

Research Article

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Growth, fecundity, and competition between aryloxyphenoxypropionate-resistant and -susceptible Asia Minor bluegrass (*Polypogon fugax*)

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Abstract

Asia Minor bluegrass (*Polypogon fugax* Nees ex Steud.) is a problem grass weed of winter crops in China, where a population has become resistant to aryloxyphenoxypropionate (APP) herbicides. The mechanism of resistance is due to an Ile-2041-Asn mutation of the *ACCcase* gene. Screen house experiments were conducted to study the growth, fecundity characteristics, and competitive ability of this aryloxyphenoxypropionate-resistant (APP-R) biotype compared with a susceptible (APP-S) biotype. When grown under noncompetitive conditions, the APP-R *P. fugax* developed more rapidly than the APP-S plants, with earlier tiller and panicle emergence and seed shedding; the APP-R *P. fugax* set seeds nearly 12 d earlier than the APP-S biotype. APP-R and APP-S biotypes had similar aboveground dry weight before the flowering stage. Fecundity of the APP-R biotype was similar to the APP-S biotype (8.57 g seeds plant⁻¹ and 0.17 g seeds panicle⁻¹ versus 8.22 g seeds plant⁻¹ and 0.13 g seeds panicle⁻¹, respectively). Ultimately, the relatively slower-developing APP-S *P. fugax* had 50% more shoot dry weight than the APP-R plants. Relative competitiveness among the APP-R and APP-S *P. fugax* biotypes was investigated through replacement series experiments. No difference in competitive ability was measured between APP-R and APP-S biotypes on the basis of shoot dry weight before the tillering stage. These results indicate that there is no apparent fitness penalty for the APP-R *P. fugax*. The shorter growth cycle of APP-R with no apparent fitness penalty suggests that growers will need begin weed control earlier and possibly include vegetative crops with an even shorter growth cycle in their rotations.

Introduction

Asia Minor bluegrass (*Polypogon fugax* Nees ex Steud.) is one of the most troublesome annual grass weeds in winter crops in China, affecting wheat (*Triticum aestivum* L.), oilseed rape (*Brassica napus* L.), and vegetable nurseries. This weed usually grows in damp lowlands or riparian areas and is also commonly found along field margins, roadsides, canal banks, and non-croplands. It generally emerges from September to October; flowering begins in early April, with seed dispersal occurring in May to June (Li 1998; Xu et al. 2014). *Polypogon fugax* is adapted to a wide range of soil environments and has increasingly become a prevalent and important weed in many regions of China (He et al. 2009; Zhang et al. 2012; Zhu et al. 2008), with serious impacts on agricultural production. It has been reported that this weed can reduce wheat yield by up to 40% (Zhang 1993).

Aryloxyphenoxypropionate herbicides (APPs) inhibit acetyl co-enzyme A carboxylase (ACCcase), a key enzyme involved in fatty-acid biosynthesis (Focke et al. 2003; Gornicki et al. 1994). In recent decades, grass weeds such as Japanese foxtail (*Alopecurus japonicus* Steud.) and American sloughgrass [*Beckmannia syzigachne* (Steud.) Fernald] had been successfully controlled by POST application of APPs. The excellent control efficacy of these herbicides for many grass weed species (>90%) encouraged their widespread and repeated use. However, the frequent use of these herbicides has resulted in selection for herbicide resistance in many weed species, with resistance to these herbicides confirmed in 48 grass weeds worldwide and 8 grass weed species in China (Heap 2018). Resistance to APPs is most commonly conferred by a target-site mutation in the *ACCcase* gene, subsequently creating an altered amino acid sequence on the ACCcase enzyme (Powles and Yu 2010). We have recently identified a *P. fugax* biotype from Qingshen County in Sichuan Province with 8- to 1,991-fold resistance to five different APP herbicides. The resistance mechanism of this biotype was a single amino acid substitution in the plastid ACCcase, Ile-2041-Asn (Tang et al. 2014).

