INCREASING HARVESTABILITY OF *PHACELIA HASTATA* SEED USING PLANT GROWTH REGULATORS

by

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DEDICATION

This thesis is dedicated to my husband, Kim, my most helpful critic and steadfast supporter. You are a continuing inspiration, especially in the search for good, creative questions and elegant solutions in science. I am ever grateful for your passionate vision and ability to articulate it.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Phacelia hastata, an excellent pollinator plant that is highly drought resistant, winter hardy, and tolerant of acid and heavy metal soils, has limited commercial availability due to inadequate seed supplies. Indeterminate flowering, lodging and seed shatter of this species make mechanical seed harvest difficult. This study was undertaken to evaluate the effects of four plant growth regulator formulations (PGRs) on seed yield, seed quality and growth characteristics of *P. hastata.* These PGRs were gibberellin, paclobutrazol, ethephon, and a hormone compound containing gibberellic acid, cytokinin and indolebutyric acid. In field experiments, foliar sprays of PGRs were applied at two rates and two timings. Plots were sprayed once, at early vegetative stage, or twice, with a sequential spray three weeks later. The exception was ethephon, which was sprayed once at time of full bloom. Treatments included plots sprayed with (1) 100 and 200 ppm gibberellic acid (2) 30 ppm paclobutrazol, (3) 2000 ppm ethephon, (4) 2500 ppm Ascend (a hormone compound consisting of cytokinin, gibberellic acid and indolebutyric acid), and (5) deionized water (Control). Two foliar applications of paclobutrazol, at a rate of 30 ppm, at one-month rosette stage and three weeks later, increased seed yield of *P. hastata* in thinned plots by 337%. In plots treated with ethephon, seed shatter was eliminated but seed yield and germination decreased. Results suggest foliar sprays of the plant growth regulator paclobutrazol on *P. hastata* regulate the flowering process, increasing harvestable seed.

INTRODUCTION

Phacelia hastata (Silverleaf phacelia, Scorpionweed), a short-lived perennial, is native to much of the western United States and Canada. It is valued as an exceptional pollinator-friendly plant (Ogle, et al., 2011); attracting and supporting pollinating insects. It is also a hardy revegetation species and a drought-resistant ornamental. Recommended for cover crops and pest management by the Farm Bill Program for Pollinator Conservation (2008), *P. hastata* provides pollen and nectar for native bees and other beneficial insects during an extended blooming period. Both wild native bees and managed honeybees, the primary pollinators for most crops in the United States and Canada, are in decline in many areas (Xerces Society, 2010). Wild, native bees, whose economic value is estimated at $3 billion per year in the United States, are at risk from habitat loss, careless pesticide use, and introduced diseases (Mader, et al., 2011). As numbers of native insects and honeybees diminish, *P. hastata's* role as a pollinator plant becomes increasingly valuable, helping sustain pollinator habitat. *Phacelia hastata* is used for both restoration of native plant communities and wildlife habitat remediation. Its hardiness and tolerance to acid/heavy metal soils make it an ideal component in seed mixes for disturbed areas on public lands (Scianna, et al., 2004). Adapted to the extreme environmental conditions in Montana, this drought-resistant ornamental is a recommended wildflower for native landscapes (U.S. Department of Agriculture, Natural Resources Conservation Service, 2001).

An insufficient seed supply limits use of many wildflowers in revegetation (Shock, et al., 2010). *Phacelia hastata*, a native forb used in seed mixtures emphasizing pollinator-friendly plants, is one such species (U.S. Department of Agriculture, Natural Resources Conservation Service, The Xerces Society for Invertebrate Conservation, San Francisco State University, 2008; U.S. Department of Agriculture, Natural Resources Conservation Service, 2011). To help meet demand, *P. hastata* seed is being increased at Bridger Plant Materials Center and released for revegetation purposes and to commercial seed producers through the Montana and Wyoming Crop Improvement Association. However, *P. hastata* seed is difficult to harvest, thereby restricting availability to growers and inhibiting broader use of this species. Low growth habit and indeterminate flowering make mechanical harvest of *P. hastata* inefficient; seed stems lodge and seed shatters throughout July–September, leaving most seed either below harvester height or on the ground at harvest time.

Reasonable approaches to address this problem might include selectively breeding for taller plants, customizing a mechanical harvester to collect seed at soil level, or using plant growth regulators (PGRs) to improve yield. As a rapid and economical solution, the question of whether PGRs can be used to improve mechanical harvest yield is examined. We focus on three growth characteristics that might be manipulated with PGRs to make seed more harvestable, namely flower stem height, lodging of flowering stems, and timing of seed shatter. Specifically, effects of gibberellic acid (GA), paclobutrazol (PBZ), ethephon, and a hormone compound containing GA, cytokinin and indolebutyric acid (COMB), are tested on seed quantity, seed quality, and growth characteristics of *P. hastata* in order to identify treatments that may improve seed yield and quality.

LITERATURE REVIEW

Plant Characteristics and Value

*Phacelia hastata (*Silverleaf phacelia) is a silky, silver-haired perennial herb with several low-lying to erect stems, 20–50 cm tall, with rapid growth rate from tap roots. Flowers are whitish to blue-lavender, broadly funnel-shaped, with five broad petal lobes, five narrow, bristly-hairy sepals and five long stamens extending well past the petals. *Phacelia hastata* has a pointed leaf shape with barbs and is distinguished from other phacelias by its prominent leaf veins. It has many flowers in branched, compact, coiled clusters (cymes). It is found on sandy or gravelly soils on flats, disturbed sites and talus or steep slopes. Habitats for this drought-tolerant species include rocky prairies, scrub, sagebrush steppe, coniferous forest, and alpine.

Phacelia hastata is recognized by pollination ecologists as attracting large numbers of native bees (Xerces Society for Invertebrate Conservation, 2013). Its extended and prolific flowering period make it an exceptional pollinator plant; possibly prolonging season-long visitation by pollinators and increasing species diversity of flower-visitors at different times during the season (Hajjar, et al., 2008). *Phacelia hastata* flowers support spring foraging bees, such as bumble and mason bees, butterflies, and beneficial wasps (C. Delphia, personal communication, 2013), including the sensitive pollen wasp, *Pseudomasaris edwardsii* (Bentler.us, 2014). Pollinator plants enhance habitat and help maintain food sources for keystone insect species, as well as provide diverse sources of pollen, improving bees' disease and pesticide resistance (Holland, 2010). *Phacelia hastata* is one of several moth-pollinated plants that co-occur with Yellowstone sand verbena (*Abronia ammophila*), a rare and highly restricted endemic of Yellowstone National Park. By supporting moth populations in the area, *P. hastata* may facilitate the reproductive success of Yellowstone sand verbena (Saunders, et al., 2005; Whipple). In addition, a rare species of miner bee, *Perditini barri*, found in Idaho, is a specialist forager and may be dependent on *P. hastata* flowers (Shepherd, 2013).

In areas where *P. hastata* thrives, such as the high elevation rangeland and sagebrush communities of Wyoming, diverse plant communities are needed to restore ecosystems threatened by energy development and residential sprawl (Winslow, et al., 2013). *Phacelia hastata* is one of the beneficial plantings recommended for mule deer, antelope, and sage grouse habitat in the Green River Basin, Wyoming (Bureau of Land Management, 2007), helping provide food sources, increased cover, and biodiversity to these landscapes. Found to reestablish naturally in disturbed areas of Yellowstone and Glacier National Parks (Majerus, 2000). *Phacelia hastata* is currently used in seed mixes for revegetation along road pullouts and in bridge repair areas in Glacier National Park (D. LaFleur, personal communication, 2013) and in seed mixtures for lodgepole pine (*Pinus contorta*) forests in Yellowstone National Park (Majerus, 2000).

Plant ecotypes from western Montana that show tolerance to arid and semi-arid climate and to acid/heavy metal soil conditions have reclamation potential (Cornish, 2007). *Phacelia hastata* is one of the top performing species tested at the Anaconda Smelter Superfund site in western Montana (Marty, 2000). This large area near Anaconda was exposed to decades of dust-fall from smelter stack emissions, which visibly altered approximately 13,000 acres of uplands (Eby, 2004). In studies at the Superfund site, beginning in 1995, twenty-nine forb species from wildland collections were evaluated at plots for percent survival, vigor, height, and seedhead production, with *P. hastata* demonstrating superior tolerance to acid/heavy metal soil conditions.

As an ornamental, its purple spiked flowers and gray-green foliage make *P. hastata* an attractive low-growing perennial. It is a hardy, USDA Hardiness Zone 3, perennial that grows in coarse, medium and fine soils, in full sun, with low supplemental water requirements, requiring no fertilizer or pest control. Due to limited seed supply, lack of knowledge about its basic requirements for greenhouse propagation, and underuse in built landscapes, it has been difficult to put into commercial production (Dougher, 2011) L. Smith, personal communication, (2012).

