

Smaller species experience mild adversity under shading in an old-field plant community

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Abstract

Plant competition experiments commonly suggest that larger species have an advantage, especially in light acquisition. However, within crowded natural vegetation, where competition evidently impacts fitness, most resident species are relatively small. It remains unclear, therefore, whether the size-advantage observed in controlled experiments is realized in habitats under intensive competition. We tested for evidence of a size-advantage in competition for light in an old-field plant community composed of herbaceous perennial species. We investigated whether larger species contributed to reduced light penetration (i.e., greater shading), and examined the impact of shade on smaller species by testing whether their abundance and richness were lower in plots with less light penetration. Light penetration in plots ranged from 0.3-72.4%. Plots with greater mean species height had significantly lower light penetration. Plots with lower light penetration had significantly lower small species abundance and richness. However, the impact of shade on small species abundance and richness was relatively small (R^2 values between 8% and 15%) and depended on how we defined "small species". Significant effects were more common when analyses focused on individuals that reached reproduction; focusing on only flowering plants can clarify patterns. Our results confirm that light penetration in herbaceous vegetation can be comparable to levels seen in forests, that plots with taller species cast more shade, and that smaller species are less abundant and diverse in plots where light penetration is low. However, variation in mean plot height explained less than 10% of variation in light penetration, and light penetration explained 5-15% of variation in small species abundance and richness. Coupled with the fact that reproductive small species were present even within the most heavily shaded plots, our results suggest that any advantage in light competition by large species is limited. One explanation is that some small species in these communities are shade tolerant.

Introduction

Evidence from neighbour removal studies clearly indicates that plant communities are highly competitive (e.g., Clements et al. 1929; Grime 1973; Tilman 1989; Gurevitch et al. 1992). Research also indicates that variation in plant functional traits is important in determining competitive ability and predicting the suppression of neighbour growth (Aarssen and Keogh 2002). For example, larger plant species are generally considered superior to smaller species when competing for pollinators (e.g., Donnelly et al. 1998), seed dispersal agents (e.g., Thomson et al. 2011), and for light (e.g., Weiner 1990; Schwinning and Weiner 1998). We refer to the competitive advantage commonly attributed to relatively tall plant species as the "size-advantage hypothesis" (e.g., Tracey and Aarssen 2014; Tracey et al. 2017).

Light is an essential resource, and light limitation can negatively impact plant growth (Bazzaz 1979; Tilman 1985; Grubb 1998). Light availability varies across the growing season (Bachmann et al. 2018), with canopy maturation (Ballaré 1994), and with community density (Givnish 1982). When competing species vary in

size, competition for light is said to be size-asymmetric (Lamb et al. 2009; DeMalach et al. 2017), with larger plants expected to dominate light competition by intercepting more light per unit size than smaller plants (Anten and Hirose 1998; DeMalach and Kadmon 2017). This growth of larger species imparts additional light limitation on smaller species while also reducing their own likelihood of being shaded (Anten 2005). When soil resources are adequate, natural communities can support the growth of tall plant species, which are able to limit the light reaching smaller plant species. For example, soil fertilization can result in increased light limitation and reduced grassland diversity (Borer et al. 2014). However, despite a perceived size-advantage in terms of expected negative impact on small species survival, growth and reproduction, small plants remain both ubiquitous and abundant within herbaceous vegetation (Aarssen et al. 2006). There is also little evidence of deterministic organization of species according to size in herbaceous communities (Schamp et al. 2008). Recent research has shown that species with larger body size in fact do not dominate neighbourhood biomass production in old-field vegetation (Tracey et al. 2017), nor do they recruit more offspring from the soil seed bank (Tracey and Aarssen 2019).

Light limitation has been studied extensively in forests (Canham et al. 1990; Canham et al. 1994; Gilliam and Roberts 2003; Gommers et al. 2013), but whether the impact of light limitation in forests is comparable to that in herbaceous vegetation remains unclear. While grasslands and old-fields are largely dominated by herbaceous species, distinct canopy layers have attributed vertical complexity to forests (Parker and Brown 2000; Miedema et al. 2019). In contrast, researchers have implied higher abundance and even distribution of light within herbaceous communities. However, several studies counter this widespread assumption, and collectively argue that light heterogeneity exists in herbaceous communities (Bazzaz 1990; Kelly and Canham 1992; Ballaré 1994; Körner 1995; Liira et al. 2002; Heger 2016; Huber et al. 2021). Herbaceous vegetation exhibits a layered canopy structure (Körner 1995; Liira et al. 2002) which, according to experimental studies, can reduce light penetration to the ground level to as low as 3% (Spehn et al. 2000), comparable to the 18-27% observed in some forests (Bartemucci et al. 2006). However, we struggled to find many published assessments of light penetration in herbaceous communities. One study found a reduction in diversity of small plant species in experimental plots under fertilization as ground-level light penetration decreased (Borer et al. 2014). Other experimental studies have also assessed the impact of light availability on herbaceous vegetation (e.g., Semchenko et al. 2012; Bachmann et al. 2018); however, analyses have yet to examine light conditions in unmanipulated communities (e.g., absent of seeding, fertilization, watering treatments).

It remains unclear how small species persist in herbaceous vegetation despite their apparent disadvantage in light competition, but the ubiquity of small species, on every scale from regional floras to local neighbourhoods, suggests that these species either avoid or tolerate low-light conditions. In woodlands, species that remain shaded under the herbaceous canopy may minimize light requirements through high photosynthetic efficiency and low light compensation points (Boardman 1977; Givnish 1988; Ballaré et al. 1997; Valladares and Niinemets 2008). In this case, there may be little to no change in small species abundance or richness associated with the amount of shade cast by taller vegetation. Smaller species may also rely on light from canopy gaps and sunflecks, which are commonly observed in forests (Chazdon and Pearcy 1991), and are likely important within herbaceous communities as well. Greater heterogeneity in canopy height in herbaceous communities and higher frequency of disturbance can increase the incidence of canopy gaps and sunflecks, allowing more light to penetrate towards the soil surface, which may thus support a greater number of small species (Chesson and Huntley 1997; Roxburgh et al. 2004). Additionally, small species may rely on early season light availability prior to canopy closure; although seasonal variation in light has been understudied in herbaceous communities, small species have been found to flower earlier in the season (Du and Qi 2010; Sun and Frelich 2011; Segrestin et al. 2020). Early growth and flowering by small species may reduce competition for light, as well as for pollinators, allowing these species to coexist with larger, later flowering species (Jensen et al. 2019).

In this study, we sought to answer two important questions concerning the presumed advantage that larger species have in light competition within a temperate mesic old-field community. First, we examined patterns of light penetration through the standing vegetation to determine whether sample plots containing taller resident species have significantly reduced light penetration. Second, we tested whether the species abundance

and richness of smaller plants were lower in sample plots where light penetration was lowest. The goal of this research was to better reconcile experimental evidence that large plant species enjoy a competitive advantage for light with the widespread prevalence of small plant species in natural communities.

