Chapter VIII

Characterization of Growth and Reproductive Ability of Imidazolinone-sensitive and –Resistant Smooth Pigweed (*Amaranthus hybridus* L.)

Abstract: Greenhouse, growth chamber, and field studies were conducted in 2000 and 2001 to compare growth and development, seed production, and seed germination of one imidazolinone-susceptible (S) and five –resistant (R1, R2, R3, R4, and R5) smooth pigweed biotypes under noncompetitive and competitive conditions. Under noncompetitive conditions in the greenhouse, rate of height increase in S smooth pigweed was similar to those in R1, R2, R3, and R5. However, growth rate at 3 to 5 wk after planting (WAP) was greatest in the R4 biotype. In both noncompetitive conditions in the greenhouse and in noncompetitive and competitive conditions in the field, R4 tended to have a more rapid rate of height increase at 3 to 5 WAP. However, height of S and R4 biotypes were similar by 8 to 9 WAP. In the greenhouse, S produced more total biomass than all R biotypes, although a greater relative proportion of total biomass was attributed to reproductive biomass in R4. Seed production in the greenhouse was similar between S and R4 biotypes, and greater than seed production of R1, R2, R3, or R5 biotypes. Seed of R4 also displayed a more rapid initial rate of germination than S, although final germination after 12 d imbibition was similar between S and R4. Vegetative and reproductive biomass accumulation in the field was density-dependent but was similar for all biotypes. Collectively, these results suggest that not all imidazolinone-resistant smooth pigweed biotypes suffer fitness penalties compared to imidazolinone-susceptible smooth pigweed, particularly under competitive conditions in the field.

Nomenclature: Smooth pigweed, *Amaranthus hybridus* L. AMACH.

Key Words: Acetolactate synthase, ALS, competition, fitness, germination, herbicide resistance, imidazolinones, imidazolinone resistance, seed production.

Introduction

At least 60 weed species resistant to acetolactate synthase (EC 4.1.3.18) (ALS)-inhibiting herbicides have been reported within the past 15 years. Recently, *Amaranthus* species have been reported more frequently than other species (Heap 2002). Biotypes of Palmer amaranth (*Amaranthus palmeri* S Wats.) (Horak and Peterson 1995; Gaeddert et al. 1997; Sprague et al. 1997), redroot pigweed (*Amaranthus retroflexus* L.) (Saari et al. 1994), prostrate pigweed (*Amaranthus blitiodes* S Wats.) (Saari et al. 1994), common waterhemp (*Amaranthus rudis* Sauer) (Foes et al. 1998; Horak and Peterson 1995; Sprague et al. 1997; Hinz and Owen 1997; Lovell et al. 1996), livid amaranth (*Amarnthus lividus* L.) (Manley et al. 1996), and smooth pigweed (Manley et al. 1996; Poston 2000; Schmenk et al. 1997;) resistant to ALS-inhibiting herbicides have been reported within the past 6 to 7 years. In all instances, repeated use of ALS-inhibiting herbicides was documented and resistance was due to an altered ALS.

Fitness is defined as the ability of an organism to establish, survive, and reproduce successfully (Silvertown 1982). Ahrens and Stoller (1983) demonstrated that triazine-resistant smooth pigweed produced less shoot biomass and seed dry weight under competitive conditions, fixed less CO_2 under saturated light and CO_2 conditions, and exhibited a significantly lower relative growth rate and net assimilation ratio than a triazine-susceptible biotype. Conrad and Radosevich (1979) concluded that triazine-resistant redroot pigweed and common groundsel (*Senecio vulgaris* L.) were less fit than their respective wild types under both competitive and non-competitive conditions and attributed reduced competitiveness in the resistant biotype to

photosynthetic inefficiency and concluded that the triazine resistance trait was only of benefit to the plant where triazine herbicides are repeatedly used. Gressel and Segel (1982) suggest that one possible result of reduced fitness in triazine-resistant weed biotypes is that the selected biotypes may continue to exist only in a population where herbicide selection pressure is great enough to kill the wild type. Based on this premise, reversion to a mostly susceptible population will likely occur over time in the absence of the herbicidal selection agent.

Interestingly, weed biotypes that have developed resistance to ALS inhibitors may not suffer fitness penalties as severe as those observed in triazine resistant weed biotype. Thompson et al. (1994) noted similar growth rates, seed production, and competitiveness in both sulfonylurea-susceptible and –resistant kochia (*Kochia scoparia* (L.) Schrad.). With sulfonylurea-resistant prickly lettuce (*Lactuca serriola* L.), reductions in biomass production compared to the wild type were observed under noncompetitive conditions, but the biotypes grew similarly in competition studies (Alcocer-Ruthling et al. 1992). In smooth pigweed, Poston et al. (2002) found that imidazolinone-susceptible smooth pigweed displayed an advantage in vegetative growth and development over three out of four imidazolinone-resistant biotypes under controlled greenhouse conditions. However, competitive advantages of susceptible smooth pigweed could not be confirmed under field conditions and it was concluded that further studies are required to determine relative growth differences.

Gressel and Segel (1982) have shown that many reproductive factors such as (1) proportion of seeds germinating at a given time, (2) rate of germination, and (3) seed size and seed yield per flower are important in determining whether a wild-type population is more fit than a selected population. Past research comparing fitness of imidazolinone-susceptible and –resistant smooth pigweed under field conditions in Virginia did not document a competitive

advantage for susceptible smooth pigweed under field conditions and concluded that further studies comparing competition as well as seed production and germination of smooth pigweed biotypes are warranted (Poston et al. 2002). In this research, work in Virginia was continued to investigate competitive ability, seed production, and seed germination of imidazolinone-susceptible and –resistant smooth pigweed.

Materials and Methods

Seed Sources

Smooth pigweed seed were collected in 1993 from four soybean fields in Somerset County, MD and one soybean field near Oak Hall, VA that had histories of repeated imazaquin use, with failure of control from imazaquin reported by farmers. Seed from an additional population were collected in 1998 from a lima bean field near Ridgely, MD were imazethapyr had been used repeatedly. In this population, failure of control from imazethapyr was reported by the farmer. Each of these four locations represented a separate farming entity with independently-owned equipment including combines (i.e., no custom harvesting), and locations were as much as 28 km apart. Equipment was not shared between any of these locations, thereby reducing the likelihood that seeds were spread from one location to another. At each location, seeds were pooled from approximately 40 different plants that had survived imazaquin or imazethapyr treatment. Samples were subsequently labeled R1, R2, R3, R4, and R5 to identify various biotypes. R1, R3, and R5 were selected by imazaquin from Somerset County, MD locations while R2 was selected by imazaquin near Oak Hall, VA and R4 was selected by imazethapyr near Ridgely, MD. Seed were collected from several plants in each field that survived imazaquin or imazethapyr applications. Seed from known imidazolinone-susceptible smooth pigweed plants were also collected from the Eastern Shore Agricultural Research and Extension Center near Painter, VA,

for use as a control biotype. This biotype was subsequently labeled S to denote susceptibility. Seed were threshed and stored under refrigeration (1 C) until needed.

