

The Effect of Reduced Light Intensity on Grass Weeds

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The effect of reduced light intensity on the growth and development of three common grass weeds, blackgrass, silky windgrass, and annual bluegrass, was studied. Two identical greenhouse experiments displaced in time were performed with six light levels aiming at 0%, 20%, 50%, 80%, 90%, and 95% shade corresponding to a mean daily light integral (DLI) of 12.4, 9.63, 7.13, 2.74, 0.95, and 0.69 mol m⁻² d⁻¹ in experiment 1 and 21.2, 18.0, 10.7, 3.71, 1.64, 1.20 mol m⁻² d⁻¹ in experiment 2. Climate screens of acrylic fabric were used to create the light levels. A DLI of 0.69 to 3.71 mol m⁻² d⁻¹ substantially reduced the plant height, the number of leaves, leaf chlorophyll content index, stomatal conductance, maximum photochemical efficiency of photosystem II, and dry matter of blackgrass. It also reduced plant height, the number of leaves, and dry matter and delayed flowering of windgrass and annual bluegrass. Annual bluegrass reacted most rapidly when light levels increased from the lowest levels by producing more leaves. DLI thresholds for blooming were estimated to be about 7.13 mol m⁻² d⁻¹ for windgrass and 1.64 mol m⁻² d⁻¹ for annual bluegrass. Annual bluegrass was able to bloom and sustain biomass even at a DLI of 1.64 mol m⁻² d⁻¹. This ability may contribute to an explanation of why annual bluegrass is among the most common weed species in highly competitive and well-fertilized crops even though it is much smaller than the two other grass species.

Nomenclature: Blackgrass, *Alopecurus myosuroides* Huds.; silky windgrass, *Apera spica-venti* (L.) Beauv.; annual bluegrass, *Poa annua* L.

Key words: Competition for light, floral diversity, phenology, physiology, shade.

Many factors affect the germination, growth, physiology, phenology, and development of plants (Yasin and Andreasen 2016). Light is a major limiting factor for plant growth, development, and biomass production (Guglielmini and Satorre 2002).

When solar radiation penetrates a canopy, it is selectively attenuated by scattering and absorption, resulting in changes in both quantity and quality of the radiation within the canopy. The solar radiation, which provides energy for the photosynthesis, will be reduced (light quantity). Wavelengths in the range of 400 to 700 nm, including red (R) light, are efficiently absorbed by chlorophyll, while far-red (FR) wavelengths (>700 nm) will be mostly reflected. Consequently, the R:FR ratio will decrease in a canopy from the 1.0 to 1.2 found in sunlight. This decline affects the photo-equilibrium of the photo-receptor phytochrome (Holmes and Smith 1977).

The phytochrome system regulates essential plant responses like induction of flowering, chloroplast development, leaf senescence, and leaf abscission (Gundel et al. 2014). In addition to this, the spectral energy distribution below a canopy is also dependent on solar elevation and sky condition but also on the age, height, leaf area index, and chlorophyll content of the crop (Holmes and Smith 1977).

Light is vital for photosynthesis and has a significant role in the competition between weeds and crops (Santos et al. 1997). Plants are exposed to varying light levels during their life spans (Valladares and Niinemets 2008). The shading ability of the crops can be used as a tool to suppress weeds, for example, by increasing crop density (Weiner et al. 2001) and by choosing tall cultivars (Garrity et al. 1992). Reduction in light quantity and quality affects spatial growth, biomass, and seed production of weeds. For instance, a quantitative light reduction of 40%, 68%, and 99% reduced the emergence, growth, biomass, and seed production of common waterhemp (*Amaranthus rudis* Sauer) (Steckel et al. 2003). The shading effect of crops can be used as a powerful tool in an integrated weed management strategy, especially against weed species that are smaller than the crop.

Weeds differ in their photosynthetic efficiency and shade tolerance. Some weed species overcome

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the adverse effect of low light by increasing their height and shoot–root partitioning (Caton et al. 1997) and by increasing their leaf area in proportion to their total plant tissue (Patterson 1979). Weeds have different levels of inherited low-light tolerance. Plant species with limited light avoidance can diminish the consequence of reduced photosynthetic active photon flux density (PPFD) by enhancing the photosynthetic rate per unit leaf area at low PPFD (Fischer et al. 2000). Plants can also reduce energy consumption via dark respiration (Regnier et al. 1988) and increase the leaf area in proportion to the total plant tissue (Patterson 1979). For example, Palmer amaranth (*Amaranthus palmeri* S. Wats.) had the ability to acclimate to 87% light reduction compared with sunlight ($1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$) in South Carolina, and texasweed [*Caperonia palustris* (L.) St. Hil.] was able to reproduce at 90% light reduction in Mississippi (Godara et al. 2012; Jha et al. 2008).

The knowledge of the response of weeds to low light intensities can be used in weed management strategies and in ecological and ecophysiological models to understand and describe competition between crops and weeds (Godara et al. 2012).

Depicting the phenological and physiological changes of weeds to low light intensities can deliver valuable information for developing mechanistic models of crop–weed competition and weed population dynamics (Brainard et al. 2005). For instance, modeling and meta-analysis explained why C_4 grasses are almost absent in low-light habitats. A biochemical model has been used to inspect the implications of interveinal distance (IVD) in leaves of C_4 grasses for low-light tolerance. This model predicted that low IVD values indicate species' ability to tolerate prolonged low light (Ogle 2003).

The objective was to study the reaction of three widespread and common grass weed species, blackgrass, silky windgrass, and annual bluegrass, to reduced intensities of light. By shading the plants, we reduced the PPFD without affecting the light quality to investigate the effect on growth and selected physiological parameters. These weeds are considered to be the most yield-reducing species in autumn-sown crops in Europe. They constitute an increasing problem to growers of winter wheat (*Triticum aestivum* L.), winter barley (*Hordeum vulgare* L.), and winter rye (*Secale cereale* L.) due to the increased area of autumn-sown cereals and the widespread occurrence of herbicide-resistant biotypes (Andreasen and Streibig 2011; Andreasen and Stryhn 2008, 2012; Jensen and Kristensen 2013; Weber and Gut 2005).

All species can germinate before and after these crops have been sown and established (Schermer 2017). While blackgrass and silky windgrass become tall plants, annual bluegrass plants are usually small. Annual bluegrass is, however, the most common weed in Denmark. Hence, we hypothesized that annual bluegrass has a better ability to adapt to low PPFD than the two tall weeds and that shading would be less efficient as a tool to control annual bluegrass than the other two weeds.

We examined their growth and development, focusing on morphology and leaf physiology in response to six light intensities in two experiments to compare their ability to grow at low light intensities.

