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Research article

Invasion success of three cool-season grasses in the northern prairie: a test of three hypotheses

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Empirical invasion ecology is laden with high context dependency. If general mechanisms underlying invasion success exist, they should be detectable in species that share biological and ecological characteristics. We carried out a growth experiment with *Agropyron cristatum*, *Bromus inermis* and *Poa pratensis* (subsp. *angustifolia*), to better understand the mechanisms underlying the invasion success of cool-season grasses in northern prairie grasslands of North America. By using a home–away approach, we tested whether 1) non-native plants have a higher performance than native plants, and whether invasiveness is 2) mediated by interactions with soils, such as a release from pathogens or enhanced mutualism, or 3) an adaptation to local soils. We compared seed size and weight of populations in Canada (non-native range) and Eurasia (native range) and carried out an experiment, in which seeds from the non-native and native ranges were planted into sterilized soil (control) and soil from a population in Canada or Eurasia, or local soils, respectively. We found inconsistent effects across species and response variables. Seed size and weight were not significantly different between native and non-native populations. The experiment showed a seed origin effect in *A. cristatum* (root and total biomass) and *B. inermis* (root biomass), with non-native populations outperforming native ones. Soil-mediated effects were supported in *A. cristatum* (root biomass) and local adaptation in *B. inermis* (root and total biomass). Germination across all species and biomass in *P. pratensis* did not respond to treatments. Despite the high similarity of our study group, our results indicate that invasiveness might be

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driven by idiosyncratic causes at the species level. Mechanisms not considered in our study, such as high propagule pressure and preadaptation could also potentially explain the invasion success across species.

Keywords: biogeographic comparison, enemy release hypothesis, evolution of invasiveness, enhanced mutualism, greenhouse experiment, invasive species

Introduction

Empirical invasion ecology suffers from high context dependency, which hampers conceptual understanding and delays transfer of knowledge to practitioners. Differences in species traits, ecosystems properties, and introduction histories are all sources of context dependencies in invasion ecology (Catford et al. 2022, Gioria et al. 2023). Hence, a detection of general mechanisms underlying invasion success should thus be most fruitful in studies that test hypotheses using species with similar traits, habitat occupation, geographic distributions, and introduction histories.

We carried out a common environment experiment to understand the invasiveness of *Agropyron cristatum* (crested wheatgrass), *Bromus inermis* (smooth brome) and *Poa pratensis* subsp. *angustifolia* (hereafter *P. pratensis*; Kentucky bluegrass) in the northern prairie grasslands of North America. These species share several biological and ecological characteristics. They are cool-season, perennial grasses native to temperate grasslands of Eurasia and have successfully invaded northern prairie grasslands (Otfinowski et al. 2007, Grant et al. 2009, Toledo et al. 2014, DeKeyser et al. 2015, Stotz et al. 2019, Palit and DeKeyser 2022, Zapisocki et al. 2022). All three species were introduced successively to North America for cultivar breeding, and have been seeded for forage production, pasture improvement, and lawn establishment, starting in the 16th century (*P. pratensis*) and at the end of the 19th and early 20th century (*A. cristatum*, *B. inermis*) (Carrier and Bort 1916, Newell and Keim 1943, Holechek 1981, Rogler and Lorenz 1983, Bashaw and Funk 1987, DeKeyser et al. 2015). They meet the definition of invasive species because they have naturalized in their non-native range, are able to successfully reproduce and have spread over a considerable area (definition sensu Richardson et al. 2000), with detrimental impacts for seminatural or natural habitats (definition sensu Ricciardi et al. 2013). While they are not regulated as noxious weeds in any Canadian prairie province or U.S. prairie state likely due to their economic use, many land and conservation managers seek to control their abundance in grasslands to preserve native biodiversity (Frid and Wilmshurst 2009, Grant et al. 2009). An understanding of their drivers of invasiveness can guide applied research, e.g. in the development of biocontrol methods, and help practitioners make informed management decisions. Although most research on the invasiveness of the grasses has focused on contrasting performance with native species in the non-native range (Ulrich and Perkins 2014, Harvey and Leffler 2020), few have tested for the role of post-introductory mechanisms by comparing performance in plants from the native and non-native range (Hierro et al. 2005, van Kleunen et al. 2010). Furthermore, a large body of experimental literature on invasiveness has addressed a single hypothesis but conceptual framework suggest that multiple mechanisms facilitate invasion success (Dai et al. 2020, Enders et al. 2020), which makes multiple hypotheses testing necessary.

In our experiment we aimed to understand whether seed origin or soil-mediated effects contribute to invasiveness in *A. cristatum*, *B. inermis* and *P. pratensis*. We crossed seeds and soils collected from populations in the non-native (Canada) and native (Eurasia) distribution ranges (n = 47 populations in total). Seed and soil source populations originated from a wide geographic gradient in the native and non-native ranges, to account for potential variability in seed performance and plant–soil relationships. We tested the following non-mutually exclusive hypotheses:

1) We tested whether in the absence of soil-mediated effects, a seed origin effect contributes to invasiveness by comparing performance in plants raised from seeds collected in the non-native and native ranges (Fig. 1a). A higher performance among invasive plants in the non-native range would be in line with the Evolution of invasiveness hypothesis, which postulates that introduced plants undergo rapid adaptive evolution in response to novel selection pressures and genetic admixture from populations of distant sources (Lee 2002, Colautti and Lau 2015). In addition, since specific origins have been selected for breeding during introduction and extensively bred for higher persistence and reproductive yield, a selection bias during introduction and admixture with cultivars post-introduction could also explain invasiveness in the non-native range (Schierenbeck and Ellstrand 2009, Scasta et al. 2015). Although our comparison would not disentangle these specific mechanisms, it could inform whether events during and post-introduction have shaped invasiveness in the three grasses.
2) We inspected whether invasiveness in the three grasses is mediated by interactions with soil biota, such as a release from enemies (Elton 1958, Keane and Crawley 2002) or enhanced mutualism (Reinhart and Callaway 2006, Sheng et al. 2022, Fig. 1b). If this hypothesis is correct, plants grown in soil inoculated with field soil from the non-native range should display higher performance than in soil inoculated with field soil from the native range, irrespective of seed origin (Fig. 1b). If invasiveness in the three grasses is mediated by interactions with soil biota, research could further explore belowground control options as a management tool. An introduction of soil pathogens from the native range could bear some biohazard risks, but a manipulation of native mycorrhizal inoculum strains in restoration and

