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Response of Ivyleaf Morningglory (*Ipomoea hederacea*) to Neighboring Plants and Objects

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Field observations of morningglory (*Ipomoea* spp.) showed that many plants grew out from places of comparable competitive advantage (alleys in field experiments with little or no vegetation) into neighboring plants or structures that provided climbing support. Of 223 native morningglory plants growing in rows and row middles in a 121-m^2 area within established corn research plots that contained no other weeds, 68% of the mature plants climbed up corn. More significant, of the 152 climbing morningglory plants, 96% grew toward and climbed the row in its closest proximity instead of growing across the row middle. Greenhouse and field experiments were initiated to determine whether morningglory grew preferentially toward certain colored structures or corn plants. Greenhouse-grown ivyleaf morningglory displayed varying frequency in locating and climbing toward black (17%), blue (58%), red (58%), white (67%), green (75%), and yellow (75%) stakes or corn (92%). Pots containing black stakes had the fewest climbing morningglory plants. In the field study, fewer ivyleaf morningglories climbed black structures compared with white- or green-colored structures or corn. The morningglory initial planting distance from colored structures or corn was also significant in the percentage of ivyleaf morningglories that exhibited climbing growth and in its final weight; morningglories that successfully located and climbed structures or corn weighed more and produced more seed than morningglories that remained on the ground. Ivyleaf morningglory appears to respond to spatial distribution of surrounding objects and possibly uses reflectance to preferentially project its stems toward a likely prospective structure for climbing.

Nomenclature: Ivyleaf morningglory, *Ipomoea hederacea* (L.) Jacq. IPOHE; corn, *Zea mays* L.
Key words: Light response, morningglory biology.

Morningglories (*Ipomoea* spp.) are annual, low-climbing vines that twine up neighboring crop plants for support as they exhibit positive phototropism to intercepted sunlight. Morningglory has been shown to have varying effects on crop yields depending on limiting resources, such as light, nutrients, and water (Cordes and Bauman 1984; Holloway and Shaw 1996; Oliver et al. 1976; Wood et al. 1999). Morningglory can reduce harvested crop quality, and in moderate populations, can reduce harvest efficiency (Buchanan et al. 1980; Cordes and Buchanan 1984; Howe et al. 1987; Murdock et al. 1986). Morningglory can grow and reproduce readily on the ground surface; however, our field observations noted that many plants appeared to grow preferentially toward upright (erect) plants or structures that provide support for a climbing growth habit.

The ability to locate a neighboring plant or object may be because of a phototropic response, a basic growth-orienting process in which unilateral light plays a central role in orienting plant shoots to grow asymmetrically. One mechanism of positive phototropic curvature or growth occurs when plants intercept light in the blue or green wavelength region (450 to 550 nm) (Aphalo and Ballare 1995; Iino 1990; Koller 1990; Parsons et al. 1984; Steinitz et al. 1985; Takemiya et al. 2005). Subsequently, an asymmetric distribution of auxin on the shaded side can lead to cell elongation and stem curvature toward the strongest sources of unilateral light (Kaufman et al. 1995). Phototropic response was also shown to be facilitated by phototropins that promote asymmetric growth in response to blue light in a low light environment (Takemiya et al. 2005).

Circumnutation is an important vine-tip movement that has been shown to facilitate twining plants' ability to find support on which to grow (Minorsky 2003). The helical movement of stem tips in circumnutation is closely related to a gravity signal and gravitropism (Yoshihara and Iino 2006). However, closely related, Yoshihara and Iino (2006) further demonstrated that circumnutation is a unique, gene-controlled movement mechanism.

Recently, gelatinous fibers have been shown to be responsible for redvine [*Brunnichia ovata* (Walt.) Shinners] tendril coiling and the coiling of numerous other vines (Meloche et al. 2007). Gelatinous fibers are fiber cells that are composed of a primary cell wall and two lignified cell walls. Gelatinous fiber formation was shown to be a result of touch stimuli, so lignin was more consistent and stronger nearer to the touched surface. This research also identified gelatinous fibers that facilitate twining stem growth in morningglory species.

