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Factors affecting germination and seed production of *Eriochloa villosa*

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Laboratory and field experiments were conducted to determine the effects of light, temperature, oxygen, and seed burial depth on seed germination and seed production of *Eriochloa villosa* without the interference of a crop. *Eriochloa villosa* seed germination did not respond to light, although it is possible that experimental conditions were not appropriate for this response to develop. Seeds germinated above 10 C and below 45 C, with germination above 85% occurring for temperatures between 20 and 40 C. Seed germination rate and total germination increased as the oxygen concentration increased to the ambient level. *Eriochloa villosa* seed emerged from 15 cm deep, with maximum emergence from 1 to 4 cm. In the field, emergence was dependent on tillage that affected the vertical distribution of seeds in the soil. Seeds emerged in the reduced-tillage field from between 0.5 and 9 cm deep in soil, with maximum emergence from 2 cm. A delay in planting greatly reduced the growth and seed production of *E. villosa*. Seed production under noncompetitive conditions was reduced by at least 75% when planting was delayed 6 to 8 wk. However, plants that emerged after July 7 still produced approximately 3,000 seeds when grown under conditions without intraspecific and interspecific competition.

Nomenclature: Woolly cupgrass; *Eriochloa villosa* [Thunb.] Kunth.

Key words: Light, oxygen, seed burial, seed germination, temperature.

Eriochloa villosa is native to East Asia and was first discovered near Portland, OR during the 1940s (Hitchcock 1950). In 1980, Strand and Miller (1980) reported that *E. villosa* had spread as far east as Wisconsin and was economically important in several states. Recent reports indicate that this weed has become so problematic in the Midwest that states are developing specific *E. villosa* management systems (Breitenbach and Hoverstad 1996; Fawcett and Kassel 1996; Mickelson and Harvey 1996; Rabaey and Harvey 1997).

Biological information on the germination, emergence, growth, and seed production of other troublesome grasses such as *Echinochloa crus-galli* (L.) Beauv., *Setaria* spp., and *Sorghum bicolor* (L.) Moench have been reported over the past 50 yr (Burnside 1965; Chepil 1946; Dawson and Bruns 1962; Maun and Barrett 1986). However, biological research on *E. villosa* is limited. Research on *E. villosa* has primarily dealt with response to herbicides (Owen et al. 1993; Rabaey et al. 1996; Rabaey and Harvey 1997; Schuh and Harvey 1989). Information on germination, emergence, growth, and seed production of *E. villosa* could be used to help model seed bank dynamics, thus helping the successful forecasting of germination trends and rational weed control in the agroecosystem (Alm et al. 1993; Forcella 1993).

The interaction of environmental conditions and the physiological state regulates seed germination in the soil (Moore et al. 1994; Taylorson 1970). An adaptation to maximize survival of an annual weed species is seed germination despite variable environmental conditions that may not reflect optimum conditions (Baskin and Baskin 1989). Low winter temperatures are known to stimulate the loss of primary dormancy for most summer annuals, including *E. villosa* (Bello et al. 1998; Totterdell and Roberts 1979). However, weed seeds exposed to low winter temperatures will not germinate unless ecophysiological factors including

light, temperature, moisture, and oxygen are adequate for germination (Egley and Duke 1985). *Eriochloa villosa* seed hulls prevented germination by impeding oxygen diffusion to the embryo (Hatterman-Valenti et al. 1996). Alternating temperatures hastened *E. villosa* seed germination but were not necessary to break dormancy after a short period of stratification (Bello et al. 1998). The objectives of this study were to examine environmental factors that affect *E. villosa* germination and emergence and to determine the seed production of this grass.

Materials and Methods

General Procedures

Eriochloa villosa seeds were harvested at physiological maturity from an indigenous population at Stratford, IA during February 1987 and 1988. Seeds were separated from soil excavated from within 5 cm of the surface. Seeds were dried at 30 C for 72 h, cleaned with an air column separator,[1] and stored dry at 5 C until used. Seeds were used within 8 mo after collection.

All seeds were disinfected with 1% sodium hypochlorite for 5 min, rinsed repeatedly with deionized water, and air-dried. Seed lot viability was nearly 100% as determined by a tetrazolium (TZ) test in which three groups of 50 seeds were presoaked in deionized water for 5 h at 25 C, bisected longitudinally, and stained in a 0.1% TZ solution at 35 C for 12 h.

