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Allelopathic Potential of Switchgrass (*Panicum virgatum* L.) on Perennial Ryegrass (*Lolium perenne* L.) and Alfalfa (*Medicago sativa* L.)

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Abstract This study investigated allelopathy and its chemical basis in nine switchgrass (*Panicum virgatum* L.) accessions. Perennial ryegrass (*Lolium perenne* L.) and alfalfa (*Medicago sativa* L.) were used as test species. Undiluted aqueous extracts (5 g plant tissue in 50 ml water) from the shoots and roots of most of the switchgrass accessions inhibited the germination and growth of the test species. However, the allelopathic effect of switchgrass declined when extracts were diluted 5- or 50-fold. Seedling growth was more sensitive than seed germination as an indicator of allelopathic effect. Allelopathic effect was related to switchgrass ecotype but not related to ploidy level. Upland accessions displayed stronger allelopathic potential than lowland accessions. The aqueous extract from one switchgrass accession was separated into phenols, organic acids, neutral chemicals, and alkaloids, and then these fractions were bioassayed to test for allelopathic potential. Alkaloids had the strongest allelopathic effect among the four chemical fractions. In summary, the results indicated that switchgrass has allelopathic potential; however, there is not enough evidence to conclude that allelopathic advantage is the main factor that has contributed to the successful establishment of switchgrass on China's Loess Plateau.

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Introduction

Switchgrass (*Panicum virgatum* L.), a warm-season perennial grass indigenous to North America, has considerable potential as a bioenergy crop. Annual dry matter yield of switchgrass ranges from 6 to 8 t/ha (Sanderson 1999). The ploidy level within this genus varies from diploid ($2n = 2x = 18$) to dodecaploid ($2n = 12x = 108$) (Hulquist and others 1996; Nielsen 1944). Switchgrass can be divided into upland and lowland ecotypes based on chloroplast DNA polymorphism. Generally, the upland ecotypes are hexaploids and octoploids, whereas lowland ecotypes are tetraploids (Hopkins and others 1996; Hulquist and others 1997).

Switchgrass adapts well to a variety of growing conditions and can improve soil quality. Ocumpaugh and others (1997) found that soil carbon content increased from 10 to 12 g/kg 3 years after the establishment of switchgrass plots. Switchgrass might be a good candidate species for the removal of radionuclides from contaminated soil (James and Lidias 1998). Because of its adaptability and high dry matter production capacity, the US Department of Energy has listed switchgrass as one of the most prominent biofuel crops.

As they coevolved with the environment, some plant species developed pathways for the production of secondary metabolites that are not required for metabolism but influence the growth and development of other organisms. This phenomenon is known as allelopathy and the secondary metabolites are known as allelochemicals. The expression of allelopathy tends to increase when plants grow under adverse circumstances, because allelopathy gives plants an advantage in competing for limited resources (George 1987; Putnam 1985). Allelopathic potential is related to plant species and is readily influenced by the environment (Curl and Truelove 1986; Kohi 1993). Allelopathic effects vary among subspecies, plant part, and plant growth stage (Leather and Einhellig 1986).

Several thousand forage grass species have been tested on China's Loess Plateau since the 1990s; however, switchgrass is the only species that has been successfully established. As a non-native species, switchgrass has the potential to reduce the growth of native forages and disturb the ecological balance in the region through allelopathy. Many studies have reported the physiological and biochemical characteristics of switchgrass, including switchgrass morphology, height, yield, forage quality, seed production, and pathogen resistance (Cornelius and Johnston 1941; Eberhart and Newell 1959; Hopkins and others 1995; Nielsen 1944; Quinn 1969). However, no studies have investigated the allelopathic effects of switchgrass on other plant species. The objective of this study was twofold: (1) to determine the allelopathic potential and its chemical basis in nine switchgrass accessions and (2) to investigate the relationship between allelopathic potential and switchgrass ecotype and ploidy level.

Materials and Methods

Sample Collection

Seeds of nine switchgrass accessions (Alamo, Black Well, Cave-in-Rock, Dakota, Forestberg, Kanlow, Nebraska 28, Pathfinder, and Sunburst) were obtained from Dr. Nobumasa Ichizen (Weed Science Center, Utsunomiya University, Japan) (Table 1). The seeds were planted in 2-m × 2-m experimental plots at the Institute of Soil and Water Conservation, Yangling, Shaanxi Province, China in April 2007. The plots were arranged in a completely randomized design and replicated three times. The distance between switchgrass rows within each plot was 30 cm.