Plant Growth Regulators and Effects

The published research on effects of PGRs on *P. hastata* is restricted to germination studies. However, work with other species suggests specific PGRs that might be used to increase harvestable seed yield by either increasing vertical height of the seed head or reducing lodging and/or seed shatter at maturity, all of which should increase harvest efficiency when using mechanical harvesters. Details follow for the PGRs considered in this study.

Using Gibberellic Acid to Increase Height

Gibberellin was first isolated in Japan in the 1930s from a fungus (*Gibberella fujikuroi*) that secretes a chemical causing abnormal elongation of rice stems, called ‘foolish seedling disease’ by Japanese farmers (Phinney, et al., 1960). In the 1950s, it was discovered that applying gibberellin to dwarf varieties of peas and maize would cause plants to grow to normal height and sometimes taller. It soon became evident that gibberellins are naturally occurring substances in higher plants and play a key role in plant growth and development (Wittwer, et al., 1958; Taiz, et al., 1991). Gibberellins are the primary hormone controlling plant height (Hartmann, et al., 2011); yet, all aspects of growth and development of higher plants can be affected by gibberellins, including seed germination, root growth, stem elongation, leaf expansion, floral induction and flower development (Phinney, et al., 1960; Mutasa-Gottgens, et al., 2009). Over 100 different forms of this endogenous plant hormone have been identified; the commonly used gibberellic acid (GA_3) promotes growth through cell enlargement and elongation (Nelson, 2003; Hartmann, et al., 2011).

Initiation of shoot and stem elongation by GA_3 is well documented for many rosette species (Brian, et al., 1955; Sachs, 1965; Hedden, et al., 2000). Sachs et al. (1959) found that in rosette plants, GA_3 causes an increase in cell number below the apical meristem, and that cell elongation in the stem occurs much later. In 1977, GA_3 was found to induce hypocotyl elongation in lettuce (*Lactuca sativa*) through increased cell elongation (Stuart, et al., 1977). A 30-fold increase in flower stem length was accomplished by GA_3 application in red beet (*Beta vulgaris*) (Goldman, et al., 1997).

Recently, Lee and Sugiyama (2011) found that GA_3-dependent cell division and elongation coincides with bolting in rosette plants; lettuce stems started to elongate three days after GA_3 treatment and continued to elongate throughout the experiment.

GA_3 may also induce or promote flowering. Stuart and Cathey (1961) found that GA_3 accelerates plant growth patterns already in progress, including flowering. For example, in greenhouse-grown lettuce treated with GA_3, flower induction occurred three days earlier (Lee, et al., 2011). However, the role of GA_3 in flowering is variable and species specific (Mutasa-Gottgens, et al., 2009). For example, in long-day and biennial plants gibberellins promote flowering while in fruit trees they inhibit it (Goldberg-Moellera, et al., 2013). New research indicates that enhanced flowering, followed by increased seed set and yield, could be achieved by modulating accumulation and degradation of gibberellins (Wagner, 2014). GA_3 has been found to regulate the transition to flowering in *Arabidopsis*, suggesting that reproductive success (and seed yield) could be adjusted by altering gibberellin accumulation before flowers form (Yamaguchi, et al., 2014).

One treatment of GA_3 used in this study, brand named Ascend®, is in combination with two other PGRs, cytokinin and indolebutyric acid (IBA), at concentrations and ratios intended to maximize plant growth and development. This treatment would have the combined effects of GA_3 and cytokinin, which promotes cell division and leaf expansion while slowing leaf aging, plus IBA, which stimulates vigorous root formation and development and increases cell elongation. Research trials by the manufacturer show improved yield potential in corn, soy, and other crops

(Winfield, 2011). Ockerse and Ralston (1967), found "a markedly synergistic growth response" to the administration of GA_3 preceding indole-3-acetic acid (IAA) in green dwarf pea. Research on interactions between plant hormones shows IAA promotes the active biosynthesis of gibberellin in pea (Ross, et al., 2001).

Using PGRs to Reduce Lodging

As *P. hastata* seed matures and gets heavier, stems tend to lodge, bending laterally near the crown and upward at the base of flower heads. Dispersal takes place from mid-July through September when uncoiling cymes release seed to the ground. This decumbent growth pattern, while an effective seed dispersal mechanism, results in seed on the plant that is too close to the ground to harvest mechanically. Two PGRs that might prevent lodging by reducing stem elongation were identified: paclobutrazol (PBZ), which is a GA-inhibitor, and ethylene.

Paclobutrazol (PBZ). GA-inhibitors such as PBZ are synthetic chemicals used to reduce unwanted longitudinal shoot growth (plant size) in many agronomic and horticultural crops (Davis, et al., 1988; Barrett, et al., 1992). They are antagonistic to gibberellins and auxins, reducing cell elongation and cell division by inhibiting GA_3 biosynthesis (Hartmann, et al., 2011). Some primary effects of these growth retardants are reduced height and thickening of flower stems (reduced internodal growth), increased root growth, early fruit set, and increased seed set (Grossmann, 1990; Nelson, 2003; Hartmann, et al., 2011).

Paclobutrazol has potential to reduce flower height of *P. hastata*, thus allowing flower stalks to remain upright and more susceptible to mechanical harvest. There is reasonable evidence to suggest that decreased flower height may allow flower stalks to remain upright. Crook and Ennos (1994) investigated lodging resistance of four wheat cultivars, finding that resistance was associated with short and light stems with high anchorage strength in the root system (stronger, widely spread roots). Effective use of PBZ reduces internode elongation, resulting in more compact plants and stouter stems in six species of greenhouse-grown ornamental plants [1] (Hickman, 1986), as well as in *Lupinus varius* L. (Karaguzel, et al., 2005), in the tropical ornamental *Pachira aquatica* (Li, et al., 2009), and in Arabidopsis (Cowling, et al., 1999).

An effect of spray application of PBZ is regulation of flowering. Karaguzel et al., (2005) found that PBZ slightly decreases time to flowering of *Lupinus varius* plants and that foliar sprays can be used to increase flower numbers without causing a decrease in flowering quality. PBZ application induces earlier flowering in begonia (Pan American Seed, 2006) and was found to accelerate flowering in the ornamental annual *Consolida orientalis* (Mansuroglu, et al., 2009). In that study, paclobutrazol had no effect on the time from sowing to flowering but increased flower number and stem diameter.

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[1] fiddleleaf fig (*Ficus liatra*), rubber plant (*Ficus elastica*), schefflera (*Brassaia achnophylla*), dipladenia (*Mandevilla*), Grape ivy, (*Cissus rhombrifolia*), German violet (*Exacum*).

Paclobutrazol is commonly used in the production of floriculture crops, with a wide range of efficacy and moderate to long-lasting responses (Runkle, 2012). In spray applications, PBZ penetrates plant stems and is translocated to the terminal bud where it reduces internode elongation (Syngenta, 2005). Since movement of the chemical occurs in the xylem and not the phloem, spray absorbed through the leaves is not readily transported to other parts of the plant. Therefore, sufficient volume of water to reach stems is needed (Whipker, 2013); label recommendations are to apply 2 qt. of spray solution over 100 sq. ft. (1.9 L/9.3 m^2). Spray timing is important. For example, PBZ causes the plant to produce smaller and more compact cells; it will not shrink cells that have elongated and must be applied before internode elongation (Faver, 2012), if height reduction is desired. In another example, spray timing influenced apple tree response (El-Khoreiby, et al., 1990), where PBZ sprays made during different parts of the growing season produced different responses in fruit characteristics of apple trees (El-Khoreiby, et al., 1990).

Ethylene. Growth retardants can be classified into two groups: GA-inhibitors and ethylene-releasing compounds (Grossmann, 1990). Ethylene (C_2H_4) is a simple chemical with a complex regulatory role in flower development and fruit ripening (Gibson, et al., 2000; Lin, 2009). Some botanic effects of ethylene became evident during the 1800s when leakage from gas street lights caused premature senescence and defoliation of nearby trees. (Abeles, et al., 1992). Ethylene, naturally produced in small quantities in most fruits and vegetables, regulates phases of plant growth, development, ripening and senescence in higher plants (Hartmann, et al., 2011). Many fruits respond with uniform ripening when exposed to an external source of ethylene (Monterey Lawn and Garden, 2012). One contact growth regulator, ethephon, is widely used in agriculture as a ripening agent. Ethephon is a synthetic compound that penetrates into tissues where it is immediately converted to ethylene (Monterey Lawn and Garden, 2012). The gas is then quickly translocated throughout the plant (Royal Society of Chemistry, 2014).