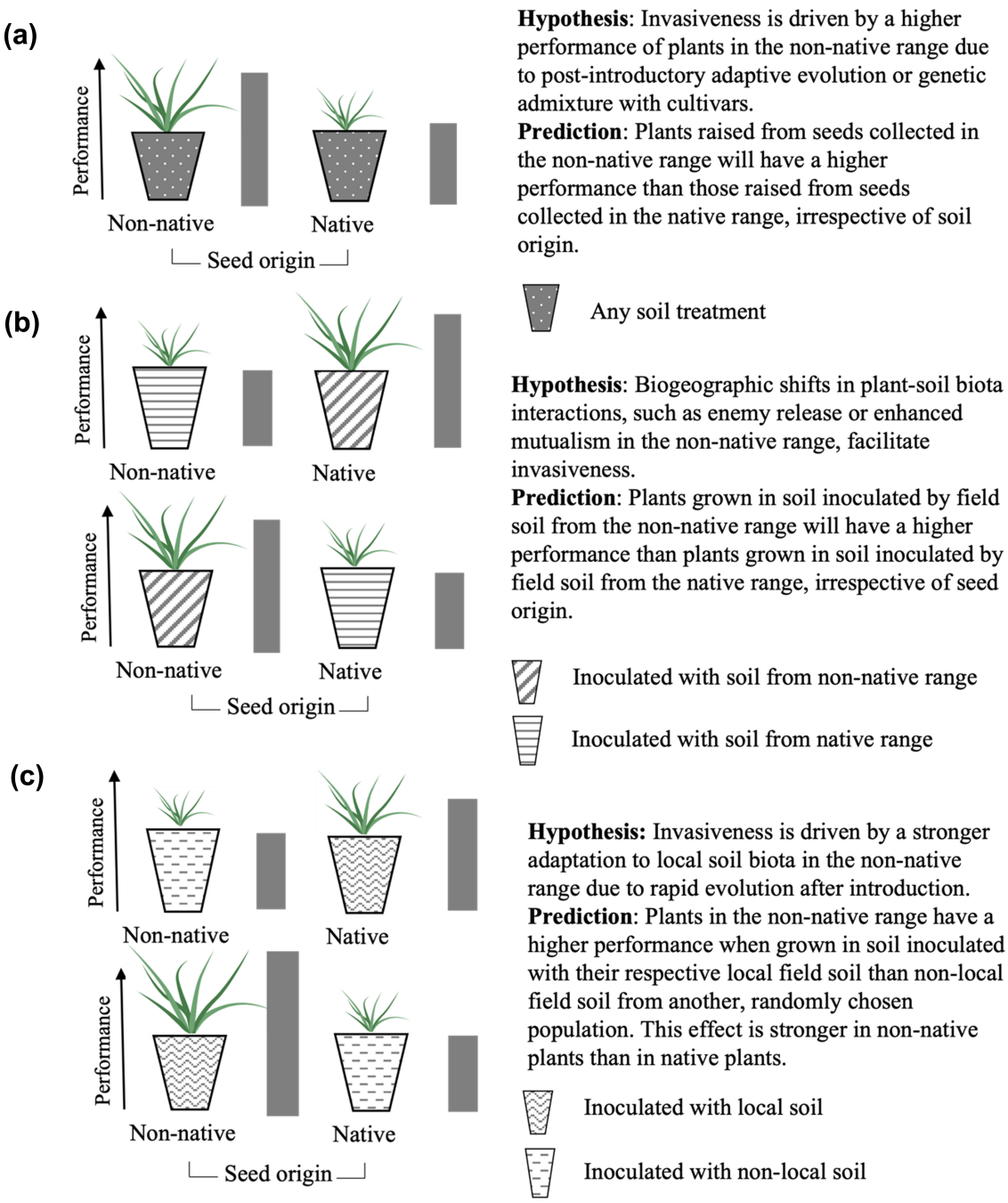


Figure 1. An overview of hypotheses and predictions explored in the experiment.

reclamation could potentially maximize benefit to native species and minimize benefit to invasive grasses.

3) We assessed whether invasiveness is driven by local adaptation to local soil biota among non-native populations, due to rapid evolutionary change and hybridization in the non-native range (Fig. 1c; Bossdorf et al. 2005, Ebeling et al. 2011). We tested this hypothesis by growing plants in sterile soil inoculated with field soil from their local population and with field soil from another, randomly chosen, non-local populations, and by growing plants in sterile soil as a control (home versus away comparison; Kawecki and Ebert 2004). Support would be provided by a significant interaction between population and soil origin, and specifically with non-native populations showing a higher performance in soils inoculated with their local field soil than in soils inoculated with non-local field soils. If local adaptation drives invasiveness, then early detection and control could decrease the likelihood that new populations adapt to local environments.

We expected to find similar drivers of mechanisms in our study species given that they were functionally similar,

originated from similar regions and invaded similar regions, thrive in similar ecosystems, and share a similar introduction history.

Material and methods

Study species

In its native range, *Agropyron cristatum* grows in arid and semi-arid grasslands in a region from the Far East, southern Siberia, to eastern Europe (Komarov 1934, Melderis 1980). *Bromus inermis* occurs in mesic steppe/prairie, meadows, forest margins, open shrub communities, and along roadsides (Komarov 1934) over a large region from Japan to Spain. *Poa pratensis* represents a complex of different subspecies, which are recognized as individual species in some floras (Komarov 1934, Edmondson 1980, Mosyakin and Fedoronchuk 1999, Király 2009). The taxon used in our study, *P. pratensis* subsp. *angustifolia* (also recognized as *P. angustifolia*), is a frequent species of meadows and mesic steppe in Eurasia (Komarov 1934) and the most common subspecies of *P. pratensis* in northern prairie grasslands (Zapisocki et al. 2022).

