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Plant–plant interactions could limit recruitment and range expansion of tall shrubs into alpine and Arctic tundra

ORIGINAL PAPER

Plant–plant interactions could limit recruitment and range expansion of tall shrubs into alpine and Arctic tundra

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Abstract

Species in cold-limited biomes are expected to expand their distribution ranges in response to climate warming. For plants, range shifts can only occur via successful recruitment beyond their current distribution limit. However, many environmental and ecological filters can act upon recruitment and establishment, thereby potentially limiting the expected climate-driven shifts. In this study, we investigate potential mechanical and chemical constraints that vegetation above the tall shrubline in alpine and Arctic tundra could impose upon the successful establishment of willow species in the Canadian Western Arctic. We collected willow seeds from an alpine and an Arctic shrubline and conducted germination trials to test (1) for seedbed preferences among three natural and one experimentally scarified seedbeds, and (2) for vulnerability to allelopathic chemicals produced by ericaceous dwarf shrub species. We found that germination was almost four times higher on manually exposed bare ground than on intact, herbaceous vegetation. Seeds of two willow species, *Salix arctica* and *Salix pulchra*, were not affected by leaf extracts from dwarf shrubs, *Cassiope tetragona* and *Vaccinum uliginosum*, but the germination of *Salix richardsonii* was reduced by as much as 24% in the presence of chemicals from *C. tetragona*. Our results suggest that biotic interactions could limit the predicted expansion of tall shrubs in the tundra by interfering with germination. Seemingly species-specific responses highlight the need for replicated studies across a wider range of species combinations. Potential range shifts may not occur as a uniform translocation of the shrubline, but could change the composition of the plant community by filtering out certain species.

Keywords Allelopathy · Seedbed · Germination · Seedlings · Shrubline · Tundra

Introduction

Ecosystem boundaries are in part controlled by temperature, and have shifted with past variations in climate as species migrated to track their climatic optimum (Davis and Shaw 2001). Under the current rapid rates of warming at the global scale (IPCC 2013), latitudinal or elevational advances in distribution limits have recently been observed in most taxa including invertebrates, plants, birds, and mammals (Chen et al. 2011). In tundra ecosystems, tall shrub species are projected to expand their range up mountain slopes and northward to higher latitudes (Post et al. 2009; Myers-Smith et al. 2011).

In sessile species such as plants, range shifts occur via the recruitment and establishment of new individuals beyond the current distribution limit. Because of the multiple environmental and ecological filters acting on regeneration (Fig. 1), these shifts are spatially heterogeneous and often lag changes in climate (Corlett and Westcott 2013; Ash et al. 2016). For instance, treelines have only advanced in around half of the sites studied in a global meta-analysis (Harsch et al. 2009). Similarly, although tundra shrubs have been expanding in the circumpolar region over the last half-century (Myers-Smith et al. 2011), most of the observed increases in growth and reproduction have only led to population infilling, and range shifts remain mostly anecdotal (but see Myers-Smith and Hik 2017). Some of the non-climatic limitations interfering with range expansion may include species traits like dispersal ability (Brooker et al. 2007; Kambo and Danby

