## Germination of Saccharum ravennae (L.) L. (Poaceae) Caryopses and Intact Spikelets

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#### ABSTRACT

Ravennagrass, Saccharum ravennae (L.) L. [synonym: Erianthus ravennae (Linn.) P. Beauv.], is a robust perennial bunchgrass grown as an ornamental in the US, but, where adapted, has become naturalized in riparian areas. Little is known about the seed size distribution and germination characteristics of ravennagrass caryopses or intact spikelets. The objectives of this study were to determine, for two populations: (i) the caryopsis size distribution, (ii) the germination of sized caryopses, (iii) the length of seedling shoots and roots from caryopses of different sizes, (iv) the germination of unsized caryopses (UC) and intact spikelets (IS), and (v) the length of seedling shoots and roots from UC and IS. Although seed production of ravennagrass is relatively low, under favorable conditions, ravennagrass can produce more than 10,000 caryopses per panicle. Caryopses germinated well within 14 d and averaged >80% germination; however, caryopses germinated >90% if their mass was >0.3 mg. Intact spikelets were slower to germinate in 14 d and had a lower percentage of abnormally germinated seed compared with caryopses. Intact spikelets also had a significantly higher percentage of firm seeds compared with caryopses and the total potential germination of IS was greater than caryopses exceeding 90%. Understanding the germination characteristics of ravennagrass will aid in the development of seeding rates and the processing of seeds for agronomic uses.

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Abbreviations: IS, intact spikelets; UC, unsized caryopses.

Sis a robust bunchgrass with culms up to 4 m tall (Hitchcock, 1951). This species is native to northern Africa, temperate and tropical Asia, and southern Europe (Chen and Phillips, 1994; eFloras, 2008; USDA National Plant Germplasm System, 2013). Ravennagrass is commonly used in ornamental plantings in the US, where it has since escaped from cultivation and become naturalized in many areas (Steury, 2004; Stevens and Ayers, 2001). Besides its use as an ornamental, ravennagrass has been used for erosion control and livestock forage at young stages (Chen and Phillips, 1994), genetic investigations (Besse et al., 1997), as a gene source for plant breeding (Janaki-Ammal, 1941), and as a bioenergy crop (Hattori et al., 2010).

Competition between seedlings of the same species can be extremely intense in cultivated fields. In general, seeds with rapid germination and high seedling vigor are favored over those that germinate slowly and have low seedling vigor (Harlan et al., 1973). Caryopsis weight has been reported to influence the rate of seedling emergence and subsequent growth in native grass species but it has not been shown to affect total germination (Kneebone and Cremer, 1955; Springer, 1991). Similarly, removal of chaff (i.e., lemmas, paleas, hairs, and awns) from caryopses has been shown to improve the rate of germination, but it has not been shown to affect total germination (Ahring et al., 1975; Springer, 1991).

Salinas et al. (1997) studied the effects of germination substrate media (organic substrate, agar, or vermiculite), chemical treatments (maceration in hydrogen peroxide, giberellins, thiourea, or a control treatment in water), and illuminance (germination under conditions of alternating light and darkness or in total darkness)

Published in Crop Sci. 56:682-688 (2016).

doi: 10.2135/cropsci2014.11.0781

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on the germination of ravennagrass caryopses. They found that ravennagrass caryopses had high germination potential with nearly complete germination on a water or agar substrate in 14 d. They also determined that germination of caryopses was stimulated by light. Their results, however, left unanswered questions regarding the distribution of caryopses by weight and number in naturalized populations of ravennagrass, the germination of ravennagrass seed with regard to seed form (i.e., IS versus caryopses) and the early growth of seedlings. Thus the objectives of this experiment were to determine, for two populations: (i) the caryopsis size distribution, (ii) the germination of sized caryopses. (iii) the length of seedling shoots and roots from caryopses of different sizes, (iv) the germination of UC and IS, and (v) the length of seedling shoots and roots from UC and IS. Determining the germination characteristics of ravennagrass will aid in understanding seeding rates and the processing of seeds for agronomic uses.