In their non-native range in North America, *A. cristatum* is frequent in semi-arid prairie grasslands (dry-mixed prairie grasslands according to the ecoregion classification of Canada and the U.S.), whereas *B. inermis* and *P. pratensis* are more frequent in more mesic grasslands (northern fescue and parkland grasslands; Otfinowski et al. 2007, Grant et al. 2009, DeKeyser et al. 2015, Zapisocki et al. 2022). In the northern prairie grasslands of Canada, *P. pratensis* subsp. *angustifolia* is the most commonly occurring *P. pratensis* subspecies (Zapisocki et al. 2022).

The study species can reproduce sexually and vegetatively. While *B. inermis* is strongly rhizomatous, *A. cristatum* forms tussocks that can be occasionally rhizomatous, and *P. pratensis* forms loose tussocks with extensive rhizomes (Flora of North America Editorial Committee 1993+). All three grass species have been bred as cultivars in their native and introduced distribution range (Williams et al. 2011, NÉBIH 2017) and have been seeded in both the introduced and native range. For instance, although *A. cristatum* is native to steppe grasslands in Central Asia, previously (in 1940–1956) this species occurred at low frequency in the region in the middle of the 20th century (Lavrenko 1991). In 1960–1970s, *A. cristatum* was frequently sown for pasture improvement and haying in Kazakhstan (Kamkin 2009). Nowadays, *A. cristatum* became one of the dominant species among grasses in originally steppe grasslands of southern Siberia, north-eastern Kazakhstan. In Ukraine, the cultivation of the three grasses does not occupy large areas, but they are represented by dozens of varieties of different origin, and there are still experiments on breeding and productivity (Bezruchko 2007, Tsurkan 2012, Bugaiov et al. 2017, SSSU 2022).

Seed and soil collection

We collected seed and soil samples across Eurasia (Germany, Hungary, Kazakhstan, Ukraine) and Canada in July and August of 2021, totaling 47 populations (Fig. 2, Supporting information). Sampling localities spanned distances of 4–4633 km within Eurasia and 1–878 km within Canada and comprised semi-natural to natural steppe or prairie grassland, without apparent anthropogenic disturbance. By acknowledging broad gradients of soil conditions within both the native and non-native range and using a high number of populations, we aimed to increase correct inference of range effects and avoid false-positive effects (Colautti and Lau 2015, Rosche et al. 2019).

At each site, we selected a random area of 10 × 10 m, in which we harvested and pooled seeds from multiple individuals. Grasses are known to undergo negative soil feedbacks (Kulmatiski et al. 2008), and invasive grasses can alter plant communities through allelopathic effects (Singh and Daehler 2023). Since we were interested in the general effect of the soil rather than soils altered by species, we collected soil samples where the study species were present but not dominant

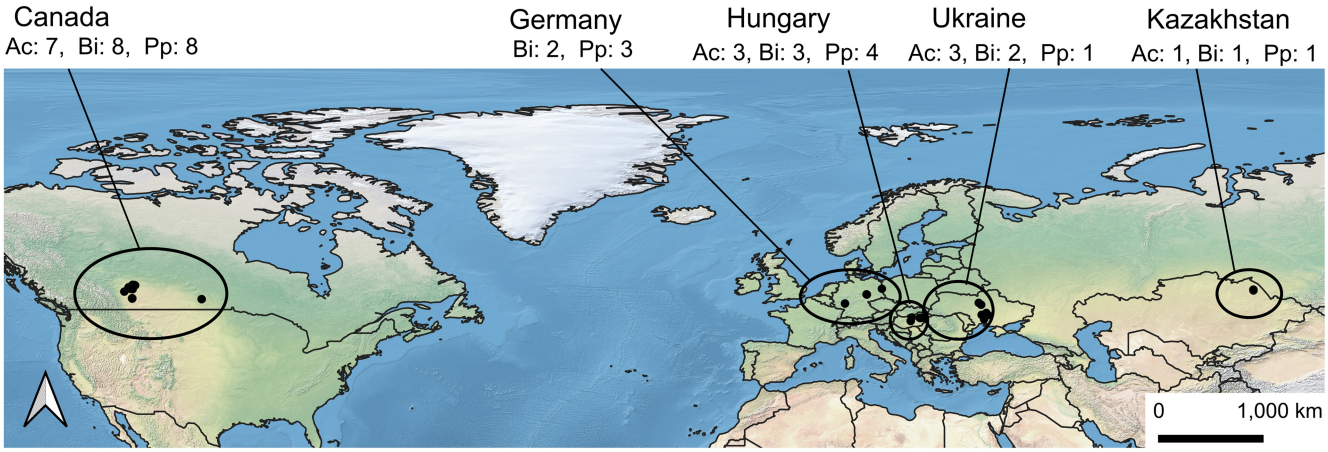


Figure 2. Geographical location of native (Eurasia) and non-native (Canada) populations of *Agropyron cristatum* (Ac), *Bromus inermis* (Bi), and *Poa pratensis* subsp. *angustifolia* (Pp) included in the experiment (total number of populations: n = 47).

and avoided sites dominated by other non-native species, i.e. either in the 10 × 10 m area or close nearby.

Samples were transported or shipped to the Wagner lab at the University of Alberta. Soil samples were air-dried and kept at ambient temperatures (20–30°C) before the experiment. Approximately 5 ml of ground soil samples were analyzed for total nitrogen and carbon in the Natural Resource Lab at the University of Alberta, using an organic elemental analyzer (dry combustion method).

Seed measurements

We assessed seed size in an image scanner using the WinSEEDLE program (Régent Instruments). For each population, we placed approximately 60 seeds into the scanner and measured the projected area of each seed. We measured the sum weight of 60 seeds in each population in an analytical scale (0.1 mg readability) and calculated the average seed weight as the ratio of the sum weight divided by the number of seeds.