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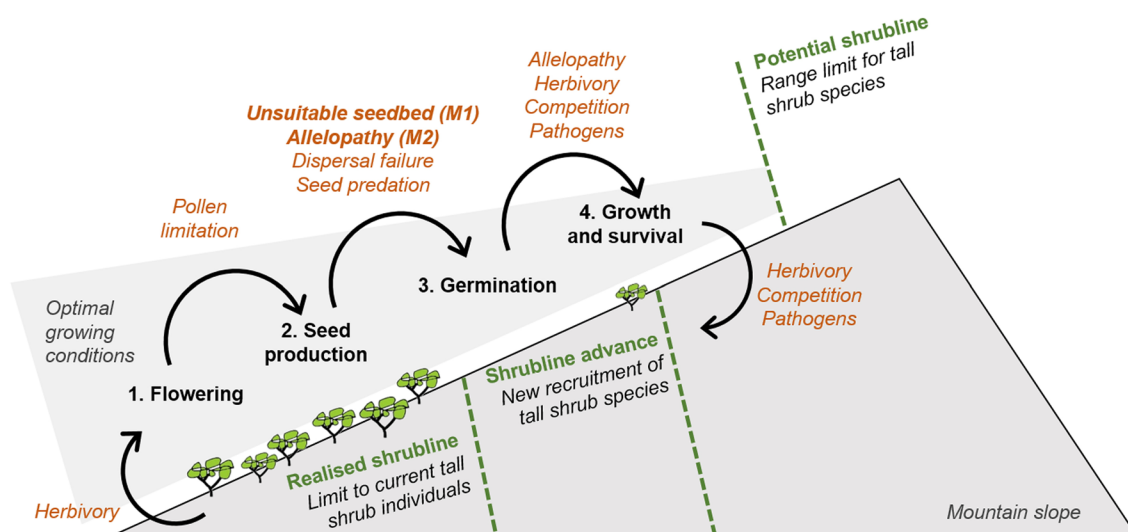
Fig. 1 Biological constraints (orange) potentially acting as ecological filters on the process of regeneration (green) above the shrubline with the mechanisms of seedbeds (mechanism 1) and allelopathy (mechanism 2) highlighted in bold, the foci of this study. (Color figure online)

2017), and a wide range of biotic interactions (reviewed in HilleRisLambers et al. 2013).

Species interactions are affected by climate change, and in turn control community assembly in environments where new species could meet their temperature requirements (Tylianakis et al. 2008; Gilman et al. 2010; Van der Putten et al. 2010). In plant communities, interactions with herbivores (Olofsson et al. 2009; Munier et al. 2010; Christie et al. 2015), soil biota (Van Grunsven et al. 2007), pathogens (Olofsson et al. 2011) and other plants (Grau et al. 2012; Liang et al. 2016) may all promote or constrain range shifts. It is therefore critical to better understand biotic interactions and incorporate them in species distribution models (Brooker et al. 2007; Hellmann et al. 2012; Meier et al. 2012).

In addition to direct competition for resources, several other types of plant–plant interactions can interfere with the establishment of a species beyond its current range. The vegetation already in place can prevent seeds from reaching a suitable seedbed. For instance, conifers at the treeline have been shown to become preferentially established after disturbance exposing the bare ground (Dufour Tremblay and Boudreau 2011). In addition, vegetation may chemically interfere with seed germination when allelopathic species are present. Allelopathy is the production of toxic compounds by some plants; when leached into the ground, these chemicals can affect the germination, growth, and survival of other species (Wardle et al. 1998). For example, some conifer seeds and seedlings are vulnerable to chemicals released by ericaceous dwarf shrubs (Nilsson and Zackrisson 1992; Dufour Tremblay et al. 2012). It is currently unknown whether these biotic controls of treeline dynamics act similarly upon shrublines at higher latitudes and elevations.

To investigate whether plant–plant interactions have the potential to limit range shifts of tall shrubs into the tundra, we carried out germination experiments using seeds of widespread and rapidly expanding willow species (*Salix* spp.) collected from an Arctic and an alpine shrubline in the Yukon Territory. Our research question was the following: Does vegetation above the tall shrubline affect the germination of shrub seeds? We experimentally tested two potential mechanisms of interference: (1) vegetation acts as a physical barrier preventing shrub seeds from reaching a suitable seedbed (M1 in Fig. 1); and (2) chemicals released by ericaceous dwarf shrubs inhibit germination (M2 in Fig. 1). Correspondingly, we predicted (1) that seeds of the tall willow shrub, *Salix pulchra* Cham. would germinate to a higher extent on bare ground than on vegetated ground, and (2) that seeds of the tall willows *S. pulchra* and *Salix richardsonii* Hooker and of the dwarf willow *Salix arctica* Pall., would germinate to a lesser extent when exposed to potentially allelopathic leachates from the ericaceous dwarf shrubs, *Vaccinium uliginosum* L. And *Cassiope tetragona* (L.) D. Don.

Materials and methods

Study sites

We conducted two germination experiments (scarification and allelopathy) on Qikiqtaruk-Herschel Island (69.568°N, 138.918°W), a Yukon territorial park in Northern Canada.