Table 1 Ecotype, ploidy level, and place of origin for switchgrass accessions in this study

Accession	Ecotype	Ploidy level	Origin
Alamo	Lowland	Tetraploid	Southern Texas 28° N
Black Well	Upland	Octoploid	Northern Oklahoma 37° N
Cave-in-Rock	Intermediate	Octoploid	Southern Illinois 38° N
Dakota	Upland	Tetraploid	Northern Dakota 46° N
Forestberg	Upland	Tetraploid	South Dakota 44° N
Kanlow	Lowland	Tetraploid	Central Oklahoma 35° N
Nebraska 28	Upland	?	Northern Nebraska 42° N
Pathfinder	Upland	Octoploid	Nebraska/Kansas 40° N
Sunburst	Upland	?	South Dakota 44° N

Note: a question mark indicates that there are contradictions in the literature

Switchgrass plants were harvested in August 2008. Samples from the same accession were combined into one sample and then divided into shoots and roots. The plant samples were placed in a freezer at −35°C for 24 h, freeze-dried under a vacuum for 36 h, and then ground to a powder.

Experiment 1

Preparation of Aqueous Extracts

A 5-g sample of root or shoot powder from each switchgrass accession was sonicated for 30 min in 50 ml distilled water, filtered through Whatman filter No. 1 paper, and then stored at −20°C until used. These samples will be referred to as undiluted extracts throughout the rest of the article. Distilled water was added to aliquots of the undiluted extracts to prepare 5- and 50-fold dilutions.

Allelopathic Bioassay

Perennial ryegrass (*Lolium perenne* L.) and alfalfa (*Medicago sativa* L.) seeds were surface-sterilized by immersion for 2 min in 1% (v/v) sodium hypochlorite followed by immersion for 2 min in 70% (v/v) ethanol. The seeds were washed with distilled water and then placed in Petri dishes (12.5 cm in diameter) on two layers of Whatman No. 1 filter paper. The Petri dishes and filter paper had been sterilized in a high-pressure steam sterilizer for 20 min. Each dish contained 20 perennial ryegrass or alfalfa seeds. A 3-ml aliquot of the test solution (undiluted, 5-fold dilution, or 50-fold dilution) was added to the filter paper. Distilled water was used as a control. Each treatment was replicated three times. The seeds were incubated at 25°C. Seed germination, seedling coleoptile/shoot length, and seedling radicle lengths were determined after 68 h for alfalfa and after 80 h for perennial ryegrass.

Experiment 2

Isolation and Bioassay of Allelochemicals in Switchgrass

Results from Experiment 1 indicated that Pathfinder had the strongest allelopathic potential among the switchgrass accessions in this study. Therefore, Pathfinder was used in a second experiment, which was designed to identify the general class of compounds with allelopathic potential in

