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Aqueous Litter Extracts of Native Grass Species Suppress Exotic Plant Species Under Allelopathic Conditions

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Abstract

Previous pasture residues can inhibit the establishment of exotic introduced plant species by exerting allelopathic effects. Concerning this issue, present research work was conducted to investigate the allelopathic potential of dominant native grass species (*Lespedeza davurica, Stipa bungeana, and Artemisia capillaris*) on the seed germination and seedling growth of exotic plant species (alfalfa and wheat). Different concentrations (2.5%, 5%, and 10%) of residue extracts of native grass species were used in the experiment. Results indicated that the aqueous extracts of *A. capillaris* and *S. bungeana* at all concentrations significantly suppressed the seed imbibition, germination potential, germination rate, germination index, seedling height, above and belowground biomass of alfalfa seedlings. Meanwhile, *L. davurica* did not show any effect on germination indexes but it significantly suppressed the seedling height of alfalfa after two weeks. However, it improved the seed imbibition, seedling height, and biomass of wheat seedlings. The greatest inhibition effect was perceived by *A. capillaris* followed by *S. bungeana* extracts. To achieve sustainable agricultural development, it is important to utilize cultivation systems that take advantage of the stimulatory and inhibitory effects of allopathic plants to regulate plant growth and development and to minimize the risk of toxicity caused by allopathic plants species.

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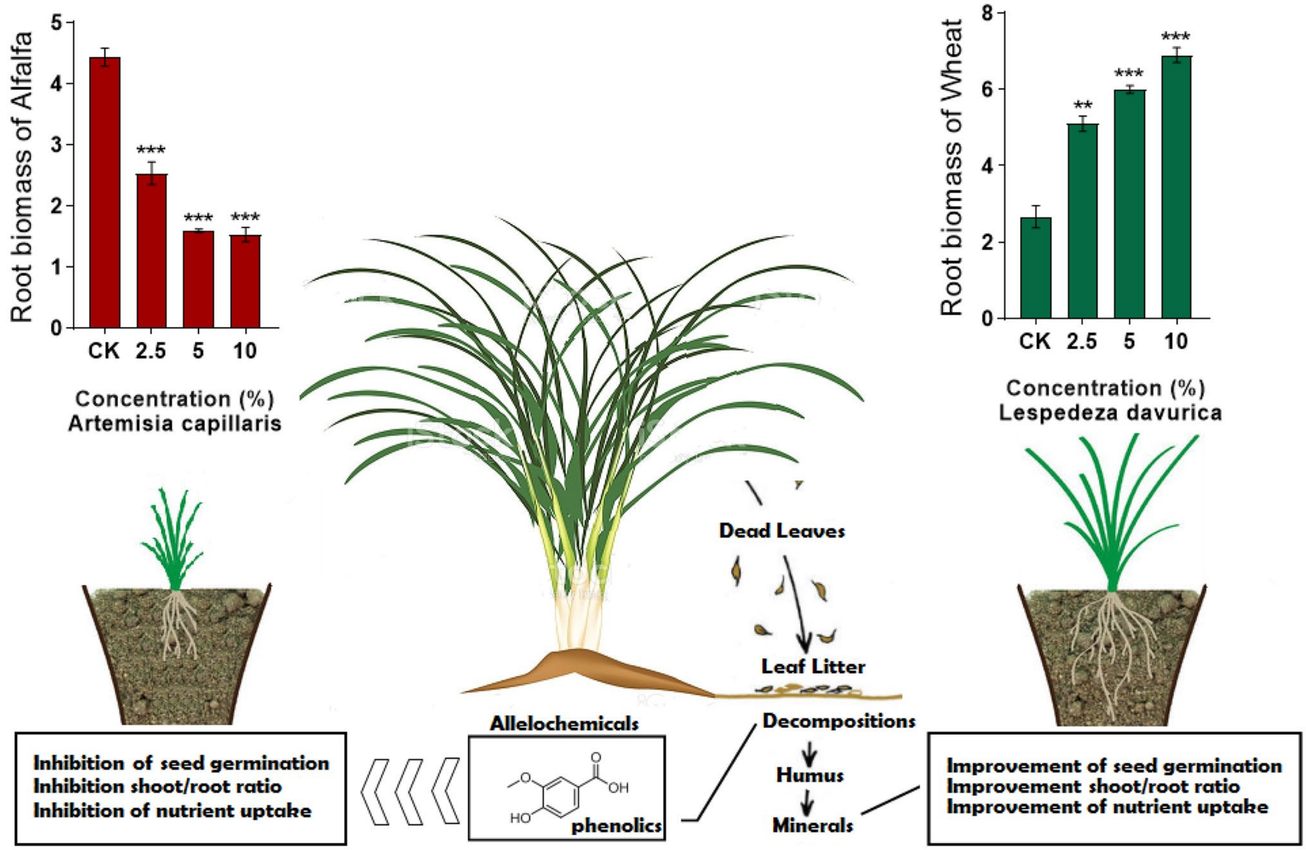
Graphical Abstract

Overall processes of allelopathy and how allelochemicals are derived from the aerial parts of plants and reveals that allelochemical compounds primarily contain phenolic compounds, terpenes, and fatty acids, which influence the seed germination, survival, growth, and development of other plants (e.g., crops or weeds).



Keywords Allelopathy · Residue extracts · Imbibition · Germination · Native species · Non-native species

Introduction

Rangeland and pastures cover more than 40% of the total land area of China (Zhou et al. 2017). These lands contribute to the long-term sustainability of livestock and forage production as they provide habitat to a variety of native plants and animals (Feng et al. 2010). To meet the global demand for forage production, species have been selected based on their ability to adapt to local environmental conditions and their rapid growth potential (Michalk et al. 2019). In many areas, exotic plants species are most effective for producing high yields (Dodet and Collet 2012). Several exotic plants species are introduced in rangelands to provide multiple ecological benefits, including, stress resistance, improved forage yield, and quality (Belnap et al. 2012; Blackburn et al. 2014; Rhodes et al. 2021). New combinations of introduced exotic and native plant species have changed rangelands into novel ecosystems (Belnap et al. 2012). The management of these novel ecosystems becomes increasingly challenging (Seastedt et al. 2008). One of the most important factors to novel plant communities is competition between plants which influences the structure and development of introduced plant communities (Blindow et al. 2016; Kegge and Pierik 2010; Kiaer et al. 2013).

Direct competition in the form of allelopathy (chemical-based communication among plants) is gaining attention due to its potential in multiple fields (Michalet et al. 2006; Scognamiglio et al. 2013). Allelopathy is a natural ecological phenomenon, that can stimulate or inhibit plant germination and growth by releasing secondary metabolites into the environment (Cheng and Cheng 2015; Farooq et al. 2011; Schandry and Becker 2019; Mushtaq et al. 2020a). Allelochemicals can affect plant growth and development in multiple ways, affecting different physiological and biochemical processes including, cell division, biosynthesis of certain hormones and proteins, uptake and transport of minerals across the membranes, water absorption, membranes permeability, stomatal conductance, photosynthesis, respiration, and protein breakdown in target plants (Ali et al. 2008; Farooq et al. 2013; Field et al. 2006; Zhang et al. 2010).

Native pasture residues exert allelopathic effects on co-occurring plants, which inhibit the seedling establishment of exotic plant species by exuding allelopathic exudates (Adomako et al. 2019; Cummings et al. 2012; Zhang et al. 2015). Likewise, allelopathy can be an important biological force that affects the germination and growth of target plants species, and consequently the population dynamics of plant species and community assembly (Mushtaq et al. 2020c; Zhang et al. 2021). The overall aim of previous research on allelopathy was the reduction of chemical pesticide inputs and consequent environmental pollution, and implementing effective methods for sustainable agricultural development (Han et al. 2013; Jabran et al. 2015; Li et al. 2010; Macías et al. 2003; Mushtaq et al. 2020b). A lot of research has been done to explore the inhibitory potential of different allelopathic crops for the sake of weed management (Bajwa et al. 2020; Farooq et al. 2011; Mushtaq et al. 2019; Nawaz et al. 2014; Sarić-krsmanović et al. 2020). The presence of weeds causes serious losses to agricultural production, both in quantitative and qualitative terms, because they constantly compete spatially with crop plants, limiting the available amount of nutrients, light, moisture, and physical space (Scavo et al. 2018; Svizzero 2021). A reduction in herbicide rates can be achieved through combining allelopathic extracts with reduced herbicide rates (Khaliq et al. 2002; Iqbal et al. 2009), based on their studies, they found that the use of these water extracts reduced herbicide application rates in certain field crops by 50 percent. Furthermore, researchers found that using sorghum extract (12 L ha^{-1} rate) for cotton, the amount of the required herbicide could be reduced by 50–60% (Cheema et al. 2003). A similar result was obtained by evaluating the effectiveness of combining sorghum and sunflower water extracts with reduced doses of some early post-emergence herbicides for weed control in wheat crops (Razzaq et al. 2010).