Materials and Methods

Experimental Procedure. We conducted a greenhouse experiment and repeated it in time (experiments 1 and 2) at the Taastrup Campus of the University of Copenhagen, Denmark (55.63°N, 12.28°E). We studied three common grass weed species: blackgrass, silky windgrass, and annual bluegrass. For each species and each treatment, 10 plastic pots (SMV, SOPARCO, Conde-sur-Huisne, France) of 4-L volume, 16-cm height, and 20-cm diameter were used and filled with the rooting medium Pindstrup mixture 2 sphagnum soil (Pindstrup Mosebrug A/S, Ryomgaard, Denmark). The base was blond peat (pH 6.0) with a dry matter content of 55 to 75 g L⁻¹ with clay granulate (40 kg m⁻³); electrical conductivity was 4 S/m. We thoroughly irrigated the pots before planting 10 seeds pot⁻¹. Three uniform-sized plants were retained per pot after thinning 11 d after sowing (DAS). When the weed species were at the 2-leaf stage (16 DAS), plants were thinned to 1 plant pot⁻¹ to obtain plants of standard size at the beginning of each experiment. When the plants were at the 2- to 3-leaf stage (18 DAS), 10 pots of each species were transferred into each level of light treatment. We used this procedure to ensure we had enough well-established plants at the same growth stage to complete the experiment. We considered plants in one pot as one replicate of treatment for each growth and harvest measurement. The experiments were randomized with 10 replications for each treatment. There were six treatments: culture in full light (control) and five lower-light intensities. We attained these conditions by constructing square tents (flat roof and side walls) of climate screen material and nonwoven acrylic fabric (Table 1) hanging over horizontal wires 120 cm above the long

Table 1. Details of shade insulation climate screens used to develop percent light-reduction levels for experiments 1 and 2.

% Light reduction	Climate screens used to develop % light reduction
0	No shade (control)
20	Single sheet used: clear prototype, manufactured by SVENSSON, AB Ludvig Svensson, Bangatan 8, 511 82 Kinna, Sweden
50	Double sheet used: one (SLS 30 Harmony) and one (clear woven), both manufactured by SVENSSON, AB Ludvig Svensson, Kinna, Sweden
80	Single sheet used: Superflor 250, manufactured by FIBERTEX Nonwovens, Aalborg, Denmark
90	Double sheet used: one (Superflor 250) manufactured by FIBERTEX Nonwovens, Aalborg, Denmark, and one (XLS 15 F FIREBREAK) manufactured by SVENSSON, AB Ludvig Svensson, Kinna, Sweden
95	Double sheet used: one (Superflor 250) manufactured by FIBERTEX Nonwovens, Svendborgvej 16, 9220 Aalborg, Denmark, and one (XLS 17 F FIREBREAK) manufactured by SVENSSON, AB Ludvig Svensson, Kinna, Sweden

edges of six greenhouse tables. The target low-light levels were 0%, 20%, 50%, 80%, 90%, and 95% light reduction in the greenhouse (Table 2). The PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) inside the tents was measured and related to the control (no shade) by percentage using a quantum sensor (LI-250 portable, LI-COR, Lincoln, NE).

We measured the light transmissions of the shade screen materials in three positions per screen by mounting them for transmission measurements in a light-integrating sphere (RTS-3Z Zenith RTS, ASD, Boulder, CO) connected to an AvaSpec-2048 spectrometer (Avantes, Apeldoorn, Netherlands).

The transmission in the 655- to 665-nm (R) and 725- to 735-nm (FR) regions were determined to investigate whether the screen material had any effect on the R:FR ratio of the light.

Plants were grown using a 16-h photoperiod under 400-W high-pressure sodium lamps (Master SON-T APIA Hg-free 400W E40, Philips, Eindhoven, Netherlands) as the supplementary light of a PPF of $281 \mu\text{mol m}^{-2} \text{s}^{-1}$ when the natural irradiance was below $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the control treatment. The average day and night temperatures were 15 C and 13 C, respectively. Pots were drip irrigated to ensure that water never became a limiting growth factor. We controlled aphids and mites biologically with blue and yellow pheromone cards (Borregaard BioPlant, Aarhus, Denmark).

The climate was monitored every minute by an air-temperature and humidity sensor (AT Delta-T RHT2nl-1158, Delta-T Devices, Cambridge, UK) and a quantum sensor (Apogee Instruments, Logan, UT) connected to a data logger (AT Delta-T GPI, Delta-T Devices, Cambridge, UK). We placed one logger with sensors permanently on the control table and a second was moved weekly between the low-light treatments. The data were used to calculate the average reduction of light for the individual treatments, and we calculated the daily light integral (DLI) or light sum ($\text{mol m}^{-2} \text{d}^{-1}$) in all treatments (Figure 1) based on the control measurements and percent reduced light in other treatments.

Phenological Variables. The growth of every plant was monitored until harvest. We counted the number of leaves per plant and measured plant height from the base of the plant to the highest point on the main stem 28 DAS. We recorded the number of days from sowing until the first flower was observed.

Table 2. Detail of actual percent light-reduction levels obtained in experiments 1 and 2 corresponding to targeted light-reduction levels of 0%, 30%, 50%, 80%, 90%, and 95% reduction of light in the greenhouse.^a

DLI ($\text{mol m}^{-2} \text{day}^{-1}$)		Fraction PPFD		Fraction of light reduction		Average % light reduction
Exp. 1	Exp.2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	
12.4	21.2	1	1	0	0	0
9.63	18	0.78	0.85	0.22	0.15	19
7.13	10.7	0.58	0.50	0.42	0.50	46
2.74	3.71	0.22	0.17	0.78	0.83	80
0.95	1.64	0.08	0.08	0.92	0.92	92
0.69	1.2	0.06	0.06	0.94	0.94	94

^a Abbreviations: DLI, daily light integral; PPFD, photosynthetic active photon flux density; Exp., experiment.

All plants were harvested individually at maturity (99 DAS for experiment 1 and 70 DAS for experiment 2), and the total aboveground dry matter biomass per plant, including stems, leaves, flowers, and seeds (mature and immature), was measured. We dried the biomass at 80 C for 48 h in a ventilated oven (TKD 150, Lytzen A/S, Soeborg, Denmark) and weighed the dry matter (ME-precision scales, Mettler Toledo A/S, Glostrup, Denmark).

