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Aminopyralid Constrains Seed Production of the Invasive Annual Grasses Medusahead and Ventenata

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Abstract

Invasive annual grasses, such as medusahead (*Taeniatherum caput-medusae* [L.] Nevski), ventenata (Ventenata dubia [Leers] Coss.), downy brome (*Bromus tectorum* L.), and Japanese brome (*Bromus japonicus* Thunb. ex Murr.), are negatively impacting millions of hectares of US rangelands. Amino acid synthesis inhibitor and photosynthesis inhibitor herbicides are sometimes used to control invasive annual grasses. Conversely, growth regulator herbicides are generally considered ineffective against invasive annual grasses. However, in a recent study of pre-emergence herbicide applications, the growth regulator aminopyralid appreciably reduced medusahead cover, primarily by killing emerging medusahead plants. Additionally, in recent studies of postemergence herbicide applications, we found the growth regulators aminopyralid, dicamba, and picloram drastically reduced downy brome and Japanese brome seed production. In these postemergence studies, growth regulators sterilized the plants without otherwise greatly affecting them. The purpose of this greenhouse study was to extend our growth regulator/plant sterility research from downy brome and Japanese brome to medusahead and ventenata. Each tested aminopyralid rate and application growth stage (late seedling, internode elongation, heading) reduced medusahead seed production to nearly zero. Picloram also reduced medusahead seed production, but not quite as consistently as aminopyralid. With ventenata, aminopyralid applied at the seedling stage reduced seed production ~95–99%. Beyond the seedling stage, however, ventenata responses to aminopyralid were highly variable. Picloram had low activity against ventenata seed production. These results contribute to a growing body of evidence suggesting it may be possible to use growth regulators to control invasive annual grasses by depleting their short-lived seedbanks.

Key Words: downy brome, growth regulator herbicide, herbicide, invasive plant, seedbank, weed

INTRODUCTION

Exotic annual grasses, such as downy brome, Japanese brome, medusahead, and ventenata negatively impact millions of hectares of US grasslands (Sheley and Petroff 1999; DiTomaso 2000; Sperry et al. 2006; Davies and Svejcar 2008). These grasses can reduce native species richness and abundances (Haferkamp et al. 2001b; Davies and Svejcar 2008), reduce livestock carrying capacities (Knapp 1996; Haferkamp et al. 2001a), alter nutrient cycling (Rimer and Evans 2006) and microbial communities (Belnap et al. 2005), and shorten wildfire return intervals (D'Antonio and Vitousek 1992). Herbicides are sometimes used alone (Shinn and Thill 2002; Ward and Mervosh 2012) and other times combined with seeding (Morris et al. 2009; Owen et al. 2011), prescribed fire, and/or grazing (Whitson and Koch 1998; Calo et al. 2012) in efforts to replace the invaders with more desirable vegetation.

The photosynthesis inhibitor herbicide tebuthiuron and the amino acid synthesis inhibitor herbicides rimsulfuron, glyphosate, and imazapic are sometimes used to control invasive annual grasses. Although these herbicides can provide partial, short-term control (~1–2 yr) of invasive annual grasses, they can damage or kill desirable perennial grass plants growing with the weeds (Lym and Kirby 1991; Monaco et al. 2005), including desirable grasses seeded around the time of herbicide application (Shinn and Thill 2004; Sheley et al. 2007; Hirsch et al. 2012).

Compared to amino acid synthesis inhibitors and photosynthesis inhibitors, growth regulator herbicides, such as aminopyralid, clopyralid, 2,4-D, dicamba, and picloram, are generally less damaging to desirable perennial grasses (Lym and Messersmith 1985; Lym and Kirby 1991; Sheley et al. 2000; Shinn and Thill 2004). Growth regulator herbicides are commonly used for controlling broadleaf weeds (Lym and Messersmith 1990; e.g., Enloe et al. 2007; Seefeldt and Conn 2011), and these herbicides have historically been considered ineffective against invasive annual grasses. However, recent anecdotal reports indicate the growth regulator herbicide aminopyralid applied pre-emergence has activity against some invasive annual grasses, including downy brome and soft brome (*Bromus hordeaceus* L.) (Kyser et al. 2012b). Moreover, a recent study found aminopyralid applied pre-emergence was as least as effective as rimsulfuron or imazapic at reducing medusahead cover (Kyser et al. 2012b).