## **MATERIALS AND METHODS**

Seeds for germination experiments were collected from two populations of ravennagrass. Population 1 was located on an old field site at 36°25′31.0″N latitude by 99°23′24.0″W longitude at 590 m elevation adjacent to a seasonal waterway. Population 2 was located adjacent to a body of water (locally known as Experiment Lake, Woodward, OK) at 36°25'37.0"N latitude by 99°25'18.5" longitude at 600 m elevation. Population 1 was approximately 2.5 km east of Population 2. Population 1 is believed to have originated from a horticultural planting that is located approximately 400 m to its south. Population 2 is believed to have originated from a horticultural planting on the southwest shoreline of Experiment Lake. The senior author first observed and collected a sample of ravennagrass on 25 Aug. 1979 along the southwest shoreline of Experiment Lake (Springer, collection #328, deposited in The Robert Bebb Herbarium at the University of Oklahoma, Norman). Since 1979, the species has spread to surround much of the perimeter of the lake shoreline (Springer, personal observation, 2015).

### **Caryopsis Weight and Size Distribution**

In 2012 and 2013, spikelets were removed by hand from 20 panicles from each population to collect seeds for germination experiments. Spikelets from each panicle were weighed and the caryopses were extracted using a Woodward laboratory air-seed shucker (Ag-Renewal, Inc., Weatherford, OK). The caryopses from each panicle were weighed and counted. Caryopses from the 20 panicles of each population were combined and four samples of UC each containing 50 caryopses were counted and weighed. The remaining caryopses were separated by density into four size classes using a South Dakota seed blower with the tube (3.8 cm inside diameter by 59.1 cm height) set at air-valve openings of 16, 20, 24, and 28 mm (Seedburo, Chicago, IL). The caryopses captured in the tube traps at each of the air-valve openings were designated as size classes 16, 20, 24, and 28. No caryopses remained in the bottom of the tube after the 28 mm blowing. Caryopses within each population and size class were weighed and counted. Mean caryopsis weight was calculated

by dividing the total caryopsis weight (mg) of each class by the number of caryopses in each class. Caryopsis size distribution percentages (based on caryopsis numbers) were calculated by dividing the number of caryopses in each class by the total number of caryopses in the sample. Caryopsis size distribution percentages (based on caryopsis weight) were calculated by dividing the caryopsis weight of each class by the total caryopses weight of the sample. Data were analyzed using a general linear mixed model with year of harvest, population, caryopsis size class, and their interactions as fixed effects and sample as a random effect (SAS Institute, 2010).

## **Germination of Sized Caryopses**

Fifty caryopses each of the 16, 20, 24, and 28 size classes within each population were placed in 7.0 by 7.0 by 2.5 cm plastic germination boxes on two layers of paper towel substrate moistened with 7 mL of distilled water. Each experimental unit was replicated four times. The germination study was conducted in a growth chamber modified to emulate a seed germinator (Springer and Tharel, 1992) set for alternating temperatures of 20°C (dark) and 30°C (light) for 8 and 16 h, respectively. Cumulative actual 'normal' and 'abnormal' germination counts were made at 7 d and 14 d (Colbry et al., 1961). At the end of 14 d, the number of firm (nongerminated, apparently dormant) caryopses was recorded. Total potential germination was determined by adding the actual number of seeds that germinated at 14 d (seedlings) and the remaining number of firm caryopses. Data were converted to percentages before analysis. Seedling shoot and root lengths were used as a measure of seedling vigor. The root and shoots of five random seedlings were measured for each size class after the 7-d germination count. This experiment was repeated twice. Data were analyzed using a general linear mixed ANOVA with population, caryopsis size class, and their interaction as fixed effects and year of harvest, replication, and replication in experiment as random effects (SAS Institute, 2010). Comparisons of means were made using LSD at  $P \le 0.05$  (Steel and Torrie, 1980).