Methods

Study site

We conducted this experiment from June to August 2006 within a 67.5 m x 50 m old-field meadow (known locally as the “Cemetery Field”) located at the Queen’s University Biological Station, north of Kingston, Ontario, Canada (44° 32’ 23” N, 76° 22’ 3” W). For about 50 years preceding this work, this field was harvested for hay annually (excluding 2005 and 2006) but has not otherwise been disturbed. In July 2005, the field was divided into 486 plots, each 1 m x 1 m, separated by 1 m laneways to minimize the impact of edge effects and disturbance during data collection (Piggott 2007). Of these 486 pre-existing plots, 49 were randomly chosen for data collection in this study.

Data collection

Monthly, from June to August 2006, we measured light intensity (photosynthetically active radiation; PAR) within each of the 49 plots using a LI-COR L1-250A light meter ($\mu\text{mol s}^{-1}\text{m}^{-2}$; LI-COR Biosciences, Lincoln, USA). Each plot was divided into nine equal squares in a 3 x 3 grid, with three measurements taken in the center of each plot row, directly above the canopy, and nine measurements taken at ground-level in each square (Fig. 1). We calculated the percentage of light penetration based on the mean light intensity at ground-level for each of the nine locations in the plot and the mean above-canopy light intensity measured above each plot row [$100 \times (\text{ground-level light intensity} / \text{above-canopy light intensity})$].

From June to August 2006, we collected abundance data by quantifying the number of rooted units per species in each plot (i.e., ramets, Schamp et al. 2016), and determined plot-level species richness from these abundance data. We monitored plot-level abundance biweekly, which was further classified into two census types: total abundance of each species (including all rooted units in a plot, both reproductive and nonreproductive), and flowering abundance of each species (including only reproductive rooted units in a plot). Species maximum height (cm) data were collected for all species in the dataset from specimens measured at the study site (not in sample plots) and in nearby old-fields at the Queen’s University Biological Station. The number of values recorded per species ranged between 5-20, and the largest value per species was used as the maximum height for that species.

Data analyses: variation in the light environment

We quantified light penetration in our grassland community to determine how much light variation exists and to identify sources of that variation. We examined light penetration across plots to assess variation across the site (‘interplot light variation’), within plots to quantify heterogeneity in light penetration (‘intraplot light variation’), and across months to determine how light penetration changed throughout the growing season (‘temporal light variation’). To quantify interplot light variation, we calculated mean light penetration (%) within a plot during one sampling event, and further calculated variance (σ^2) between these means for each month (N=3). For intraplot light variation, we calculated the variance in light penetration within each plot for each month (N=147). Finally, to quantify temporal variation, we calculated variance in mean light penetration for each plot across months (June, July, August; N=49).

Additionally, to assess how light penetration levels differ across June, July, and August, we performed a one-way repeated measures ANOVA using mean light penetration as the response variable and plot as the within-subject factor, followed by a Bonferroni post hoc test to determine significant differences between months. We visually assessed normality and checked for equal variances among months using a Mauchly’s test for sphericity. For these analyses, we used the ‘anova_test’ and ‘pairwise_t_test’ functions from the package ‘rstatix’ v0.6.0 (Kassambara 2020).

Data analyses: species size effects on — and responses to — light penetration

Because there is no standard definition of “small species” we compared two approaches: 1) small species were regarded as those smaller than the first quartile of species height for all species in the focal community (‘1st quartile’, <53.25 cm, N=15), 2) small species were regarded as those smaller than the median of species height in the community (‘median’, <83 cm, N=29; Fig. 2). Comparing results across these two definitions allowed us to test whether any significant patterns were sensitive to our method of defining small species.

We tested whether plots with larger species had lower light penetration. Specifically, we fit linear models with mean plot height (mean plot-level maximum height weighted by species plot-level abundance) and large species abundance (including all species which are not considered “small” by either definition, >83 cm) as predictors and mean light penetration as the response variable. We also tested whether small species abundance and richness responded to variation among plots in light penetration. We fit linear models with small species abundance and richness (for both ‘1st quartile’ and ‘median’ defined small species) as response variables. Light penetration and mean intraplot variation in light penetration (calculated for each plot at each sampling event and averaged across months) were our predictor variables. We checked the variance inflation factor to ensure that there was not a high degree of multicollinearity between our variables.

We used the package ‘stats’ from R.4.0.3 (R Core Team 2020) for modeling, and checked statistical assumptions using residual vs. fitted, normal quantile-quantile, scale location, and constant leverage plots (‘ggfortify’ v.0.4.11; Tang 2016). We log₁₀-transformed variables where necessary to meet assumptions. For our multiple linear regressions, we used the Akaike Information Criterion corrected for small sample sizes for model selection (AICc). Where multiple models were within two units of the lowest AICc score, we used the full model average (via the ‘model.avg’ function from the ‘MuMIn’ v1.43.17 package; Bartoń 2020) to determine the significance of predictors.

Finally, to assess the collective response of small species to light availability, we performed distance-based redundancy analyses (dbRDA) using Bray-Curtis dissimilarities. Additionally, we used the ‘decorana’ function from the package ‘vegan’ v.2.5-6 (Oksanen 2019) to confirm linearity of responses. We conducted RDA with mean light penetration and mean intraplot variation as possible predictors using the ‘capscale’ function from ‘vegan’ v.2.5-6 (Oksanen 2019). We compared models using AICc scores, selecting the model with the lowest score.

Results

Variation in the light environment

Light penetration within our old-field site ranged from 0.3-72.4% ($n = 440$, $\mu = 16.6\% \pm 12$; Fig. S1A). The highest variance in light penetration occurred between plots ($n = 3$, median interplot variance=77.3), followed by variance across months ($n = 49$, median temporal variance = 57.4) with within-plot light penetration varying the least ($n = 147$, median intraplot variance = 26.2; Fig. 3). Intraplot variance in light penetration ranged from 0.07-1546.5 ($n = 147$, $\mu = 88.3 \pm 15.3$; Fig. S1B). Mean light penetration was highest in June (20.2%), lowest in July (13.6%), and slightly higher in August (15.9%). Light penetration differed significantly across months (repeated measures ANOVA, $F_{2,96} = 9.2$, $P < 0.001$; Fig. 4); with a posthoc test revealing that light penetration in June was significantly different than in both July (Bonferroni, $P_{\text{adj}} < 0.001$; Fig. 4A) and August (Bonferroni, $P_{\text{adj}} = 0.036$; Fig. 4B), but that the last two months did not significantly differ (Bonferroni, $P_{\text{adj}} = 0.4$; Fig. 4C). High variance in light penetration among sample plots further justified our plot-level approach to hypothesis testing.