Although foliar sprays of ethephon are broadly used for increased lateral branching in floriculture crops and may delay flowering if applied close to the time of flower initiation (Latimer, et al., 2012), responses vary widely among plant species and with varying application techniques, timings and concentrations. Of interest to this study, ethephon has been shown to lower lodging risk in barley (Foster, et al., 1993) and control lodging, thus enhancing yields, in small grains (Green, et al., 1985). Bratsch and Mack (1990), found spray application of ethephon on sweet corn reduced lodging in some treatments and compared favorably to mechanical topping for reducing plant height and improving yield

In addition to decreased lodging, ethylene can increase reproductive development and crop uniformity. It initiates reproductive development in pineapple (Monterey Lawn and Garden, 2012) and accelerates post-harvest ripening in many fruits such as apples, pears and bananas (Washington State University, 2014). Recent advances in ethylene research indicate ethylene is a key regulator of many survival and competition mechanisms in plants (Lin, 2009). Ethylene is now thought of as part of a regulatory signaling network, acting as a mediator that responds to and coordinates growth dynamics and developmental events (Yoo, et al., Article in Press), controlling such responses as synchronizing flowering time, flower development and seed dispersal.

MATERIALS AND METHODS

Study Area

The study site, located four miles southeast of Bridger, Montana at the U.S. Department of Agriculture Natural Resources Conservation Service, lies at an elevation of 1118 m (3665 feet) in USDA Plant Hardiness Zone 4a (2012). When plots were seeded on November 28, 2012, warm, dry conditions prevailed, with total precipitation 7.6 inches (19 cm) lower than the calendar year average (Table 1). During the 2013 growing season of 154 days (May 2–October 5), total precipitation was 0.4 inches (1 cm) greater than the long-term mean of 11.7 inches (30 cm). Also, the mean temperature was slightly warmer (+1.7° F, +0.9° C) than the long-term average of 45.7 ° F (7.2° C) (Table 2). Soils at the site consist of Halverson and Heldt silty clay loams (U.S. Department of Agriculture, 2014).

Experimental Design

At the field site**,** treatments were arranged in a randomized complete block design, with seven replicates per treatment. The field consisted of 16 rows with furrow irrigation channels between rows. The outside row on each side was left untreated to reduce edge effects. Each of the 14 inner rows contained eight randomized treatments (GA, 2XGA, PBZ, COMB, ethephon, GA-twice, 2XGA-twice, PBZ-twice) and two controls, one for each spray timing (Table 2). The ethephon treatment was placed on the west end of the treatment blocks by itself, addressing concerns about ethylene drift and allowing

Table 1 *Weather Data for the Bridger Plant Materials Center, November, 2012–October, 2013*

Month	°F Max.	°F Min.	°F Mean	Long-term Mean	Dep. from Long-term Mean	°F Soil Temperature Mean	2012	Long-term Mean	Departure from Mean	Number Days Ppt.	Avg. Wind Speed
	Mean Monthly Air Temperature						Total Monthly Precipitation				
							in.	*in.*	*in.*		*mph*
November	51.4	28	39.7	33.4	6.3	40.6	0.15	0.49	-0.34	2	9.18
December	36.5	15.1	25.8	24.7	1.1	53.6	0.12	0.4	-0.28	2	2.52
January	35.7	13.9	24.8	25.9	-1.1	27.1	0.31	0.48	-0.25	9	8.4
February	39.1	19.3	29.2	27.4	1.8	29.5	0.48	0.33	0.05	8	7.6
March	52.1	23.2	37.7	35.6	2.1	37.7	0.21	0.73	-0.56	11	7.8
April	54.1	27.6	40.9	43.9	-3	45.9	0.86	1.41	-0.76	15	7.9
May	69.6	43.7	56.7	53.2	3.5	61.6	1.82	2.21	-0.49	11	7.4
June	80.4	50.5	65.5	62.2	3.3	71.7	0.51	1.85	-1.03	8	6.4
July	89.2	57.4	73.3	70.1	3.2	80.8	0.69	0.73	-0.04	9	6.1
August	89.9	56.5	73.2	67.8	5.4	74.7	0.85	0.78	0.07	5	5.7
September	76.5	50.2	66.1	57.9	8.2	66	2.32	1.17	1.15	12	6.4
October	53.7	32.2	43	46.6	-3.6	44.5	2.8	1.11	1.69	12	6.3
Yearly Total[z]							11.12	11.69	-0.79	104	81.7
Monthly Mean	60.7	34.8	48.0	45.7	2.3	52.8					6.8

Note. 2013 Growing Season 28°F: 154 days, May 2-October 5. Adapted from Bridger Plant Materials Center Annual Technical Reports, 2012 and 2013, *US Department of Agriculture Natural Resources Conservation Service*. [z] November 2012–October 2013.

expansion of the thinned block length to include ten plants in full bloom on the day of treatment. All other plots had dimensions of 7.3 by 1.8 m (24 by 6 feet). Thinned plots (n odd numbered rows) were thinned to ten plants per plot.

Procedures

P. hastata seed (G1 seed collected from the Anaconda Superfund Site in 2010[2]) was obtained from Bridger Plant Materials Center and planted on November 28, 2012. Each row was seeded using a Kincaid, 4-row, precision cone planter at the rate of 25 bulk seed/linear foot (0.3 m) within a row. Rows were spaced 30 inches (0.76 m) apart, on center. During the 2013 growing season the plot was hand weeded two times. Rows were flood irrigated on 14 May and 27 June 2013. Thinned plots were created by removing all but ten plants per plot, resulting in approximately one-foot spacing between plants. Unthinned plots of the same dimensions were located next to each thinned plot and remained as seeded. For consistency and convenience, plots were treated and harvested in pairs, with each treatment sprayed on both thinned and unthinned plots, with the exception of ethephon, which was sprayed on thinned plots only.

Gibberellic acid (GA), double concentration gibberellic acid (2XGA), paclobutrazol (PBZ), combined hormone (COMB), ethephon and Control 1, were sprayed once. In addition, GA, 2XGA, PBZ, and Control 2 were sprayed sequentially, once on 25-June and again three weeks later (Table 2). Using a handheld 2L backpack

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[2] Seed is assigned a generation number based on how many field generations the seed lot is removed from the parental stock (Bohl, et al., n.d.), in this case, one generation.

sprayer, foliar sprays were applied until foliage was thoroughly wet, but not dripping from leaves. The application date for first treatment was scheduled based on manufacturer recommendations, plant phenology, and field conditions. All PGRs were sprayed on the same date to allow comparison of effects. Treatments began as soon as possible after plots were established, weeded, thinned, and when weather conditions allowed (dry, calm conditions in the morning). None of the PGRs were labeled for application to *P. hastata*, thus timings and rates of applications were based on recommendations for closest related species and desired effects, along with the practical considerations noted above. In order to spray plants in full bloom, ethephon plots were sprayed on the second spray date (18-July), on ten plants, in thinned plots only. Unthinned plots were not sprayed with ethephon because full bloom requirements could not be met.

Harvest date was determined using a visual assessment of seed maturity, when initial blooms were shattering. Seed samples were hand rubbed and designated as ripe at the hard dough stage. In consultation with the staff at Bridger, and anticipating a relatively concentrated period of seed maturation, I established a harvest timing criterion, whereby harvest would occur when at least 40% of the seed samples appeared ripe. Plants were harvested by hand and combined into one sample per plot. For each sample, all stems were cut at 10 cm above soil surface to approximate the height of a machine harvester. Samples were placed in paper bags in a drying room (24° C) for two weeks, and weighed (cut mass). Samples were then cleaned by removing leafy plant material and debris using a rubbing board, screens and a seed blower. Seeds were subsequently weighed (seed mass) and counted (seed count). The mass of one hundred seeds (hundred-seed mass) was calculated from seed mass and seed count measurements. Seed germination and viability (tetrazolium choloride, TZ) tests were conducted by the Montana State Seed Lab in Bozeman, Montana. Standard procedures included germination under light at 15° C (59° F) for 12 days (Association of Official Seed Analysts, 1993). No pretreatment was applied. Only non-germinated seeds were tested for viability via the TZ test.

Supplementary data regarding plant growth characteristics were collected at harvest on one plant chosen randomly from each thinned plot. Maximum distance from ground level to the top of tallest bloom or seed head (bloom height), maximum diameter of rosette (plant diameter), number of stems blooming, and number of stems greater than 10 cm in height (tall stems) were measured. This height was chosen to approximate mechanical harvest height.

Table 2

Treatment Details of Foliar Sprays of Plant Growth Regulators on P. hastata.