## **Germination of UC and IS**

Intact spikelets were obtained by examining spikelets under a purity workboard and diaphanoscope (Seedburo Equipment Co., Chicago, IL). Four replicates of 50 IS or UC were germinated from each population using the same germination procedures, experimental conditions, and seedling measurements as described in the previous germination test. Data were analyzed with a general linear mixed model ANOVA with population, seed form (IS or UC), and their interaction as fixed effects and year of harvest, replication, and replication in experiment as random effects (SAS Institute, 2010). Comparisons of means were made using LSD at  $P \le 0.05$  (Steel and Torrie, 1980).

## **RESULTS AND DISCUSSION**

Population 1 was 2.5 km east of Population 2 and although the two populations were in close proximity, they are believed to be derived from different ornamental plantings that escaped cultivation. Based on a wind dispersal model developed by Schmidt (1918) that accounts for turbulence, a ravennagrass seed (e.g., intact spikelet containing a caryopsis) released from a height of 4 m and falling at a rate of

**Table 1.** Caryopsis weight and distribution percentages (on the basis of caryopsis number and weight) of Saccharum ravennae by caryopsis size class.

				Distribution of caryopses by							
Size	Caryopsis weight (mean ± SE)			Numb	er (mean ± SE)		Weight (mean ± SE)				
class†	Population 1	Population 2	<i>P</i> >  t ‡	Population 1	Population 2	<i>P</i> >  t ‡	Population 1	Population 2	<i>P</i> >  t ‡		
	mg			%			%				
16	0.21 ± 0.01	0.18 ± 0.01	0.01	57.5 ± 0.04	$35.4 \pm 0.04$	0.01	$40.2 \pm 0.06$	$38.7 \pm 0.06$	0.04		
20	$0.32 \pm 0.01$	$0.32 \pm 0.01$	0.85	$29.7 \pm 0.04$	$40.6 \pm 0.04$	0.11	$37.3 \pm 0.06$	$27.2 \pm 0.06$	0.17		
24	0.41 ± 0.01	$0.42 \pm 0.01$	0.70	$9.6 \pm 0.04$	17.8 ± 0.04	0.21	$16.0 \pm 0.06$	$21.9 \pm 0.06$	0.10		
28	0.47 ± 0.01	$0.51 \pm 0.01$	0.11	$3.2 \pm 0.04$	$6.2 \pm 0.04$	0.63	$6.5 \pm 0.06$	$12.2 \pm 0.06$	0.08		
UC	0.27 ± 0.01	$0.32 \pm 0.01$	0.01	-	_	-	_	-	-		
IS	$0.63 \pm 0.02$	$0.72 \pm 0.03$	0.01	_	_	_	-	_	_		

† Size classes determined by an seed blower with air-valve openings of 16, 20, 24, and 28 mm; UC, unsized caryopses; IS, intact spikelets.

‡ Probability of difference between populations within a size class.

 $0.57 \pm 0.08$  m s<sup>-1</sup> (mean  $\pm$  SD; Springer, unpublished data, 2015) would travel distances of 180 to 730 m when exposed to a horizontal wind velocity of 20 m s<sup>-1</sup> (approximately 45 mile per hour wind speed). The average wind speed at Woodward, OK in October to November, when ravennagrass is shattering seeds, is 4.7 m s<sup>-1</sup> from the south (Oklahoma Mesonet, 2015). The average maximum wind speed gust in October to November is 20.5 m s<sup>-1</sup> from the south. On the basis of this information, it is unlikely that these two populations were derived from the same source materials or that migration has occurred between the two populations. A detailed genetic analysis, however, would need to be performed to verify that each population is distinct.