Herbicide resistance may or may not confer fitness penalties in the resistant populations. Development of effective management strategies for herbicide-resistant weeds requires an understanding of the resistance-endowing mechanism and its potential fitness variation. Previous studies have determined that different mutations in the ACCase gene conferred varied pleiotropic effects along with ACCase-inhibitor resistance. For instance, plants segregating for Ile-1781-Leu mutation exhibited similar relative growth rate, biomass accumulation, and seed production compared with susceptible plants for smooth barley [*Hordeum murinum* L. ssp. *glaucum* (Steud.) Tzvelev], blackgrass (*Alopecurus myosuroides* Huds.), and rigid ryegrass (*Lolium rigidum* Gaudin) in the absence of herbicide selection (Menchari et al. 2008; Shergill et al. 2016; Vila-Aiub et al. 2005). Green foxtail [*Setaria viridis* (L.) P. Beauv] plants with the Ile-1781-Leu mutation had greater fitness than susceptible plants when grown in the greenhouse or in the field (Wang et al. 2010). However, *A. myosuroides* plants containing the Asp-2078-Gly mutation and *L. rigidum* plants with the Asp-2078-Gly or the Cys-2088-Arg mutation exhibited a fitness cost (Menchari et al. 2008; Vila-Aiub et al. 2009).

It has been acknowledged that biotypes with similar genetic backgrounds should be involved for the quantification of fitness cost with the resistance genes (Délye et al. 2015). Here we only detected one aryloxyphenoxypropionate-resistant (APP-R) biotype of *P. fugax*; to minimize differences in environmental factors, a susceptible (APP-S) biotype was collected from adjacent areas of the same field with similar growing conditions, and then F₂ seeds of the two biotypes grown in the greenhouse under the same conditions were used in this study. A previous study indicated that the APP-S biotype had increased germination and emergence rates compared with the APP-R biotype (Tang et al. 2015). The main objective of the present research was to determine (1) the growth and fecundity of the APP-R and APP-S biotypes (2) and their competitive ability in replacement series experiments in the absence of APP herbicide application. This information will increase our understanding of the potential fitness differences between the APP-R and APP-S biotypes and could be helpful for the overall development of resistance management strategies.

Material and Methods

Plant Material

Polypogon fugax seeds were originally collected in 2012 from APP-R and APP-S plants found in or nearby a grower's field in Qingshen County, Sichuan Province, China (Tang et al. 2015). The APP-R and APP-S *P. fugax* biotypes were separately cultivated in a screen house (an 8 m by 20 m chamber framed with 2-cm iron mesh and covered overhead with a transparent plastic cover to prevent rain damage) for 2 yr at the China National Rice Research Institute (CNRRI; 30.04°N, 119.55°E), Hangzhou, Zhejiang Province, China. A whole-plant dose–response experiment was conducted to confirm the resistance level of the F₂ plants of APP-R *P. fugax* in the CNRRI screen house. At the 3-leaf stage, the APP-R biotype survived a clodinafop-propargyl application rate of 48 g ai ha⁻¹, whereas, the APP-S biotype was completely controlled. The F₂ plants of the APP-R biotype were 1,965-fold more resistant to clodinafop-propargyl compared with the F₂ plants of the APP-S biotype (data not shown). Seeds collected from F₂ plants of the two biotypes in May 2014 were used in this study. The collected seeds were air-dried in the shade for 10 d, then cleaned and stored in paper bags at 4 C until being conditioned for experiments. Seed germination rates were close to 95% and 75% in

a preliminary experiment in the incubator (15/5 C fluctuating day/night temperatures, 12-h light/12-h dark) for the APP-R and APP-S biotypes, respectively (data not shown).

Noncompetitive Growth and Seed Production

A screen house experiment was conducted at the CNRRI. Seeds of each biotype (APP-R and APP-S) were sown in plastic trays (24 cm by 18 cm by 5 cm) containing a potting medium (1:1:1:2 vegetable garden soil/compost/peat/dolomite) with pH 6.3 and 13.7% organic matter. Plants were grown in a screen house with average day/night temperatures of 20/10 C under natural light (average intensity of 700 mmol m⁻² s⁻¹). Seeds were planted on November 9, 2015, and November 12, 2016. The trays were watered every 48 h. After emergence, seedlings at the 1-leaf stage were transplanted to plastic pots (12-cm diameter, 10-cm height) containing the same medium described earlier. The seedlings were transplanted on November 19, 2015, and November 23, 2016, respectively. Each pot contained a single APP-R or APP-S *P. fugax* seedling. Pots were placed in a completely randomized design with 120 pots for each biotype. No supplemental fertilizer was applied, and plants were periodically rotated on the bench to minimize environmental variation. For growth rate studies, four randomly selected plants of each biotype were harvested weekly for 15 consecutive weeks beginning 3 wk after transplant. The plants were clipped at the soil surface, bagged, and dried at 70 C for 72 h. The dry weight of each sample was measured.

