

Effects of canopy shade on the morphology, phenology, and seed characteristics of Powell amaranth (*Amaranthus powellii*)

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Characterizing the response of weeds to canopy shade is important for improved understanding of crop–weed competition and weed population dynamics. In 2000 and 2001, field studies were conducted in central New York state to examine the influence of three neighbor types (none, broccoli, or broccoli plus winter rye) and two locations (between or within rows of broccoli) on the morphology, phenology, and seed germination characteristics of Powell amaranth. Reductions in light availability and in the ratio of red-to-far red light were associated with increases in (1) partitioning of dry weight to stem tissue, (2) stem elongation, and (3) specific leaf area. Canopy shade also resulted in fewer main leaves at flowering and a reduced rate of leaf appearance but had no effect on the number of days to flowering. The relationship between Powell amaranth fecundity and aboveground dry weight was allometric, with both parameters declining significantly under competition. The weight of seeds produced did not vary significantly according to the competitive environment experienced by the maternal parent. However, the germination percentage of viable seeds was 40 to 50% lower for seeds maturing on plants grown under competition than without competition. Reductions in the number of main leaves at flowering and increased seed dormancy may be adaptive responses to canopy shade. Both mechanistic crop–weed competition models and population dynamic models would benefit from incorporation of data on the phenotypic plasticity of morphology, phenology, and seed germination characteristics of weeds.

Nomenclature: Powell amaranth = green pigweed, *Amaranthus powellii* S. Wats. AMAPO; broccoli, *Brassica oleracea* L. var. *italica* PLENCK ‘Marathon’; winter rye, *Secale cereale* L.

Key words: Shade avoidance, flowering time, seed dormancy, stem elongation, specific leaf area, allometry, phenology, red-far red ratio, competition, light quality.

Characterizing the response of weeds to shade is critical for improved understanding of crop–weed competition and weed population dynamics. Crop–weed competition models depend on estimation of plant phenology, carbon partitioning, height, and leaf area development (Kropff and van Laar 1993). Similarly, population dynamic models depend on estimates of weed fecundity and seed germination characteristics (Cousens and Mortimer 1995). Unfortunately, for many species, inadequate empirical information is available to parameterize such models under different competitive environments (Bussan and Boerboom 2001). Often, modelers have had to use data from plants grown under artificial conditions in the glasshouse or under noncompetitive conditions in the field (Cousens and Mortimer 1995). Because weeds show such a high degree of phenotypic plasticity in response to competition (Ballaré 1999; Morgan and Smith 1976), such experimental practices may limit the usefulness of mechanistic models (Ball and Shaffer 1993; Brainard and Bellinder 2004a; McDonald and Riha 1999).

Under competition for light, plants exhibit several well-known “shade-avoidance” responses, including accelerated stem extension growth, retarded leaf development, and strengthened apical dominance (Morgan and Smith 1976). These shade-avoidance responses are largely mediated by light-stable phytochromes in response to shifts in the ratio of red-to-far red light (R–FR), although changes in irradi-

ance and shifts in blue light also play an important role (reviewed in Ballaré 1999). Such shade-avoidance responses may improve plant fitness by increasing capture of the most limiting resource under diverse environmental conditions (Bradshaw 1965; Sultan 1987, 2000). Stem elongation in particular has received considerable attention as an example of “adaptive plasticity” (Schmitt 1997; Sultan 2000).

The physiological mechanisms and ecological consequences of shifts in flowering time in response to shade are less well understood. Under artificial conditions, plants subjected to reduced R–FR ratios often flower both at a lower node and in fewer days than nonshaded controls receiving the same total irradiance (Davis and Simmons 1994; Kadman-Zahavi and Ephrat 1974; Smith and Whitelam 1997). In contrast, under reduced irradiance conditions, the rate of leaf appearance generally declines, and the timing of flowering is often delayed (McLachlan et al. 1993a). Under canopy shade, both the R–FR ratio and irradiance decline, and, thus, the impact of shade on the timing of flowering is difficult to predict. In most cases, competition results in either no change or a delay in the onset of reproduction (Weiner 1988). Despite the importance of flowering time in determining plant fitness (Cohen 1976; King and Roughgarden 1982; Shitaka and Hirose 1998), the effect of shade on flowering time has received relatively little attention in the ecological literature. Smith and Whitelam (1997) sug-

gested that reductions in flowering time in response to reduced R–FR ratios may be adaptive because it increases the probability of seed production in the face of impending death from competition. Alternatively, changes in flowering time may be the indirect consequence of physiological trade-offs and may be maladaptive if they result in premature partitioning away from light-capturing tissue (Cohen 1976).

Plants may also respond to competition for light through changes in the dormancy status of their seeds. Increased dormancy in seeds maturing under shade may be another form of adaptive shade avoidance because germination under competitive environments might reduce the probability of seedling survival. In fact, increased dormancy of seeds maturing under low R–FR ratios has been observed for *Aradopsis thaliana* (McCullough and Shropshire 1970) as well as *Piper auritum* (Orozco-Segovia et al. 1993). In redroot pigweed (*Amaranthus retroflexus* L.), Kigel et al. (1977) found that seeds maturing under reduced irradiance (without a concomitant reduction in the R–FR ratio) and short day lengths were less dormant than those receiving high irradiance under short day lengths (although the effect of irradiance on seed dormancy was the opposite under long day lengths). Alternatively, changes in characteristics of seeds maturing under high competition may be an indirect consequence of physiological constraints such as reduced photosynthate available for seed coat development. The latter explanation may be more helpful for understanding why some species including velvetleaf (*Abutilon theophrasti* Medicus) (Bello et al. 1995; Nurse and DiTommaso 2004), exhibit reductions in dormancy under canopy shade. In any case, understanding the impact of maternal competitive environment on the dormancy status of seeds may be helpful for improving models of population dynamics because such models are often sensitive to assumptions relating to seed germinability (Cousens and Mortimer 1995; Grundy 2003).

Although many shade-avoidance responses have been investigated under greenhouse conditions, few field studies exist. Although growth chamber studies can provide interesting information on the mechanisms of shade-avoidance responses, they may not reflect responses likely to occur in the field. Among studies investigating shade effects on weeds, many use neutral shade cloth (e.g., Kigel et al. 1977). Because canopy shade is not neutral, and light quality often has a very different effect on plant characteristics than irradiance (Ballaré 1999; Rajcan et al. 2002), results from such studies may not accurately reflect responses likely to occur under leaf canopies.

The objectives of this study were to evaluate the influence of competition for light under field conditions on characteristics of Powell amaranth typically associated with shade avoidance (i.e., specific stem length [SSL], specific leaf area [SLA], partitioning coefficients), as well as on characteristics less often considered part of the shade-avoidance syndrome, namely flowering time and seed dormancy.

Materials and Methods

Experimental Procedures

Field experiments were conducted at the H. C. Thompson Vegetable Research Farm in Freeville, NY, in 2000 and 2001 on a Howard gravel loam soil (loamy-skeletal mixed mesic Glosoboric Hapludalf). This experiment was part of

a larger experiment with multiple objectives reported elsewhere (Brainard and Bellinder 2004a, 2004b). The main factor analyzed in this research was neighbor type: none, broccoli, or broccoli and winter rye. Within plots containing broccoli, Powell amaranth was grown both between and within rows. Each treatment was replicated five times in a randomized complete block design.

