

Adaptive Responses of Field-Grown Common Lambsquarters (*Chenopodium album*) to Variable Light Quality and Quantity Environments

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Field experiments were conducted to determine whether exposure to reduced red:far-red light ratios (R:FR) typical of crop–weed environments was associated with adaptive changes in morphology, productivity, and fecundity of common lambsquarters. Plants were grown in reduced or ambient R:FR environments (both in full sunlight) until initiation of flowering, after which plants were grown in full sunlight or partial shade. At initiation of flowering, plants that had been exposed to reduced R:FR exhibited greater specific leaf area, stem elongation, main stem leaf area, specific stem length, and main stem mass compared with plants exposed to ambient R:FR. However, biomass allocation to stems, leaves, and roots did not differ between vegetative-stage R:FR treatments. At the end of flowering, morphology and productivity of plants exposed to partial shade did not differ between vegetative-stage R:FR treatments. In contrast, plants exposed to full sunlight during flowering after exposure to reduced R:FR during the vegetative stage had less total plant mass, less total leaf area, greater stem elongation, greater specific stem length, and a greater ratio of main stem to total stem mass compared with plants exposed to ambient R:FR during the vegetative stage. At physiological maturity, plants exposed to reduced R:FR during the vegetative stage and to partial shade during the reproductive stage had less total seed mass and fewer seeds compared with plants exposed to ambient R:FR during the vegetative stage and to partial shade during the reproductive stage. Fecundity of plants exposed to full sunlight during the reproductive stage did not differ between vegetative-stage R:FR treatments. These results indicate that exposure of common lambsquarters to reduced R:FR during the vegetative stage was maladaptive at later stages of growth in competitive environments, and suggest that interactions of light quality and quantity are important determinants of common lambsquarters fecundity.

Nomenclature: Common lambsquarters, *Chenopodium album* L. CHEAL.

Key words: Competition, weed–crop interactions, light quality, red:far-red ratio, modeling.

Light serves not only as a resource for plants, but also as a source of many cues that trigger plant responses to the surrounding environment (Aphalo and Ballaré 1995; Ballaré 1999). Previous research has shown that many important responses of plants to variable light environments are mediated by light wavelength-sensitive photoreceptors. Plants have signal-transducing photoreceptors belonging to three major classes: red (R) and far-red (FR) wavelength-sensitive phytochromes, UV-A/blue wavelength-sensitive cryptochromes, and phototropins (Ballaré 1999; Franklin and Whitelam 2004). Of these, the phytochrome class of photoreceptors has been the most widely studied at molecular, cellular, and whole-plant levels (Franklin and Whitelam 2004). Many studies involving *Arabidopsis thaliana* mutants have characterized the genetic and biochemical basis of plant responses to changes in the spectral composition of light. These and other studies have shown that phytochromes play a critical role in mediating morphological responses of plants to changes in the ratio of R to FR wavelengths (R:FR) (Casal et al. 1998; Franklin and Whitelam 2004; Weinig 2000).

Because green plants preferentially absorb light in the R and blue regions of the visible spectrum, light microenvironments adjacent to plants tend to be depleted in R wavelengths and enriched in FR wavelengths (Ballaré 1999; Smith 1982). Therefore, reduced R:FR, whether occurring alone or together with reduced photosynthetically active radiation (PAR), is a reliable indicator of impending or actual shade (Aphalo and Ballaré 1995; Smith 1982). Well-documented phytochrome-mediated responses of plants to reduced R:FR include stem elongation, suppression of branching or tillering, shifts in biomass allocation to stems, roots, and leaves, changes

in leaf anatomy and morphology, alterations in leaf and shoot orientation, increased apical dominance, and early flowering (Ballaré and Casal 2000; Kasperbauer 2000).

Numerous studies conducted in controlled environments and in the field have documented plant morphological changes in association with changes in R:FR. Studies involving dicotyledonous species have demonstrated that plants exposed to reduced R:FR exhibit greater internode length (Board 2001; Causin and Wulff 2003), greater plant height (Mahoney and Swanton 2008; Rajcan et al. 2002), reduced ratio of leaf mass to stem mass (LSR) (Causin and Wulff 2003), greater specific leaf area (SLA) (Causin and Wulff 2003), increased branch orientation away from nearby neighbors (Novoplansky 1990, 1991), greater leaf area (Heraut-Bron et al. 2001), reduced leaf number and more steeply inclined leaves (van Hinsberg and van Tienderen 1997), and reduced total plant mass (Causin and Wulff 2003) when compared with plants exposed to ambient R:FR.

Few studies have determined the effects of R:FR-mediated alterations in weed and crop morphology on competitive ability under field conditions (Ballaré and Casal 2000). Such responses could have important consequences for modeling competition for light in crop–weed communities (Rajcan and Swanton 2001; Rajcan et al. 2004). Most plant species, in particular weed species, are characterized by a high degree of morphological plasticity in changing light environments. A better understanding of this plasticity could help explain the underlying basis for phenomena such as critical periods for weed removal and economic thresholds for weed control that are only described empirically (Holt 1995; Rajcan and Swanton 2001). Also, most process-based models of plant competition, which are primarily driven by resource availability and use, tend to neglect plant morphological plasticity as influenced by the light environment (Aphalo et al. 1999). Furthermore, the lack of process-based descriptions of biomass allocation is a fundamental weakness inherent in

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most simulation models of plant growth and development (Grace 1991).

Greater understanding of plant morphological responses to the light environment could improve methods of biomass partitioning in models describing weed growth and competition with crop plants (Aphalo and Ballaré 1995; Grace 1991; Rajcan and Swanton 2001). For instance, simulation of jimsonweed (*Datura stramonium* L.) growth and competitive effect on corn (*Zea mays* L.) was greatly improved when the model INTERCOM was modified to include plasticity of height and SLA that occurred under competitive conditions for light (Cavero et al. 2000). Conversely, these adjustments did not improve simulations when the model was parameterized to describe growth in monocultures of either species.

Most plant growth simulation models describe competitive interactions that occur only when resources (such as light) become limiting. If responses occurring before the onset of resource limitation are important to outcomes of competition, then characterization of these responses might improve process-based models of crop-weed competition. Previous studies have typically focused on early-vegetative-stage plant responses to altered R:FR but have seldom addressed the implications of these responses for long-term competitive ability through the reproductive stage to physiological maturity. It is important to know not only whether plastic growth responses to altered R:FR occur early in plant development but also to know whether or not these responses confer greater (or less) competitive ability during later development in different types of competitive environments.

