Received: 22 January 2017 | Revised: 10 March 2017 | Accepted: 13 March 2017
DOI: 10.1002/rra.3149

WILEY

RESEARCH ARTICLE

Giant hogweed at its northern distribution limit in North America: Experiments for a better understanding of its dispersal dynamics along rivers

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Funding Information
Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: 194613-2013; Fonds de recherche du Québec Nature et Technologies, Grant/Award Number: 2015-PR-181294; Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec, Grant/Award Number: PV-3.2-2014-002

Abstract

We studied the reproduction and dispersal of giant hogweed (*Heracleum mantegazzianum*) at its northern distribution limit in North America (Québec, 2014–2016) to better understand the invasion dynamics of the species along rivers. Seeds were collected from a riparian population to conduct germination, floatation, and dispersal experiments. Data were analysed in comparison with a real invasion case that was initiated about 10 years ago along a river system. In Québec, giant hogweed individuals produce on average 14,000 to 16,000 seeds with a germination rate of 75–85%. Seeds with endosperm that fall in water likely sink within 5 hr. Along a small brook, most disperse over short distances (<40 m) in summer, although some can travel 100–300 m. These data suggest that late-summer or early-fall water dispersal of seeds would not explain the magnitude and rapidity of the invasion patterns observed along streams. We suggest that late-fall and, especially, spring floods are the most efficient dispersal vectors for giant hogweed seeds and are likely responsible for the establishment of populations kilometres downstream from introduction points along river systems. The spread of giant hogweed would consequently be less influenced in the near future by a rise in temperature than by a change in the magnitude or timing of flood events.

KEYWORDS

flood, germination rate, *Heracleum mantegazzianum*, invasive plant, riparian corridor, seed floatation, sexual reproduction

1 | INTRODUCTION

Giant hogweed (Apiaceae: *Heracleum mantegazzianum* Sommier & Levier; hereafter, GH) figures amongst the most studied invasive plants of the world (Hulme et al., 2013). The species was introduced from the Caucasus Mountains (southern Russia and eastern Georgia) as ornamental plant in England in 1817 and in North America probably at the beginning of the 20th century (Jahodová et al., 2007; United States Department of Agriculture, 2017). GH is now present in 19 European countries, notably in the Czech Republic, Denmark, Germany, Great Britain, and Switzerland, and in northeastern and northwestern North America (Biota of North America Program, 2017; DAISIE European Invasive Alien Species Gateway, 2017). It has rapidly spread in these countries/regions from parks and gardens to river and road corridors (Pergl, Pyšek, Perglová, & Jarošík, 2012; Thiele, Schuckert, & Otte, 2008). This plant is considered a serious public health problem (Reinhardt, Herle, Bastiansen, & Streit, 2003). Contact with the sap can cause severe photodermatitis, including third-degree burns, if the skin is subsequently exposed to sunlight or other sources of ultraviolet radiation (Chan, Sullivan, O'Sullivan, & Eadie, 2011; Klimaszyk, Klimaszyk, Piotrowiak, & Popiołek, 2014; Pfurtscheller & Trop, 2014). In the province of Québec (Canada), 21% of landowners with GH have reported photodermatitis cases (Lavoie, Lelong, Blanchette-Forget, & Royer, 2013).

The number of GH populations has recently increased in northeastern North America, especially in New York State (from 346 in 2007 to 1309 in 2015; Kraus, 2016) and Québec (from a few populations in 2006 to 169 in 2012, and 276 in 2015; Page, Wall, Darbyshire, & Mulligan, 2006; Lavoie et al., 2013; Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques du Québec, 2017a). Most of the new populations likely established from seeds produced by individuals planted in gardens,

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and then spread by wind, water, or humans over short or long distances (Lavoie et al., 2013).

Several studies have been conducted in Europe, and especially in the Czech Republic, on the reproduction, dispersal, and effects of GH. The plant is monocarpic, reproducing only once in its lifetime, usually at 3 to 5 years of age, and does not spread vegetatively (Pergl, Perglová, Pyšek, & Dietz, 2006). An individual may produce up to 10,000–20,000 seeds (Perglová, Pergl, & Pyšek, 2007). Most seeds (>90%) are dispersed over very short distances (<10 m), but because they are buoyant, some can be transported by water along rivers, potentially over several kilometres (Caffrey, 1994; Clegg & Grace, 1974; Moravcová et al., 2007; Pergl, Müllerová, Perglová, Herben, & Pyšek, 2011). Germination rates in laboratory experiments can be very high (>90%). In nature, seeds massively germinate the next spring season, and only very small fractions (1–3%) are still present in the seed banks 2 to 3 years after their production (Krinke et al., 2005; Moravcová, Pyšek, Pergl, Perglová, & Jarošík, 2006).