## **Caryopsis Weight and Size Distribution**

The number of caryopses per inflorescence varied from <10 to >10,000. The average caryopsis weight was 0.27  $\pm$  0.01 mg for Population 1 and 0.32  $\pm$  0.01 mg for Population 2 (Table 1). Caryopsis weight, however, varied between years. Caryopsis weight averaged  $0.28 \pm 0.01$  mg in 2012 and averaged  $0.31 \pm 0.1$  mg in 2013. Caryopsis weight averaged  $0.20 \pm 0.01$  mg for Size Class 16,  $0.32 \pm$ 0.01 mg for Size Class 20,  $0.42 \pm 0.01$  mg for Size Class 24, and  $0.49 \pm 0.01$  mg for Size Class 28 (Table 1). The average spikelet weight (0.68  $\pm$  0.01 mg) was 2.3  $\pm$  0.01 times heavier than the average caryopsis weight (0.30  $\pm$  0.01 mg, Table 1). Harlan and Ahring (1960) reported several conversion factors that represent the relationship between caryopsis weight and spikelet weight for various species from the tribe Andropogoneae. They reported a range in conversion factors from 1.54  $\pm$  0.023 for yellow bluestem [Bothriochloa ischaemum (L.) Keng] to  $2.20 \pm 0.022$  for indiangrass [Sorghastrum nutans (L.) Nash]. The conversion factor for ravennagrass (2.3  $\pm$  0.01) falls slightly outside the range reported for introduced and native grasses.

A year  $\times$  caryopsis size class interaction and a plant population  $\times$  caryopsis size class interaction occurred for the caryopsis size distributions by number and by weight. More than 55% of the caryopses in Population 1 were in Size Class 16 compared to 35% of the caryopses in



Fig. 1. Seed size distribution (percentage by seed number) of *Saccharum ravennae*: the interaction of plant population with caryopsis size class.

Population 2 (Fig. 1). In 2012, nearly 40% of the caryopses were in Size Class 16 compared to >50% in 2013 (Fig. 2). Caryopsis Size Class 16 in Population 1 accounted for >40% of the total caryopsis weight compared with caryopsis Size Class 20 in Population 2 (Fig. 3). In 2013, approximately 80% of the weight was equally distributed between caryopsis Size Classes 16 and 20, whereas, in 2012, approximately 60% of the caryopsis weight was unequally distributed between caryopsis Size Classes 16 and 20 (approximately 25% in Class 16 and 35% in Class 20, Fig. 4). Differences in caryopsis weight and distribution were possibly explained by differences in precipitation patterns during 2012 and 2013. During the April to October growing season in 2012, plants received 200 mm of precipitation. For the same time period in 2013, plants received 410 mm of precipitation. In 2012, the average seed set was 17 and 8% for Populations 1 and 2, respectively. In 2013, the average seed set was 50 and 55% for Populations 1 and 2, respectively. Thus, precipitation is an important factor for seed production, as well as caryopsis weight and distribution. These findings agree with Springer (1989) for big bluestem (Andropogon gerardii



Fig. 2. Seed size distribution (percentage by seed number) of *Saccharum ravennae*: the interaction of year of harvest with caryopsis size class.



Fig. 3. Seed size distribution (percentage by seed weight) of *Saccharum ravennae*: the interaction of plant population with caryopsis size class.



Fig. 4. Seed size distribution (percentage by seed weight) of *Saccharum ravennae*: the interaction of year of harvest with caryopsis size class.

Vitman), where drought reduced the percentage of seed set, but disagree with Springer (1991) for big bluestem where drought increased the percentage of smaller caryopses. The number of caryopses per culm was reduced by approximately 50% in big bluestem during a drought year (208 caryopses during an average precipitation year versus 100 caryopses during a drought year; Springer, 1989). In contrast, the number of caryopses per spike was reduced by approximately 85% in ravennagrass during a drought year (3700 caryopses during an average precipitation year versus 600 during a drought year). Significantly fewer caryopses per spike in ravennagrass could lead to heavier caryopses during a drought year (Fig. 4).