Greenhouse Experiments

Seed from S, R1, R2, R3, R4, and R5 smooth pigweed populations were planted into 43- by 53-cm greenhouse flats[1] containing a commercial potting soil mix[2] on June 22, 2000 and June 16, 2001. Seed were germinated and seedlings allowed to develop for several days before being transplanted into 10- by 10-cm square pots filled with potting soil. Seedlings at the one-true-leaf stage were transplanted into each pot. Plants were maintained in the greenhouse under natural sunlight and sprinkler irrigation. Plants were fertilized[3] weekly to maintain active growth.

Data were collected over the course of 8 wk beginning approximately 2 wk after seeding and 1 wk following transplanting. Shoot height was measured weekly for each plant. The majority of seedlings were judged to be mature by 8 WATR. At that time, all biomass above the soil level was harvested and separated into vegetative and reproductive (inflorescence) portions. The reproductive portion included the rachis, utricles, seeds, perianth segments, and bracts. Fresh weight for each plant portion was recorded immediately following harvest. Reproductive portions were then allowed to air-dry for five d. Seed from reproductive portions of each plant were then successively cleaned using size 10, 18, and 30-mesh sieves[4]. Estimation of seed production per plant followed procedures used by Weaver (1984). To estimate seed production per plant, 0.1 g samples were collected from total cleaned seed of each plant and were manually counted. Seed number per g of fresh inflorescence and per plant was extrapolated from these values. Mean weight of 100 seed was also determined for each biotype. A completely randomized design with six replications was used in the greehouse study and the study

was repeated. Population by study interactions were not detected, therefore all data were combined across studies. Non-linear regression analysis techniques similar to those employed by Chism et al. (1992) were used to generate growth curves and to compare growth in different smooth pigweed populations. Shoot height data were regressed to fit the sigmoidal model:

$$y = a / (1 + e^{(-(x-c)/b)}) \quad [1]$$

where y is shoot height in cm, x is WAP, a is a magnitude constant, b is a rate constant, c is the y intercept, and e is the base of the natural logarithm. Because a general nonlinear model was used to generate growth curves for all populations, comparisons between regression coefficients could be made using techniques described by Chism et al. (1992) to establish significant differences between regression lines. Approximate R^2 values were calculated to assess goodness of fit for individual regression equations.

Growth Chamber Experiments

Germination experiments were also conducted to investigate viability and germination rate of smooth pigweed biotypes. Seed from each biotype were drawn from seed lots used in greenhouse experiments. One hundred seed of each biotype were placed on Whatman No. 3 filter paper[5] in 10-cm petri dishes[6] moistened with 10 mL of distilled water. Petri dishes were placed in a growth chamber[7] at alternating temperatures of 30/20 C (12 h) under alternating light and darkness with a 12-h photoperiod (fluorescent lights, 20.5 $\mu E*sec^{-1}*m^{-2}$). Germination was recorded every 2 d for a period of 12 d. Additional water was added as needed. A seed was recorded as germinated when its radicle had emerged to a length of 2 mm. The experimental treatments for the growth chamber experiment were smooth pigweed biotype (S, R1, R2, R3, R4, or R5). Treatments were completely randomized within the growth chamber.

Growth chamber experiments included six replications of treatments and the experiment was repeated. Population by experiment interactions were not detected, therefore germination data were combined across both experiments. Germination data was fit to the Gompertz equation (Draper and Smith 1981):

$$f = a * e^{(-e(-(x-c)/b))} \quad [2]$$

Where f is germination (%), a is the upper asymptote for late germination, b is a rate constant, c is the inflection point of the curve, x is time (days imbibition), and e is the base of the natural logarithm.

Competitive and Noncompetitive Growth in the Field

Noncompetitive and competitive densities were used in field experiments to investigate noncompetitive and competitive growth characteristics of smooth pigweed biotypes. Seed from S, R1, R2, R3, and R4 smooth pigweed populations were planted and germinated as previously described. The R5 biotype from greenhouse and growth chamber experiments was not used in field experiments. Evenly sized one-true-leaf-stage seedlings were transplanted into 5.7-cm square peat cups filled with potting soil and grown in the greenhouse under natural sunlight and sprinkler irrigation to approximately 6-cm tall before being transplanted into the field. Plot size used for field experiments was 1- by 1-m with a 2 m separation between plots. Field experiments consisted of smooth pigweed grown at three densities: one plant m^{-2} (noncompetitive), 16, or 36 plants m^{-2} (competitive). For noncompetitive treatments, one plant from each biotype was planted in the center of each plot. At the competitive density of 16 plants m^{-2}, eight S and eight of each R biotype were planted 25 cm apart (S/R1, S/R2, S/R3, S/R4). At the competitive density of 36 plants m^{-2}, 18 S and 18 of each R biotype were planted 17 cm apart (S/R1, S/R2, S/R3, S/R4). At both competitive densities, smooth pigweed biotypes were planted

in an alternating fashion (SRSRSR etc.). Competitive effects of R biotypes on each other were not assessed. Plant height in all plots was measured at 2, 3, 4, 5, 7, and 9 WATR. At 10 WATR, plant stem diameter at ground level was measured, plants were then harvested at ground level, and vegetative and reproductive portions of each plant were separated as described previously. Subsampling procedure for height measurements, stem diameter, and plant harvest was: 1 plant per plot (S or R) for 1 plant m^{-2} noncompetitive densities, 8 plants per plot (4S, 4R) for 16 plants m^{-2} densities, and 16 plants per plot (8S, 8R) for 36 plants m^{-2} densities. Experimental design for the field experiment was a randomized complete block with three replications. All populations behaved similarly over years in field studies and data were combined across years. Height data were fit to the sigmoidal model given in Equation 1.

Statistical Analyses

Analysis of variance (ANOVA) was performed on all smooth pigweed biomass and seed production data in SAS[8]. Sums of squares were partitioned to evaluate linear, quadratic, and higher order effects as well as study by biotype interactions for greenhouse and growth chamber experiments or year by biotype and/or density interactions for field experiments. Data measured over time (plant height or germination) were analyzed using repeated measures techniques with multivariate ANOVA to control for correlation structure (Meridith and Stehman 1991). Regression analysis was used to determine the degree of association between smooth pigweed biotype and measured data in greenhouse and growth chamber experiments and between smooth pigweed biotype, density, and measured data in field experiments. Where a nonlinear equation was fit to height and germination data, biologically realistic equations that appropriately described the data were used to characterize relationships (Cousens et al. 1987). An approximate coefficient of determination (R^2) for

nonlinear equations was obtained by subtracting the ratio of the residual sums of squares (RSS) to the corrected total sums of squares (CTSS) from 1 (i.e., $R^2 = 1 - RSS/CTSS$). For all plant biomass and seed data, means were separated using Fisher's protected LSD test at the $\alpha = 0.05$ level.