PGR Code Names	Active Ingredient[z]	Brand Name	Manufacturer	Rates (ppm)	Growth stage at application	Date(s) of Application
Control 1	Water with surfactant				Pre-bloom	25-Jun
COMB	[y]Cytokinin (0.090%) Gibberellic acid (0.030%) Indolebutyric acid (0.045%)	Ascend®	Winfield Solutions LLC, Saint Paul, MN	2500	Pre-bloom	25-Jun
PBZ	Paclobutrazol (0.4%)	Bonzi®	Syngenta Crop Protection, Inc., Greensboro, NC	30	Pre-bloom	25-Jun
GA	Gibberellin A3 (40%)	RyzUp Smartgrass®	Valent Biosciences, Libertyville, IL	100	Pre-bloom	25-Jun
2XGA	Gibberellin A3 (40%)	RyzUp Smartgrass®	Valent Biosciences, Libertyville, IL	200	Pre-bloom	25-Jun
Ethephon	Ethephon (3.9%)	Florel®	Lawn and Gardens Products, Inc., Fresno, CA	2000	Once, at bloom	18-Jul
Control 2	Water with surfactant				Pre-bloom + 3 weeks later	25-Jun and 18-Jul
PBZ-twice	Paclobutrazol (0.4%)	Bonzi®	Syngenta Crop Protection, Inc., Greensboro, NC	30	Pre-bloom + 3 weeks later	25-Jun and 18-Jul

GA-twice	Gibberellin A3 (40%)	RyzUp Smartgrass®	Valent Biosciences, Libertyville, IL	100	Pre-bloom + 3 weeks later	25-Jun and 18-Jul
2XGA-twice	Gibberellin A3 (40%)	RyzUp Smartgrass®	Valent Biosciences, Libertyville, IL	200	Pre-bloom + 3 weeks later	25-Jun and 18-Jul

[z]Adjuvants Interlock® (3125 ppm), a deposition aide and drift control agent and Preference ® (625 ppm), a nonionic surfactant, were added to gibberellin treatments and Controls.
[y]Cytokinin, as Kinetin

Statistical Analysis

Analysis of variance (ANOVA) was used to test the null hypotheses that, among all treatments and their controls, there were no differences with respect to all measured variables (SAS version 9.4, SAS Institute, Inc., Cary, North Carolina). Errors made in the collection and seed cleaning processes (i.e. one labelling error, one sample was lost during seed cleaning) and elimination of a third sequential spray of GA resulted in unequal sample sizes. ANOVA tests were conducted using general linear means (PROC GLM). Where significant differences were detected, means were separated using the Tukey-Kramer post-hoc procedure. Statistical tests assumed significance at $\alpha = 0.05$ level.

RESULTS

Seed Quantity and Quality

Among treatments sprayed once, there were no significant differences. Foliar applications of PBZ sprayed twice (PBZ-twice) increased seed mass, seed count, and hundred-seed mass in thinned plots, while in unthinned plots, no differences from controls were significant. In thinned plots (Figure 1), seed mass for plants sprayed with PBZ-twice was 337% greater than for Control 2 ($p = 0.02$) and 444% greater than for plants sprayed with GA-twice ($p = 0.006$). A second spray of GA was not helpful in increasing seed yield; GA sprayed once produced greater seed mass than GA-twice ($p = 0.05$). Seed mass in unthinned plots varied among blocks and treatments (Table 3).

Similar to seed mass, seed count in thinned plots (Figure 3) sprayed with PBZ-twice was 303% higher than Control 2 ($p = 0.02$) and 298% higher than GA-twice ($p=0.03$). For seed count in unthinned plots (Figure 4), both Block and Treatment effects were significant (Table 3) with no differences found using the Tukey test. The highest means were COMB and PBZ-twice while the lowest means were GA-twice and 2X GA-twice.

Higher hundred-seed mass (Figure 5) was found in thinned plots for PBZ-twice and 2XGA treatments while the lowest hundred-seed mass was found under GA- twice treatment (PBZ-twice vs. GA-twice $p=0.02$ and 2XGA vs. GA-twice $p=0.04$), but were not different from the controls. Differences in hundred-seed mass were not detected among unthinned plots.

Ethephon treatment produced lower germination rates than Control 1 ($p = 0.03$), GA-twice ($p = 0.03$) and 2XGA-twice ($p < 0.01$) (Figure 6). Lower germination was also found under COMB treatment compared to 2X GA-twice ($p = 0.04$). No other differences were detected among PGR treatments with respect to germination or viability of harvested seed (Table 3).

Plant Measurements

With foliar applications of these plant growth regulators, no differences were observed in cut mass, plant diameter, bloom height or percent tall stems in either thinned or unthinned plots, with the following exceptions. Cut mass and plant diameter were increased with two applications of GA in thinned plots only (Figures 7 and 8). In thinned plots, the cut mass of plants sprayed with 2X GA-twice was greater than Control 2 ($p = 0.03$). Cut mass of plants sprayed with a single spray of GA was also greater than Control 2 (p=.02). Plant diameter in thinned plots sprayed with 2X GA-twice was greater than ethephon, sprayed once (p=.04).

Harvest Timing Decisions

The protracted flowering season of *P. hastata* leads to considerable variation in the timing of seed maturity, making harvest timing decisions difficult. During the 2013 growing season, the indeterminate nature of *P. hastata* was especially evident; a single *P. hastata* plant in our study might display flower buds, blooms, post-bloom stems, mature seed on stems, and seed shatter on any given day from July through August. In mid-July, a visual assessment suggested that a significant amount of mature seed was on the ground or on flower stems lying below the four-inch cutting height of a mechanical harvester, yet no single plot met harvesting requirements. As a result, the harvesting criterion was not met and decision to harvest was made based on field observation and sampling. Logistical considerations required that we harvest all plots at once, whereas ideally, we would have harvested by treatment.

Table 3.
Two-way ANOVA for variables measured in thinned and unthinned plots

	Thinned[z]				Unthinned			
Measured variable	F (Block)	P (Block)	F (PGR)	P (PGR)	F (Block)	P (Block)	F (PGR)	P (PGR)
Seed mass (g)	3.95	< 0.01	3.21	< 0.01	5.15	< 0.01	2.67	0.02
Seed count	4.12	< 0.01	2.79	0.01	5.11	< 0.01	2.65	0.02
Hundredseed mass (g)	2.21	0.06	3.03	0.01	4.29	< 0.01	1.72	0.12
Germination (%)	0.89	0.51	3.60	< 0.01	NA	NA	NA	NA
Viability (%)	0.22	0.97	1.27	0.28	NA	NA	NA	NA
Cut mass (g)	2.96	0.02	2.66	0.01	7.68	< 0.01	1.13	0.36
Plant diameter (cm)	0.60	0.73	2.08	0.05	1.08	0.38	1.94	0.08
Bloom height (cm)	0.34	0.91	0.73	0.68	0.63	0.64	0.83	0.58
Number of stems	0.94	0.47	0.78	0.64	0.48	0.75	0.96	0.48
Tall stems (%)[y]	1.46	0.21	1.47	0.19	0.34	0.85	1.46	0.20

[z]All variables are measured per plant, in thinned plots. [y]Proportion of stems >10 cm height.