To our knowledge, there are no data on the reproduction and dispersal of GH in North America. At the northern limit of the invaded range (Bas-Saint-Laurent, Québec City, and Saguenay regions in northeastern Québec), the climate is considerably cooler and wetter (mean annual temperature, 2.8–5.0 °C; total annual precipitation, 930–1190 mm) than in the Czech localities (5.5–8.5 °C; 475–850 mm) where most of the data on reproduction were collected (Government of Canada, 2017; Lavoie et al., 2013; Moravcová, Perglová, Pyšek, Jarošík, & Pergl, 2005; Moravcová et al., 2006; Perglová, Pergl, & Pyšek, 2006; Perglová et al., 2007), which cautions against transposing Czech data to the North American context without discernment. However, on the basis of the distribution of the species in northern Europe, Page et al. (2006) predicted that GH could easily tolerate the cold continental climates of Canada. Furthermore, climate warming could favor a northward expansion of the species in Canada by improving reproductive conditions as has recently been observed for the invasive Japanese knotweed (*Reynoutria japonica* Houttuyn; Groeneveld, Belzile, & Lavoie, 2014; Duquette et al., 2016); on the other hand, a warmer climate could also be responsible of a decline of well-established populations located in the United States because of the absence of temperatures cold enough to break seed dormancy (Pyšek, Kopecký, Jarošík, & Kotková, 1998). Additional data on the reproductive biology of the species are urgently needed to better evaluate the potential of GH to invade new North American regions.

Dispersal of GH seeds requires further investigation, because our understanding of this phenomenon is essentially based on computer modelling rather than field data (Pergl et al., 2011). Models generally conclude that long-distance (>10 m) seed dispersal is the driving force of a GH invasion and that short distance dispersal alone cannot account for the observed invasion patterns (Nehrbass et al., 2007; Pergl et al., 2011). Walker, Hulme, and Hoelzel (2003) and Moenickes and Thiele (2013) estimated that dispersal along rivers significantly contributes to the spread of GH at the landscape level. However, to date, knowledge on water dispersal of GH seeds relies only on a single poorly detailed floatation test (Clegg & Grace, 1974), in which seeds were scattered on a water surface under "turbulent" or "undisturbed" conditions: seeds remained afloat 1 or 2 days (turbulent) or 3 days (undisturbed). Clegg and Grace (1974) concluded that "with a hypothetical river surface velocity of 0.1 m s^{-1}, a seed could thus be transported 10 km if unhindered" (p. 228). No field data have since been gathered to verify this hypothesis.

We studied the reproduction and dispersal of GH near its northern distribution limit in North America (Québec) over a 3-year period (2014–2016). Seeds were collected from a riparian population to conduct germination and floatation experiments. A dispersal experiment under field conditions was also conducted to determine the distance over which GH seeds are spread by water. We hypothesized that the number of seeds produced by GH individuals and the viability level would be lower in Québec than in the Czech Republic, because of the colder and wetter climate, but nevertheless high enough to trigger an invasion. We also hypothesized that a high proportion of the seeds dispersed by water would travel over distances 100–1000 m, that is, over one or two orders of magnitude larger than the known short dispersal distance (<10 m), which would explain why the species spreads so readily in riparian habitats. Data were analysed in comparison with a real invasion case that was initiated about 10 years ago along a river system to better understand the dispersal dynamics of GH in riparian habitats.

2 | MATERIAL AND METHODS

2.1 | Study area

The GH population that was selected for this study was located along the Fourchette Brook (hereafter FBk), at Saint-Isidore, near Québec City, in Québec, Canada (46°38′ N, 71°06′ W; alt.: 140 m a.s.l.). FBk is the main tributary of the Le Bras River, which flows into the Etchemin River that ends its course into the St. Lawrence River at the town of Lévis, across the river from Québec City. The mean annual temperature in the study area is 5 °C, the mean temperature of the coldest month (January) –12 °C, and that of the warmest month (July) 19 °C. The mean annual precipitation totals 1178 mm, 23% of which fall as snow. The mean annual number of degree days (>0 °C) totals 2,825, but at the GH seed harvest day (this study), it was 2,281 (September 1, 2014), 2145 (August 27, 2015) and 2210 (August 29, 2016), which was close to or 3–6% higher than the mean value registered at these dates (2150; Government of Canada, 2017). Total precipitation received (mm) at the seed harvest day was 753 (2014), 784 (2015), and 876 (2016), again close to the mean value registered at theses dates (770 mm), except for 2016, which was 14% wetter (Government of Canada, 2017).