Results and Discussion

Greenhouse Experiments

ANOVA indicated that experiment effects for plant height over time, biomass production, and seed production were not significant; therefore, data were averaged over experiments.

Growth

Under noncompetitive conditions in the greenhouse, plant height increased significantly over time in all biotypes and growth patterns best fit the sigmoidal model (Equation 1). Predicted maximum plant height (coefficient *a*) for the S biotype was similar to R1, R4, and R5 but was larger than R2 or R3 (Table 8.1, Figure 8.1). During the period of 3 to 5 WAP, however, R4 had a more rapid rate of growth than the S biotype (coefficient *b*). More rapid growth of the R4 biotypes during the period of 2 to 4 WAP was confirmed within each of these measurement times, as R4 plants were significantly taller than S plants at 2, 3, and 4 WAP, but heights were similar at 6 and 8 WAP. Inflection points (coefficient *c*) of growth curves were similar for all biotypes.

Biomass production

Total biomass production under noncompetitive conditions in the greenhouse differed between smooth pigweed biotypes, as S biomass production was 44, 19, 46, 51, and 9% greater than R1, R2, R3, and R4 biotypes, respectively (Figure

8.2). Reproductive biomass was also greatest in S and R4 biotypes. Reproductive biomass was 9.01 and 9.7 g, respectively, in S and R4 biotypes compared to 5.9 to 7.5 g in R1, R2, R3, or R5 biotypes. Although reproductive biomass in R4 was similar to S and greater than other R biotypes, R4 produced significantly less vegetative biomass than S, R2, and R5. Therefore, R4 devoted more resources to reproductive purposes than other R biotypes and had a greater ratio of reproductive biomass to total biomass than all other biotypes.

Seed production

Smooth pigweed seed production per plant also differed between populations and reflected differences seen in reproductive biomass production. Total seed production per plant was higher in S and R4 biotypes than in R1, R2, R3, and R5 biotypes. Estimated seed production per plant based on seed counts from cleaned samples of each population were 3530 and 3960 seed per plant for S and R4 biotypes, respectively, and 2040 to 2460 seed per plant for R1, R2, R3, and R5 biotypes (Figure 8.3). Seed weight was similar between biotypes, ranging from 40 to 48 mg per 100 seed (data not presented).

Seed germination

Seed germination of all biotypes increased significantly during the 12 d observation period (Figure 8.4). Germination patterns for all biotypes best fit the Gompertz model (Equation 2). Regression coefficient a (upper asymptote for predicted late germination) was different in all R biotypes compared to S. However, not all a values were lower than a values for S. Upper asymptote values for R1 and R5 were significantly lower than that for S (lower predicted final germination in R1 and R5). Conversely, upper asymptote values for R2, R3, and R4 were greater than that of S (greater predicted final germination than S). Regression coefficient b for R1, R2,

R3, and R4 was similar to that for S although germination between 4 and 10 d was lower for R5. R1 and R3 inflection points of curves as indicated by coefficient c were similar to c values for S while inflection point for R2, R4, and R5 were slightly lower than S, indicating slightly higher germination compared to S in these biotypes, particularly during early periods of imbibition (2 to 6 d). Final germination after 12 d imbibition was 78 to 93% in S, R1, R4, and R5 biotypes, 64% in R5, and 45% in R3.

Field Experiments

Due to lack of a density by biotype by year interaction, data for plant height over time, stem diameter, and biomass production from field experiments were averaged over years.

Growth

The R5 biotype used in growth studies in the greenhouse and germination studies in the growth chamber was not used in field studies. ANOVA revealed that growth of all biotypes was heavily influenced by plant density. Significant main effects occurred for plant density and biotype. Height data over time across densities and within densities were best fitted to the sigmoidal model (Equation 1). Averaged over smooth pigweed biotypes, mean plant height over time increased from 28 to 165 cm, 28 to 154 cm, and from 25 to 135 cm during the period of 2 to 9 WAP for smooth pigweed densities of 1, 16, and 36 plants m^{-2}, respectively (Figure 8.5). Smooth pigweed growing under noncompetitive conditions (1 plant m^{-2}) were significantly taller than smooth pigweed growing at the competitive density of 36 plants m^{-2} at 4, 5, and 7 WAP and were taller than smooth pigweed growing at densities of 16 and 36 plants m^{-2} at 9 WAP.

Differences in growth data over time between biotypes occurred at each density, with differences occurring primarily between S and R4 biotypes. At

the noncompetitive density of 1 plant m^{-2}, plant heights of all biotypes were similar at 2 and 3 WAP (Figure 8.6A). At 4 WAP, the R4 biotype was similar in height to S and taller than R1, R2, and R3 biotypes. At 5 WAP, R4 was taller than all other biotypes. By 9 WAP, however, plant height was similar for all biotypes. Comparison of regression coefficients revealed that sigmoidal regression coefficients *a*, *b*, and *c* for R4 were different from those of S (Table 8.2). Although R1 and R4 had lower predicted maximum height than S, a lower *b* coefficient value in R4 compared to S indicated more rapid growth during the period of 3 to 5 WAP. Further, the lower inflection point (coefficient *c*) for R4 shifts its growth curve slightly to the left, also indicative of more rapid early-season growth.

At the competitive density of 16 plants m^{-2}, differences in growth of S and R4 biotypes were also evident. R4 smooth pigweed was significantly taller than all other biotypes at 2, 3, 4, 5, and 7 WAP (Figure 8.6B). Similar to growth under noncompetitive conditions, height of all biotypes was similar at 9 WAP. Declination of the rapid growth phase of R4 by 9 WAP resulted in lower predicted maximum height (coefficient *a*) in R4. Lower *b* and *c* values for R4 compared to S indicate more rapid growth at 2 to 5 WAP, resulting in a lower inflection point thereby causing the R4 curve to again be shifted slightly to the left. Inflection point for R1 was also slightly lower than that of S.

At the most competitive density of 36 plants m^{-2}, differences in growth between S and R4 biotypes were still apparent (Figure 8.6C). Plant competition from heavier densities resulted in fewer height differences between biotypes within each measurement time. However, comparisons of nonlinear regression coefficients nonetheless indicated differences in growth over time between S and R4 biotypes. Similar to differences in regression coefficients between S and R4 biotypes at 1 and 16 plants m^{-2}, R4 had a lower predicted maximum height following more rapid growth earlier in the season.

At all three densities, R4 began its rapid growth phase earlier than most other biotypes, but this rapid growth phase also began to decline earlier than in other biotypes.

Biomass production

Similar to smooth pigweed height data, biomass production was also heavily influenced by smooth pigweed density. However, biomass production was similar across all biotypes at each density. Average vegetative, reproductive, and total biomass across all biotypes was 3542, 1752, and 5294 g per plant at 1 plant m^{-2}; 292, 144, and 436 g per plant at 16 plants m^{-2}; and 92, 36, and 127 g per plant at 36 plants m^{-2} (Figure 8.7). Similarly, biomass of S and R biotypes within each biotype combination at competitive densities were comparable (data not presented). All biotypes responded similarly to density and no competitive advantage was seen in any portion of biomass accumulation in any S to R combination. Similar to results observed with biomass production, smooth pigweed stem diameter was influenced only by plant density. Averaged over all biotypes, mean stem diameter was 54.4 mm at the noncompetitive density of 1 plant m^{-2}, 18.4 mm at 16 plants m^{-2}, and 11.0 mm at 36 plants m^{-2} (data not presented).