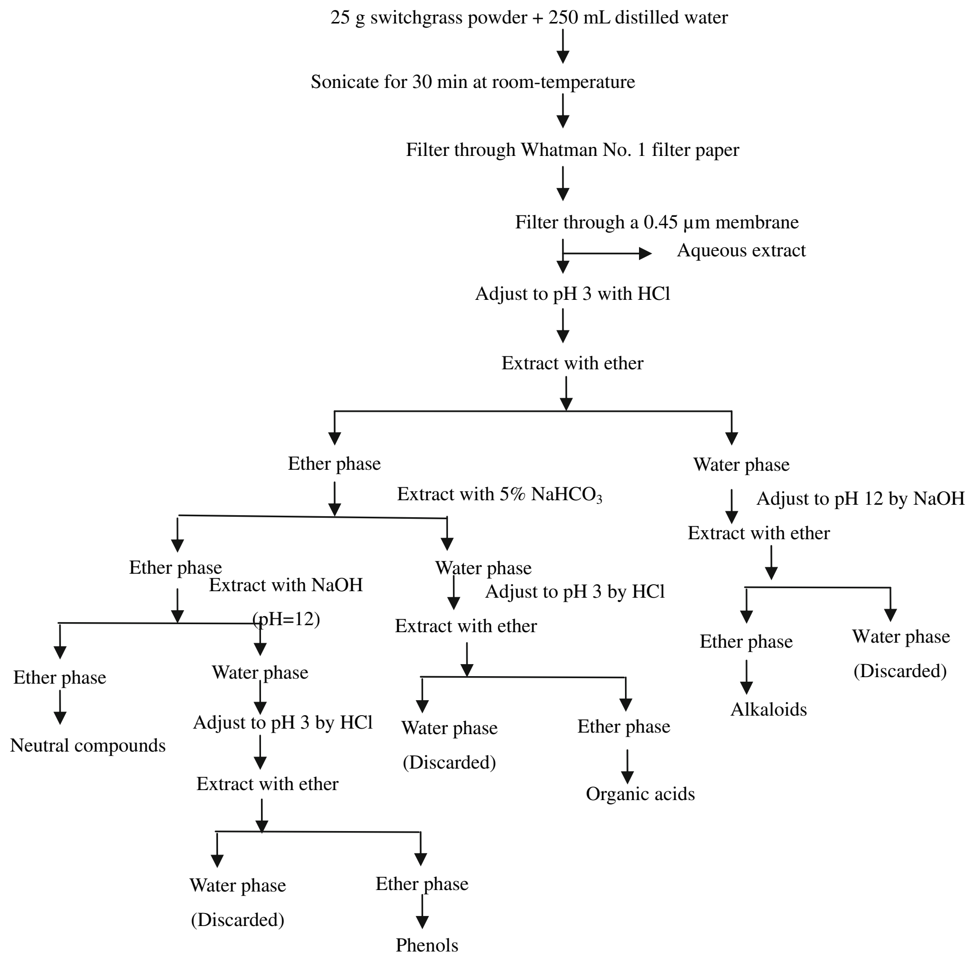

Fig. 1 Extraction procedure for isolating allelochemicals in switchgrass

switchgrass. The extraction procedure is shown in Fig. 1. Briefly, a 25-g sample of powder (Pathfinder, whole plant) was sonicated in 250 ml distilled water for 30 min, filtered through Whatman No. 1 filter paper, and then filtered again through a 0.45-μm membrane (Xinya Co., Shanghai, China). The solution was separated into four fractions (neutral compounds, phenols, alkaloids, and organic acids) by adjusting the pH of the solution by either HCl or NaOH and then extracting with ether. After separation, ether was removed from the samples by low-temperature rotary evaporation and then distilled water was added to bring each sample back to the original volume (250 ml). These extracts will be referred to as undiluted extracts. Distilled water was added to aliquots from each sample in order to prepare 5-fold and 10-fold dilutions. The effect of these fractions on the germination and growth of perennial ryegrass was determined using the allelopathic bioassay described in Experiment 1.

Statistical Analysis

Analysis of variance was performed using JMP 6.0 software (SAS Institute Inc., Cary, NC, USA). Least significant difference (LSD) between the means was calculated and cluster analysis was conducted using DPS 6.55 software (DPS Soft Inc., Hangzhou, China). Differences between means were considered significant at $P \leq 0.05$ and $P \leq 0.01$.

Results and Discussion

Allelopathic Effect of Switchgrass Roots

Undiluted aqueous root extracts from six of the switchgrass accessions significantly reduced perennial ryegrass germination rates (Table 2). In comparison, root extracts from only three of the switchgrass accessions inhibited alfalfa germination. Undiluted root extracts from Dakota, Pathfinder, and Sunburst significantly inhibited both perennial ryegrass and alfalfa germination. The 5- and 50-fold diluted extracts had no significant effect on germination rates of either test species.

Compared to seed germination, seedling growth was a more sensitive indicator of the allelopathic effect of switchgrass root extracts (Table 3). Undiluted aqueous

Table 2 Allelopathic effects of aqueous switchgrass extracts on perennial ryegrass and alfalfa germination rates

Switchgrass accession	Perennial ryegrass germination rate (%)		Alfalfa germination rate (%)	
	Root extracts	Shoot extracts	Root extracts	Shoot extracts
Alamo				
Undiluted	82.5	70.0	72.5	76.7
5-fold dilution	97.5	83.3	65.0	63.3
50-fold dilution	95.0	90.0	65.0	70.5
Black well				
Undiluted	45.0**	93.7	62.5	50.0
5-fold dilution	85.0	93.3	77.5	63.3
50-fold dilution	95.0	90.0	72.5	90.0
Cave-in-rock				
Undiluted	25.0**	83.3	57.5	66.7
5-fold dilution	72.5	93.3	67.5	76.7
50-fold dilution	90.0	93.3	87.5	70.0
Dakota				
Undiluted	50.0**	23.3**	40.0*	0**
5-fold dilution	76.7	90.0	77.5	60.0
50-fold dilution	89.0	86.7	90.0	66.7
Forestberg				
Undiluted	60.0*	30.0**	55.0	0**
5-fold dilution	93.3	86.7	90.0	80.0
50-fold dilution	97.7	80.0	70.0	83.3
Kanlow				
Undiluted	100	80.0	67.5	76.7
5-fold dilution	80.0	86.7	67.5	56.7
50-fold dilution	90.0	83.3	85.0	90.0
Nebraska 28				
Undiluted	70.0	16.7**	60.0	0**
5-fold dilution	84.3	90.0	77.5	63.3
50-fold dilution	89.0	93.3	85.0	56.7
Pathfinder				
Undiluted	43.3**	16.7**	12.5**	0**
5-fold dilution	70.0	86.7	60.0	70.0
50-fold dilution	94.3	96.7	80.0	70.0
Sunburst				
Undiluted	33.3**	3.3**	22.5**	0**
5-fold dilution	70.0	90.0	67.5	73.3
50-fold dilution	84.7	96.7	77.5	76.7
Control	91.0	93.3	80.0	68.3