Twelve plants of each biotype were retained for reproductive studies. The number of days after transplant (DAT) was recorded for the initial visible appearance of a developing tiller, flower, and inflorescence. After flowering, each panicle was gently enclosed in a pollination bag for seed collection. The seeds reaching physiological maturity (characterized by yellow seed color) were harvested from each plant and then dried in the shade for 1 wk. Seeds were separated manually and cleaned, and seed yield was measured as grams of seed per plant, and the number of panicles per plant and grams of seed per panicle were calculated. Aboveground biomass of each plant was also recorded as described for the growth rate experiment.

Competitive Growth Study

The relative competitive ability of the APP-R and APP-S biotypes was also compared under the aforementioned screen house conditions in November 2014 and 2015. A replacement series experiment was conducted at the CNRRI using a completely randomized design with four replicates in November 2014. This experiment was repeated in December 2015. *Polypogon fugax* seedlings were transplanted into plastic pots (25-cm diameter, 15-cm height) and equally distributed in 2 by 2, 3 by 3, or 4 by 4 grids (Jolliffe 2000; Shrestha et al. 2010) to achieve final densities of 4, 9, and 16 plants pot⁻¹, or 82, 184, and 327 plants m⁻². These levels of *P. fugax* infestation are not uncommon in wheat or oilseed rape fields in south China. Five biotype proportions (100:0, 75:25, 50:50, 25:75, and 0:100) were used at each density level, and each individual APP-R and APP-S *P. fugax* plant was marked with a plastic stake to ensure proper identification throughout the experiment. In the 9 plants pot⁻¹ density, planting ratios were based on 8 plants and an APP-R or APP-S *P. fugax* plant was randomly assigned as the 9th plant to complete the planting grid. Plants were cut at the soil surface at 90 DAT before panicles appeared, dried at 70 C for 72 h, and weighed for shoot dry weight. Individual plant shoot dry weight data were subjected to ANOVA.

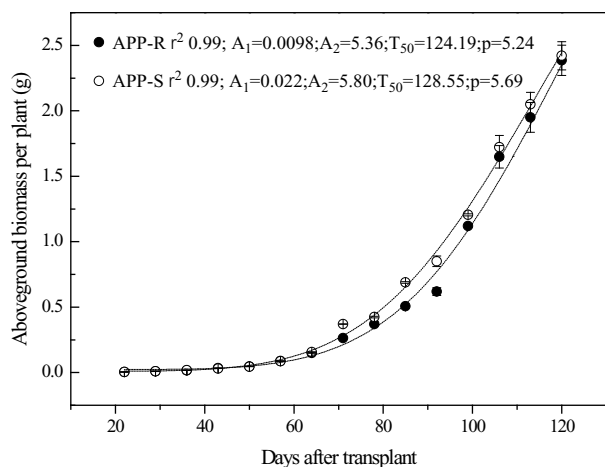


Figure 1. Aboveground shoot dry biomass of aryloxyphenoxypropanoate-resistant (APP-R) and aryloxyphenoxypropanoate-susceptible (APP-S) *Polygonum fugax* biotypes grown under noncompetitive conditions. Vertical bars represent SEs. The line represents a four-parameter sigmoid model, $W = A_2 + (A_1 - A_2)/(1 + x/T_{50})^p$, fit to the data, where A_2 = the lower limit, A_1 = the upper limit, p = the slope at the T_{50} , and T_{50} is the days after transplant when W is 50% of the maximum.

Statistical Analysis

A completely randomized design was used in all experiments, and each experiment was repeated once. Data obtained from screen house experiments were tested for normality, and ANOVA was performed using SPSS software (v. 13.0; SPSS, Chicago, IL). No interactions ($P > 0.05$) occurred between year and biotype for any of the parameters. Therefore, data from the two experimental repetitions were pooled. Mean comparison was performed using Student's t test, and the overall differences were significant ($P = 0.05$).