In this research, imidazolinone-susceptible smooth pigweed growth potential over time was similar to R1, R4, and R5 and greater than R2 and R3 in the greenhouse. However, R4 displayed a more rapid rate of growth at 3 to 5 WAP. Similar growth patterns were seen at 1, 16, and 36 plants m^{-2} in the field, where the magnitude of the phase of rapid growth (3 to 5 WAP) was greater in R4, but began to decline earlier than S. At each density, height of R4 was equal to or greater than height of S at 3 to 5 WAP, but heights were similar at 9 WAP. More rapid growth at 3 to 5 WAP in the greenhouse did not translate into more biomass accumulation, however, as the S biotype produced more total biomass than any R biotype. The R4 biotype contributed

more energy to reproductive purposes in the greenhouse, however, as reproductive to total biomass ratios were higher in R4 than in any other biotype. Biotypic differences were less pronounced in the field. Neither S nor R biotypes displayed any definitive competitive advantages in biomass accumulation under noncompetitive or competitive conditions in the field, as vegetative, reproductive, and total biomass was similar between biotypes at each density and between S and R biotypes at competitive densities of 16 and 36 plants m^{-2}. In the greenhouse, estimated seed production was similar between S and R4 biotypes and greater than seed production in all other biotypes. As observed with early growth in R4, this biotype also exhibited more rapid germination in the early periods of imbibition in growth chamber experiments. Maximum germination was similar between S, R1, R3, and R4 biotypes. Germination potential of S was greater than that of R3 or R5.

Although the R4 biotype displayed a faster initial rate of growth than S in both greenhouse and field conditions, this generally did not result in long-term advantages in fitness of R4 over S. However, R4 may exhibit a short-term, early-season competitive advantage in growth during the first 3 to 5 wk. These experiments also indicated that R4 is likely more competitive than the other R biotypes in most characteristics that were evaluated. Of all the R biotypes investigated, R4 was the most similar to S in these experiments.

Gill et al. (1996) suggested that at least four S and R biotypes are required to definitively estimate biotypic differences. In our studies, five R biotypes were used in greenhouse and growth chamber experiments and four of these five R biotypes were used in field experiments. However, only one S biotype was included in these experiments. Since resistance was widespread at all locations where R populations were collected (essentially 100% resistance), it was extremely difficult to collect seed from S plants from the same location or from adjacent locations. Based on this premise, we

cannot conclude that reduced growth and biomass accumulation in R2 and R3 and reduced seed production in R1, R2, R3, and R5 compared to S is linked to imidazolinone resistance. Additionally, reduced competitive ability was not documented for most parameters in the imidazolinone-resistant R4 biotype. Collectively, these results suggest that all imidazolinone-resistant smooth pigweed biotypes may not suffer extensive fitness penalties compared to imidazolinone-resistant smooth pigweed biotypes, particularly under competitive conditions in the field.

Sources of Materials

[1]Sutton universal greenhouse flat, inside dimensions 51 by 40 by 5.7 cm, Wetzel, Inc., 1345 Diamond Springs Road, Virginia Beach, VA 23455.

[2]Pro-Mix BX, Premier Horticulture, Inc., Red Hill, PA 18076.

[3]Peters 20-20-20 professional soluble plant food, Wetzel, Inc., 1345 Diamond Springs Road, Virginia Beach, VA 23455.

[4]U.S. Standard Testing Sieves, Fisher Scientific Company. Fair Lawn, NJ 07410.

[5]Whatman No. 3 filter paper, Whatman International, Ltd, Maidstone, England.

[6]Falcon 1029 petri dishes, 100 by 15 mm dimensions, Becton Dickinson Labware, Lincoln Park, New Jersey 07035.

[7]Percival incubation chamber, Boone, Iowa 50036.

[8]Statistical Analysis Systems (SAS) software, Version 7.0, SAS Institute, Inc., Box 8000, SAS Circle, Cary, NC 27513.

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Table 8.1. Nonlinear regression coefficients for growth curves in Figure 8.1 (smooth pigweed growth in the greenhouse) and Figure 8.4 (smooth pigweed germination) for one imidazolinone-susceptible and five –resistant smooth pigweed biotypes[a].

	Regression coefficients					
	Smooth pigweed growth in the greenhouse[b]			Smooth pigweed germination[c]		
Biotype	a	b	c	a	b	c
S	104.6 ± 6.80	1.50 ± 0.30	4.10 ± 0.30	76.46 ± 2.00	1.60 ± 0.20	3.44 ± 0.15
R1	99.7 ± 6.40	1.59 ± 0.28	4.12 ± 0.31	*44.38 ± 3.29	2.28 ± 0.59	3.72 ± 0.37
R2	*91.8 ± 5.30	1.40 ± 0.25	4.00 ± 0.26	*82.38 ± 2.77	1.65 ± 0.26	*3.02 ± 0.19
R3	*89.7 ± 5.84	1.60 ± 0.30	3.86 ± 0.31	*93.58 ± 0.65	1.60 ± 0.05	3.45 ± 0.04
R4	97.8 ±4.90	*1.19 ± 0.24	3.18 ± 0.22	*90.23 ± 1.09	1.37 ± 0.09	*2.50 ± 0.07
R5	99.6 ± 6.20	1.31 ± 0.27	3.77 ± 0.28	*60.90 ± 1.89	*1.10 ± 0.20	*3.02 ± 0.19

[a]Coefficients followed by an * are significantly different from the coefficient for the S biotype based on comparisons of regression coefficients using 95% confidence intervals for each regression coefficient. Coefficients are parameter estimates ± standard errors.

[b]Smooth pigweed growth curves fit to the sigmoidal model: $y = a/(1 + e^{(-(x-c)/b)})$.

[c]Smooth pigweed germination curves fit to the Gompertz equation: $f = a*e^{(-e(-(x-c)/b))}$.

Table 8.2. Nonlinear regression coefficients for growth curves in Figure 8.5 (effect of plant density on smooth pigweed growth) and Figure 8.6 (A: smooth pigweed growth at 1 plant m^{-2}; B: 16 plants m^{-2}; and C: 36 plants m^{-2}) for one imidazolinone-susceptible and four –resistant smooth pigweed biotypes in the field.