Physiological Variables. Chlorophyll content index (CCI) was measured nondestructively 59 DAS with a Chlorophyll Content Meter CCM-200 (OPTI-SCIENCE, Hudson, NH) using a fully expanded leaf from each plant. Stomatal conductance (g_s) ($\text{mmol m}^{-2} \text{s}^{-1}$) was measured from the lower leaf surface of 1 leaf plant^{-1} 62 DAS by using a leaf porometer (SC-1, Decagon Devices, Pullman, WA). Chlorophyll fluorescence was measured as the maximum photochemical efficiency of photosystem II (F_v/F_m of PSII) at 67 DAS with a portable Handy-PEA Plant Efficiency Analyzer (Hansatech Instruments, Norfolk, UK) using a fully expanded leaf from each plant. CCI, g_s , and F_v/F_m were only measured using blackgrass, because the leaves of silky windgrass and annual bluegrass were too narrow to mount in the sensor heads.

Statistical Analysis. The experiment was performed as a random design with 10 replicates of each treatment. Data were analyzed using the Statistix-8 software (Statistix-8, Tallahassee, FL) to test the effect of reduced light on the growth and biomass production of the three grass weed species. The data were homogeneous and normally distributed (tested by descriptive data analysis) and are presented as the mean of 10 replicates in the graphs. We analyzed data with linear and nonlinear regression analysis using Sigma Plot v. 12.5 (Systat Software, San Jose, CA). We compared the regression coefficients using a t -test (considered significantly different if $P \leq 0.05$). The relationships between plant heights vs. DLI, the number of leaves per plant vs. DLI, CCI vs. F_v/F_m , and g_s vs. DLI were described by a logarithmic function:

$$y = a + b \ln(x) \quad [1]$$

where a is the intercept and b is the slope coefficient, respectively.

For the variable “the number of days to first flowering,” the data were fit to an exponential decay curve:

$$y = a * \exp(-b * x) \quad [2]$$

where a is the intercept and b is the slope coefficient, respectively. We used a sigmoidal function to characterize the effect of DLI on dry matter accumulation:

$$y = a / (1 + \exp(-(x - x_0) / b)) \quad [3]$$

where a is the maximum value of the dry matter per plant (g) for each plant species, x is the DLI ($\text{mol m}^{-2} \text{day}^{-1}$), x_0 represents the magnitude of DLI to reach 50%, halfway between minimal and maximal DLI values, and b is the slope coefficient.

Results and Discussion

We achieved a mean DLI of 12.4, 9.63, 7.13, 2.74, 0.95, and 0.69 $\text{mol m}^{-2} \text{d}^{-1}$ in experiment 1 and 21.2, 18.0, 10.7, 3.71, 1.64 and, 1.20 $\text{mol m}^{-2} \text{d}^{-1}$ in experiment 2 when using screens for 0%, 20%, 50%, 80%, 90%, and 95% reduction of light, respectively (Figure 1). All climate screens had $\leq 2\%$ difference in transmission between 655 to 665 nm and 725 to 735 nm, which left the R:FR ratio unaffected in all the treatments (unpublished data). In general, low light substantially affected the phenology of the grass species (Figure 2). Low light resulted in reduced dry matter, plant height, number of leaves, CCI, g_s , and F_v/F_m in the weeds under study (Figures 2, 3, 4, 5, and 6). The relationship between plant heights and the daily light integral of all species was well described using a logarithmic function (Figures 3, 5, and 6). The height of blackgrass was almost the same at DLI 7.13 to 21.2 $\text{mol m}^{-2} \text{d}^{-1}$, which included the three highest light levels in both experiments. Plant height of blackgrass decreased significantly at DLI 3.71 $\text{mol m}^{-2} \text{d}^{-1}$ and below ($b = 4.70$ for experiment 1 and 3.10 for experiment 2) (Figure 3; Table 3). The relation between plant height and DLI followed the same curve shape for all species, but the curves were displaced from each other in the two experiments (Figures 3, 5, and 6).

The number of leaves was closely related to DLI in all species, with the regression lines more or less overlapping in the two experiments (Figures 3, 5, and 6). Annual bluegrass showed the strongest response (producing more leaves) when the light level increased from the lowest levels ($b = 2.25$ and 2.35 [Figure 6] in the two experiments in comparison to the range 1.10 to 1.73 in the other two species [Figures 3 and 5; Table 3]). We could only measure the physiological parameters F_v/F_m and CCI on blackgrass. Figure 4 shows the relationship

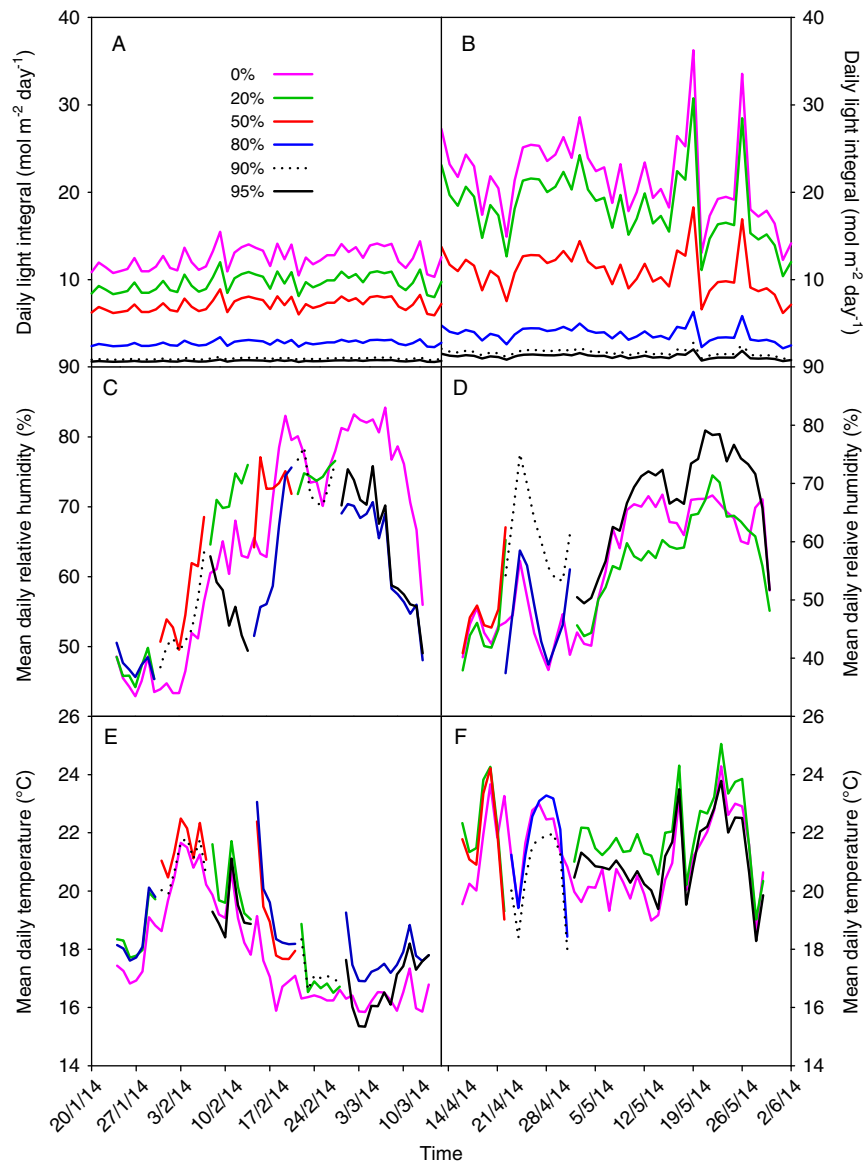


Figure 1. Daily light integral (A and B), daily mean relative humidity (C and D), and daily mean temperature (E and F) for experiment 1 (A, C, and E) and experiment 2 (B, D, and F) of 0%, 20%, 50%, 80%, 90%, and 95% reduced light levels.