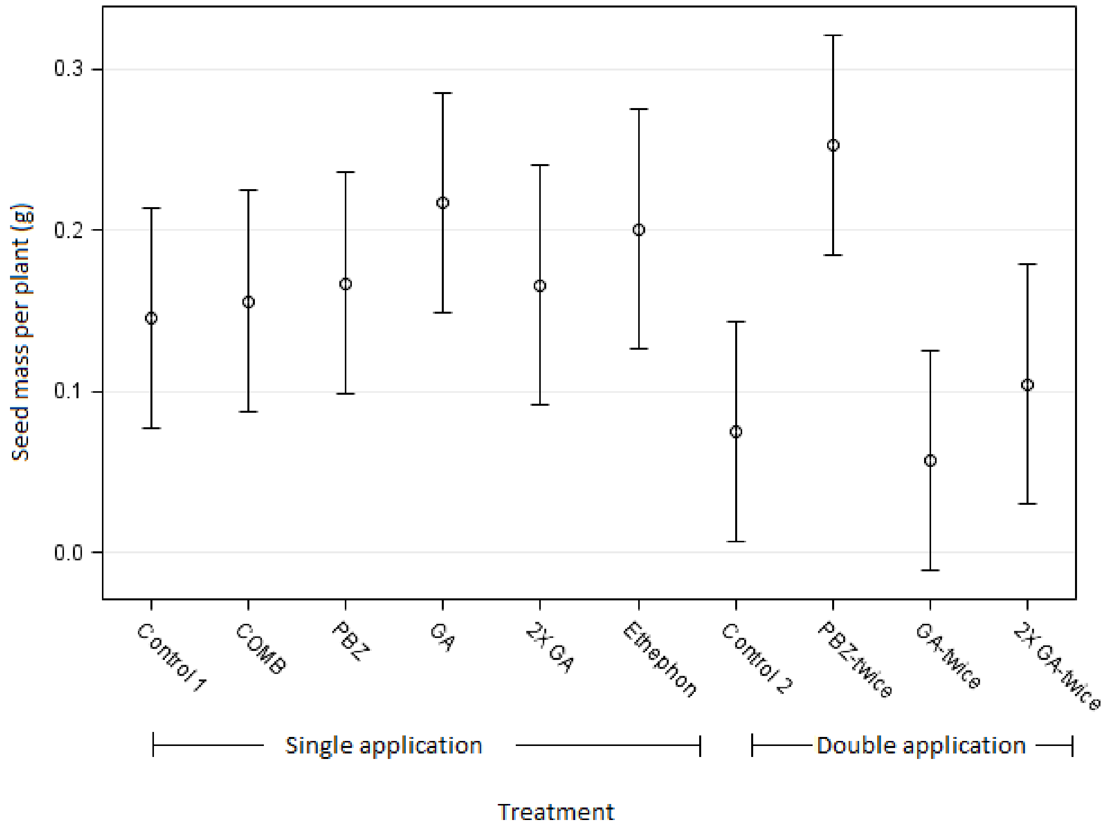

Figure 1. Effects of plant growth regulators on seed mass in thinned plots. Circles indicate least squares means and error bars indicate 95% confidence limits. Seed mass per plant varied among treatments, F (9, 57) = 3.21, p <0.01. For a description of treatments, see Table 2. n = 7 for all treatments except 2XGA, ethephon and 2XGA-twice where n=6.

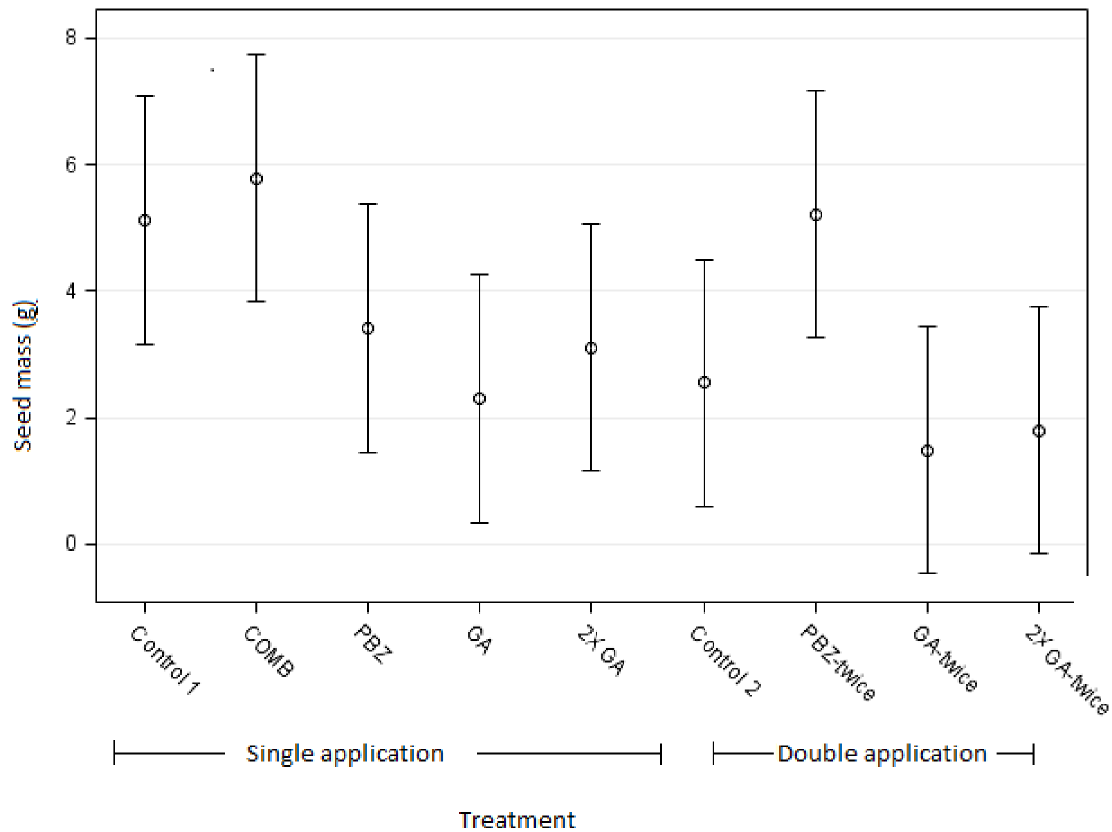

Figure 2. Effects of plant growth regulators on seed mass in unthinned plots. Ethephon was not sprayed on unthinned plots. Circles indicate least squares means and error bars indicate 95% confidence limits. Seed mass per plant varied among treatments, F (8, 54) = 2.67, p = 0.02. For a description of treatments, see Table 2. n = 7 for all treatments.

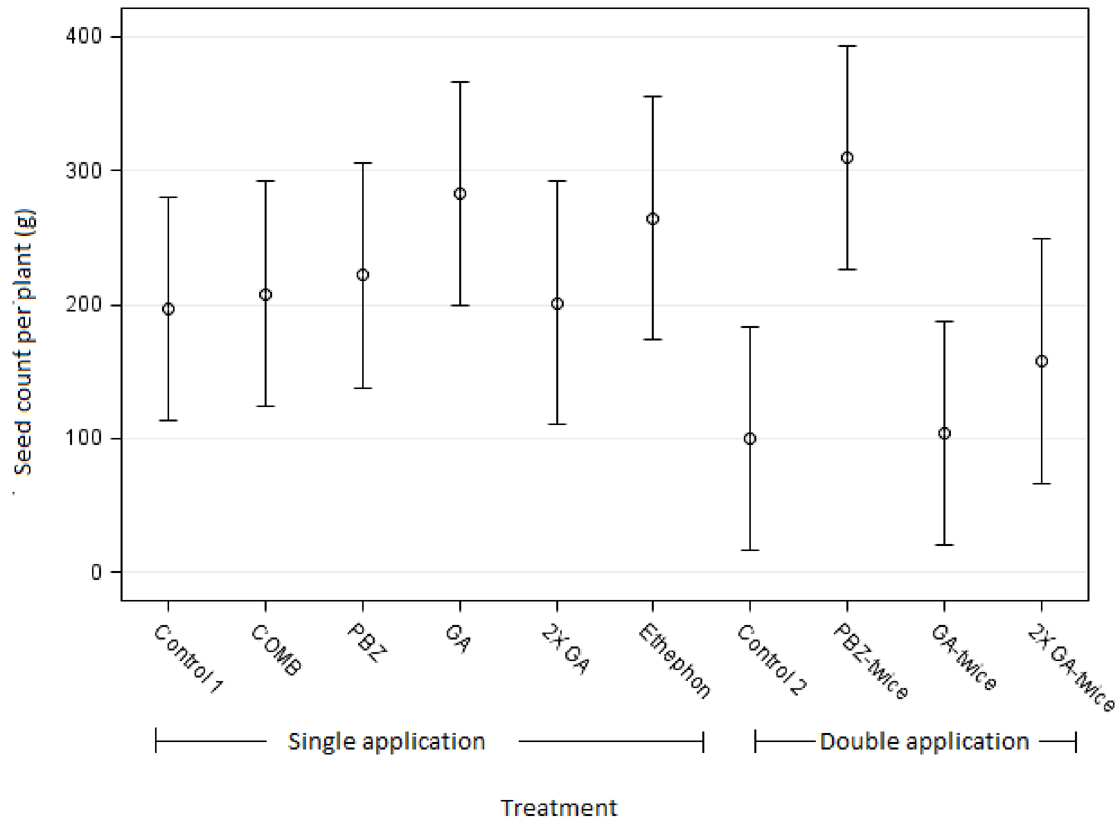

Figure 3. Effects of plant growth regulators on seed count in thinned plots. Circles indicate least squares means and error bars indicate 95% confidence limits. Seed count per plant varied among treatments, F (9, 57) = 2.79, p = 0.01. For a description of treatments, see Table 2. n = 7 for all treatments except 2XGA, ethephon and 2XGA-twice where n=6