	Regression coefficients[ab]								
	Smooth pigweed density (plants m^{-2})								
	1			16			36		
Biotype	a	b	c	a	b	c	a	b	c
S	193.9 ± 8.6	1.90 ± 0.2	5.10 ± 0.2	174.8 ± 5.3	1.73 ± 0.10	5.04 ± 0.2	148.9 ± 5.3	1.77 ± 0.13	4.93 ± 0.18
R1	*172.0 ± 5.4	1.72 ± 0.1	4.90 ± 0.2	168.8 ± 5.8	1.61 ± 0.13	*4.68 ± 0.2	147.2 ± 5.2	1.64 ± 0.13	4.63 ± 0.17
R2	182.1 ± 4.1	1.78 ± 0.1	4.99 ± 0.1	167.1 ± 5.5	1.66 ± 0.12	4.93 ± 0.2	148.0 ± 5.9	1.70 ± 0.14	4.93 ± 0.20
R3	222.9 ± 57.8	2.62 ± 0.7	6.43 ± 1.6	168.8 ± 5.2	1.83 ± 0.10	5.12 ± 0.2	144.1 ± 5.4	1.77 ± 0.14	4.80 ± 0.19
R4	*168.5 ± 4.5	*1.35 ± 0.1	*3.84 ± 0.1	*153.3 ± 3.9	*1.42 ± 0.12	*3.75 ± 0.1	*138.3 ± 4.3	*1.36 ± 0.13	*4.02 ± 0.14

[a]Coefficients followed by an * are significantly different from the coefficient for the S biotype based on comparisons of regression coefficients using 95% confidence intervals for each regression coefficient. Coefficients are parameter estimates ± standard errors.

[b]Smooth pigweed growth curves for all densities fit to the sigmoidal model: $y = a/(1 + e^{(-(x-c)/b}$).

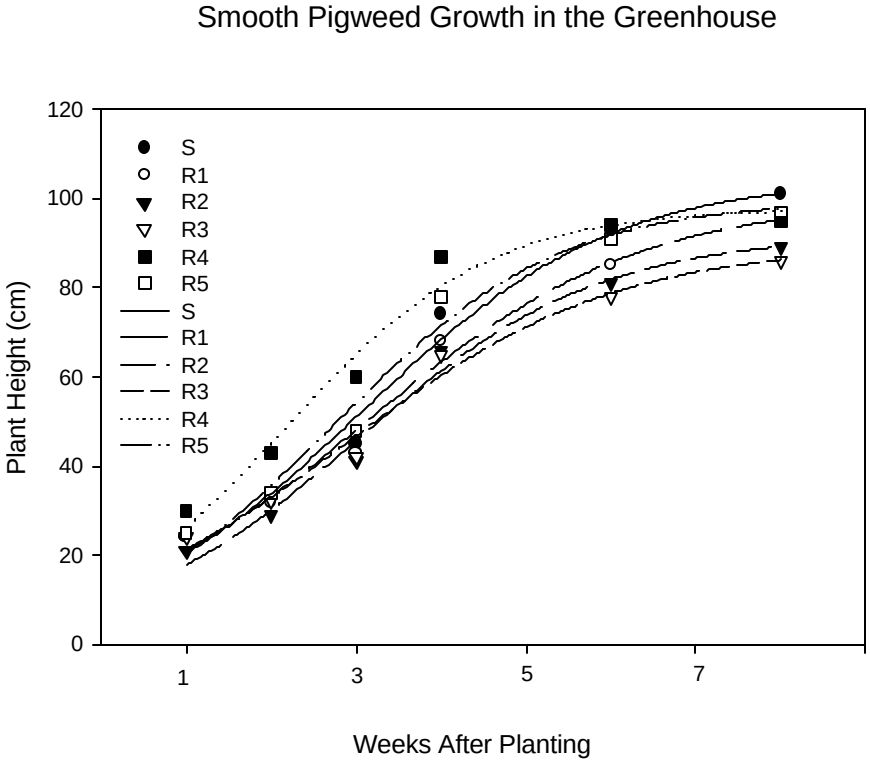

Figure 8.1. Noncompetitive growth of smooth pigweed biotypes in the greenhouse. Regression equations are $y = 104.6/(1 + e^{(-(x-4.1)/1.5)})$, $R^2 = 0.99$; $y = 99.7/(1 + e^{(-(x-4.12)/1.6)})$, $R^2 = 0.98$; $y = 91.8/(1 + e^{(-(x-4.0)/1.4)})$, $R^2 = 0.98$; $y = 89.7/(1 + e^{(-(x-3.86)/1.6)})$, $R^2 = 0.97$; $y = 97.8/(1 + e^{(-(x-3.18)/1.19)})$, $R^2 = 0.96$; and $y = 99.6/(1 + e^{(-(x-3.77)/1.31)})$, $R^2 = 0.96$ for S, R1, R2, R3, R4, and R5 biotypes, respectively.

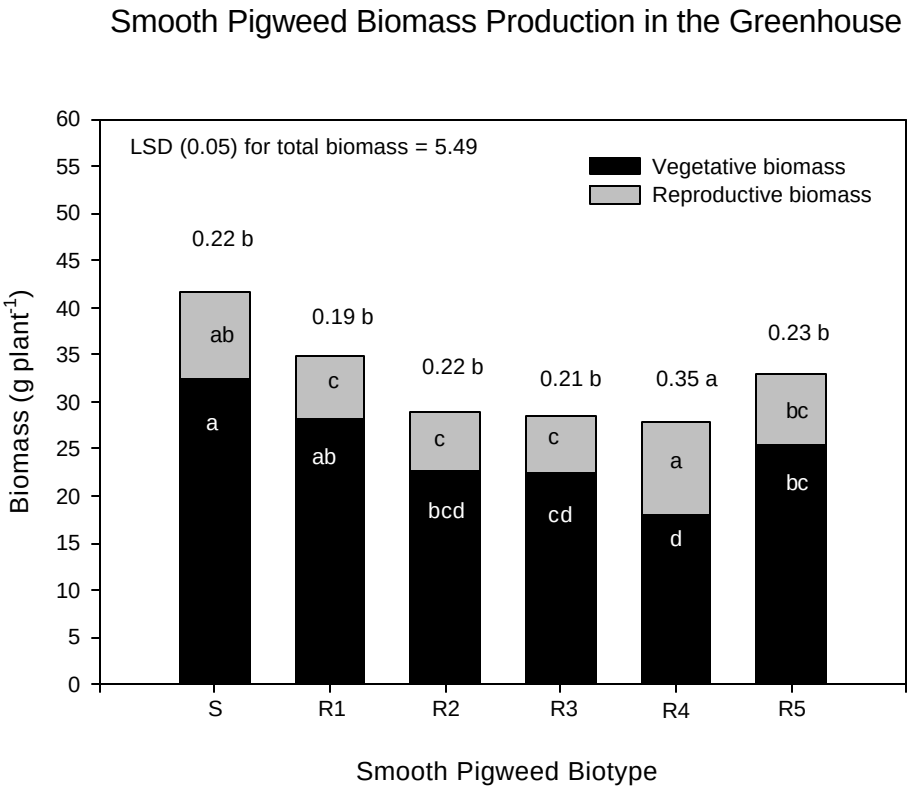

Figure 8.2. Vegetative, reproductive, and total shoot biomass production for imidazolinone-susceptible (S) and -resistant (R1, R2, R3, R4, and R5) smooth pigweed biotypes in the greenhouse. Portions of bars with the same letter are not different according to Fisher's protected LSD (P=0.05). Numbers above the bars are ratios of inflorescence biomass to total biomass for each biotype. Ratios followed by the same letter are not significantly different according to Fisher's protected LSD (P=0.05).