#### **Germination of Sized Caryopses**

The cumulative caryopsis germination percentages at 7 and 14 d varied with population and caryopsis size class  $(P \le 0.05)$ . Population 1 had greater caryopsis germination at the end of the 7-d, 14-d, and total potential germination periods than Population 2 (Table 2). The germination percentage of caryopses in Size Class 16 was lower than other size classes at the end of the 7-d and 14-d germination periods ( $P \le 0.05$ ). This trend was also found for big bluestem, where Size Class 35 had lower seed germination compared with other size classes (Springer, 1991). These data suggest that a threshold caryopsis weight exists, allowing for equal germination among seed size classes. The threshold seed size for big bluestem was  $\ge 1.55$  mg in weight for caryopses (Springer, 1991). The threshold seed size for ravennagrass was  $\ge 0.3$  mg for caryopses.

The percentage of firm seed (nongerminated caryopses at the end of the 14-d germination period) was less than 1% among the caryopses size classes and did not contribute significantly to the total potential germination (Table 2). Although a germination threshold was found to exist, 80% or more of the caryopses in all seed classes germinated in 14 d. This is similar to what Salinas et al. (1997) reported. The total caryopsis germination percentage (sum of 14-d cumulative germination percentage and percentage firm seed) varied among caryopsis size classes ( $P \le 0.05$ ) and followed the same trends as the 7-d and 14-d cumulative germination percentages (Table 2).

The percentage of abnormally germinated caryopses decreased as the caryopsis size class increased ( $P \leq 0.05$ ). Size Class 16 had the largest percentage of abnormally germinated seed (5.8%), Size Classes 20 and 24 had intermediate percentages (3.6–3.5%), and Size Class 28 had the lowest percentage (2.5%, Table 2). This was expected because the Woodward air-seed shucker tends to damage smaller caryopses more than larger caryopses (Springer, personal observation) and cracked or broken caryopses tend to lead to abnormal germination.

**Table 2.** Effects of plant population and caryopsis size class (of sized caryopses) of *Saccharum ravennae* on cumulative 7-d and 14-d germination percentage, percentage of firm seed, total potential germination percentage, abnormal germination percentage, shoot and root lengths of 7-d seedlings, and seed unit weight.

		Cumulative germination		Firm seed	Total	Abnormal	Shoot length	Root length	Seed unit
Variable	Level	7 d	14 d	14 d	germination†	germination	7 d	7 d	weight
				%		<u> </u>	m	m ———	mg
Population	1	91.7 ± 1.5 a‡	93.0 ± 1.4 a	0.16 ± 0.07 a	93.2 ± 1.4 a	3.1 ± 0.6 a	13.8 ± 0.2 a	11.4 ± 0.2 b	028 ± 0.01 b
	2	85.7 ± 1.5 b	88.1 ± 1.4 b	$0.03 \pm 0.07 \text{ a}$	88.1 ± 1.4 b	4.6 ± 0.6 a	13.7 ± 0.2 a	12.1 ± 0.2 a	031 ± 0.01 a
Size class	16	76.8 ± 2.1 b	80.0 ± 2.0 b	0.01 ± 0.10 b	80.0 ± 2.0 b	5.8 ± 0.8 a	10.3 ± 0.3 d	$8.8\pm0.3$ c	0.20 ± 0.01 d
	20	89.4 ± 2.1 a	91.7 ± 2.0 a	0.01 ± 0.10 b	91.7 ± 2.0 a	3.6 ± 0.8 ab	12.7 ± 0.3 c	11.2 ± 0.3 b	$0.32 \pm 0.01 \text{ c}$
	24	93.6 ± 2.1 a	94.7 ± 2.0 a	0.06 ± 0.10 ab	94.8 ± 2.0 a	3.5 ± 0.8 ab	15.2 ± 0.3 b	13.1 ± 0.3 a	0.42 ± 0.01 b
	28	95.0 ± 2.1 a	95.8 ± 2.0 a	0.32 ± 0.10 a	96.1 ± 2.0 a	$2.5 \pm 0.8$ b	16.8 ± 0.3 a	13.8 ± 0.3 a	0.49 ± 0.01 a

† The sum of 14-d cumulative germination percentage and the firm seed percentage.

 $\ddagger$  Means within columns followed by the same letter are not significantly different at  $P \le 0.05$ .

