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Note

# Potential role of the seed bank in spreading invasive plants in a tundra-edge environment

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## Abstract

Although relatively infrequent, invasions by non-native plants at high latitudes are increasingly recognized as an emerging problem. Churchill, MB, Canada is unusual as over 100 non-native species have been found in human-disturbed areas, making it an outlier amongst subarctic habitats. Although these non-native species have persisted almost exclusively within town, some occur in isolated locations throughout the local road network. Most of these non-native species have been observed in areas with a history of soil movement (e.g., for construction or road repairs), suggesting that they have been moved within the soil, likely either germinating from seeds or growing clonally from root and rhizome fragments. Using a greenhouse experiment, we found evidence that soils from human-disturbed sites can contain a substantial non-native seed bank. In particular, we grew a significantly higher number of non-native seedlings from translocated soils compared with uninvaded soils. These germinated non-native species are native to Europe but have widely invaded temperate regions. This study provides the first direct evidence that movement of seed-contaminated soil is a significant source of local non-native species spread. Future warming in Arctic regions may increase seed production of these species, leading to increased spread and persistence via contaminated soil.

**Key words:** non-native plants, seed bank, tundra, invasive species spread

## Introduction

Invasions by non-native plant species are a concern worldwide (Mack et al. 2000; Simberloff et al. 2013), although not all regions are equally at risk. In the northern hemisphere, invasions tend to peak at mid-latitudes and decline poleward (Guo et al. 2021). For instance, in Canada, temperate areas have a higher proportion of invaders than northern regions, reflecting higher population density with its associated disturbance, trade, and travel, as well as a less severe climate; 42% of the 1937 plant species of the heavily populated Toronto region are non-native in origin (Cadotte 2021). In contrast, subarctic and Arctic Canada have historically been much less affected by invasions. These regions remain dominated by native vegetation, reflecting their harsh climates, short growing seasons, and spatial isolation from population centers (Carlson and Shephard 2007; Langor et al. 2014, p. 201).

Despite this general pattern, non-native plant species are increasingly being recorded at northern latitudes (Wasowicz et al. 2020). This trend likely is being accelerated by ongoing climate change: polar climates are warming faster than anywhere else on Earth (Hassol 2004; Anisimov et al. 2007; Bush and Lemmen 2019). At the same time, shipping and other forms of transportation are increasing, and human populations are growing (Post et al. 2009; Ricciardi et al. 2017). These changes are exposing northern ecosystems to an elevated risk of invasion (Sanderson et al. 2012; Smith et al. 2012; Alsos et al. 2015; Conservation of Arctic Flora and Fauna and Protection of the Arctic Marine Environment 2017; Ricciardi et al. 2017; Rew et al. 2020). Many plant species are extending their range poleward (Hughes 2000; Walther et al. 2002; Parmesan 2006; Chen et al. 2011; Pauchard et al. 2016; Rew et al. 2020), including non-native species such as sweet clover (*Melilotus*) in Alaska (Conn et al. 2008). Similarly, invasive plant species have also become a problem in the Antarctic (Bergstrom and Chown 1999; Frenot et al. 2005; Rew et al. 2020). Consequently, invasions in high-latitude ecosystems are recognized as an emerging problem (Sanderson et al. 2012; Ricciardi et al. 2017; Rew et al. 2020).

The town of Churchill, MB, Canada (58°N 94°W), on Hudson Bay at the boreal/tundra interface, is a hotspot for northern invasions. In 1929, a railway link was established, and grain shipments to Europe began. Churchill became a major port, and is still the only town on Hudson Bay with a permanent land link to southern Canada. Churchill has also served as a military base, and is a major destination for tourism and research. As a result of its history of trade and transportation, more than 100 non-native plant species have been recorded in this town of 900 people, an unusually high number for this latitude. Most of these non-native plant species likely arrived as contaminants in agricultural shipments (Beckett 1959; Staniforth and Scott 1991; Scott 1996; Kent et al. 2018).

Many subsequently failed to establish lasting populations, and production of viable seed is likely low, but some have persisted since at least 1959 (Staniforth and Scott 1991; Scott 1996; Kent et al. 2018).