Another proposed mechanism for the ability of morningglory to climb neighboring green vegetation located in proximity may be due to detection of light in intense red and far-red wavelengths (600 to 800 nm) (Aphalo and Ballare 1995; Ballare et al. 1995; Britz and Galston 1983; Iino 1990; Koller 1990). In this mechanism, phytochromes detect light quality, specifically, the balance between red and far-red light. Ballare et al. (1995) showed that cucumber (*Cucumis sativus* L.) without phytochrome-B responded less to far-red light compared with wild types. Open canopies, such as the artificial light gaps created in corn within this study, have light that contains a high red to far-red ratio. As a canopy closes (because of increased plant height and width), the ratio of red

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to far-red becomes smaller approaching the ground. For most plants, nearby vegetation causes initiation of shade-avoidance reactions (Ballare et al. 1995; Iino 1990). Skotropism, or growth toward darkness, has been shown to facilitate location of a tropical arboreal vine's host tree (Strong and Ray 1975). This directional growth mechanism has been shown to lead a vine directly to support, whereas positive phototropism can only lead a vine into an area where there may be support.

Research has shown that field dodder (*Cuscuta planiflora* Engelm.) exhibits a phototropic curvature toward regions of lowered red to far-red light (Orr et al. 1996a), which aids field dodder in host location and attachment. In another study with dodder, near-vertical seedlings were grown in white light and then cyclically illuminated from above with red light for 4 h, followed by red plus far-red light for 4 h (Orr et al. 1996b). Time-lapsed video showed that stems grew toward red light and away from far-red light and that the latter response was reversible. In a different dodder study, phototropic curvature toward a host was due to the plant's ability to detect and grow toward light transmitted by green leaves (Benvenuti et al. 2005). Spectral distributions (red to far-red ratios) and phytochrome equilibria have been measured in canopies composed of *Brassica* spp. or tobacco (*Nicotiana tabacum* L.) plants (Smith et al. 1989). Measurements were taken of radiation traveling vertically downward and radiation traveling horizontally. Radiation measures in these canopies were shown to be depleted in the 400 to 690 nm wavelength range and increased in the 690 to 800 nm wavelength range. Smith et al. (1990) hypothesized that the detection of spectral quality by the phytochrome system would allow for the detection and proximity of neighboring plants. Results also showed that lowered red to far-red radiation produced by a 12-cm-high *Brassica* spp. was detected by a radiospectrometer up to 30 cm away and up to 45 cm away from a 30-cm-high tobacco stand. In a controlled soybean [*Glycine max* (L.) Merr.] experiment, plants exposed to 5 min of far-red light at the end of each day had longer internodes and fewer branches than plants not exposed to far-red light (Kasperbaur 1987). Dry-matter partitioning in this field study was also related to red to far-red light ratios.

We are not aware of any published literature concerning responses of morningglory to neighboring plants and objects. Based on our observation in the field, we hypothesized that morningglory preferentially grows toward structures that reflect regions of more intense reflected solar radiation or altered light quality. Characterizing that response would allow for a better determination of the sphere of influence of morningglory and its potential for interference. Therefore, studies were initiated to investigate the response of morningglory to neighboring corn plants and different-colored objects.

Methods and Materials

Field Survey. All morningglories growing within two separate, established corn experiments (totaling 121 m^2) infested with native morningglory were characterized as exhibiting climbing or nonclimbing habit. The corn was planted in mid-March, and the survey was conducted in late-June. Row spacing for corn was 92 cm. For morningglory climbing corn, the distance from the emergence site of the morningglory plant to the corn plant was recorded. For nonclimbing morningglory plants, the distance from the apical meristem to nearest corn plant was recorded. In each case, morningglory species were also identified. Data were subjected ANOVA to determine whether trial effects were significant. Both chi-square analysis and Fisher's exact tests (SAS, 1998) were used to determine significance of presence or absence of climbing growth habit as well as possible species effects on climbing habit.

