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Review

Breaking seed dormancy of switchgrass (*Panicum virgatum* L.): A review

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ABSTRACT

Switchgrass (*Panicum virgatum* L.) is a perennial warm-season grass identified as a model species for bioenergy feedstock production. Established switchgrass stands are very resilient to the environmental fluctuations; however, seed dormancy and weak seedling vigor make establishment difficult. Breaking seed dormancy of switchgrass is a first step to reduce risk of establishment failure and the costs associated with reseeding. Many studies have reported a myriad of methods to break seed dormancy of switchgrass, including chemical, mechanical, thermal, and hormonal seed treatments. Length of seed storage, storage conditions (e.g., temperature and humidity), and prior soil conditions (e.g., soil salinity and fertilizer rates) affect switchgrass seed dormancy. Strong interactions exist among germination, seedling emergence, and soil conditions; therefore, treated seeds tested in soil media will generate more accurate results following dormancy breaking techniques. This paper reviews the current methods used to break switchgrass seed dormancy.

1. Introduction

Switchgrass (*Panicum virgatum* L.) is a perennial warm-season grass identified as a model species for bioenergy feedstock. The Oak Ridge National Laboratory administered the Biofuels Feedstock Development Program (BFDP), and that selected switchgrass through herbaceous crop screening trials conducted from 1985 to 1992 [1]. Switchgrass is an erect, long lived, and native perennial grass that originates east of the Rocky Mountains and south of 55° N latitude in North America [2]. Switchgrass exists as two ploidy levels (tetraploid and

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octaploid), and two distinct cytotypes (lowland and upland) with ecotypes of northern or southern origin [3]. The cytotypes are determined based on the chloroplast DNA polymorphism [4]. Lowland cultivars perform better under flooded conditions, while upland cultivars grow better under moderate soil moisture [5]. The two cytotypes differ not only in habitat and size of clones, but also differ in morphology of vegetative organs [5]. Lowland cultivars have larger, wider, and coarse stems, leaves, ligules, and panicles compared to upland cultivars [6]. The lowlands cultivars produce 10 Mg ha^{-1} y^{-1} on average higher biomass due to the thick tillers compared to upland cultivars [7–13]. The number of tillers per plant is lower in lowland cultivars with 30–75 [14] while upland cultivars have 80–120 tillers [15,16]) although the tillers of upland cultivars are thinner [5]. Major lowland and upland cultivars were summarized by Seepaul et al. [17] in terms of ploidy level, cytotype, latitude, origin, and plant hardiness zone (Table 1). A diffuse panicle produces 200–1000 kg ha^{-1} of seeds depending upon lodging level [18,19]. Established switchgrass stands are very resilient to environmental fluctuation; however, seed dormancy and weak seedling vigor make establishment difficult [2,20].

Seed dormancy is defined as intact viable seeds that failed to germinate under favorable condition for germination [2]. It is an ecological adaptation of the plant species to survive under adverse environmental conditions. There are two seed dormancy mechanisms; embryo imposed and seed coat imposed dormancy [21]. The embryo imposed dormancy can be further categorized into two types; morphological and physiological. Morphological dormancy is caused when the embryo is immature or undeveloped, while physiological dormancy is caused by some germination inhibitors which may be contained in embryo [21]. Examples of the inhibitor include abscisic acid, coumarin, catechins, tannins, and phenols [22]. Seed coat imposed dormancy prevents germination through the presence of chemical inhibitor, low permeability of the seed coat, and/or disturbed gas/water exchange to inhibit embryo respiration [21]. Under natural field conditions, dormant seeds are exposed to temperature alternations, humidity, soil moisture, and light regimes, through which seed dormancy may be reduced [23–25]. Switchgrass produces high concentration of dormant seeds due to its short history as cultivated plant species. Seed labels for native grasses often include viable dormant seeds in a total germination percentage. Despite the high total germination percentage on the label, seedling emergence in the field is often low. A recent study using an electron scanning microscope revealed that seed coat dormancy may be the major cause of switchgrass seed dormancy [26] although reports of embryo dormancy exist [27]. According to the study, the pericarp was the primary barrier to oxygen and water exchange followed by the lemma and palea as secondary barriers. There was no evidence of a germination inhibitor in these structures, and that the endosperm did not affect dormancy of switchgrass seeds [26].