Therefore, our first objective was to determine the effects of common lambsquarters exposure to reduced R:FR during the vegetative stage on morphology and biomass production at the initiation of flowering. We hypothesized that exposure to reduced R:FR during the vegetative stage would be associated with plastic morphological responses such as increased stem elongation, reduced branching, and increased SLA compared with plants exposed to ambient R:FR. Our second objective was to determine whether responses of plants exposed to reduced R:FR during the vegetative stage were affected by exposure to full sunlight or partial shade during the reproductive stage. We hypothesized that plants exposed to reduced R:FR during the vegetative stage would be adaptive (i.e., would increase productivity or fecundity) when grown in partial shade during the reproductive stage, but not when grown in full sunlight. We also hypothesized that plants exposed to ambient R:FR during the vegetative stage would be adaptive when grown in full sunlight during the reproductive stage, but not when grown in partial shade. A better understanding of the adaptive responses of common lambsquarters to variable light quality and quantity environments should improve our ability to predict outcomes of crop-weed competition.

Materials and Methods

Site Description and Field Procedures. Field experiments were conducted in 2004 and 2005 at the University of Wisconsin, Arlington Agricultural Research Station (UW-AARS), near Arlington, WI. The soil type was a Plano silt loam (fine-silty mesic Typic Argiduoll) with 3.3% organic matter and pH 7.0. Soil was chisel-plowed in November. Nitrogen (180 kg ha^{-1}) was applied in mid-April, followed

by seedbed preparation with a soil finisher in early May. Glyphosate- and European corn borer [*Ostrinia nubilalis* (Hübner)]-resistant 'DeKalb 50-20 RR2/YGCB' corn seed was planted at a rate of $80,000 \text{ seeds ha}^{-1}$ in 76-cm east-west oriented rows on May 7, 2004 and May 10, 2005. Tefluthrin ($0.15 \text{ kg ai ha}^{-1}$) was applied in-furrow at planting to protect corn from corn rootworm (*Diabrotica* spp.) infestation. Before corn emergence, $1.85 \text{ kg ai ha}^{-1}$ S-metolachlor, $0.17 \text{ kg ai ha}^{-1}$ mesotrione, and $0.69 \text{ kg ai ha}^{-1}$ simazine were applied for weed control.

On June 15, 2004 and June 14, 2005 (at approximately the fifth-leaf stage of corn), common lambsquarters seeds were planted in 11.4-L plastic pots (156 pots total) filled with a 50:50 sand:silt loam mixture that had been screened to remove large soil aggregates, rocks, and organic debris. The sand was sharp coarse quartz sand and the silt loam was as described above. The seeds had been hand harvested in the fall of 2003 from plants located in fields with a history of continuous corn production at the UW-AARS. The seeds were stored at -5 C . The same seed source was used in 2004 and 2005 experiments. Pots were placed 1.8 m apart equidistant between two rows of corn (reduced R:FR environment) or 1.8 m apart in an open (crop-free) field area (ambient R:FR environment). The experimental area for each R:FR environment measured 35 m (north-south) by 32 m (east-west). Pots were placed on plastic saucers so roots would not contact the field soil. Seedlings were thinned to one per pot shortly after emergence. Pots were watered as needed to maintain field capacity and treated as needed with 20-10-20 plant fertilizer¹ solution containing 200 ppm N (Volenberg and Stoltenberg 2002).

Treatment Description. From emergence (first appearance of cotyledons, June 20 in 2004 and June 19 in 2005) until the initiation of flowering (first visible flowers, July 28 in 2004 and July 26 in 2005), potted common lambsquarters plants were exposed to either a reduced R:FR treatment (as mediated by neighboring corn plants) or an ambient R:FR treatment (no corn neighbors in open field). Both R:FR treatments were applied in the absence of shade (ambient PAR). To prevent shading of target common lambsquarters plants by neighboring corn plants, PAR was measured continuously (described below) and corn neighbor rows were thinned and corn plants were trimmed to maintain ambient PAR. Neighbor corn plants were thinned to a 1.5-m-wide row spacing on June 18, 2004 and June 21, 2005 and to a 2.3-m-wide row spacing on July 6, 2004 and June 30, 2005. In addition, corn plants were trimmed to a height of approximately 1.5 m on July 14, 2004 and July 8, 2005 to prevent shading of target common lambsquarters plants.

At the onset of the reproductive stage (initiation of flowering), randomly selected common lambsquarters plants from each R:FR treatment were destructively harvested for morphological characterization (described below). The remaining plants were subsequently exposed to one of two PAR treatments (full sunlight or partial shade provided by neighbor corn plants) during the reproductive stage. Target plants exposed to reduced R:FR during the vegetative stage were divided randomly into two groups and placed either in full sunlight or partial shade. Similarly, target plants exposed to ambient R:FR during the vegetative stage were divided randomly into two groups and placed in either full sunlight or

partial shade. Exposure to full sunlight was achieved by placing the pots of target plants 1.8 m apart in the open field area. Exposure to partial shade was achieved by placing pots of target plants 1.8 m apart located equidistant between two rows of corn neighbor plants spaced 1.5 m apart.

At the end of flowering (pollination cessation), which occurred on August 23, 2004 and August 16, 2005, target plants were randomly selected from each R:FR and PAR treatment combination and destructively harvested. In 2004, unusually cold temperatures from August 5 to August 16 (data not shown) extended the flowering period. Exposure of all remaining target plants to PAR treatments was maintained for the duration of the reproductive stage. At physiological maturity (when seeds were fully ripened), which occurred on September 20 in each year, the remaining target plants were destructively harvested to determine total shoot mass and seed production.