In other recent research, we found that postemergence applications of the growth regulators dicamba, picloram, and aminopyralid, but not 2,4-D, drastically reduced seed production of downy brome (Rinella et al. 2013) and Japanese brome (Rinella et al. 2010a, 2010b). This suggests growth regulators

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could be used to help control invasive annual grasses by depleting their short-lived seedbanks (Hulbert 1955; Burnside et al. 1996; Smith et al. 2008). In our studies, the majority of the decline in seed production resulted from growth regulators inducing plant sterility, not from the herbicides reducing plant size or survival. Similarly, studies of wheat and other grass crops have shown growth regulators can cause sterility without otherwise substantially impacting plant growth, particularly when the herbicides are applied from jointing to heading (Friesen et al. 1968; Rinella et al. 2001; Sikkema et al. 2007).

The purpose of the study described here was to extend our growth regulator research from Japanese brome and downy brome to medusahead and ventenata. Medusahead has been estimated to impact negatively nearly 1.0 million ha (2.4 million acres) in 17 western states (Duncan et al. 2004). If aminopyralid consistently induces high levels of sterility in medusahead, then this, combined with findings of Kyser et al. (2012b), would suggest a wide range of aminopyralid application timings could be used to control this aggressive invader. To our knowledge, no studies have been published on the biology or control of ventenata, but this invasive annual grass is spreading rapidly in some western states, including Idaho, Oregon, and Washington. Ventenata was the topic of a special symposium at the 2011 annual meetings of the Western Society of Weed Science, and this illustrates the growing concern over this species (Pavek et al. 2011).

In a greenhouse, we evaluated medusahead and ventenata seed production responses to growth regulators applied at three growth stages. The specific growth regulators we evaluated were picloram and aminopyralid, because these herbicides appeared most effective at reducing invasive annual grass seed production in our Japanese brome and downy brome research. We developed two hypotheses based on our previous research. Our first hypothesis was that aminopyralid and picloram would drastically reduce medusahead and ventenata seed production at all rates and timings of application. Our second hypothesis was that the herbicides would have only minor effects on medusahead and ventenata biomass production.

METHODS

Experimental Design and Measurements

Ventenata and medusahead seeds were collected July 2010 from a grassland site near Monument, Oregon (lat 44.819870, long −119.420866). Fungal infections have hindered our previous efforts to grow seed-bearing invasive annual grasses in the greenhouse. Therefore, in October 2011 (Experiment 1) and November 2012 (Experiment 2), seeds were coated with a powder formulation of the fungicides captan (N-trichloro-methylthio-4-cyclohexene-1, 2-dicarboximide) and carboxin (A 5, 6-dihydro-2-methyl-N-phenyl-1, 4-oxathiin-3-carboxamide) at a rate of 19.55% and 0.45% by weight, respectively. Seeds were planted in flats (51 × 26 × 6 cm) containing commercial potting soil (Sunshine Mix 1, Sun Gro Horticulture, Inc., Bellevue, WA). When medusahead and ventenata seedling heights averaged 5.1 cm and 1.9 cm, respectively, flats were transferred to a growth chamber held at 6°C with an 8-h photoperiod to induce vernalization. Flats were maintained in the growth chamber for 60 d, during which time soils were kept moist. Following vernalization, two medusahead seedlings per pot (21 cm diam × 21 cm, 7.6 L) were planted in 56 pots and two ventenata seedlings per pot (18.5 cm diam × 16.5 cm, 2.9 L) were planted in 28 pots containing the previously described potting soil mix, and the pots were placed in a greenhouse. Greenhouse temperatures were 18°C (day) and 10°C (night) until mid-March, when the daytime temperature was raised to 21°C. To attain desired day and nighttime temperatures, temperatures were gradually increased beginning 2 h before sunrise and gradually decreased beginning 2 h after sunset. Plants received no artificial light and were watered when soils appeared dry.