In response to crop allelopathy, it is important to screen putatively allelopathic accessions, different screening techniques have been developed (Li et al. 2015). However, direct field screening imposes limitations, as it is time-consuming, requires large amounts of space and labor, and can be expensive, especially when there are large collections of crop germplasm to be screened (Wu et al. 2001). The potting method (Putnam and Duke 1974), and rhizosphere soil method (Fujii et al. 2005) as a medium for the screening of allelochemical activity under greenhouse are the most convenient methods (Macias et al. 2007; Farooq et al. 2011). It has been suggested that each specific method depends on the researcher's goals, bioassay species, the availability of analytical instruments and that the screening results by laboratory methods should be further confirmed by field testing (Wu et al. 2001).

Though, previous literature has reported the effects of various native pastures and weeds allelopathic effects on co-occurring plants. Yet, little information is available on how native dominant pasture species of *Lespedeza davurica*, *S. bungeana*, and *A. capillaris* could affect the seed germination and seedling establishment of introduced species (wheat and alfalfa). Therefore, the present study was conducted to determine whether *L. davurica, S. bungeana,* and *A. capillaris* had allelopathic effects on introduced exotic plant species, and how different concentrations of residue extracts from these pastures would affect seed germination and seedling growth of alfalfa and wheat seedlings. Results from this study would help in the understanding of interactions among plants communities, which may help modify crop cultivation patterns with resulting yields increments.

Materials and Methods

Plant Material and Treatments

A pot experiment was conducted at the Tian Shui Grassland Research Station in Huanxian county, Gansu province, Northwest China (37.12°N, 106.82°E; 1650 m in elevation). Plastic pots (20 cm height and 18 cm diameter) were filled with soil collected from natural grassland (0–10 cm soil profile). The physicochemical properties of soil are presented in Table 1. High-quality alfalfa (30) and wheat (10) seeds were planted in each pot. The aqueous litter extracts were applied to each pot before the commencement of the seed sowing. Overall, there were 10 treatments including 0 (control), 2.5% *L. davurica* extract, 2.5% *S. bungeana* extract, 2.5% *A. capillaris* extract, 5.0% *L. davurica* extract, 5.0% *S. bungeana* extract, 5.0% *A. capillaris* extract*,* 10.0% *L. davurica* extract, 10.0% *S. bungeana* extract and 10.0% *A. capillaris* extract. Each treatment was replicated three times. The pots were organized in a completely randomized design (CRD) and placed inside the glasshouse under a relative humidity of 60 ± 5%, ambient temperature regimes ranging from 16.5 to 22.2 °C, soil temperature ranging from 12.1 to 16.6 °C, and a day/night cycle of 14/10 h.

Donor Plant Species

Lespedeza davurica, Stipa bungeana, and *Artemisia capillaris* were used which are the dominant plant species in the semi-arid grasslands of northwest China. *Lespedeza*

Table 1 Soil physicochemical properties

Measured character	Value and units	Measured character	Value and units
pH	7.6	Soil components	Sand (59.44%)
Electrical conductivity (EC)	112.1 us cm^{-1}		Silt (24.21%)
Cation Exchange Capacity	7.8 cmol kg^{-1}		Clay (16.13%)
Available N	29.98 mg kg^{-1}	Soil texture	Sandy loam
Available P	1.35 mg kg^{-1}	Total carbon	8.63 g kg^{-1}
Available K	172.4 mg kg^{-1}	Organic carbon	6.65 g kg^{-1}
Bulk density	1.27 g cm^{-3}	Microbial carbon	0.143 g kg^{-1}

davurica is a C3 perennial leguminous shrub that contributes 64.3% of the aboveground biomass. Due to its drought resistance and ability to grow in barren areas, it plays an important role in maintaining the area's unique natural sceneries (Xu et al. 2015). *Artemisia capillaris* is also a perennial plant, which contributes 75.6% of total aboveground biomass production (Hou et al. 2002). *Stipa bungeana* observed higher biomass production and has tolerance for the trampling of livestock (Na et al. 2010).

Receptor Plants

Alfalfa (*Medicago sativa* L.) and wheat (*Triticum aestivum* L.) crop seeds were used as receptor species. Healthy wheat and alfalfa seeds with regular shape, uniform size, and good germination potential were collected. Seeds of these species were obtained from the Huanxian grassland research station.

The Aqueous Litter Extracts Preparation

Litters of *L. davurica, S. bungeana*, and *A. capillaris* were collected from the experimental field of grassland research station Huanxian County. After cleaning with distilled water and air drying, litter extracts were prepared according to the method of Han et al. (2019). Briefly, the grass samples were ground and then passed through a mesh. The grounded plant samples (100 g) were soaked in 1000 ml of distilled water and shaken for 24 h at 25 °C. These aqueous litter extracts were centrifuged at 180 r min^{-1}. The supernatants were filtered through a 0.45 µm membrane and 2.5, 5, and 10% aqueous extracts of *Lespedeza davurica, Stipa bungeana*, and *Artemisia capillaris* were prepared. The litter extracts were stored in a refrigerator at 4 °C, until usage.

Seed Imbibition

Effects of litter extract from *L. davurica*, *S. bungeana*, and *A. capillaris* on seed imbibition were measured in a separate petri dish experiment. Thirty seeds of alfalfa and 10 seeds of wheat were placed separately in 9-cm Petri dishes with filter paper and soaked in aqueous extracts of various concentrations (2.5, 5, and 10%). Simultaneously, distilled water was used for the control treatment. The treatments were placed in a growth chamber (Westinghouse, Electrolux home products, Australia) at 25 °C under dark conditions. Each treatment combination was repeated thrice. Based on the differences in weight, the seed imbibition was determined at 0, 4, 8, 12, 16, 20, and 24 h.

Germination Experiment

The seed emergence was monitored over 12 days and the germinated seeds were counted daily. The seedling height was determined at two days intervals until the end of the experiment. After 18 days of germination, seedlings were carefully removed, and washed. The dry weight (DW) of seedlings was determined after oven-drying the samples for 48 h at 75 °C. The germination rate, germination potential, and germination index were calculated following the procedures of Kamran et al. (2021).

$$\textbf{Germination potential}\ (\%) = \frac{\text{number of seeds germinated on 3rd day}}{\text{the total numbers of seeds}} \times 100$$

$$\textbf{Germination rate}\ (\%) = \frac{\text{number of seeds germination}}{\text{total numbers of seeds}} \times 100$$

$$\textbf{Germination index (GI)} = \Sigma\left(\frac{\text{Gt}}{\text{Dt}}\right)$$

where Gt stands for the number of seeds emerging on a given day, and Dt stands for the time after setting the seeds for germination.

Calculation of the root-to-shoot ratio was based on the dry weight of the seedlings using the formula:

$$\textbf{Root/Shoot ratio} = \frac{\text{root dry weight}}{\text{shoot dry weight}}$$

Allelopathy Response Index (RI)

The allelopathic response index (RI), which represents the intensity of the allelopathic effect, was calculated using the formula described by Williamson and Richardson (1988) as follows:

$$RI = 1 - C/T$$

where C represents control data, and T represents treatment data. **RI > 0** showed that seedling germination or seedling growth was promoted.**RI < 0** showed an inhibitory effect.

Absolute values of the RI refer to the intensity of allelopathy.