FBk is 30-km long and its mean annual water flow is 0.07 m^3/s (Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques du Québec, 2017b). Its watershed covers 120 km^2. The brook is bordered by agricultural lands (corn, forage, and soybean) over 80% of its course (Michaud, Deslandes, Desjardins, & Grenier, 2009; Pelletier, 2005). River banks are essentially clayey, sandy, or loamy, with some rocky sections, and covered by a herbaceous riparian strip about 5 to 6-m wide in cultivated areas; elsewhere, river banks are tree-covered.

About 2005 (exact introduction year unknown), some GH individuals were planted a few meters from FBk, at a site located

7.5 km from the source of the brook. GH has since spread along FBk: in 2014, the river banks were heavily infested (up to 110–275 individuals per m^2), especially over the first 8 km downstream from the introduction point, with the exception of the kilometer 1 where the river banks are rocky (Figure 1a). High numbers of individuals were also detected from 11 to 12 km, and at 14 and 15 km from the introduction point. A few were noted as far as 20, 23, and 26 km downstream, on the banks of the Le Bras and Etchemin Rivers. Flowering individuals were recorded over the first 11 km (2013) or 18 km (2014) of the invaded stretch of the brook. No individual was detected upstream from the introduction point (Boivin & Brisson, 2016; Lavoie, 2016).

2.2 | Field sampling

GH individuals selected for sampling were located on one of the most heavily invaded sections of FBk, about 2–3 km downstream from the introduction point. At this location (Pieriane Farm), the brook is bordered by cultivated fields (corn, soybean, and forage) over its entire course. The vegetated riparian strip is 6-m wide and is colonized by GH and 69 other vascular plant species (55% of which are exotic), mainly grasses, such as *Alopecurus pratensis* Linnaeus, *Bromus inermis* Leysser, *Elymus repens* (Linnaeus) Gould, and *Phalaris arundinacea* Linnaeus (Lavoie, 2016).

In 2014, 2015, and 2016, 20 flowering individuals were haphazardly selected within small quadrats used as control sites for eradication experiments initiated in 2014 (Boivin & Brisson, 2016). Once the seeds formed but before their release (2014, August 4; 2015, August 3; 2016, July 28), the terminal umbel—which alone produce about 45% of the seeds (Perglová et al., 2006)—of each individual was wrapped with an Agribon AG-19 (2014) or AG-15 (2015 and 2016) white textile sheet (Polymer Group, San Luis Potosi, Mexico); the other umbels were eliminated (Figure 2). The AG-19 sheet has an 85% light transmission, and considering the low germination rate of seeds collected in 2014, we hypothesized a higher light transmission sheet (AG-15: 90%) could increase seed viability; this sheet was thus used in 2015 and 2016. However, in 2016, five additional individuals were wrapped with an AG-19 sheet for comparison purposes. Seeds were collected once mature (light brown and dry appearance), that is, at the end of August—beginning of September (2014, September 1; 2015, August 27; 2016, August 29), then air-dried, cleaned, weighed, and placed in open paper bags. Seeds were stored at room temperature (22 °C) until the beginning of germination and floatation experiments.

2.3 | Germination

A total of 150 seeds per GH individual were haphazardly selected to conduct germination experiments; malformed or completely blackened seeds were not selected. Seeds were deposited on a wet filter paper in five petri dishes (30 seeds per dish). About 4–5 mL of water was added to each dish to create a thin film of free water. Seeds were then stratified under cold (3–6 °C) and dark conditions for germination. Water was added throughout the experiments (1 or 2 times per week) to keep the filter paper wet. Dishes were checked once a week to detect germinating seeds, which were counted then discarded. The experiments were terminated when the germination rate reached an asymptote (about 100 days). Significant differences between years for seed production, seed weight, and germination rate were tested using multiple linear regression models with sampling year as dummy variable, calculated with Stata (StataCorp, 2013).