The five medusahead herbicide treatments were aminopyralid at 0.069 (half rate) or 0.120 (full rate) $kg \cdot ae \cdot ha^{-1}$, picloram at 0.21 (half rate) or 0.42 (full rate) $kg \cdot ae \cdot ha^{-1}$, and a no-herbicide control. The three ventenata treatments were aminopyralid at 0.120 $kg \cdot ae \cdot ha^{-1}$, picloram at 0.42 $kg \cdot ae \cdot ha^{-1}$, and a no-herbicide control. These are common rates for broadleaf weed control, and these rates greatly reduced Japanese brome (Rinella et al. 2010a, 2010b) and downy brome (Rinella et al. 2013) seed production in previous research. Herbicides were applied with the use of a CO_2-pressurized backpack sprayer with 4-XR TeeJet 8200VS nozzles (T-Jet Technologies Wheaton, IL) calibrated to deliver 131 $L \cdot ha^{-1}$. Herbicide treatments were applied with the applicator, while the experimenter walked parallel to the pots arranged in a row.

The three growth-stage treatments were seedling, internode elongation, and heading. These treatments were applied 102, 134, and 191 d after planting (Experiment 1) and 98, 139, and 167 d after planting (Experiment 2), respectively. At the seedling stage, medusahead and ventenata plants were approximately 14 and 4 cm tall, respectively. At the internode elongation stage, tillering was complete but no inflorescences were visible. At the heading stage, flowering had begun. Pots were arranged in the greenhouse in a randomized complete block design (medusahead: four blocks × four herbicide treatments × three plant growth stages + eight nontreated controls × two experiments = 112 pots; ventenata: four blocks × two herbicide treatments × three plant growth stages + four nontreated controls × two experiments = 56 pots).

Seeds were clipped from plants when the seeds were ripe but had not yet dropped from the plants. Seeds were stored at room temperature in paper bags and approximately 4 mo after harvest, seeds were subjected to a germination test. Germinable seeds per pot was estimated by multiplying seeds per pot by germination ratios. Germination ratios were estimated by incubating 200 seeds in 100 × 15-mm petri dishes (≤ 33 seeds per dish). Each dish contained a piece of filter paper supported by a polyurethane foam disc. Distilled water was supplied continuously via a cotton wick inserted in a hole in the center of the disc. Seeds were recorded as germinable and removed from petri dishes if radicles and coleoptiles exceeding 5 mm in length developed within 30 d. Medusahead seeds had long awns, which were removed prior to germination tests. A 12-h photoperiod was supplied with cool-white fluorescent bulbs ($PAR = 28\ \mu mol \cdot m^{-2} \cdot s^{-1}$), and the temperature was held at 21 and 15°C during light and dark periods, respectively. After seeds were clipped from plants, plants were clipped at soil level,

