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Light Quality and the Critical Period for Weed Control in Soybean

Emily Green-Tracewicz, Eric R. Page, and Clarence J. Swanton*

The critical period for weed control (CPWC) is an integral component of integrated weed management strategies. Several studies have defined the CPWC in soybean under varying agronomic conditions, yet none have described the mechanisms involved in crop yield losses caused by weed competition. We hypothesized that under nonresource-limiting conditions, morphological changes resulting from the expression of shade avoidance could be used to define a period of developmental sensitivity to low red-to-far-red ratio (R : FR) that would overlap with the defined CPWC in soybean. Two experiments (a sequential harvest and a weed addition/removal series) were conducted in 2008 and 2009 under controlled environmental conditions to address this hypothesis. Two light-quality treatments were used: (1) high R : FR ratio (i.e., weed-free), and (2) low R : FR ratio (i.e., weedy). The low R : FR ratio treatment induced shade avoidance responses in soybean, which included increases in height, internode length, and the shoot : root ratio, as well as a reduction in biomass accumulation and leaf number. Using the morphological changes in biomass and leaf number observed in the weed addition/removal series, a period of developmental sensitivity to low R : FR was defined between the first trifoliate (V1) and third trifoliate (V3) stages of soybean development. This period was found to be very similar to the CPWC previously defined by field studies of soybean–weed competition.

Nomenclature: Soybean, *Glycine max* (L.) Merr.

Key words: *Glycine max*, soybean, red to far-red ratio, competition theory, shade avoidance, physiological costs, phenotypic plasticity.

Successful integrated weed management (IWM) systems require an understanding of crop–weed interactions (Swanton et al. 2008). The outcome of these interactions can be described using the experimental framework of the CPWC. The CPWC is defined as the interval in the life cycle of a crop that must remain free of weeds to prevent unacceptable crop yield losses (Zimdahl 1980). The concept of the CPWC, first described by Nieto et al. (1968), is comprised of a weed-addition and -removal series. In the weed addition series, the crop is kept weed-free for increasing periods of time, after which emerging weeds are no longer controlled. In the weed removal series, weeds are allowed to emerge and grow for increasing lengths of time until weed control is affected at predetermined intervals (i.e., days after emergence, growth stages). The addition series determines the point in the development of the crop when weed emergence events can be left uncontrolled without causing yield losses, whereas the removal series gives an indication of the earliest stage of development at which weeds can cause unacceptable yield losses. When combined, a critical period can be identified that describes when weed control should be employed in order to prevent unacceptable yield losses.

The CPWC has been defined for numerous crop species, across a range of environments and under a variety of cultivation and planting practices (Halford et al. 2001; Hall et al. 1992; Knezevic et al. 2003; Nieto et al. 1968; Weaver et al. 1992). In Ontario, the critical weed-free period for soybeans has been observed to occur from emergence until the fourth trifoliate (V4)stage of development (Van Acker et al. 1993). Similar studies in soybeans also have defined the CPWC under no-till (Halford et al. 2001) and narrow row planting practices (Knezevic et al. 2003). Under no-till practices, the CPWC in soybean was longer when compared to conventional tilled systems and occurred from the second trifoliate (V2) to the appearance of first flower (R1) stage of development (Halford et al. 2001). Conversely, Knezevic et al. (2003) found that the critical timing for weed removal occurred later, at the V4 stage of soybean development, when soybean row spacing decreased from 76 to19 cm. Although it is clear from these studies that the CPWC can be influenced by cropping systems practices, it is also affected by the time of weed emergence relative to the crop and the density of the emerging weed population.