**Table 3.** Effect of plant population and seed form [unsized caryopses (UC) or intact spikelets (IS)] of *Saccharum ravennae* on cumulative 7-d and 14-d germination percentage, percentage of firm seed, total potential germination percentage, abnormal germination percentage, shoot and root lengths of 7-d seedlings, and seed unit weight.

		Cumulative germination		Firm seed	Total	Abnormal	Shoot length	Root length	Seed unit
Variable	Level	7 d	14 d	14 d	germination†	germination	7 d	7 d	weight
				%			m	m ———	mg
Population	1	68.8 ± 3.4 a‡	80.2 ± 3.0 a	11.3 ± 2.2 a	91.5 ± 1.7 a	3.2 ± 0.8 a	11.6 ± 0.4 a	$8.4 \pm 0.3$ b	$0.46 \pm 0.01$ b
	2	59.0 ± 3.4 b	74.2 ± 3.0 b	14.7 ± 2.2 a	88.9 ± 1.7 a	3.0 ± 0.8 a	11.1 ± 0.4 a	9.5 ± 0.3 a	0.54 ± 0.01 a
Seed form	UC	84.2 ± 3.4 a	86.7 ± 3.0 a	0.3 ± 2.2 b	86.9 ± 1.7 b	6.0 ± 0.8 a	12.7 ± 0.4 a	10.2 ± 0.3 a	$0.30 \pm 0.01$ b
	IS	43.6 ± 3.4 b	67.7 ± 3.0 b	25.7 ± 2.2 a	93.4 ± 1.7 a	0.2 ± 0.8 b	10.0 ± 0.4 b	7.8 ± 0.3 b	0.68 ± 0.01 a

† The sum of 14-d cumulative germination percentage and the firm seed percentage.

 $\ddagger$  Means within columns followed by the same letter are not significantly different at  $P \le 0.05$ .

# Seedlings Shoot and Root Lengths From Sized Caryopses

#### **Germination of UC and IS**

Shoot lengths of seedlings that germinated in 7 d varied with caryopsis size class ( $P \leq 0.05$ ). As caryopsis size increased, there was a corresponding increase in seedling shoot length (Table 2). Root length of seedlings that had germinated in 7 d varied with plant population and caryopsis size class ( $P \leq 0.05$ ). The seedling root lengths of Population 1 were shorter (11.4 mm) than those of Population 2 (12.1 mm, Table 2). Like seedling shoot length, there were also incremental increases in seedling root lengths up to Size Class 24, where seedling root length appeared to peak (Table 2).

It was not surprising to find that heavier caryopses produced seedlings with longer roots and shoots, since heavier caryopses would be expected to have larger embryos and carbohydrate reserves. These observations are similar to those reported for buffalograss [Buchloë dactyloides (Nutt.) Engel.], indiangrass, sand bluestem (Andropogon hallii Hack.), sideoats grama [Bouteloua curtipendula (Michx.) Torr.], and switchgrass (Panicum virgatum L.) by Kneebone and Cremer (1955) and for big bluestem by Springer (1991). Therefore, seedling establishment would be expected to be greater for larger caryopses than for smaller caryopses because of greater seedling vigor (Harlan et al., 1973). The 7-d and 14-d cumulative germination percentages of UC and IS varied with population and seed form  $(P \le 0.05)$ . Seeds from plant Population 1 had a greater germination rate compared to Population 2 at the end of the 7-d and 14-d germination periods (Table 3). Likewise, UC had a greater germination rate compared to IS at the end of the 7-d and 14-d germination periods (Table 3). The percentage of firm seed, total potential germination percentage, and percentage of abnormally germinated seed varied with seed form (P < 0.05) but not with plant population (Table 3). The percentage of firm seed for IS was 25% greater than that of UC and the total potential germination of IS was approximately 6% greater than that of UC (Table 3). In contrast, the percentage of abnormally germinated seeds was greater for UC than for IS (Table 3).