The sensitive effect (SE) value is used as an indicator to evaluate allelopathy potential effects, and calculated as the sum of the corresponding RI of germination, root, and shoot biomass (Ma et al. 2020).

Statistical Analysis

All the data in figures and tables are presented as mean ± SE ($n = 3$). The ANOVA analyses were performed using SPSS software, version 20.0 (SPSS Inc., Chicago, IL, USA). Significant differences among treatments were determined according to the Fisher's least significant difference (LSD) test at $P < 0.05$. All the figures were constructed using Excel 2010 (Microsoft, USA) and Origin 9.2 software (OriginLab OriginPro 2015, USA).

Results

Effects of Grass Aqueous Litter Extracts on Alfalfa and Wheat Seed Imbibition

The water uptake by alfalfa seeds was decreased by increasing the concentration of aqueous extracts, with the greatest impact caused by *A. capillaris* extracts. It was observed that the seeds imbibed with distilled water absorb more water than those treated with *S. bungeana* and *A. capillaris* litter extracts during the same period (Fig. 1B, C). Initially, *S. bungeana* had a minor effect on alfalfa seed's weight but over time, its effects became more evidential and decreased seed weight by 14.28, 15.23, 16.55, and 16.11% at 12, 16, 20, and 24 h, respectively compared to control (Fig. 1B). Similarly, the seed weight of alfalfa treated with a high concentration of *A. capillaris* dropped significantly by 16.71, 15.30, 14.28, 15.61, and 15.23% after 8, 12, 16, 20, and 24 h, respectively compared to control (Fig. 1C). On the contrary, the litter extracts of *A. capillaris* and *S. bungeana litter* did not show any inhibitory effects on the seed weight of wheat. Instead, the lower concentration of *L. davurica* (2.5%) improved the seeds' weight by 3.9, 3.82, 3.72% after 16, 20, and 24 h, respectively compared to control (Fig. 1A).

Effects of Grass Aqueous Litter Extracts on Alfalfa and Wheat Seed Germination

The results indicated that aqueous litter extracts of *A. capillaris* and *S. bungeana* significantly ($P < 0.05$) inhibited the seed germination indices of alfalfa at each concentration. Among the three-donor species, the *A. capillaris* aqueous litter extracts showed the greatest allelopathic effects on alfalfa, and reduced seed germination potential by 26, 47, and 60%, germination rate by 22, 28, and 43%, and germination index by 23, 34, and 54% after they were exposed to 2.5, 5, and 10% concentrations, respectively (Fig. 2). A similar trend was also observed in alfalfa under the application of litter extract of *S. bungeana* that reduced seed germination potential by 12, 15, and 39% seed germination rate by 11, 21, and 32% and seed germination index by 7, 20, and 36% with 2.5, 5, and 10% concentration, respectively. However, no significant effects of *L. davurica* were observed on germination indices of alfalfa (Fig. 2). In addition, our findings indicated that litter extracts of all dominant grass species did not show any significant ($p > 0.05$) effect on seed germination indices of wheat at all concentrations (Fig. 2). Overall, results revealed that alfalfa-grass germination indices were more sensitive than wheat crops (Fig. 2).

Effects of Grass Aqueous Litter Extracts on Alfalfa and Wheat Seedling Height

Aqueous litter extracts of *L. davurica, S. bungeana*, and *A. capillaris* inhibited seedling growth of alfalfa. Initially, *L. davurica* had a minimal effect on an alfalfa seedling's height but over time, its effects became more prominent and decreased seedling height by 16.98, 22.56, and 30.90% after 14, 16, and 18 days compared to control, respectively (Table 2). Similarly, the height of alfalfa seedlings dropped significantly by 25.53, 19.81, 23.76, and 29.69% after 12, 14, 16, and 18 days, respectively as compared to control at high concentration of *S. bungeana* (Table 2). Throughout the experiment, *A. capillaris* litter extract had the strongest inhibition effect upon the seedling height of alfalfa, and there was a significant ($P < 0.05$) reduction in height by 44.11, 37.95, 32.27, 29.24, 30.59, and 34.09% after 8, 10, 12, 14, 16 and 18 days when compared to control, respectively

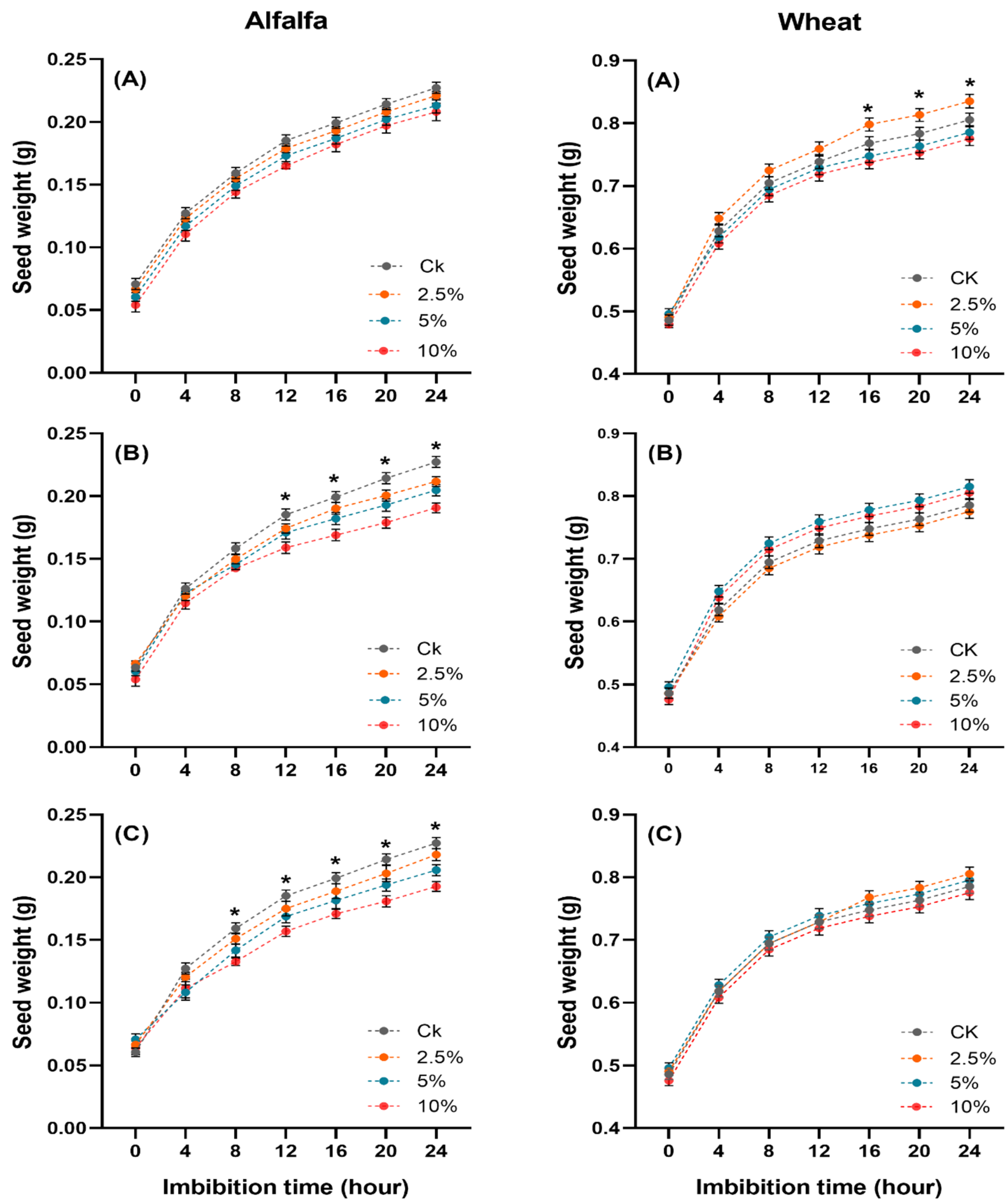


Fig. 1 Effects of different aqueous litter extract concentrations (0, 2.5, 5, and 10%) of three dominant native grass species *Lespedeza davurica* (**A**), *Stipa bungeana* (**B**), and *Artemisia capillaris* (**C**) on seed imbibition of the target introduced exotic plant species of alfalfa and wheat. Values are means ± SE ($n = 3$). Star * indicate significant ($P < 0.05$) differences between treatments

(Table 2). On the contrary, litter extracts of *A. capillaris* and *S. bungeana* did not show any inhibitory effects on the seedling growth of wheat. Instead, the higher concentration of *L. davurica* ($P < 0.05$) enhanced the seedling height by 30.81, 19.60, and 8.55% at high concentrations after 10, 14, and 16 days, respectively (Table 3).