Although the persistence of these non-native species demonstrates that they can survive locally given the right conditions, nearly all have remained restricted to the townsite and other human-disturbed areas, and almost none have spread from this reservoir into nearby boreal forest and tundra habitats (Kent et al. 2018). An exception to this restricted spread has been plant species associated with soil that was being moved to new locations for purposes such as construction, for road and powerline repairs, and as waste soil dumped near roadsides (Kent et al. 2018). Such transported soil could contain dormant seeds of non-native plant species. Many of the invaders in the Churchill area do produce seed, and some of the most abundant are annuals that depend on seed production for local persistence (e.g., *Thlaspi arvense*, *Capsella bursa-pastoris*). Alternatively, translocated soils might contain viable root and rhizome fragments or might be colonized by seed dispersal from nearby invaded sites.

In this preliminary study, we aim to document whether viable seeds of non-native plant species are present in the seed bank of translocated soil. Soil samples collected from areas invaded by non-natives and from uninvaded areas were sieved and incubated in a greenhouse, and emerging seedlings were counted and identified. Germination of non-native species from samples originating in invaded sites would suggest that seed-contaminated soil may be a significant source of local spread of these invaders.

# Materials and methods

## Study site and soil sampling

Soil was collected in August of 2021 from sites in and near the town of Churchill and other human-modified areas (Fig. S1). All sites were north of the continuous treeline, although an outlier of white spruce (*Picea alba*) occurs close to the Churchill Northern Studies Center (CNSC) site. At each site, roughly 500 $\text{cm}^3$ of soil was collected to a depth of 10 cm and stored in plastic bags. We also recorded the five most abundant vascular plant species at each site.

Two different sampling strategies were used. First, to compare the seed bank of previously invaded and uninvaded areas, soil was collected from 12 sites containing a conspicuous population of one or more non-native species (*Linaria vulgaris*, *Plantago major*, *Silene alba*, etc.); there is also evidence of human modification and soil addition at these sites. Each invaded site was paired with an uninvaded site 2–5 m away; these sites have little-to-no anthropogenic disturbance, and are assumed to have never been previously invaded. Eight such pairs of sites were in or near town, including roadsides and adjacent areas with a history of disturbance and (or) soil dumping. The remaining four pairs of sites were associated with roadside power transmission poles between the town and the airport. These poles had been recently replaced, apparently with soil additions, and we first observed populations of non-native plants at these sites in August 2019.

We used a different sampling strategy to better describe the seed bank in a single recently invaded site. Twelve soil samples were collected from invaded areas at the CNSC (58°N 93°W), six from each side of the main road. Soil had been recently added to repair the road and parking area at the entrance to the site (likely in 2020), and the roadside contained large populations of non-native species, notably *L. vulgaris*, *S. alba*, *P. major*, and *Matricaria matricarioides*.

## Seed germination procedure

Soil samples were transported to the University of Toronto Mississauga (UTM) in Mississauga, ON (43°N 79°W) where they were refrigerated for 45 days before use. All samples were then passed through a ~2 mm mesh to remove rocks, roots, and other coarse organic material. Sieving risks removing some seeds, but laboratory trials confirmed that even seeds of large-seeded invaders, such as *L. vulgaris* and *S. alba*, could readily pass through these sieves. Four hundred milliliters of sieved soil from each sample was then spread over 5000 mL of sterile sand in a 54 cm × 26 cm greenhouse tray.

Trays were placed in a climate-controlled greenhouse on 29 November 2021 and maintained for 10 weeks until 7 February 2022. To compensate for short winter days, supplemental artificial lighting was used to maintain 16 h of daylight (similar to early spring in Churchill), with an 18 °C/10 °C daytime/nighttime temperature cycle and a relative humidity set point of 60%. Trays were watered three times a week, at which point germinating seedlings were also noted. Any seedlings observed were counted, classified into morphospecies, and then removed to prevent them from being re-counted at subsequent samplings. A few seedlings from each morphospecies were then transferred into small pots and maintained until they grew sufficiently to be identified to species with reasonable confidence.