Species size and light penetration

Light penetration was significantly lower in plots with greater plot-level mean height ($R^2 = 0.08$, $P = 0.025$; Fig. 5) but was unassociated with large species abundance. Mean intraplot variation in light penetration was significantly positively correlated with mean light penetration (Spearman correlation, $\rho = 0.49$, $P < 0.001$; Fig. S2).

Small species abundance and richness in plots were significantly higher in plots with high light penetration, but not for both definitions of small species. Small species under the ‘1st quartile’ definition had significantly

higher flowering abundance in plots with higher light penetration ($R^2 = 0.08$, $P = 0.027$; Fig. 6A). Median flowering abundance and richness were significantly higher in plots with increased light penetration (Abundance: $R^2=0.1$, $P = 0.012$; Richness: $P = 0.014$, $R^2 = 0.1$; Figs. 6B,D). The richness of small species (1st quartile) did not significantly change with light penetration (Fig. 6C, Table S1). Within-plot variation in light penetration was not significantly related to small species abundance or richness using either definition (Table S1).

The composition of small plant species defined using the median significantly changed with mean plot-level light penetration (dbRDA1, $P = 0.031$, pseudo- $F_{1,47} = 2.06$; Fig. 7), but was unaffected by mean intraplot variation. Mean plot-level light penetration explained 4.2% of the total variation in plot composition for ‘median’ small species. Eighteen species had higher abundances associated with higher light penetration (as demonstrated by positive loadings along the light penetration axis), while eight species tended to have lower abundances associated with higher light penetration (as demonstrated by negative loadings along the light penetration axis; Fig. 7). Conversely, ‘1st quartile’ small species composition was unaffected by mean light penetration or mean intraplot variation, and neither were retained as axes.

We performed analyses using both total abundance and flowering abundance; however, because the analyses of flowering abundance were more informative, we have focused on these. Half of the analyses using the total number of individuals demonstrated significant relationships between light penetration and small species abundance and richness, compared to two-thirds of analyses using only the number of flowering individuals. We provide further information on analyses using the total number of individuals in the supplementary material (Fig. S3-S7).

Discussion

Understanding variation in the light environment

To understand the effects of light limitation on small plant species in a herbaceous plant community, we first characterized variation in light penetration within-plots, among-plots, and across time through the growing season. Despite existing assumptions that light is not heterogeneously distributed within herbaceous communities, light penetration across plots in our community ranged from 0.3-72.4% (Fig. S1A). Light penetration also varied within plots and across the growing season, and the degree of variance in light penetration among intraplot, interplot, and temporal measures was similar (Fig. 3). Light penetration significantly increased from June to July as well as from June to August but did not differ between July and August; thus, maximum canopy development was reached by July.

Analyses of light penetration through the canopy of natural herbaceous plant communities are rare (e.g., Kelly and Canham 1992); those that exist are often conducted on communities that have been subjected to an experimental treatment. These include various fertilization (e.g., Urbas and Zobel 2000; Semchenko et al. 2012; Borer et al. 2014), watering (e.g., Semchenko et al. 2012), mowing (e.g., Urbas and Zobel 2000; Bachmann et al. 2018), herbivory (e.g., Izaguirre et al. 2006; Borer et al. 2014), and shading or illumination treatments (e.g., Urbas and Zobel 2000; Izaguirre et al. 2006; Semchenko et al. 2012). Varied experimental treatments, along with differences among studies in how the light environment is quantified (e.g., 5cm from the ground by Kelly and Canham 1992; 3-150 cm from the ground by Bachmann et al. 2018), make it difficult to compare across studies, and to get a general sense of light environments in herbaceous communities. However, when species richness was manipulated via seeding, analyses of old-field meadow and grassland communities have described ranges of percent light penetration similar to our community, with averages as low as 13% in 8-species mixtures (Spehn et al. 2000), 20-32% in 16-species mixtures (Bachmann et al. 2018), and 3% in 32-species mixtures (Spehn et al. 2000). Within our community, total species richness ranged from 13-29 among plots; thus, the ranges of light penetration and species richness recorded in our non-experimental study site are comparable to findings from experimental herbaceous study sites.

Because the herbaceous canopy lacks shrubs and trees, it is a widely held view that light is both highly abundant and relatively homogenous within herbaceous communities. However, average light penetration within our community (5-29%) is comparable to 18-27% light penetration through a mixed wood temperate

forest (Bartemucci et al. 2006) and, for some plots, 0.4-6.7% light penetration through a tropical forest (Valladares et al. 2002). While herbaceous canopies are likely slower to close, many small plant species in herbaceous communities persist underneath these canopies. While shade tolerance is generally accepted as supporting the ability of small plant species to survive in forest understories, it remains an open question whether shade tolerance plays a similar role in herbaceous plant communities.

Testing hypotheses related to species size and light penetration

According to the size-advantage hypothesis, larger species are competitively superior to smaller species, mainly due to their ability to intercept light, shading plants below (e.g., Schwinning and Weiner 1998; Anten 2005; Tracey and Aarssen 2014; Tracey et al. 2017). Consistent with this, we found that light penetration significantly decreased with mean plot height (Fig. 5). Importantly, the height of species in sample plots, as measured here, left approximately 90% of variation in plot-level light penetration unexplained. Some of this unexplained variation is inevitably due to the way in which we estimated plot height – future assessments based on measuring the heights of all plant species in plots would be of benefit but were not possible for this study. Regardless, this result highlights that while tall species have the capacity to shade smaller plants, the biological significance of this advantage may be greatly reduced by the size distributions of tall species in plots, and by other factors that contribute to variation in composition within herbaceous plant communities. Inevitably, other factors, like the available soil nutrients, can limit the height of the canopy by controlling which species can persist (Borer et al. 2014). Large species with large minimum reproductive size thresholds (Tracey and Aarssen 2019) may be less likely to persist in low soil nutrient settings and self-thinning among tall plant species may create regular gaps, allowing light to reach smaller species (Schamp and Aarssen 2014). Thus, nutrient limitation and competition among tall species may decrease the abundance of large plant individuals per area, simultaneously increasing light penetration and altering the importance of light as a previously limited resource. Herbivory can also impact canopy development directly, and indirectly by influencing plant investments in herbivore defense.

We found evidence that small species abundance and richness are limited by light penetration; these patterns were consistent when we considered reproductive plants and small species were defined as those below the median height of species in the community, but inconsistent when small species were defined as those in the first quartile of species heights in the community. These findings were less consistent across both definitions of small species when we did not focus on reproductive plants (Table S1). Importantly, the coefficients of determination (R^2) for regressions between light penetration and our response variables, when significant, ranged between 8-11% (Fig. 6). Furthermore, only 4.2% of the variation in the composition of small species, defined using the median, was explained by light penetration (Fig. 7). Low light penetration had a significant, but meagre impact on small species abundance and richness in this community.