Common Lambsquarters Measurements. For harvests conducted at the initiation of flowering and end of flowering, shoot height was measured before plants were clipped at the soil surface, after which the leaves, stems, and reproductive structures were separated. Leaf area was measured using a planimeter.² Roots were recovered by washing the soil from root masses by hand (Cornelissen et al. 2003). All plant parts were dried to a constant mass at 70 C. Root:shoot ratio (RSR, g g^{-1}) was calculated as the ratio of dry root mass to dry shoot mass. Specific stem length (SSL, cm g^{-1}) was calculated as the ratio of main stem length to main stem mass. SLA ($\text{cm}^2 \text{g}^{-1}$) was calculated as the ratio of leaf area to leaf mass. LSR (g g^{-1}) was determined as the ratio of leaf mass to stem mass. Leaf area ratio (LAR, $\text{cm}^2 \text{g}^{-1}$) and leaf mass ratio (LMR, g g^{-1}) were determined as the ratios of leaf area and leaf mass to total plant mass, respectively. Nodes along the main stem were counted. Leaves were collected separately from the upper and lower halves of each shoot to assess vertical adaptations in leaf area distribution (LAD). The length of the main stem was divided by the number of nodes to determine average internode length. Plant elongation was calculated as plant height relative to total plant mass (cm g^{-1}), following Schmitt et al. (1995). Stem mass was measured separately from branches and the main stem to determine changes in allocation of stem mass between branches and the main stem (main stem ratio, MSR).

At physiological maturity, common lambsquarters shoots were harvested and oven-dried at 70 C for a minimum of 1 wk to a constant mass, then weighed to determine dry shoot mass. Seeds were separated from shoot mass by manual screening and using an air column seed blower³ to remove leaf and stem particles; cleaned seeds were subsequently weighed to determine total seed mass. A 0.1-g subsample of seeds was weighed and counted; the ratio of subsample seed number to subsample seed mass was used to estimate the total seed number for each sample. Mass per seed was calculated as the subsample mass divided by the subsample seed count. Harvest index (HI) was determined as total seed mass divided by total shoot mass.

Environmental Measurements. To determine the approximate R:FR composition of light in the reduced and ambient R:FR treatment environments, several series of spectral reflectance measurements were made during the vegetative

stage using a spectroradiometer⁴ fitted with a 25° field of view foreoptic. Measurements were made on clear days near noon and were repeated in 12 representative locations within the reduced R:FR environment and 12 representative locations within the ambient R:FR environment. At each location, the sensor optic was oriented horizontally at the same height as the apex of target plant shoots and spectral reflectance was measured in four or eight cardinal directions. A reference reflectance spectrum (total reflectance from a white reference panel aimed at direct radiation) was also collected at each location. Spectral irradiances at 645 and 735 nm were used to calculate R:FR ratios; these values approximate the phytochrome action peaks in green plants (Kasperbauer 1987).

To ensure that only light quality (R:FR), and not light quantity, was altered in the reduced R:FR treatments, PAR was measured continuously during the vegetative stage using quantum line PAR sensors.⁵ In the reduced R:FR environment, one line sensor was placed between two corn rows in a position that resulted in measurement of PAR in the interrow area occupied by the target common lambsquarters plants. A second line sensor was placed in the ambient R:FR environment. Mean PAR was logged at 15-min intervals throughout the vegetative stage. To account for possible slight differences between the two line sensors, PAR data were adjusted using a calibration curve. PAR data were monitored daily to detect onset of interrow shading by neighboring corn plants, which were immediately thinned and trimmed (described above) as needed to avoid shading of common lambsquarters plants.

Thigmomorphogenesis, or the formation of thicker and shorter stems, can result from the mechanical perturbations of plant stems caused by winds (Jaffe and Forbes 1993). If wind speeds differed between the two R:FR treatments, some plant responses to light quality such as stem elongation could be obscured. Therefore, wind speed was measured during the vegetative stage to determine whether wind speed differed between the reduced R:FR and ambient R:FR environments. Average and maximum wind speeds were measured with a portable hand-held weather station⁶ (equipped with a National Institute of Standards and Technology-calibrated impeller) during times of light (0 to 8 km h^{-1}) and moderate (8 to 24 km h^{-1}) winds. On each measurement date, 12 measurements were taken in each R:FR environment. For each measurement, the portable weather station was placed slightly above pot level so that the impeller faced the prevailing direction of the wind. After 30 s, average and maximum wind speeds were recorded. To mitigate possible temporal differences in wind speeds, measurements were alternated between the R:FR environments.

Experimental Design and Statistical Analysis. The experimental design was completely random; the experimental unit was one target common lambsquarters plant. At the initiation of flowering, 18 and 12 target plants per treatment were sampled in 2004 and 2005, respectively. At the end of flowering, six plants per treatment were sampled in each year. At physiological maturity, four to six plants per treatment were sampled in 2004, whereas nine plants per treatment were sampled in 2005. ANOVA was conducted for each harvest and treatment combination. Before ANOVA, data were subjected to Levene's test (Brown 1974) for heteroscedasticity and were transformed when necessary. When ANOVA

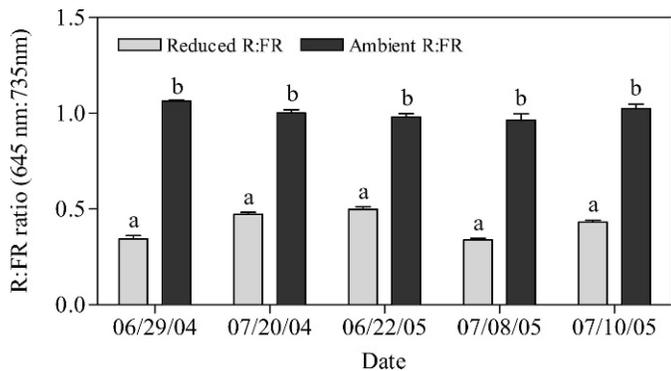


Figure 1. Mean red:far-red light (R:FR) values (\pm standard error of the mean) in reduced R:FR and ambient R:FR treatments in 2004 and 2005. Mean R:FR values designated by different lowercase letters differed between treatments according to t tests ($\alpha = 0.05$) for all measurement dates (MM/DD/YY).

indicated year-by-treatment interactions, pairwise comparisons of treatment means were conducted within each year using Bonferroni's adjustment (Schaffer 1995). When a response was determined to differ between R:FR treatments, the natural logarithm (\ln) of the response was regressed against \ln total mass to determine whether the response was ontogenetic (attributed to typical plant development) or plastic (a response distinct from the ontogenetic trajectory). A plastic response is indicated if regression coefficients differ between treatments (Causin and Wulff 2003).

Within each measurement date, Student's t tests (Steel and Torrie 1980) were conducted to compare mean R:FR values, maximum wind speeds, and average wind speeds between reduced R:FR and ambient R:FR treatments. To compare vegetative-stage PAR between R:FR treatments, PAR in the reduced R:FR treatment was regressed against PAR in the ambient R:FR treatment; a slope close to or equal to 1 indicated similar PAR between R:FR treatments.