## Statistical analysis

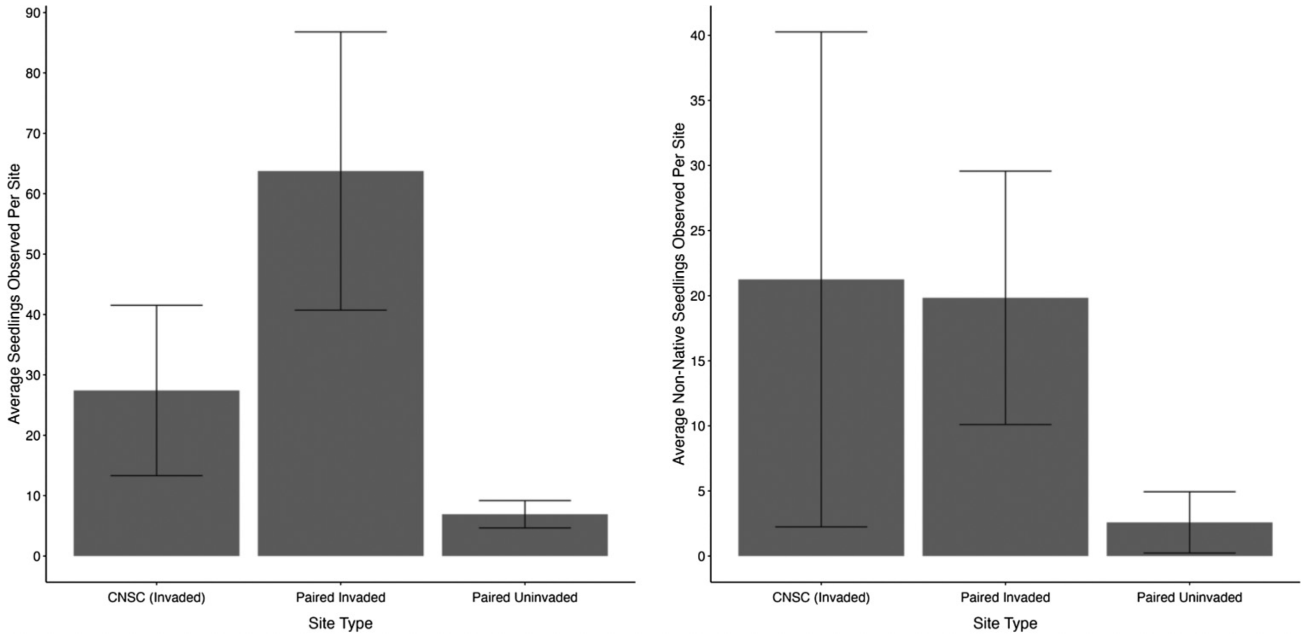
Analyses were performed in R (version 4.1.3). Since this is a descriptive study, the primary focus is simply on the total number of seedlings of each species observed. Nonparametric two-sided Wilcoxon's signed-rank tests were also used to compare seedling counts between paired invaded and uninvaded sites, since quantile–quantile comparison plots indicated non-normal distributions. Mean ± standard error (SEM), medians, and total counts of emerged seedlings are reported.

# Results

## Overall germination

By the end of the experiment (70 days), a total of 1177 seedlings had germinated from samples of all soil types (Fig. S2). These totals exclude a small number of seedlings that died before they could be adequately examined and categorized. Germination rate plateaued after about 60 days, suggesting that few ungerminated seeds remained at this point (Fig. S2). On average, paired invaded samples produced the greatest number of seedlings (63.75 ± 25.75 per sample, median = 12) (Fig. 1*a*). Soils from paired uninvaded sites

**Fig. 1.** Mean number of seedlings germinated per soil sample ± standard error (SEM) from the three site types. (*a*) All seedlings germinated. (*b*) Identified seedlings of non-native species.



produced significantly fewer seedlings (6.92 ± 3.51, median = 1) than paired invaded soil samples ($V = 68$, $p = 0.025$). Soils sampled from recently invaded sites at the CNSC produced an intermediate number of seedlings (27.42 ± 9.45, median = 0). The number of seedlings per sample varied substantially, ranging from a low of 0 (7 out of 12 paired uninvaded plots, 1 of 12 paired invaded plots, and 1 of 12 CNSC plots) to 2 samples with more than 100 seedlings (318 and 127, both from paired invaded plots).