The allelopathy experiment was replicated in the Kluane region of the Southwest Yukon Territory (61.027°N, 138.411°W, Fig. 2). These two sites are 1000 km apart and represent both Arctic and alpine tundra ecosystems where tall shrubs are thought to be expanding their ranges.

Qikiqtaruk is underlain by ice-rich permafrost (Burn and Zhang 2009) and harbours several types of tundra vegetation (described by Smith et al. 1989), including the Herschel type characterised by moist acidic tussock tundra, and the Komakuk type comprising herbaceous tundra disturbed by freeze–thaw processes. Alpine habitats of the Kluane Region are underlain by bedrock containing permafrost. The alpine zone is characterised by willow-dominated tall shrub tundra transitioning to dwarf shrub and herbaceous tundra at around 1600-1900 m elevation (Myers-Smith 2011).

On Qikiqtaruk, both experiments were set up in front of a window in an unheated warehouse. The average daily minimum, mean and maximum temperatures during the 10 days spanning both experiments were 7.4/12.0/18.0 °C, respectively, measured by iButton Thermochron data loggers (±1 °C, model DS1921G-F5, Dallas Semiconductor Corporation, Dallas, TX, USA) with hourly recording. In Kluane, the allelopathy experiment was set up in a laboratory (average daily minimum, mean and maximum temperatures were 18.9/21.0/24.1 °C, respectively, measured as above over 9 days). A scarification experiment was initially also set up in Kluane, but coincided with a week of unusually high temperatures. The laboratory not being climate controlled, this resulted in the seedlings drying out and dying within 48 h after emerging, and the experiment was discontinued.

Study species

Salix pulchra and *Salix richardsonii* are willow species with an erect growth form. They are widespread in the Western Arctic and dominant species at our study sites; on Qikiqtaruk, they approximately reach their northern distribution limit (Argus 2007). *Salix arctica* is a dwarf willow widely distributed in the circumpolar region all the way up to the High Arctic, over 80°N (Argus 2007). It is a dominant species on Qikiqtaruk and could therefore greatly contribute to woody plant encroachment there. However, germination of this species is highly variable both spatially and temporally, and thus expansion could be limited by regeneration failures (Boulanger-Lapointe et al. 2016). This is why we included this species in the experiment despite it being far from its leading range edge. Willows are capable of spreading clonally, but while this certainly contributes to the infilling of existing populations (Myers-Smith et al. 2011), colonisation of new sites in a range shift context requires establishment from seed. Willows tend to be early-successional plants characterised by fast growth rates (Bret-Harte et al. 2002) and the production of great numbers of small, wind-dispersed seeds that can recolonize sites rapidly after disturbances (Brinkman 1974; Forbes et al. 2001).

Vaccinium uliginosum, a blueberry, is an ericaceous deciduous dwarf shrub known to have allelopathic effects on conifer seeds (Dufour Tremblay et al. 2012). *Cassiope tetragona* is an ericaceous evergreen dwarf shrub for which no allelopathic effects have yet been reported; however, it has been shown to interfere with the growth of Arctic

Allelopathy experiments

Shrub species	Treatment
Salix pulchra	Control
Salix richardsonii	*Cassiope tetragona*
Salix arctica	

Shrub species	Treatment
Salix pulchra	Control
Salix richardsonii	*Cassiope tetragona*
	Vaccinium uliginosum