These results, in combination with the above results showing that large species contribute only slightly to patterns of light penetration, provide useful context for understanding the conundrum of small species diversity in natural systems in spite of experimental observations that small species are at a competitive disadvantage. First, light penetration in herbaceous systems is relatively low, but less so earlier in the growing season (i.e., June in this study system). It is possible that some small species take advantage of higher light penetration early in the growing season. This is consistent with observations that smaller plant species often flower earlier in the season (Du and Qi 2010; Sun and Frelich 2011; Segrestin et al. 2020). Second, within-plot variation in light penetration, reflecting heterogeneity in plot canopy structure, had no impact on small species abundance and richness, suggesting that local sunflecks are relatively unimportant in maintaining small species in herbaceous communities. This may be because plots with more variation in canopy structure tended to be less shaded on average, reducing the role of sunflecks as a critical source of light. Third, the fact that small species richness is only modestly impacted by light penetration suggests that many small species possess some mixture of shade avoidance and shade tolerant strategies that allow them to persist in shaded conditions. Shade tolerance may contribute to increased reproductive economy in smaller species (Aarssen 2008). Shade tolerant species implement morphological and physiological traits which increase efficiency of carbon gain and stress tolerance, allowing them to persist under low light conditions (Valladares

and Niinemets 2008). Additionally, small species richness, defined using the 1st quartile, was no lower when light penetration was lowest, indicating that the richness of the 25% smallest species in the community was maintained under increasingly low light availability. Adaptation to low light levels via phenotypic plasticity in morphological traits may explain the persistence of small species richness under low light (Ballaré 1994; Urbas and Zobel 2000; Hallik et al. 2009; Niinemets et al. 2015), as some individuals may express traits associated with greater light capture (e.g., high specific leaf area; Valladares and Niinemets 2008), thus maintaining species presence under reduced abundance. The characteristics of the light environment in our community, and likely the characteristics of many resident small species ensure that any disadvantage they suffer in competition for light is minimal.

The effects of shading on small species abundance and richness were more consistently observed and stronger in general when we focused on reproductive individuals in sample plots. This demonstrates that although ‘median’ small species were able to persist under low light with no detected loss in abundance or richness, some were not successful enough to reach reproductive maturity. The presence of flowering individuals in a sample plot is evidence of a species’ capacity to successfully establish in that environment. Our results make it clear that light penetration does indeed affect which small species can find success, but its impact on small species abundance and richness is relatively minor (8-15% of variation explained). Our results also support the contention that focusing censuses on flowering species when studying coexistence, can clarify plant community dynamics (Schamp et al. 2016, Schamp and Jensen 2019).

Conclusion

The size of resident species in old-field vegetation plots had a significant impact on light penetration; however, it appears that this impact is quite limited. This should be studied further, with more thorough assessments of plot-level height, to clarify the degree to which large species have the capacity to shade smaller species in herbaceous communities. Small plant species abundance and richness were significantly lower when light penetration was lower; however, this impact was once again relatively small. Our results are consistent with the results of competition experiments that reveal a size-advantage in competition, but add context by demonstrating that, in our study community, this advantage has only a very small impact on small species. Several possible explanations exist. For example, mitigating impacts on large plants, like herbivory, may reduce the capacity for large species to outcompete small species for light. It is also possible that one or more of several characteristics of small species (early season growth and reproduction, shade tolerance) contribute to greater reproductive economy of small species (Aarssen 2008). This study also adds to the sparse body of literature on the light environment in unmanipulated herbaceous plant communities.

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References

- Aarssen LW. 2008. Death without sex- the ‘problem of the small’ and selection for reproductive economy in flowering plants. *Evol. Ecol.* 22: 279-298.
- Aarssen LW, Keogh T. 2002. Conundrums of competitive ability in plants: what to measure? *Oikos*. 96(3): 531-542.
- Aarssen LW, Schamp BS, Pither J. 2006. Why are there so many small plants? Implications for species coexistence. *J. Ecol.* 94(3): 569-580.
- Anten NPR, Hirose T. 1998. Biomass allocation and light partitioning among dominant and subordinate individuals in *Xanthium canadense* stands. *Ann. Bot.* 82(5): 665-673.

- Anten NPR. 2005. Optimal photosynthetic characteristics of individual plants in vegetation stands and implications for species coexistence. *Ann. Bot.* 95(3): 495-506.
- Bachmann D, Roscher C, Buchmann N. 2018. How do leaf trait values change spatially and temporally with light availability in a grassland diversity experiment? *Oikos*. 127(7): 935-948.
- Ballaré CL. 1994. Light gaps: sensing the light opportunities in highly dynamic canopy environments. — In: Caldwell, M. M. and Pearcy, R. W. (eds), *Exploitation of environmental heterogeneity by plants*. Academic Press, pp. 73-110.
- Ballaré CL, Scopel AL, Sánchez RA. 1997. Foraging for light: photosensory ecology and agricultural implications. *Plant Cell Environ.* 20(6): 820-825.
- Bartemucci P, Messier C, Canham, CD. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. *Can. J. For. Res.* 36(9): 2065-2079.
- Bartoń K. 2020. MuMIn: Multi-Model Inference. R 1.43.17.
- Bazzaz FA. 1979. The physiological ecology of plant succession. *Annu. Rev. Ecol. Evol. Syst.* 10(1): 351-371.
- Bazzaz FA. 1990. The response of natural ecosystems to the rising global CO₂ levels. *Annu. Rev. Ecol. Evol. Syst.* 21(1): 167-196.
- Boardman NK. 1977. Comparative photosynthesis of sun and shade plants. *Annu. Rev. Plant Physiol.* 28(1): 355-377.
- Borer ET, Seabloom EW, Gruner DS...Yang LH. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*. 508(1): 517-520.
- Buhk C, Alt M, Steinbauer MJ, Beierkuhnlein C, Warren SD, Jentsch A. 2017. Homogenizing and diversifying effects of intensive agricultural land use on plant species beta diversity in Central Europe—A call to adapt our conservation measures. *Sci. Total Environ.* 576(1): 225-233.
- Canham CD, Denslow JS, Platt WJ, Runkle JR, Spies TA, White PS. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20(5): 620-631.
- Canham CD, Finzi AC, Pacala SW, Burbank DH. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* 24(2): 337-349.
- Chazdon RL, Pearcy RW. 1991. The importance of sunflecks for forest understory plants. *BioScience*. 41(11): 760-766.
- Chesson P, Huntly N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.* 150(5): 519-553.
- Clements FE, Weaver JE, Hanson HC. 1929. *Plant competition. An analysis of community functions*. Washington: Carnegie institution.