## Seedling identities

A total of 12 seedling morphospecies (734 individuals) was classified to the species level (Table 1); further analyses focus on this subset. In most cases, at least some examples flowered, allowing confirmation of species identity. Three other non-flowering morphospecies (130 individuals) were tentatively identified to genus. Of the 313 remaining unidentified seedlings, 312 individuals occurred in a single sample (a paired invaded plot). This sample contained at least two different species, possibly including a native *Draba*; however, despite transplantation to individual pots, none of these seedlings survived until flowering. No obvious greenhouse contaminants were observed, and as noted above, pots frequently contained no seedlings during the experiment. However, *Veronica peregrina* has not been previously reported from the Churchill area (Scott 1996) raising questions about its provenance.

Only 3 (*Potentilla norvegica*, *Poa sp.*, *Ribes oxyacanthoides*) of the 12 identified species are native to Manitoba (Table 1). *Festuca* sp. also likely is a native, since there are no locally known introduced members of this genus (Scott 1996); however, since it was only tentatively identified, we have excluded it from further analysis. The remaining nine identified species are native to Europe, but they are also commonly established in southern Canada, consistent with our assumption that these populations originated from southern locations. Of the four identified species with at least 36 seedlings (i.e., an average of ≥1 seedling per sample), three were introduced (*T. arvense*: 313 seedlings in 18 samples; *C. bursa-pastoris*: 100 seedlings in 8 samples; and *M. matricarioides*: 71 seedlings in 2 samples) and one was native (*P. norvegica*: 207 seedlings in 12 samples).

Paired invaded soil samples tended to contain more seeds of identified natives (11.92 ± 23.33, median = 1) than other soil types (paired uninvaded: 1.92 ± 3.59, median = 1 and CNSC: 3.67 ± 7.33, median = 044). Nonetheless, the difference between paired invaded and paired uninvaded sites was not significant ($V = 29$, $p = 0.14$). Aside from a small sample size, the reason is that the majority of the natives in paired uninvaded sites germinated from a single sample containing 97 *P. norvegica*. Seedlings of identified non-natives were most abundant in soil samples from the CNSC (21.25 ± 19.01, median = 1), followed by paired invaded (19.83 ± 9.73, median = 13) and paired uninvaded soils (2.58 ± 2.35, median = 0) (Fig. 1*b*). Samples from paired invaded plots consistently produced more non-native seedlings than samples from paired uninvaded plots ($V = 43.5$, $p = 0.015$).

At least 40 plant species were identified in the survey of aboveground vegetation at the sampled sites (Table 2). Fireweed (*Chamaenerion angustifolium*) was the most abundant species, present at 29 of the 36 sampled sites. Of the four most common species identified by germination, *T. arvense* occurred aboveground in 16 sites, *C. bursa-pastoris* in 7, *P. norvegica* in 6, and *M. matricarioides* in 5. Although small sample sizes make statistical analysis difficult, it is apparent that non-native species occurring aboveground, were often, but

**Table 1.** Number of individuals of each species emerging from the three types of soil samples, ordered by total abundance ($N = 12$ samples per soil type).

| Species | Family | Status in Manitoba | CNSC soils | Paired invaded soils | Paired uninvaded soils |
|---|---|---|---|---|---|
| ***Thlaspi arvense*** | Brassicaceae | Introduced | 200 | 88 | 25 |
| ***Potentilla norvegica*** | Rosaceae | Native | 44 | 141 | 22 |
| ***Capsella bursa-pastoris*** | Brassicaceae | Introduced | 43 | 57 | |
| ***Matricaria matricarioides*** | Asteraceae | Introduced | 8 | 63 | |
| *Rumex* sp. | Polygonaceae | Unknown | | 60 | 10 |
| *Festuca* sp.* | Poaceae | Unknown | 26 | 12 | 8 |
| ***Chenopodium album*** | Amaranthaceae | Introduced | 3 | 13 | |
| ***Silene alba*** | Caryophyllaceae | Introduced | | 16 | |
| *Poa sp.* | Poaceae | Unknown | 4 | | 10 |
| ***Galeopsis tetrahit*** | Lamiaceae | Introduced | | 1 | 3 |
| ***Linaria vulgaris*** | Plantaginaceae | Introduced | | | 2 |
| ***Veronica peregrina*** | Plantaginaceae | Native | | 1 | 1 |
| ***Ribes oxyacanthoides*** | Grossulariaceae | Native | | 1 | |
| ***Stellaria media*** | Caryophyllaceae | Introduced | | | 1 |
| ***Taraxacum officinale*** | Asteraceae | Introduced | 1 | | |
| Unknown** | Unknown | Unknown | | 312 | 1 |
| Total | | | 329 | 765 | 83 |