between the two parameters at high, intermediate, and low DLI. At high (DLI 10.7 to 21.2 mol m⁻² d⁻¹) and intermediate (DLI 3.71 to 9.63 mol m⁻² d⁻¹) light, F_v/F_m was unaffected, even though the green pigmentation decreased with decreasing DLI. At low DLI (0.69 to 2.74 mol m⁻² d⁻¹) the leaves were paler with a low CCI, and F_v/F_m decreased (Table 3). In blackgrass, g_s was also measured and followed a logarithmic function with increasing DLI (Figure 3; Table 3), with plants exhibiting maximum g_s in full light (DLI 21.2 mol m⁻² d⁻¹) and minimum at DLI 0.69 mol m⁻² d⁻¹.

We harvested plants 99 DAS in experiment 1 and 70 DAS in experiment 2. Blackgrass was unable to flower within this time limit. We fitted an exponential decay curve (Equation 2) to describe the response of

annual bluegrass and silky windgrass to initiate first flowering at different levels of DLI (Figures 5 and 6). Flowering was just delayed for annual bluegrass at reduced light levels, while silky windgrass was unable to flower at DLI below 7.13 mol m⁻² d⁻¹. Some annual bluegrass plants were able to flower at DLI 1.64 mol m⁻² d⁻¹ (Figure 6). The windgrass plants were able to flower at DLI 7.13 mol m⁻² d⁻¹ (Figure 5). All species produced substantially lower dry matter at low DLI 0.69 to 3.71 mol m⁻² d⁻¹ than at higher DLI 7.13 to 21.2 mol m⁻² d⁻¹ in both experiments (Figures 3, 5, and 6; Table 3).

When solar radiation penetrates a plant canopy, the R:FR ratio changes and affects signaling for seed germination and elongation growth. Our focus was not on seed germination, because seeds of these weed

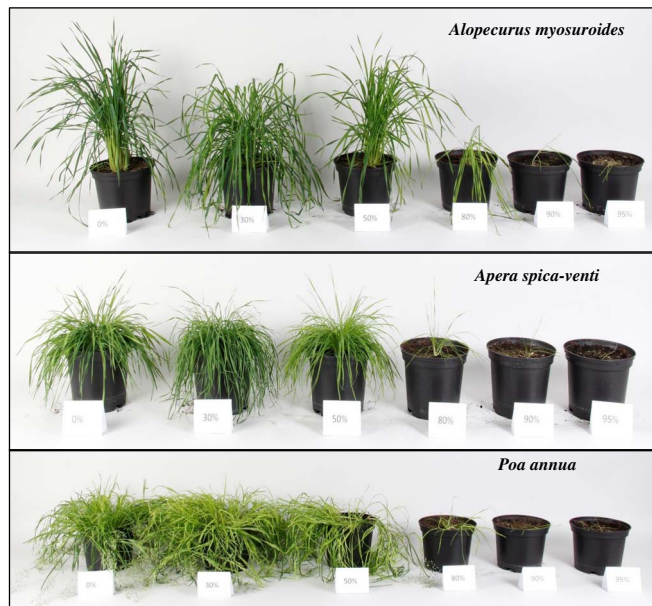


Figure 2. Image showing the effect of light reduction (0%, 20%, 50%, 80%, 90%, and 95%) on plant size and morphology of blackgrass (*Alopecurus myosuroides*), silky windgrass (*Apera spica-venti*), and annual bluegrass (*Poa annua*) (plants from experiment 1). The light-reduction levels resulted in daily light integrals of 12.4, 9.63, 7.13, 2.74, 0.94, and 0.69 mol m⁻² d⁻¹.

species can germinate before and after autumn-sown crops have been established (Schermer 2017) when the R:FR ratio is still high. Plants are affected by the decreasing R:FR under a canopy and often react by increased elongation growth and reduced branching (Gundel et al. 2014). However, it is not realistic in a greenhouse experiment to simulate the combination of decreasing light level with a decrease in R:FR that corresponds to that shade level in a canopy. We therefore decided to focus on biomass production alone by decreasing the absolute light level to create different DLIs for the different treatments. The light quality (R:FR) was not significantly affected by the climate screens. This means that the effect on plant height that is found in these shade experiments should be considered as a minimum effect on plant height, since any additional decrease of the R:FR ratio would further enhance the elongation growth (Gundel et al. 2014). As mentioned earlier, other physiological factors are also affected by the light quality, and our experiments therefore do not reflect field conditions completely, although they give a good indication of the effect of reduced light quantity. Field experiments would be valuable to improve the understanding of the importance of light quality for the development of the plant species.

The three species showed some common responses to reduced light intensities. In general,