The experimental fields were moldboard plowed, disked, fertilized with 785 kg ha⁻¹ of 13:13:13 (N–P–K) fertilizer, and field cultivated before transplanting. Ammonium nitrate fertilizer (34:0:0) was side-dressed 2 to 3 wk after transplanting at a rate of 165 kg ha⁻¹. These relatively high fertilizer rates were used to minimize belowground competition for nutrients. Likewise, natural rainfall was supplemented with frequent irrigation to minimize competition for water.

Broccoli, MarathonTM, was seeded in the greenhouse in late June and transplanted at the three- to five-leaf stage on July 20 in both years. Broccoli transplants were spaced at 38 cm in-row and 76 cm between-row. Plots were two rows wide and 4.6 m long. Immediately after broccoli transplanting, winter rye was seeded broadcast into the standing broccoli crop at a rate of 125 kg ha⁻¹ using an S-tine cultivator with a seed box mounted in front of the tines. The cultivator was set so that broadcast rye seed was incorporated into the top 2.5 to 5 cm of soil in both the between-row and in-row environments.

Powell amaranth seeds were collected from between 20 and 30 plants in adjacent vegetable production fields in the fall before each trial and stored at 5 C until the next summer. In plots containing broccoli or broccoli and rye, 12 Powell amaranth plants were established in each location (between-row or in-row) within each plot by hand sowing seeds immediately after rye seeding, and thinned to one Powell amaranth plant per location at the two-leaf stage. Plants in the “between-row” competitive environments were seeded equidistant from neighboring rows of broccoli (at least 38 cm from nearest broccoli plant), whereas those in the “in-row” competitive environment were seeded equidistant from neighboring broccoli plants within a row (19 cm from the nearest broccoli plant). Powell amaranth in the no-neighbor treatment was sown directly down the center of each plot in a single row, with 28 cm between plants. In the no-neighbor treatment, every other plant was removed at the time of flowering (to obtain six plants per plot spaced at 56 cm) to minimize intraspecific competition. In all plots, all weeds other than the seeded Powell amaranth were removed through a combination of cultivating and hoeing.

Light Measurements

In 2000, the availability of light to Powell amaranth plants was measured by using a CI-110 Digital Plant Canopy Imager.¹ Digital images were taken under cloudy skies or before sunrise and analyzed to calculate the solar beam transmission coefficient. In 2001, light availability was estimated using a 1-m line sensor.² Total incident photosynthetic photon flux density (PPFD) was measured above each plot before each measurement of transmitted PPFD. Transmitted PPFD was measured by placing the line sensor parallel to crop rows either directly adjacent to broccoli stems (in-row) or equidistant from adjacent rows (between-row). Measurements were taken between 11:00 A.M. and 1:00 P.M.

at approximately half the average Powell amaranth height 22 and 38 d after transplanting (DATR) in 2000 and 25 and 41 DATR in 2001. Light measurements 41 DATR in 2001 were not made in the in-row environment because of substantial interference of the large broccoli plants with the 1-m line sensor at half the height of the Powell amaranth plants.

In 2001, the ratio of red (655 to 665 nm)-to-far red (725 to 735 nm) light (R–FR) was measured using a LI-COR 1800 spectroradiometer with remote sensor.³ Because R–FR perception at the stem is thought to be most relevant for stem elongation (Ballaré et al. 1987), spectral measurements were made in the horizontal direction at one-half the average height of weed target plants. Measurements were made on August 9, 17, 20, and 30. Measurements were initially made in all four cardinal directions but subsequently limited to the northern orientation because of minimal directional variation. No measurements were made in the in-row environment on August 30 because no change in the R–FR ratio had been observed between the previous two measurement dates.

Plant Measurements

Two plants from each plot were monitored and the time of flowering recorded when floral primordia were visible to the naked eye. At flowering, plant height and the number of leaves on the main stem (node number) were recorded. Plants were then clipped at the soil surface and divided into leaf blade and stem plus petiole tissue. In addition, a random subsample of 8 to 10 leaf blades from each plant was separated and photocopied to estimate SLA. Each plant component was dried for 5 d at 65 C and weighed. Photocopied leaf images were scanned and analyzed for leaf area using Scion Image® software.⁴ In late September, just before the first hard frost (65 DATR), all remaining weeds were harvested and separated into leaf blade, stem plus petiole, and reproductive parts. Leaf blade, stem, and petiole tissues were dried for 5 d at 65 C and weighed. To avoid loss of seed viability, reproductive tissue was air dried for 20 d at approximately 30 C before weighing.

Powell amaranth seed was separated by sieving and air column separation (see Brainard and Bellinder 2004a). Seeds were weighed, and seed number was estimated from the weight of 100 randomly selected seeds. A subsample of 100 seeds from each plot was dried for 48 h at 90 C and weighed. Seeds from both years were stored dry in glass jars at approximately 20 C and tested for germination and viability in November 2001. After initial germination testing, jars were transferred to a refrigerator at 5 C and stored dry for an additional 2 yr before retesting in November 2003. At each testing date, the germinability of 100 (November 2001) or 50 (November 2003) seeds from two plants from each plot were tested in 9-cm-diam petri dishes in a growth chamber set at 30/25 C (day/night) with a photoperiod of 16/8 (light/dark) and PPFD of approximately 250 (2001) or 150 (2003) $\mu\text{mol m}^{-2} \text{s}^{-1}$. Germinated seeds (radicle > 2 mm) were counted and removed every 24 h for 10 d. Seeds that did not germinate during this period were transferred to petri dishes containing 5 ml of gibberillic acid (GA_3 ; 0.002 M) and placed in an incubator at 35/30 C (day/night) with a photoperiod of 16/8 (light/dark) and PPFD of approximately 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for an additional

5 d to induce further germination. Seeds that did not germinate with GA_3 (< 5% of seeds) were tested for viability using tetrazolium chloride (1%).

SLA ($\text{cm}^2 \text{g}^{-1}$) was calculated by dividing the leaf area of the leaf subsamples by the leaf dry weight. SSL (cm g^{-1}) was calculated by dividing the height of each individual by its stem dry weight. Following Stoller and Myers (1989), the stem leaf ratio (SLR) was calculated by dividing the dry weight of stem tissue by the dry weight of leaf tissue. The number of degree days to flowering was calculated using average temperature data from a local weather station and assuming a base temperature of 10 C (McLachlan et al. 1993a). Percentage germination was calculated as the percentage of viable seed, not total seed number.

Statistical Analysis

Data were subjected to analysis of variance using the general linear model procedures of the Statistical Analysis System (SAS 1999). Contrasts were used to compare mean responses of (1) plants grown without competition vs. plants grown with competition (“broccoli effect”) and (2) plants competing with broccoli vs. those competing with both broccoli and rye (“rye effect”). Separate contrasts were conducted for each location (between-row vs. in-row). Weed dry weight and seed number were log transformed and percentage germination data arcsine square root transformed before statistical analysis to improve assumptions of normality and equal variance of population distributions. The regression procedures of SAS (1999) were used to test whether shoot dry weight and seed production were related according to the allometric equation (Persall 1927):

$$\ln(S) = m \cdot \ln(W) + b \quad [1]$$

where S is the number of seeds per plant, W is the total shoot dry weight of the plant in grams, and m and b are the slope and intercept of the best-fit regression line.