* and ** denote significant differences in germination between the aqueous extract treatment and distilled water (control) at 95 and 99% confidence levels, respectively

extracts from the roots of eight switchgrass accessions inhibited the growth of perennial ryegrass and alfalfa seedlings. Kanlow was the only accession that did not exhibit an allelopathic effect on perennial ryegrass seedling growth, whereas Alamo was the only accession that did not exhibit an allelopathic effect on alfalfa seedling growth. Perennial ryegrass seedling growth was inhibited by treatment with fivefold diluted extracts from Cave-in-Rock and Sunburst. Alfalfa seedling growth was inhibited by fivefold diluted extracts from Pathfinder and Sunburst. The 50-fold diluted extracts had no significant effect on seedling growth of either test species.

Allelopathic Effect of Switchgrass Shoots

Undiluted shoot extracts from five switchgrass accessions (Dakota, Forestberg, Nebraska 28, Pathfinder, and Sunburst) significantly inhibited both perennial ryegrass and alfalfa germination (Table 2). The 5- and 50-fold diluted extracts had no significant effect on germination rates of

Table 3 Allelopathic effect of aqueous extracts from switchgrass roots on perennial ryegrass and alfalfa seedling growth

Switchgrass accession	Perennial ryegrass		Alfalfa	
	Radicle length (cm)	Coleoptile length (cm)	Radicle length (cm)	Shoot length (cm)
Alamo				
Undiluted	0.99**	0.57*	1.29	0.96
5-fold dilution	1.80	1.01	1.20	0.86
50-fold dilution	1.86	1.05	1.15	1.09
Black well				
Undiluted	0.05**	0.23**	0.39**	0.32**
5-fold dilution	1.53	0.89	1.05	1.24
50-fold dilution	2.03	1.09	1.05	1.02
Cave-in-rock				
Undiluted	0.00**	0.07**	0.08**	0.22**
5-fold dilution	0.71**	0.36**	0.73	0.77
50-fold dilution	1.71	1.07	1.36	1.31
Dakota				
Undiluted	0.86**	0.18**	0.20**	0.12**
5-fold dilution	1.54	0.65	0.87	0.54
50-fold dilution	1.59	0.70	0.92	0.51
Forestberg				
Undiluted	0.92**	0.17**	0.48**	0.14**
5-fold dilution	1.42	0.62	0.86	0.46
50-fold dilution	1.90	0.96	0.82	0.42*
Kanlow				
Undiluted	1.77	0.96	0.86	0.41*
5-fold dilution	1.87	0.99	1.24	0.89
50-fold dilution	2.16	1.23	1.36	1.24
Nebraska 28				
Undiluted	1.22	0.50**	0.53**	0.27**
5-fold dilution	1.67	0.94	0.88	0.53
50-fold dilution	1.55	0.93	0.82	0.50
Pathfinder				
Undiluted	1.15*	0.48**	0.00**	0.03**
5-fold dilution	1.48	0.80	0.23**	0.22**
50-fold dilution	1.90	1.14	0.87	0.51
Sunburst				
Undiluted	0.78**	0.35**	0.04**	0.04**
5-fold dilution	1.06**	0.86	0.41**	0.37*
50-fold dilution	1.56	0.91	1.00	0.52
Control	1.75	0.99	1.19	0.82

* and ** denote significant differences in coleoptile/shoot and radicle growth between the aqueous extract treatment and distilled water (control) at 95 and 99% confidence levels, respectively

either test species. As previously observed, seedling growth was more sensitive than germination rate as an indicator of allelopathic potential (Table 4). Undiluted shoot extracts from all nine switchgrass accessions inhibited perennial ryegrass seedling growth. Treatment with fivefold diluted extracts from Dakota, Nebraska 28, Pathfinder, and Sunburst resulted in a significant decrease in seedling growth. Undiluted aqueous extracts from the shoots of six accessions significantly inhibited alfalfa seedling growth; however, the effect of 5- and 50-fold diluted extracts was not significant.