Greenhouse Experiment. Experiments were conducted in a glass greenhouse maintained at approximately 25 $\pm$ 2 C with a 16-h day of natural lighting and an average midday photosynthetic flux density of 700 μmol/m^2/s. Two completely randomized experiments were conducted using three replications of each treatment. Treatments were 30-cm corn plants or six different 30-cm-tall, colored stakes. Stake colors (all semigloss) were black, bright red, light blue, light yellow, medium green, and white.[1] Four ivyleaf morningglory seed were sown 18 cm opposite both stakes and corn plants and, upon emergence, thinned to one universal-size plant per pot. Pots were watered daily taking care not to physically disturb the morningglories. The experiments were conducted in 15-L black pots containing 10 cm of potting soil[2] thus leaving approximately 20 cm of space between the potting soil and the pot top. This method created an environment in which the morningglory received direct sunlight for approximately 2.5 h and indirect and reflected light off the colored stakes or corn for the remainder of day. This method also shielded morningglory from reflected stake color from neighboring pots. Circumnutation movement was not inhibited or monitored in this study. Morningglory plants were characterized as exhibiting climbing or nonclimbing habit on stakes or corn plants at daily intervals after emergence. The spectral quality of reflected solar radiation of each stake was measured at the initial morningglory establishment location using a LICOR 1800 radiospectrometer[3] capable of measuring every 2 nm, from 200 nm to 1,200 nm; readings were averaged over five consecutive measurements. Red (600 to 699 nm) to far-red (700 to 800 nm) ratios were also calculated. Data were subjected to ANOVA, and means were separated using Fisher's protected LSD at the 5% probability level.

Field Experiment. The experiment was conducted at the Central Crops Research Station near Clayton, NC, in 2001 and 2002. Soil was a Norfolk loamy sand (fine-loamy, siliceous, thermic Typic Paleudults) with 1.8% organic matter and pH of 5.8. Greenhouse-grown ivyleaf morningglory plants at cotyledon growth stage were transplanted into a field experiment containing a split-split plot design with randomized plots and three replications of each treatment. The main plot factor was structure color consisting of 4.5 by 9.5 by 244 cm wood structures, painted black, green, or white,[4] or 183-cm corn. The first subplot factor was initial morningglory distance from either a corn plant or painted structure within a plot. Initial distances were 15, 30, 61, 91, or 122 cm. The second subplot factor was either east or west orientation of morningglory's initial transplanted location relative to the corn plant or painted structure. This factor was chosen to evaluate directional solar radiation impacts on growth habit. Corn was established, and the painted structures were placed in the field when the corn reached a mature height of 184 cm. The structures were placed 60 cm into the ground and oriented with the 9.5-cm side facing east and west. Morningglories were transplanted immediately after. Corn and morningglories were watered as needed with care taken not to physically disturb plants. Plots were kept weed free by hand-weeding with similar care. If morningglories grew within 5 cm of a structure, a trellis system extending 3 cm out from structure surface on which the morningglory could climb was erected using 5-cm drywall screws and nylon twine. The trellis was erected to help facilitate climbing because the painted structure was extremely smooth. Again, circumnutation movement was not inhibited or monitored in this study. At each experiment's termination after 4 mo, each morningglory's habit was characterized as climbing or nonclimbing. Morningglory plants had set seed and were beginning to senesce at experiment termination. For nonclimbers, distances from apical meristems to corn or structure were recorded. At final harvest, each morningglory's total dry aboveground biomass and seed production was determined. Reflected solar radiation for each structure-color was taken early in the season, as previously described, and was initiated when sun was at solar noon. Blue and green absorbance maximums were tested for correlation of intensity of reflected light at these wavelengths with percentage of morningglories successfully locating and climbing structures and corn. Also, red (600 to 699 nm) to far-red (700 to 800 nm) ratios were calculated and tested for correlation with percentage of morningglories successfully locating and climbing structures and corn.

Data were subjected to ANOVA with sums of squares partitioned to reflect a split-split-plot treatment structure and trial effects. The three different-colored structures and corn were considered main plots, the two planting orientations were considered subplots, and the six initial planting distances were considered sub-subplots. Residuals were plotted, and logarithmic transformations conducted on data where variance increased with increasing means. Following ANOVA, treatment or log-transformed treatment means were compared using Fisher's Protected LSD test at the 5% probability level. Where main effects were significant, regressions were used to explain the relationship of measured response over time.

Results and Discussion

Field Survey. ANOVA indicated no differences in the percentage of morningglories that climbed corn between the two trials surveyed, so data were combined for presentation. Also, there was no difference in response among morningglory species; therefore, data were combined across species for presentation. A total of 223 morningglory plants, consisting of entireleaf morningglory (*Ipomoea hederacea* var. *integriuscula* Grey), ivyleaf morningglory, pitted morningglory (*Ipomoea lacunosa* L.), and tall morningglory [*Ipomoea purpurea* (L.) Roth] were characterized. Out of the 223 morningglories characterized, a significant majority (68% of the morningglories that were large enough contacted and climbed the corn) had done so successfully (data not shown). More notably, of the 152 that exhibited climbing habit, a majority (96%) grew to the row closest to the point of morningglory emergence.