Results and Discussion

Light Availability and Light Quality

The presence of a broccoli crop significantly reduced light availability at half the Powell amaranth height within 25 DATR in both years (Table 1). For example, in 2000, light availability within rows of broccoli was 39% at 22 DATR and 9% at 38 DATR. In 2000, light availability for plants emerging between-row was further reduced by the presence of winter rye. For example, at 22 DATR, the addition of rye to the between-row environment reduced light availability from 95 to 42%. Within rows of broccoli, the addition of rye had no significant effect on measured light availability in either year. Rapid shading from broccoli negated the effect of rye in-row.

Although no direct statistical comparisons between years can be made (due to differences both in the timing and method for measuring solar irradiance), cumulative light availability to Powell amaranth was greater in 2001 compared with 2000, especially in competitive environments. PPFD from a local weather station was approximately 11% greater in 2001 than in 2000 (Brainard and Bellinder 2004b). In addition, higher average temperatures in 2001 (19.4 C) compared with 2000 (18.3 C), and much higher

TABLE 1. Light availability at one-half the height of Powell amaranth under different competitive environments, 2000 and 2001. Data are means with standard errors shown in parentheses.^a

No. Treatment	Light availability ^b			
	2000		2001	
	22 DATR	38 DATR	25 DATR	41 DATR
	%			
1 None	100 (0)	100 (0)	100 (0)	100 (0)
2 Broccoli				
Between-row	95 (2)	41 (10)	77 (5)	61 (9)
In-row	39 (9)	9 (2)	22 (6)	NA
3 Broccoli + rye				
Between-row	42 (1)	23 (9)	62 (10)	46 (8)
In-row	22 (0)	7 (2)	17 (3)	NA
	P values			
Contrasts				
Broccoli effect ^c				
Between-row	0.014	< 0.001	0.001	0.002
In-row	< 0.001	< 0.001	< 0.001	NA
Rye effect ^d				
Between-row	0.001	0.051	0.096	0.258
In-row	0.198	0.814	0.584	NA

^a Abbreviations: DATR, days after transplantation; NA, not available.

^b Photosynthetically active radiation at one-half the Powell amaranth height divided by PAR above broccoli canopy.

^c Broccoli effect compares treatments 1 vs. (2 and 3).

^d Rye effect compares treatment 2 vs. 3.

temperatures during the first week after broccoli transplanting in 2001 (22.3 °C) compared with 2000 (17.1 °C), favored more rapid emergence and growth of the warm-adapted C₄ Powell amaranth compared with the cool-adapted C₃ rye and broccoli plants (Brainard and Bellinder 2004a, 2004b). Cool temperatures (e.g., 2000) delay the relative emergence time of Powell amaranth and shift the competitive advantage toward rye and broccoli (Brainard and Bellinder 2004b). Broccoli yield and rye biomass in a companion study in a neighboring field were not significantly different in 2000 and 2001 (Brainard and Bellinder 2004b). However, Powell amaranth plants in 2001 were approximately twice as tall as plants in 2000 for most treatments (Table 2), resulting in greater light interception under competition.

The pattern of reductions in the R–FR ratio due to broccoli (Figure 1) were similar to the pattern of reductions in light availability in 2001 (Table 1). However, whereas rye had no detectable effect on measured light availability in 2001, it did significantly and rapidly reduce the R–FR ratio for weeds growing between rows. For example, by 28 DATR, the R–FR ratio was 0.59 in broccoli, compared with only 0.11 in broccoli plus rye treatments in the between-row environment. Horizontally reflected far-red light from neighboring rye plants (as opposed to increased filtering of red light from direct shade) probably accounts for this difference. Ballaré et al. (1987) demonstrated that such early reductions in the R–FR ratio due to horizontally reflected far-red light can induce shade-avoidance responses before actual shading (reductions in irradiance) begins.

Powell Amaranth Biomass

Powell amaranth aboveground dry weight both at flowering and at the termination of the experiment was significantly

influenced both by broccoli and rye in the between-row location (Table 2). However, as with light availability, the addition of rye had no significant effect on Powell amaranth dry weight in the in-row environment. Belowground dry weight was not measured in this experiment. Generally, canopy shade either results in little change (Brainard and Bellinder 2004b) or an increase (Causin and Wulff 2003; Rajcan et al. 2002) in partitioning to shoot tissue relative to root tissue.

Although no statistical comparisons can be made, Powell amaranth dry weight was far greater in 2001 compared with 2000, especially under competitive environments (Table 2). This difference is probably attributable to warmer temperatures and higher irradiance in 2001 compared with 2000, which resulted in more rapid emergence and growth of Powell amaranth relative to broccoli and rye (Brainard and Bellinder 2004b). Using a simulation model in combination with historic climate data, Brainard and Bellinder (2004a) showed that such year to year variation is not unusual and that results for 2000 are more representative of long-term averages than those for 2001.

Phenology

Main leaf (node) number at flowering was significantly lower for plants grown under competition than for plants grown alone (Table 3). For example, in 2000, main leaf number was reduced from 12 for weeds growing alone to eight for weeds growing within rows of broccoli and rye. In 2001, the presence of broccoli resulted in significantly fewer main leaves at flowering, but rye had no additional effect on main leaf number. These results are consistent with previous studies demonstrating a reduction in main leaf number due to reductions in the R–FR ratio observable in many

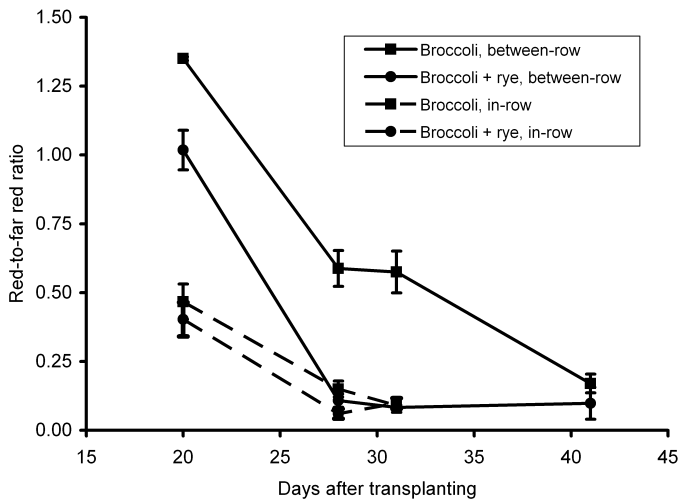


FIGURE 1. Mean (\pm SE) ratio of red-(655 to 665 nm)-to-far red (725 to 735 nm) light under different competitive environments, 2001. Measurements were taken horizontally at half the height of Powell amaranth grown in competition with broccoli (squares) or broccoli and rye (circles), either between-row (solid lines) or in-row (dotted lines).

plants (Smith and Whitelam 1997) including barley (*Hordeum vulgare* L.) (Davis and Simmons 1994) and redroot pigweed (Kadman-Zahavi and Ephrat 1974). Studies involving phytochrome-deficient mutants also suggest the importance of perceiving the R–FR ratio in controlling the reductions in main leaf number at flowering (Devlin et al. 1999; Halliday et al. 1994).