The time of weed emergence is perhaps the most important factor determining the magnitude of crop yield losses (Dew 1972; Kropff et al. 1992). It has been established from critical period and weed threshold studies that weeds emerging with the crop result in greater yield losses than if they emerge later in crop development (Bosnic and Swanton 1997; Cowan et al. 1998; Knezevic et al. 1994). Indeed, many studies have observed that the CPWC can begin during the very early stages of crop seedling development when weeds emerge at or near the time of crop emergence (Hall et al. 1992; Van Acker et al.1993; Weaver et al. 1992). For example, Van Acker et al. (1993) found that the critical period in soybean could occur as early as 9 d after emergence if weeds were allowed to emerge at the same time as the crop. Similarly, Hall et al. (1992) observed that the onset of the CPWC in maize could occur as early as the three-leaf-tip stage of development. The onset of the CPWC also can be influenced by the rate of nitrogen fertilizer applied at planting, which supports the traditional view that crop–weed competition for resources might, in part, explain the observed yield losses under field conditions (Evans et al. 2003). However, it has been suggested recently that resource independent factors, such as light or hormonal signalling, also might play a role in determining the onset and outcome of crop–weed competition prior to resource limitation (Green-Tracewicz et al. 2011; Page et al. 2009; Rajcan et al. 2004).

Weed seedlings present at or near the time of crop emergence have the potential to alter the R : FR ratio of the light environment surrounding crop seedlings. The decrease in the R : FR of light reflected from the leaf surface of weeds

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has been proposed as a potential mechanism initiating crop–weed competitive interactions (Liu et al. 2009; Page et al. 2009; Rajcan et al. 2004; Rajcan and Swanton 2001). This decrease in the R : FR of reflected light has been viewed traditionally as a pre-emptive indicator of impending competition for resources (Ballaré et al. 1987, 1990; Smith 1992; Smith et al. 1990). Reflected light with a low R : FR induces a shade avoidance response in crop seedlings, which is characterized by stem and petiole elongation, the suppression of branching, and changes in biomass partitioning (Ballaré et al.1987, 1990; Kasperbauer 1987; Schmitt and Wulff 1993; Smith 1982). Several studies have suggested that soybeans can express these phenotypic changes in response to low R : FR light (Bradburne et al. 1989; Hunt et al. 1989; Kasperbauer 1971; Kasperbauer et al. 1984). These changes, however, have not been regarded as a potential mechanism contributing to the onset and outcome of soybean–weed competition. In this study, we explore the sensitivity of soybean seedlings to changes in the R : FR of reflected light. We hypothesized that under non-limiting resource conditions, morphological changes resulting from the expression of shade avoidance could be used to define a period of developmental sensitivity to low R : FR that would overlap with the defined CPWC in soybean.

Materials and Methods

A critical-period-of-weed-control experiment was simulated in controlled growth facilities in 2008 and 2009 to examine the morphological and phenological response of soybeans to the absence and presence of weed competition. A University of Guelph soybean variety OAC 01-26 (2,700 heat units) was selected for this study. The two series that comprise field-critical period studies were simulated using weed-addition and -removal series. Soybean seedlings were grown under equal light quantities (i.e., photosynthetic photon flux density or PPFD), and in two contrasting R : FR environments. The two light quality treatments were: (1) high R : FR ratio (i.e., weed-free), measured as upward-reflected light from Turface (Turface MVP®, Profile Products LLC, Buffalo Grove, IL), a baked clay medium; or (2) low R : FR ratio (i.e., weedy), measured as upward-reflected light, from perennial ryegrass (*Lolium perenne* L.). Perennial ryegrass was chosen because of its quick establishment and ability to reflect a consistent R : FR.