For growth rate studies, shoot dry weight (W) at time T was fit using the following four-parameter log-logistic equation:

$$W = A_2 + \frac{A_1 - A_2}{1 + \exp \{b[\log(x)] - \log T_{50}\}} \quad [1]$$

where A_2 = the lower limit, A_1 = the upper limit, b = the slope at the T_{50} , and T_{50} is the DAT when W is 50% of the maximum.

Results and Discussion

Noncompetitive Growth and Phenological Development

Phenologically, the APP-R and APP-S *P. fugax* biotypes were similar, with no distinguishing characteristics between them before panicle emergence. The relationship between *P. fugax* plant biomass and establishment time was described by a logistic regression model (Figure 1). Aboveground dry shoot biomass of APP-R and APP-S *P. fugax* was similar at each harvest (21 to 112 DAT), and no difference ($P > 0.05$) in average dry shoot biomass was detected at 120 DAT until the emergence of panicles. This result is in agreement with an Ile-2041-Asn *A. myosuroides* biotype, for which no differences in vegetative biomass were determined (Menchari et al. 2008). Similar results were also reported in several other grass weed species segregating for Ile-1781-Leu mutation (Menchari et al. 2008; Shergill et al. 2016; Vila-Aiub et al. 2005). The slightly reduced dry biomass produced by the APP-R plants during the vegetative growth phase could be partly related to the moderately

Table 1. Time for aryloxyphenoxypropanoate-resistant (APP-R) and aryloxyphenoxypropanoate-susceptible (APP-S) *Polygonum fugax* biotypes grown in a screen house to reach different phenological stages in terms of days after transplant (DAT)^a

Biotype	Tiller emergence	Panicle emergence	Seed shedding
	DAT		
APP-R	14.8 (2.3) b	120.8 (0.8) b	142.9 (0.9) b
APP-S	20.9 (1.1) a	130.3 (0.8) a	154.7 (1.6) a

^a Data were averaged over 2 yr. SEs are in parentheses. Means within a column for biotype followed by the same letter are not different according to Student's t test at $P = 0.05$.

reduced ACCase enzyme activity reported in *A. myosuroides* (Délye et al. 2003).

The APP-R biotype exhibited accelerated phenological development compared with the APP-S biotype under noncompetitive conditions (Table 1). The APP-R *P. fugax* reached tiller and panicle emergence and seed-shedding stages earlier than the APP-S biotype. The average time for these stages was 15, 121, and 143 d, respectively, for the APP-R biotype, which was about 6, 10, and 12 d, respectively, earlier than the APP-S biotype. Similar phenomena were reported in a *H. murinum* biotype containing the Ile-2041-Asn mutation, for which the date of panicle emergence was 20 d earlier than for the susceptible biotype (Shergill et al., 2016). Wang et al. (2010) determined that *Setaria* spp. mutants segregating the ACCase 1781 allele flowered earlier, and they were shorter at maturity than the susceptible plants. These differences in plant growth may affect control practices based simply on crop growth stage. The APP-R plants may be at a more advanced growth stage of phenological development than the APP-S biotype at the time of POST herbicide application, or the advanced APP-R plants maybe already dropping seeds by the time hand weeding is conducted (when panicles of most weeds emerged). Therefore, differences in plant phenology need to be taken into consideration when developing APP-R *P. fugax* management strategies.

Inflorescence Characteristics and Seed Production

The beginning of inflorescence development can be identified by the elongation of the shoot meristem as it undergoes the transition from vegetative to reproductive growth. The inflorescence shape of the APP-R and APP-S biotypes at the panicle emergence stage were similar; however, obvious and noticeable differences appeared as the inflorescence expanded. All panicles of the APP-S biotype appeared very open, with relatively loose branches (Figure 2). In contrast, the shape of the panicle of the APP-R plants was more compact, and the branches appeared close to the rachis during flowering.