Reductions in the leaf appearance rate in response to competition were similar to reductions in main leaf number at flowering (Table 3). For example, in 2000, the leaf appearance rate was 33% lower under the most-shaded cropping environment (broccoli plus rye in-row) than the least-shaded environment (none). These results are consistent with findings from other studies demonstrating slower leaf appearance under canopy shade or reduced irradiance. Leaf appearance rate of redroot pigweed was reduced 42 to 80% under shade from corn (*Zea mays* L.) (McLachlan et al. 1993a). Growth chamber experiments with redroot pigweed suggest that such declines in leaf appearance rate are the result of reduced irradiance but not reduced R–FR ratio (Rajcan et al. 2002).

Competitive environment had no significant effect on the number of degree days to flowering in either year (Table 3). Mean number of degree days to flowering was 266 in 2000 and 258 in 2001.

Our results are consistent with the observation that competition generally results in either no change or a delay in flowering (Weiner 1988). Apparently, under field conditions, reductions in the number of main leaves at flowering due to reduced R–FR ratio were largely offset by reductions in the leaf appearance rate due to reduced irradiance. The relative magnitude of these two effects may determine the impact of canopy shade on the timing of flowering. In vegetable production systems with relatively short canopies, the relative importance of R–FR ratio effects may be greater than in production systems involving taller crops like corn.

Reductions in main leaf number at flowering due to a reduced R–FR ratio may be an adaptive response that prevents delays in flowering under canopy shade and increases

the probability of seed production in the face of impending death through competition (Smith and Whitelam 1997). On the other hand, reductions in the main leaf number at flowering may be maladaptive under some competitive environments because it involves the potentially costly trade-off associated with reductions in allocation of photosynthate to light harvesting tissue (leaves and stem) (Cohen 1976; Shitaka and Hirose 1998).

Morphological Responses

Competition from broccoli (in-row) and from broccoli plus rye significantly increased Powell amaranth SLA (leaf area divided by leaf dry weight) in 2000 (Figure 2A). In 2000, SLA values increased from 200 cm² g⁻¹ in the absence of competition to almost 400 cm² g⁻¹ in competition with broccoli in-row. In 2000, competition with broccoli plus rye resulted in a doubling of SLA relative to broccoli alone in both the between-row and in-row locations ($P = 0.0139$ and $P = 0.0020$, respectively). In contrast, in 2001, competition with broccoli had no significant effect on SLA (Figure 2B). In 2001, Powell amaranth plants competing with broccoli plus rye had significantly greater SLA than those competing with broccoli alone in the between-row environment ($P = 0.0139$) but not in the in-row environment ($P = 0.6562$).

SLA generally declines in response to reductions in the R–FR ratio (Morgan and Smith 1976), reductions in irradiance (Rajcan et al. 2002; Stoller and Myers 1989), and decreased temperatures (Charles-Edwards et al. 1986). The effect of temperature may explain higher SLA values under the warmer conditions of 2001 compared with 2000, in the absence of competition. Smaller differences in SLA across competitive environments in 2001 were probably the result of smaller reductions in light availability or R–FR ratio associated with broccoli and rye plots compared with 2000.

It is possible that observed differences in SLA across competitive environments reflect the indirect effect of changes in plant size rather than a direct plastic response to competition. Such allometric effects may more effectively explain shifts in partitioning and other plant characteristics than phenotypic plasticity (Weiner and Thomas 1992). However, evidence from other studies demonstrates that under competitive environments, SLA did not vary significantly with size for either redroot pigweed (Knezevic et al. 1999; Senesac 1985) or Powell amaranth (Senesac 1985). SLA values for Powell amaranth were consistent with reported values from greenhouse-grown plants of both Powell amaranth and redroot pigweed (Rajcan et al. 2002; Senesac 1985) but significantly higher than reported values for field-grown redroot pigweed (Knezevic et al. 1999; McLachlan et al. 1993b).

As with SLA, the SSL (ratio of stem length to stem dry weight) increased significantly under more competitive environments (Figures 2C and 2D). SSL ranged from 38 to 581 cm g⁻¹ in 2000 and from 23 to 58 cm g⁻¹ in 2001 in the least (none) and most (broccoli plus rye in-row) competitive environments, respectively. In both years, plants grown in competition with broccoli had higher SSLs than those grown alone ($P = 0.0012$; $P = 0.0001$). The addition of rye to treatments increased SSL in 2000 ($P = 0.0033$) but not in 2001 ($P = 0.3490$). Between-row plants grown in competition with broccoli and rye were almost twice as

TABLE 3. Main leaf number at flowering, rate of leaf appearance, and degree days to flowering for Powell amaranth under different competitive environments, 2000 and 2001. Data are means with standard errors shown in parentheses.

No. Treatment	Main leaf number at flowering		Rate of leaf appearance		Degree days to flower	
	2000	2001	2000	2001	2000	2001
1 None	12.2 (0.6)	14.4 (0.4)	4.7 (0.3)	5.8 (0.0)	260 (8)	247 (7)
2 Broccoli						
Between-row	12.4 (0.8)	13.2 (0.2)	4.8 (0.4)	5.3 (0.2)	260 (8)	250 (5)
In-row	9.8 (0.7)	12.6 (0.2)	3.7 (0.3)	4.8 (0.2)	266 (4)	263 (11)
3 Broccoli + rye						
Between-row	9.2 (0.9)	12.6 (0.8)	3.4 (0.4)	4.8 (0.3)	271 (3)	265 (5)
In-row	8.0 (0.7)	11.4 (0.5)	3.0 (0.3)	4.3 (0.1)	271 (4)	267 (7)
	P values					
Contrasts						
Broccoli effect ^a						
Between-row	0.125	0.035	0.141	0.001	0.381	0.271
In-row	0.002	0.002	0.003	< 0.001	0.193	0.062
Rye effect ^b						
Between-row	0.006	0.437	0.007	0.033	0.138	0.189
In-row	0.090	0.130	0.128	0.032	0.455	0.726

^a Broccoli effect compares treatments 1 vs. (2 and 3).

^b Rye effect compares treatment 2 vs. 3.

tall as those grown with broccoli alone at the time of flowering (Figure 3; Table 2), despite accumulating only 18% of the dry weight (data not shown). Mechanistic models of weed-crop competition often implicitly assume that plant height is independent of competitive environment or reduced by competition (Kropff and van Laar 1993). Our results suggest that under some situations of crop-weed competition this assumption is questionable and may lead to significant errors in model predictions.

Biomass partitioning to stem and leaf tissue during the vegetative stage was significantly influenced by competitive environment in both years (Figures 2C and 2F). In both years, plants grown in competition with broccoli allocated more dry weight to stem tissue relative to leaf tissue ($P < 0.0001$ and $P = 0.0288$). For example, in 2000, the stem-leaf dry weight ratio (SLR) ranged from 0.35 for plants grown in the absence of competition to 1.13 for between-row plants grown under competition with broccoli and rye. In 2000, the addition of rye increased partitioning to stem tissue for plants growing in the between-row environment ($P = < 0.0001$) but not for those growing in the in-row environment ($P = 0.2093$). However, in 2001, the addition of rye had no effect on partitioning.