Comprehensive Assessment of Allelopathic Potential of Switchgrass

For comparative purposes, the magnitude of inhibition or stimulation was determined using the allelopathic assessment method designed by Williamson and Richardson

Table 4 Allelopathic effect of extracts from switchgrass shoots on perennial ryegrass and alfalfa seedling growth

Switchgrass accession	Perennial ryegrass		Alfalfa	
	Radicle length (cm)	Coleoptile length (cm)	Radicle length (cm)	Shoot length (cm)
Alamo				
Undiluted	0.94**	0.26**	1.02	0.74
5-fold dilution	1.56	0.71	0.79	0.69
50-fold dilution	1.86	0.85	1.22	0.67
Black well				
Undiluted	1.14	0.42**	0.52	0.53*
5-fold dilution	1.75	0.74	0.78	0.63
50-fold dilution	1.70	0.72	1.71	1.10
Cave-in-rock				
Undiluted	0.79**	0.36**	0.78	0.62
5-fold dilution	1.99	0.82	1.46	1.05
50-fold dilution	1.89	0.81	1.29	0.87
Dakota				
Undiluted	0.00**	0.07**	0.00**	0.00**
5-fold dilution	0.75**	0.91	0.77	0.95
50-fold dilution	1.37	0.90	1.38	1.11
Forestberg				
Undiluted	0.00**	0.08**	0.00**	0.00**
5-fold dilution	1.12	0.86	1.17	1.28
50-fold dilution	1.30	0.88	1.20	1.15
Kanlow				
Undiluted	1.14	0.40**	0.66	0.91
5-fold dilution	1.62	0.65	0.66	0.85
50-fold dilution	1.72	0.80	1.32	1.20
Nebraska 28				
Undiluted	0.00**	0.04**	0.00**	0.00**
5-fold dilution	0.75**	0.88	0.61	1.00
50-fold dilution	0.99*	1.14	0.72	0.87
Pathfinder				
Undiluted	0.00**	0.06**	0.00**	0.00**
5-fold dilution	0.58**	0.87	0.93	1.16
50-fold dilution	1.22	0.90	0.74	0.98
Sunburst				
Undiluted	0.00**	0.02**	0.00**	0.00**
5-fold dilution	0.93**	0.83	0.64	1.10
50-fold dilution	1.31	0.91	1.28	1.19
Control	1.60	0.87	1.21	1.13

* and ** denote significant differences in coleoptile/shoot and radicle growth between the aqueous extract treatment and distilled water (control) at 95 and 99% confidence levels, respectively

(1988). In this method, the allelopathic response index (RI) was calculated based on the formula $RI = (T/C) - 1$, where T is the germination rate or growth response of the test species treated with undiluted aqueous extracts and C is the germination rate or growth response of the test species treated with distilled water (control). A positive RI value indicates that the switchgrass-derived extract stimulated germination or seedling growth, whereas a negative RI value indicates that the extract inhibited germination or seedling growth. The absolute value of RI reflects the intensity of the allelopathic effect.

In this study, RI values for nine switchgrass accessions were determined at undiluted extract for alfalfa and ryegrass; then the mean RI values were calculated (Fig. 2). Each bar on the graph represent the mean of 54 RI values (9 accessions × 3 repeats × 2 test species) times 3 repeats. Results from this analysis indicated that allelopathic inhibition from aqueous shoot extracts was stronger than from

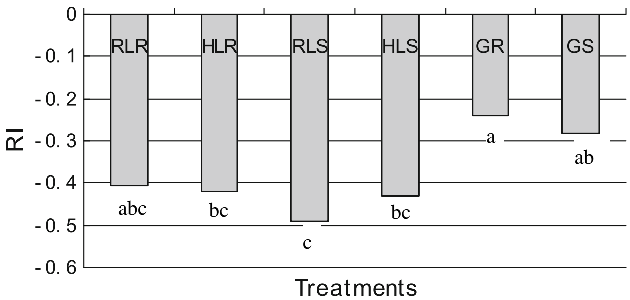

Fig. 2 Allelopathic RI for germination, coleoptile/shoot growth, and radicle growth in response to treatment with aqueous extracts from switchgrass shoots or roots. RLR, effect of root extracts on radicle growth; HLR, effect of root extracts on coleoptile/shoot growth; RLS, effect of shoot extracts on radicle growth; HLS, effect of shoot extracts on coleoptile/shoot growth; GR, effect of root extracts on germination; GS, effect of shoot extracts on germination. Bars with different lowercase letter(s) are significantly different at $P < 0.05$