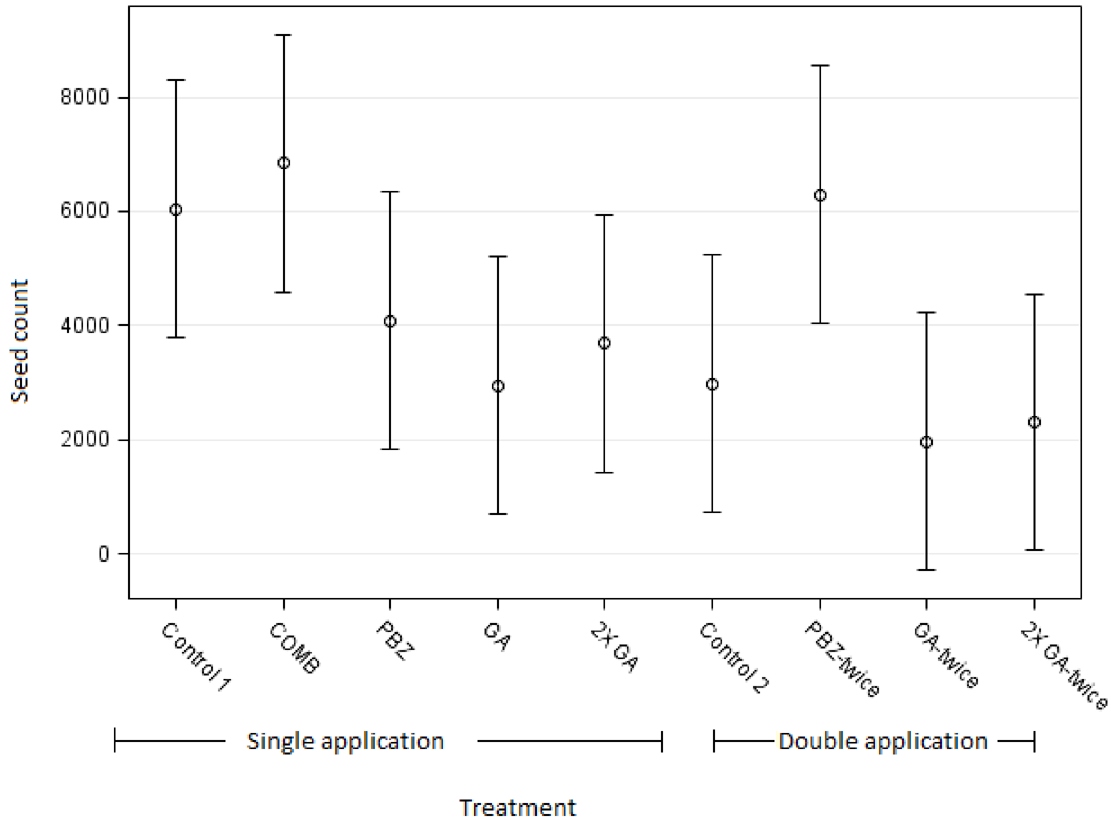

Figure 4. Effects of plant growth regulators on seed count in unthinned plots. Ethephon was not sprayed on unthinned plots. Circles indicate least squares means and error bars indicate 95% confidence limits. Seed count per plant varied among treatments, F (8, 54) = 2.65, p = 0.02. For a description of treatments, see Table 2. n = 7 for all treatments

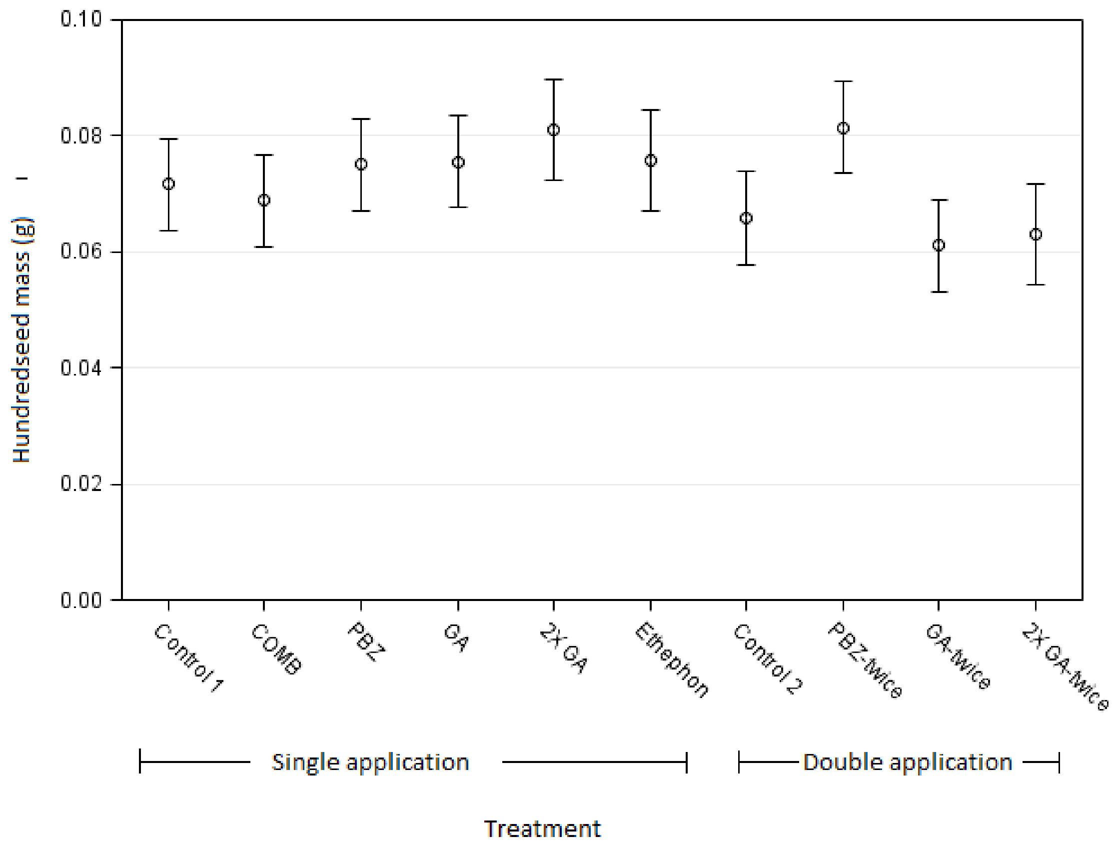

Figure 5. Effects of plant growth regulators on hundred-seed mass in thinned plots. Circles indicate least squares means and error bars indicate 95% confidence limits. Hundred-seed mass per plant varied among treatments, F (9, 57) = 3.03, p = 0.01. For a description of treatments, see Table 2. n = 7 for all treatments except 2XGA, ethephon and 2XGA-twice where n=6

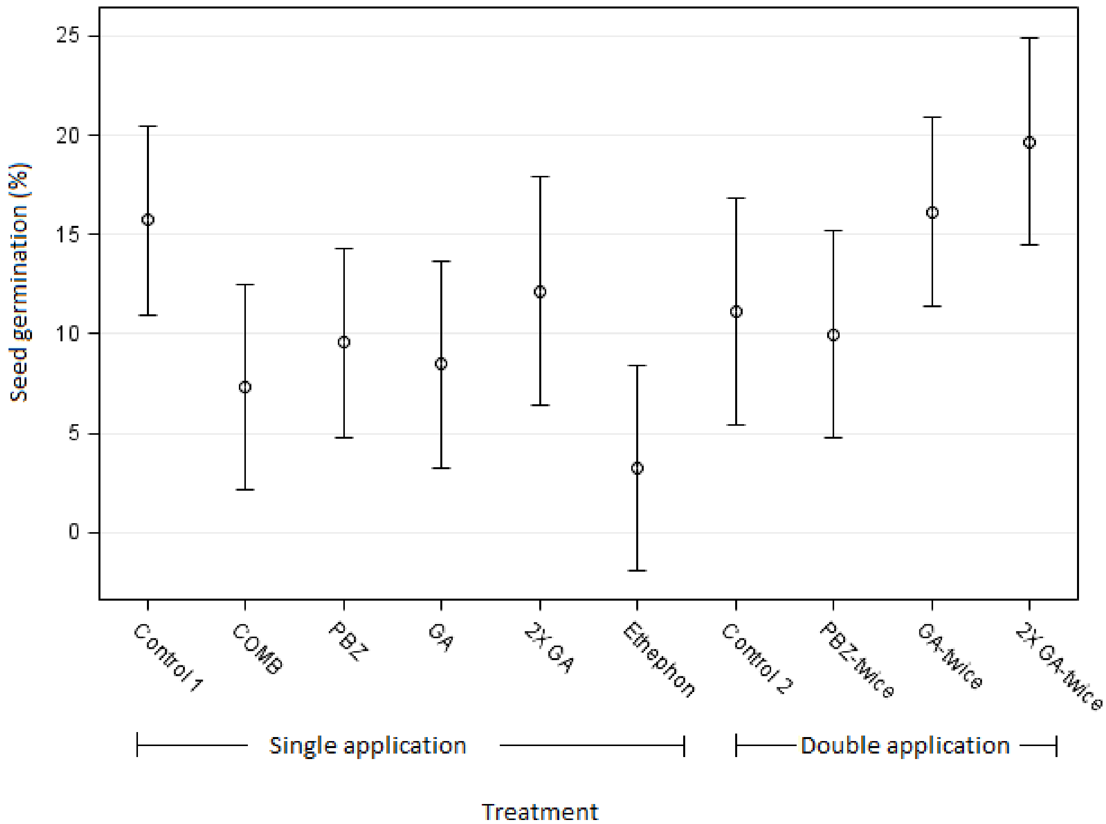

Figure 6. Effects of plant growth regulators on seed germination in thinned plots. Circles indicate least squares means and error bars indicate 95% confidence limits. Seed germination per plant varied among treatments, F (9, 51) = 3.60, p <0.01. For a description of treatments, see Table 2. n = 7 for Control 1, PBZ and GA-twice. n = 6 for COMB, GA, ethephon, PBZ-twice and2XGA-twice. n = 5 for 2XGA and Control 2.