The observed increases in biomass partitioning to stem tissue under competition in this study most likely represent plastic responses to reductions in the R-FR ratio resulting from competition. In growth chamber experiments involving redroot pigweed, Rajcan et al. (2002) found that reductions in the R-FR ratio (while holding irradiance fixed) resulted in increases in biomass partitioning to stem tissue, whereas reductions in irradiance (while holding R-FR ratio fixed) resulted in decreases in biomass partitioning to stems. Reductions in irradiance (without changes in the R-FR ratio) were also correlated with reductions in partitioning to stem tissue in tumble pigweed (*Amaranthus albus* L.) (Stoller and Myers 1989). In contrast with our results, corn-induced

shade resulted in reduced biomass partitioning to stem tissue in redroot pigweed (McLachlan et al. 1993b). Such differences in biomass partitioning may be the indirect consequence of reduced irradiance on plant size or developmental stage (Samson and Werk 1986; Weiner and Thomas 1992). Because *Amaranthus* spp., like most plants, partition more dry weight to stem tissue relative to leaf tissue later in their development (Knezevic et al. 1999; Kropff and van Laar 1993; Senesac 1985), delayed development or reduced size should result in a reduction in SLR. However, because SLR increased in this study, allometry is not a plausible explanation for observed differences in partitioning. The highest observed SLR occurred in the broccoli plus rye (between-row) treatment that was characterized by significant reductions in horizontal R-FR ratios (Figure 1) but relatively modest reductions in light availability (Table 1). Plants growing in-row also experienced reductions in R-FR ratios as well as greater reductions in irradiance than between-row plants. This additional reduction in irradiance of in-row plants may have tempered increases in SLR.

Reproductive Allocation and Seed Production

Increased competition led to a significant reduction in the percentage of total plant weight allocated to seeds in 2000 but not in 2001 (data not shown). However, in contrast to SLR, differences in allocation to seeds across competitive environments within a given year can probably be explained largely by plant size (Samson and Werk 1986).

The fit of the allometric equation relating total Powell amaranth dry weight to total seed number was better in 2001 ($R^2 = 0.97$) than in 2000 ($R^2 = 0.84$) (Figure 3). Deviations from the allometric equation in 2000 may be due to the greater level of competition observed in that year. Powell amaranth subjected to greater competition may undergo weight-independent changes in biomass allocation to-

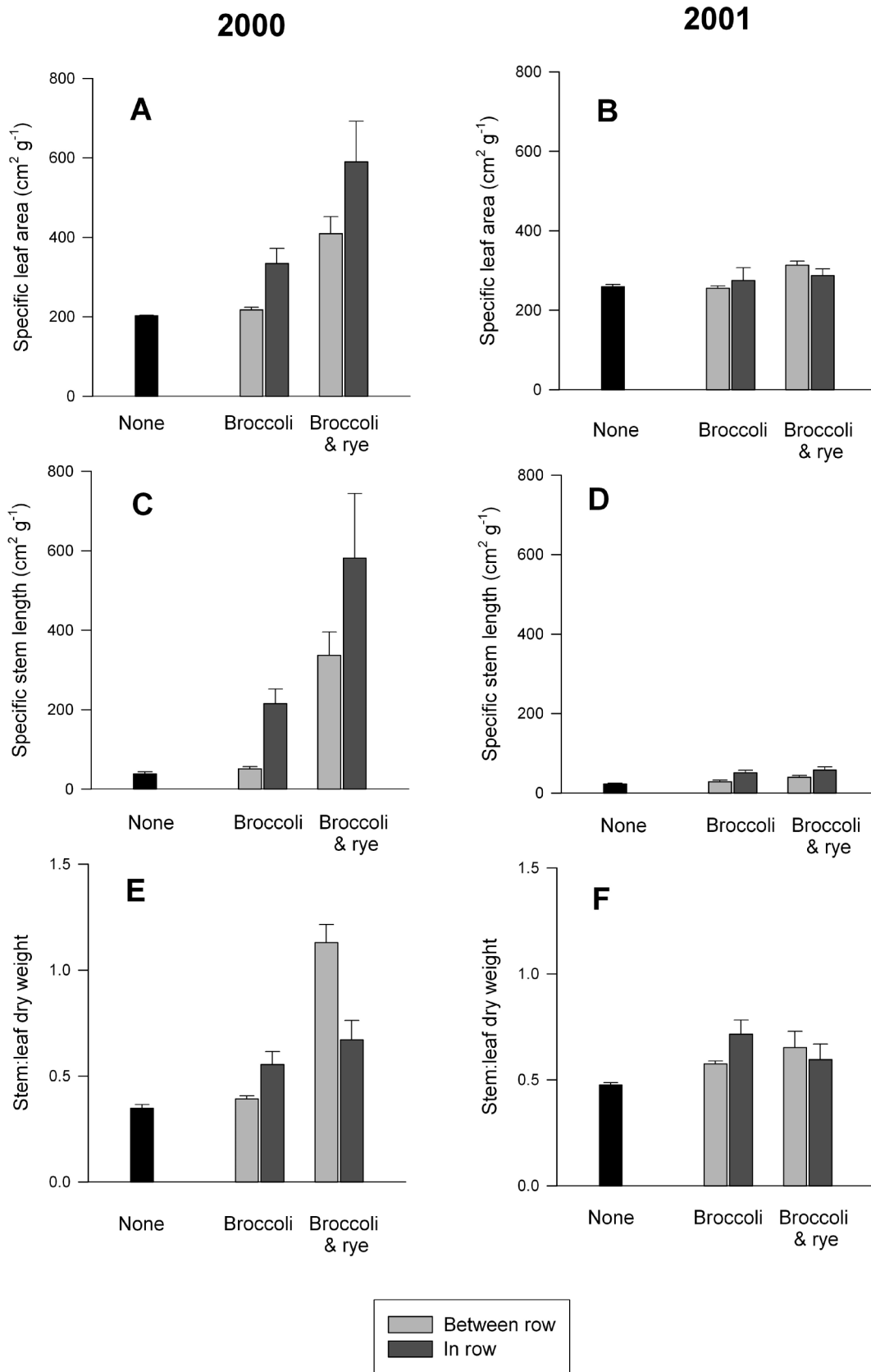


FIGURE 2. Mean (\pm SE) specific leaf area (A and B), specific stem length (C and D), and ratio of stem dry weight to leaf dry weight (E and F) at the time of flowering (20–25 DATR) in 2000 (A, C, and E) and 2001 (B, D, and F) for Powell amaranth growing in different competitive environments. For plots containing broccoli, weeds growing both in-row and between-row are presented.