Experimental preparation

In early November 2021, we set up a growth chamber experiment in the BIOTRON facility at the Department of Biological Sciences, at the University of Alberta, using seed and soil from populations in the native and non-native ranges as experimental factors. We created background soil by mixing commercially available loamy soil and sand to a 3:1 ratio and autoclaving it in bags (filled to about a maximum of 20 cm depth) for two 3 h cycles at 121°C, followed by 30 min of drying on a liquid cycle in a Getinge Model 533LS Steam Sterilizer to retain moisture. The usage of sterilized soil allowed us to inspect effects across a standard substrate and to single out soil biota as a possible cause driving soil-mediated effects and local adaptation. Soil inoculum was prepared by sieving each field-collected soil sample in a 2 mm sieve. All tools, materials, and surfaces brought into contact with soil and seed treatments were sterilized after usage to avoid cross-contamination among samples by one of two methods: material soaked in 10% bleach solution (5.25% aqueous NaOCl) for 20 min or surfaces sprayed with 70% EtOH solution.

Experimental treatments

We filled growth pots with 650 ml of sterilized background soil and in each pot, added soil treatments, and planted seeds from a seed population in the native or non-native range. Soil treatments comprised the following levels: 1) control soil (sterilized background soil only), 2) inoculation with local soil from the site where seeds were collected, or inoculum with soil from another, randomly chosen population in 3) Canada, or 4) Eurasia (Supporting information). For treatments that required an inoculum, we added 40 ml of field-collected soil to pots, and lightly mixed the background soil and inoculum soil using a sterilized metal spatula. Pots with a control soil treatment comprised 690 ml background soil to yield a soil volume comparable to inoculated pots. By growing plants in sterilized background soil with small amounts of live soil inoculum (6%) and by including a sterilized control treatment, we aimed to understand whether effects are driven by soil biota and to ensure that effects are not confounded by abiotic differences among field soils (Brinkman et al. 2010). Our treatments allowed us to compare performance of plants from different seed sources (Canada versus Europe) and plants grown in soils of different origin (Canada versus Europe; local versus non-local). We replicated seed and soil treatments using seed and soil populations as replicates. In addition, we used four pots nested in population combinations as additional replicates. For instance, seed population AG-CAN-04 was planted in control soil pots (n = 4 pots), in pots inoculated with local soil (4 pots each with AG-CAN-04 soil), pots inoculated with soil from other Canadian populations (4 pots, each inoculated with soils from AG-CAN-03, AG-CAN-06, AG-CAN-07 or AG-CAN-09, respectively), and pots inoculated with soil from Eurasian populations (4 pots, each inoculated with soils from AG-HUN-02, AG-HUN-03, AG-KAZ-01 or AG-UKR-03, respectively). Given that populations in Eurasia were collected from distant subregions, we aimed to cross seeds and soil between subregions as much as possible to avoid a dominating effect of a single subregion. In total, our experiment encompassed 752 pots across all species and treatments.

Due to a low number of ripe seeds, four out of 47 seed populations were planted with less than four seeds per pot (populations AG-CAN_03, AG-CAN_06, BR-GER-01 and PO-GER-01).

Growth experiment

Pots were randomly distributed across 32 growth trays (blocks), which were in turn randomly distributed on a greenhouse bench. Plants were grown with 12 h of light at 20°C and 12 h of darkness at 12°C and were watered every three days with approximately 10 ml. These conditions were set to mimic growth condition in the early growing season. Light sources encompassed fluorescent growth lights with 86 Watt (Phillips PLUS T8 High Output lamps). The experiment was started on 1 December 2021. After three weeks, plants were thinned to the tallest individual to keep the number of individuals per pot constant and avoid the effect of competition, which was not assessed in the experiment. We measured max. plant height every two weeks and harvested when this metric showed a stagnation. *Agropyron cristatum* and *B. inermis* were harvested after 10 weeks and *P. pratensis* after 12 weeks. In pots that did not show any germination within the first three weeks (8.4% pots), we planted four additional seeds, then thinned after three weeks and harvested three weeks later than the remaining pots.

Response variables

We evaluated the success of germination three weeks after the start of the experiment by assessing the presence or absence

of emerged seedlings. Pots without germination that had to be reseeded after three weeks were not included in the subsequent analysis of germination. Furthermore, after thinning, we assessed plant height increase as a proxy for increase in growth by measuring the longest leaf of each plant every two weeks starting with the fifth week. Dried biomass was measured at the end of the experiment, after harvesting the shoot and root components, washing the roots, and drying each sample for 48 h at 70°C.

Statistical analysis

We assessed differences in seed size between native and non-native populations using linear mixed-effects models in the 'lme4' package (Bates et al. 2015; ver. 1.1-28) in R (www.r-project.org), using population as a random effect. Differences in average seed weight per population between the native and non-native range were assessed using a *t*-test in R.

We analyzed the outcomes of our experiment using linear mixed-effects models for each response variable. Although the random effects structure slightly differed among these models, we employed the same fixed effects and the same approach to test hypotheses. We tested our first hypothesis of higher performance in the non-native range by inspecting the effect of seed origin in each model (native versus non-native). To explore whether invasiveness is driven by soil-mediated effects, we inspected the effect of soil treatment in each model. If the latter was significant, we used a post hoc test to verify that plants in pots inoculated with soil from Canada showed a higher performance than those inoculated with soil from Eurasia. To investigate whether invasiveness is driven by local adaptation, we inspected whether there was a significant interactive effect of soil treatment and seed origin in our models. If the latter was significant, we tested whether non-native plants had a significantly higher performance in pots inoculated with non-local soils. All statistical analyses were conducted as ANOVA tables using type III sum of squares, as implemented in the 'car' package (Fox and Weisberg 2019) in R. Models were validated by inspecting residuals.

Germination success

We analyzed germination success using generalized linear mixed-effects models with a binomial error family in the 'lme4' package. Seed origin, soil treatment, and their interaction were used as fixed effects, and block, soil population, seed population, and pot ID as random effects. Due to a singular fit, seed population was dropped as a random effect for *B. inermis*. To facilitate model convergence, we removed pot ID from random effects in *P. pratensis*.