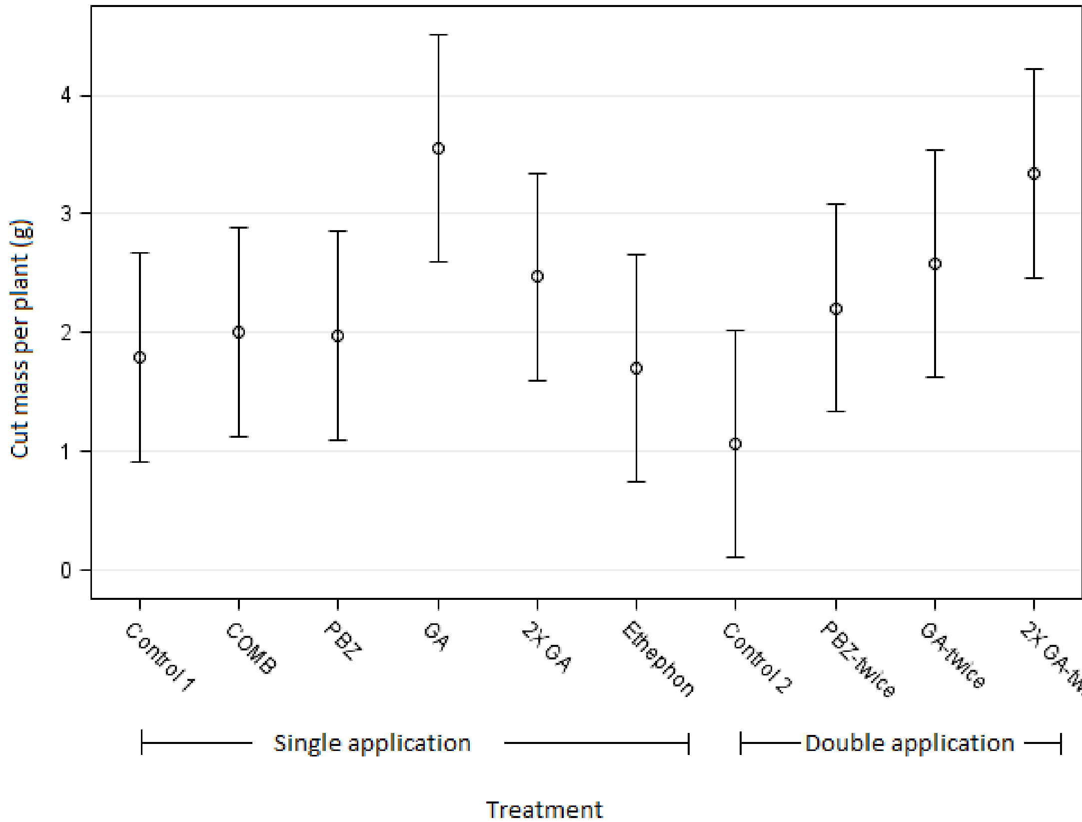

Figure 7. Effects of plant growth regulators on cut mass in thinned plots. Circles indicate least squares means and error bars indicate 95% confidence limits. Cut mass per plant varied among treatments, F (9, 56) = 2.66, p = 0.01. For a description of treatments, see Table 2. n = 7 for all treatments except GA, ethephon, Control 2 and GA-twice where n=6

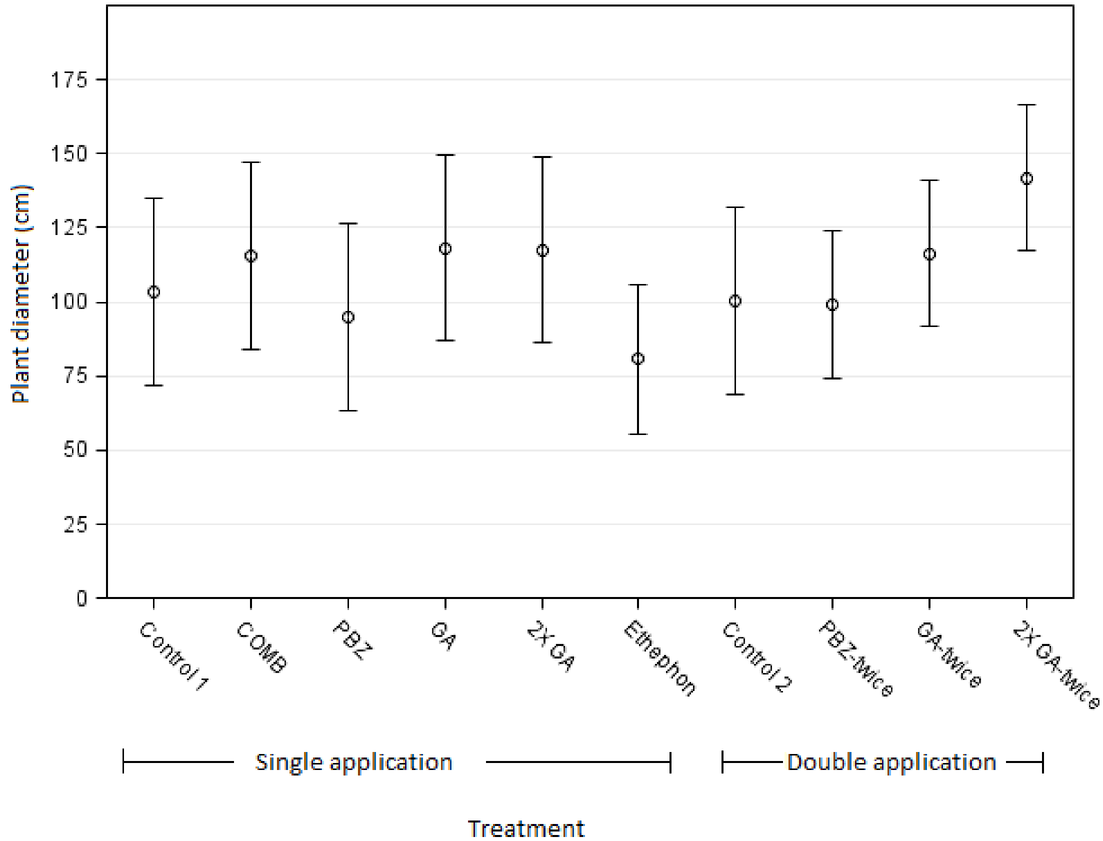

Figure 8. Effects of plant growth regulators on plant diameter in thinned plots. Circles indicate least squares means and error bars indicate 95% confidence limits. Plant diameter varied among treatments, F (9, 56) = 2.08, p = 0.05. For a description of treatments, see Table 2. n = 5 for all treatments except ethephon, where n = 6 and PBZ-twice, GA-twice, and 2XGA-twice where n = 10

DISCUSSION AND CONCLUSION

Although *P. hastata* is valued for a number of important applications—for example, improving insect pollinator habitat, revegetating difficult sites, and providing drought-resistant ornamentals—it is not widely used because seed is not readily available. Underlying causes of this problem can be traced to the characteristics of *P. hastata* itself. The species' low growth habit and protracted flowering period combine to make mechanical harvesting inefficient, thereby frustrating efforts to grow commercially viable quantities of seed. This study primarily considers whether select PGRs might be used to facilitate mechanical harvest by 1) increasing flower stem height, 2) reducing lodging, and/or 3) synchronizing the timing of seed maturation. Secondarily, it asks whether the PGR treatments examined affect seed quality (i.e., germination rate or viability), recognizing that increasing seed yield at the expense of seed quality may provide no overall benefit to growers.

PGRs examined in this study include gibberellic acid (GA), paclobutrazol (PBZ), ethephon and a combined hormone (COMB). For each, detailed findings are discussed below.

Gibberellic Acid

Gibberellins play a role in many processes of plant development (Wright, 1993) and are well known to promote uniform growth through cell enlargement (Blazquez, et al., 1998). We anticipated that GA would encourage rapid elongation of flower stalks, thereby increasing flower stem height, resulting in increased seed harvest via mechanical harvester.

