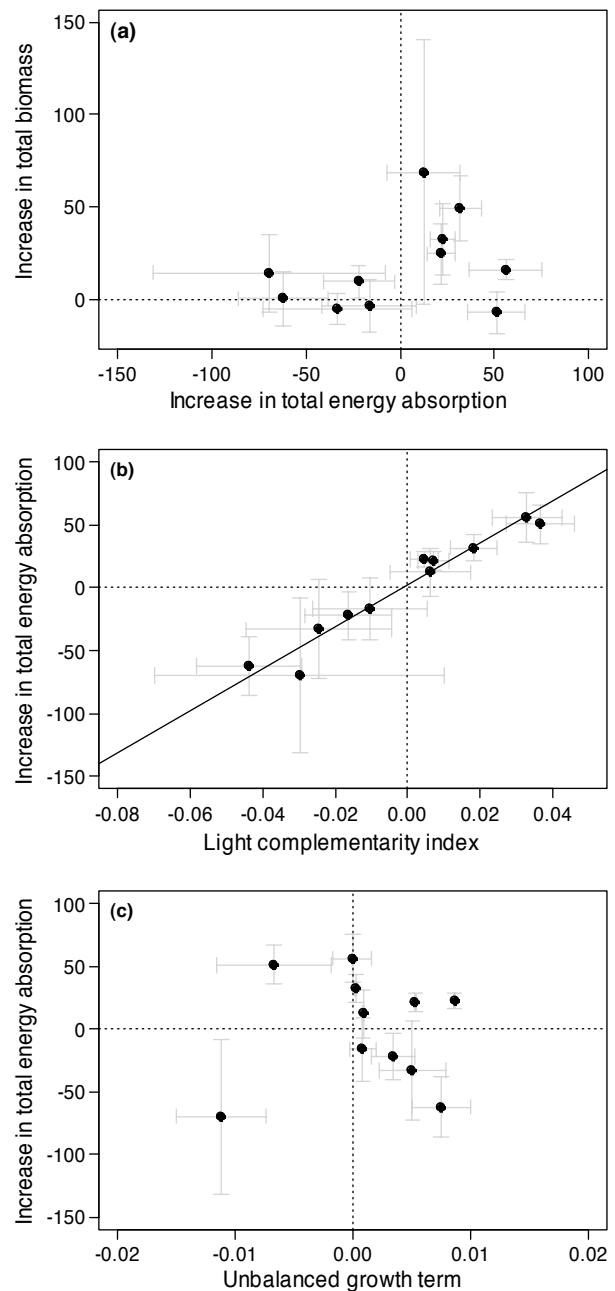


Figure 5. Application of the model of light competition in plant communities (Yachi and Loreau 2007) to data from the June harvest in 2005 (mean \pm SEM of all ten pairwise and the full five species mixture). The regression line was fitted using reduced major axis analysis. (a) relationship between increase in total biomass (δB) and increase in total energy absorption (δE), (b) relationship between increase in total energy absorption (δE) and the light complementarity index (LC) and (c) relationship between increase in total energy absorption (δE) and the unbalanced growth term (UG).

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 understory species which accounted for changes in relative yields between high fertility and shade treatments in the experiments of Fridley (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 and Hector unpubl.). 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 and 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 (δE) and the increase in total biomass (δB) 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.

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Appendix 1.

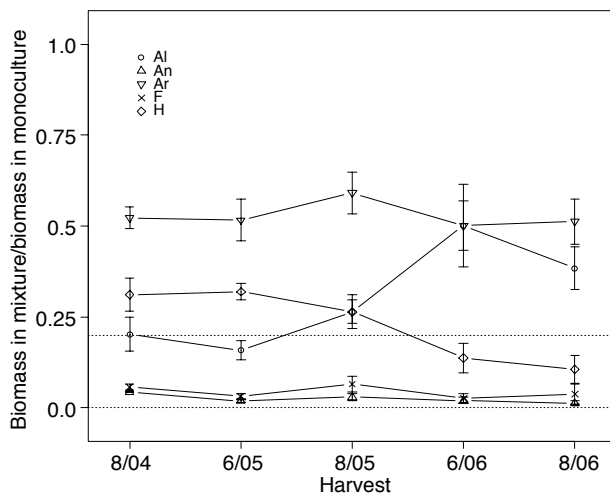


Figure A1. Development of relative biomass in all replicates of the full five species mixture over all three years (all five harvests). Al: *Alopecurus pratensis*; An: *Anthoxanthum odoratum*; Ar: *Arrhenatherum elatius*; F: *Festuca rubra*; H: *Holcus lanatus*.