The ACCase Ile-2041-Asn substitution has been observed in other grass weed species (Scarabel et al. 2011; Tang et al. 2012; Yu et al. 2007). There has, however, been no report of any inflorescence variation linked with this mutation in these species. Morphological and structural alternations associated with target site-resistant biotypes have been reported in some weed species (Nandula et al. 2015; Tardif et al. 2006). To eliminate the possibility of the APP-R and APP-S biotypes belonging to different species, we carried out multigene approaches that use combinations of variable noncoding and relatively conserved coding regions of the plastid genome (Burgess et al. 2011; Yu

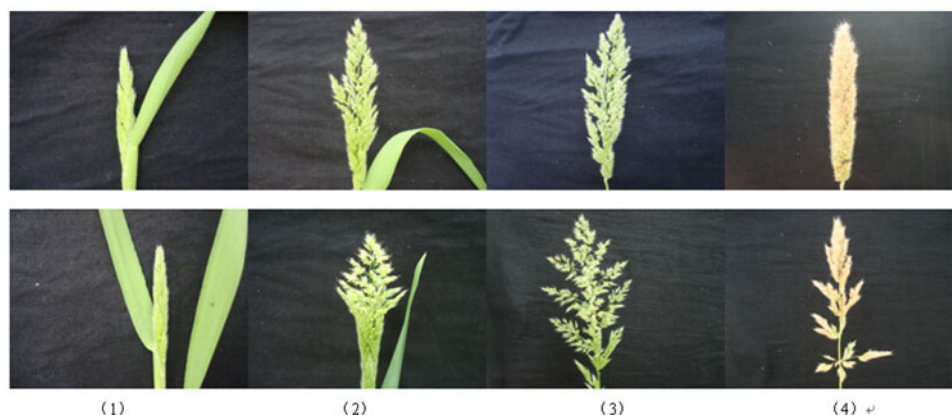


Figure 2. Inflorescence characteristics of aryloxyphenoxypropanoate-resistant (APP-R, top row) and aryloxyphenoxypropanoate-susceptible (APP-S, bottom row) *Polygogon fugax* biotypes. (1) Panicle emergence stage; (2) inflorescence expansion stage; (3) inflorescence fully expanded; (4) seed maturity stage.

Table 2. Seed production for aryloxyphenoxypropanoate-resistant (APP-R) and aryloxyphenoxypropanoate-susceptible (APP-S) *Polygogon fugax* biotypes under noncompetitive conditions^a

Biotype	Panicle no. plant ⁻¹	Seed weight		Aboveground biomass after seed harvest
		g plant ⁻¹	g panicle ⁻¹	g plant ⁻¹
APP-R	54.82 (4.64) b	8.57 (0.38) a	0.1664 (0.0135) a	11.58 (0.49) b
APP-S	64.00 (3.95) a	8.22 (0.26) a	0.1313 (0.0053) a	22.35 (0.40) a

^aData were averaged over 2 yr. SEs are in parentheses. Means within a column for biotype followed by the same letter are not different according to Student's *t* test at *P* = 0.05.

et al. 2012). Results indicated that there were no differences in nuclear ribosomal internal transcribed spacer region (ITS; GenBank accessions KP135427 and KP135428 for APP-R and APP-S *P. fugax*, respectively) and *rbcL* (GenBank accessions KP135425 and KP135426) and *matK* (GenBank accessions KP135423 and KP135424) coding regions of the two biotypes (data not shown). These results indicated that both APP-R and APP-S biotypes belong to *P. fugax*.

The link between the altered ACCase enzyme caused by the Ile-2041-Asn substitution and the inflorescence variation observed in the APP-R biotypes is not clear. In our previous study, we analyzed the transcriptomes of the APP-R biotype and a susceptible biotype of *P. fugax* and found 12 unigenes were differentially expressed at the early flowering stage, which provides a genomic resource for understanding the molecular basis of early flowering (Zhou et al. 2017). Whether this mutation has such a large impact in other species, and what eventual link this would have with the morphological variation that we have observed, would be worth examining.