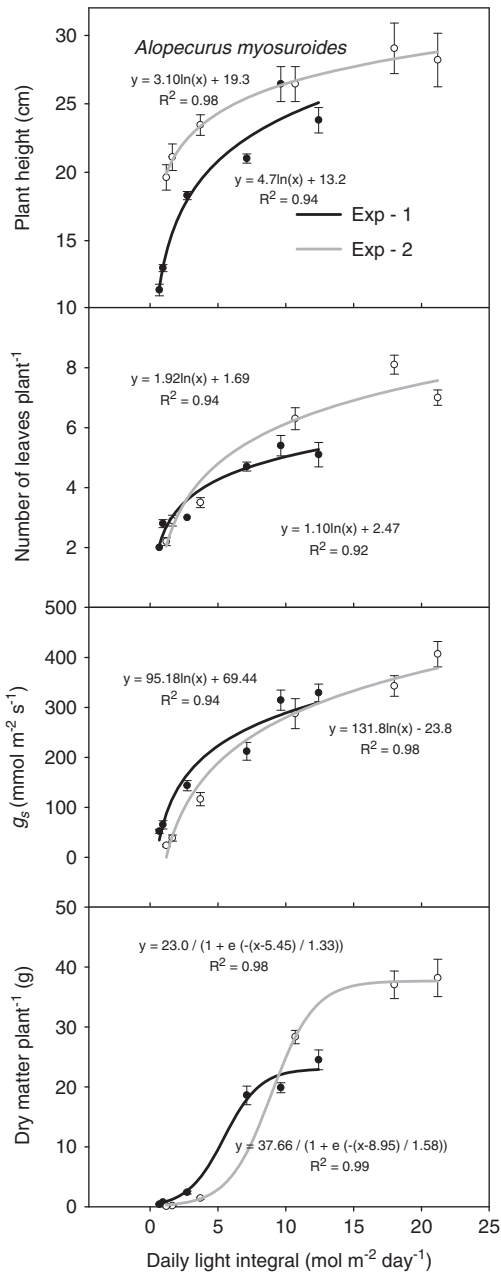


Figure 3. The relation between plant height, number of leaves plant per plant, stomatal conductance (g_s), and dry matter per plant for blackgrass regressed under six reduced light levels of 0%, 20%, 50%, 80%, 90%, and 95%, which correspond to daily light integrals of 12.4, 9.63, 7.13, 2.74, 0.94, and 0.69 mol m⁻² d⁻¹ for experiment 1 (closed symbols) and 21.2, 18.0, 10.7, 3.71, 1.64, and 1.20 mol m⁻² d⁻¹ for experiment 2 (open symbols), respectively. The data show mean values of $n = 10 \pm SE$.

they produced less biomass, but they differed from each other in their ability to produce flowers and leaves. Blackgrass did not flower at all, probably due to lack of vernalization, and silky windgrass needed a higher DLI than annual bluegrass before it was able to flower. Annual bluegrass is a relatively small plant compared with the other two species and is able to

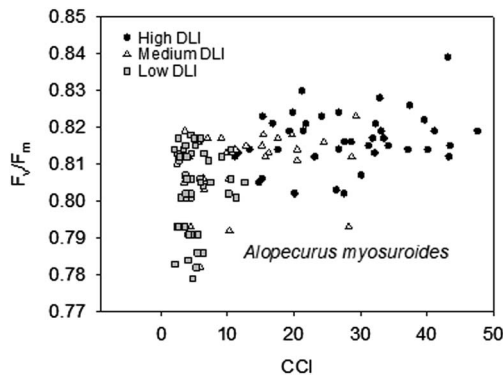


Figure 4. The relation between maximum photochemical efficiency (F_v/F_m) and chlorophyll content index (CCI) for blackgrass (*Alopecurus myosuroides*) regressed under six reduced light levels of 0%, 20%, 50%, 80%, 90%, and 95%, which correspond to daily light integrals (DLIs) of 12.4, 9.63, 7.13, 2.74, 0.94, and 0.69 $\text{mol m}^{-2} \text{d}^{-1}$ for experiment 1 and 21.2, 18.0, 10.7, 3.71, 1.64, and 1.20 $\text{mol m}^{-2} \text{d}^{-1}$ for experiment 2, respectively. The data show mean values of $n = 10 \pm \text{SE}$. The symbols represent high DLI (10 to 21 $\text{mol m}^{-2} \text{d}^{-1}$, filled circles), intermediate DLI (3 to 9 $\text{mol m}^{-2} \text{d}^{-1}$, open triangles), and low DLI (0.69 to 2 $\text{mol m}^{-2} \text{d}^{-1}$, filled squares) with pooled data from the two experiments.

produce many generations during a year (Warwick 1979). Seeds were not counted, but seed production was observed at the lowest DLIs for annual bluegrass. This weed's ability to produce flowers and seeds in low light intensities and to rapidly increase its number of leaves even if light intensity only increases a little helps to explain why it is among the most common weeds.

The mathematical models described the relation between DLI and growth responses of the three species well. In most cases, number of leaves per plant, CCI, g_s , and dry matter of blackgrass and the number of leaves and dry matter of silky windgrass and annual bluegrass showed overlap between the two experiments, indicating that light intensity has a strong influence on these parameters. Plant height showed the least uniformity between the two experiments for the three species.

Our study showed that the g_s of blackgrass was significantly affected by the reduction of DLI from 18 to 0.69 $\text{mol m}^{-2} \text{d}^{-1}$ in both experiments. Unfortunately, only blackgrass had leaves wide enough to be measured with the porometer, but here the g_s dropped from 390 $\text{mmol m}^{-2} \text{d}^{-1}$ at high DLI to 40 $\text{mmol m}^{-2} \text{d}^{-1}$ at reduced light conditions (Figure 3). When plants are well watered, light is the most important factor for regulation of stomatal opening, even though other environmental factors such as low air humidity or high CO_2 concentration may counteract a light signal to increase g_s (Merilo et al. 2014).

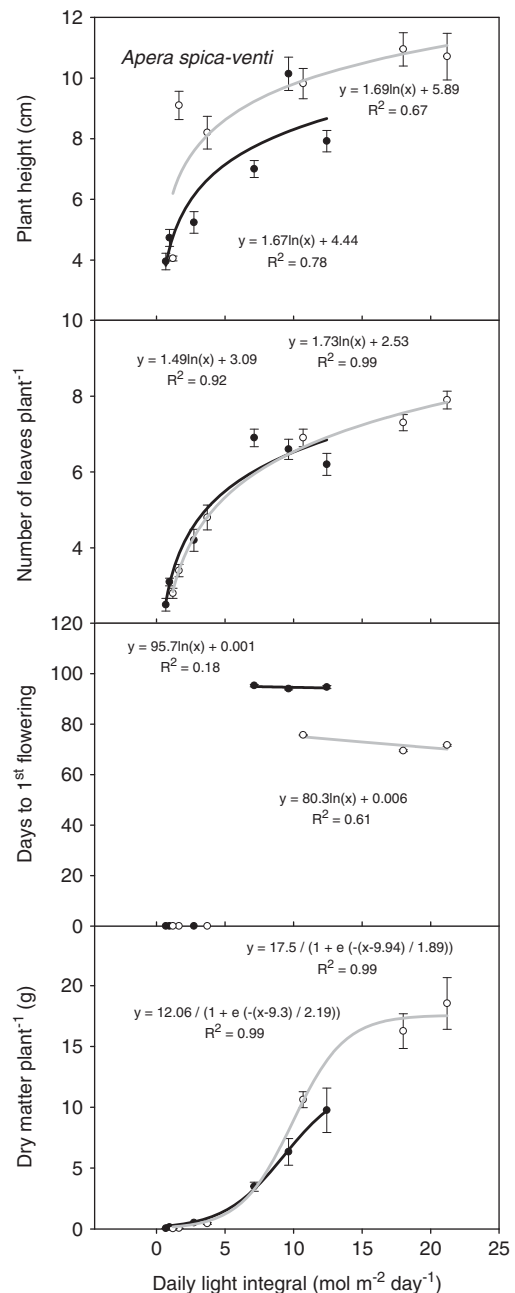


Figure 5. The relation between plant height, number of leaves plant per plant, number of days to first flowering, and dry matter plant per plant of silky windgrass (*Apera spica-venti*) regressed on six light levels, as in Figure 3.