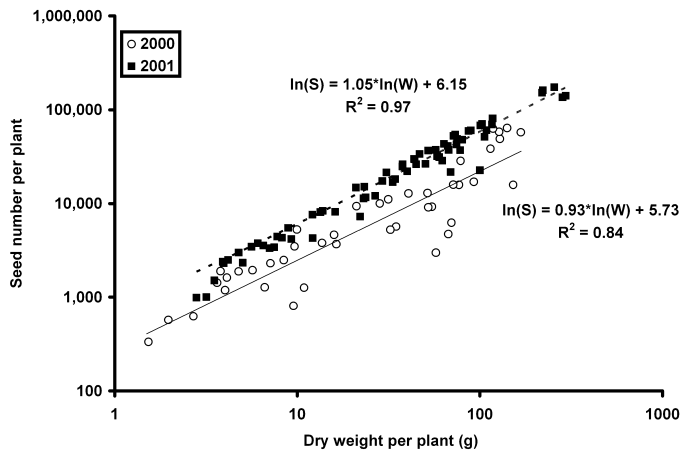


FIGURE 3. Regression of natural logarithm of seed number per plant vs. natural logarithm of total dry weight for Powell amaranth in 2000 and 2001.

ward structures that increase competitive ability (e.g., stem), leaving less assimilate for reproduction (Weiner 1988). However, insufficient data are available to test this hypothesis in our experiments.

The nature of the relationship between plant weight and seed number (Equation 1: parameters m and b) also varied across the 2 yr (Figure 3). Lower seed production for a given weight observed in 2000 may be due to a lower level of seed maturity at the time of broccoli harvest. Previous studies involving redroot pigweed have also found considerable variation across years in the relationship between seed weight and either plant size (McLachlan et al. 1995) or plant height and stem diameter (Mohler and Callaway 1995).

Such year to year variation in fecundity–weight relationships implies that the use of a single allometric equation may lead to significant errors in model predictions (Brainard and Bellinder 2004b; Cousens and Mortimer 1995). However, use of allometric equations may be an improvement on the assumption used in some models (Kropff and van Laar 1993) of a fixed harvest index (partitioning coefficient to reproduction) for weeds because harvest indices often vary considerably with plant size (Samson and Werk 1986). Partitioning coefficients may also vary considerably with competitive environment (Knezevic et al. 2001), although most studies fail to separate the effects of plant size and competition on reproduction (Weiner 1988).

Seed Characteristics

Powell amaranth seed weight was not influenced by maternal competitive environment (Table 4). The competitive environment experienced by the mother plant also had little effect on seed viability (Table 4). Seeds from the 2000 season that had matured in competition with broccoli and rye had slightly lower viability (88%) than those maturing with broccoli alone (98%) when tested 1 yr after harvest. Similarly, seeds from 2001 maturing in competition with broccoli had slightly lower viability (90%) than those maturing without competition (97%) after storage for 2 yr. However, in all other cases, maternal competitive environment had no significant effect on viability. Overall, seed viability declined during 2 yr of storage from 93 to 88% for 2000 seed and from 94 to 91% for 2001 seed.

Powell amaranth seed germination at 30/25 C was not significantly different for plants growing in-row and be-

TABLE 4. Seed dry weight and percentage viability of seeds maturing under different competitive environments, 2000 and 2001. Seed viability was tested both in November 2001 and November 2003. Data are means with standard errors shown in parentheses.

No. Treatment	Seed dry weight		Seed viability			
	2000	2001	2000 ^a		2001	
			November 1 ^b	November 3	November 1	November 3
mg/100 seeds		%				
1 None	44 (2)	45 (2)	94 (2)	88 (2)	93 (3)	97 (2)
2 Broccoli						
Between-row	46 (1)	47 (2)	98 (1)	92 (3)	97 (3)	90 (1)
In-row	38 (3)	46 (2)	93 (4)	85 (6)	92 (5)	90 (1)
3 Broccoli + rye						
Between-row	45 (2)	46 (1)	88 (2)	88 (5)	97 (2)	86 (4)
In-row	NA ^{c,d}	44 (2)	NA	NA	92 (4)	92 (2)
P values						
Contrasts						
Broccoli effect ^e						
Between-row	0.687	0.669	0.764	0.427	0.157	0.019
In-row	0.086	0.793	0.756	0.552	0.802	0.119
Rye effect ^f						
Between-row	0.959	0.763	0.029	0.806	0.963	0.238
In-row	NA	0.397	NA	NA	0.989	0.717

^a Year of harvest.

^b Date of viability/germination testing.

^c Insufficient seeds were produced to measure seed weight and viability.

^d Abbreviation: NA, not available.

^e Broccoli effect compares treatments 1 vs. (2 and 3).

^f Rye effect compares treatment 2 vs. 3.

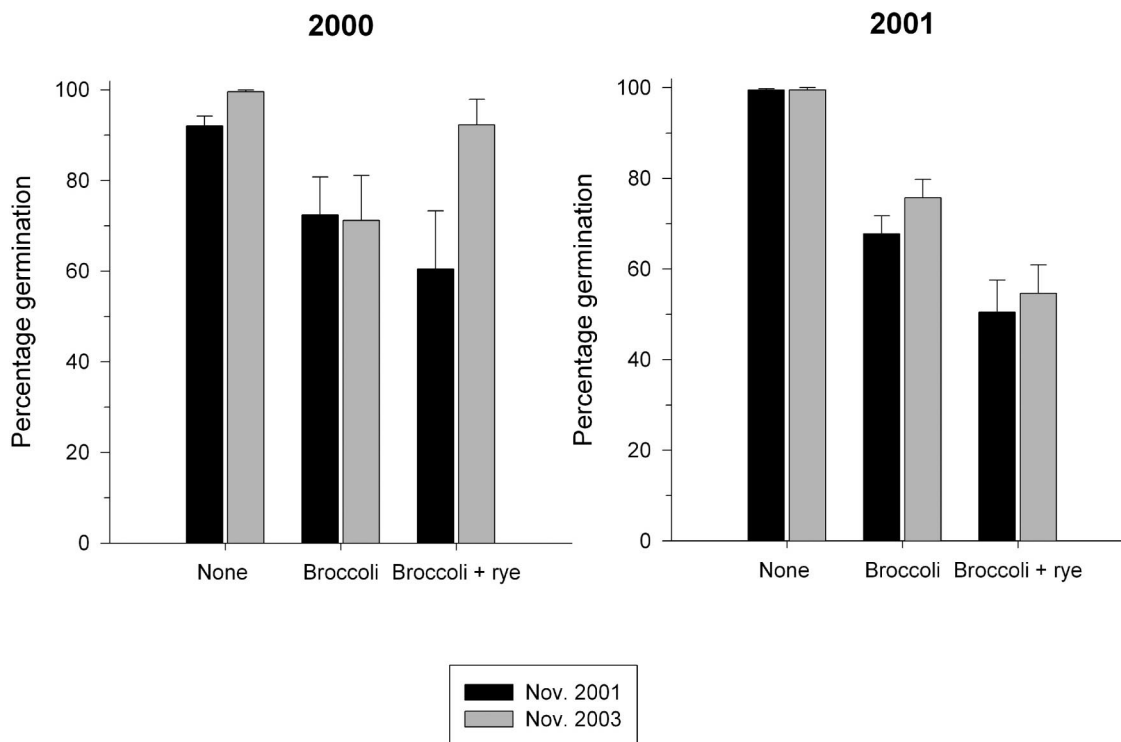


FIGURE 4. Mean (\pm SE) percent germination of viable seed of Powell amaranth maturing under different competitive environments in 2000 and 2001 and tested at 30/25 C in light in November 2001 and November 2003. Germination percentages for plants growing in-row and between-row did not vary significantly, so data were pooled within each competitive environment.

tween-row. Therefore, data were pooled within each competitive environment. Powell amaranth seed germination was significantly influenced by maternal competitive environment in both years (Figure 4). Among seeds produced in 2000, the germination of viable seed after 1 yr of storage was 92% for seed maturing in the absence of competition compared with 60% for seeds maturing in competition with broccoli plus rye. However, after an additional 2 yr of storage, the effect of maternal environment on germination was no longer significant. For seeds produced in 2001, after 2 mo of storage, the germination of viable seeds was approximately 50% lower for seeds that matured under competition with broccoli plus rye compared with seeds that matured in the absence of competition. After two additional years of storage, there was little change in the nature of these relationships.