Plant height

We used linear mixed-effects models in the 'nlme' package (Pinheiro et al. 2022) to analyze how seed origin, soil treatment, time, and the two-way interactions between these factors affected plant height during weeks 5–9 (*A. cristatum*, *B. inermis*) and 5–11 (*P. pratensis*). Given that height was measured on the same plant (repeated measures), we incorporated different variance–covariance structures that account for temporal autocorrelation and heterogeneous variance with time. Models were compared based on their AICc using the 'MuMIn' package (Bartoń 2022). The best model was identified as the one with the lowest AICc and AICc ≥ 2 to other models. For all species, a model type without any autocorrelation estimates and homogeneous variance emerged as the best solution (data not shown). The 'nlme' package has the advantage of modeling residual correlation and variance but it is restricted in its use of multiple additive (or crossed) random effects (Gałecki and Burzykowski 2013). Hence, we included only plant ID nested in block for this analysis and did not include soil or seed population as additional random effects. We validated the normal distribution and homoscedasticity of residuals graphically and used least-square mean tests in the 'emmeans' package (Lenth 2022) for pairwise post hoc comparisons in case predictors showed a significant effect.

Dry biomass

Total dried biomass, dried shoot biomass, and dried root biomass were analyzed using generalized least-squares and linear mixed-effects models in the 'lme4' package. Throughout the analysis, seed origin and soil treatments were used as a fixed effect, while block, soil population, and seed population as random effects. When analyzing root biomass in *A. cristatum*, soil population showed very little variance, which resulted in singular fits. Hence, we removed this random effect in the respective model. We used least-square mean tests in the 'emmeans' package for pairwise post hoc comparisons.

Results

Seed origin effect

Across all species, populations from the non-native range did not have larger seeds or heavier seeds than populations from the native range (Supporting information). Similarly, the analysis of the growth experiment showed germination and increase in height (Supporting information) were similar between non-and native populations, except that *B. inermis* plants from Eurasia grew overall larger and faster than plants from Canada (Supporting information) and *P. pratensis* from Eurasia grew slightly faster compared to plants from Canada (Supporting information). The analysis of biomass did not yield any seed origin effects (Fig. 3, Supporting information), except for *A. cristatum* root, shoot, and total biomass (Fig. 3a, d, g, Supporting information) and *B. inermis* root biomass (Fig. 3e, Supporting information), which were higher in non-native than native populations.

Soil treatment effect

Root biomass in *A. cristatum* was higher in soils inoculated with field soil from Canada than inoculated with field soil from Eurasia (Fig. 4d, Supporting information). However,

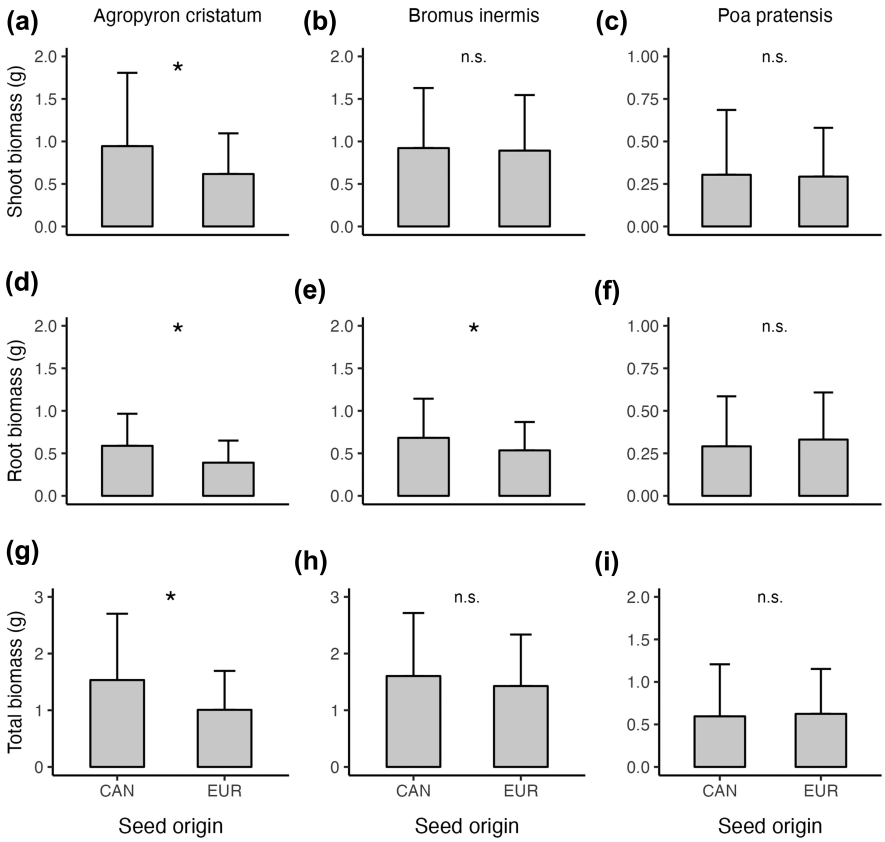


Figure 3. Shoot, root, and total biomass in response to seed origin in *A. cristatum*, *B. inermis*, and *P. pratensis* (mean + 1 SE). Asterisks indicate statistically significant differences ($p < 0.05$). n.s. = not significant. See the Supporting information for the accompanying ANOVA table.

none of the other response metrics across species responded to soil treatments in accordance with our hypothesis (Table 1).

Although soil treatment affected *A. cristatum* height (Supporting information), the trend was not in line with our hypotheses, with plants growing higher in control and local soils than in soil from Eurasia, but not in non-local soil from Canada (Supporting information). In *B. inermis*, soil treatment showed a significant effect on plant height (Supporting information) but pairwise differences were not significant in the post hoc test (Supporting information). In *A. cristatum*, soil treatment had a significant effect on total biomass (Supporting information) but this effect was driven by a lower total biomass in soils from Eurasia compared to local soils (Fig. 4g).