In general, g_s is regulated to accommodate the need for CO_2 for photosynthesis, and even when plants have the same potential for photosynthesis through equal light acclimation, a stress-induced decrease in photosynthesis will be followed by a decrease in g_s (Sharma et al. 2015).

Since our data for blackgrass is based on g_s , they do not allow precise comparisons of carbon gain of adjacent light treatments, but the lowest light treatments showed a drastic drop in g_s , which indicated

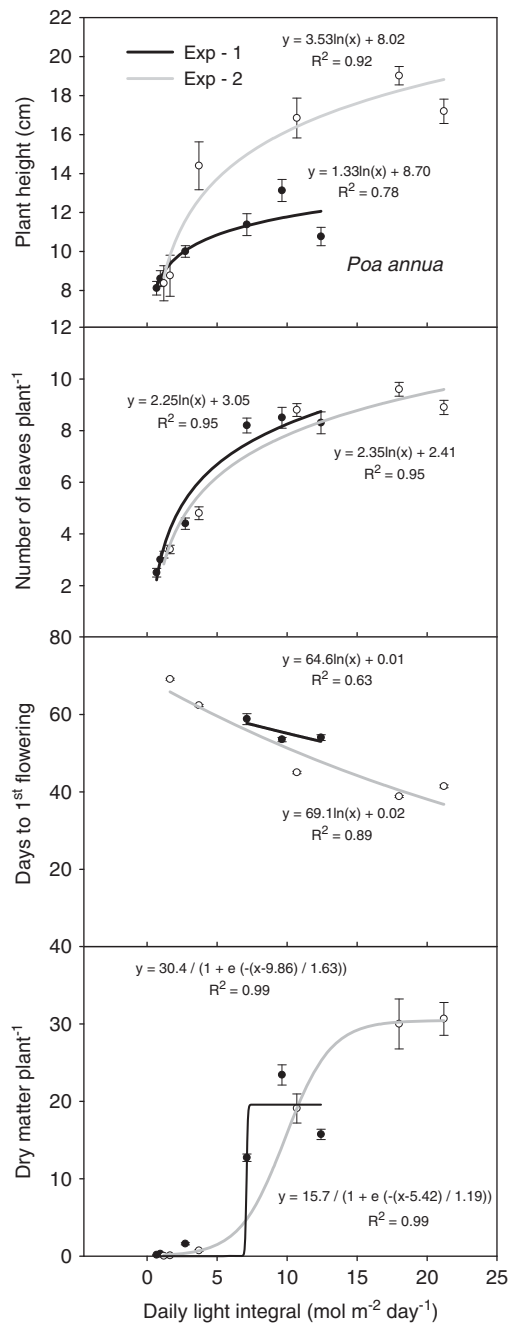


Figure 6. The relation between plant height, number of leaves plant per plant, days to first flowering, and dry matter plant per plant of annual bluegrass (*Poa annua*) regressed on six light levels, as in Figure 3.

that those treatments had a considerably lower carbon gain in situ compared with the high light treatments, which was as expected. We also found that a light reduction of more than 50% ($\text{DLI} \leq 10.7 \text{ mol m}^{-2} \text{ d}^{-1}$) significantly reduced g_s per unit leaf area of blackgrass, which is in concordance with Merilo et al. (2014), who studied the response of wheat, barley, saltwater cress [*Thellungiella salsuginea* (Pall.) O. E. Schulz], cultivated tobacco (*Nicotiana tabacum* L.), and common rockrose [*Helianthemum nummularium*

(L.) Mill.] and found that when the light intensity decreased from 150 to $0 \mu\text{mol m}^{-2} \text{ s}^{-1}$, the g_s dropped along a gradient for these species.

The air humidity and temperature also affect g_s through their effects on the leaf-to-air vapor pressure deficit (Merilo et al. 2014). Due to limited numbers of humidity and temperature sensors and data loggers, we could not measure humidity and temperature every day in all the treatments, but except for the control, the sensors were moved between treatments at regular intervals (Figure 1). Except for a couple of days in mid-February, the mean daily temperature was kept with ca. 2 C difference between the treatments and relative humidity within 15%. Even though the tents were open along the edge of the table the air circulation in the tents was slightly restricted, and the mean daily temperature was ca. 1 C lower in the control than in the shade treatments. However, on most days, the air humidity in the control was within the same range as in the shade treatments. Because the order of the treatments is mixed within each experiment, we do believe that the light effect dominates as affecting the g_s .

We did not measure humidity and temperature every day during the experiment for all treatments, but Figure 1 shows that the mean daily temperature did not vary significantly between treatments. However, the variation in mean daily relative humidity seemed to vary, especially between control and a light intensity reduction of 95%. Although water was not a limiting factor in these experiments, this variation in relative humidity may have influenced stomatal conductance. We would expect a higher relative humidity in a dense crop (corresponding to the experiment at 95% shading).

We have described the relationship between F_v/F_m and CCI at different DLIs by dividing data from the two experiments into three groups: low (0.69 to $2.74 \text{ mol m}^{-2} \text{ d}^{-1}$), medium (3.71 to $9.63 \text{ mol m}^{-2} \text{ d}^{-1}$), and high (10.7 to $21.2 \text{ mol m}^{-2} \text{ d}^{-1}$) DLI. This enabled us to make a realistic estimation of leaf senescence. At high and intermediate DLI, the plants could maintain a high F_v/F_m despite a clear variation in pigmentation measured as CCI. At low DLI, however, the uniformly low CCI was accompanied by a wider range of F_v/F_m , with many of the palest leaves showing a clear drop in F_v/F_m . Normally F_v/F_m is lowest in high light treatments, since those plants are most easily photoinhibited (Barth et al. 2001; Li et al. 2010). In our case, the opposite was found. Because the reduced maximum photochemical efficiency of PSII in blackgrass was found in the palest leaves, we interpreted this as a sign of senescence. Plants in the lowest DLI treatment were lacking light and deteriorated. This is in

Table 3. Summary of regression equations of growth and physiological parameters for blackgrass, silky windgrass, and annual bluegrass under varying levels of daily light integral in two independent repeated experiments.^{a,b}