- DeMalach N, Kadmon R. 2017. Light competition explains diversity decline better than niche dimensionality. *Func. Ecol.* 31(9): 1834-1838.
- DeMalach N, Zaady E, Kadmon R. 2017. Light asymmetry explains the effect of nutrient enrichment on grassland diversity. *Ecol. Let.* 20(1): 60-69.
- Donnelly SE, Lortie CJ, Aarssen LW. 1998. Pollination in *Verbascum thapsus* (Scrophulariaceae): the advantage of being tall. *Am. J. Bot.* 85(11): 1618-1625.
- Du G, W Qi. 2010. Trade-offs between flowering time, plant height, and seed size within and across 11 communities of a QingHai-Tibetan flora. *Plant Ecol.* 209: 321-333.
- Garnier E, Lavorel S, Ansquer P, Zarovali MP. 2007. Assessing the effects of land use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Ann. Bot.* 99(5): 967-985.
- Gilliam FS, Roberts MR, editors. 2003. The herbaceous layer in forests in eastern North America. New York (NY): Oxford University Press. p. 48-86.
- Givnish TJ. 1982. On the adaptive significance of leaf height in forest herbs. *Am Nat.* 120(3): 353-381.
- Givnish TJ. 1988. Adaptation to sun and shade: a whole-plant perspective. *Aust. J. Plant Physiol.* 15(2): 63-92.
- Gommers CMM, Visser EJW, St Onge KR, Voesenek LACJ, Pierik R. 2013. Shade tolerance: when growing tall is not an option. *Trends Plant Sci.* 18(2): 65-71.
- Grime JP. 1973. Competitive exclusion in herbaceous vegetation. *Nature.* 242(1): 344-347.
- Grubb PJ. 1998. A reassessment of the strategies of plants which cope with shortages of resources. *Perspect. Plant Ecol.* 1(1): 3-31.
- Gurevitch J, Morrow LL, Wallace A, Walsh JS. 1992. A meta-analysis of competition in field experiments. *Am. Nat.* 140(4): 539-572.
- Hallik L, Kull O, Niinemets Ü, Aan A. 2009. Contrasting correlation networks between leaf structure, nitrogen and chlorophyll in herbaceous and woody canopies. *Basic Appl. Ecol.* 10(4): 309-318.
- Heger T. 2016. Light availability experienced in the field affects ability of following generations to respond to shading in an annual grassland plant. *J. Ecol.* 104(5): 1432-1440.
- Huber M, Nieuwendijk NM, Pantazopoulou CK, Pierik R. 2021. Light signalling shapes plant-plant interactions in dense canopies. *Plant Cell Environ.* 44(4): 1014-1029.
- Izaguirre MM, Mazza CA, Biondini M, Baldwin IT, Ballaré CL. 2006. Remote sensing of future competitors: impacts on plant defenses. *PNAS.* 103(18): 7170-7174.
- Jensen AM, Schamp BS, Belleau A. 2019. Evidence of temporal niche separation via low flowering time overlap in an old-field plant community. *Oecologia.* 189(4): 1071-1082.
- Kassambara, A. 2020. rstatix: Pipe-Friendly Framework for Basic Statistical Tests. R

- package version 0.6.0. <https://cran.r-project.org/web/packages/rstatis/>
- Kelly VR, Canham CD. 1992. Resource heterogeneity in oldfields. *J. Veg. Sci.* 3(4): 545-552.
- Körner C. 1995. Scaling from species to vegetation: the usefulness of functional groups. In: Schulze ED and Mooney HA. (eds), *Biodiversity and Ecosystem Function*. Springer-verlag, Berlin, p. 117-140.
- Lamb EG, Kembel SW, Cahill JF. 2009. Shoot, but not root, competition reduces community diversity in experimental mesocosms. *J. Ecol.* 97(1): 155-163.
- Liira J, Zobel K, Mägi R, Molenberghs J. 2002. Vertical structure of herbaceous canopies: the importance of plant growth-form and species-specific traits. *Plant Ecol.* 163(1): 123-134.
- Miedema LJ, Capmoureres V, Anand M. 2019. Impact of land composition and configuration on the functional trait assembly of forest communities in southern Ontario. *Ecosphere*. 10(3): 1-13.
- Niinemets Ü, Keenan TF, Hallik L. 2015. A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytol.* 205(3): 973-993.
- Oksanen JF, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H. 2019. *vegan: Community Ecology Package*. R 2.5-6.
- Parker GG, Brown MJ. 2000. Forest canopy stratification—is it useful? *Am. Nat.* 155(4): 473-484.
- Piggott G. 2007. Effects of density and light use efficiency on plant community invasibility [bachelor's thesis]. Kingston (ON): Queen's University.
- Roxburgh SH, Shea K, Wilson JB. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology*. 85(2): 359-371.
- Schamp BS, Chau J, Aarssen LW. 2008. Dispersion of traits related to competitive ability in an old-field plant community. *J. Ecol.* 96(1): 204-212.
- Schamp BS, Aarssen LW. 2014. Plant species size and density-dependent effects on growth and survival. *J. Veg. Sci.* 25: 657-667.
- Schamp BS, Aarssen LW, Piggott GJS, Dante SK. 2016. The impact of non-reproductive plant species on assessments of community structure and species co-occurrence patterns. *J. Veg. Sci.* 27(4): 668-678.
- Schamp BS, Jensen A. 2019. Evidence of limiting similarity revealed using a conservative assessment of coexistence. *Ecosphere* 10(8): e02840.
- Schwinning S, Weiner J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*. 113(4): 447-455.
- Segrestin J, Navas M, Garnier E. 2020. Reproductive phenology as a dimension of the phenotypic space in 139 plant species from the Mediterranean. *New Phytol.* 225: 740-753.