Effects of Grass Aqueous Litter Extracts on Alfalfa and Wheat Biomass

The aboveground biomass of alfalfa was significantly ($P < 0.05$) affected by *L. davurica* extract as compared to the control. The application of *L. davurica* at 2.5 and 5% concentration increased the aboveground biomass by 53.31 and

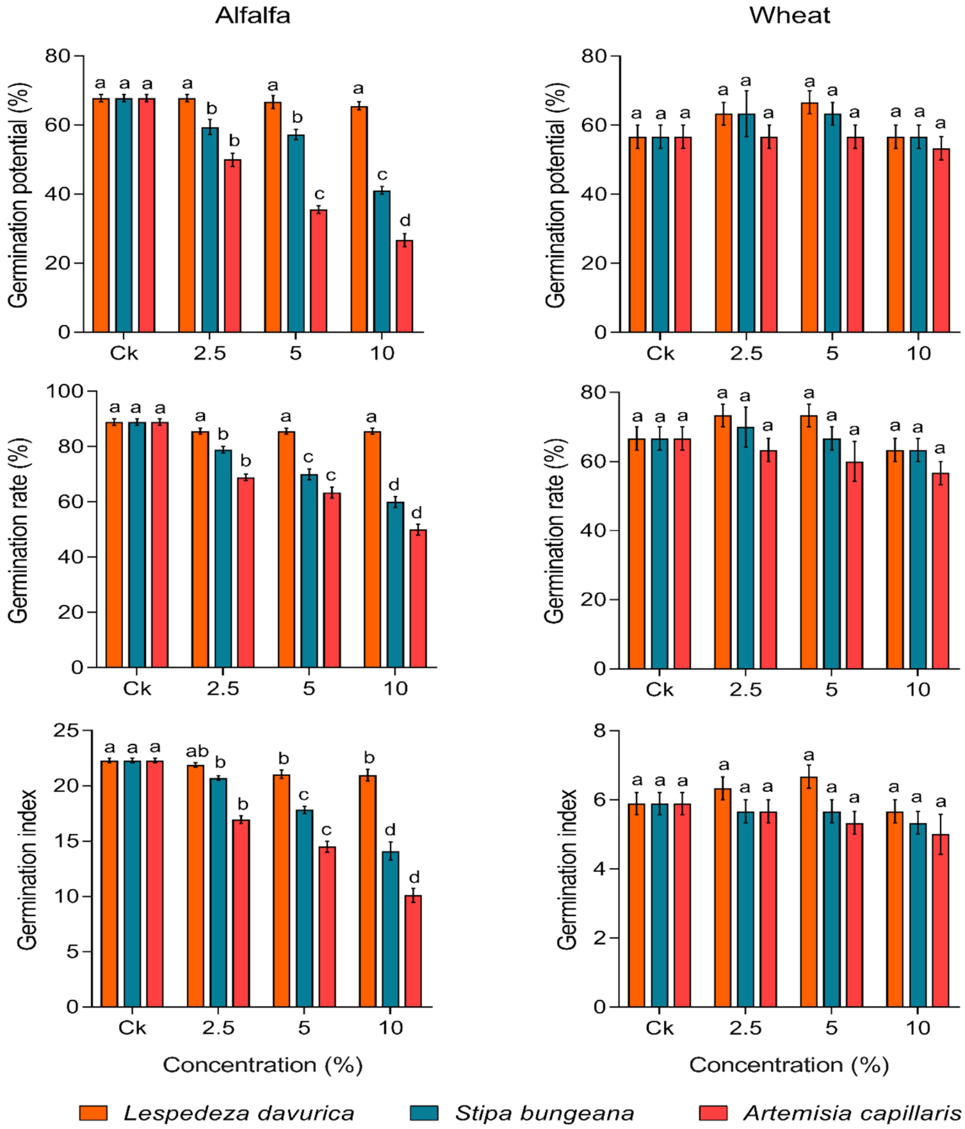


Fig. 2 Effects of different aqueous litter extract concentrations (0, 2.5, 5 and 10%) of three dominant native grass species *Lespedeza davurica, Stipa bungeana*, and *Artemisia capillaris* on seed germination potential (GP), germination rate (GR), and germination index (GI) of the target introduced exotic plant species of alfalfa and wheat. Values are means ± SE ($n = 3$). Different letters indicate significant ($P < 0.05$) differences between treatments

41.33% while the highest concentration (10%) did not show any significant effect (Fig. 3). However, *S. bungeana* extract significantly decreased the aboveground biomass of alfalfa at all concentrations compared to the control treatment. It reduced the aboveground biomass by 33.73, 38.92, and 60.40% at 2.5, 5, and 10% extract concentrations, respectively (Fig. 3). The *A. capillaris* extract showed variable effects at different concentrations, by improving the aboveground biomass by 31.75% at low concentration (2.5%), while significantly reducing the aboveground biomass by 30.53 and 54.48% at medium (5%) and high concentration (10%) compared to control, respectively (Fig. 3).

Belowground biomass of alfalfa was also significantly ($P < 0.05$) affected by *L. davurica, S. bungeana*, and *A. capillaris* as compared to the control. The application of *L. davurica* at low concentration (2.5%) did not show any significant effects but it reduced the belowground biomass by 9.76, and 18.03% at 5 and 10% concentration compared to control, respectively (Fig. 3). However, *S. bungeana* and *A. capillaris* showed negative effects on the belowground biomass of alfalfa at all concentrations. Application of *S. bungeana* decreased the belowground biomass by 9.76, 12.01, and 54.12%, while *A. capillaris* reduced it by 42.84, 64.09, and 65.45% at 2.5, 5, and 10% concentrations when compared to the control treatment, respectively (Fig. 3).

The litter extract of *L. davurica* at 2.5% concentration increased the aboveground biomass of wheat by 30.55%, while the other concentrations did not show any significant effects (Fig. 3). The *S. bungeana* litter extracts showed no significant effects on wheat aboveground biomass (Fig. 3). Similarly, *A. capillaris* had no significant effect at low concentrations but it reduced the wheat aboveground biomass by 16.66% at high concentration (10%) as compared with the control (Fig. 3). In comparison to control, *L. davurica and S.*

Table 2 Effects of different aqueous litter extract concentrations (0, 2.5, 5, and 10%) of three dominant native grass species *Lespedeza davurica*, *Stipa bungeana*, and *Artemisia capillaris* on seedling height (cm) of the target introduced exotic plants alfalfa. Values are means ± SE ($n = 3$)