An analysis of field-collected soil showed that total carbon and nitrogen were similar in the native and non-native ranges, except in *P. pratensis*, where non-native soils had higher carbon and nitrogen content (Supporting information).

Local adaptation (Seed origin × Soil treatment effect)

Bromus inermis was the only species to show support for the local adaptation hypothesis, with a significant interactive effect of soil treatment and seed origin on root and total biomass, and a marginally significant effect on shoot biomass (Supporting information). In line with the hypothesis, plants from non-native populations produced more biomass in local soils than in non-local soils (mean total biomass: 1.895 g versus 1.191 g, least-square mean test, $t = -3.23$, $p = 0.031$; mean root biomass: 0.793 g versus 0.505 g, $t = -3.20$, $p = 0.028$; mean shoot biomass: 1.101 g versus 0.688 g, $t = -2.85$, $p = 0.089$; Fig. 5a–b). By comparison, plants from native populations did not produce more biomass in local than in non-local soils (least-square mean test: mean total biomass: 1.195 g versus 1.340 g, $t = 0.64$, $p = 0.998$; mean root biomass: 0.430 g versus 0.479 g, $t = 0.53$, $p = 0.999$, mean shoot biomass: 0.764 g versus 0.861 g, $t = 0.64$, $p = 0.998$; Fig. 5b, d). In addition, *B. inermis* plants from Canada grown in their local soils produced 45% more root biomass compared to plants from Eurasia grown in their local soils (least-square mean test, 0.793 g versus 0.430 g, $t = 3.43$, $p = 0.024$).

Discussion

Although our study tested hypotheses in a set of species that are biologically and ecologically similar, it showed that the factors contributing to invasiveness are likely idiosyncratic. An evolution of invasiveness and soil-mediated effects likely contribute to invasiveness in *A. cristatum* and local adaptation to invasiveness in *B. inermis*.

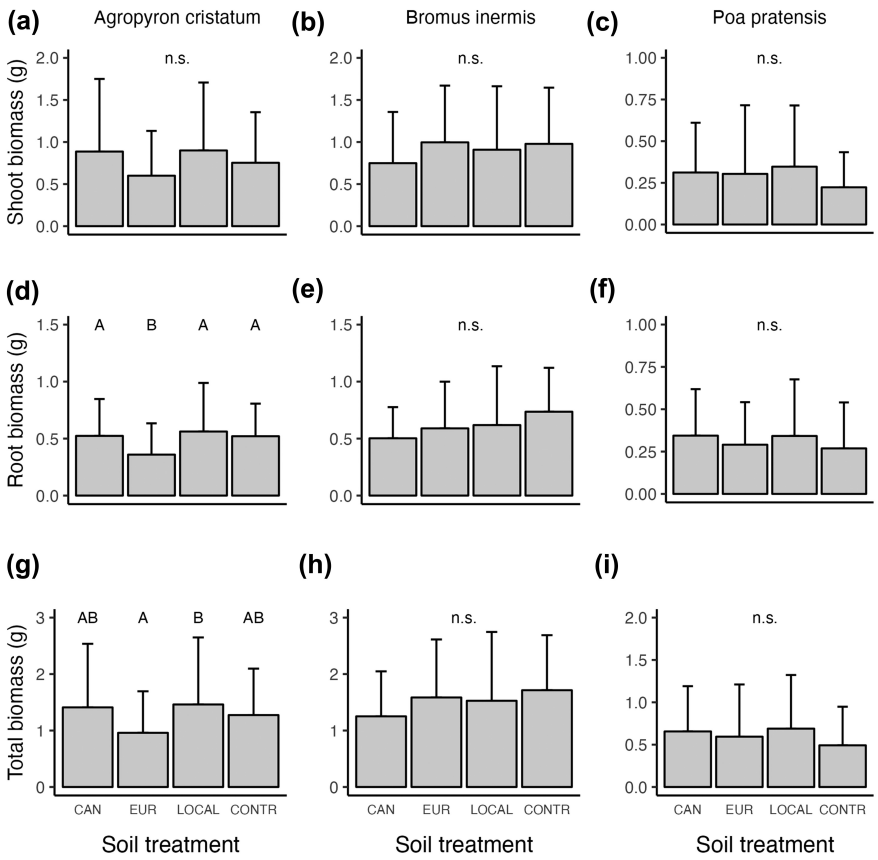


Figure 4. Shoot, root, and total biomass in response to soil treatment in *A. cristatum*, *B. inermis*, and *P. pratensis* (mean + 1 SE). Different letters indicate statistically significant differences ($p < 0.05$). n.s. = not significant. See the Supporting information for the accompanying ANOVA results.

Seed performance, germination and plant height

Across our study species, we did not find any differences in seed size and seed weight between native and non-native populations. Similarly, seed germination rates did not vary in response to our experimental factors. The germination results contrast with findings by a meta-analysis, which found that seeds from non-native population tended to germinate at greater percentages than seeds from native populations (Gioria and Pyšek 2017). We did not assess germination speed, but our results suggest that germination success within three weeks is comparable in native and non-native populations. High performance at this early life stage could be a reason why the species were selected for economic use and at least partly explain their high competitiveness and invasiveness in natural communities.

Varying support for a seed origin effect

We hypothesized that plants from the non-native range would have heavier and larger seeds and show a higher performance in the experiment, irrespective of the soil treatment they were grown in, potentially due to an evolution of invasiveness (Lee 2002, Colautti and Lau 2015) or admixture with cultivars in the non-native range (Schierenbeck and Ellstrand 2009, Scasta et al. 2015). Our analysis revealed complex results, with root, shoot, and total biomass in *A. cristatum* and root biomass in *B. inermis* supporting the hypothesis, and the remaining response metrics refuting it. Our mixed results across species are in line with a review by Hinz and Schwarzlaender (2004), which found that six out of 14 investigated species showed higher plant vigor in the non-native than in the native range, when using standardized environmental conditions. This review also found that the outcome often depended on the studied parameters. Similarly, in a meta-analysis of home-away comparisons in plants, Parker et al. (2013) found on average a higher size and fecundity in introduced plants, but the outcome was variable among species. These combined results suggest that there is considerable uncertainty in our understanding of the evolution of invasiveness in the new range.