Several explanations may account for the observed reductions in germination for seeds maturing under more competitive environments. First, exposure of maternal plants to reduced R-FR ratios may have reduced seed germinability. Reductions in the maternal R-FR environment can increase seed dormancy in some light-sensitive plant species like Powell amaranth (reviewed in Gutterman 2000; McCullough and Shropshire 1970; Orozco-Segovia et al. 1993). A second possibility is that reduced irradiance during maturation influenced seed germination characteristics. However, reductions in irradiance during maturation are associated with reductions in seed dormancy in several species including velvetleaf (Bello et al. 1995; Nurse and DiTommaso 2004) and thorn apple (*Datura ferox* L.) (Sanchez et al. 1981). Likewise, for redroot pigweed, Kigel et al. (1977) found that seeds maturing under low irradiance (without reductions in R-FR ratio) and short days had less

dormant seeds than those maturing under high irradiance and short days. These results suggest that changes in the R-FR under competition may have been responsible for differences in seed dormancy in our study.

Changes in offspring seed characteristics in response to maternal stresses may represent an important form of adaptive plasticity (Fenner 1985; Sultan 1996). Increased seed dormancy in response to canopy shade during seed maturation may be adaptive, if there is a positive correlation between maternal and offspring environments and strong selection pressure against germination under canopy shade (Sultan 1996). On the other hand, if the mechanism of dormancy requires diversion of photosynthate away from structures that enhance fitness (e.g., stem), the cost of dormancy under competitive conditions (e.g., lower light interception and fewer offspring) might outweigh the benefit (higher probability of survival of each offspring). Such trade-offs might explain why large-seeded species like velvetleaf, for which seed coat thickness influences dormancy, exhibit reduced dormancy under low irradiance, whereas small-seeded species like Powell amaranth, for which physiological dormancy is important, exhibit increased dormancy when maturing under canopy shade. Maternal environmental effects on seed dormancy may also be viewed as a mechanism for increasing variability in germination characteristics and hence preventing catastrophic mass germination (Fenner 1985; Gutterman 2000). However, the adaptive significance of maternal environmental effects on seed dormancy cannot be evaluated without monitoring the fate of seeds produced under different conditions (Fenner 1985).

The significance of observed differences in Powell amaranth dormancy will depend in part on environmental conditions during the winter. For *Amaranthus quitensis* Kunth,

Nisensohn and Faccini (1993) reported almost complete loss of dormancy after 6 mo of seed burial. Egley (1989) reported that for redroot pigweed, 20% of dormant seed buried in the fall was dormant when recovered the next spring, but dormancy was reduced to 2% in soil amended with nitrate. In cases where dormancy is readily broken during the winter, seed longevity may be more important than seed dormancy in determining population dynamics. Although we did not detect any differences in the rate of loss of viability of seeds under dry, soilless conditions, seeds from different competitive environments may behave differently when buried in the field.

To summarize, the presence of neighboring plants significantly influenced both the quantity and quality of light experienced by Powell amaranth. Reductions in solar irradiance and the R-FR ratio were associated with increases in SLA, SSL, and partitioning to stem tissue, as well with reductions in the rate of leaf appearance, the number of main leaves (nodes) at flowering, and the germinability of seeds produced. Although many studies have examined morphological responses to shade, few previous studies have examined the influence of competition for light under field conditions on plant phenology and characteristics of seeds produced. Reductions in main leaf number at flowering may be an adaptive response that prevents delays in flowering that would otherwise occur as a result of reductions in the rate of main leaf appearance under competition. Similarly, increased dormancy of seeds maturing under shade may be an adaptive response that reduces the probability of germination of offspring under unfavorable (shaded, competitive) conditions. Regardless of their adaptive significance, characterization of these often overlooked responses is critical for improving our understanding of weed population dynamics, weed-crop competitive interactions, and weed evolution and should improve our ability to better understand the long-term impact of weed management choices.

Sources of Materials

¹ CI-110 Digital Plant Canopy Imager, CID Inc., 4018 NE 112th Avenue, Suite D-8, Vancouver, WA 98682.

² Sunfleck Ceptometer, Decagon Devices Inc., P.O. Box 835, Pullman, WA 99163.

³ LI-COR 1800. LI-COR Inc., 4421 Superior Street, Lincoln, NE 68504.

⁴ Scion Corporation, 82 Woman's Mill Court, Suite H, Frederick, MD 21701.

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Literature Cited

Ball, D. A. and M. J. Shaffer. 1993. Simulating resource competition in multispecies agricultural plant communities. *Weed Res.* 33:299-310.
 Ballaré, C. L. 1999. Keeping up with the neighbours: phytochrome sensing and other signaling mechanisms. *Trends Plant Sci.* 4:97-102.
 Ballaré, C. L., R. A. Sanchez, A. L. Scopel, J. J. Casal, and C. M. Ghersa. 1987. Early detection of neighbour plants by phytochrome perception of spectral changes in reflected sunlight. *Plant Cell Environ.* 10:551-557.