Day after germination seedling height alfalfa (cm)									
Doner species	Concentration (%)	4	6	8	10	12	14	16	18
Lespedeza davurica	CK	1.35 ± 0.06^{a}	2.11 ± 0.15^{a}	3.36 ± 0.08^{a}	3.82 ± 0.06^{a}	4.5 ± 0.18^{a}	5.30 ± 0.03^{a}	5.85 ± 0.17^{a}	6.6 ± 0.14^{a}
	2.5	1.32 ± 0.03^{a}	1.85 ± 0.12^{a}	3.32 ± 0.20^{a}	3.70 ± 0.11^{a}	4.5 ± 0.05^{a}	5.17 ± 0.16^{a}	5.6 ± 0.15^{a}	5.8 ± 0.15^{b}
	5	1.23 ± 0.03^{a}	1.78 ± 0.05^{a}	3.26 ± 0.14^{a}	3.49 ± 0.15^{a}	4.4 ± 0.13^{a}	4.86 ± 0.17^{ab}	5.09 ± 0.36^{ab}	5.42 ± 021^{b}
	10	1.13 ± 0.08^{a}	1.7 ± 0.15^{a}	3.1 ± 0.06^{a}	3.38 ± 0.30^{a}	4.2 ± 0.20^{a}	4.4 ± 0.30^{b}	4.53 ± 023^{b}	4.56 ± 0.29^{c}
	SEM	0.0379	0.0690	0.0679	0.0885	0.0595	0.1371	0.1860	0.2372
	P	ns	ns	ns	ns	ns	*	*	*
Stipa bungeana	CK	1.24 ± 0.03^{a}	2.11 ± 0.15^{a}	2.7 ± 0.11^{a}	3.3 ± 0.11^{a}	4.7 ± 0.18^{a}	5.30 ± 0.03^{a}	5.85 ± 0.17^{a}	6.6 ± 0.14^{a}
	2.5	1.16 ± 0.08^{a}	1.66 ± 0.12^{a}	2.6 ± 0.05^{a}	3.3 ± 0.52^{a}	4.24 ± 0.03^{b}	5.08 ± 0.23^{ab}	4.95 ± 0.18^{b}	5.65 ± 0.28^{b}
	5	1.12 ± 0.05^{a}	1.58 ± 0.12^{a}	2.5 ± 0.11^{a}	3.1 ± 0.18^{a}	3.7 ± 0.03^{c}	4.69 ± 0.15^{bc}	4.90 ± 0.05^{b}	5.21 ± 0.32^{bc}
	10	1.05 ± 0.03^{a}	1.55 ± 0.17^{a}	2.5 ± 0.18^{a}	3.1 ± 0.21^{a}	3.5 ± 0.11^{c}	4.25 ± 0.14^{c}	4.46 ± 017^{b}	4.64 ± 0.20^{c}
	SE	0.0345	0.0894	0.0607	0.1320	0.1512	0.1397	0.1668	0.2401
	P	ns	ns	ns	ns	*	*	*	*
Artemisia capillaris	CK	1.2 ± 0.03^{a}	1.6 ± 0.08^{a}	3.4 ± 0.08^{a}	3.82 ± 006^{a}	4.74 ± 018^{a}	5.30 ± 0.03^{a}	5.85 ± 0.17^{a}	6.6 ± 0.14^{a}
	2.5	1.2 ± 0.08^{a}	1.5 ± 0.05^{a}	2.32 ± 0.14^{b}	3.14 ± 0.12^{b}	4.14 ± 021^{a}	4.84 ± 0.12^{b}	4.62 ± 0.20^{b}	5.22 ± 0.23^{b}
	5	$1.1 \pm 0.03a$	1.4 ± 0.14^{a}	2.0 ± 0.08^{Bc}	2.56 ± 0.17^{c}	3.48 ± 0.20^{b}	4.2 ± 0.15^{c}	4.53 ± 0.17^{b}	4.72 ± 027^{bc}
	10	1.1 ± 0.12^{a}	$1.4\ 0.12^{a}$	1.9 ± 0.11^{c}	2.37 ± 0.17^{c}	3.21 ± 0.17^{b}	3.75 ± 0.14^{d}	4.06 ± 0.20^{b}	4.35 ± 0.29^{c}
	SE	0.0272	0.0556	0.1792	0.1812	0.1986	0.1864	0.2157	0.27761
	P	ns	ns	*	*	*	*	*	*

Different letters and * indicate significant ($P < 0.05$) differences between treatments according to Fisher's least significant difference (LSD) test. Ns indicates no significant results

bungeana donor species improved wheat belowground biomass but *A. capillaris* did not show any significant results. The results showed that *L. davurica* at all concentrations significantly ($P < 0.005$) improved the belowground biomass by 100, 125, and 150% at 2.5, 5, and 10% concentrations respectively compared with control (Fig. 3). *S. bungeana* significantly improved belowground biomass only at low concentrations by 172 and 75% at 2.5 and 5% concentrations respectively but did not show any improvement at high concentrations when compared to control (Fig. 3).

Effects of Grass Aqueous Litter Extracts on the Root-to-Shoot Ratio of Alfalfa and Wheat

Applications of *L. davurica* at low concentrations (2.5 and 5%) and *A. capillaris* litter extract at all concentrations significantly ($P < 0.05$) inhibited the root-to-shoot ratio of alfalfa as compared to the control. Meanwhile, *S. bungeana* significantly improved the root-to-shoot ratio by 35.83, 43.75, 15.41% at 2.5, 5, and 10% concentrations, respectively (Fig. 4). Contrariwise, *A. capillaris* extracts significantly decreased the root-to-shoot ratio (56.66, 48.33, 24.16%) at all concentrations (2.5, 5, and 10%) respectively, while application of *L. davurica* extracts significantly reduced the root-to-shoot ratio only at low concentrations 2.5 and 5%, by 34.16, and 36.66%, respectively, while did not show any effect at high concentration (Fig. 4). In addition, the data showed that the root-to-shoot ratio of wheat was significantly ($P < 0.05$) increased with the application of *L. davurica* and *S. bungeana* litter extracts as compared to the control treatment. The *L. davurica* significantly improved the root-to-shoot ratio by 55.63, 124.81, and 181.95% at 2.5, 5, and 10% concentrations, respectively (Fig. 4). Similarly, our results indicated that *S. bungeana* litter extracts at concentrations 2.5, 5, and 10% significantly improved the root-to-shoot ratio by 175.18, 89.47, and 36.84, respectively compared with control (Fig. 4). The litter extract of *A. capillaris* at all concentrations did not show any inhibitory or regulatory effects on root-to-shoot ratios of wheat crop (Fig. 4).

Allelopathy Response Index (RI)

The litter extract from *L. davurica* grass showed the weakest sensitive effect while *S. bungeana* and *A. capillaris* aqueous litter extracts at concentrations of 2.5, 5, and 10% were negative and had inhibition effects on alfalfa germination and seedling growth (Table 4). Meanwhile, the response of wheat aqueous litter extracts of *L. davurica, S. bungeana,*

Table 3 Effects of different aqueous litter extract concentrations (0, 2.5, 5, and 10%) of three dominant native grass species *Lespedeza davurica, Stipa bungeana*, and *Artemisia capillaris* on seedling height (cm) of the target introduced exotic plants Wheat. Values are means ± SE ($n = 3$)