Results and Discussion

Environmental Measurements. Red:Far-Red. Mean R:FR was less in the reduced R:FR treatment than in the ambient R:FR treatment on each measurement date (Figure 1). Over time, mean R:FR values in the ambient R:FR treatment were approximately 1.0 and were similar to expected values for ambient R:FR spectral content, which are typically about 1.15 (Smith 1982). Mean R:FR values measured in the reduced R:FR treatment ranged from about 0.3 to 0.5, within the 0.1-to-0.7 range of R:FR values that have been measured under natural canopies (Smith 1982) and in crop-weed communities (Markham and Stoltenberg 2009). Since these measurements were conducted near noon, they likely represent the greatest R:FR ratios that common lambsquarters plants were exposed to, since R:FR decreases with solar angle and at twilight (Smith 1982).

Various methods have been used to expose targeted plants to altered light quality environments. Typical methods include surrounding plants with cylinders made of color-coated or dye-impregnated plastic films (Causin and Wulff 2003; Novoplansky 1991), filtering light from bulbs or using special bulbs that emit particular wavelengths (Alokam et al. 2002; Rajcan et al. 2002; van Hinsberg and van Tienderen 1997), directing specific wavelengths onto a specific plant part

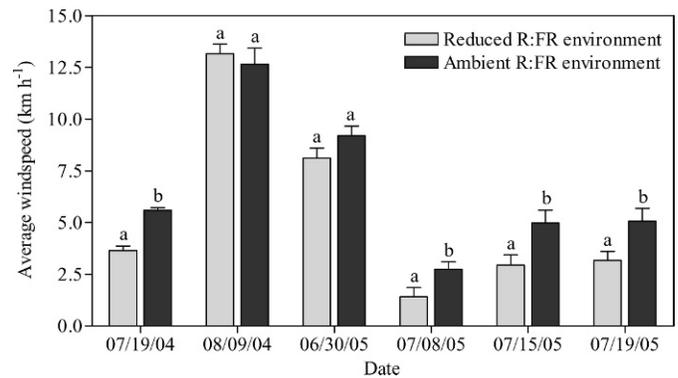


Figure 2. Average wind speeds (\pm standard error of the mean) in reduced and ambient red:far-red light (R:FR) treatments on six dates (MM/DD/YY) in 2004 and 2005. Average wind speeds designated with different lowercase letters differed between treatments within date according to two-tailed Student's t tests ($\alpha = 0.05$).

using colored light-emitting diodes (Deregibus et al. 1985; Héraut-Bron et al. 1999; Schuerger et al. 1997), and simply using neighboring plants to mediate R:FR (Kasperbauer 1987; Smith et al. 1990).

The method used to mediate R:FR is of great importance; choosing a method that does not mimic or closely represent natural light signals may produce results of little value. For instance, Collins and Wein (2000) investigated three smartweed (*Polygonum*) species' responses to R:FR environment altered by living plants or artificial green cellophane plants. Target plant response to living vs. artificial neighbor plants differed, even though the measured R:FR did not differ between neighbor types. Moreover, the responses varied among species. The authors did not speculate on the possible causes of these observed differences, but their results highlight the importance of methods used to alter R:FR.

Evidence suggests that the direction of sensed light signals as well as the quality, or spectral composition, is important. Horizontally propagated light striking plant internodes, especially the uppermost internode, is thought to elicit the greatest response (Casal and Smith 1988). However, slight changes in the angle of light incidence have been demonstrated to be associated with changes in stem elongation of tobacco (*Nicotinia tabacum* L.) (Seavers and Smith 1997). This may be a possible mechanism for distinguishing self-reflected light from light reflected by neighbors. Because natural light environments are highly complex and dynamic, both spatially and temporally, and since responses to this heterogeneity have not been fully characterized, alteration of R:FR with neighboring plants, or at least plantlike structures, may be the most conservative approach to altering R:FR. A drawback, however, is that precisely controlling the spectral content, directionality, and intensity of the R:FR treatments using plants can be difficult (Dale and Causton 1992).

Wind Speed. When wind speeds were low ($< 8.0 \text{ km h}^{-1}$), the mean wind speed was less in the reduced R:FR treatment than in the ambient R:FR treatment (Figure 2). In contrast, at moderate wind speeds ($> 8.0 \text{ km h}^{-1}$), mean wind speeds did not differ between the R:FR treatments. Since the thigmomorphogenetic effect (the formation of thicker and shorter stems) is most pronounced when plants are exposed to moderate to high wind speeds ($> 8.0 \text{ km h}^{-1}$) (Jaffe and

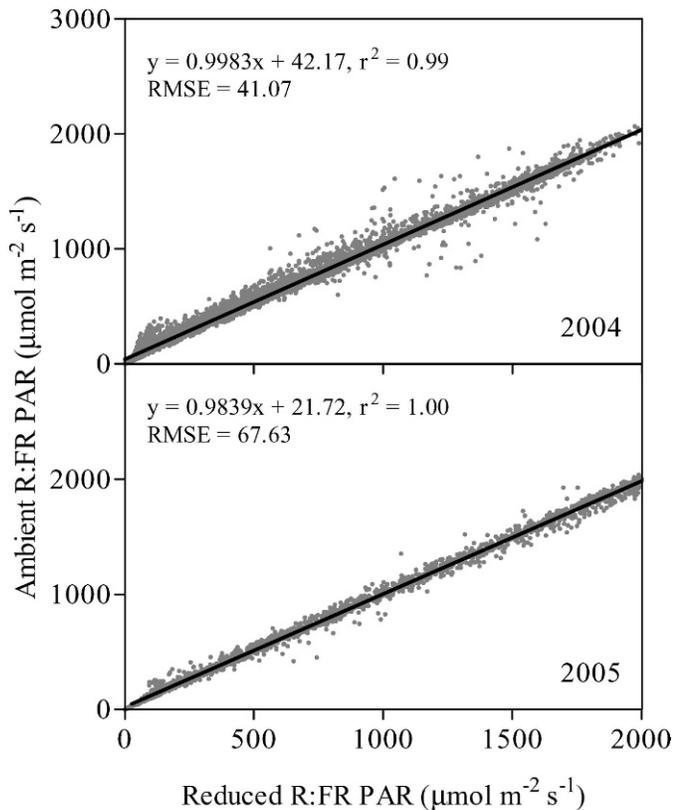


Figure 3. The relationship between photosynthetically active radiation (PAR) in ambient and reduced red:far-red light (R:FR) treatments in 2004 and 2005. Symbols are data pairs (x, y) representing PAR measured at the same time point within each of the R:FR treatments.