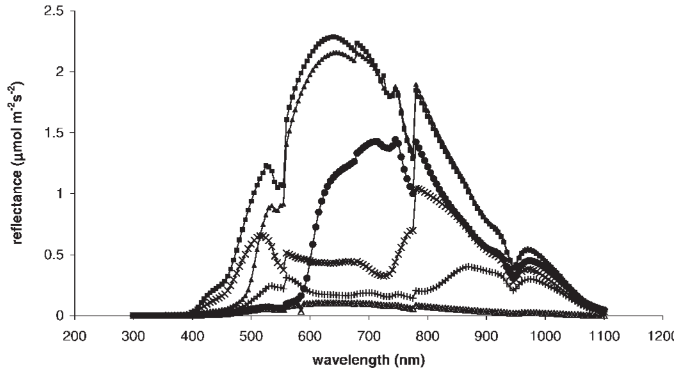

Figure 1. Reflected spectra of stakes in greenhouse study for white (■), yellow (▲), red (●), blue (×), green (+), and black (Δ) stakes at 15 cm.

Greenhouse Study. ANOVA indicated there was no treatment by experimental run interaction; therefore, data were combined for presentation. The red to far-red ratios for the colored stakes were as follows: red, 1.5; white, 1.2; yellow, 1.1; green, 0.93; blue, 0.78; black, 0.70; and corn, 0.51. The white stake had the greatest total reflected photon-flux density compared with all other stakes, and the black stake had the least (Figure 1). Greenhouse-grown morningglory displayed varying degrees of positive growth response toward corn and all colored stakes. The frequency of locating and climbing by the 12 morningglory plants for each treatment were as follows: black (17%), blue (58%), red (58%), white (67%), green (75%), and yellow (75%) stakes or corn (92%) (Table 1). The black-stake treatment had fewer morningglories growing toward and climbing the stakes relative to all other treatments. There was no correlation between red to far-red ratio and the frequency of morningglory climbing habit.

Field Study. There was no treatment by year interaction; therefore, data were combined for presentation. Reflected blue light had an absorbance maximum of 480 nm, and reflected green light had an absorbance maximum of 528 nm for all structures at all initial distances (data not shown). White structures reflected more blue light at 15- and 30-cm initial

Table 1. Frequency of greenhouse grown ivyleaf morningglory that successfully located and climbed stakes and corn.

Treatment	Frequency
	%
Black stake	17
Blue stake	58
Corn	92
Green stake	75
Red stake	58
White stake	67
Yellow stake	75
LSD[a]	34

[a] Means were separated using Fisher's Protected LSD on nontransformed data.

Table 2. Photon-flux densities at 480 nm (blue absorbance maximum) and 528 nm (green absorbance maximum) for white-, green-, or black-colored structures and corn located in the field.

		Initial distance (cm)					
		15	30	61	91	122	
Treatment	Wavelength	Photon-flux density					LSD[a]
	nm	μmol/m²/s²					
White structure	480	0.41	0.28	0.20	0.18	0.16	0.04
Green structure	480	0.11	0.10	0.09	0.09	0.09	0.03
Black structure	480	0.08	0.08	0.07	0.06	0.05	0.03
Corn	480	0.14	0.14	0.14	0.14	0.13	0.03
LSD[b]		0.07	0.06	0.08	0.08	0.09	
White structure	528	0.41	0.27	0.20	0.18	0.15	0.04
Green structure	528	0.17	0.13	0.11	0.10	0.10	0.03
Black structure	528	0.08	0.07	0.07	0.06	0.05	0.03
Corn	528	0.20	0.19	0.17	0.15	0.14	0.03
LSD[b]		0.08	0.06	0.08	0.09	0.11	

[a] Means within column were separated using Fisher's Protected LSD on nontransformed data.

[b] Means within row were separated using Fisher's Protected LSD on nontransformed data.

distances than did any other treatment and also at 61-cm initial distance compared with black or green structures (Table 2). Morningglories grown in plots containing white or green structures or corn at 15- or 30-cm initial distance received more reflected green light than morningglories grown in plots containing black structures (Table 2). At the 61-cm initial distance, morningglories grown in plots containing white structures or corn received more green light than did morningglories grown in plots containing green or black structures. However, differences in blue or green light did not appear to influence morningglory growth habit.