Light Effects

Intact nondormant *E. villosa* seeds were imbibed between two moistened blue blotter papers[2] in 6-cm petri dishes for

24 h in the dark before exposing groups of 25 seeds to no light, red light (600 to 660 nm), or far-red light (700 to 760 nm) for 10, 15, and 20 min. Experiments were established in the dark. A spectroradiometer[3] was used to measure irradiance from the tungsten lamps. Seeds were returned to the dark at 25 C after the light treatment, and germination was evaluated 6 d after treatment (DAT). Seeds were considered germinated if the radicle had protruded from the seed.

Temperature Effects

A two-way thermogradient plate with 25 thermocouples was used to determine the effect of temperature on germination. The thermogradient plate had thermocouples spaced 32 cm apart, resulting in regions with constant temperatures ranging from a minimum temperature of 5 C to a maximum temperature of 50 C. Twenty-five intact nondormant seeds were placed between two moistened blue blotter papers[2] within the regions of constant temperature. Seeds were observed daily for 6 d and considered germinated when the radicle had protruded from the seed. Temperatures above 25 C caused localized drying, and consequently seeds were moistened every 10 h throughout the experimental period.

Oxygen Effects

Three groups of 25 intact nondormant seeds were placed in a 125-ml serum bottle[4] with 36 g of sterilized fine sand[5] moistened with 8 ml of deionized water. Each serum bottle was sealed with a rubber stopper and crimped with a tear-off aluminum seal[4] before it was flushed and filled with an oxygen, nitrogen, and carbon dioxide gas mixture. Carbon dioxide was added at 2% (v/v). The oxygen level of the inlet gas mixture was measured with an oxygen electrode[6] and adjusted so that seeds were subjected to 0, 2, 4, 8, 16, 21, 35, and 45% oxygen. Nitrogen was added at 98 to 43% (v/v) depending on the oxygen level in the gas mixture. Seeds were observed daily for 6 d and considered germinated when the radicle had protruded.

Soil Depth Effects

The effect of seed depth on germination and seedling emergence was investigated under controlled and field conditions. In the growth chamber, groups of 50 intact nondormant seeds were planted in a pasteurized 2:1 (v/v) soil: sand mixture at depths of 0, 1, 2, 4, 6, 8, 10, 15, or 20 cm. Treatments were placed in growth chambers maintained at a 30:20 C temperature regime with a 16:8 h thermoperiod. Seedling emergence was evaluated every 2 d for 10 d.

In the field during 1987 and 1988, seedling emergence was evaluated from an indigenous E. villosa population in a minimum-tillage field (one pass with a chisel plow followed by one pass with a finishing disk) that was Zea mays L. the previous year. The tillage regime results in a uniform distribution of weed seeds throughout the depth of tillage (Pareja et al. 1985). The soil type was a Browton silty clay loam (Mesic Typic Haplaquolls) with a pH of 8 and 5.2% organic matter. Five 3 by 7.5–m quadrants were arbitrarily selected within the infested area before weed emergence. From each quadrant, 50 seedlings (4- to 6-leaf) were arbitrarily selected and excavated to determine the length of the mesocotyl from the seed to ground level. Plots were sampled in May and June. All seedlings were removed after the initial sampling. Emergence depth data were segregated into 10 groups for each sampling date. Sampling depths were the same as in the growth chamber experiment.

Seed Production

Field experiments were conducted during 1987 and 1988 near Stratford, IA on a field with an indigenous infestation of E. villosa. The soil was a Browton silty clay loam (Mesic Typic Haplaquolls) with a pH of 8 and 5.2% organic matter. Nondormant seeds were planted approximately 2 cm deep biweekly for 10 wk starting May 12. In 1988, seeds that were planted at the last planting date did not germinate because of drought conditions. Plots were thinned to 5 seedlings when plants reached the 6- to 8-leaf stage and were maintained in a weed-free, noncompetitive environment throughout the experiment. Preliminary studies showed that a maximum of 5 plants per 2 m² could be grown without overlapping aerial parts and thus were considered noncompetitive. Environmental data were recorded hourly from a nearby weather station until the time of harvest in September.

Statistical Analysis

All studies were arranged as randomized complete blocks, replicated three times, and repeated, except for the field depth of emergence study, which was arranged in a completely randomized design, replicated five times, and repeated. Data were pooled over the two experiments when there was no time interaction. Percentage values were arcsine transformed and subjected to analysis of variance with Fisher's Protected LSD test ($P < 0.05$) for mean separation. Transformations did not affect the interpretation of the data; thus nontransformed means are presented.