Experimental Design. Our experimental design eliminated direct effects of competition and allelopathy, such that root systems of soybean seedlings and perennial ryegrass were isolated. Soybean seeds were germinated in wet vermiculite for 48 h prior to planting. Germinated seeds with emerged radicles of equal size were planted in 8-cm-diam, 10-cm-tall, 355-ml plastic cups (Plastic cups, Dart Container Corporation, Mason, MI), at a depth of 2 cm (one seed per cup). These cups were then positioned within 8-cm-diam, 18-cm-tall pots (Pots, Consolidated Bottle Co., Toronto, Ontario, Canada) (1-L natural cylinder modified to 18 cm). These cylindrical pots were further centered within 25-cm-diam, 19-cm-tall 6-L pots (Pots, Airlite Plastics Company, Omaha, NE), and the area surrounding the cylindrical pot was filled with Turface or seeded with perennial ryegrass 4 wk prior to planting. Similar methodology has been reported previously (see Liu et al. 2009; Page et al. 2009). Soybean plants and perennial ryegrass within each pot were fertigated separately to field capacity daily with a nutrient solution as described by Page et al (2011). This design ensured that there was no direct competition for water or nutrients. In order to minimize the potential for shading, perennial ryegrass was manually clipped to maintain its height below the unifoliate leaves of soybean seedlings.

The growth cabinet (Conviron 6050, model PGW36, Controlled Environments Ltd., Winnipeg, Manitoba, Canada) was set to deliver a 25 : 15 C thermoperiod and a 16 : 8 (day : night) hour photoperiod. Light reflected from the Turface and perennial ryegrass was characterized over the course of experimental runs. A point quantum radiometer (LI-190SA, LI-COR Biosciences Lincoln, NE), with a cosine-corrected sensor on a fiber-optic cable was used to measure incoming and reflected PPFD at the top of soybean seedlings (approximately 700 μmol m^{-2} s^{-1}). The R : FR ratio of incoming irradiance was quantified at the top of soybean seedlings using a point sensor (SKR 110, 660/730nm, Skye Instruments, Ltd., Llandrindod Wells, Powys, U.K.).

The incoming or ambient R : FR ratio of the growth cabinet did not differ between treatments (R : FR ~2.2). The R : FR of light reflected from the surface of Turface and perennial ryegrass was determined by positioning the sensor downward, 10 cm above either Turface (R : FR = 1.9 ± 0.04) or perennial ryegrass (R : FR = 0.48 ± 0.04).

The experiment was arranged as a split-block design with light quality treatments (i.e., weedy or weed-free) as the whole plot factor and stage of development as the split-plot factor. The experiment was repeated twice, and each repetition contained five replications. The growth chamber was split into weedy and weed-free by a white opaque plastic divider to minimize any potential contamination of R : FR between treatments. All experimental units within a whole-plot were randomized every 3 d to reduce edge effects on light quantity. Treatments consisted of weed additions and removals at the first trifoliate(V1), V2, V3, V4, and sixth trifoliate (V6) stages of soybean developmental (Fehr et al. 1971), as well as control treatments of continuously weedy and weed-free, lasting from emergence to the sixth trifoliate (V6). Additions and removals occurred when ≥ 50% of soybeans grown in the high R : FR treatment entered the respective developmental stages. Destructive biomass harvests also were conducted at each of these timings in order to document soybean seedling development in continuously weedy or weed-free conditions.

At each time of transfer, the number of trifoliate leaves per plant, plant height, and internode elongation parameters were recorded for soybean seedlings in the control treatments (continuously weedy and weed-free). Soybean height was determined by pulling trifoliate vegetation upwards and measuring from the surface of the Turface to the tip of tallest trifoliate. Internode length was measured on the main stem, which included hypocotyl, epicotyl, and second trifoliate (V2)-to-V6 stages of soybean development.

The final harvest of all weed-addition and -removal treatments occurred 4 d after the V6 transfer, at approximately the seventh trifoliate (V7) developmental stage. Fully expanded trifoliates were cut at the end of the petioles and young leaflets at the undeveloped nodes. An area meter (LI-COR 3100 Area Meter, LI-COR Biosciences Lincoln, NE) was used to determine leaf area. The aboveground biomass

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harvested included leaf, stem, and pods. Belowground biomass (roots) was separated from stems and washed prior to all plant tissue being dried in a forced-air oven at 80 C to a constant weight.