There was no difference in red to far-red ratios between initial distances for plots containing green (0.78) and black (0.87) structure colors (Table 3). Corn had red to far-red ratios of 0.50, 0.58, 0.61, 0.72, and 0.82 for the respective initial distances of 15, 30, 61, 91, and 122 cm. These data show that morningglories grown in plots with corn were subjected to more far-red light at 15- and 30-cm initial distances than morningglories grown in plots containing any other colored structures and at 61 cm, when compared with green- and black-colored structure. The white-colored structures treatment had red to far-red ratios of 1.55, 1.12, 1.00, 0.98, and 0.96 for the respective initial distances of 15, 30, 61, 91, and 122 cm. However, there was no correlation between red to far-red ratio and morningglory climbing response. The white structures reflected more red light at 15, 30, and 61 cm initial distances and had the greatest total reflected photon-flux density at all wavelengths at all initial distances compared with black or green structures or corn (data not shown). The green structures had higher total reflected photon-flux density at all initial distances compared with black structures.

The main plot factor (structure color) was significant for climbing growth, with fewer morningglories climbing black structures compared with white- or green-colored structures or corn (Table 4). The subplot factor (initial distance) was also significant for the percentage of morningglories that climbed (Figure 2). Morningglories planted within 46 cm of white or green structures or corn located and climbed $\geq$ 78% of the time. Morningglories planted within 46 cm of black structures located and climbed $\leq$ 21% of the time. As initial distance increased, the number of morningglories that successfully located and climbed all colored structures and corn decreased. Morningglories were observed to initiate stem branching as early as the eight-leaf growth stage (data not shown). Also, at 3 wk after planting, morningglories that had not located and climbed structure or corn tended to branch more than those that were growing toward a structure or corn.

The main plot factor was also significant for aboveground biomass, with morningglory plants in the plots containing

Table 3. Red to far-red ratios for white-, green-, and black-colored structures and corn located in the field.

	Initial distance (cm)					
	15	30	61	91	122	
Treatment	Photon-flux density					LSD[a]
	μmol/m²/s²					
White structure	1.55	1.12	1.0	0.98	0.96	0.13
Green structure	0.79	0.78	0.79	0.78	0.78	0.11
Black structure	0.86	0.88	0.87	0.88	0.87	0.10
Corn	0.50	0.58	0.61	0.72	0.82	0.11
LSD[a]	0.23	0.27	0.18	0.25	0.26	

[a] Means were separated using Fisher's Protected LSD on nontransformed data.

Table 4. Percentage of morningglories in field study that successfully located and climbed objects and average dry weight for morningglories in field study grown in plots containing white, green, and black structure or corn.

Treatment	Successful climbing	Dry weight
	%	g
White structure	64	127
Green structure	67	125
Black structure	10	88
Corn	61	118
LSD[a]	21	22

[a] Means were separated using Fisher's Protected LSD on nontransformed data.

black structures having less biomass (Table 4). This result reflects that morningglories that successfully located and climbed structures had greater growth than those that remained on the ground. The initial planting distance was also significant for morningglory biomass (decreasing weight with increasing initial distance), likely reflecting decreasing climbing habit with increasing initial distance (Figure 3). Increased morningglory biomass (as a result of climbing) resulted in increased production of seed (Figure 4).

Ivyleaf morningglory tended to respond to the spatial distribution of surrounding objects and preferentially projected its growth toward the most likely prospective regions for climbing. However, because of a lack of correlation between red to far-red ratios and the percentage of morningglories that successfully located and climbed structure, phototropism because of the red to far-red light ratio is unlikely to be the mechanism by which morningglory growth responds. Also, intensity of blue and green light was not correlated to the percentage of morningglories that successfully located and climbed structure. Further research is necessary to elucidate mechanisms triggering the preferential growth exhibited by morningglory. However, these data show that if morningglory is located within 46 cm of corn, 78% of the time it will successfully locate and climb neighboring plants. Also, these data show that as morningglories successfully locate and climb structures, seed production increases. Because many crops are planted with row spacing of 76 to 90 cm, the success of morningglory in locating and climbing the crop readily illustrates reasons why control of morningglory is critical.