Forbes 1993), wind speed was not likely an important confounding factor in our experiments.

Photosynthetically Active Radiation. In 2004 and 2005, linear regressions of PAR in the ambient R:FR treatment vs. PAR in the reduced R:FR treatment had R^2 values of 0.99 and 1.00, respectively (Figure 3). Also, the daily total PAR in the reduced R:FR treatment was within 1 to 3% of PAR in the ambient R:FR treatment (data not shown). Therefore, PAR probably did not elicit a differential effect on common lambsquarters responses to R:FR treatments.

A few studies have determined that the exposure to reduced R:FR alone is not sufficient to alter plant responses in the absence of shade (Marcuvitz and Turkington 2000). Reduced light quantity is known to elicit several of the same responses (e.g., stem elongation, changes in leaf size and structure) that are also associated with reduced R:FR (Smith 1982). Many studies of R:FR effects have been conducted in controlled environments. However, the relatively low PAR typically achieved in growth chambers (rarely in excess of 500 to 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$) could potentially cause some of the same morphological responses caused by reduced R:FR, thereby confounding results (Smith 1982). Furthermore, low PAR has been shown to interact antagonistically with reduced R:FR with respect to changes in common lambsquarters stem elongation and specific leaf area (Morgan and Smith 1981), further complicating interpretations of results from studies conducted within controlled environments. In our study we achieved a reduced R:FR treatment environment that

included typical ambient PAR, which should have minimized or eliminated possible confounding effects.

Common Lambsquarters Morphology at the Initiation of Flowering. For common lambsquarters plants exposed to reduced R:FR or ambient R:FR treatments during the vegetative stage and measured at the initiation of flowering, R:FR treatment-by-year interactions were not significant ($\alpha = 0.05$, data not shown); therefore, data were pooled across years for ANOVA. Plant height, number of main stem nodes, RSR, LSR, and LMR did not differ ($P > 0.05$) between the reduced R:FR and ambient R:FR treatments (Table 1). However, stem elongation (plant height mass^{-1} , cm g^{-1}), internode length, SSL, MSR, SLA, LAD, and LAR were greater ($P < 0.05$) for plants exposed to reduced R:FR than those exposed to ambient R:FR, whereas total plant mass and total leaf area were less for plants exposed to reduced R:FR than for plants exposed to ambient R:FR.

These common lambsquarters growth and morphological responses are similar to those observed by Causin and Wulff (2003), who found that at equal PAR, whole plant mass of common lambsquarters decreased and SLA increased with exposure to reduced R:FR. Increased SLA is one of the most commonly reported responses of plants to reduced R:FR (Kasperbauer 1971; van Hinsberg and van Tienderen 1997). Conversely, a few studies have shown that SLA was affected more by changes in PAR levels than by changes in R:FR (Mahoney and Swanton 2008; Marcuvitz and Turkington 2000; Morgan and Smith 1981).

Similarly, conflicting results have been reported for the effect of reduced R:FR on biomass production. Alokam et al. (2002), Deregibus et al. (1983), and Lee et al. (1997) reported decreased biomass in association with reduced R:FR; however, Sleeman et al. (2002) and van Hinsberg and van Tienderen (1997) found that R:FR treatment did not affect total plant mass. Decreased total plant mass may sometimes be associated with reduced PAR, as photosynthesis is limited at low PAR levels. However, reduced PAR is an unlikely explanation for the observed differences in common lambsquarters plant mass in our study since PAR was similar between the ambient and reduced R:FR treatment (Figure 3).

Although common lambsquarters total leaf area was less in reduced R:FR than in ambient R:FR treatments, this was likely due to biomass differences, as LSR and LMR did not differ between treatments (Table 1). Furthermore, LAR was greater for plants exposed to reduced R:FR than for plants exposed to ambient R:FR. Since LMR did not differ between R:FR treatments, greater SLA for plants exposed to reduced R:FR than ambient R:FR was probably the principal factor associated with differences in LAR. Plants typically increase SLA in response to shade to maximize light interception per unit of leaf mass (Morgan and Smith 1981). Greater SLA in response to reduced R:FR would be beneficial if shade occurred after the vegetative stage, but during the vegetative stage, greater SLA would have been maladaptive since all leaves were exposed to ambient PAR. An explanation for less total plant mass in association with reduced R:FR is that leaves of plants exposed to reduced R:FR had lower photosynthetic capacity per unit leaf area due to greater SLA, which led to less photosynthetic assimilation and biomass accumulation (Kasperbauer 1971).

Table 1. Morphological characteristics of common lambsquarters at the initiation of flowering after exposure to reduced or ambient red : far-red light (R : FR) treatments during the vegetative stage. Data were pooled across 2 yr (2004 and 2005) for analysis.

Morphological characteristic	Mean value \pm SE		P value
	Reduced R : FR	Ambient R : FR	
Plant height (cm)	34.6 \pm 1.6	30.6 \pm 1.0	0.092
Total plant mass (g)	6.9 \pm 0.9	9.6 \pm 0.7	0.001
Stem elongation (plant height mass ⁻¹ , cm g ⁻¹)	5.94 \pm 0.32	3.49 \pm 0.18	< 0.0001
Total leaf area (cm ²)	576 \pm 39	735 \pm 32	0.001
Internode length (cm)	1.40 \pm 0.05	1.24 \pm 0.03	0.027
Number of nodes	22.8 \pm 0.9	22.7 \pm 0.9	0.982
Root : shoot ratio (RSR, g g ⁻¹)	0.22 \pm 0.02	0.21 \pm 0.01	0.886
Specific stem length (SSL, cm g ⁻¹)	35.0 \pm 1.9	25.7 \pm 1.4	< 0.0001
Main stem : total stem mass (MSR, g g ⁻¹)	0.48 \pm 0.01	0.39 \pm 0.01	< 0.0001
Specific leaf area (SLA, cm ² g ⁻¹)	187 \pm 5	159 \pm 3	< 0.0001
Leaf area distribution (LAD, cm ² cm ⁻²)	0.35 \pm 0.02	0.26 \pm 0.01	< 0.0001
Leaf : stem ratio (LSR, g g ⁻¹)	1.56 \pm 0.05	1.59 \pm 0.04	0.771
Leaf area ratio (LAR, cm ² g ⁻¹)	94.1 \pm 3.7	80.8 \pm 2.4	0.003
Leaf mass ratio (LMR, g g ⁻¹)	0.50 \pm 0.06	0.51 \pm 0.04	0.624

Another explanation for less biomass accumulation in association with reduced R : FR is that exposure to reduced R : FR may have resulted in a reduction in UV-protective phenolic compounds. Since plants in the reduced R : FR treatment were exposed to ambient PAR, a reduction in UV-protective phenolics could have led to an increase in UV damage to leaves, thereby reducing photosynthetic capacity and consequent biomass accumulation. For example, Weinig et al. (2004) showed that jewelweed (*Impatiens capensis* Meerb.) plants that were exposed to reduced R : FR had lower phenolic concentrations than plants exposed to ambient R : FR.