Seeds with high levels of dormancy provide a low germination fraction, resulting in sporadic seedling emergence in the field. Reseeding cost was estimated to be 36% of the total establishment cost in switchgrass production, which is not offset by simply increasing yield [28]. Various treatments have been examined to break dormancy of switchgrass seeds

Table 1 – Summary of major cultivars of switchgrass.

Genotype	Ploidy level[a]	Cytotype	Latitude	Origin	PHZ[b]	Remarks	References	Seed g^{-1}
Alamo	T	Lowland		Southern TX	6	Selected for biomass		1059
Kanlow	T	Lowland	35°14′15.32″ N	Wetumka, OK	5			1064
Tusca		Lowland		Mississippi		Selected for herbicide tolerance from Alamo		
Expresso		Lowland		Mississippi		Selected for improved germination		
Cave in Rock	H	Lowland/upland	37°28′09.18″ N	Cave in Rock, IL	4b		[87]	573
Shelter	H	Lowland/upland	39°23′46.36″ N	St. Mary's, WV	4		[88]	
Blackwell	H	Upland	36°48′16.12″ N	Blackwell, OK	5a		[87]	619
Carthage	O	Upland		Southern IL				
Dacotah	T	Upland		North Dakota	4a	Early maturity, winter hardy, high stand density, persistent	[89]	
Forestburg	T	Upland	44°01′19.94″ N	Forestburg, SD	3b-4b	Early maturity, excellent winter hardiness and persistence, good seed potential	[90]	643
Shawnee	O	Upland	37°28′09.18″ N	Cave in Rock, IL		High forage yield and quality from Cave in Rock	[91]	654
Summer	T	Upland		Southern NE	4			
Sunburst	H	Upland	42°51′43.69″ N	Union County, SD		Winter hardy, leafy, heave-seeded, superior seedling vigor	[88,92]	623
Trailblazer	H	Upland		Nebraska		High forage quality, high IVDMD	[93]	588

Notes: Seed g^{-1} of different cultivars were averaged over four replicates obtained in the Forage Laboratory at Washington State University, Prosser.
[a] T, H, and O indicate tetraploid, hexaploid, and octaploid, respectively.
[b] PHZ: Plant hardiness zone.
Note: Modified from Seepaul et al. [17].

because reduction of dormancy is the first critical step for successful stand establishment. Currently, the Association of Official Seed Analysts (AOSA) recommends a moist pre-chill treatment at 5 °C for 14 days for switchgrass seeds [29]. Pre-chill may mimic the wintering of the seeds and stimulate mobilization of seed carbohydrate reserves [30] and lipid [31] by moist and cold stratification [32]. Although the moist pre-chill treatment breaks seed dormancy of switchgrass seeds, the effect is limited under a condition where seeds remain wet [33]. If the seeds are desiccated completely for mechanical planting, the pre-chilled seeds revert to dormancy [33]. Based on the observation, Shen et al. [33] explained that dormancy and germination are a continuous process, rather than on or off process [33]. To prevent the reversion, the primary dormancy must be completely removed from the seeds by extending pre-chill periods to 42 days [33]. Newly harvested seeds expressed more dormancy reversion than aged seeds [33–35]. Moist pre-chill treatments are useful for inducing small-scale seed germination improvement; however, treatment time is long (e.g., weeks), and the application is limited due to the dormancy reversion [33].

2. Chemical treatments

Treatment time can be shortened with chemical scarification, which takes minutes to hours instead of weeks as required for the pre-chill method. A 15-min treatment with 1.5 mol L^{-1} chloroethanol solution increased germination of the lowland cultivar Alamo from 50% in the untreated control to 87% [36]. Despite the positive results, it was not recommended due to the toxicity. Chemical scarification damages the margins of the lemma, allowing entry of water and gas into the seeds [37]. The acid concentration and duration of application are important criteria controlling efficacy [37]. Sulfuric acid at 16.8 mol L^{-1} increased germination of freshly harvested cv. Alamo (94%), cv. Kanlow (68%), and cv. Caddo (68%) switchgrass seeds compared to untreated seeds of these cultivars (52%, 16%, and 48%, respectively) with 10 min of treatment time [36]. In contrast, diluted sulfuric acid (8 mol L^{-1}) increased germination by 14% with 5 min treatment from 46% in the un-treated control [37]. The efficacy of chemical seed treatment depends upon many factors including cultivar, harvest method, seed production environment, and harvest year [36,38]. For example, Sarath and Mitchell [39] observed that several seed lots harvested in the same field had different responses to reactive nitrogen species and peroxide.