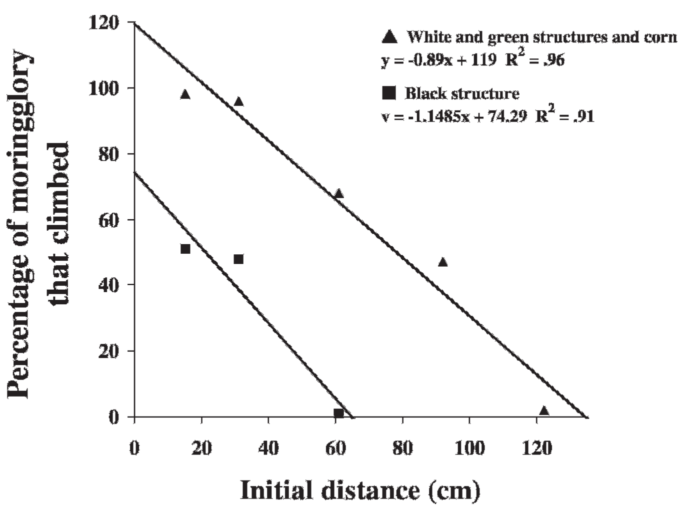

Figure 2. Percentage of morningglories in field study that successfully located and climbed black structure (■), or white and green structures and corn (▲) as influenced by initial distance.

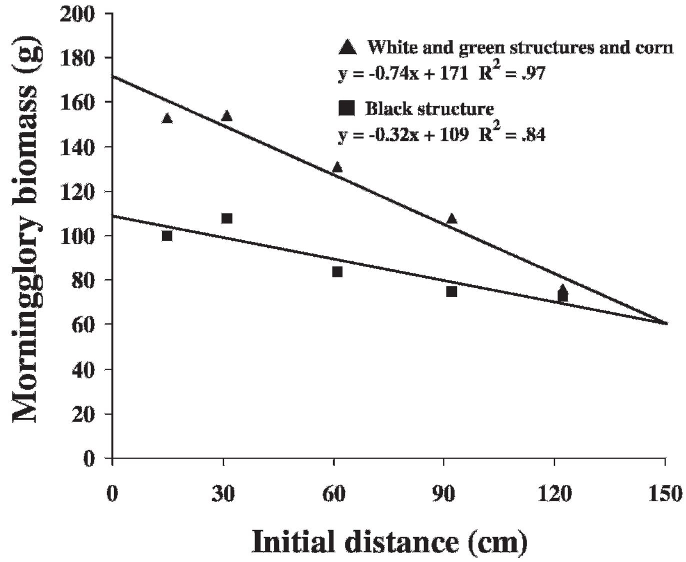

Figure 3. Average morningglory biomass in a field study containing a black structure (■), or white and green structures and corn (▲) as influenced by initial distance.

Sources of Materials

[1] Premium Spray Enamel Paint. Orgill, Inc., Memphis, TN 38101.

[2] Metro-Mix 360, Scotts-Sierra Horticulture Products Co., 14111 Scottslawn Road., Marysville, OH 43041.

[3] LI-COR Biosciences Inc., 4308 Progressive Avenue, P.O. Box 4000, Lincoln, NB 68504.

[4] Glidden America's Finest Outdoor Exterior Semi-Gloss Paint. The Glidden Co., Cleveland, OH 44115.

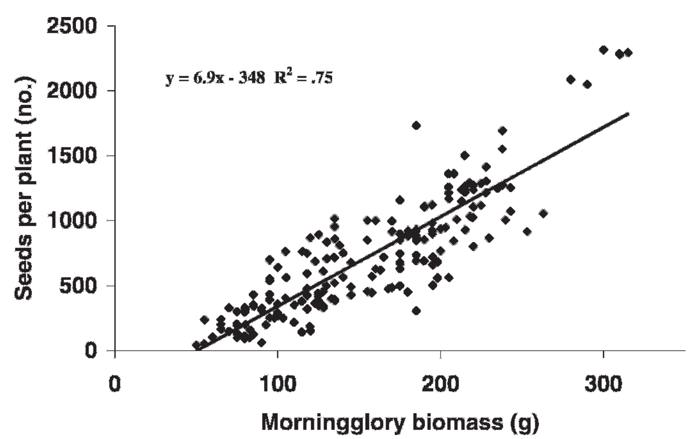

Figure 4. Seed per plant as influenced by morningglory biomass in field study.

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