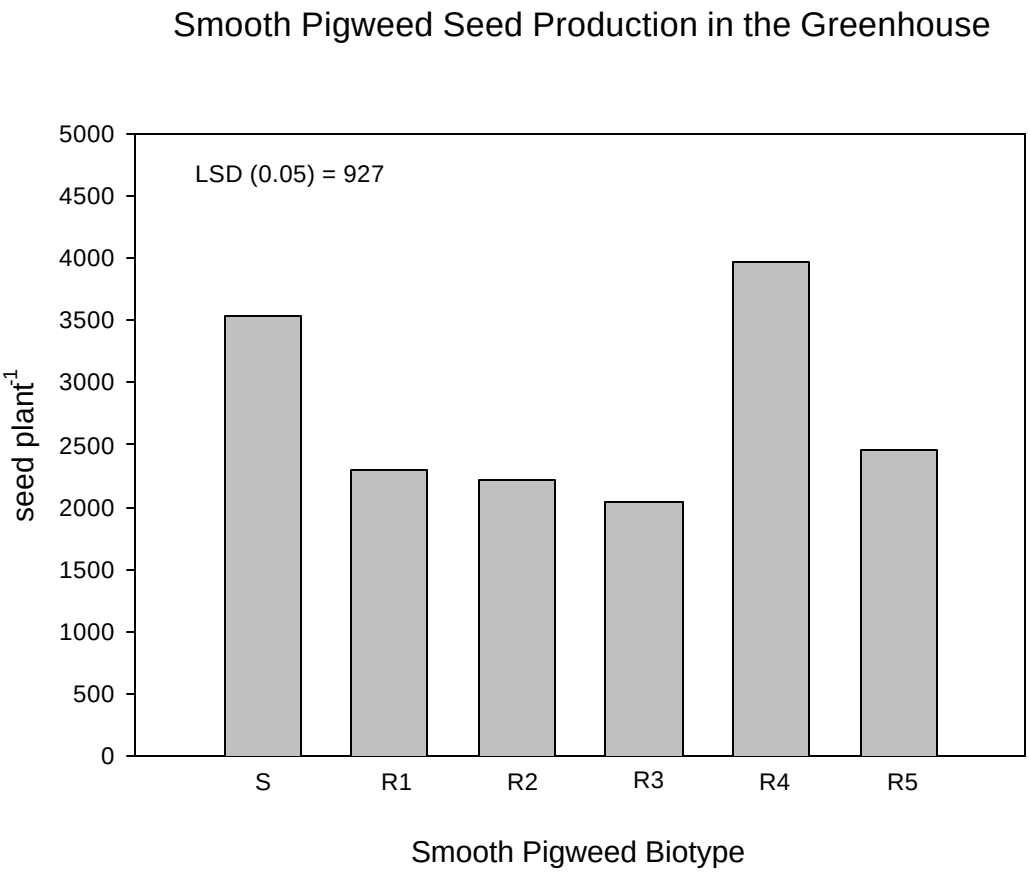

Figure 8.3. Seed production per plant for imidazolinone-susceptible (S) and -resistant (R1, R2, R3, R4, and R5) smooth pigweed biotypes in the greenhouse.

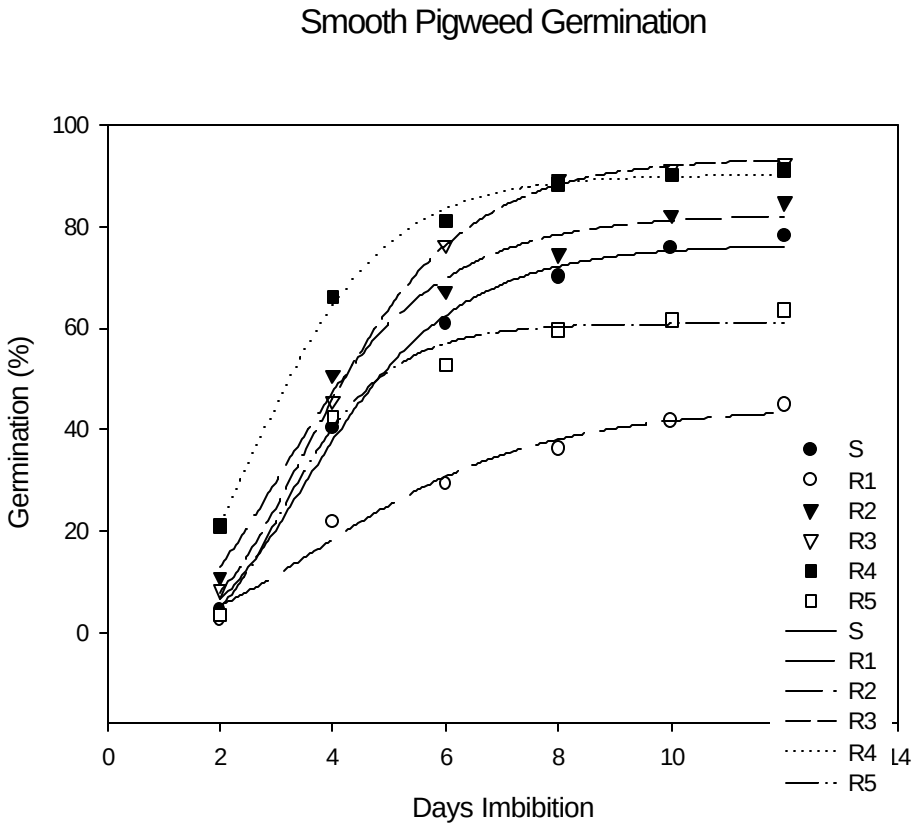

Figure 8.4. Smooth pigweed germination over a 12 d imbibition period. Regression equations for percent germination are $y = 76.46*e^{(-e^{(-(x-3.44)/1.6)})}$, $R^2 = 0.99$; $y = 44.38*e^{(-e^{(-(x-3.72)/2.28)})}$, $R^2 = 0.96$; $y = 82.38*e^{(-e^{(-(x-3.02)/1.65)})}$, $R^2 = 0.98$; $y = 93.58*e^{(-e^{(-(x-3.45)/1.6)})}$, $R^2 = 0.99$; $y = 90.23*e^{(-e^{(-(x-2.5)/1.37)})}$, $R^2 = 0.99$; and $y = 60.9*e^{(-e^{(-(x-3.02)/1.1)})}$, $R^2 = 0.98$ for S, R1, R2, R3, R4, and R5 biotypes, respectively.