**Note:** Taxa identified to the species level are in **bold**. *Likely native; no non-native *Festuca* is known to occur locally (Scott 1996).
**Includes at least two species of seedling.

not always, present in the seed bank at the same site. For instance, for the most frequently identified non-natives, *T. arvense* occurred below ground at 13 of the 16 sites where it was identified aboveground, *C. bursa-pastoris* at 3 of 7 sites, and *M. matricarioides* at 1 of 5 sites. Some non-native species conspicuously aboveground were nearly absent as seedlings. For instance, *L. vulgaris* was present aboveground and often abundant at 16 sites, but only two seedlings were grown from one soil sample from a single site. Another often-abundant species, *S. alba*, was detected belowground at two of the sites where it was present aboveground. Some species were detected belowground at sites where they were not observed aboveground. For example, *Chenopodium album* was found in seven soil samples but only noted aboveground at one of these sites. Likewise, *L. vulgaris* was absent aboveground at the single site where it was present in the soil. These examples could indicate presence of a persistent soil seed bank but low establishment success.

## Discussion

Although non-native plants are common in the town of Churchill, few have spread beyond town limits. Exceptions to this rule are usually found in areas where significant human disturbance has occurred, particularly in areas where soil has recently been moved or dumped. The results of this study indicate that one reason for this association is that viable seeds of non-native plants commonly occur in transported invaded soils.

The invaded soils that we sampled included several highly disturbed areas in or near town, including a series of soil dumps close to the Port of Churchill. These sites are close to the railway line, which likely is the original source of these invaders, and typically contain fertile organic-rich soils with large populations of invaders. Movement of such soils to other locations by humans, such as the power transmission poles and the roadsides at the CNSC, would result in the transportation of germinable seeds over long distances (upwards of 25 km by road, the distance between the Port and the CNSC). Transported soil would also offer a disturbed, competitor-free seedbed suitable for the growth of these invaders. Once established, these species could add their own seeds to the soil, creating a seed bank. In contrast, when we sampled uninvaded soils, seeds of non-natives were nearly absent. This evidence supports our assumption that uninvaded sites have not previously supported a population of non-native species. It is likely that the lack of human disturbance and soil modification is a barrier to non-native species establishment at these sites.

Persistent seed banks are often associated with non-native plants and can increase population longevity as well as spread (Gioria et al. 2021). The most abundant species that we detected were annuals or short-lived perennials, including both non-natives (*T. arvense*, *C. bursa-pastoris*, *M. matricarioides*) and natives (*P. norvegica*). These plants are dependent on seed production for persistence. As well, seed banking may buffer them against variable environmental conditions, such as late frosts or cool summers, which may be especially important for these species as they are near the edge of their environmental tolerances. Interestingly, one non-native species that we grew from our soil samples, *L. vulgaris*, was not previously known to set viable seeds in Churchill (Staniforth and Scott 1991), although it does flower there and can produce apparently mature but non-germinable seeds (*pers. obs.* 2023). Instead, it has been presumed to persist as rhizomes. Given

**Table 2.** Occurrence of plants identified in the seed bank and (or) in aboveground vegetation, ordered by total abundance below ground ($N = 36$ soil samples).