3. Physical treatments

Mechanical scarification breaks seed coat dormancy by cracking the pericarp and increasing gas and water entry to the seeds [40]. Emery cloth [41] and sand paper [42] increased germination of switchgrass seeds (unknown cultivar) by 85%; however, rubbing seeds by hand is inefficient in a large-scale operation. The "Forsberg Cylinder," an emery-cloth-based scarifying device invented by Forsbergs, Inc. (Thief River Falls, Minnesota, USA) improved germination of cv. Sunburst and cv. North Dakota switchgrass seeds from 73% to 30% in controls to 82% and 55%, respectively [43]. Large-scale seed treatment may be possible with this type of scarifier. While, further research is needed to establish the effectiveness and economic applicability of mechanical scarification.

Germination of switchgrass is sensitive to temperatures, and the sensitivity differs among cultivars. In the field switchgrass seeds germinate when soil temperatures are between 10.0 °C [44] and 15.5 °C [45], with seedling growth is enhanced at 26.6 °C [17,46] with a 16/8 h day/night photoperiod [47]. Optimum temperature for germination is cultivar-specific. Switchgrass cultivar, cv. Summer, tolerates higher temperature for germination (28.6 °C), while others (cv. Cave in Rock, cv. Dacotah, cv. Expresso, cv. Forestburg, cv. Kanlow, cv. Sunburst, cv. Trailblazer, and cv. Tusca) prefers 24.0–28.2 °C for germination [17]. These cultivars do not germinate at temperatures above 45 °C [17]. Germination of switchgrass has been recorded as low as 8 °C [17]. While extreme soil temperatures may inhibit switchgrass germination, temperature fluctuations enhance germination of switchgrass [48]. Germination of 6-month old switchgrass seeds at constant 20 °C was 38% lower than germination under 35/20 °C day/night temperatures (88%) [48]. Temperature fluctuation intend to mimic the surface soil temperature regime to which seeds are typically exposed to in early spring, and under extreme conditions may result in freeze-thaw scarification of seeds [49,50]. Fluctuations between −80 °C for 2 h followed by thawing at 20 °C (or room temperature) for 2 h reduced dormancy of alfalfa seeds from 60 to 14% [50]. Similarly, seedling emergence of frozen switchgrass seeds was greater (value not reported) than unfrozen seeds in three out of four years of study [51]. Temperature fluctuations between freezing seeds at −80 °C or −20 °C for 1 h followed by thawing seeds at room temperature (one freeze-thaw cycle) were repeated up to five cycles to investigate influence of freeze-thaw scarification of dormancy of switchgrass [52]. The freeze-thaw scarification had no influence on germination of switchgrass. One hour for each freezing and thawing may be too short regimes to break seed dormancy of switchgrass. Increasing freezing time may more accurately mimic the soil condition in early spring. Further research is needed to determine optimal treatment temperatures and duration of freeze-thaw scarification on switchgrass seeds.

4. Plant hormones

Plant hormones are important growth regulators controlling initiation of germination [2]. Gibberellin promotes breakdown of starch stored in the endosperm through enzymatic reactions, whereas abscisic acid depresses the action of gibberellin [2]. Water imbibition of seeds increased gibberellin concentration [2]. There were strong interactions between plant hormones (e.g., abscisic acid, gibberellin, and fluridone) and temperature during germination, seed coats, and seed lots [53]. Osmo-conditioning of cv. Cave in Rock, cv. Dakotah, and cv. Jersey 50 switchgrass seeds in a solution of polyethylene glycol and 1 mmol L^{-1} gibberellin increased germination by 19% [54]. There is a strong correlation between nitric oxide (NO) signaling pathways and dormancy mechanisms in warm season grasses [27]. Exogenously applied nitric oxide