Greater stem elongation, internode length, and plant height are also common responses to reduced R : FR (Franklin and Whitelam 2005; Smith 1982). Changes in stem elongation and the relative biomass allocation between leaves and stems are considered to be the most consistent responses of most plants to reduced R : FR (Smith 1982). In many instances, plants exposed to reduced R : FR have increased biomass allocation to stems compared with leaves (i.e., LSR is reduced) (Causin and Wulff 2003; Mahoney and Swanton 2008; Morgan and Smith 1981), but in other instances (Weinig 2000) LSR has been insensitive to altered R : FR. In instances of greater biomass allocation to stems than leaves, this would likely be beneficial only if vertical adaptations in leaf area provided a substantial increase in access to light (Dudley and Schmitt 1996; Smith 1982; Weinig 2000).

Although common lambsquarters plants exposed to reduced R : FR were more elongated and had longer internodes than plants exposed to ambient R : FR (Table 1), plant height, internode number, and LSR were not affected by R : FR. Comparing plant heights to detect elongation responses is problematic, because height is confounded with plant size and vigor (Weinig et al. 2004). Thus, since plant mass was greater in the ambient R : FR treatment than in the reduced R : FR treatment, stem height relative to mass (or stem elongation) was greater for plants in the reduced R : FR treatment.

Greater total plant mass of common lambsquarters exposed to ambient R : FR compared with reduced R : FR during the vegetative stage (Table 1) suggests that ontogeny of plants may have differed between the vegetative-stage R : FR environments. Observations of morphological plasticity can be attributed to either passive plasticity associated with an ontogenetic trajectory or to more complex plasticity resulting

both from ontogeny and responses to changing environmental variables (McConnaughay and Coleman 1999; Wright and McConnaughay 2002). Many allometric relationships describing biomass allocation patterns that vary with environmental factors can also vary with ontogeny, i.e., ontogeny can vary among individuals of the same age exposed to different environmental treatments. Therefore, distinguishing ontogenetic plasticity from more complex plasticity resulting from responses to environmental factors that vary independently from ontogeny is important (Huber and Stuefer 1997; McConnaughay and Coleman 1999; Wright and McConnaughay 2002). The relationships between common lambsquarters total plant mass and internode length, MSR, SLA, and LAD differed between reduced R : FR and ambient R : FR treatments (Figure 4), indicating that differences in responses were likely due to complex plasticity rather than solely due to passive plasticity associated with plant development (ontogeny). In contrast, the linear relationships between total plant mass and SSL, total plant mass and total leaf area, and total plant mass and LAR did not differ between R : FR environments (data not shown), indicating that passive plasticity alone may explain differences in these traits between R : FR treatments.

Common Lambsquarters Morphology at the End of Flowering. Treatment-by-year interactions were not significant (data not shown) for common lambsquarters morphology at the end of flowering after exposure to reduced or ambient R : FR treatments during the vegetative stage and exposure to partial shade during flowering. Consequently, data were pooled across years for analysis. However, biomass and morphological characteristics of these plants were not affected by R : FR treatment during the vegetative stage (data not shown).

For common lambsquarters plants exposed to reduced or ambient R : FR during the vegetative stage, and to full sunlight during flowering, treatment-by-year interactions were not significant (data not shown) for plant morphology, so data were pooled across years for analysis. For these plants, many morphological characteristics did not differ ($P > 0.05$) between R : FR treatments. However, stem elongation, SSL, and MSR were greater ($P < 0.05$) for plants exposed to reduced R : FR in the vegetative stage than those exposed to ambient R : FR (Table 2). Total plant mass and total leaf area

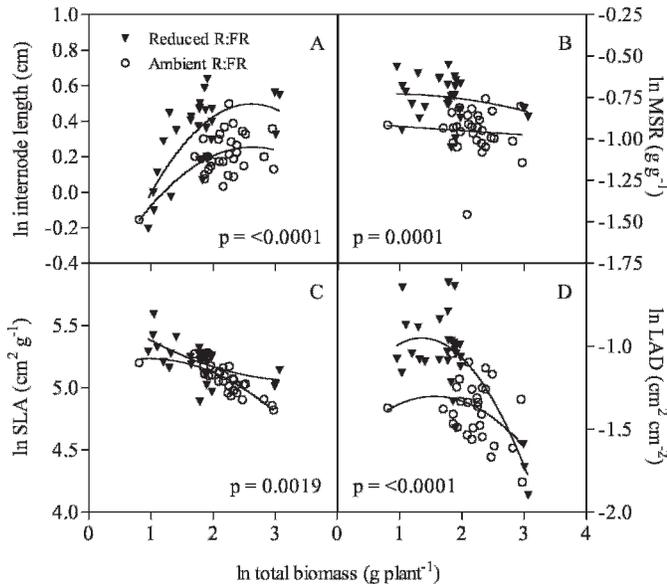


Figure 4. The relationship between common lambsquarters (A) ln internode length, (B) ln main stem mass: total stem mass (MSR), (C) ln specific leaf area (SLA), and (D) ln leaf area distribution (LAD) and ln total mass in reduced (▼) and ambient (○) red:far-red light (R:FR) treatments at the initiation of flowering. Regression equations: (A, ▼) $y = -0.819 + 1.001x - 0.192x^2$, $r^2 = 0.47$; (A, ○) $y = -0.612 + 0.659x - 0.126x^2$, $r^2 = 0.34$; (B, ▼) $y = -0.74 + 0.03x - 0.02x^2$, $r^2 = 0.05$; (B, ○) $y = -0.90 - 0.02x - 0.0001x^2$, $r^2 = 0.01$; (C, ▼) $y = 5.70 - 0.37x + 0.05x^2$, $r^2 = 0.36$; (C, ○) $y = 5.13 + 0.20x - 0.10x^2$, $r^2 = 0.70$; (D, ▼) $y = -1.467 + 0.767x - 0.284x^2$, $r^2 = 0.61$; (D, ○) $y = -1.664 + 0.465x - 0.149x^2$, $r^2 = 0$. Differences between regression equations (reduced vs. ambient) are indicated by P values and data were pooled across 2004 and 2005.

were less for plants exposed to reduced R:FR than for plants exposed to ambient R:FR. Relationships between total mass and total leaf area, SSL, and MSR indicated that leaf area and SSL responses to vegetative-stage R:FR treatments were ontogenetic, whereas the MSR response was due to more complex plasticity (data not shown). These relationships are consistent with the results discussed above for measurements made at the initiation of flowering.