Scarification experiment

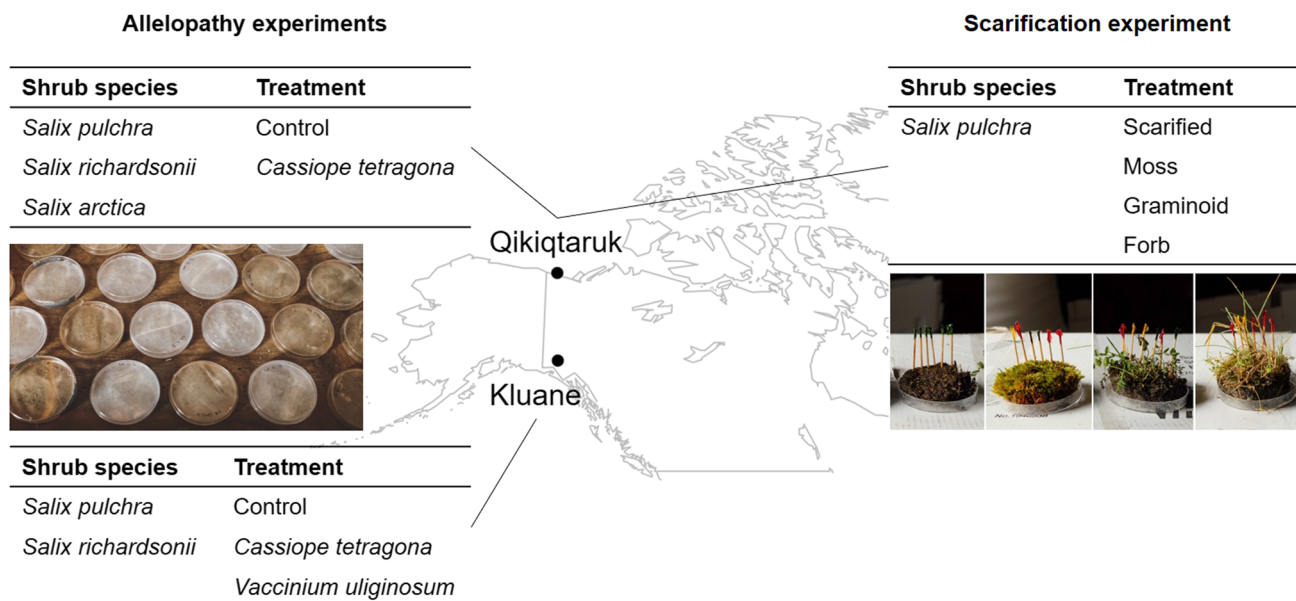| Shrub species	Treatment
Salix pulchra	Scarified
	Moss
	Graminoid
	Forb

Qikiqtaruk

Kluane

Fig. 2 Location of the two field sites in the Western Canadian Arctic and details of the experiments carried out at each research station using seeds from local shrubline tundra sites

graminoids (Michelsen et al. 2012). These dwarf shrubs typically come in later during succession (Lambert 1972) and have higher investments in reproduction and defences.

Scarification experiment

Our first objective was to test whether seedbed type influenced willow germination. The four seedbeds tested were (1) moss-dominated; (2) grass-dominated; (3) forb-dominated; and (4) scarified. For each treatment, we collected four discs (10 cm diameter, ca. 3 cm deep) of undisturbed tundra vegetation on Qikiqtaruk. Cover of the target vegetation type for the moss, grass and forb treatments was over 90% on each disc. For the scarified discs, we randomly collected discs with a mixed cover of grasses and forbs and carefully stripped them of all above-ground vegetation to expose the organic soil. Samples were collected in a ca. 50-m-by-50-m plot on a south-facing ridge belonging to the Komakuk vegetation type (Smith et al. 1989) and brought back to the warehouse.

Catkins of *Salix pulchra* were collected at a nearby site. Only ripe catkins were collected, and no more than 10 catkins per individual shrub were harvested to reduce genetic bias. Seeds were all pooled together before sowing on the discs.

On all discs, 36 seeds were sown in a six-by-six arrangement, with a toothpick marking the emplacement of each row to facilitate monitoring. The discs were misted twice daily with a spray-bottle containing distilled water to prevent seeds from drying. Emergence was monitored daily until no further germination occurred.

Allelopathy experiment

Our second objective was to test whether willow seeds were vulnerable to potentially toxic compounds leached from the leaves of two ericaceous dwarf shrubs. Allelopathy experiments were run at both field sites (Fig. 2). In the alpine shrub tundra of Printer's Pass (Ruby Range mountains, Kluane), we collected ca. 200 ripe catkins of *S. pulchra* and *S. richardsonii* following the sampling protocol described in the previous section. Around 100 g of fresh leaves of *Vaccinium uliginosum* and *Cassiope tetragona* were collected in the same area. Leachates were prepared by soaking 75 g of leaves in 500 mL of distilled water for 24 h to obtain a 15% solution (Dufour Tremblay et al. 2012).