[27] and hydrogen peroxide, which enhances NO production [32], increased germination of cold-stratified switchgrass, big bluestem (*Andropogon gerardi* Vitman), and indiangrass [*Sorghastrum nutans* (L.) Nash] seeds. Conversely, the presence of NO scavengers resulted in reduced germination [27]. Low concentrations of ethylene (25 μmol L^{-1}), gibberellin (0.25 mmol L^{-1}), and kinetin (0.1 mmol L^{-1}) did not increase germination of cv. Blackwell and cv. Cave in Rock [38].

5. Seed storage/after ripening periods

Thick seed coats preventing radicle emergence are often weakened over time by temperature fluctuations, fungal attack, fire, after-ripening periods, or enzymes produced from the embryo both in natural and controlled environments [21]. However, when the storage periods become too long, seed viability decreases as a result of peroxidation of polyunsaturated fatty acids, and damage to cell membranes and DNA [55]. High temperature accelerates seed aging at 60 °C [56,57], although optimal storage periods, temperature, and storage methods (e.g., see dbag, plastic containers, and paper bags) are cultivar- and seed lot-specific [34,35,58]. Two seed lots (1995 and 1996) of cv. Alamo and accession 746 (upland ecotype) were stored at three different conditions: cold (7 °C with 550 g kg^{-1} humidity), room temperature (21 °C with ambient humidity), and a warehouse condition (−1 °C–38 °C with ambient humidity) for 1, 5, 7, 9, and 11 months [34]. Initial germination percentages were 24% and 76% for cv. Alamo and 1% and less than 1% for accession 746 for seed lots 1995 and 1996, respectively [34]. For both seed lots, storage at room temperature was optimal for breaking dormancy. For the 1995 seed lot, germination was increased by 50% after one month of storage for Alamo and after five months of storage for accession 746 at room temperature [34].

Seed storage at subfreezing temperatures can increase the germination percentage of switchgrass. Germination of switchgrass was improved from 10 to 76% after storing at 4 °C for 49 days [41], from 30 to 53% at 4 °C for 300 days [57], from 78 to 90% after storing at 23 °C for 90 days [38], from 43 to 69% after storing at 23 °C for one year [59], and from 27 to 88% after storing at 25 °C for one year [23]. These results indicate that storage temperature between 4 °C and ambient temperature may break switchgrass dormancy [60]. Effect of storage temperatures below 4 °C on dormancy breaking of switchgrass has shown conflicting results among studies [23,38,41,51,61]. For instance, freezing switchgrass seeds for 14, 31, 49, and 54 days did not break seed dormancy [41], and storing cv. Blackwell and cv. Cave in Rock seeds at −8 °C for 90 days, 180 days, 2 years, and 4 years had little influence on germination [38]. Switchgrass seeds stored at −23 °C for one year showed little germination improvement as compared to seeds stored at 25 °C [23]. Storage at −20 °C had little influence upon dormancy of cv. Alamo [61]. Storage temperature at −20 °C reduced germination of cv. TEM-LoDorm, Alamo-based cultivar with reduced post-harvest seed dormancy [61]. Although storage of switchgrass seeds at freezing temperatures have been found to have little influence on germination improvement, enhanced seedling emergence and vigor [51] was observed when seeds were stored at freezing temperatures for several weeks.

6. Miscellaneous methods

Miscellaneous methods have been reported in the effort to break seed dormancy of switchgrass. Such methods include karrikinolide smoke ($C_8H_6O_3$; [62]), bacterial [63] and fungal [64] inoculation, seed priming [63], electromagnetic radiation [65], and ultrasounds [66]. Karrikinolide smoke was found to improve germination and seedling vigor in some plant species native to ecosystems with frequent fires [67,68]. In one study, two-month-old cv. Alamo seeds were soaked in karrikinolide solution for 24 h and planted in a pot with potting mix [62]. The pots were placed in greenhouse under 12 h day length at day/night temperatures of 32/20 °C. No difference was observed between the treated and untreated seeds; however, application of karrikinolide in different forms, such as gas applied with irrigation water, may improve germination of switchgrass seeds [62].