Statistical Analyses. All statistical analyses were performed in SAS 9.1 (Statistical package, SAS Institute, Cary, NC) with a Type I error rate set at $\alpha = 0.05$. Destructive harvests of soybean seedlings at the V1, V2, V3, V4, and V6 developmental stages were analyzed as a split-block design using PROC MIXED. Fixed effects included treatment, sampling time and their interaction. Random effects included repetitions of the experiment, replicates (repetitions), and replicates by treatment (repetitions). The degrees of freedom for all tests of fixed effects were calculated using the Satterthwaite approximation (Satterthwaite 1946). Prior to analysis, all physiological parameters were $\log_{10}$ transformed to correct for heterogeneity of error variance. Preplanned contrasts were used to compare the treatment effect within a sampling time.

Seedlings harvested at maturity from the weed-addition and -removal treatments were analyzed as separate series using nonlinear regression. Each of the measured physiological parameters was regressed against the natural logarithm of the number of growth stages spent in weed-free or weedy environments, respectively, using PROC NLIN. The absolute value of the shape parameters of the regression equations of weed-addition and -removal series were compared using paired *t*-tests.

Results and Discussion

Sequential Biomass Harvests. Soybean seedlings developing in the weed or low R : FR environment displayed typical shade avoidance responses, such as increases in soybean height, internode elongation, and a shift in the shoot : root ratio. As early as the first harvest time (i.e., the V1 stage of soybean development), soybeans grown in the weedy treatment were 25% taller than plants in the weed-free treatment ($P < 0.0001$; Figure 1A). Soybean seedlings in the weedy treatment were consistently taller than those in the weed-free treatment until the V6 stage of soybean development, at which time no differences were detected ($P = 0.9995$). Similarly, hypocotyl and epicotyl internode elongation increased in the weedy compared to the weed-free treatment ($P = 0.0210$; $P = 0.0002$, respectively, data not presented). The shoot : root ratio was larger in the weedy compared to the weed-free treatment at the first two harvest intervals (Table 1); however, after these stages no differences were detected between treatments.

Leaf area per plant and trifoliate number were reduced in the weedy compared to weed-free treatment (Table 1). Similarly, soybean seedlings developing in the weedy treatment accumulated less leaf biomass, root biomass, and total plant biomass than those developing in a weed-free environment (Table 1). These reductions were detected early and persisted throughout the duration of the experiment. For example, the trifoliate number per plant was reduced in weedy compared to the weed-free as early as the V2 stage of soybean development (0.75 vs. 1.4 trifoliolates, respectively; $P = 0.0004$; Figure 1B). This difference between treatments continued throughout the experiment and at the V6 stage of soybean development,