Results and Discussion

Light Effects

Seed germination was greater than 95% regardless of the light treatment (data not shown), suggesting that E. villosa seeds are not photoblastic or responsive to light. However, it is possible that the seeds may not have developed photoblastic characteristics because they received a dormancy-breaking cold temperature but were never buried in the soil. Taylorson (1972) showed that several weed species, including E. crus-gali, a nondormant population that initially germinated in the dark, became dependent on light for germination after burial.

Seed germination under all light conditions may have also resulted from the germinating temperature. Gallagher and Cardina (1998) showed that with Amaranthus retroflexus L., there was no evidence that red light promoted germination at 30 C, whereas 3,000 µmol m^{-2} s^{-1} of red light was necessary for maximum germination at 20 C. They suggested that this might be an adaptation that enabled seeds, in the absence of light, to sense warm temperatures at shallow soil depths, where the probability of seedling survival was greater.

TABLE 1. Effect of temperature and time on the germination of nondormant *Eriochloa villosa* seeds.[a]

Temperature (C)	Germination period (d)		
	2	4	6
		%	
10	0 e	0 d	0 c
15	33 d	33 c	100 a
20	84 b	97 a	99 a
25	95 a	100 a	100 a
30	100 a	100 a	100 a
35	97 a	100 a	100 a
40	64 c	84 b	85 b
45	0 e	0 d	0 c

[a] Data are the means of six replications of 25 seeds per treatment. Means within a column followed by the same letters are not significantly different (P < 0.05).

TABLE 2. Effect of oxygen level and time on the germination of nondormant *Eriochloa villosa* seeds.[a]

Oxygen concentration (%)	Germination period (d)		
	2	4	6
		%	
0	0 f	0 d	0 d
2	20 e	36 c	51 c
4	36 d	47 b	87 b
8	76 c	98 a	100 a
16	93 b	100 a	100 a
21	100 a	100 a	100 a
30	100 a	100 a	100 a
45	100 a	100 a	100 a

[a] Data are the means of six replications of 25 seeds per treatment. Means within a column followed by the same letters are not significantly different (P < 0.05).

Temperature Effects

Temperature affected total germination and the rate of seed germination (Table 1). *Eriochloa villosa* seeds required a temperature above 10 C but below 45 C for germination. Optimum germination occurred over a broad range of temperatures between 20 and 35 C. Seed germination rate increased with increasing temperatures, reaching 100% 2 DAT for the 30 C temperature. As temperature increased above 35 C, the germination rate declined.

Setaria faberi (L.) Herrm. is considered one of the most common competitive grasses in *Z. mays* and *Glycine max* (L.) Merr. production systems in the Midwest (Knake 1990). However, *S. faberi* emerges when soil temperatures reach 10 to 17 C and ceases at 30 C or more (Knake 1990), whereas *E. villosa* will continue to germinate at 40 C. This extended germination period may make *E. villosa* more difficult to control than *S. faberi* and may explain the reported season-long emergence (Deneke 1998; Mickelson and Harvey 1999).

Hartzler et al. (1999) reported that *E. villosa* consistently emerged before *S. faberi* in the field. However, results from this study indicated that the lowest germination temperature was similar to that reported for *S. faberi* (Knake 1990). The discrepancy between these reports may have occurred because the temperatures used in our research were constant. Previous research has shown that fluctuating temperatures hasten *E. villosa* germination and can overcome the detrimental effects of low oxygen concentration in comparison to a constant temperature (Bello et al. 1998).

Oxygen Effects

The oxygen concentration affected *E. villosa* germination rate and total germination (Table 2). Germination was inhibited in the anoxic atmosphere but increased with higher
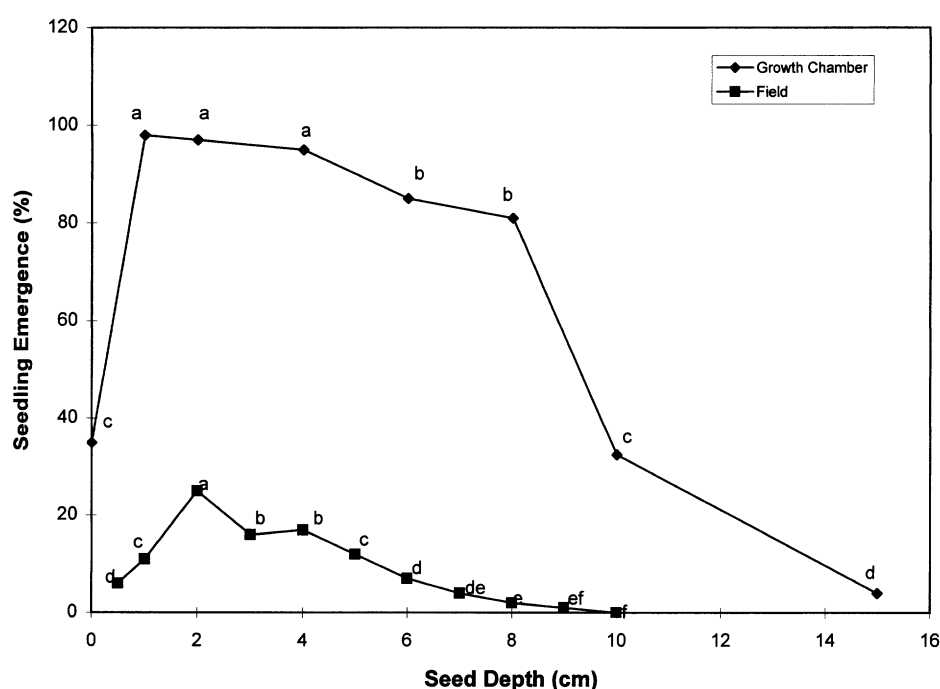