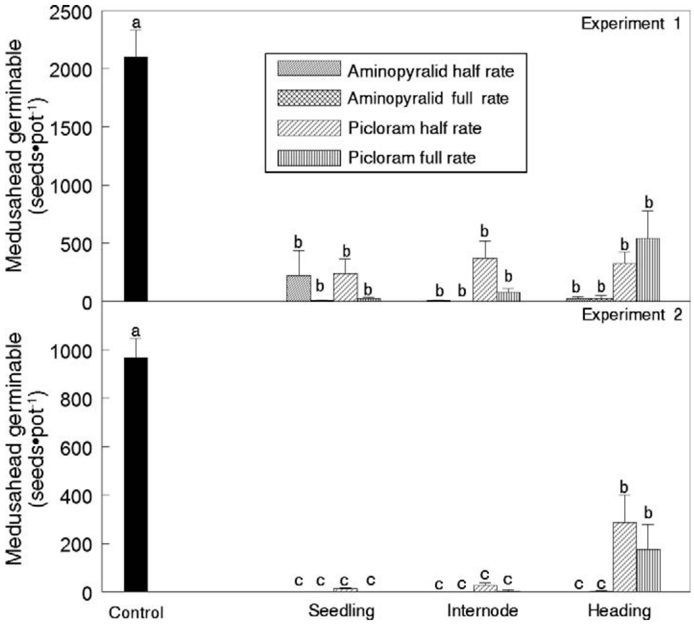

Figure 1. Effects of growth regulator herbicides on viable seed production of medusahead. Herbicide half and full rates were 0.069 and 0.120 kg · ae · ha^{-1} for aminopyralid and 0.21 and 0.42 kg · ae · ha^{-1} for picloram, respectively. Bars denote standard errors, and treatments without a letter in common are significantly different ($P < 0.05$).

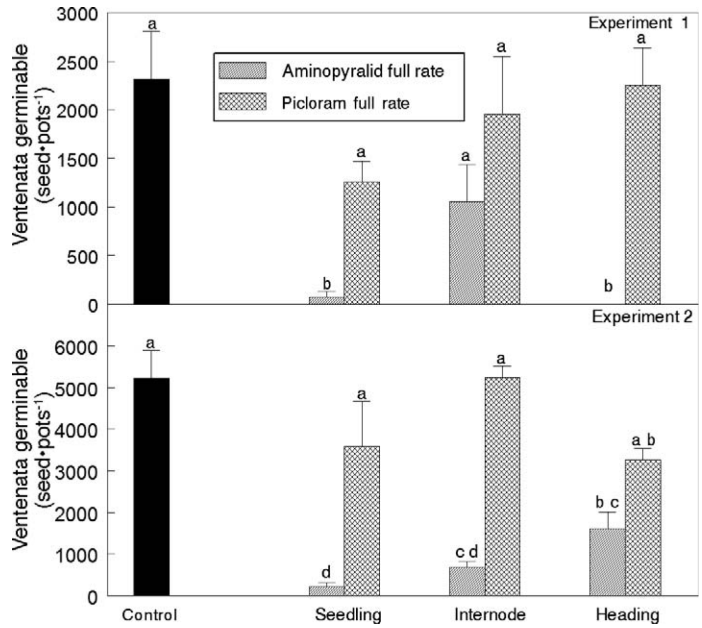

Figure 2. Effects of growth regulator herbicides on viable seed production of ventenata. Herbicide half and full rates were 0.069 and 0.120 kg · ae · ha^{-1} for aminopyralid and 0.21 and 0.42 kg · ae · ha^{-1} for picloram, respectively. Bars denote standard errors. and treatments without a letter in common are significantly different ($P < 0.05$).

placed in a drying oven at 60°C for 2 d and weighed in order to assess herbicide effects on biomass.

Statistical Analysis

The medusahead seed production data did not follow a normal distribution because no viable seeds occurred in 51 pots, so 51 of 104 data values equaled zero. Therefore, the bootstrap procedure was used to simulate *P* values for assessing statistical differences among all treatment combinations within each experiment (Efron and Tibshirani 1993).

Linear regression models were used to analyze the ventenata seed data and medusahead and ventenata biomass data. The responses were ventenata seeds per pot and ventenata and medusahead biomass per pot. The independent variables were experiment, block, growth stage, herbicide, herbicide rate (in the case of medusahead), and all two- and three-way interactions not involving block. Histograms of model residuals supported the regression assumption that, conditional on the independent variables, the response data were approximately normally distributed with constant variance, so the data were not transformed. Statistical differences among treatments were calculated from uncertainty estimates on the regression parameters with the use of methods outlined by Gelman and Hill (2007). All analyses were performed with the use of Mathematica® (Wolfram Research 2007).