On Qikiqtaruk, around 150 catkins were collected for *S. pulchra*, *S. richardsonii* and *S. arctica*. As *V. uliginosum* is not locally abundant, we only used a leachate of *C. tetragona* in this experiment. The leaf extract was prepared as described above.

Seeds were sown on filter paper in 9-mm Petri dishes (25 seeds per dish in Kluane; 50 seeds per dish on Herschel Island). At the start of the experiment, 3 mL of either leaf extract (*C. tetragona* or *V. uliginosum*) or distilled water (control treatment) were put in every dish. We added 2 mL of the same treatments the following day, then kept all dishes moist as needed with distilled water for the duration of the experiment. In Kluane, we set up eight replicate dishes of the factorial design (all combinations of species and treatments). On Qikiqtaruk, we set up four replicate dishes. The dishes were spatially randomised and rotated daily to avoid spatial effects. We monitored emergence daily until no further germination occurred.

Statistical analyses

Analyses were conducted using generalised linear models with a binomial distribution (logit link function) to account for germination rates being constrained between 0 and 1. Germination rates were not zero-inflated. For the scarification experiment, which was conducted with a single species, we used seedbed as the explanatory variable. For the allelopathy experiments, we ran separate models for the two study locations, using treatment (control, *V. uliginosum* extract, *C. tetragona* extract) and willow species as interacting explanatory variables. When means differed significantly among treatments, we conducted Tukey's post hoc tests using the "lsmeans" package. All analyses were conducted in R v. 3.3.2 (R Core Team 2016).

Results

Scarification experiment

Emergence of *Salix pulchra* was significantly higher on scarified ground than on forb- or grass-dominated ground, and intermediate on moss-covered ground (Fig. 3; Table 1A). Germination started within 24 h of sowing and ceased after 4 days.

Allelopathy experiment

On Qikiqtaruk (Fig. 4a; Table 1B), *S. pulchra* and *S. richardsonii* had high and similar germination rates, but the germination of *S. richardsonii* was reduced in the presence of *C. tetragona* leaf extract, while that of *S. pulchra* was not. *Salix arctica* experienced much lower germination that was not affected by the allelopathic treatment.

In Kluane (Fig. 4b; Table 1C), the germination of *S. richardsonii* was slightly lower than that of *S. pulchra,* and like on Qikiqtaruk, was reduced in the presence of *C. tetragona* leaf extract compared to the control. Extract of *V. uliginosum* had no effect on either *S. richardsonii* or *S. pulchra*.
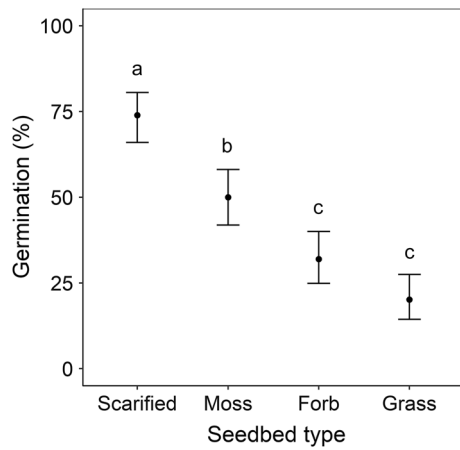
Fig. 3 Germination of *Salix pulchra* presenting higher on scarified ground than on forb- or grass-covered ground, and intermediate on moss. Dots represent binomial model estimates (error bars are 95% confidence intervals), and letters indicate significant differences between treatments, as identified by Tukey's post hoc test

Discussion

In this study, we demonstrated that willow seeds preferentially germinated on bare ground. Moreover, our experiments revealed a potential vulnerability of some shrub species to chemical interference from ericaceous dwarf shrubs. Together, these findings have implications for expected range shifts and community composition changes under climate warming. Our results suggest that the community already in place above the shrubline may physically or chemically impede shrub recruitment. Biotic interactions are likely to shape future vegetation trajectories in the tundra, and it is critical to gain a better understanding of the mechanisms involved to predict more accurately future range expansion of shrub species.