Similar to those of other species of the tribe Andropogoneae, the UC of ravennagrass germinate more rapidly than IS (Ahring, 1963; Springer, 1991, 2005; Springer et al., 2001). The slow germination rate of IS can be attributed to chemical compounds in glumes, lemmas, and paleas and from waxy compounds that act as moisture barriers to seed germination (Ahring et al., 1975). Thus, given enough time, the dormant nongerminated (firm seeds) caryopses within spikelets of ravennagrass should germinate when the chemical(s) and/or barrier(s) that prevents the viable caryopses within IS to germinate within the 14-d breakdown (Springer, unpublished data, 2015).

If not for the high percentage of abnormally germinated seed in UC, the total potential germination of IS and UC would have been similar. As previously discussed, caryopsis extraction methods tend to damage smaller caryopses more than larger caryopses. Because the caryopses of IS are not disturbed, the percentage of abnormally germinated seeds was low.

## Seedlings Shoot and Root Lengths From UC and IS

Shoot lengths of seedlings that had germinated in 7 d varied with seed form ( $P \le 0.05$ ) but not with plant population. The average shoot length of UC was 2.7 mm longer than those from IS (Table 3). The root lengths of seedlings that had germinated in 7 d varied with plant population and seed form ( $P \le 0.05$ ). Seedlings from plant Population 2 had longer root lengths ( $9.5 \pm 0.3$  mm) than Population 1 ( $8.4 \pm 0.3$  mm, Table 3). Likewise, root lengths of seedlings that had germinated in 7 d were greater for UC ( $10.2 \pm 0.3$  mm) than those of IS ( $7.8 \pm 0.3$  mm, Table 3). Because the germination of IS is slower than that of UC, the shoots and roots at the end of the 7-d germination period was longer for UC than for IS. These findings were comparable to those reported for big bluestem (Springer, 1991).

## CONCLUSIONS

Ravennagrass is a robust perennial bunchgrass that is palatable to livestock only in its young stages of growth. In the US, it is grown as an ornamental but, where adapted, has become naturalized in riparian areas. Although seed production of ravennagrass is relatively low, under favorable conditions, it can produce more than 10,000 caryopses per panicle. The amount of precipitation received each year influences the number and weight percentage distributions of caryopses. In drier years, fewer but heavier caryopses are produced; in wetter years, more but lighter caryopses are produced. More than 80% of caryopses germinated in 14 d. Caryopses germinated >90% if the caryopsis mass was  $\geq 0.3$  mg. Caryopses within IS were slower to germinate in 14 d than bare caryopses and had a lower percentage of abnormally germinated seed compared with UC. Intact spikelets also had a significantly higher percentage of firm seeds compared with caryopses and the total potential germination of IS was greater than that of caryopses. This species has escaped cultivation in the eastern and southern US, becoming established in riparian areas. Rapid seed germination and the fact that it is relatively unpalatable to livestock and wildlife may help to explain its success in escaping cultivation. Nongerminated (firm seeds) dormant caryopses of IS may accumulate in the environment, producing a seed bank but research to test the amount and longevity of seed in the environment would need to be conducted.

Ravennagrass has the potential to be grown as a bioenergy crop. Under irrigation, mature plants will average  $5.2 \pm 0.7$  kg (mean  $\pm$  SD) of biomass above a 0.3 m height (Springer, unpublished data, 2013). At 5000 plants ha<sup>-1</sup>, ravennagrass has the potential to produce  $25.9 \pm 3.4$  Mg of biomass per hectare a year. To develop ravennagrass into a viable energy crop, research is needed to determine the optimum seeding rates and plant densities to sustain long-term biomass production.

#### **Acknowledgments**

Thanks are given to W. Cooper and E. Friend for their dedicated assistance throughout this investigation. Mention of a trademark or a proprietary product does not constitute a guarantee or warranty of the product by USDA and does not imply approval to the exclusion of other suitable products. All programs and services of the USDA are offered on a nondiscriminatory basis without regard to race, color, national origin, religion, sex, age, marital status, or handicap.

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