In our study, the response metrics that were significantly different between non-native and native population yielded only small effect sizes. This might be explained by the broad spatio–environmental gradients we sampled, which raises the question as to whether the detected differences translate into fitness advantages in the field. To fully corroborate the hypothesis of higher performance in the non-native range, future research should explore how biomass production changes under competition and whether origin also influences reproductive fitness and success.

Table 1. Summary of the experimental outcome, with cells indicating inference by different response variables and across different species. G: germination, H: plant height, NA: not applicable, RB: root biomass, SB: shoot biomass, SS: seed size, SW: seed weight, TB: total biomass. *: support for scientific hypothesis, –=no support for scientific hypothesis.

	Hypothesis explaining invasiveness in the non-native range		
	Seed origin effect	Soil treatment effect	Soil × Seed effect
	Higher performance	Soil mediated effects	Local adaptation to soil biota
Agropyron cristatum	SS: –	NA	NA
	SW: –	NA	NA
	G: –	G: –	G: –
	H: –	H: –	H: –
	SB: *	SB: –	SB: –
	RB: *	RB: *	RB: –
	TB: *	TB: –	TB: –
Bromus inermis	SS: –	NA	NA
	SW: –	NA	NA
	G: –	G: –	G: –
	H: –	H: –	H: –
	SB: –	SB: –	SB: –
	RB: *	RB: –	RB: *
	TB: –	TB: –	TB: *
Poa pratensis	SS: –	NA	NA
	SW: –	NA	NA
	G: –	G: –	G: –
	H: –	H: –	H: –
	SB: –	SB: –	SB: –
	RB: –	RB: –	RB: –
	TB: –	TB: –	TB: –

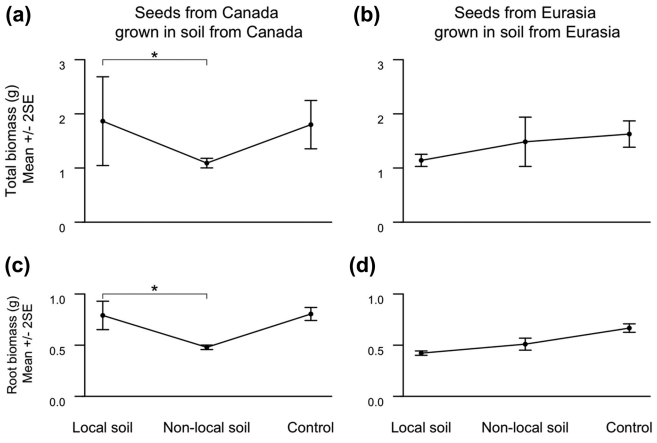


Figure 5. Interaction plots showing the total biomass (a, b) and root biomass (c, d) of *B. inermis* plants grown from seed from Canada (a, c) and Eurasia (b, d) in local and non-local soil from their respective region and control soil. See the Supporting information for the accompanying omnibus tests. Asterisks show significant interactions among treatment combinations according to least-squares means test.

In contrast to our expectation, *B. inermis* aboveground and total biomass and all biomass metrics of *P. pratensis* showed a similar performance in native and non-native populations. Such a lack in trait differences between native and non-native populations was also found in *Dactylis glomerata*, a perennial Eurasian grass species that is invasive in more mesic regions of North America (Leifso et al. 2012). Our results indicate that post-introductory acquisition of higher performance does not contribute to invasiveness in *P. pratensis*, or contributes to invasiveness to some extent in *B. inermis*. This result raises the question whether invasiveness is driven in part by a general pre-adaption in the species, such as high germination performance, highly competitive ability, and productivity. These species-level traits have been likely the reason why the species have been used for agronomic purposes and breeding in the native and introduced range (Bezruchko 2007, Williams et al. 2011). Furthermore, the lack of any seed origin effects might be explained by the fact that breeding was not restricted to the introduced range but also occurred in the native range and that some cultivars were developed from both Eurasian and North American cultivar parents (Bezruchko 2007, Williams et al. 2011, Marinich 2015). If an admixture between wild and cultivated plants occurred in both ranges, trait differences between the non-native and native ranges would be blurred. However, this hypothesis does not explain why seed effects were found in *A. cristatum* but not in *B. inermis* and *P. pratensis*, as breeding in the native range occurred in all three grasses. Although speculative, this discrepancy might be linked to a higher historic proximity of sampled *A. cristatum* populations to areas seeded by cultivars. Testing such a scenario would require linking standardized growth studies on trait differentiation with genomic analyses of natural populations and introduced cultivars.

Soil–plant interactions as drivers of invasiveness

Agropyron cristatum was the only species that demonstrated soil-mediated effects as drivers of invasiveness. Its individuals produced more root biomass when grown in pots inoculated with soils from Canada than in soil from Eurasia, irrespective of seed origin. This difference cannot be contributed to differences in soil nutrients as non-native and native field soils in the species did not differ in their soil nutrient status and we used only a small percentage of soil inoculum.

In order to understand whether the effect is due to soil enemy release versus enhanced mutualism, it is important to analyze and compare soil pathogen and mycorrhizal composition, as well as quantify mycorrhizal colonization in plants grown in soils from Canada and Eurasia. If a release from soil enemies is driving invasion success, biocontrol options should be potentially explored. The reason why only *A. cristatum* displayed soil-mediated effects is unclear. The species occurrence in semi-arid regions suggests that it might have adaptations to soils with lower nutrient status and nutrient-pulses, such as a close association with mycorrhizae, which could allow the species to more fully exploit mycorrhizal communities in the introduced range. To solve this question,

future studies need to compare plant–mycorrhizal relationships across the three species, and in individuals grown in soils from the native and introduced ranges.