| | Number of individuals | Number of sites | |
|---|---|---|---|
| Species | Seed bank | Seed bank | Aboveground |
| *Thlaspi arvense* | 313 | 18 | 16 |
| *Potentilla norvegica* | 207 | 12 | 6* |
| *Capsella bursa-pastoris* | 100 | 8 | 7 |
| *Matricaria matricarioides* | 71 | 2 | 5 |
| *Rumex* sp. | 70 | 4 | 2 |
| *Festuca sp.* | 46 | 12 | |
| *Chenopodium album* | 16 | 7 | 4* |
| *Silene alba* | 16 | 2 | 5 |
| *Poa sp.* | 14 | 4 | 2 |
| *Galeopsis tetrahit* | 4 | 2 | 2 |
| *Linaria vulgaris* | 2 | 1 | 16 |
| *Veronica peregrina* | 2 | 2 | |
| *Ribes oxyacanthoides* | 1 | 1 | 4 |
| *Stellaria media* | 1 | 1 | |
| *Taraxacum officinale* | 1 | 1 | 1 |
| *Chamaenerion angustifolium* | | | 29 |
| *Salix* spp. | | | 9 |
| *Hedysarum mackenzii* | | | 6 |
| *Leymus mollis* | | | 5 |
| *Crepis tectorum* | | | 4 |
| *Plantago major* | | | 4 |
| *Solidago multiradiata* | | | 4 |
| *Shepherdia canadensis* | | | 3 |
| *Achillea* sp. | | | 2 |
| *Dryas integrifolia* | | | 2 |
| *Equisetum arvense* | | | 2 |
| *Erigeron* sp. | | | 2 |
| *Hordeum jubatum* | | | 2 |
| *Matricaria ambigua* | | | 2 |
| *Parnassia palustris* | | | 2 |
| *Poa sp.* | | | 2 |
| *Tanacetum huronense* | | | 2 |
| *Arnica alpina* | | | 1 |
| *Betula glandulosa* | | | 1 |
| *Castilleja raupii* | | | 1 |
| *Descurainia* sp. | | | 1 |
| *Gentianella* sp. | | | 1 |
| *Juncus* sp. | | | 1 |
| *Lomatogonium rotatum* | | | 1 |
| *Potentilla cf. egedei* | | | 1 |
| *Pyrola rotundifolia* | | | 1 |
| *Salix reticulata* | | | 1 |
| *Taraxacum lacerum* | | | 1 |
| *Urtica dioica* | | | 1 |

**Note:** Nomenclature follows Scott (1996). *May include similar species.

the small mesh size of the sieves we used, it is unlikely that vegetative fragments could have contaminated our samples. Instead, it may be that this species can mature seeds in unusually warm or favourable years.

Some of the most prominent species aboveground were very scarce in the germinable seed bank. In some cases, this may be because the greenhouse environment failed to provide necessary conditions for germination; however, other factors may also help to explain these discrepancies. For instance, despite abundant local seed production, the most frequent aboveground plant, *Chamaenerion angustifolium*, was absent from our germination trials. This species does not form persistent seed banks (Grime et al. 1998), instead regenerating from rhizomes while spreading to new sites via wind dispersal of seeds. Similarly, *L. vulgaris* was often very abundant above ground at our sites but very scarce in germination trials, even though this species can produce seeds capable of multiyear dormancy (Saner et al. 1995). Instead, the lack of germinable seeds may reflect infrequent production of viable seeds, as noted above. In contrast, *T. arvense* was abundant in both the aboveground vegetation and the germinated seed bank. This annual depends on abundant seed production and is known to have a persistent seed bank (Warwick et al. 2002).

## Limitation and applications

This study is intended to be a first step rather than a comprehensive description of the seed bank; however, the small number of samples examined is sufficient to confirm that viable seeds of some locally common invaders occur in the soil in our study area. Although it is perhaps not surprising that weedy invaders are represented in invaded soils (Gioria et al. 2021), this study confirms suspicions that some of the most prominent invaders in the Churchill area are unintentionally being locally transported by movement of invader-contaminated soil. This suggests that soil movement is an important mechanism for local spread and helps to explain the strong association of invaders with human-disturbed sites. In particular, the local road network may be an important corridor for non-native species invasions through soil movement for construction, roadside repairs, or disposal. Restricting excavation of soil from invaded areas may be an effective way of reducing further spread.

Movement of soil may represent an increasing problem as the local climate continues to warm. Air temperatures in the Hudson Bay region were relatively stable until the 1990s but are now rapidly increasing (Hochheim and Barber 2010), and in particular, temperatures in the Churchill area have been increasing at an accelerating rate (Mulder et al. 2017). These increasing temperatures may lead to increased seed production and a higher rate of germination and establishment by non-native species currently at the edge of their climatic range, though increased interannual variation may work to counter this effect (Mulder et al. 2017). Notably, species, such as *L. vulgaris*, believed currently to be persisting vegetatively may begin to produce viable seeds, at least in warmer years. Such species may be on the cusp of becoming significantly more invasive as the climate continues to warm.

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### Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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### Competing interests

The authors declare there are no competing interests.

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## Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjb-2023-0019.

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