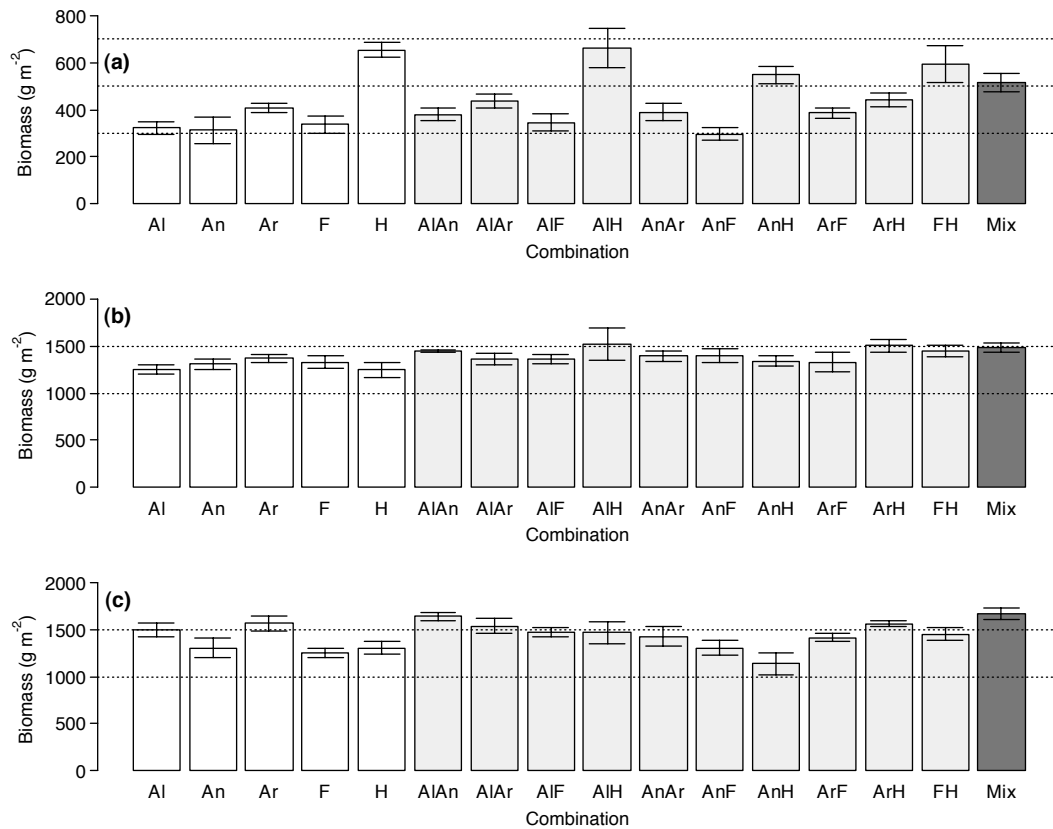


Figure A2. Mean whole-year biomass (g m^{-2} ; \pm SEM) of each combination in the experiment in (a) 2004, (b) 2005 and (c) 2006. White bars denote monocultures, light grey bars pairwise and dark grey the full five-species mixture. Al: *Alopecurus pratensis*; An: *Anthoxanthum odoratum*; Ar: *Arrhenatherum 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.