FIGURE 1. Effect of depth on *Eriochloa villosa* seedling emergence. Points represent the emergence percentage of 50 seeds per depth planted in the growth chamber. Field data represent the percentage of seedlings total emerging from each depth. A total of 250 *E. villosa* seedlings each from two sample periods were evaluated. Means within a curve followed by the same letter are not significantly different (P < 0.05).

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TABLE 3. Effect of planting date on *Eriochloa villosa* yield.[a]

Planting date	Dry weight (g)	Tillers per plant	Panicles per plant	Racemes per panicle	Seeds per raceme	Seeds per plant
1987						
May 12	381 a	56 a	800 a	6.4 a	26 a	123,500 a
May 26	369 a	59 a	900 a	6.2 a	34 a	164,170 a
June 9	245 a	32 b	350 b	5.3 b	34 a	57,860 b
June 23	76 b	18 c	125 b	5.1 b	15 b	8,910 bc
July 7	30 b	12 c	55 b	4.2 c	12 b	2,650 c
1988						
May 12	117 a	31 a	200 a	6.4 a	25 a	28,200 a
May 26	112 a	21 b	170 b	5.3 b	16 b	13,060 b
June 9	58 b	12 c	120 c	5.1 b	15 b	9,000 c
June 23	36 c	4 d	80 d	4.1 c	14 b	5,360 d
July 7	—	—	—	—	—	—

[a] Data are the means of three replications of three plants per treatment. Means within a column and year followed by the same letters are not significantly different ($P < 0.05$).

oxygen concentrations, reaching a maximum at normal atmospheric oxygen concentration. Seed germination rate also increased as the oxygen concentration increased to the ambient level. Seeds exposed to 16% oxygen germinated sooner and with greater than 90% germination 2 DAT when compared with concentrations less than 16%. By 4 and 6 DAT, seeds subjected to 8% oxygen also germinated above 90%.

The lack of seed germination in an anoxic condition was expected because only a few species are capable of germination in the absence of oxygen (Kennedy et al. 1992). Likewise, the positive effect of increased oxygen on total germination was expected because *E. villosa* germination was reduced by limiting oxygen to the embryo (Hatterman-Valenti et al. 1996).

Soil Depth Effects

Planting depth significantly affected seedling emergence (Figure 1). In the growth chamber, no single depth clearly favored emergence. Greater than 90% *E. villosa* seedling emergence was observed from 1, 2, and 4 cm deep. Seedling emergence decreased as planting depth increased beyond 4 cm, but at 6 and 8 cm, seedling emergence was still 82 and 85%, respectively. Placing seeds on the soil surface reduced seedling emergence to 35%, which was similar to emergence from 10 cm. *Eriochloa villosa* seeds were able to emerge from 15 cm (4%), whereas none emerged from 20 cm deep.

Eriochloa villosa seeds are large in comparison to *S. faberi* even though vegetative growth is similar (Deneke 1998). Therefore, emergence from depths beyond the maximum for *S. faberi* (7.5 cm) reported by Fausey and Renner (1997) was expected. *Sorghum halepense* (L.) Pers. has seeds that are

similar in size to *E. villosa*. McWhorter (1972) reported that *S. halepense* emerged from 15 cm deep in a sandy loam soil, whereas none emerged from this depth in a clay soil. Therefore, *E. villosa* seedling emergence characteristics are more similar to *S. halepense*, even though vegetative growth is similar to *S. faberi*.

The depth in the field with the highest percentage of *E. villosa* seedlings was 2 cm with 25% (Figure 1). Seedling emergence was significantly less from depths above and below 2 cm, and no seedlings emerged from deeper than 9 cm.