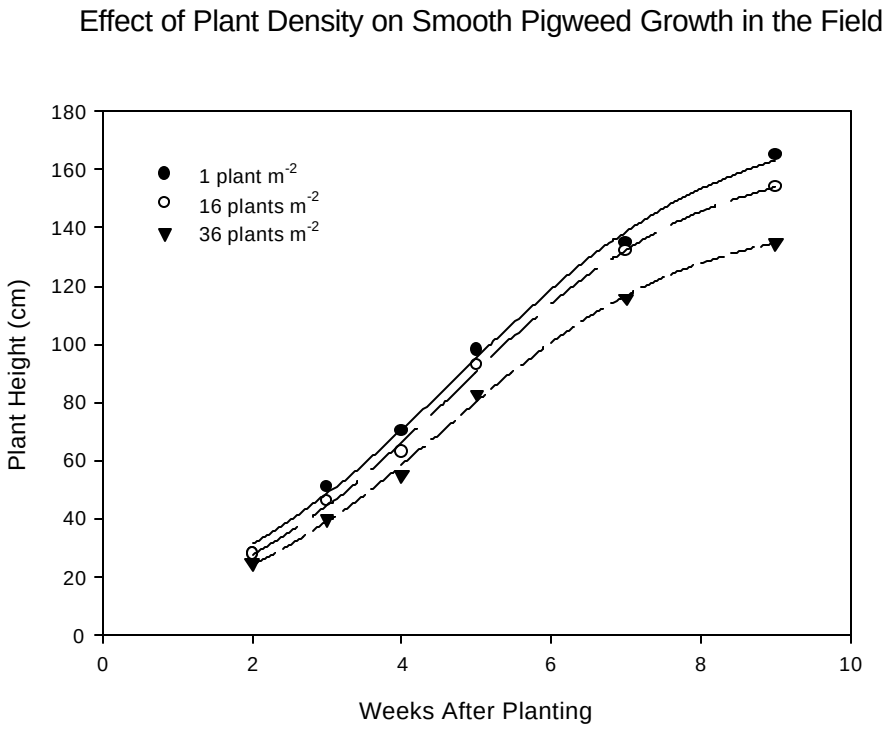

Figure 8.5. Effect of plant density on smooth pigweed shoot growth in the field. Data are averaged over smooth pigweed biotyp Regression equations for plant height are $y = 178.5/(1 + e^{(-(x-4.76)/1.79)})$, $R^2 = 0.99$; $y = 165.5/(1 + e^{(-(x-4.68)/1.67)})$, $R^2 = 0.99$; and $y = 144.3/(1 + e^{(-(x-4.63)/1.64)})$, $R^2 = 0.99$ for smooth pigweed densities of 1, 16, and 36 plants m^{-2}, respectively.

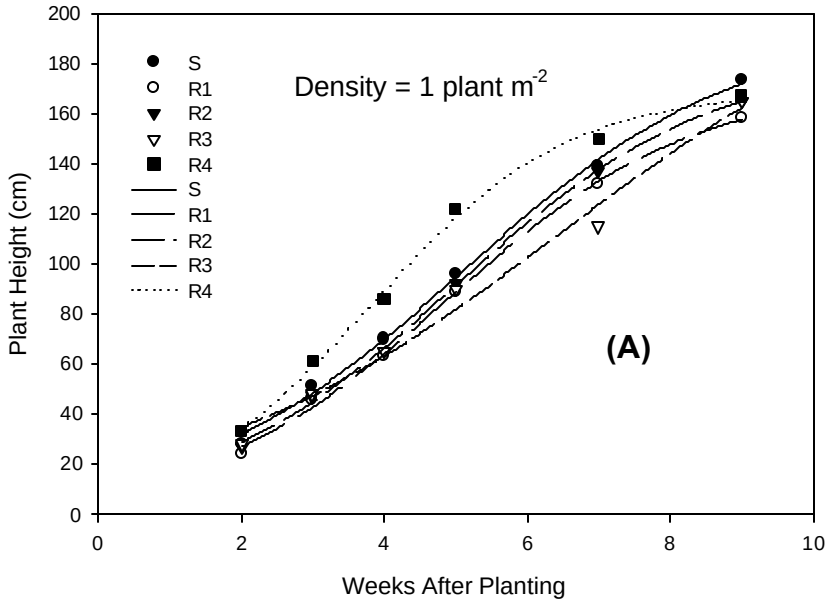

Figure 8.6A. Noncompetitive growth of smooth pigweed biotypes at 1 plant m^{-2}.
Regression equations for density = 1 plant m^{-2} are $y = 193.9/(1 + e^{(-(x-5.1)/1.9)})$, $R^2 = 0.99$; $y = 172.0/(1 + e^{(-(x-4.9)/1.7)})$, $R^2 = 0.99$; $y = 182.1/(1 + e^{(-(x-5.0)/1.78)})$, $R^2 = 0.99$; $y = 222.9/(1 + e^{(-(x-6.43)/2.62)})$, $R^2 = 0.99$; and $y = 168.53/(1 + e^{(-(x-3.84)/1.35)})$, $R^2 = 0.97$ for S, R1, R2, R3, and R4 biotypes, respectively.