RESULTS

In support of our first hypothesis, all aminopyralid and picloram treatments significantly reduced viable medusahead seed production (Fig. 1; $P < 0.01$), and all aminopyralid rate and timing combinations had statistically equivalent effects on medusahead seed production (Fig. 1; $P > 0.05$). According to treatment means, all aminopyralid treatments reduced medusahead seed production > 90%, and aminopyralid applied at the internode and heading stages reduced seed production 96–100% (Fig. 1). Compared to aminopyralid, picloram appeared somewhat less damaging to medusahead seed production, particularly when applied at the heading stage (Fig. 1). However, picloram was significantly less effective than aminopyralid only at the heading timing in Experiment 2 ($P < 0.01$).

The herbicides had highly variable effects on ventenata seed production, so the ventenata data do not strongly support our first hypothesis. Like medusahead seed production, ventenata seed production was reduced more by aminopyralid than picloram ($P < 0.05$), except perhaps at the internode timing in Experiment 1 ($P = 0.25$) and the heading timing in Experiment 2 (Fig. 2; $P = 0.09$). Aminopyralid applied at the seedling growth stage provided the most consistent reductions in ventenata seed production (Fig. 2).

The data generally support our second hypothesis that herbicides would have only minor effects on biomass production. However, full rates consistently reduced medusahead biomass when applied at the seedling stage (Fig. 3; $P < 0.01$). Only three herbicide treatments applied after the seedling stage significantly reduced medusahead biomass, and only in Experiment 1 (Fig. 3; $P < 0.05$). Ventenata biomass did not vary significantly among treatments ($P > 0.05$), although seedling-stage applications appeared to slightly reduce ventenata biomass (Fig. 4).

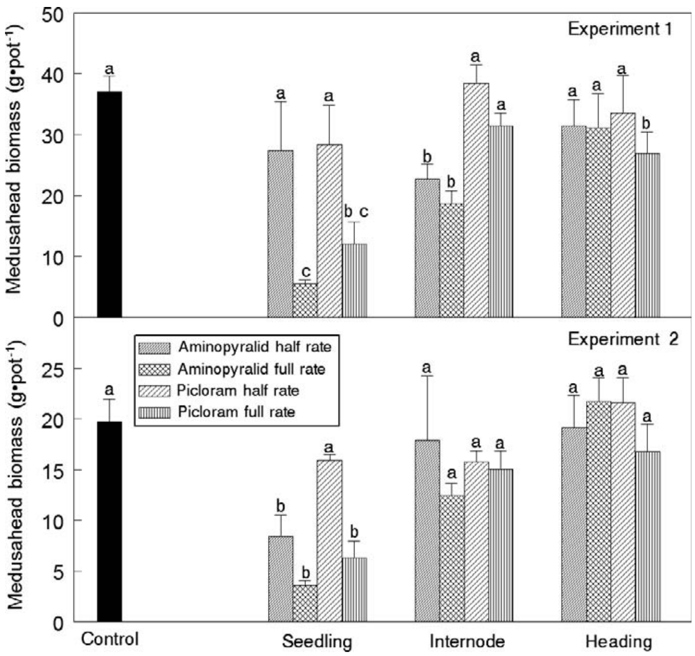

Figure 3. Effects of growth regulator herbicides on medusahead biomass. Herbicide rates were 0.120 kg · ae · ha^{-1} for aminopyralid and 0.42 kg · ae · ha^{-1} for picloram. Bars denote standard errors and treatments without a letter in common are significantly different ($P < 0.05$).