Morphological plasticity enables plants to express adaptive phenotypes that are suited to local environmental stresses (Weinig 2000). However, to demonstrate that observed plastic responses are adaptive it is necessary to show that the environmentally induced expression of a particular phenotype

is adaptive in the inductive environment but also maladaptive in a noninductive environment (Dudley and Schmitt 1996; Schmitt et al. 1995; Weinig et al. 2004). Morphological adaptations associated with exposure to reduced R:FR induced by neighboring plants that occur before the onset of shading are thought to increase competitive ability of early emerging weed species, which are usually associated with the greatest crop yield loss (Rajcan et al. 2002).

Our results suggest initially that vegetative-stage exposure to reduced R:FR did not affect the competitive ability of common lambsquarters grown in partial shade during flowering, as plant morphology was similar between treatments at the end of flowering (data not shown). However, at the initiation of flowering, when these plants were placed in partial shade, many morphological characteristics differed between R:FR treatments (Table 1). Since total plant mass in the reduced R:FR treatment was less than in the ambient R:FR treatment at the initiation of exposure to partial shade, the lack of morphological differences between treatments at end of flowering suggests that plants exposed to reduced R:FR were more competitive when placed in partial shade than plants exposed to ambient R:FR. In contrast, if no competitive advantage was conferred by reduced R:FR during the vegetative stage, then plants from the ambient R:FR treatment, which had greater total plant mass at the beginning of the partial shade treatment, would probably have maintained their relative advantage.

For plants grown in full sunlight during flowering, prior exposure to reduced R:FR during the vegetative stage was associated with less total plant mass and leaf area at the end of flowering than for plants exposed to ambient R:FR (Table 2). When placed in full sunlight at the initiation of flowering, plants from the reduced R:FR treatment had less total plant mass than plants from the ambient R:FR treatment (Table 1). However, in contrast to the effects of partial shade, this size asymmetry continued into the reproductive stage (Table 2), indicating that vegetative-stage exposure to reduced R:FR was not associated with a competitive advantage for plants later exposed to full sunlight. At the initiation of flowering, total mass of plants exposed to ambient R:FR was 39% greater than plants exposed to reduced R:FR (Table 1). By the end of flowering, this size differential was the same; total mass of plants exposed to vegetative-stage ambient R:FR was 39% greater than for plants exposed to vegetative-stage reduced R:FR (Table 2).

Table 2. Morphological characteristics of common lambsquarters at the end of flowering after exposure to reduced or ambient red:far-red light (R:FR) treatments from emergence to initiation of flowering and exposure to full sunlight during flowering. Data were pooled across 2 yr (2004 and 2005) for analysis.

Morphological characteristic	Mean value ± SE		P value
	Reduced R:FR	Ambient R:FR	
Plant height (cm)	73.3 ± 1.8	72.8 ± 1.4	0.853
Total plant mass (g)	35.8 ± 2.8	49.5 ± 3.8	< 0.0001
Total leaf area (cm ²)	1,290 ± 85	1,820 ± 155	0.001
Stem elongation (plant height mass ⁻¹ , cm g ⁻¹)	2.18 ± 0.16	1.56 ± 0.11	< 0.0001
Internode length (cm)	1.78 ± 0.07	1.81 ± 0.11	0.946
Number of nodes	40.9 ± 1.8	40.4 ± 2.1	0.864
Root:shoot ratio (RSR, g g ⁻¹)	0.23 ± 0.02	0.23 ± 0.02	0.782
Specific stem length (SSL, cm g ⁻¹)	17.1 ± 1.1	14.2 ± 1.1	0.003
Main stem:total stem mass (MSR, g g ⁻¹)	0.36 ± 0.01	0.31 ± 0.01	0.004
Specific leaf area (SLA, cm ² g ⁻¹)	131.5 ± 3.1	127.5 ± 4.6	0.502
Leaf area distribution (LAD, cm ² cm ⁻²)	0.12 ± 0.02	0.12 ± 0.02	0.616
Leaf:stem ratio (LSR, g g ⁻¹)	0.83 ± 0.02	0.84 ± 0.03	0.763
Leaf area ratio (LAR, cm ² g ⁻¹)	36.9 ± 1.5	36.8 ± 1.5	0.969
Leaf mass ratio (LMR, g g ⁻¹)	0.29 ± 0.01	0.30 ± 0.01	0.646

Table 3. Morphological characteristics for common lambsquarters at physiological maturity after exposure to reduced or ambient red : far-red light (R : FR) treatments from emergence to initiation of flowering, and partial shade or full sunlight during the reproductive stage.

Morphological characteristic	Mean value ± SE					
	Partial shade during reproduction			Full sunlight during reproduction		
	Reduced R : FR	Ambient R : FR	P value	Reduced R : FR	Ambient R : FR	P value
Total shoot mass (g plant ⁻¹)	44.1 ± 2.2	50.6 ± 2.6	0.052	54.6 ± 1.9	59.6 ± 3.6	0.159
Total seed mass (g plant ⁻¹)	13.3 ± 0.7	18.1 ± 1.3	0.009	18.2 ± 1.3	19.6 ± 1.6	0.583
Seed number (no. plant ⁻¹ × 10 ⁴)	2.83 ± 0.17	3.58 ± 0.22	0.024	3.77 ± 0.26	3.99 ± 0.30	0.869
Seed mass (mg seed ⁻¹)	0.48 ± 0.02	0.50 ± 0.02	0.530	0.49 ± 0.03	0.49 ± 0.03	0.744
Harvest index (g g ⁻¹ seed mass shoot mass ⁻¹)	0.30 ± 0.01	0.36 ± 0.02	0.112	0.34 ± 0.02	0.34 ± 0.03	0.877

Thus, vegetative-stage exposure to reduced R : FR was likely maladaptive for competitive ability during the vegetative stage, but not so for competitive ability during the reproductive stage in a sunlit environment.