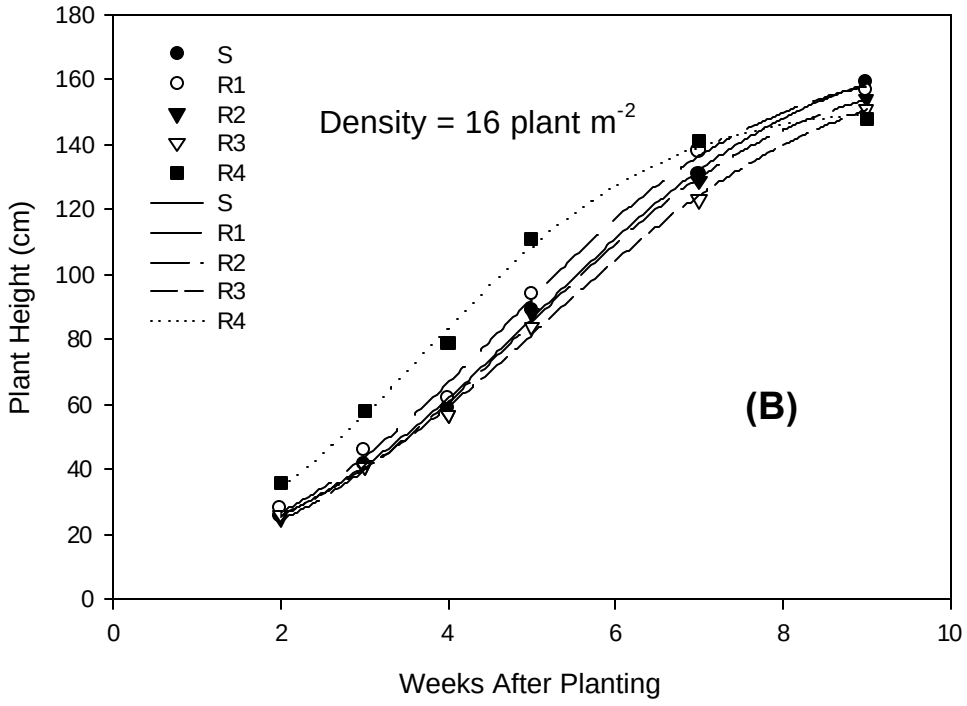

Figure 8.6B. *C*ompetitive growth of smooth pigweed biotypes at 16 plants m^{-2}. Regression equations are $y = 174.8/(1 + e^{(-(x-5.04)/1.73)})$, $R^2 = 0.99$; $y = 168.8/(1 + e^{(-(x-4.68)/1.61)})$, $R^2 = 0.99$; $y = 167.1/(1 + e^{(-(x-4.93)/1.66)})$, $R^2 = 0.99$; $y = 168.8/(1 + e^{(-(x-5.12)/1.83)})$, $R^2 = 0.99$; and $y = 153.3/(1 + e^{(-(x-3.75)/1.42)})$, $R^2 = 0.99$ for S, R1, R2, R3, and R4 biotypes, respectively.

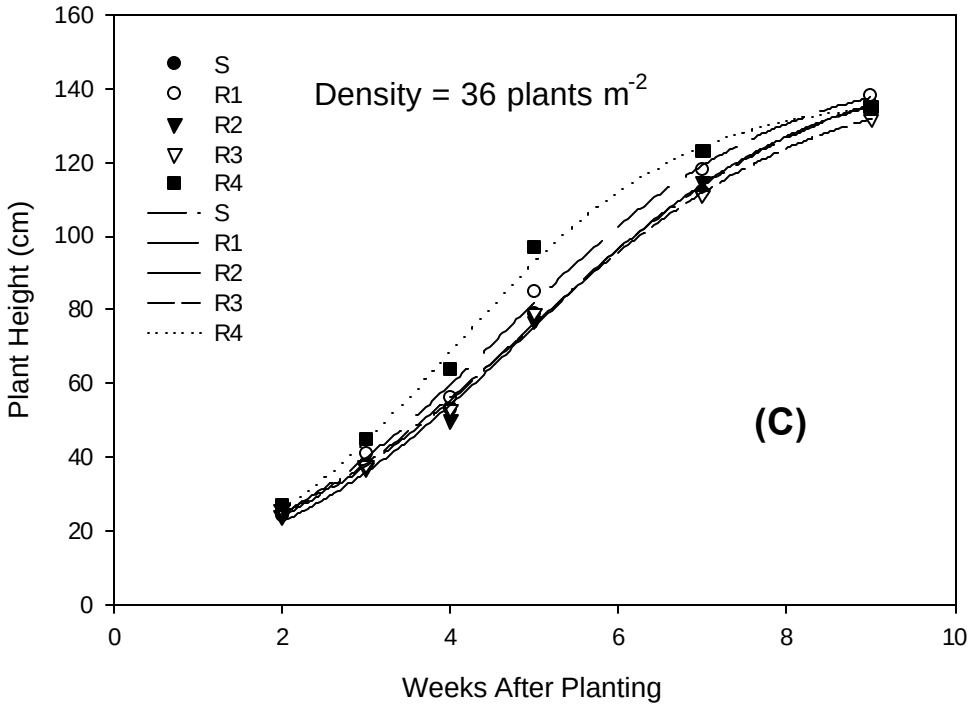

Figure 8.6C. Competitive growth of smooth pigweed biotypes at 36 plants m^{-2}. Regression equations are $y = 148.9/(1 + e^{(-(x-4.93)/1.77)})$, $R^2 = 0.99$; $y = 147.2/(1 + e^{(-(x-4.63)/1.64)})$, $R^2 = 0.99$; $y = 148.0/(1 + e^{(-(x-4.93)/1.7)})$, $R^2 = 0.99$; $y = 144.1/(1 + e^{(-(x-4.8)/1.77)})$, $R^2 = 0.99$; and $y = 138.3/(1 + e^{(-(x-4.02)/1.36)})$, $R^2 = 0.97$ for S, R1, R2, R3, and R4 biotypes, respectively.

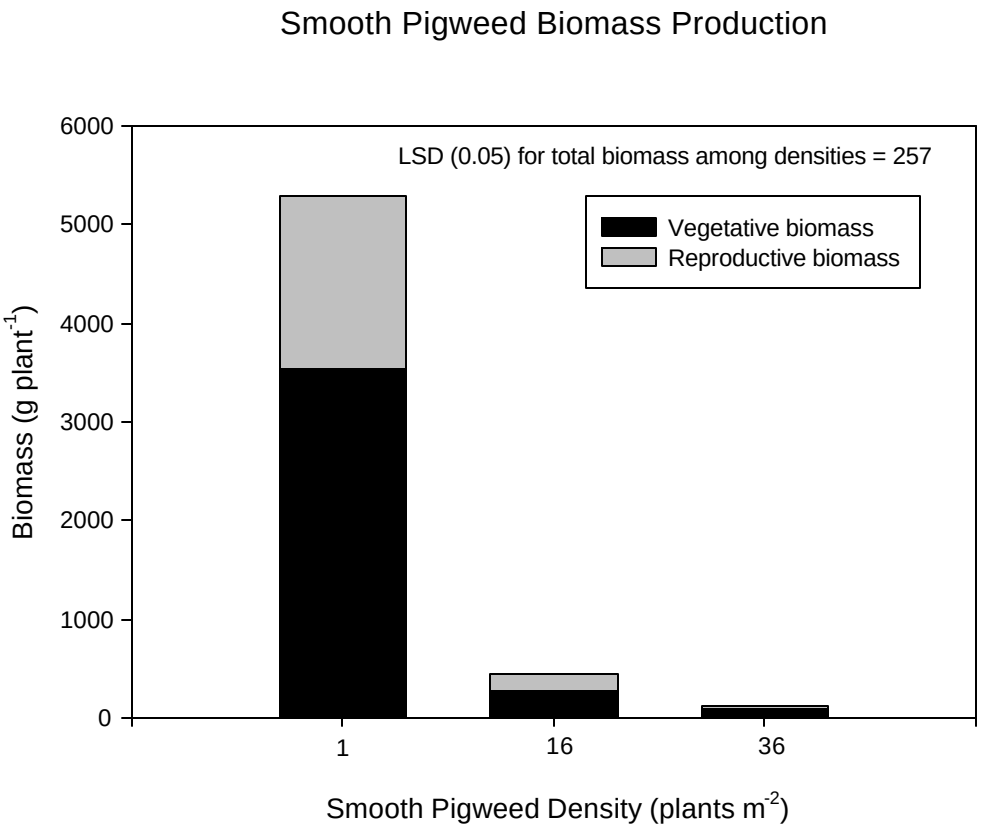

Figure 8.7. Smooth pigweed vegetative, reproductive, and total biomass as influenced by plant density in the field.