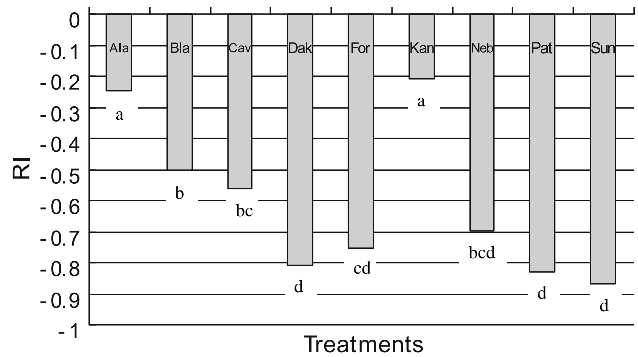

Fig. 4 The mean RI values of each switchgrass. Ala stands for Alamo; Bla stands for Black Well; Cav stands for Cave-in-Rock; Dak stands for Dakota; For stands for Forestberg; Kan stands for Kanlow; Neb stands for Nebraska 28; Pat stands for Pathfinder; Sun stands for Sunburst. Bars with different lowercase letter(s) are significantly different at $P < 0.05$

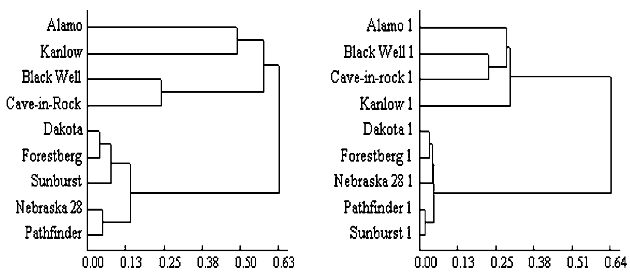

Fig. 3 Cluster analysis for allelopathic potential of switchgrass on perennial ryegrass (*left*) and alfalfa (*right*). The title of the *x*-axis is Euclidean distance

root extracts, although the difference was not significant. Furthermore, the effect of aqueous extracts on the germination rate of the test species was less than the effect of the extracts on coleoptile/shoot and radicle growth. This supports our previous observation that seedling radicle and coleoptile/shoot growth was more sensitive than germination rate as an indicator of allelopathic potential.

We used RI values of shoot, root, and germination of each switchgrass at undiluted extract for alfalfa and ryegrass in cluster analysis (Fig. 3), and the mean RI values of each switchgrass were also determined (Fig. 4). Cluster analysis showed that allelopathic effects of the nine switchgrass accessions were similar for perennial ryegrass and alfalfa. Furthermore, the switchgrass accessions could be divided into two groups based on allelopathic potential. Accessions with strong allelopathic potential were Dakota, Forestberg, Nebraska 28, Pathfinder, and Sunburst, whereas accessions with weak allelopathic potential were Alamo, Black Well, Cave-in-Rock, and Kanlow.

The nine switchgrass accessions in this study included two lowland ecotypes, one intermediate ecotype, and six upland ecotypes (Table 1). Ploidy levels ranged from tetraploid (4*n*) to octoploid (8*n*). Among the nine accessions, allelopathic potential was weakest for tetraploid accessions Alamo and Kanlow followed by octoploid accessions Black Well and Cave-in-Rock (Fig. 4). Allelopathic potential was stronger for the other five accessions, which included both tetraploid and octoploid levels. Kim and Shin (1998) and Olofsdotter and others (1999) found that allelopathy was more influenced by genetics than environment, and Inderjit and Mallik (1997) found that allelopathy was strongly influenced by habitat, ecology, and environmental factors. Our results suggested a relationship between ecotype and allelopathic potential (Fig. 3; Table 1). Specifically, allelopathic potential was stronger for upland ecotypes compared to lowland ones. For example, water stress can promote root exudation (Curl and Truelove 1986) and enhance the concentration of allelopathic compounds in the tuber and rhizosphere of purple nutsedge (*Cyperus rotundus* L.) (Kohi 1993). One possible explanation for stronger allelopathic potential among the upland switchgrass accessions in our study is that allelopathy is influenced by ecotype, possibly due to genomic evolution in adaptation to environmental changes, and allelopathy would help switchgrass to survive and compete for limited resources in the dry and therefore environmentally adverse upland habitat.

Many researchers have examined the role of allelopathy in the invasion of exotic plants. One of the most studied examples is the production of (–)-catechin by spotted knapweed (*Centaurea stoebe*). Results from some of these studies led to the "novel weapons hypothesis" (Bais and others 2002, 2003; Perry and others 2005; Weir and others 2003), which states that invasive plants release allelochemicals that native plants have never encountered. These allelochemicals inhibit the growth of native plants, thus giving advantage to the invasive species (Bais and others 2003; Callaway and Ridenour 2004). Other researchers have expressed doubt about this hypothesis, pointing out that leaching would prevent the allelochemical from attaining toxic levels (Blair and others 2005, 2006; Qin and others 2007).