Day after germination seedling height wheat (cm)									
Doner species	Concentration (%)	4	6	8	10	12	14	16	18
Lespedeza davurica	CK	3.13 ± 0.56^{b}	5.99 ± 0.67^{a}	8.59 ± 0.87^{a}	10.87 ± 0.88^{b}	14.70 ± 1.14^{a}	18.06 ± 0.69^{b}	22.06 ± 0.59^{a}	24.44 ± 0.60^{b}
	2.5	4.60 ± 0.22^{a}	7.82 ± 0.41^{a}	10.72 ± 0.45^{a}	13.35 ± 0.11^{a}	17.32 ± 0.38^{a}	20.74 ± 0.56^{a}	23.17 ± 0.36^{a}	25.53 ± 0.49^{ab}
	5	5.39 ± 0.26^{a}	7.86 ± 1.06^{a}	10.22 ± 1.41^{a}	13.90 ± 0.44^{a}	17.37 ± 0.97^{a}	20.77 ± 0.68^{a}	22.83 ± 0.77^{a}	25.36 ± 0.15^{ab}
	10	4.96 ± 0.08^{a}	7.37 ± 0.99^{a}	10.38 ± 0.65^{a}	14.22 ± 0.22^{a}	17.46 ± 1.02^{a}	21.60 ± 0.14^{a}	22.65 ± 1.84^{a}	26.53 ± 0.13^{a}
	SE	0.3156	0.4198	0.4648	0.4228	0.5285	0.4619	0.3110	0.2730
	P	*	ns	ns	*	ns	*	ns	*
Stipa bungeana	CK	3.13 ± 0.56^{a}	5.99 ± 0.67^{a}	8.59 ± 0.87^{a}	10.87 ± 0.88^{a}	14.70 ± 1.14^{a}	18.06 ± 0.69^{a}	22.06 ± 0.59^{a}	24.44 ± 0.60^{a}
	2.5	3.58 ± 0.09^{a}	6.48 ± 1.08^{a}	9.36 ± 1.08^{a}	11.74 ± 1.12^{a}	15.46 ± 0.83^{a}	18.62 ± 0.72^{a}	22.07 ± 0.46^{a}	24.60 ± 0.38^{a}
	5	3.71 ± 1.04^{a}	6.62 ± 1.14^{a}	8.98 ± 0.83^{a}	11.14 ± 1.09^{a}	14.94 ± 1.22^{a}	17.50 ± 1.20^{a}	20.82 ± 1.06^{a}	23.74 ± 0.48^{a}
	10	4.06 ± 0.62^{a}	7.16 ± 0.92^{a}	9.84 ± 1.03^{a}	12.22 ± 1.32^{a}	15.74 ± 0.47^{a}	18.91 ± 0.72^{a}	20.97 ± 0.83^{a}	24.41 ± 0.99^{a}
	SE	0.3054	0.4329	0.4321	0.5023	0.4311	0.3993	0.3729	0.29622
	P	ns	ns	ns	ns	ns	ns	ns	ns
Artemisia capillaris	CK	3.13 ± 0.56^{a}	5.99 ± 0.67^{a}	5.59 ± 0.87^{a}	10.87 ± 0.88^{a}	14.70 ± 1.14^{a}	18.06 ± 0.69^{a}	22.06 ± 0.59^{a}	24.44 ± 0.60^{a}
	2.5	4.62 ± 0.28^{a}	8.17 ± 0.09^{a}	11.16 ± 0.47^{a}	13.62 ± 0.39^{a}	18.12 ± 0.76^{a}	21.24 ± 1.03^{a}	23.04 ± 1.41^{a}	25.06 ± 0.66^{a}
	5	3.01 ± 1.35^{a}	5.24 ± 2.43^{a}	10.07 ± 2.08^{a}	11.35 ± 2.75^{a}	15.36 ± 3.17^{a}	18.25 ± 3.53^{a}	20.54 ± 3.02^{a}	22.44 ± 3.27^{a}
	10	4.29 ± 0.42^{a}	7.27 ± 1.02^{a}	9.91 ± 0.70^{a}	12.18 ± 0.27^{a}	15.59 ± 0.19^{a}	19.18 ± 0.46^{a}	21.27 ± 0.32^{a}	24.41 ± 0.73^{a}
	SE	0.3931	0.6751	0.5857	0.7034	0.8368	0.8931	0.7786	0.8023
	P	ns	ns	ns	ns	ns	ns	ns	ns

Different letters and * indicate significant ($P < 0.05$) differences between treatments according to Fisher's least significant difference (LSD) test. Ns indicates no significant results

and *A. capillaris* is presented in (Table 5). The data revealed that the aqueous litter extracts of *L. davurica,* at low concentrations of 2.5 to 5% were positive and had promotional effects, while *A. capillaris* extracts at all tested concentrations inhibited germination, aboveground and belowground biomass, whereas, *S. bungeana* showed inhibition effects only at high concentrations. These results suggested that wheat is more insensitive to aqueous litter extracts as compared to alfalfa (Table 5).

Discussion

Allelopathy is an important mechanism of interference in which one plant releases bioactive compounds into the surrounding environment that affect the growth of neighboring plants, and the majority of plants can attain a dominating position through allelopathic effects (Latif et al. 2017). Seed imbibition is an important phase of seed germination (Wang et al. 2011). With some exceptions (Chon et al. 2004), the impact of allelochemicals on seed imbibition is rarely addressed in allelopathic studies. Results from the present study indicated a decrease in water uptake by alfalfa seeds with increasing concentration of aqueous extracts, suggesting the negative impact of *S. bungeana* and *A. capillaris* allelopathy on seed imbibition. A similar trend of changes was observed regarding water uptake of receptor plant species that suggested the inhibition of water uptake by allelopathic species (Han et al. 2008). Further, the inhibitory effect of allelochemicals from black mustard leaves was investigated, and increasing its concentration significantly inhibited water uptake by wild barley seeds (Tawaha and Turk 2003). In the present study, the litter extract of *L. davurica* at a low concentration significantly improved the wheat seeds' weight as compared to the controlled group. In general, it is assumed that physiologically active substances activated the embryo and other associated structures, which led to increased water absorption due to elasticity in the cell walls (Kamaraj and Padmavathi 2012; Renugadevi et al. 2008).

The seed germination potential of a plant depends on the speed and uniformity of seed germination (Kamran et al. 2021). The germination rate is dependent on survival rate and population density, while the germination index generally reflects the receptor plant seeds' germination process (Siri-Udom et al. 2017). Our results portrayed that the *S. bungeana* and *A. capillaris* extracts significantly inhibited the seeds germination potential, seed germination

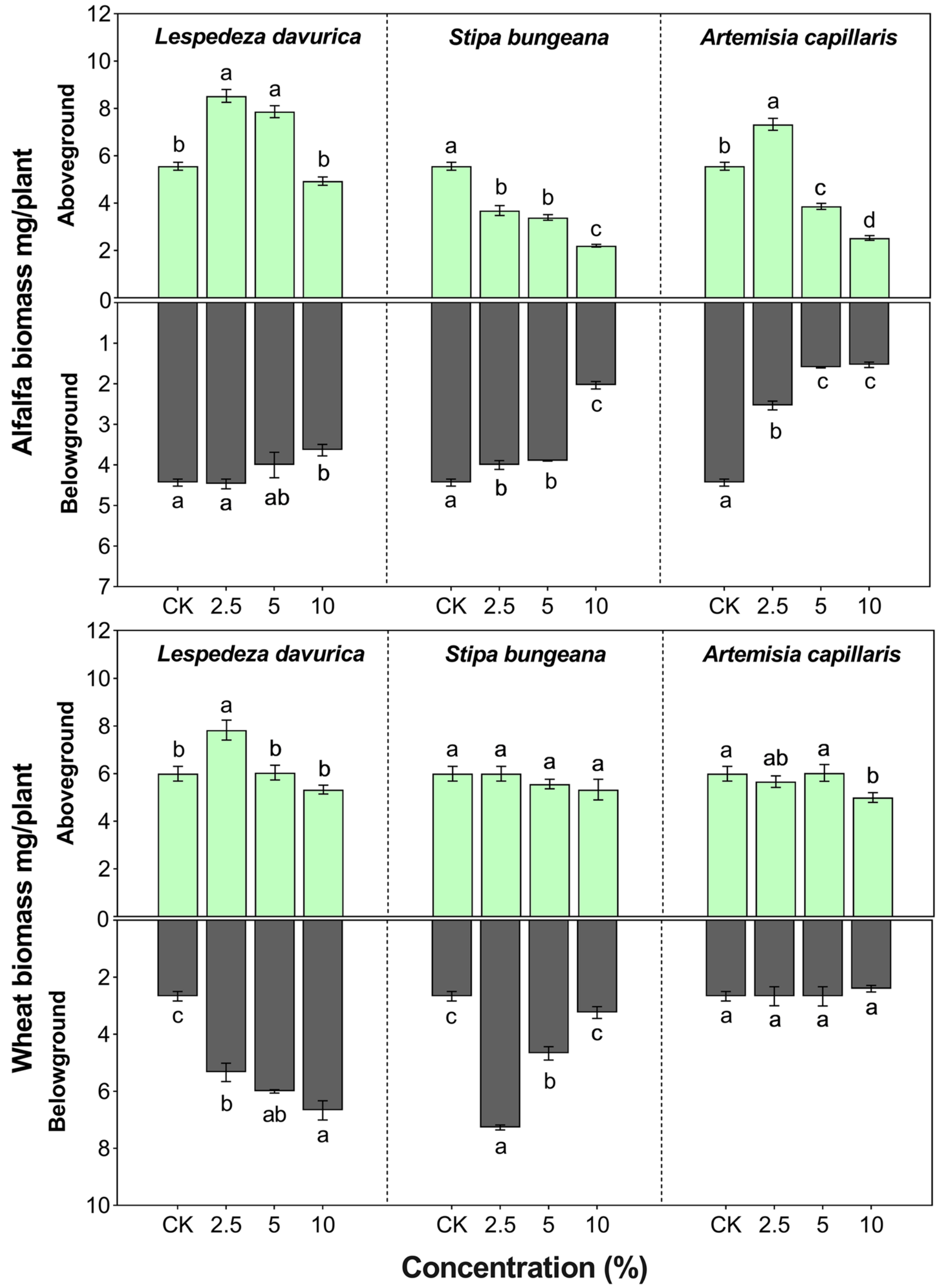


Fig. 3 Effects of different aqueous litter extract concentrations (0, 2.5, 5, and 10%) of three dominant native grass species *Lespedeza davurica*, *Stipa bungeana*, and *Artemisia capillaris* on aboveground, and belowground biomass of the target introduced exotic plant species of alfalfa and wheat. Values are means ± SE ($n = 3$). Different letters indicate significant ($P < 0.05$) differences between treatments