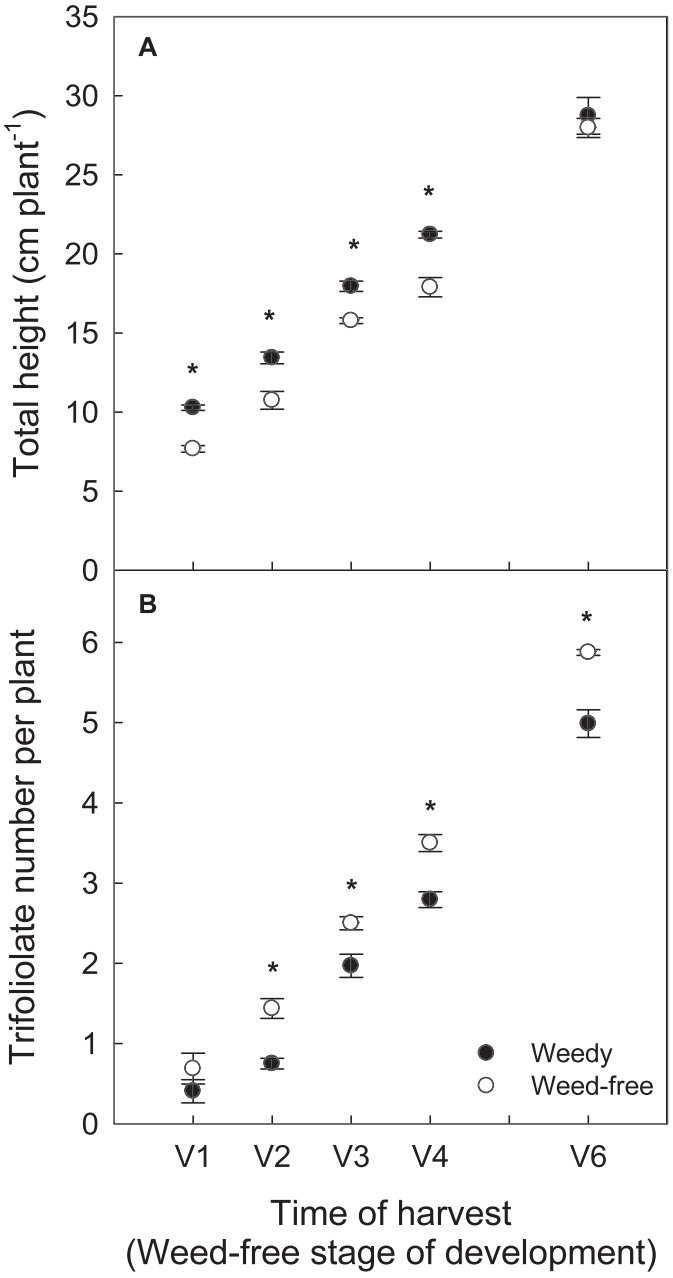


Figure 1. Plant height (A) and trifoliolate leaf number (B) of soybean seedlings developing under continuously weedy or weed-free conditions. ANOVAs for soybean height and trifoliate number indicated significant treatment by time interactions ($P < 0.0004$, and $P < 0.0142$, respectively).

weed-free plants had, on average, 1 trifoliate more than weedy plants ($P < 0.0001$). Leaf biomass and leaf area in the weedy treatment were reduced as early as the V1 stage and persisted until the V6 stage of soybean development. Differences in total biomass between treatments were also observed by V3 and persisted until the V6. At final harvest (V7), differences in partitioning among roots, stems, and leaves were apparent between treatments (Figure 2). Soybean plants that developed under continuously weedy conditions had less total plant biomass (6.5 g vs. 11.1 g) and partitioned less to roots (2.5 g vs. 4.8 g) and more to the stem (1.4 g vs. 2 g).

Final Biomass Harvest (40 Days after Emergence): Addition and Removal Series. In the weed removal series,

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Table 1. The effect of the Red : Far-red ratio on leaf area, root, stem, and leaf, total biomass, and the shoot : root ratio (± SE) by stage of soybean development.