Germination of Kanlow strains (MAFF-305828, MAFF-305830, and MAFF-305842) was increased by 52% upon inoculation with the mycorrhizal fungus *Sebacina vermifera* [64]. This fungal inoculant also enhanced plant height and root length. Inoculated seeds produced 75, 113, and 18% greater shoot biomass in the first, second, and third harvest, respectively, as compared to the shoot biomass from untreated seeds [64]. The increased shoot biomass was attributed to improved nutrient acquisition through the symbiotic relationship with *S. vermifera* [64]. Solid-matrix priming with post-priming heat treatment of cv. Cave in Rock, cv. Trailblazer, and cv. Nebraska 28 seeds increased the average shoot dry matter by 56%, the number of adventitious roots by 91%, and the number of tillers by 138% compared to untreated controls [63].

Ultrasound treatments have been reported to promote breaking of seed dormancy in dicots [69,70] and monocots [71]. The ultrasound may disrupt plant cells surrounding the seeds, increasing gas and water entry [66]. Wang et al. [66] applied ultrasound treatments with various sonication times, temperatures, and ultrasound output power levels to cv. Alamo and cv. Summer seeds. The optimum treatment was a sonication time of 22.5 min at 39.7 °C with an output power of 348 W [66]. Funk et al. [65] reported at the *In Vitro* Biology meeting in 2010 that electromagnetic radiation for 20–25 min increased germination of switchgrass and improved seedling vigor in terms of shoot and root length.

7. Effect of seed size upon seed dormancy

Seed properties vary greatly between the seed lots within and among cultivars [72]. Two seed lots expressing the same germination percentage differ in their emergence percentage by 40%, seed number per gram by 200 seeds, and seeding rates by 5 kg ha^{-1} when aiming at pure live seed of 300 m^{-2} [73]. (Table 2; [73]). Larger seeds within a cultivar expressed a greater percentage of germination than smaller seeds [74–76], although results between studies have been inconsistent [58].

Table 2 – Two seed lots with same germination percentage expressing different seed characters.

Seed quality test	Unit	Seed lot 2060	Seed lot 2061
Germination	%	66	66
Total viable seed (Germinated and dormant seed)	%	94	85
Greenhouse pot test	%	80	38
Seeds g^{-1}		480	680
Desired seeding rate	PLS m^{-2}	300	
Greenhouse number of seedlings emerged	g^{-1}	384	258
Bulk seeding rate	kg ha^{-1}	7.8	11.6

Note: Adapted from Vogel [73].

Blackwell seeds screened with 1.27, 1.15, and 1.06 mm emerged at 82, 64, and 32%, respectively [74]. In a study conducted by Aiken and Springer [76], seeds were separated by size using air valve settings of 40, 50, 60, and 80°. Seed weight between each setting was in the range of 80–460 μg (8–46 mg/100 seeds) depending upon cultivar. Germination of cv. Alamo, cv. Blackwell, cv. Cave in Rock, cv. Kanlow, and cv. Trailblazer was improved as seed size increased, while seed size had no influence on germination of Pathfinder. The time required for germination was longer in seeds ≤1.06 mm than larger seeds between 1.15 and 1.27 mm [74]. Seed weight is typically greater in early-flowering than late-flowering cultivars [77]. Upland cultivars flower earlier than lowland cultivars, while there are difference of flowering within upland ecotypes; sunburst flowers earlier than cv. Blackwell and cv. Pathfinder. The 1000 seed weight of cv. Sunburst was the heaviest (6.7 g) as compared to 1000 seed weight of cv. Blackwell (5.2 g) and cv. Pathfinder (5.3 g) [76]. Seed count of other switchgrass cultivars are summarized in Table 3. The advantage of larger and heavier seeds has been shown to last up to 10 weeks after emergence in greenhouse experiments [78] and in the field [79].