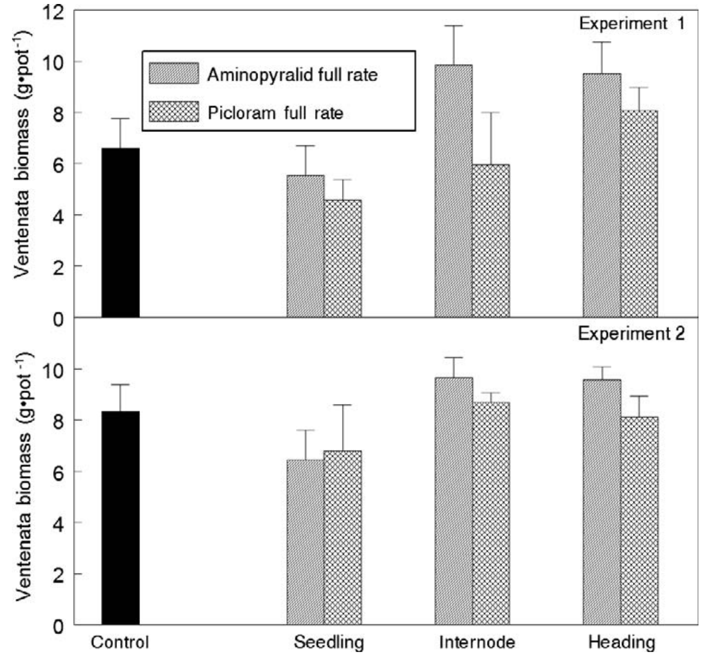

Figure 4. Effects of growth regulator herbicides on ventenata biomass. Herbicide rates were 0.120 kg · ae · ha^{-1} for aminopyralid and 0.42 kg · ae · ha^{-1} for picloram. Bars denote standard errors. There were no significant differences between treatments ($P < 0.05$).

DISCUSSION

In order to explore potential management roles for our treatments, it is useful to consider past medusahead herbicide research. Kyser et al. (2012a) found glyphosate reduced medusahead seed production ~95% during the year of application, which compares favorably with our seed production results. In addition, glyphosate had the advantage of controlling established medusahead plants (Kyser et al. 2012a). However, glyphosate control of medusahead is not entirely consistent: Glyphosate provided only ~61% medusahead control at one site in another study (Kyser et al. 2013). Moreover, glyphosate has the disadvantage of being potentially damaging to perennial forage grasses (Lym and Messersmith 1994; Lym 2000).

Imazapic, the herbicide most researched on medusahead, sometimes provides nearly 100% control of this weed (Sheley et al. 2007, 2012), and imazapic occasionally continues partially controlling medusahead 2 yr after application (Kyser et al. 2007, 2013). But in some studies imazapic provided only ~30–75% medusahead control (Shinn and Thill 2002; Monaco et al. 2005), and like glyphosate, imazapic can damage desirable perennial grasses growing with medusahead (Shinn and Thill 2002; Monaco et al. 2005).

It is yet to be seen if our growth regulator treatments will provide more consistent control of medusahead than glyphosate or imazapic. It is clear that growth regulators pose less risk to established perennial grass plants (Lym and Messersmith 1985; Lym and Kirby 1991; Sheley et al. 2000; Shinn and Thill 2004). However, growth regulators may reduce seed production of perennial grasses that are at susceptible growth stages when medusahead is treated. But because perennial grasses rely heavily on vegetative propagation for population growth, growth regulator applications are unlikely to reduce perennial grass populations appreciably. Instead, perennial grass populations often increase when growth regulators are used to control weedy species (Lym and Messersmith 1985; Sheley et al. 2000).

In addition to perennial grasslands, medusahead is also a problem in annual grasslands because it reduces forage production of desirable annual forage grasses such as wild oat (*Avena fatua* L.), slender oat (*Avena barbata* Pott ex Link), and Italian ryegrass (*Lolium perenne* L. subsp. *multiflorum* [Lam.] Husnot) (Kyser et al. 2012b). It is somewhat risky to use glyphosate and imazapic to control medusahead in annual grasslands because these herbicides could damage annual forage grasses. Conversely, it may be possible to use aminopyralid to control medusahead seed production without risking damage to annual forage grasses, because medusahead generally begins producing seed after other annual grasses have completed seed production (McKell et al. 1962). In a current study, we are testing aminopyralid applications made before medusahead flowers but after other annual grasses have completed seed production.