- Semchenko M, Lepik M, Gotzenberger L, Zobel K. 2012. Positive effect of shade on plant growth: amelioration of stress or active regulation of growth rate? *J. Ecol.* 100(2): 459-466.
- Spehn EM, Joshi J, Schmid B, Diemer M, Korner C. 2000. Above-ground resource use increases with plant species richness in experimental grassland ecosystems. *Funct. Ecol.* 14(3): 326-337.
- Sun S, Frelich LE. 2011. Flowering phenology and height growth pattern are associated with maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland species. *J Ecol.* 99: 991-1000.
- Tang Y, Horikoshi M, Li W. 2016. ggfortify: unified interface to visualize statistical result of popular R packages. *R J.* 8.2: 478-489.
- Thomson FJ, Moles AT, Auld TD, Kingsford RT. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *J. Ecol.* 99(6): 1299-1307.
- Tilman D. 1985. The resource-ratio hypothesis of plant succession. *Am. Nat.* 125(6): 827-852.
- Tilman D. 1989. Ecological experimentation: strengths and conceptual problems. In: Likens GE. *Long-Term Studies in Ecology*. Springer, New York, NY.
- Tracey AJ, Aarssen LW. 2014. Revising traditional theory on the link between plant body size and fitness under competition: evidence from old-field vegetation. *Ecol Evol.* 4(7): 959- 967.
- Tracey A, Irwin E, Mcdonald B, Aarssen L. 2017. Species with larger body size do not dominate neighbourhood biomass production in old-field vegetation. *J Veg Sci.* 28(3): 616-626.
- Tracey AJ, Aarssen LW. 2019. Resident species with larger size metrics do not recruit more offspring from the soil seed bank in old-field meadow vegetation. *J Ecol.* 107: 1067–1078.
- Urbas P, Zobel K. 2000. Adaptive and inevitable morphological plasticity of three herbaceous species in a multi-species community: field experiment with manipulated nutrients and light. *Acta Oecol.* 21(2): 139-147.
- Valladares F, Skillman JB, Pearcy RW. 2002. Convergence in light capture efficiencies among tropical forest understory plants with contrasting crown architectures: a case of morphological compensation. *Am. J. Bot.* 89(8): 1275-1284.
- Valladares F, Niinemets U. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annu. Rev. Ecol. Evol. Syst.* 39: 237-257.
- Weiner J. 1990. Asymmetric competition in plant populations. *Trends Ecol Evol.* 5(11): 360-364.

Figures

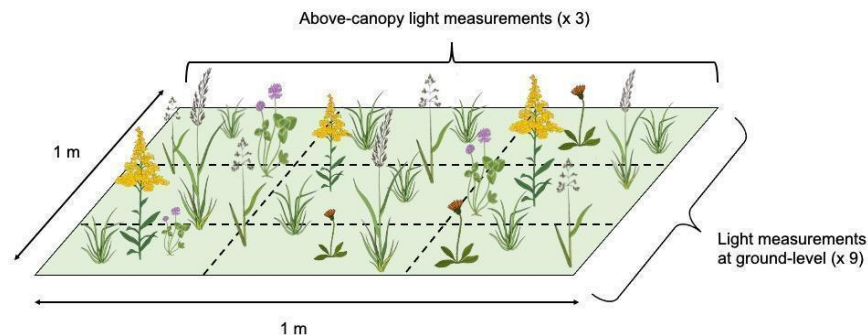


Figure 1: Experimental plot setup for measuring light penetration. Plots were laid out in 1 m x 1 m squares divided into a 3 x 3 grid for a total of nine equal subsections within each plot. We took three light intensity measures ($\mu\text{mol s}^{-1}\text{m}^{-2}$) at the center of each row directly above the canopy, with an additional nine measurements (one in each subsection) at the ground-level. We then calculated three measures of percentage of light penetration for each plot by taking the mean light intensity at the ground-level for each row and using the equation: $100 \times (\text{ground-level light intensity} / \text{above-canopy light intensity})$.

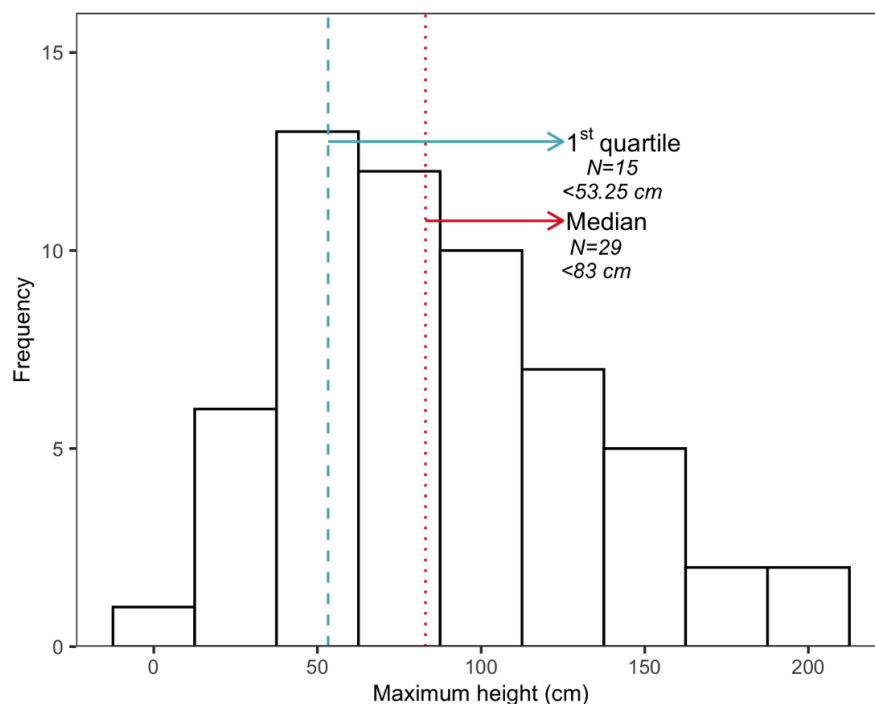


Figure 2: Frequency of maximum height (cm) values for species that occur at our old-field site (N=58). Vertical lines mark the cutoff points for each of the small species definitions: species below the first quartile ('1st quartile'; dashed light blue, N=15, <53.25 cm), and species below the median height ('median', dotted light red, N=29, <83 cm).