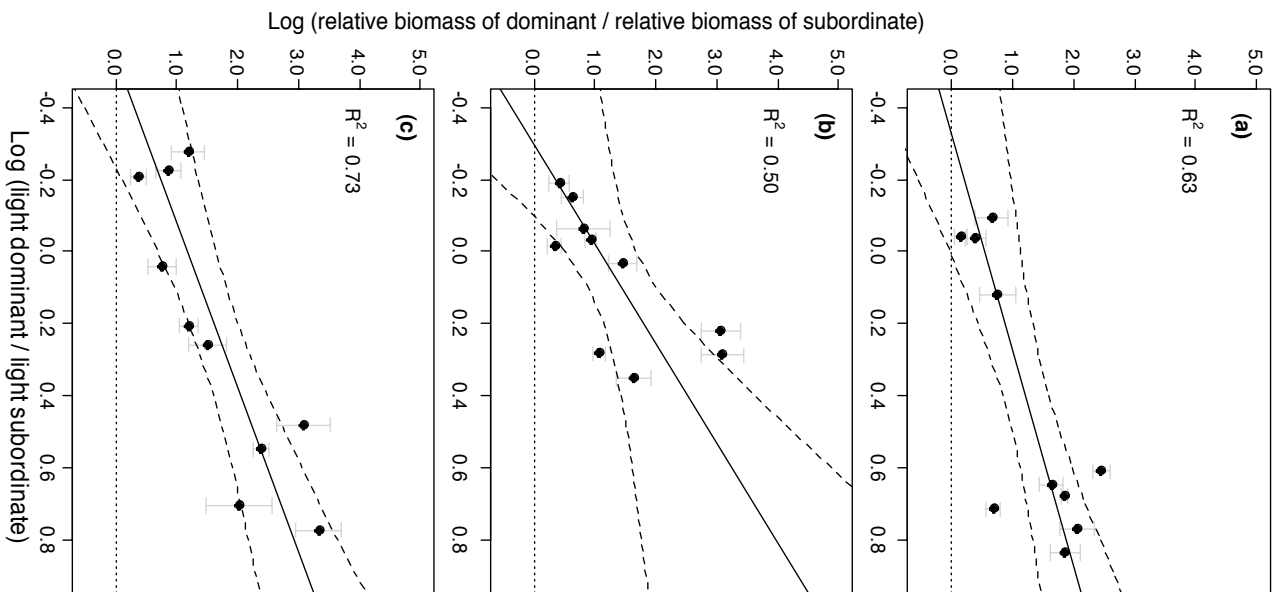


Figure A3. Linear regression slopes and 95% CI for the relationships between the biomass ratio and the log ratio of relative difference in light interception as measured at the begin of the growing season in (a) 2004, (b) 2005 and (c) 2006.

Table A1. Parameters used in the Yachi and Loreau (2007) method. For details see text.

| Abbreviation | Description | Method of determination |
|--|---|---|
| δB | Increase in total biomass | Calculated from biomass at harvest |
| L_0 (L_{0i} , L_{0mix}) | Light intensity above canopy | Measured in the experiment |
| L_G (L_{Gi} , L_{Gmix}) | Light intensity below canopy | Measured in the experiment |
| ΔE (ΔE_i , ΔE_{i-max}) | Light energy absorbed | Calculated from L_0 and L_G |
| LAI (LAI_{mono-i} , LAI_{mix}) | Leaf area index | Calculated from measured leaf area |
| q_i | Species-specific light absorption rate per unit leaf area | Measured in the experiment |
| \bar{q} | Average of all q_i among species in a mixture | Calculated from q_i |
| g (q , LAI) | Increasing function of q and of LAI | Calculated from q and of LAI |
| ΔE_{max} (ΔE_{i-max} , $\Delta E_{mix-max}$) | Theoretical maximum light energy | Calculated from L_0 and g (q , LAI) |
| E (e_i , e_{mix}) | Light absorption efficiency | Calculated from ΔE and ΔE_{max} |
| LC | Light complementarity index | Calculated from e_i and e_{mix} |
| UG | Unbalanced growth term | Calculated from e_i and g (q , LAI) |
| δE | Increase in total light energy absorption | Calculated from L_{0mix} , g (q , LAI) LC and UG |