Switchgrass is the only forage grass to be successfully introduced on China's Loess Plateau. The observation that undiluted aqueous extracts from switchgrass shoots and roots inhibited perennial ryegrass and alfalfa growth suggested that allelopathy might promote switchgrass stand establishment in this environment. However, allelopathic effects disappeared when the aqueous extracts were diluted. Thus, this study confirms allelopathic potential in switchgrass, but there is not enough evidence to conclude that allelopathy is the main factor that has contributed to the successful establishment of switchgrass on the Loess Plateau.

Chemical Basis for the Allelopathic Potential of Switchgrass

The RI analysis indicated that Pathfinder is one of the switchgrasses that had the strongest allelopathic potential among nine switchgrass accessions (Fig. 3); therefore, we chose to use Pathfinder as plant material for the extraction procedure in Experiment 2. An aqueous extract from Pathfinder was separated into four chemical fractions (neutral compounds, phenols, organic acids, and alkaloids) and then the allelopathic effect of these fractions was bioassayed on perennial ryegrass. Perennial ryegrass was chosen because previous results indicated that it was more sensitive than alfalfa to allelopathy by switchgrass. Data indicated that undiluted concentrations of all four chemical fractions significantly inhibited perennial ryegrass germination and seeding growth (Table 5). Fivefold dilutions of the phenolic and organic acid fractions inhibited seedling growth but not germination. Fivefold dilutions of the alkaloid fraction inhibited seedling growth and germination, and 10-fold dilutions of the alkaloid fraction inhibited seedling growth. This simply assay showed that the alkaloid fraction had the strongest allelopathic potential among the four chemical fractions. Future studies will be done to identify the allelochemical in the alkaloid fraction as well as the allelochemical's level of activity.

Conclusions

Allelopathic potential of switchgrass was related to its ecotype but not dependent on its ploidy level. Upland accessions displayed stronger allelopathic potential than lowland ones. The results support the hypothesis that adaptation to adverse environmental conditions will give

Table 5 Allelopathic effect of chemical fractions separated from switchgrass extracts on perennial ryegrass germination and growth

Chemical fraction	Perennial ryegrass		
	Root length (cm)	Shoot length (cm)	Germination rate (%)
Neutral fraction			
Undiluted	0.04**	0.06**	33.3**
5-fold dilution	1.13	0.54	96.7
10-fold dilution	1.11	0.46	88.3
Phenolic fraction			
Undiluted	0.00**	0.00**	0.0**
5-fold dilution	0.39**	0.31**	80.0
10-fold dilution	1.20	0.56	90.0
Organic acid fraction			
Undiluted	0.01**	0.01**	10.0**
5-fold dilution	0.82**	0.44	90.0
10-fold dilution	1.06	0.52	88.3
Alkaloid fraction			
Undiluted	0.00**	0.00**	0.0**
5-fold dilution	0.04**	0.15**	45.0**
10-fold dilution	0.36**	0.32**	78.3
Aqueous fraction			
Undiluted	0.01**	0.00**	5.0**
5-fold dilution	0.74**	0.62	81.7
10-fold dilution	0.73**	0.41	70.0
Control	1.11	0.53	81.7

* and ** denote significant differences in coleoptile/shoot and radicle growth between the aqueous extract treatment and distilled water (control) at 95 and 99% confidence levels, respectively

rise to an increase in the allelopathic potential of some plant species or ecotypes. In other words, allelopathy is the result of a species' or ecotype's adaptation to the environment. This study indicated that switchgrass has allelopathic potential; however, the allelopathic effect declined sharply when plant extracts were diluted with water. This leads us to conclude that allelopathic effects of these accessions are limited in the natural environment. It is unlikely that allelopathy is the primary factor accounting for the adaptability of switchgrass to diverse environments.

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References

Bais HP, Walker TS, Stermitz FR, Hufbauer RA, Vivanco JM (2002) Enantiomeric-dependent phytotoxic and antimicroial activity of (±)-catechin A rhizosecreted racemic mixture from spotted knapweed (*Centaurea maculosa*). Plant Physiology 128:1173–1179

Bais HP, Vepachedu R, Gilroy S, Callaway RM, Vivanco JM (2003) Allelopathy and exotic plants: from genes to invasion. Science 301:1377–1380

Blair AC, Hanson BD, Brunk GR, Marrs RA, Westra P, Hufbauer RA (2005) New techniques and findings in the study of a candidate allelochemical implicated in invasion success. Ecological Letters 8:1039–1047