Variables	Exp.	Equation parameters	Blackgrass, estimates (SE)	Silky windgrass, estimates (SE)	Annual bluegrass, estimates (SE)
Plant height (cm)	1	<i>a</i>	13.2 (0.97)**	4.44 (0.71)**	8.70 (0.57)**
		<i>b</i>	4.70 (0.58)**	1.67 (0.43)**	1.33 (0.34)**
		R ²	0.94	0.78	0.78
	2	<i>a</i>	19.3 (0.39)**	5.89 (1.19)**	8.02 (1.02)**
		<i>b</i>	3.10 (0.19)**	1.69 (0.58)*	3.53 (0.49)**
		R ²	0.98	0.67	0.92
Number of leaves plant ⁻¹	1	<i>a</i>	2.47 (0.25)**	3.09 (0.35)**	3.05 (0.40)**
		<i>b</i>	1.10 (0.15)**	1.49 (0.21)**	2.25 (0.24)**
		R ²	0.92	0.92	0.95
	2	<i>a</i>	1.69 (0.47)*	2.53 (0.13)**	2.41 (0.51)**
		<i>b</i>	1.92 (0.23)**	1.73 (0.06)**	2.35 (0.25)**
		R ²	0.94	0.99	0.95
Days to first flowering	1	<i>a</i>	—	95.7 (2.23)**	64.6 (7.65)ns
		<i>b</i>	—	0.001 (0.002)ns	0.01 (0.01)ns
		R ²	—	0.18	0.63
	2	<i>a</i>	—	80.3 (6.81)*	69.1 (4.74)**
		<i>b</i>	—	0.006 (0.005)ns	0.02 (0.00)**
		R ²	—	0.61	0.89
g _s (mmol m ⁻² s ⁻¹)	1	<i>a</i>	69.44 (19.20)*	—	—
		<i>b</i>	95.18 (11.58)**	—	—
		R ²	0.94	—	—
	2	<i>a</i>	-23.84 (19.05)ns	—	—
		<i>b</i>	131.82 (9.28)**	—	—
		R ²	0.98	—	—
Dry matter plant ⁻¹ (g)	1	<i>a</i>	23.00 (1.43)**	12.06 (0.85)**	15.76 (0.14)
		<i>b</i>	1.33 (0.30)*	2.19 (0.21)**	1.19 (0.03)
		X ₀	5.45 (0.55)**	9.30 (0.40)**	5.42 (0.07)
		R ²	0.98	0.99	0.99
	2	<i>a</i>	37.66 (0.33)**	17.57 (0.66)**	30.43 (0.16)**
		<i>b</i>	1.58 (0.12)**	1.89 (0.62)*	1.63 (0.11)**
		X ₀	8.95 (0.15)**	9.94 (0.44)**	9.86 (0.07)**
		R ²	0.99	0.99	0.99
CCI vs. F _v /F _m		<i>a</i>	0.006 (0.001)**	—	—
		<i>b</i>	0.79 (0.002)**	—	—
		R ²	0.25	—	—

^a Estimates for equation parameters are based on the regression with SE in parentheses. It included equation parameters, *y*-intercept (*a*), slope coefficient (*b*), and coefficient of determination (R²) for logarithmic and exponential-decay curves. For sigmoid curves, equation parameters are: maximum slope or upper limit (*a*), slope at inflection (*b*), and daily light integral recorded to attain 50% dry matter (X₀) = EC₅₀, and coefficient of determination (R²).

^b Abbreviations: Exp., experiment; g_s, stomatal conductance; CCI, chlorophyll content index; F_v/F_m, maximum photochemical efficiency of photosystem II.

*Significant: P ≤ 0.05; **highly significant: P ≤ 0.01; ns, nonsignificant: P > 0.05.

line with the findings of DeEll and Toivonen (1999), who described the correlation between loss of hue in broccoli (*Brassica oleracea* L. var. botrytis L.) as it became paler and, consequently, F_v/F_m decreased as the senescence progressed.

Like blackgrass, silky windgrass is a widespread and aggressive winter annual weed species, especially in winter cereals (Andreasen and Stryhn 2012; Weber and Gut 2005). Silky windgrass showed stunted plants with significantly fewer leaves and less dry matter when exposed to reduced DLI (0.69 to

3.71 mol m⁻² d⁻¹) in both experiments. Silky windgrass did not flower at DLI < 7.13 mol m⁻² d⁻¹ until 99 DAS in experiment 1 and 70 DAS in experiment 2. A similar decline in plant growth and reduction in dry matter caused by light reduction has been reported by Patterson (1980).

Annual bluegrass is native to Europe (Warwick 1979) and is a common weed in many summer and winter annual cereal crops (Andreasen and Streibig 2011; Jensen and Kristensen 2013). Annual bluegrass responded to the adverse effect of low light

with a combination of morphological and physiological reactions. Plants did not increase growth but were able to maintain growth, biomass, and number of leaves at reduced DLI (1.64 to 2.74 mol m⁻² d⁻¹). Burian and Winter (1976) found that photosynthetic efficiency of annual bluegrass in response to short daylight conditions resulted in reduced net dry matter production, photosynthetic rates, and lower chlorophyll *a* and *b* content. DLI ≤ 1.20 mol m⁻² d⁻¹ hardly enabled annual bluegrass to grow and flower. Benvenuti et al. (1994) also found that light reduction delayed flowering of the weeds velvetleaf (*Abutilon theophrasti* Medik.), jimsonweed (*Datura stramonium* L.), and johnsongrass [*Sorghum halepense* (L.) Pers.].

The smallest variation between the two experiments was found for the number of leaves per plant in the three species. Therefore, it can be suspected that other climate parameters than light affect plant height and total dry weight, whereas the number of leaves seems more strictly light regulated.

The DLI reaches approximately 68 mol m⁻² d⁻¹ in the field during peak summer in northern Europe at 58.37°N (Niinemets et al. 2004). The DLI from early May to early August was approximately 23% in the range of 50 to 68 mol m⁻² d⁻¹, 69% in the middle range of 20 to 50 mol m⁻² d⁻¹, and 8% in 5 to 20 mol m⁻² d⁻¹ based on 3 yr of field measurements. Ninety percent of incident light may be absorbed by a dense canopy of barley (Christensen and Goudriaan 1993). Therefore, one can expect a light level in the range of DLI 0.5 to 6.5 mol m⁻² d⁻¹ in the middle of the summer under a closed canopy of cereals like barley. In our experiments, the three lowest light treatments (DLI 0.69 to 3.71 mol m⁻² d⁻¹) corresponded to the light intensities under a closed barley canopy. Annual bluegrass is a relatively small plant, but its ability to acclimate to reduced light conditions and grow, flower, and set seeds at low light intensities makes it successful in reduced-light environments. In our experiments, annual bluegrass was able to bloom and sustain biomass even at DLI 1.64 mol m⁻² d⁻¹. This attribute of annual bluegrass may explain why it is among the most common weed species, even in highly competitive and well-fertilized cereal crops and even though it is much smaller than blackgrass and silky windgrass.