The postemergence applications we tested may be more effective against medusahead than the pre-emergence aminopyralid applications of Kyser et al. (2012b). Treatment means from Kyser et al. (2012b) indicate pre-emergence applications reduced medusahead cover by 52–69%, and aminopyralid did not significantly reduce seed production of those medusahead plants that survived aminopyralid exposure. Assuming a 1:1 relationship between cover and seed production, these results suggest aminopyralid applied pre-emergence at 0.12 kg · ae · ha^{-1} reduced medusahead seed production 52–69%. In contrast, our estimates suggest this same aminopyralid rate applied at internode and heading stages consistently reduced medusahead seed production > 95% (Fig. 1). Moreover, we observed that nearly halving the postemergence rate from 0.12 to 0.069 $kg \cdot ae \cdot ha^{-1}$ did not compromise control of medusahead seed production (Fig. 1), whereas medusahead control declined with declining pre-emergence rate at one or more of three sites in the Kyser et al. (2012b) study.

Picloram did not sharply reduce ventenata seed production, and ventenata responses to aminopyralid were quite variable (Fig. 2). Future research may identify better herbicides for this invader of increasing concern. It is unclear why the growth regulators were more effective against medusahead than ventenata. In both species, and all cereal and weed grasses of past studies, growth regulators reduced germinable seed production by causing normal seeds to be replaced with shriveled, nongerminable seeds lacking endosperm (e.g., Rinella et al. 2001, 2010a). Growth regulator modes of action are not completely understood, but it is known that differences in herbicide metabolism and target site sensitivity cause grass species to differ in their responses to growth regulators (Cobb 1992; Sterling and Hall 1997; Grossmann 2003). Metabolism and target site characteristics likely explain variation between ventenata and medusahead responses, as well as variation in responses to different growth regulators, rates, and timings.

Medusahead responses in the field will likely mirror our greenhouse results. Growth regulator effects on wheat (*Triticum aestivum* L.) and Japanese brome seed production did not vary greatly between the greenhouse and field (Rinella et al. 2001, 2010a, 2010b). One potential caveat involves our seedling stage results. Medusahead, downy brome, and other winter annual grasses emerge in fall and remain as seedlings until warm wet conditions stimulate rapid spring growth. By applying our seedling stage treatments after vernalization, we simulated seedling applications at the onset of rapid spring growth. Had we applied the herbicides prior to vernalization, ~60 d earlier, we would have simulated applications to newly emerged seedlings. In this case, medusahead seed production might have been greater, because the seedlings would have had more time to metabolize the herbicides before producing seed.

Invasive forbs commonly grow in association with invasive annual grasses on degraded range sites (e.g., Sheley et al. 2004; Rinella et al. 2010a; Ortega and Pearson 2011). In the case of medusahead, yellow starthistle (*Centaurea solstitialis* L. CENSO.) appears to be the most commonly associated invasive forb (Sheley and Larson 1994; Shinn and Thill 2002). Medusahead can increase in abundance after herbicides are used to control yellow starthistle (DiTomaso et al. 2006). It may be possible to avoid this problem by applying aminopyralid pre-emergence or at growth stages when yellow starthistle and medusahead are both susceptible to aminopyralid (Kyser et al. 2011, 2012b).

IMPLICATIONS

The growth regulator herbicides aminopyralid and picloram applied postemergence drastically reduced medusahead seed production in this study. This implies growth regulators may be useful for controlling medusahead, because populations of this annual invader decline rapidly when adult plants are prevented from replenishing the seedbank (Young et al. 1998). Growth regulators have the advantage over other invasive annual grass herbicides of being generally less damaging to desirable perennial grasses (e.g., Shinn and Thill 2002). However, because growth regulators can reduce seed production in many grass species, these herbicides may reduce seed production in native annual grasses. Moreover, like all other herbicides used to control invasive annual grasses, growth regulators can damage desirable forbs and shrubs (Rinella et al. 2009; Davies and Sheley 2011; Ortega and Pearson 2011; Louhaichi et al. 2012). Therefore, caution is warranted in planning and executing herbicide applications for invasive annual grass control. Combined with results from Kyser et al. (2012b), our results suggest a wide range of aminopyralid application timings (i.e., pre-emergence, late seedling, internode, heading) may be effective against medusahead, whereas other herbicides are only highly effective pre-emergence (e.g., imazapic) and/or early postemergence (e.g., imazapic, glyphosate).

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