Blair AC, Nissen SJ, Brunk GR, Hufbauer RA (2006) A lack of evidence for an ecological role of the putative allelochemical (±)-catechin in spotted knapweed. Journal of Chemical Ecology 32:2327–2331

Callaway RM, Ridenour WM (2004) Novel weapons: a biochemically based hypothesis for invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2:436–443

Cornelius DR, Johnston CO (1941) Difference in plant type and reaction to rust among several collections of *Panicum virgatum* L. Journal of American Society of Agronomy 33:115–124

Curl EA, Truelove B (1986) The rhizosphere. Springer, New York

Eberhart SA, Newell LC (1959) Variation in domestic collections of switchgrass, *Panicum virgatum* L. Agronomy Journal 51:613–616

George RW (1987) Allelochemicals. American Chemical Society, Washington, DC

Hopkins AA, Vogel KP, Moore KJ, Johnson KD, Carlson IT (1995) Genotypic variability and genotype × environment interactions among switchgrass accessions from the Midwestern USA. Crop Sciences 35:565–571

Hopkins AA, Taliaferro CM, Murphy CD, Christian D (1996) Chromosome number and nuclear DNA content of several switchgrass populations. Crop Sciences 36:1192–1195

Hulquist SJ, Vogel KP, Lee DJ, Arumuganathan K, Kaeppler S (1996) Chloroplast DNA content and nuclear DNA content variations among cultivars of switchgrass, *Panicum virgatum* L. Crop Sciences 36:1049–1052

Hulquist SJ, Vogel KP, Lee DJ, Arumuganathan K, Kaeppler S (1997) DNA content and chloroplast DNA polymorphisms among switchgrasses from remnant Midwestern prairies. Crop Sciences 37:595–598

Inderjit, Mallik AU (1997) Effect of phenolic compounds on selected soil properties. Forest Ecology and Management 92:11–18

James AE, Lidias W (1998) Potential remediation of 137Cs and 90Sr contaminated soil by accumulation in alamo switchgrass. Water, Air, and Soil pollution 104:339–352

Kim KU, Shin DH (1998) Rice allelopathy research in Korea. In: Olofsdotter M (ed) Proceedings of the workshop on allelopathy in rice. International Rice Research Institute, Manila, Makati City, pp 39–44

Kohi K (1993) Allelopathy and water stress of purple nutsedge (*Cyperus rotundus* L.). M.S. thesis, University of Hawaii, Honolulu

Leather GR, Einhellig FA (1986) Bioassays in the study of allelopathy. In: Putnam AR, Tang CS (eds) The science of allelopathy. Wiley, New York, pp 133–145

Nielsen EL (1944) Analysis of variation in *Panicum virgatum*. Journal of Agricultural Research 69:327–353

Ocumpaugh WR, Sanderson MA, Hussey MA, Read JC, Tischler CR, Reed RL (1997) Evaluation of switchgrass cultivars and cultural methods for biomass production in the southcentral U.S. Final project report for Subcontract 19x-LS128C. Oak Ridge National Lab, Oak Ridge

Olofsdotter M, Navarez D, Rebulanan M, Streibig JC (1999) Weed suppressing rice cultivars—does allelopathy play a role? Weed Research 39:441–454

Perry LG, Thelen GC, Ridenour WM, Weir TL, Callaway RM, Paschke MW, Vivanco JM (2005) Dual role for an allelochemical: (±)-catechin from *Centaurea maculosa* root exudates regulates conspecific seedling establishment. Journal of Ecology 93:1126–1135

Putnam AR (1985) Weed allelopathy. In: Duke SO (ed) Weed physiology, volume I: reproduction and ecophysiology. CRC Press, Boca Raton, pp 131–155

Qin B, Lau JA, Kopshever J, Callaway RM, McGray H, Perry LG, Weir TL, Paschke MW, Hierro JL, Yoder J, Vivanco JM, Strauss S (2007) No evidence for root-mediated allelopathy in *Centaurea solstitialis*, a species in a commonly allelopathic genus. Biology Invasions 9:897–907

Quinn JA (1969) Variability among high plains populations of *Panicum virgatum*. Bulletin of the Torrey Botanical Club 96:20–41

Sanderson MA (1999) Switchgrass cultivars and germplasm for biomass feedstock production in Texas. Bioresource Technology 67:209–219

Weir TL, Bais HP, Vivanco JM (2003) Intraspecific and interspecific interactions mediated by a phytotoxin, (−)-catechin, secreted by the roots of *Centaurea maculosa* (spotted knapweed). Journal of Chemical Ecology 29:2397–2412

Williamson GB, Richardson D (1988) Bioassays for al-telepathy: measuring treatment responses with independent controls. Journal of Chemical Ecology 14(1):181–187