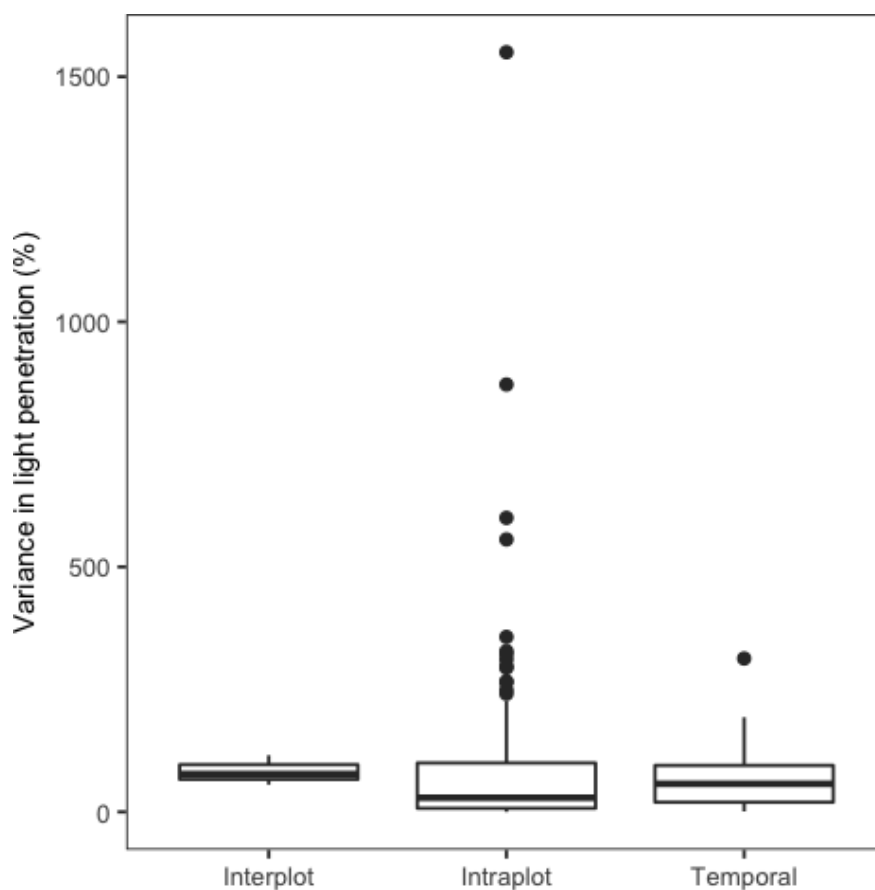


Figure 3: Interplot, intraplot, and temporally driven variance in light penetration (calculated as $100 \times$ ground-level light intensity/above canopy light intensity; $\mu\text{mol s}^{-1}\text{m}^{-2}$). To quantify intraplot variation, variance was calculated within each plot for each month ($N=147$, median=26.2). For interplot variation, mean light penetration was calculated for each plot, and variance in these means was calculated for each month ($N=3$, median=77.3). Temporal variation was also quantified using mean light penetration for each plot. Variance in individual plot means across months (June, July, August) were calculated ($N=49$, median=57.4). Boxes represent the 25th to 75th percentiles of the data, and whiskers represent the 10th and 90th percentiles.

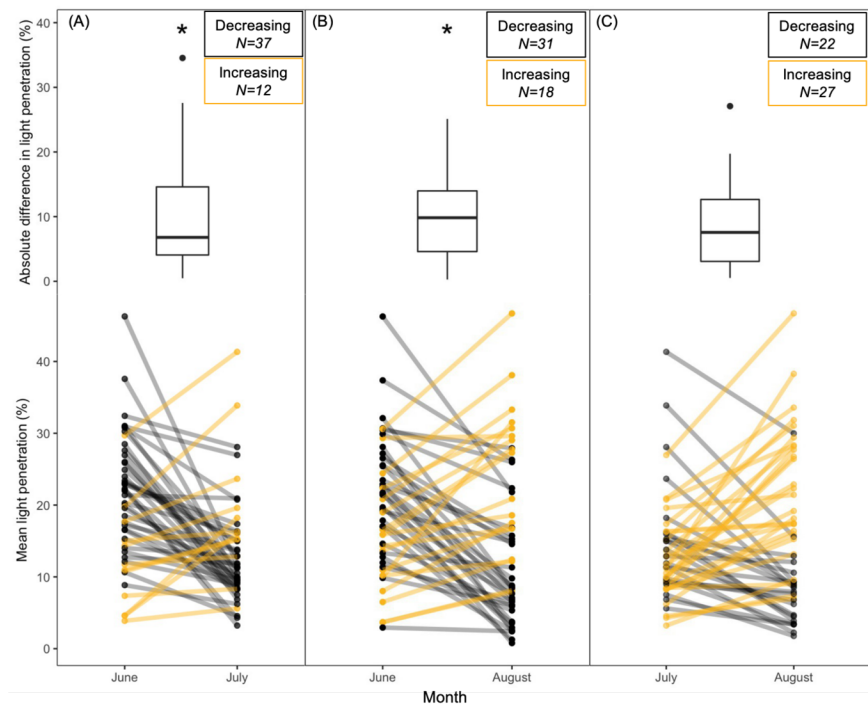


Figure 4: Comparisons of light penetration (%) between June and July (A), June and August (B), and July and August (C). Boxplots show absolute differences in light penetration within each plot between month pairings. Line plots show change in mean light penetration for each plot between month pairings. Mean light penetration at the plot level was significantly different between months (repeated measures ANOVA, $F_{2,96}=9.2$, $P < 0.001$). Mean light penetration in June was significantly higher than in July (Bonferroni, $P_{\text{adj}} < 0.001$) and August (Bonferroni, $P_{\text{adj}} = 0.036$). July and August did not significantly differ (Bonferroni, $P_{\text{adj}} = 0.4$). Between June and July, 37 plots decreased in light penetration while 12 plots increased. Between June and August, 31 plots decreased in light penetration, while 18 plots increased. Between July and August, 22 plots decreased in light penetration while 27 plots increased. Boxes represent the 25th to 75th percentiles of the data, and whiskers represent the 10th and 90th percentiles. Lines coloured in black represent plots that decreased in light penetration from the first to the second month, and lines coloured in goldenrod represent plots that increased in light penetration from the first to the second month. Month pairings marked by an asterisk (*) significantly differed in mean light penetration.

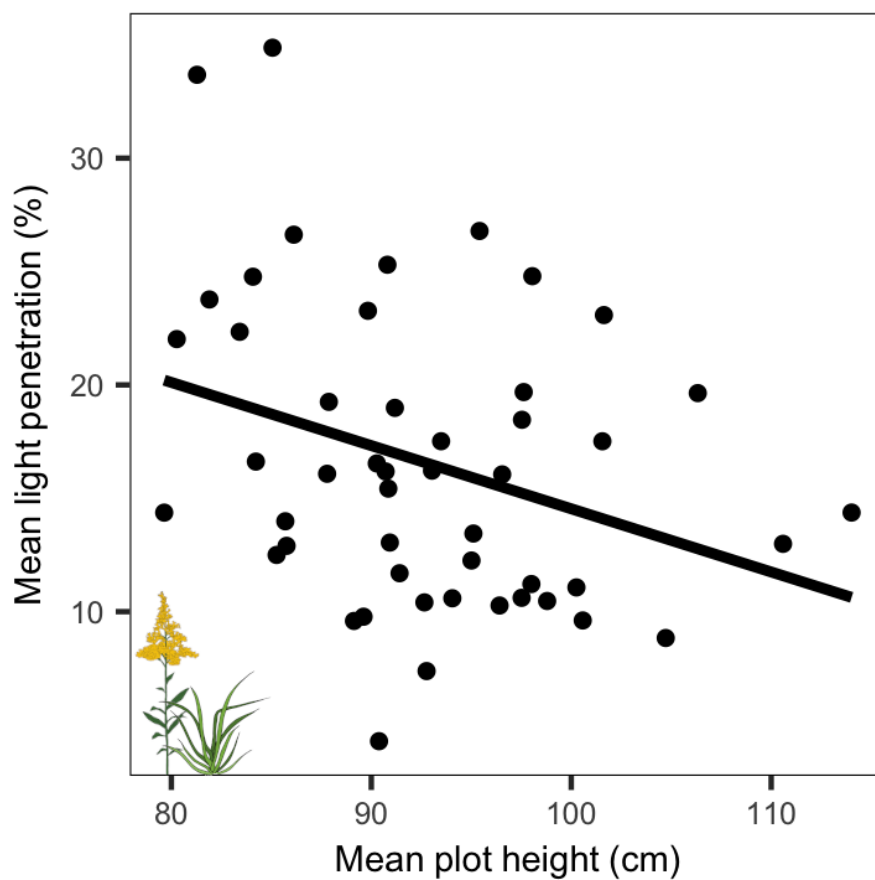


Figure 5: Mean plot-level maximum height weighted by species plot-level abundance (‘mean plot height’, cm) vs. mean light penetration (%) per plot. Mean light penetration significantly declined with mean plot height ($P = 0.025$, $R^2 = 0.08$).