The aboveground biomass and the number of panicles per plant were lower in the APP-R biotype (54.8 panicles plant⁻¹) compared with the APP-S biotype (64.0 panicles plant⁻¹) under noncompetitive conditions (Table 2); however, the APP-R biotype produced greater weight of seeds per panicle than the APP-S biotype (0.1664 vs. 0.1313 g seeds panicle⁻¹, respectively). The APP-R biotype had relatively greater 1,000-seed weight (150 vs. 145 mg) than the APP-S biotype (Tang et al. 2015); fewer panicles with greater weight resulted in no significant differences in seed production among the APP-R and APP-S biotypes. This trend indicates that the fecundity is not related to the ACCase resistance trait. These results are in agreement with a previous report that determined no differences in seed production between the Ile-2041-Asn ACCase *A. myosuroides* and susceptible plants (Menchari et al. 2008). Also, seed production and weight levels were found to be

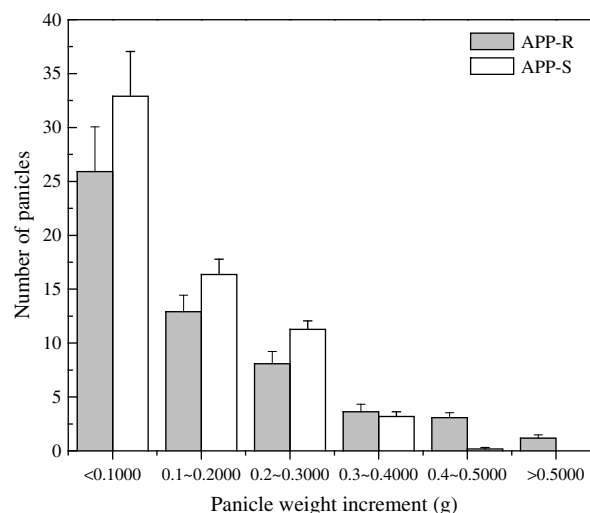


Figure 3. Panicle weight increments of aryloxyphenoxypropanoate-resistant (APP-R) and aryloxyphenoxypropanoate-susceptible (APP-S) *Polygogon fugax* biotypes seedlings. Vertical bars represent SEs.

the same in ACCase inhibitor-resistant and ACCase inhibitor-susceptible sterile oat (*Avena sterilis* L.), *H. murinum*, and *L. rigidum* (Shergill et al. 2016; Travlos 2013; Vila-Aiub et al. 2005).

Frequency distributions of seed weights per panicle for APP-R and APP-S biotypes of *P. fugax* were also determined (Figure 3). The APP-R biotype developed more high-yield panicles (more total seed weight per panicle), with 7.6%, 6.2%, and 2.6% panicles, respectively, at the panicle weight increments of 0.3 to 0.4 g, 0.4 to 0.5 g, and >0.5 g, respectively, compared with 5.0%, 0.3%, and 0%, respectively, for the APP-S biotype. This resulted in similar seed production per plant, and there were no differences among the APP-R and APP-S biotypes regarding their total seed mass per plant (*P* > 0.05). However, the