percentage, and seed germination index of alfalfa and the inhibitory effects of the extracts increased with increasing concentrations. These results are consistent with results from a previous study that reported the inhibition of barley seeds by *Artemisia annua* aqueous extracts (Salman et al. 2017). The inhibition effects of these extracts on germination could be attributed to the presence of water-soluble inhibitory allelochemicals affecting the physiological processes of receptor plants (Dai et al. 2021; Knudsmark Jessing et al. 2014; Tian et al. 2020). For an instant, phytotoxins found in Artemisia species are known to be or can be converted into germination-inhibitory chemicals (Wei et al. 2020). Moreover, various components such as chlorogenic acid, luteolin, gallic acid, p-coumaric, β-pinene, and γ-curcumene identified in *A. capillaris* (Jung et al. 2012; Nigam et al. 2019; Vokou et al. 2003; Won 2009), several flavonoids (quercetin, epicatechin, and rutin) isolated from *L. davurica* (Xu et al. 2010) are known to have inhibitive effects on membrane permeability, mitochondrial respiration, protein synthesis, and enzymatic activities and therefore, might be responsible for delaying the seed germination (Chowhan et al. 2013; Ertani et al. 2016;

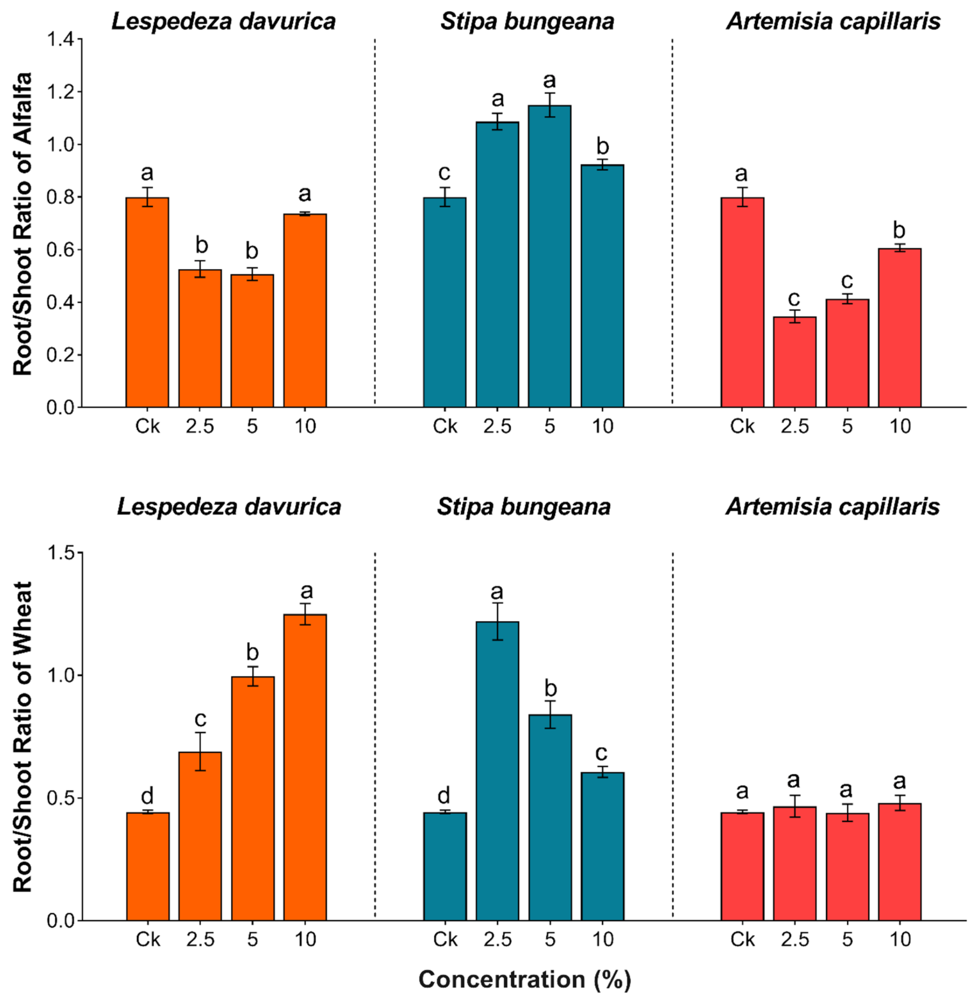


Fig. 4 Effects of different aqueous litter extract concentrations (0, 2.5, 5, and 10%) of three dominants native grass species *Lespedeza davurica, Stipa bungeana,* and *Artemisia capillaris* on Root/shoot ratio of the target introduced exotic plant species of alfalfa and wheat. Values are means ± SE ($n = 3$). Different letters indicate significant ($P < 0.05$) differences between treatments

Table 4 Effects of different aqueous litter extract concentrations (2.5, 5, and 10%) of three dominant native grass species *Lespedeza davurica, Stipa bungeana*, and *Artemisia capillaris* on response index (RI) of the target introduced exotic plants of alfalfa

Doner species	Concentration (%)	Response index (RI)			Sensitive effect (SE)
		Germination rate	Aboveground biomass	Belowground biomass	
Lespedeza davurica	2.5	−0.04	0.35	0.01	0.31
	5	−0.04	0.29	−0.12	0.13
	10	−0.04	−0.13	−0.22	−0.39
Stipa bungeana	2.5	−0.13	−0.34	−0.11	−0.58
	5	−0.27	−0.33	−0.14	−0.74
	10	−0.49	−0.82	−1.19	−2.50
Artemisia capillaris	2.5	−0.29	0.24	−0.76	−0.81
	5	−0.41	−0.45	−1.79	−2.64
	10	−0.78	−1.21	−1.90	−3.89

The positive values indicate promotion effects and negative values indicate inhibition effects

Ferreira and Aquila 2000; Jmii et al. 2020; Kato-Noguchi et al. 2010; Ozaki and Kato-Noguchi 2016). Moreover, an indirect consequence of allelopathic inhibition of germination due to reduced water uptake (Tawaha and Turk 2003). The allelopathic effect of *A. capillaris* extracts was stronger than that of *S. bungeana*. However, there was very little or no inhibition effect of *S. bungeana* and *A. capillaris* extracts on seed germination of wheat. Previously, some studies have reported that the metabolic systems in plants are disrupted only when the concentration of

Table 5 Effects of different aqueous litter extract concentrations (2.5, 5, and 10%) of three dominant native grass species *Lespedeza davurica, Stipa bungeana*, and *Artemisia capillaris* on response index (RI) of the target introduced exotic plants of wheat

Doner species	Concentration (%)	Response index (RI)			Sensitive effect (SE)
		Germination rate	Aboveground biomass	Belowground biomass	
Lespedeza davurica	2.5	0.09	0.23	0.50	0.81
	5	0.09	0.00	0.56	0.65
	10	−0.06	−0.13	0.60	0.41
Stipa bungeana	2.5	0.03	−0.01	0.63	0.65
	5	0.00	−0.08	0.43	0.34
	10	−0.06	−0.14	0.17	−0.03
Artemisia capillaris	2.5	−0.06	−0.06	−0.03	−0.15
	5	−0.14	−0.01	−0.06	−0.20
	10	−0.18	−0.20	−0.11	−0.49

The positive values indicate promotion effects and negative values indicate inhibition effects

extracts reaches a certain level (Kato-Noguchi et al. 2017). Therefore, we conclude that the difference in the inhibition effects might be related to the tolerance mechanism of plants, and hence, alfalfa was more sensitive to the applied extracts compared to wheat. These findings are in agreement with those of Zhang et al. (2017) who reported differential effects of extracts tested on various plant species.