Scarification experiment

Willows are pioneer species in boreal and tundra succession, producing a large number of small seeds that can be wind-dispersed over long distances and rapidly colonise disturbed sites (Walker et al. 1986). Our dedicated germination study found that emergence of willow seedlings was higher on bare ground than on ground covered by herbaceous vegetation, supporting succession theory. These results also agree with observations of higher abundance and performance of shrubs on ground disturbed by thermokarst processes (Lantz et al. 2009). More widely, our results align with treeline studies that have shown increased conifer recruitment on exposed mineral soil (Dufour Tremblay and Boudreau 2011). Few similar experiments have been conducted with shrub species, but our results are in accordance with those of Graae et al.

Table 1 Model outputs from binomial logistic regressions to explain germination of tundra willows as a function of (A) ground layer composition and (B–C) allelopathic effects of ericaceous dwarf shrubs at two field sites

	Estimate	SE	z value	p
(A) Scarification—Qikiqtaruk				
Scarified (intercept)	1.04	0.19	5.37	<0.0001
Moss	−1.04	0.26	−4.07	<0.0001
Forb	−1.80	0.26	−6.82	<0.0001
Grass	−2.42	0.28	−8.51	<0.0001
Contrasts			*z ratio*	
Scarified—moss	1.04	0.26	4.07	**0.0003**
Scarified—forb	1.80	0.26	6.82	**<0.0001**
Scarified—grass	2.42	0.28	8.51	**<0.0001**
Moss—forb	0.76	0.24	3.10	**0.0106**
Moss—grass	1.38	0.27	5.17	**<0.0001**
Forb—grass	0.62	0.27	2.27	0.1058
Sample size: 16				
Null deviance: 156.15 on 15 df				
Residual deviance: 58.21 on 12 df				
(B) Allelopathy—Qikiqtaruk				
Intercept	0.87	0.16	5.62	<0.0001
TreatmentCAS	0.31	0.23	1.36	0.1747
SpeciesSR	−0.02	0.22	−0.11	0.9130
SpeciesSA	−2.23	0.23	−9.52	<0.0001
TreatmentCAS:SpeciesSR	−0.94	0.31	−3.02	0.0025
TreatmentCAS:SpeciesSA	−0.16	0.33	−0.49	0.6263
Contrasts			*z ratio*	
SP: C– CAS	−0.31	0.23	−1.36	0.1747
SR: C–CAS	0.62	0.21	2.98	**0.0028**
SA: C–CAS	−0.15	0.24	−0.61	0.5447
Sample size: 24				
Null deviance: 298.185 on 23 df				
Residual deviance: 36.565 on 18 df				
(C) Allelopathy—Kluane				
Intercept	0.10	0.16	6.25	<0.0001
TreatmentCAS	−0.26	0.22	−1.20	0.2294
TreatmentVAC	−0.46	0.21	−2.14	0.0326
SpeciesSR	−0.85	0.21	−4.01	<0.0001
TreatmentCAS:SpeciesS R	−0.24	0.30	−0.81	0.4200
TreatmentVAC:SpeciesSR	0.12	0.30	0.41	0.6806
Contrasts			*z ratio*	
SP: C–CAS	0.50	0.22	1.20	0.4521
SP: C–VAC	0.46	0.22	2.14	0.0825
SP: CAS–VAS	−0.16	0.21	0.95	0.6120
SR: C–CAS	0.50	0.20	2.50	**0.0335**
SR: C–VAC	0.34	0.20	1.70	0.2059
SR: CAS–VAC	−0.16	0.20	−0.81	0.6982
Sample size: 48				
Null deviance: 110.254 on 47 df				
Residual deviance: 42.834 on 42 df				