Common Lambsquarters Morphology and Productivity at Physiological Maturity. For common lambsquarters exposed to partial shade during the reproductive stage and measured at physiological maturity, year-by-treatment interactions were not significant (data not shown), so data were pooled across years for analysis. R : FR treatment during the vegetative stage did not affect total shoot mass (g plant⁻¹), seed mass (mg seed⁻¹), or HI (g g⁻¹, total seed mass shoot mass⁻¹), but seed number (no. seed plant⁻¹) and total seed mass per plant (g plant⁻¹) were less for plants exposed to reduced R : FR than ambient R : FR (Table 3). Relationships between total shoot mass and total seed number per plant and total seed mass per plant indicated that the response of seed production to vegetative-stage R : FR treatments was ontogenetic and varied only as function of plant size (data not shown).

For common lambsquarters exposed to full sunlight during the reproductive stage, year-by-treatment interactions were not significant (data not shown), so data were pooled for analysis. For these plants, morphological characteristics were not affected by R : FR treatments during the vegetative stage (Table 3).

Few previous studies have investigated the effect of vegetative-stage exposure to altered R : FR on plant fecundity, which is commonly cited as a key aspect of plant fitness (Dudley and Schmitt 1996; Weinig and Delph 2001). Evidence from a few studies has shown that phytochrome-mediated elongation responses are advantageous for plants grown in dense (shaded) stands and disadvantageous (with respect to fitness as quantified by fecundity) for plants grown in less dense stands (Dudley and Schmitt 1996; Schmitt et al. 1995). For instance, in a rare example of research conducted under field conditions to assess the impact of vegetative-stage exposure to reduced R : FR on plant fitness (total reproductive output over the lifetime of the plant), Dudley and Schmitt (1996) exposed seedlings of jewelweed to either reduced or ambient R : FR, resulting in plants with either elongated or nonelongated phenotypes, respectively. Groups of each phenotype were subsequently transplanted into dense and open stands. Results indicated that in dense stands, elongated phenotypes were more fit than nonelongated types, whereas in open stands, nonelongated phenotypes were more fit than elongated types.

Conversely, our results suggest that exposure to reduced R : FR during the vegetative stage was maladaptive and associated with a reproductive disadvantage for common lambsquarters grown in partial shade during the reproductive

stage. However, exposure to reduced R : FR during the vegetative stage was not associated with a reproductive disadvantage for plants grown in full sunlight during the reproductive stage. These results are consistent with those of Causin and Wulff (2003), who reported that common lambsquarters plants exposed to reduced R : FR produced a similar number or fewer seeds than plants exposed to ambient R : FR. Although Mahoney and Swanton (2008) found that common lambsquarters seed production was about 50% less in low light levels compared with high light levels in growth cabinet studies; seed production was not affected by R : FR treatments at low light levels. Reduced seed production associated with R : FR-mediated shade avoidance responses may be due in part to accelerated flowering, which may serve to ensure species survival in highly competitive environments (Smith and Whitelam 1997).

Vegetative-stage exposure to reduced R : FR may also have been maladaptive for plants later exposed to partial shade because plastic responses early in life history can be associated with reduced plasticity to the same stimuli later in the life of the plant. Weinig and Delph (2001) demonstrated that velvetleaf (*Abutilon theophrasti* Medic.) seedlings exposed to an initial reduced R : FR treatment were elongated but that these elongated seedlings were subsequently less responsive to another exposure to R : FR when compared with seedlings that were initially treated with spectrally neutral shade. These authors also pointed out that their results highlight the importance of understanding how the expression of traits varies across life history stages and how early developmental responses may condition later responses.

The results of our study demonstrate that biomass production and morphology of common lambsquarters measured at initiation of flowering varied with vegetative-stage exposure to altered R : FR (Table 1). At the end of flowering, vegetative-stage exposure to reduced R : FR was associated with a competitive or adaptive advantage for plants grown in partial shade during flowering, but by physiological maturity, fecundity was less for these plants compared with plants exposed to ambient R : FR during the vegetative stage (Table 3). In contrast, vegetative-stage exposure to reduced R : FR was not associated with a reproductive disadvantage for plants grown in full sunlight during the reproductive stage (Table 3), but it was unclear whether this exposure was explicitly maladaptive.

Although demonstrable adaptive responses were induced by changes in light quality, these responses had associated costs, such as reduced fecundity or reduced responsiveness to light signals at later stages of development. However, responses of adaption or maladaptation associated with vegetative-stage R : FR exposure were inconsistent. Also, some of the effects of altered R : FR exposure were probably transient to some

extent (Dale and Causton 1992), as plants sense and respond to both R:FR and PAR throughout their life histories. Furthermore, responses to light quality environments are likely affected by responses to other important environmental variables (temperature, photoperiod, and wind) and the integration of all these results produces a particular phenotype (Smith 1982; Weinig 2000). Thus, progress toward gaining a more complete understanding of phenotypic plasticity, which may be the most critical determinant of plant competitive ability (Aphalo and Ballaré 1995), will occur more readily when the effects of these interacting variables on plant morphology and development are more clearly understood.

Sources of Materials

¹ 20-10-20 General Purpose Peter's Professional Fertilizer, Scotts-Sierra Horticultural Products Company, 14111 Scottslawn Rd., Marysville, OH 43401.

² LI 3100C Area Meter, LiCor Biosciences, 4421 Superior Street, Lincoln, NE 68504. <http://www.licor.com>

³ Oregon Seed Blower, Hoffman Manufacturing, Inc., 16541 Green Bridge Rd., Jefferson, OR 97352.

⁴ ASD Field Spec Spectroradiometer, Analytical Spectral Devices, Inc., 5335 Sterling Drive, Suite A, Boulder, CO 80301. info@asdi.com

⁵ LI-191 Quantum Line Sensor, LiCor Biosciences, 4421 Superior Street, Lincoln, NE 68504. <http://www.licor.com>

⁶ Kestrel 3000 Pocket Weather Meter, Nielsen-Kellerman Co., 21 Creek Circle, Boothwyn, PA 19061. <http://www.nkhome.com/ww/3000.html>

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