The lack of any support for soil-mediated effects as drivers of invasiveness in *B. inermis* and *P. pratensis* is in line with a recent meta-analysis that showed no support for the enhanced mutualism hypothesis (Bunn et al. 2015). However, it contrasts with the results of another meta-analysis that found 57% of considered experiments (n = 8, out of 14) to support the enemy release hypothesis (Prior and Hellmann 2015). There are several possible explanations for a lack of soil-mediated effects in *B. inermis* and *P. pratensis*. In theory, natural selection for generalist plant–soil biota relationships (Lankau and Keymer 2018) could have nullified any soil-mediated advantage in the non-native range. This explanation would echo the proposed hypothesis that plant enemy release is strongest for species that co-evolved with specialist enemies in the native range (Mitchell and Power 2003, Heger and Jeschke 2018). Soil enemies of *B. inermis*, for example plant parasitic nematodes, may also be similar between native and introduced habitats, not providing the escape that is often attributed to this hypothesis. Alternatively, it is possible that the effect of soil pathogens or nematodes on *B. inermis* is minimal (Otfinowski et al. 2016). Furthermore, interactions with soil biota might be mediating invasiveness to a smaller extent compared to interaction partners, like aboveground herbivores, seed predators (Maron and Vilà 2001), or competitors (Callaway et al. 2011), or anthropogenic factors, like increased propagule pressure and economic use (Bucharova and van Kleunen 2009). The lack of a soil treatment effect could have also resulted from a cultivation bias of soil biota in the greenhouse conditions (Sýkorová et al. 2007). In theory, an increase in nutrient content due to soil sterilisation could have masked soil-mediated effects but this effect was likely negligible because sterilized background soil had a lower nutrient content than field collected soils and we kept the inoculum rate deliberately low (6%). Finally, the lack of soil enemy release might be linked to the species' large distribution ranges, and indirectly to their relatively long residence time, which could have led to a buildup of soil enemies or mutualists to a level that is comparable to the native range (Agrawal et al. 2005).

Local adaptation in non-native *B. inermis* populations

We expected that local adaptation could contribute to invasiveness in the non-native range, which would be manifested in a significant interaction between seed and soil treatments. Specifically, populations in Canada grown in their local soil would show a higher performance than in non-local soil from other sites in Canada, and this local adaptation effect would be stronger than among populations in Eurasia. In our experiment, only *B. inermis* total and root biomass yielded results in line with this expectation. Since biomass of plants from Canada did not differ between local soils and control soils, the local adaptation effect must be linked to an adaptation to soil biota. The fact that biomass was higher in local than in non-local soils in non-native *B. inermis* suggests that populations have adapted to local soil mutualists or escaped local pathogens. In general, our results contrast with several studies that did not find evidence of local adaptation in grassland plant species, such as in *Stipa capillata* (Wagner et al. 2011) and *Aster amellus* (Pánková et al. 2014). A study on four *Acacia* species found that neither non-native nor native populations showed signs of local adaptation to soils (Birnbaum and Leishman 2013). However, our results are in line with a study by Sherrard and Maherali (2012), which found evidence of positive local adaptation in non-native *B. inermis* populations in Ontario linked to soil biota. It is noteworthy that the home site advantage in this study was linked to a decrease in mycorrhizal colonization, which implies that non-native *B. inermis* populations avoid parasitic effects of root colonization by mycorrhizal fungi. This suggestion is corroborated by a lack of significant mycorrhizal relationships in *B. inermis* Great Plains populations (Reinhart et al. 2017) and an ability of non-native populations to escape colonization by mycorrhizae (Grman 2012).

Although we detected local adaptation in Canadian *B. inermis* populations, we did not detect any local adaptation in the species native populations. This result is similar to findings for *Conyza canadensis* by Sheng et al. (2022) which found stronger local adaptation to mutualists in the introduced range than the native range. Meanwhile, *B. inermis* seeds from Eurasia grown in Eurasian soils did not differ in biomass production from plants grown in other soil treatments. Our result is striking given that native populations in Eurasia spanned a larger spatial gradient, five-time the distances of Canadian populations. Although speculative, it might reflect a more pronounced spatial mosaic of selective pressure by local parasitic mycorrhizal colonization in the non-native range than in the native range. Future research should compare mycorrhizal colonization, composition, and effects on *B. inermis* plant growth among populations in the native and non-native ranges. Furthermore, our results could also indicate an escape of locally bred varieties in the introduced range. The fact that only *B. inermis* showed signs of local adaptation among our study species might be due to a stronger reliance on rhizomatous reproduction on a local patch scale, which should diminish the importance of gene flow among populations and increase genetic differentiation.

Conclusions

Our study examined three factors that could contribute to the invasion success of *A. cristatum*, *B. inermis* and *P. pratensis* in northern prairie grasslands. Given that *A. cristatum* showed signs of an evolution of invasiveness, the next step would be to clarify to what extent this finding translates into increased competitive ability in its non-native populations. *Agropyron cristatum* was also the only species to show signs of soil-mediated invasiveness. To disentangle the mechanisms driving soil-mediated effects, future research needs to differentiate between effects of soil pathogens and mutualists and

would benefit from a better understanding of differences in soil biota communities between steppe and prairie grasslands. The fact that non-native *B. inermis* populations showed positive local adaptation to soil biota warrants further studies on the role of parasitic mycorrhizal fungi as selection pressures in the home and non-native ranges, and the role of locally bred cultivars.

We considered three hypotheses to explain the invasiveness of three species with similar biological and ecological characteristics. Although some of our hypotheses partially explain invasiveness in individual species, none of the hypotheses was supported across all study species, which suggests that mechanisms driving invasiveness are more idiosyncratic than previously assumed, and hypotheses must be tested on a species-by-species level. Such an empirical approach would be slower and more cost intensive but could potentially provide a more accurate understanding of invasion success. Finally, invasion success in *A. cristatum*, *B. inermis* and *P. pratensis* might be driven by general mechanisms not investigated in our study but shared across the species, such as high propagule pressure through seeding, interbreeding with cultivars, interspecific interactions, or a generally high competitive ability due to pre-adaptation.

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Data availability statement

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.23152721.v2 (Villasor et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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