Single and double concentrations of GA, sprayed once or twice, yielded no difference from controls in seed yield or quality. GA sprayed twice compared unfavorably with PBZ sprayed twice, producing lower seed mass and hundredseed mass, but was not different from control. Percent germination and viability were not different from controls, indicating no measureable effect on seed quality. There might be an association with GA_3 and higher germination rates, but this study was underpowered to detect it (2XGA-twice vs. Control 2, $p = 0.47$). Viability data ranged from 76% to 89% but was not different among treatments. While two applications of double concentration GA did increase cut mass, stem height and percent tall stems were not different from controls. GA's effect on vegetative mass and plant diameter did not translate into increased seed yield. Further trials with higher rates and/or different timings of GA may show a more pronounced response.

Low seed yields, in this study, may be due to GA's ability to induce early flowering under some applications. GA is known to synchronize flowering under greenhouse conditions in a variety of floricultural crops (Latimer, et al., 2012) and under field conditions in coffee (*Coffea arabica* L.) (Schuch, et al., 1990; Masarirambi, et al., 2010). Time of flower emergence can have a significant influence on time of seed maturity (Kulkarni, et al., 2006). For example, GA accelerates flower bud development in artichoke, significantly advancing maturity (Harms, et al., 1988). In this study, GA may have induced early flowering in *P. hastata*, resulting in early seed shatter compared to PBZ treated plots. This would decrease the amount of seed available on harvest day, which was chosen to coincide with overall field maturity. Investigating the effects of GA on timing of seed maturation (through synchronization of flowering) in *P. hastata* could prove useful.

Paclobutrazol

The efficient growth retardant, paclobutrazol, can cause a substantial depletion in the levels of active GAs throughout a plant (Ribeiro, et al., 2011) and is used by growers to control plant height in ornamental species, with height reduction effects primarily seen in stem, petiole and flower stalk tissue (Pilon, 2006; Latimer, et al., 2012). Depending on the plant species and concentration applied, paclobutrazol has been found to both strengthen flower stems (Halevy, 1986) and reduce stem diameter (Tsegaw, et al., 2005). Conflicting responses to paclobutrazol treatment are common and are often species specific. For example, paclobutrazol has been widely used to accelerate flowering in various perennial species (Halevy, 1986; Mukadam, et al., 2013), but can delay flower development in velvet grass (Hampton, et al., 1992).

Pertinent to this study, suitable application of paclobutrazol can increase seed quantity and improve seed quality in grass and grain crops (Pan, et al., 2013; Hampton, et al., 1992). The hypothesis that PBZ reduces lodging in *P. hastata*, thus allowing more harvestable seed, was tested by spraying both single and sequential applications of paclobutrazol. Although no reduction of lodging was found with applications of paclobutrazol, floliar sprays of PBZ-twice increased seed yield compared to Control, with no resulting decrease in germination or viability of seed.

In thinned plots, we observed that two sprays (30 ppm at one-month rosette stage and three weeks later) of paclobutrazol (PBZ-twice) increased seed mass, seed count and hundred-seed mass of *P. hastata*. This result is similar to that of Hampton et al. (1992), who found that spray applications of paclobutrazol increased seed yield of a first year crop of velvet grass (*Holcus lanatus*). However, findings from this study differed from those of Hampton et al. in other respects. Hampton et al. also found that velvet grass stem length was reduced and lodging prevented. In this study, the number of stems and percent tall stems did not differ from the control, in either thinned or unthinned plots. Similarly, in unthinned plots, possible differences were found in seed mass, but not in stem length or lodging.

While PBZ treatments were used in an attempt to reduce lodging of *P. hastata*, the potential impact of paclobutrazol application on timing of seed maturation was only identified during the course of field work. Delaying harvest in *P. hastata* can lead to crop loss due to seed shatter (J. Scianna, personal communication). The higher seed yield and quality at harvest in PBZ-twice plots could indicate that fewer seeds were shed than in untreated plots. Wiltshire and Hebblethwiate (1990) found an increase in seed yield as harvest was delayed in *Lolium perenne* L. treated with the growth regulator (GA-biosynthesis inhibitor) triapenthenol, which is chemically similar to PBZ. They noted that optimum harvest time in a growth regulated seed crop will be different from that of an untreated crop due to the delay in crop maturity caused by triazols. Basing harvest timing decisions on seed moisture content within each treatment, rather than harvesting all plots on the same day, would be an improved approach in future studies. In that way, the hypothesis that differences in seed yield between treated and untreated plots are independent of harvest date and of seed moisture content at harvest could be tested.

An alternative hypothesis is that the surfactant suppresses seed yield in *P. hastata*. Preference®, the adjuvant chosen for this study, has both crop-derived and petroleum-based active ingredients and is recommended by the manufacturer for use with the GA_3 formulation used in this study. The addition of the wetting agent and surfactants was intended to help coverage and cuticle penetration in *P. hastata*. In comparing treaments sprayed twice, it appears that the nonionic surfactant applied to all treatments except PBZ may have been phytotoxic. Both GA_3 treatments and Control 2 produced lower seed mass, seed count, and hundred-seed count than PBZ-twice.

Ethephon

We hypothesized that spray application of ethephon would control lodging and synchronize the timing of seed maturation in *P. hastata*. Reduced lodging and reduced seed shatter were apparent in plots sprayed with ethephon at time of full bloom, with 100% of blooms remaining upright without shedding seed. However, plots sprayed with ethephon showed decreased germination rates without increases in seed yield. This is possibly due to early flower senescence caused by ethylene, the primary hormone responsible for flower senescence and fruit ripening (Taiz, et al., 1991; Latimer, 2009). Decreases in seed quality after application of ethephon were found by Yang, (2006). In that study, application of ethephon at an early grain-filling stage reduced grain-filling rate and grain weight in rice (*Oryza sativa* L.).

One of a multitude of effects of ethylene on crops is timing of senescence, which determines yield and reproductive success. Grierson (2012), notes that timing of hormone treatments can enable senescence to be manipulated in *Arabidopsis* and proposes this control of “ethylene-mediated senescence” could improve yield, quality and longevity. In this study, spray applications of ethephon yielded reduced lodging and percent germination, possibly due to early flower senescence. Further investigation is needed to establish a possible cause-and-effect relationship between ethylene and seed development in *P. hastata.*

Combination Hormone

Following discussions with people in the agricultural crop protection industry, it appeared that a combination hormone like Ascend® might have potential to affect flower stem height and increase yield. This hormone combination was offered for our use and was included in the trials. Anticipating a synergistic effect from GA_3 plus cytokinin and IBA, single sprays of COMB were sprayed at the recommended rate. COMB treatments increased seed mass and seed count in unthinned plots as compared to GA-twice, but did not differ from control. There were no differences from control in germination and viability. Because unthinned plots mimic actual field conditions for seed production of *P. hastata*, the high means for seed mass and seed count are of interest for directing future studies.

Conclusion

In the agronomic and floriculture industries, GA_3 and its inhibitors are commonly used to control plant height (Wittwer, et al., 1958; Nickell, 1982; Hartmann, et al., 2011). Application of these plant growth regulator treatments did not increase flower stem height or number of bloom stems at time of harvest. Foliar sprays of GA-twice increased cut mass with no resulting increase in seed yield or quality. Sequential sprays of paclobutrazol increased seed mass and seed count of *P. hastata* in thinned plots. In addition, ethephon spray eliminated seed shatter with accompanying decreases in seed yield.

During the course of the study, a number of factors emerged as having primary importance for improving seed yield in *P. hastata* (e.g. timing of seed maturity and continuous flowering until frost). Anecdotal observations in the field indicate these factors are an issue that easily overwhelms the effects of the PGRs used in this study and is one that merits its own research. Indeterminate flowering may be the single greatest factor causing poor seed yield, and deserves a closer look. In addition, visual inspection of the field in the year following this study (2^{nd} year plants) suggests that growth patterns (e.g. asynchrony of bloom) and the need for PGRs could be very different in more mature *P. hastata* plants. A recommended approach is to learn *P. hastata's* growth curve and apply PGRs during or slightly before its rapid growing phase and monitor weekly to evaluate need for a PGR application, with careful attention paid to timing of harvest. Because the plant hormone must be in contact with the leaf/stem surfaces in order to be absorbed, higher concentrations and/or more frequent spray applications of these PGRs may be necessary in plants with hairy leaves, such as *P. hastata.* Time of day, humidity, and temperature at time of application, as well as spray volume, are some factors that influence efficacy of these PGRs. Harvestable seed yield could be improved with further refinement of spray protocols for paclobutrazol on 2nd year *P. hastata* under field conditions.

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