Phenotypic parameter	Treatment		P value
	Weed-free	Weedy	
V1: Unifoliate			
Leaf area (cm^2 $plant^{-1}$)	19.1 (0.64)	9.8 (0.58)	< 0.0001
Root biomass (g $plant^{-1}$)	0.067 (0.0063)	0.038 (0.0046)	1.0000
Stem biomass (g $plant^{-1}$)	0.097 (0.0038)	0.095 (0.0145)	0.9923
Leaf biomass (g $plant^{-1}$)	0.084 (0.0053)	0.048 (0.0037)	< 0.0001
Total biomass (g $plant^{-1}$)	0.25 (0.004)	0.18 (0.020)	0.9987
Shoot : Root	2.7 (0.32)	4.8 (1.25)	0.0025
V2: 1st trifoliolate			
Leaf area (cm^2 $plant^{-1}$)	57.5 (1.87)	31.6 (1.83)	< 0.0001
Root biomass (g $plant^{-1}$)	0.48 (0.069)	0.20 (0.055)	0.3249
Stem biomass (g $plant^{-1}$)	0.13 (0.006)	0.14 (0.007)	1.0000
Leaf biomass (g $plant^{-1}$)	0.32 (0.011)	0.16 (0.008)	< 0.0001
Total biomass (g $plant^{-1}$)	0.93 (0.06)	0.50 (0.060)	0.3309
Shoot : Root	1.1 (0.22)	3.1 (0.85)	0.0035
V3: 2nd trifoliolate			
Leaf area (cm^2 $plant^{-1}$)	150.3 (3.38)	85.8 (2.14)	< 0.0001
Root biomass (g $plant^{-1}$)	0.83 (0.122)	0.58 (0.105)	0.5022
Stem biomass (g $plant^{-1}$)	0.26 (0.016)	0.23 (0.017)	0.9518
Leaf biomass (g $plant^{-1}$)	0.88 (0.028)	0.56 (0.044)	< 0.0001
Total biomass (g $plant^{-1}$)	2.0 (0.15)	1.4 (0.16)	0.0392
Shoot : Root	1.6 (0.19)	1.7 (0.25)	0.9011
V4: 3rd trifoliolate			
Leaf area (cm^2 $plant^{-1}$)	240.2 (5.40)	151.4 (7.86)	< 0.0001
Root biomass (g $plant^{-1}$)	1.3 (0.07)	0.93 (0.161)	0.0587
Stem biomass (g $plant^{-1}$)	0.44 (0.03)	0.38 (0.028)	0.9119
Leaf biomass (g $plant^{-1}$)	1.6 (0.08)	1.1 (0.09)	< 0.0001
Total biomass (g $plant^{-1}$)	3.3 (0.11)	2.4 (0.27)	< 0.0001
Shoot : Root	1.6 (0.15)	1.8 (0.21)	1.0000
V6: 5th trifoliolate			
Leaf area (cm^2 $plant^{-1}$)	535.9 (14.44)	343.0 (9.12)	< 0.0001
Root biomass (g $plant^{-1}$)	3.8 (0.22)	2.5 (0.17)	< 0.0001
Stem biomass (g $plant^{-1}$)	1.2 (0.05)	1.0 (0.05)	0.8396
Leaf biomass (g $plant^{-1}$)	3.4 (0.13)	2.5 (0.12)	0.0134
Total biomass (g $plant^{-1}$)	8.4 (0.32)	6.2 (0.29)	< 0.0001
Shoot : Root	1.2 (0.08)	1.4 (0.09)	0.9998

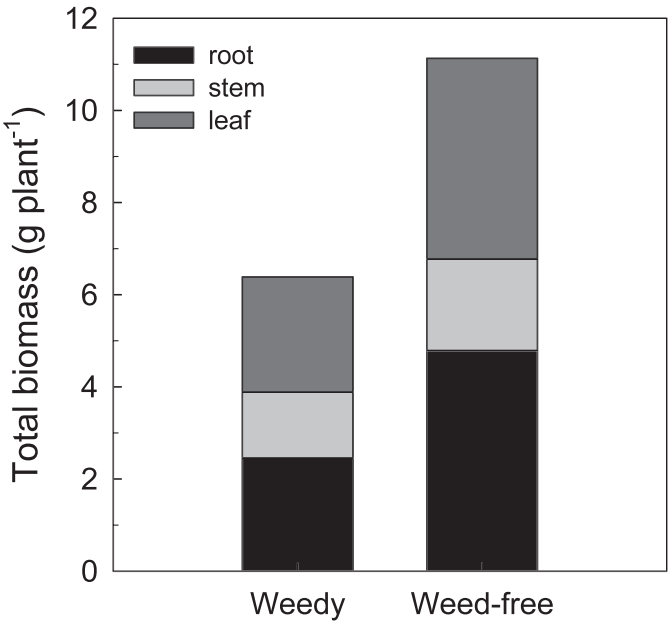


Figure 2. Soybean biomass partitioning of leaf, stem, and root components sampled at the sixth trifoliolate/first flower (V7) stage of soybean development. Bars represent the total plant biomass of soybeans harvested from continuously weedy and weed-free treatments at V7. ANOVA for soybean total biomass indicated that there was a significant treatment response ($P < 0.0001$).