Species codes are *SP Salix pulchra*, SR: *Salix richardsonii*, *SA Salix arctica*. Allelopathic treatments are coded *C* for control, *CAS* for *Cassiope tetragona* leachate, and *VAC* for *Vaccinium uliginosum* leachate. For each model, pairwise post hoc contrasts are presented using Tukey's post hoc test, and significant contrasts are bolded
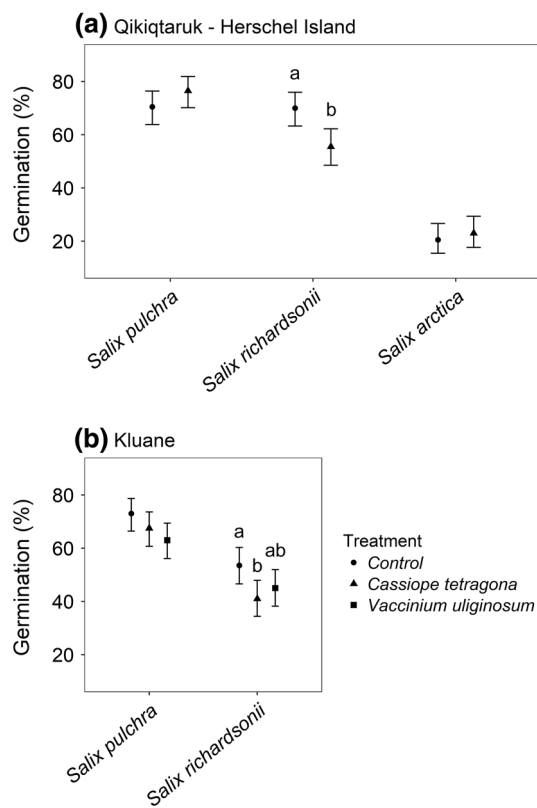
Fig. 4 Effect of leaf extracts from *Cassiope tetragona* and *Vaccinium uliginosum* on seed germination of three willow species from **a** Qikiqtaruk and **b** Kluane. Dots represent binomial model estimates (error bars are confidence intervals), and letters indicate significant differences between treatments, as identified by Tukey's post hoc test

(2011), who found consistently higher germination of tundra species on bare ground.

Willows typically produce short-lived seeds that must germinate within a few days of ripening (Bliss 1958; Brinkman 1974). It therefore seems likely that when seeds are dispersed on dense, tall vegetation, they cannot always reach the ground and meet their moisture requirement for germinating, and rapidly lose viability. On the contrary, seeds that fall onto bare ground can germinate within a day, as we observed during this study. We found that the moss seedbed had intermediate rates of germination, which could be due to high water retention capacity compared to herbaceous vegetation. In stressful environments, mosses can facilitate recruitment by sheltering seedlings from herbivores and temperature extremes (Wheeler et al. 2011; Lett et al. 2017).

We cannot generalise our observations to all tundra shrub species, as it is likely that species-specific traits like seed longevity play an important role in these interactions. Nonetheless, our results suggest that vegetation above the shrubline might act as a physical barrier for establishment of some dominant tundra shrub species. In a context of vegetation encroachment and decrease in bare ground at our field

site (Myers-Smith et al. in review), and in the tundra biome in general (Elmendorf et al. 2012), there might be limited opportunities for shrubline advance. This could lead to an increasing reliance on disturbance for regeneration (Lantz et al. 2010; Frost et al. 2013) as optimal recruitment microsites become sparser.

Allelopathy experiment

At both sites, the germination of *Salix richardsonii* was reduced when seeds were exposed to *C. tetragona* leaf extracts. In addition to producing allelopathic compounds, ericaceous species can change soil nutrient status and chemical properties (Bloom and Mallik 2006). Previously, negative effects of *C. tetragona* on the growth of graminoids have been explained by the labile carbon in the extracts promoting nutrient uptake by soil biota, thereby depleting resources for plants (Michelsen et al. 1995). As our seeds were placed directly on sterile filter paper without the possibility of third-party interactions, our results suggest that the leaves of *C. tetragona* may contain allelopathic compounds affecting the germination of some species. Alternatively, other chemical properties of the solution, such as reduced pH, could have affected germination. Edaphic factors are important in controlling shrub distribution: for instance, *Salix pulchra* is more tolerant to acidic soils than *S. richardsonii* (Swanson 2015). More work will be needed to validate our findings and identify the precise mechanism of interference. The very low germination of *Salix arctica* is unsurprising: unlike the other two species, it is a late disperser with conditionally dormant seeds (Densmore and Zasada 1983).