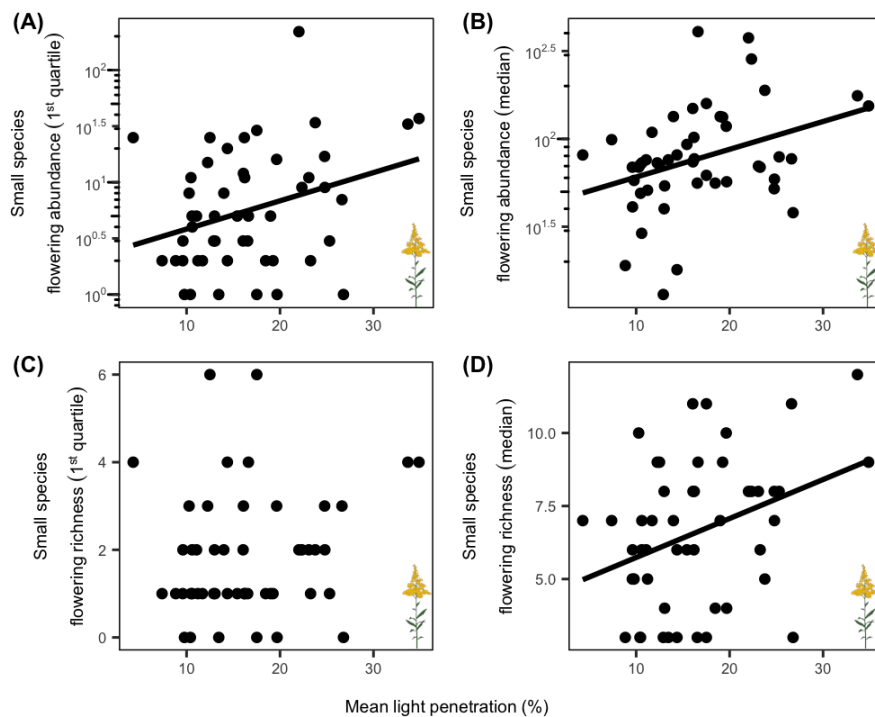


Figure 6: Flowering abundance of small species under the first quartile height ('1st quartile'; A), flowering abundance of small species under the median height ('median', B), flowering richness of '1st quartile' small species (C) and flowering richness of 'median' small species (D) vs. mean light penetration (%) per plot. We used log₁₀ transformations on '1st quartile' and 'median' small species flowering abundance and fit all with linear models. Flowering '1st quartile' small species (A; $P = 0.027$, $R^2 = 0.08$), flowering 'median' small species (B; $P = 0.012$, $R^2 = 0.11$) as well as richness of flowering 'median' small species (D; $P = 0.014$, $R^2 = 0.10$) significantly declined as mean light penetration decreased. Flowering '1st quartile' species richness was not significantly affected by light penetration (C).

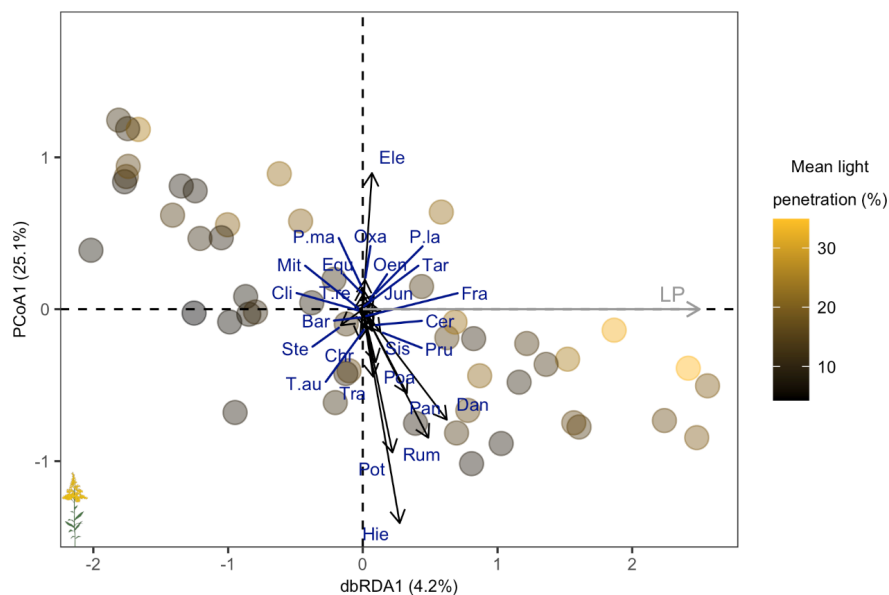


Figure 7: Distance-based redundancy analysis (dbRDA) ordination for composition of flowering species smaller than the median height ('median', $N = 26$, $<83\text{cm}$) with mean light penetration as a constrained axis. Light penetration ('LP', grey arrow) explained 4.2% of the total variation in 'median' species flowering abundance among plots (dbRDA1, $P = 0.031$, pseudo- $F_{1,49}=2.06$). Each point represents a plot. Species abbreviations are as follows: Bar *Barbarea vulgaris* ; Cer *Cerastium fontanum* ; Chr *Chrysanthemum leucanthemum* ; Cli *Clinopodium vulgare* ; Dan *Danthonia spicata* ; Ele *Eleocharis compressa* ; Equ *Equisetum arvense* ; Fra *Fragaria virginiana* ; Hie *Hieracium aurantiacum* ; Jun *Juncus tenuis* ; Mit *Mitchella repens* ; Oen *Oenothera perennis* ; Oxa *Oxalis stricta* ; Pan *Panicum capillare* ; P.la *Plantago lanceolata* ; P.ma *Plantago major* ; Poa *Poa pratensis* ; Pot *Potentilla recta* ; Pru *Prunella vulgaris* ; Rum *Rumex acetosella* ; Sis *Sisyrinchium montanum* ; Ste *Stellaria graminea* ; Tar *Taraxacum officinale* ; Tra *Tragopogon pratensis* ; T.au *Trifolium aureum* ; T.re *Trifolium repens* .