leaf area and biomass (stem, leaf, and total biomass) were reduced progressively as the duration of time spent in the weedy environment increased (Table 2, Figure 3A and B). Similarly, seedlings in the weed-addition series accumulated less leaf area and biomass (stem, leaf, and total biomass) as the duration of time spent in the weedy environment increased; however, these reductions were smaller than those observed in the weed removal series (Table 2). Trifoliate number per plant and root biomass also declined with increasing durations of time spent in the weedy environment in both the weed-addition and -removal series (Table 2, Figure 3C and D). There were, however, no differences between series in the levels of the declines with respect to these two growth parameters.

A rapid reduction in total biomass per plant and the underlying component biomasses was observed if weeds were present up to and including the V2 stage of soybean development (i.e., the 2 : 5 interval, Figure 3B). After this period of exposure, increasing the duration of time in a weedy environment had little additional impact on total biomass accumulation. If weeds were introduced after the V2 stage of soybean development in the weed addition series, there also was little impact on total biomass accumulation (Figure 3A). Taken together, these results suggest that the impact of weedy or low R : FR signals on biomass accumulation was greatest during the period lasting from emergence to the V2 stage of soybean development.

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Table 2. Nonlinear regression parameters for weed-addition and -removal series. Seedlings growth components were regressed against the number of growth stages spent in weed-free or weedy conditions, respectively (e.g., Figure 3). The absolute values of the shape parameter of these nonlinear regressions were compared using paired *t*-tests.

Regression Parameter	Trifoliolates	Leaf area	Root biomass	Stem biomass	Leaf biomass	Total biomass
Weed addition						
Intercept	5.95	511.6	2.84	1.57	2.67	7.08
Shape[a]	0.6179a	144.6a	1.002a	0.194a	1.023a	2.217a
Weed removal						
Intercept	6.63	613.3	4.11	1.4	3.71	9.20
Shape	−0.658a	−68.557b	−0.962a	−0.048b	−0.679b	−1.659b

[a] Shape parameters within a column followed by the same letter are not significantly different at $P < 0.05$ level.

Previous field trials have shown that the critical period for weed control in soybean lasts from emergence to the V4 stage of development (Halford et al. 2001; Van Acker et al. 1993). In this study, the shade-avoidance response induced by the presence of weeds caused temporal changes in soybean height, internode elongation, and the shoot : root ratio during the same period of development observed by Van Acker et al. (1993) and Halford et al. (2001). These temporal changes were followed closely by or were overlapped by reductions in trifoliate number and biomass accumulation that lasted until the end of the experiment at the V7 stage of development.

Based on the reductions in total biomass and trifoliate number per plant observed in the current study, we suggest that a period of R : FR sensitivity exists between the V1 and V3 stages of soybean development (Figure 3). Traditionally, crop–weed competition studies conducted under field conditions have utilized percent yield loss for determining the CPWC. Although this study did not directly measure the impact of weed addition or removal on soybean yield, it has been previously demonstrated that soybean seedlings that developed in a weedy or low R : FR environment had lower per plant yields than seedlings from a weed-free or ambient R : FR environment (Green-Tracewicz et al. 2011).