Data from the controlled and field experiments are not contradictory. Results from the field experiment show the pattern of *E. villosa* emergence in a reduced-tillage system. Pareja et al. (1985) found 85% of all weed seeds in the top 5 cm of soil in a reduced-tillage system compared with 28% in the conventional system. Buhler and Mester (1991) reported that the mean depth of emergence for *S. faberi* and *Setaria viridis* (L.) Beauv. in a loamy sand was 1.3, 2.3, and 3.1 cm for no-till, chisel plow, and conventional tillage systems, respectively. Likewise, Yenish et al. (1992) reported that under a reduced-tillage system, most weed seeds were distributed in the upper 3 cm of soil. Thus, although *E. villosa* has the potential to emerge from a soil depth of 15 cm, field emergence may be more dependent on the effect tillage has on the vertical distribution of seed in the soil. Furthermore, conditions that were optimum for germination and emergence were likely consistent at all depths in the growth chamber, whereas in the field, these conditions were encountered over a relatively narrow range of soil depths.

Seed Production

Eriochloa villosa growth and seed production in the absence of crop interference varied between years (Table 3). This variation was partly caused by differences in rainfall distribution during the growing season (Table 4). Total rainfall from May through August 1987 was 54% more than during 1988 (62 cm and 28 cm, respectively).

The planting date significantly affected all growth characteristics (Table 3). In 1987, *E. villosa* seeds planted during May produced the most tillers, panicles, and racemes, whereas plants from the last two planting dates (June 23

TABLE 4. Monthly rainfall, temperature, and long-term averages.

Month	Rainfall 1987	Rainfall 1988	Rainfall 48-yr	Temperature 1987	Temperature 1988	Temperature 48-yr
	mm			C		
May	57	35	99	19	20	16
June	84	32	121	23	24	21
July	195	25	112	24	24	23
August	162	75	109	21	24	22
September	46	105	77	18	19	18

and July 7) produced the fewest tillers, panicles, and racemes. Similarly, plant dry matter accumulation and the number of seeds per raceme were greatest from seeds planted on or before June 9. *Eriochloa villosa* dry matter accumulation was reduced 92% by an 8-wk delay in planting. Total seed production was the greatest for planting on or before June 9. The greatest number of seeds produced by a plant (164,170) occurred when seeds were planted on May 26, whereas less than 3,000 seeds were produced when planting was delayed until July 7. This difference was mainly attributed to the 80% decrease in tiller production when planting was delayed.

In 1988, each successive planting date resulted in less plant tiller, panicle, and total seed production (Table 3). Delaying the planting date also reduced racemes and the number of seeds per raceme. Seeds planted on May 12 produced more racemes and more seeds per raceme than any other planting date. Dry matter accumulation, however, did not differ during May but did decrease with successive planting dates thereafter.

A delay in planting greatly reduced the growth and seed production capabilities of *Abutilon theophrasti* Medicus and *S. faberi* (Oliver 1979; Schreiber 1965). Oliver (1979) suggested that reductions in *A. theophrasti* growth and seed production were caused by the changing photoperiod. *Eriochloa villosa* seed production under noncompetitive conditions was reduced at least 75% when planting was delayed 6 to 8 wk. However, plants that emerged after July 7 still produced approximately 3,000 seeds.

The total seeds per plant values represent the seed production under noncompetitive conditions and would likely be reduced with competitive crops. Pecinovsky (1994) showed that *Z. mays* competition reduced *E. villosa* dry matter accumulation and seed production 6-fold and 11-fold, respectively, at an *E. villosa* density of five plants per square meter. Furthermore, Mickeleson and Harvey (1999) reported that delaying *E. villosa* emergence until the V2, V5, or V10 *Z. mays* stage further reduced seed production.

The results of this study indicated that *E. villosa* seeds germinate over a wide temperature range (above 10 C and below 45 C) with an optimum temperature between 20 and 35 C. *Eriochloa villosa* seed germination did not respond to light but required oxygen. *Eriochloa villosa* seeds can emerge from a 15-cm soil depth in an artificial soil mixture in a growth chamber, but most emergence occurred from 1 to 4 cm in the field, depending on tillage's effect on the vertical distribution of seeds. *Eriochloa villosa* seed production was variable depending on date of emergence and environmental conditions, even under noncompetitive conditions. Delaying the emergence of *E. villosa* 6 to 8 wk greatly reduced growth and seed production. However, plants that emerged after July 7 still produced approximately 3,000 seeds.

Sources of Materials

Acknowledgment

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