Seedling height is one of the most important indicators to study the effects of the liquid extract on the seedling growth of recipient species. A significant reduction in plant growth, in terms of shoot length, was evident in the present study. The decrease in shoot length of the alfalfa seedlings was directly proportional to the increase in the concentration of allelopathic plant extracts used in the experiment. The shoot length of alfalfa was inhibited by the *L. davurica, S. bungeana,* and *A. capillaris* litter extracts in a concentration-dependent manner. *A. capillaris* extract was most effective in suppressing the shoot growth of alfalfa. Similar effects inhibitive effects on shoot length of wheat and field mustard were previously reported after treating with Artemisia species extracts (Mallik et al. 2015). Shoot elongation of the lettuce plant was found to be inhibited by the application of Artemisinin extracts in a dose-dependent manner (Yan et al. 2015). The growth inhibition of target species with *A. capillaris* might be the result of the presence of bioactive compounds like neochlorogenic acid, 7-hydroxycoumarin, ursolic acid, and caffeic acid (Nigam et al. 2019). Previously, the detrimental effects of these compounds on different crops have been reported by various studies (Ladhari et al. 2018; Rawat et al. 2013; Selvi and Kadamban 2009). The defense mechanism of the wheat crop is considered to be more robust than that of alfalfa as a receptor plant. In the present investigation, the litter extract of *L. davurica* at a high concentration significantly improved the wheat seedling height as compared to the controlled group. We hypothesize that litter extracts of *L. davurica* contain complex carbohydrates as well as unknown diffusible allelochemicals that might have stimulated the response of wheat seedlings, leading to higher shoot lengths. Previously, researchers have observed that rice hull extracts promoted the growth of different plants, including wheat, by stimulating their shoot length (Seyyednejad et al. 2010). The primary effects of allelochemicals include altering the permeability of the plant cell membrane, which may result in secondary effects, such as changes in water and mineral absorption potentials, pH variations, mutations of enzymes resulting either in stimulatory or inhibitory effects (Barkosky et al. 2000; Gatti et al. 2010; Majeed et al. 2012). In response to allopathic stress, carbohydrates and protein contents of the target plant build up more proline as a stress indicator; consequently, plant growth is either enhanced or inhibited (Al-Johani et al. 2012; Batish et al. 2007).

Among the allopathy effects, inhibition of plant biomass is one of the major constraints. The present study revealed both positive and negative allelochemical impacts upon introduced species. Previous studies have shown that low concentrations of few extracts show positive interaction and promote growth; meanwhile, higher concentrations resist the growth of recipient species (Arowosegbe and Afolayan 2013; Wang et al. 2018). The application of *L. davurica* litter extract at low concentrations significantly improved alfalfa aboveground biomass but inhibited belowground biomass at high concentrations compared to control treatment. On the other hand, *S. bungeana* litter extracts decreased the above and belowground biomass at all concentrations, while *A. capillaris* showed positive effects at low concentrations on aboveground biomass, but had inhibitive effects at high concentrations on above- and belowground biomass of alfalfa when compared to control. We conclude that different concentrations of the plant aqueous extract have different influences on the growth behavior of the same plant species. Previously, Yuan and Hou have also reported that the allelochemicals inhibitive effects greatly depend on the concentration of the extract (Yuan and Hou 2010). Similarly, fresh and dry weights of *Plantago ovate* were both reduced after treatment with *A. annua* extract (Moussavi-Nik et al. 2011). Several plant species produce allelochemicals that reduce the quantum efficiency of photosystem II, resulting in a reduction of photosynthesis assimilation (Colom and Vazzana 2003). In the present study, the application of *S. bungeana* and *A. capillaris* litter extracts could be attributed to their inhibitive effects on reducing the photosynthetic activity of alfalfa seedlings. Root growth (belowground biomass) was more sensitive to allelochemicals present in *A. capillaris* litter extract than shoot growth (aboveground biomass), which was also confirmed by a previous study (Khan and Kato-Noguchi 2016). In another study, *Achillea biebersteinii* (Asteraceae) extract significantly reduced the rate of root growth compared to pepper shoot growth (Abu-Romman 2011). In plants, the root system is most sensitive to allelochemicals, which is the result of direct contact between the root system and toxic phytochemicals and due to the high permeability of root tissues (Abd El-Gawad 2016; Abu-Romman and Ammari 2015; Nishida et al. 2005). However, wheat aboveground dry biomass was significantly improved when it was treated with *L. davurica* litter extract at low concentrations, meanwhile; a gradual increase in the belowground biomass with increased concentrations of *L. davurica* extracts was observed. At the same time, *S. bungeana* did not show any significant effects on wheat aboveground biomass but significantly improved belowground biomass of wheat at low concentrations. These results are consistent with the findings of Hozayn et al. (2015), who carried out pot and field experiments to investigate the allelopathic effects of *Casuarina equisetifolia* leaf litter and observed an improving effect on the growth of wheat. Similarly, (Brockman and Brennan 2017), established that foliar application of moringa leaf extract increased some morphological growth parameters of wheat crop. Musyimi and Uzoma (Musyimi et al. 2015; Uzoma et al. 2019) suggested that the stimulatory effect on the morphological growth parameters corresponded to an increase in total chlorophyll and phenolic content.

The root/shoot ratio is a very reliable indicator of morphological, physiological, and biochemical changes in developing seedlings. In the present investigation, it was found that *L. davurica,* at low concentrations while *A. capillaris* at all concentrations significantly decreased the root/shoot ratio of alfalfa as compared to control. The correlation analysis also showed that the reduction in root/shoot ratio was the result of inhibition of root dry biomass production rather than shoot dry biomass (Zohaib et al. 2018). The possible reason might be the direct contact of roots with allelopathic leachates resulting in inhibition of root length. The retarded root system restricted the ability of the individual plants to compete for underground resources such as water, reducing above-ground growth (Merrill et al. 2002). The decreased values of root/shoot ratios were also reported in two different varieties of rice due to aqueous extracts *of Ageratum Borreria* (Gogoi et al. 2002). In the present study, higher values of root/shoot ratios were observed in wheat when treaded with aqueous litter extracts of *L. davurica,* and *S. bungeana* as compared to control. A similar trend was noticed in seedlings of *Sorghum bicolor* L. and *Cenchrus americanus* L. when treated with extracts of aspidium rhizomes (Bhalerao et al. 2000). Another study also investigated that, aqueous extracts of sterile oat, and aleppo grass strongly affected seedling growth parameters especially the root/shoot ratio of common purslane and alfalfa (Othman et al. 2018). Several physiological and metabolic alterations take place due to allelochemicals (D'Abrosca et al. 2013), such as phenolics, terpenoids, and organic acids, are or can be converted into inhibitory compounds (Wei et al. 2020). *A. capillaris* major components identified, acenaphthylene (37.91%), 4-carene (10.61%), β-pinene (12.08%), and γ-curcumene (9.92%), that could lead to positive or negative interactions (Vokou et al. 2003). Flavonoids (kaempferol, tamarixetin, luteolin, quercetine, epicatechin, trifolin, isoorientin, and rutin) were isolated from *L. davurica* (Xu et al. 2010).

Conclusion

In summary, our results demonstrated that previous pasture residues inhibit the establishment of introduced exotic plant species by exerting allelopathic effects, the potential of allelochemicals varied from one species to another depending on the concentration of the aqueous extract. The wheat germination indices were more resistant to allelopathic chemicals at all concentrations in comparison to alfalfa. Among all donor plant species, *Artemisia capillaris* and *Stipa bungeana* showed the most inhibitive effects on seed imbibition, germination, and morphological indices of alfalfa. So, introducing exotic crops to grassland previously cultivated with *Artemisia capillaris* and *Stipa bungeana* should be observed for their impacts on the proceeding crops. This study provides a basis for establishing and managing cultivated grasslands for future food stability and economic development.

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Author Contributions FH conceived and designed the experiment. MUG and YH performed the experiments. MT contributed to reagents/materials/analysis tools. MUG wrote the manuscript. MK assisted in data analysis and English language revision. All authors read and approved the final manuscript.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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