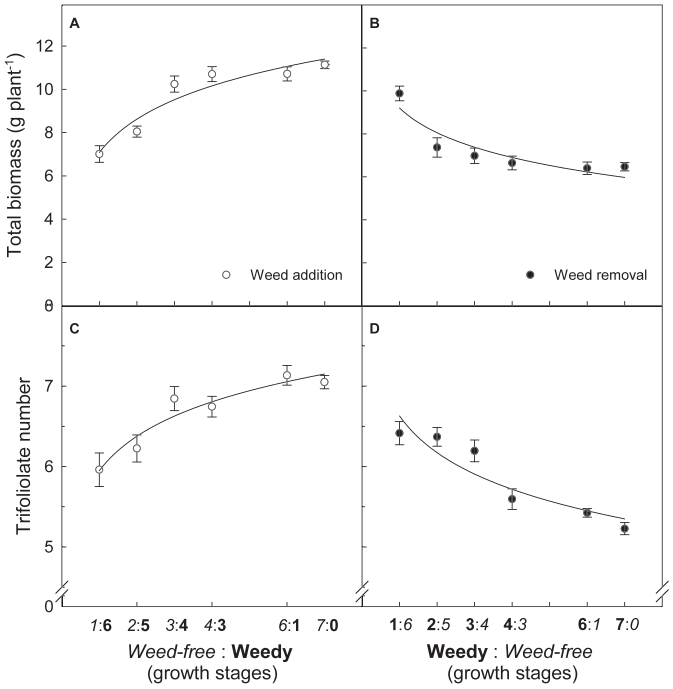


Figure 3. Total soybean biomass (A and B) and trifoliate number (C and D) at the V7 stage of soybean development from the weed addition (A and C) and weed removal series (B and D). The X-axis refers to V stages spent in weed-free or weedy conditions, respectively. For example a duration of 2 : 5 indicates that a soybean seedling emerged and grew in a weed-free environment for two V stages, after which it was transferred to a weedy environment for five growth stages and was harvested at V7. The equations of the regression lines for total biomass were: weed addition (Total biomass = [Leaf tips = 2.217 × Ln(growth stages weed-free) + 7.08]; weed removal [Leaf tips = −1.659 × Ln(growth stages weedy) + 9.2]. The equations of the regression lines for leaf tips were: weed addition [Leaf tips = 0.6179 × Ln(growth stages weed-free) + 5.95]; weed removal [Leaf tips = −0.658 × Ln(growth stages weedy) + 6.63].

Sensitivity to R : FR signals in dicots has been attributed to the internodal regions of developing seedlings, and it is well established that low R : FR signals increase soybean height, internode length and the shoot : root ratio (Ballaré et al. 1990, 1991; Casal et al. 1986; Hunt et al. 1989; Kasperbauer 1987). Furthermore, exposure to low R : FR can decrease soybean lateral branching, pod number, and grain yield per plant, while increasing the plant-to plant variability in yield and yield components (Green-Tracewicz et al. 2011). In previous studies, the proximity, number and size of leaves of neighbouring plants influenced the amount of FR light received and the resulting changes to soybean growth (Kasperbauer 1971, 1987; Kasperbauer et al. 1984). For example, Kasperbauer (1987) and Kasperbauer and Karlen (1994) observed that soybeans planted in north/south rows received more FR light at the beginning and end of each day, which increased plant height and reduced lateral branching. The authors attributed this response to the heliotropic movement of soybean leaves and the directed reflection of FR light as the leaves faced the sun at low solar angles. The results of these studies support our findings that soybean seedlings are capable of detecting and responding to reflected light with low R : FR early in their development, and that their response can have lasting effects on growth, development and yield at maturity.

In summary, our results indicate that changes in the R : FR of reflected light can alter soybean physiological and phenological development during the early stages of the growing season. Under non-limiting resource conditions, low R : FR-reflected light reduced the rate of leaf appearance and biomass accumulation in soybean seedlings. These changes were used to determine a period of sensitivity to low R : FR between the V1 and V3 stages of soybean development. This result was very similar to the CPWC that has been observed under field conditions. This period of soybean sensitivity to the R : FR ratio did not persist beyond the V3 stage of development. The addition of weeds after this time had little effect on soybean growth and development.

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