Bello, I. A., M. D. Owen, and H. M. Hatterman-Valenti. 1995. Effect of shade on velvetleaf (*Abutilon theophrasti*) growth, seed production, and dormancy. *Weed Technol.* 9:452-455.
 Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* 13:115-155.
 Brainard, D. C. and R. R. Bellinder. 2004a. Assessing variability in fecundity of *Amaranthus powellii* using a simulation model. *Weed Res.* 44:1-15.
 Brainard, D. C. and R. R. Bellinder. 2004b. Weed suppression in a broccoli-winter rye intercropping system. *Weed Sci.* 52:281-290.
 Bussan, A. J. and C. M. Boerboom. 2001. Modeling the integrated management of velvetleaf in a corn-soybean rotation. *Weed Sci.* 49:31-41.
 Causin, H. F. and R. D. Wulff. 2003. Changes in the responses to light quality during ontogeny in *Chenopodium album*. *Can. J. Bot.* 81:152-163.
 Charles-Edwards, D. A., D. Doley, and G. M. Rimmington. 1986. *Modelling Plant Growth and Development*. Orlando, FL: Academic. 234 p.
 Cohen, D. 1976. The optimal timing of reproduction. *Am. Nat.* 110:801-807.
 Cousins, R. and M. Mortimer. 1995. *Dynamics of Weed Populations*. Cambridge: Cambridge University Press. 332 p.
 Davis, M. H. and S. R. Simmons. 1994. Far-red light reflected from neighbouring vegetation promotes shoot elongation and accelerates flowering in spring barley plants. *Plant Cell Environ.* 17:829-836.
 Devlin, P. F., P.R.H. Robson, S. R. Patel, L. Goosey, R. A. Sharrock, and G. C. Whitelam. 1999. Phytochrome D acts in the shade-avoidance syndrome in *Arabidopsis* by controlling elongation growth and flowering time. *Plant Physiol.* 119:909-915.
 Egley, G. H. 1989. Some effects of nitrate-treated soil upon the sensitivity of buried redroot pigweed (*Amaranthus retroflexus* L.) seeds to ethylene, temperature, light and carbon dioxide. *Plant Cell Environ.* 12:581-588.
 Fenner, M. 1985. *Seed Ecology*. New York: Chapman and Hall. 151 p.
 Grundy, A. C. 2003. Predicting weed emergence: a review of approaches and future challenges. *Weed Res.* 43:1-11.
 Gutterman, Y. 2000. Maternal effects on seeds during development. Pages 59-84 in M. Fenner, ed. *Seeds: The Ecology of Regeneration in Plant Communities*. New York: CABI.
 Halliday, K. J., M. Koornneef, and G. C. Whitelam. 1994. Phytochrome B and at least one other phytochrome mediate the accelerated flowering response of *Arabidopsis thaliana* L. to low red/far-red ratio. *Plant Physiol.* 104:1311-1315.
 Kadman-Zahavi, A. and E. Ephrat. 1974. Opposite response groups of short-day plants to the spectral composition of the main light period and end-of-day red or far-red irradiations. *Plant Cell Physiol.* 15:693-699.
 Kigel, J., M. Ofir, and D. Koller. 1977. Control of the germination responses of *Amaranthus retroflexus* L. seeds by their parental photothermal environment. *J. Exp. Bot.* 28:1125-1136.
 King, D. and J. Roughgarden. 1982. Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. *Theor. Popul. Biol.* 1:1-15.
 Knezevic, S. Z., M. J. Horak, and R. L. Vanderlip. 1999. Estimates of physiological determinants for *Amaranthus retroflexus*. *Weed Sci.* 47:291-296.
 Knezevic, S. Z., R. L. Vanderlip, and M. J. Horak. 2001. Relative time of emergence affects dry matter partitioning. *Weed Sci.* 49:617-621.
 Kropff, M. J. and H. H. van Laar, eds. 1993. *Modelling Crop-Weed Interactions*. Wallingford, UK: CABI. Pp. 25-30, 157.
 McCullough, J. M. and W. Shropshire, Jr. 1970. Physiological predetermination of germination responses in *Arabidopsis thaliana* (L.) Heynh. *Plant Cell Phys.* 11:139-148.
 McDonald, A. J. and S. J. Riha. 1999. Model of crop:weed competition applied to maize: *Abutilon theophrasti* interactions. I. Model description and evaluation. *Weed Res.* 39:355-369.
 McLachlan, S. M., S. D. Murphy, M. Tollenaar, S. F. Weise, and C. J. Swanton. 1995. Light limitation of reproduction and variation in the allometric relationship between reproductive and vegetative biomass in *Amaranthus retroflexus* (redroot pigweed). *J. Appl. Ecol.* 32:157-165.
 McLachlan, S. M., C. J. Swanton, S. F. Weise, and M. Tollenaar. 1993a. Effect of corn-induced shading and temperature on rate of leaf appearance in redroot pigweed (*Amaranthus retroflexus* L.). *Weed Sci.* 41:590-593.
 McLachlan, S. M., M. Tollenaar, C. J. Swanton, and S. F. Weise. 1993b. Effect of corn-induced shading on dry matter accumulation, distri-

- bution, and architecture of redroot pigweed (*Amaranthus retroflexus*). *Weed Sci.* 41:568–573.
- Mohler, C. L. and M. B. Callaway. 1995. Effects of tillage and mulch on weed seed production and seed banks in sweet corn. *J. Appl. Ecol.* 32:627–639.
- Morgan, D. C. and H. Smith. 1976. Linear relationship between phytochrome photoequilibrium and growth in plants under simulated natural radiation. *Nature* 262:210–212.
- Nisensohn, L. and D. Faccini. 1993. Persistence of redroot pigweed seeds in no-till soil. *Turrialba* 43:138–142.
- Nurse, R. E. and A. DiTommaso. 2004. Influence of Photoperiod and Corn Competition on Reproduction, Seed Germination, and Seedling Vigor in Velvetleaf (*Abutilon theophrasti* Medic.). *Weed Science Society of America Abstracts No. 308*. Lawrence, KS: Weed Science Society of America. [CD-ROM computer file]
- Orozco-Segovia, A., M. E. Sanchez-Coronado, and C. Vazquez-Yanes. 1993. Effect of maternal light environment on seed germination in *Piper auritum*. *Funct. Ecol.* 7:395–402.
- Persall, W. H. 1927. Growth studies. VI. On the relative sizes of growing plant organs. *Ann. Bot.* 41:549–556.
- Rajcan, I., M. AghaAlikhani, C. J. Swanton, and M. Tollenaar. 2002. Development of redroot pigweed is influenced by light spectral quality and quantity. *Crop Sci.* 42:1930–1936.
- [SAS] Statistical Analysis System. 1999. SAS/STAT User's Guide Version 7-1. Cary, NC: Statistical Analysis System Institute. 1030 p.
- Samson, D. A. and K. S. Werk. 1986. Size dependent effects in the analysis of reproductive effort in plants. *Am. Nat.* 127:667–680.
- Sanchez, R. A., G. Eyherabide, and L. de Miguel. 1981. The influence of irradiance and water deficit during fruit development on seed dormancy in *Datura ferox* L. *Weed Res.* 21:121–132.
- Schmitt, J. 1997. Is photomorphogenic shade avoidance adaptive? Perspectives from population biology. *Plant Cell Environ.* 20:826–830.
- Senesac, A. F. 1985. Aspects of the Biology and Control of Pigweed (*Amaranthus* spp.) in New York. Ph.D. dissertation. Cornell University, Ithaca, NY. 188 p.
- Shitaka, V. and T. Hirose. 1998. Effects of shift in flowering time on the reproductive output of *Xanthium canadense* in a seasonal environment. *Oecologia* 114:361–367.
- Smith, H. and G. C. Whitelam. 1997. The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. *Plant Cell Environ.* 20:840–844.
- Stoller, E. W. and R. A. Myers. 1989. Response of soybeans (*Glycine max*) and four broadleaf weeds to reduced irradiance. *Weed Sci.* 37:570–574.
- Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evol. Biol.* 21:127–178.
- Sultan, S. E. 1996. Phenotypic plasticity for offspring traits in *Polygonum persicaria*. *Ecology* 77:1791–1807.
- Sultan, S. E. 2000. Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci.* 5:537–542.
- Weiner, J. 1988. The influence of competition on plant reproduction. Pages 228–245 in J. L. Doust and L. L. Doust, eds. *Plant Reproductive Ecology: Patterns and Strategies*. New York: Oxford University Press.
- Weiner, J. and S. C. Thomas. 1992. Competition and allometry in three species of annual plants. *Ecology* 73:648–656.

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