8. Effect of soil conditions upon seed dormancy

Seed dormancy of grasses is associated with soil conditions such as salinity [25,80–82] and fertilizer rate [83,84]. Although established switchgrass stands are resilient to soil temperature and pH fluctuations, germinating seeds and emerging seedlings are sensitive to these soil parameters [25]. The optimum soil pH and temperature ranges for germination and emergence of cv. Dacotah, ND3743, cv. Summer, cv. Sunburst, cv. Trailblazer, cv. Shawnee, OK NU2, and cv. Cave in Rock were pH 6–8 and 23–25 °C [25]. Salt tolerance of switchgrass was examined with sodium sulfate (120 mmol L^{-1}), magnesium sulfate (100 mmol L^{-1}), and a mixture of these salts (66 mmol L^{-1}, 33 mmol L^{-1}) [79]. Switchgrass germination decreased from 71% in control to 57% with the sodium sulfate treatment. A second report demonstrated that NaCl concentrations above 500 mmol L^{-1} reduced germination of Cave in Rock by 30% [81]. The lowland cultivars cv. Alamo and cv. Kanlow expressed salt tolerance compared to the upland cultivars cv. Dacotah, cv. Forestburg, and PV-1777, with respect to germination [82]. Reduced germination under high salt concentrations was shown to result from inhibition of adenosine monophosphate (AMP) for some cool-season grasses and legumes [85]. However, AMP had no effect on germination of switchgrass and western wheatgrass (*Agropyron smithii* Rydb).

The relation between switchgrass dormancy (cv. Blackwell, cv. Cave in Rock, and cv. Pathfinder) and agricultural practices, such as N rates, was examined by Mullen et al. [86] at Ames, Iowa. Nitrogen rates were 0, 90, and 180 kg ha^{-1}. The N rate of 180 kg ha^{-1} increased germination of pre-chilled cv. Cave in Rock seeds but decreased germination of pre-chilled cv. Blackwell and cv. Pathfinder, and the results were highly variable between cultivars and years. In addition to N fertilizer, compost application increased seedling emergence of switchgrass. Green compost, mixed compost, and coffee compost all increased switchgrass seedling emergence and vigor [84]. Coffee compost amendments between 50 and 200 mg L^{-1} increased germination of all tested cultivars except cv. Alamo, and cv. Alamo germination was improved by green compost at 50 mg L^{-1} [84].

Table 3 – Seed count g^{-1} of cv. Kanlow harvested in 2008, 2010, and 2011, cv. Blackwell and cv. Trailblazer harvested in 2010 and 2011.

Cultivar	Seed lot	Seed count (g^{-1})
Kanlow	2008	1818
	2010	1235
	2011	1149
Blackwell	2010	917
	2011	578
Trailblazer	2010	787
	2011	787

Note: Adapted from Kimura et al. [52].

9. Conclusion

Seed dormancy of switchgrass must be overcome for successful stand establishment. This will be a first step to reduce establishment risk and the cost associated with reseeding. Many studies have reported the effects of chemical, mechanical, thermal, and hormonal seed treatments upon switchgrass seed dormancy. Seed storage duration and conditions are associated with switchgrass seed dormancy. Smaller seeds (e.g., lowland cultivars) typically have higher dormancy compared to larger seeds (e.g., upland cultivars); however, freshly harvested seeds have a high level of dormancy regardless of seed size. Degree of dormancy cannot be predicted easily by cultivar since there are complex interactions between seed dormancy and environmental conditions such as soil parameters (e.g., salinity) micro- and macro-environments during seed production, and management practices (e.g., fertilizer rates). Therefore, it is difficult to select one dormancy breaking treatment that reduces dormancy of all cultivars and seed lots of switchgrass seeds. However, the combination of temperature regimes and storage length is easily attainable among all treatments previously introduced in this review since it is applicable for large quantities of seed within safe and controlled conditions.

The effectiveness of dormancy-breaking treatments has been demonstrated on small amount of seeds in petri dishes and growth chambers. However, planting the treated seeds in pots or in the field more accurately reveals the true response of seeds following dormancy-breaking treatments because soil conditions significantly influence germination and seedling emergence of switchgrass. It will be helpful for seed suppliers or producers to include actual germination percentage without viable dormant seeds and method used to reduce switchgrass seed dormancy on seed labels so increased seedling emergence in the field may be better estimated resulting in adequate switchgrass stands within the window for successful establishment.

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