All three of our focal research species are found at the shrubline in the Kluane region (Myers-Smith and Hik 2017) and are widely distributed on Qikiqtaruk (Smith et al. 1989), yet they each have different habitat preferences. Interestingly, *Salix richardsonii* is spatially segregated from *C. tetragona* on Qikiqtaruk, the former being typically associated with other canopy-forming willows, and the latter mostly found with other evergreen shrubs and *Betula nana* in the Komakuk vegetation type characterised by soil disturbance from freeze–thaw processes (Smith et al. 1989). These habitat preferences likely reflect the different tolerance and plasticity of willow species to soil characteristics and other environmental and succession-related characteristics: throughout the Yukon Territory, *Salix richardsonii* is most commonly found on alluvial sites or floodplains, while *Salix pulchra* has a wider range of habitats (Cody 1996). The higher environmental plasticity of *S. pulchra* might be partially linked to the apparent absence of vulnerability to chemical interference from common ericaceous dwarf shrubs, although further studies will be required to test this specifically.

The fact that only one out of three willow species seemed vulnerable to allelopathy raises the issue of replication in this study and the question of the specificity of biotic interactions. Species-specific allelopathic responses have been reported at the treeline, with for instance black spruce, but not larch, being affected by ericaceous species (Dufour Tremblay et al. 2012). However, the scarcity of similar studies and low sample sizes make it difficult to rule out experimental artefacts and identify general patterns. To validate our findings and make them more generally applicable to the tundra biome, we call for more tests of allelopathic effects with these and other species in the Arctic region.

Biotic filters for shrubline expansion

While shrub encroachment in the tundra biome has received considerable attention, shrublines are understudied, with only six studies focusing specifically on range shifts (reviewed in Myers-Smith and Hik 2017). A study of 14 elevational shrublines in the Kluane region, one of our field sites, consistently found younger willows at higher elevations, a pattern suggestive of climate-driven range expansion (Myers-Smith and Hik 2017). However, we still have a poor understanding of the local factors that may mitigate the speed of shrubline advances. Our results and the lack of comparable studies highlight the need to better understand plant–plant interactions within tundra communities. Standardised replication of our experiments at more sites and with a more diverse range of tundra species could help determine whether biotic interactions are likely to be a major constraint to shrub expansion above the shrubline.

The biotic interactions investigated in this study, i.e. interaction with ground cover and allelopathy, are only a subset of all the possible interactions that may affect seedling establishment above the shrubline. Notably, below-ground interactions in the tundra are still poorly understood, and it is unclear whether some positive associations, like those arising from mycorrhizal symbionts and other interactions with soil microbiota (Grau et al. 2010; Pellissier et al. 2013; Sedlacek et al. 2014), may balance out negative interactions like allelopathy. The growth and survival of seedlings could be positively or negatively affected by the presence of taller plants through nurse effects or competition, respectively: the direction and importance of these interactions can even vary across life-stages (e.g. seed–seedling conflicts; Cranston and Hermanutz, 2013).

Overall, the realised extent of range shifts depends not only on climate suitability but also on biotic interactions within the new community (HilleRisLambers et al. 2013). Therefore, range shifts of Arctic and alpine shrublines will almost certainly be slower than predicted by climate envelope models. The species-specific nature of biotic interactions may act as an ecological filter where the advance of some species may be limited or prevented by the presence of competitors, allelopathic plants, or selective herbivores. Thus, it is unlikely that tundra shrubline range shifts will occur as intact plant communities moving to higher elevations or latitudes; instead, filtering will occur, with biotic interactions leading to different species assemblages forming beyond the current range limit.

Conclusion

Climate change is altering ecosystem boundaries, and a growing research focus is to achieve the integration of biotic interactions into predictive models of climate-driven range shifts. While treelines have received extensive attention and the effects of a wider range of plant–plant interactions on recruitment are starting to be better understood, it is unclear whether those mechanisms have the same importance at high-elevation and high-latitude shrublines. Our two simple experiments showed that the effects of two types of plant–plant interactions, namely seedbed type and allelopathy, are also relevant processes partly limiting germination at and above Arctic and alpine shrublines. Acknowledging the high spatio-temporal variability in seed production and viability in northern environments, we call for replication of these types of studies to gain a better understanding of the constraints acting upon regeneration in the tundra biome.

Author Contributions S.A.B. designed the study with inputs from all authors. S.A.B. and I.M.S. conducted the experiments. S.A.B. analysed the data. S.A.B. wrote the manuscript with inputs from all authors.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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