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Literature Cited

- Andreasen C, Streibig JC (2011) Evaluation of changes in weed flora in arable fields of Nordic countries—based on Danish long-term surveys. *Weed Res* 51:214–226
- Andreasen C, Stryhn H (2008) Increasing weed flora in Danish arable fields and its importance for biodiversity. *Weed Res* 48:1–9
- Andreasen C, Stryhn H (2012) Increasing weed flora in Danish beet, pea and winter barley fields. *Crop Prot* 36:11–17
- Barth C, Krause GH, Winter K (2001) Responses of photosystem I compared with photosystem II to high-light stress in tropical shade and sun leaves. *Plant Cell Environ* 24:163–176
- Benvenuti S, Macchia M, Stefani A (1994) Effects of shade on reproduction and some morphological characteristics of *Abutilon theophrasti* Medicos, *Datura stramonium* L. and *Sorghum halepense* L. Pers. *Weed Res* 34:283–288
- Brainard DC, Bellinder RR, DiTommaso A (2005) Effects of canopy shade on the morphology, phenology, and seed characteristics of Powell amaranth (*Amaranthus powellii*). *Weed Sci* 53:175–186
- Burian K, Winter C (1976) Effect of different daylength on the productivity of grasses. *Photosynthetica* 13:401–408
- Caton BP, Foin TC, Hill JE (1997) Phenotypic plasticity of *Ammannia* spp. in competition with rice. *Weed Res* 37:33–38
- Christensen S, Goudriaan J (1993) Deriving light interception and biomass from spectral reflectance ratio. *Remote Sens Environ* 43:87–95
- DeEll JR, Toivonen PMA (1999) Chlorophyll fluorescence as an indicator of physiological changes in cold-stored broccoli after transfer to room temperature. *J Food Sci* 64:501–503
- Fischer AJ, Messersmith CG, Nalewaja JD, Duysen ME (2000) Interference between spring cereals and *Kochia scoparia* related to environment and photosynthetic pathways. *Agron J* 92:173–181
- Garrity DP, Movillon M, Moody K (1992) Differential weed suppression ability in upland rice cultivars. *Agron J* 84:586–591
- Godara RK, Williams BJ, Geaghan JP (2012) Effect of shade on Texasweed (*Cyperus palustris*) emergence, growth, and reproduction. *Weed Sci* 60:593–599
- Guglielmini AC, Satorre EH (2002) Shading effects on spatial growth and biomass partitioning of *Cynodon dactylon*. *Weed Res* 42:123–134
- Gundel PE, Pierik R, Mommer L, Ballaré CL (2014) Competing neighbors: light perception and root function. *Oecologia* 176:1–10
- Holmes MG, Smith H (1977) The function of phytochrome in the natural environment. II. The influence of vegetation canopies on the spectral distribution of natural daylight. *Photochem Photobiol* 41:539–545
- Jensen PK, Kristensen K (2013) Annual grasses in crop rotations with grass seed production—a survey with special focus on *Vulpia* spp. in red fescue production. *Acta Agr Scand* 63:604–611
- Jha P, Norsworthy JK, Riley MB, Bielenberg DG, Bridges W Jr (2008) Acclimation of Palmer amaranth (*Amaranthus palmeri*) to shading. *Weed Sci* 56:729–734

- Li H, Jiang D, Wollenweber B, Dai T, Cao W (2010) Effects of shading on morphology, physiology and grain yield of winter wheat. *Eur J Agron* 33:267–275
- Merilo E, Jõesaar I, Brosché M, Kollist H (2014) To open or to close: species-specific stomatal responses to simultaneously applied opposing environmental factors. *New Phytol* 202: 499–508
- Niinemets Ü, Kull O, Tenhunen JD (2004) Within-canopy variation in the rate of development of photosynthetic capacity is proportional to integrated quantum flux density in temperate deciduous trees. *Plant Cell Environ* 27:293–313
- Ogle K (2003) Implications of interveinal distance for quantum yield in C₄ grasses: a modeling and meta-analysis. *Oecologia* 136:532–542
- Patterson DT (1979) The effects of shading on the growth and photosynthetic capacity of itchgrass (*Rottboellia exaltata*). *Weed Sci* 27:549–553
- Patterson DT (1980) Shading effects on growth and partitioning of plant biomass in cogongrass (*Imperata cylindrica*) from shaded and exposed habitats. *Weed Sci* 28:735–740
- Regnier EE, Salvucci ME, Stoller EW (1988) Photosynthesis and growth responses to irradiance in soybean (*Glycine max*) and three broadleaf weeds. *Weed Sci* 36:487–496
- Santos BM, Morales-Payan JP, Stall WM, Bewick TA, Shilling DG (1997) Effects of shading on the growth of nutsedges (*Cyperus* spp.). *Weed Sci* 45:670–673
- Scherner A (2017). Tillage and Crop Rotation Effects on the Soil Seed Bank, Weed Germination, Emergence, and Herbicide Dissipation in Winter Cereals. Ph.D thesis. Aarhus, Denmark: Department of Agroecology, Faculty of Science and Technology, Aarhus University. 135 p
- Sharma DK, Andersen SB, Ottosen CO, Rosenqvist E (2015) Wheat cultivars selected for high F_v/F_m under heat stress maintain high photosynthesis, total chlorophyll, stomatal conductance, transpiration and dry matter. *Physiol Plantarum* 153:284–298
- Steckel LE, Sprague CL, Hager AG, Simmons FW, Bollero GA (2003) Effects of shading on common waterhemp (*Amaranthus rudis*) growth and development. *Weed Sci* 51: 898–903
- 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, Griepentrog HW, Kristensen L (2001) Suppression of weeds by spring wheat *Triticum aestivum* increases with crop density and spatial uniformity. *J Appl Ecol* 38:784–790
- Warwick SI (1979) The biology of Canadian weeds: 37 *Poa annua* L. *Can J Plant Sci* 59:1053–1066
- Weber E, Gut D (2005) A survey of weeds that are increasingly spreading in Europe. *Agron Sustain Dev* 25:109–121
- Yasin M, Andreasen C (2016) Effect of reduced oxygen concentration on the germination behavior of vegetable seeds. *Hortic Environ Biotechnol* 57:453–461

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