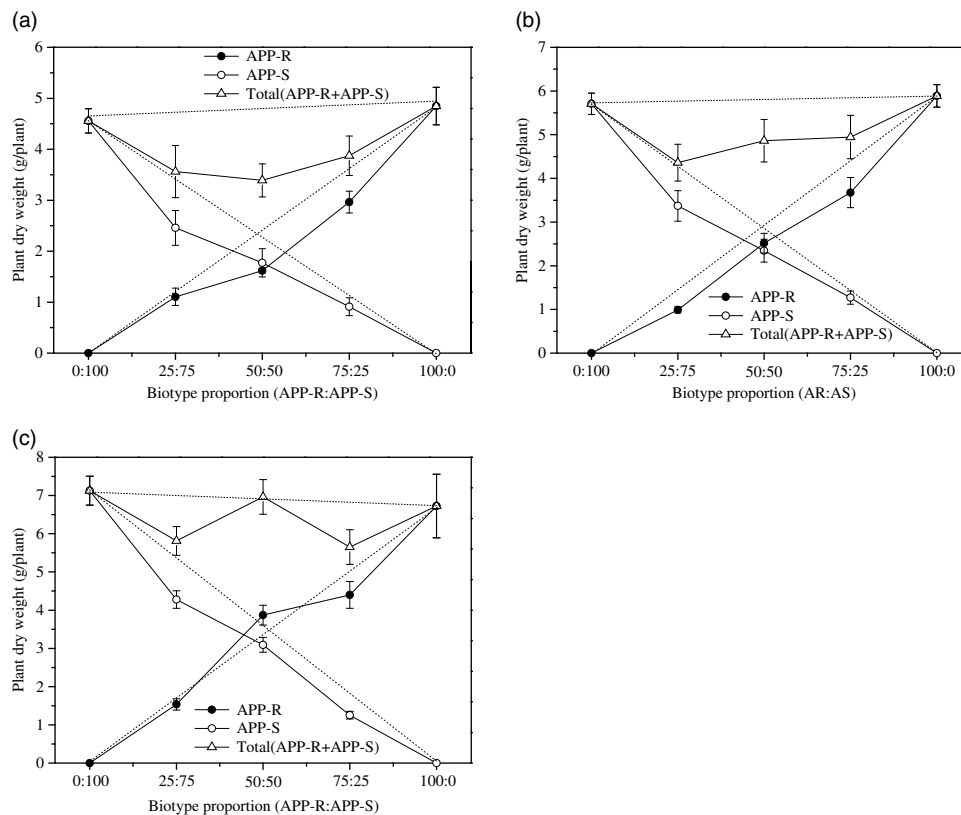


Figure 4. Replacement series diagrams for plant biomass of aryloxyphenoxypropanoate-resistant (APP-R) and aryloxyphenoxypropanoate-susceptible (APP-S) *Polypogon fugax* biotypes of 4 (A), 9 (B), and 16 (C) plants pot^{-1} densities grown under competitive conditions at different proportions. Vertical bars represent SEs. Dotted lines represent the expected hypothetical values for two equally competitive biotypes.

aboveground shoot dry weight (11.6 vs. 22.4 g plant^{-1} , respectively) after seed harvest was different between the APP-R and APP-S biotypes ($P < 0.05$). This may be attributed to physiological differences resulting in a more efficient transformation of the resources available for flowering and seed production for the APP-R biotype (Bourdôt et al. 1996; Kumar and Jha 2016).

Competitive Study

When the APP-R and APP-S biotypes were grown in mixtures under competitive conditions, the aboveground shoot dry weight before tiller emergence of the APP-R biotype plants was similar to that of the APP-S biotype ($P > 0.05$) and in general terms corresponded to the theoretical response of two biotypes having equal competitive ability (Figure 4). At the three tested densities, individual shoot dry weights of APP-R and APP-S biotypes were similar in monoculture and were not different in any proportions of mixture. This implies that there is no apparent competitive disadvantage for this particular APP-R biotype, and the APP-R plants are likely to persist in the population when the use of ACCase-inhibiting herbicide is discontinued. Similar results have been reported in ACCase inhibitor-resistant and ACCase inhibitor-susceptible giant foxtail (*Setaria faberi* Herrm.), *L. rigidum*, and *A. sterilis* (Gill et al. 1996; Travlos 2013; Wiederholt and Stoltenberg 1996), but the ACCase-resistance mechanism was unknown in these studies. Studies with the Ile-1781-Leu mutation in *L. rigidum* and *A. myosuroides* also indicated no differences in competitive

abilities compared with the susceptible biotypes (Menchari et al. 2008; Vila-Aiub et al. 2005).

The results of the current study revealed that the Ile-2041-Asn mutation had no negative effects on the fitness of APP-R *P. fugax*. In our previous study, seeds of the APP-R biotype had reduced germination and emergence percentage and a less adaptive range under same treatment conditions compared with the APP-S biotype (Tang et al. 2015), indicating that the APP-R biotype may have stronger dormancy and a longer persistence period in the soil. These results also indicated that for a similar seedbank, APP-S *P. fugax* will emerge and be controlled with continued APP herbicide selection pressure, whereas the APP-R population will increase.

Finally, to assess fitness costs associated with mutant ACCase alleles, it is critical that the resistant and susceptible individuals share a similar genotype or that a group of plants having the same genotype be investigated (Cousens et al. 1997; Strauss et al. 2002; Vila Aiub et al. 2009). Although we collected several other accessions of *P. fugax* from different areas, no other resistant biotypes were found. The many panicles, desynchronous flowering, and self-crossing characteristic of *P. fugax* make crossing efforts unlikely. To unequivocally attribute fitness cost endowed by the ACCase-inhibiting herbicide resistance alleles, F_2 populations from similar environments were used in this study. While impact of resistance on plant fitness can be altered by several factors (Warwick and Black 1994), we did not measure any differences other than rate of maturity.

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