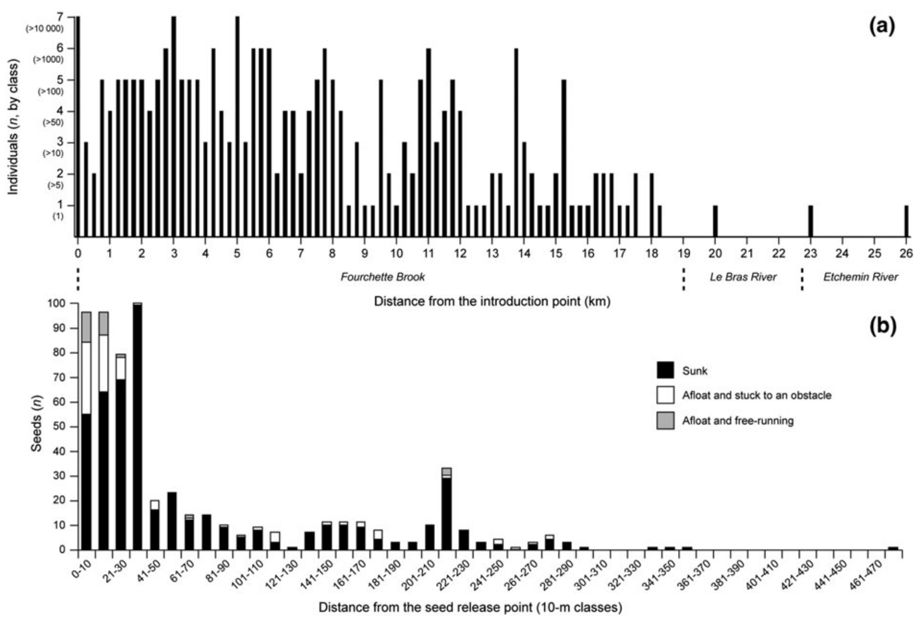

FIGURE 1 (a) Number of giant hogweed (*Heracleum mantegazzianum*) individuals detected along the Fourchette Brook, Le Bras River and Etchemin River (Québec, Canada) in June 2014 (adapted from Lavoie, 2016). This survey was done every 250 m downstream from the introduction point of the species. The number of individuals was estimated over a 50-m distance at each sampling station and using seven population classes; (b) number and position of giant hogweed seeds marked and released in Fourchette Brook and recovered 17–23 hr later. The status of the seeds (sunk, afloat and free-running, and afloat but stuck to an obstacle) is indicated

FIGURE 2 Terminal umbel of a giant hogweed (*Heracleum mantegazzianum*) individual wrapped with an Agribon AG-15 textile sheet used to collect seeds (photograph: E. Groeneveld). [Colour figure can be viewed at wileyonlinelibrary.com]

2.4 | Viability

A seed viability experiment was conducted with seeds collected in 2014, given their relatively low germination rates, at least compared to Czech data (Moravcová et al., 2005). A total of 150 seeds per individual were again haphazardly selected for a tetrazolium viability test. A buffer solution was first produced by mixing 5.68 g of Na_2HPO_4 to 3.63 g of KH_2PO_4 in 1 L of deionized water. A tetrazolium solution was obtained by adding 10 g of 2,3,5-triphenyl-2H-tetrazolium chloride (Sigma-Aldrich, St. Louis, Missouri, USA) in 1 L of the buffer solution. The resulting solution was stored (3–6 °C) in a bottle designed for light sensitive material. Seeds were preconditioned by placing them between two filter papers in petri dishes, then soaking in water (5 mL) during 16 hr at 22 °C. Seeds were cut to expose their embryo, soaked into 2.5 mL of tetrazolium solution during 24 hr at 22 °C, then examined under a binocular microscope. Pink- or red-colored embryos were considered viable, because they showed the activity of dehydrogenase enzymes used in the respiration process (Association of Official Seed Analysts, 2002; Elias, Copeland, McDonald, & Baalbaki, 2012).

2.5 | Floatation

Two floatation experiments, inspired by van den Broek, van Diggelen, and Bobbink (2005) and Rouifed, Puijalon, Viricel, and Piola (2011), were conducted with GH seeds. In the first experiment, 16 beakers were filled with water (2 L); eight were equipped with a small aquarium air pump (Marina 200; Hagen, Baie d'Urfé, Québec, Canada) to constantly generate bubbles and turbulence (moving water treatment vs. standing water treatment). Fifty seeds haphazardly selected among the ones sampled in 2014 were deposited in each of the 16 beakers. They were checked every hour to count the number of seeds that remained afloat. Before checking, air pumps were switched off to allow seeds to sink, and in all beakers, water was stirred for 5 s to break surface tension. Only seeds with endosperm (85% of the seeds) were retained for calculating floatation time. These seeds were easy to identify after the first 5 h of the experiment, that is, once saturated with water. The second experiment was a repetition of the first, but with seeds collected in 2016 (91% with an endosperm), which had a significantly higher seed weight (+68%) than those collected in 2014; floatation time can be negatively correlated to weight (Planchuelo, Catalán, & Delgado, 2016).

2.6 | Dispersal

A GH dispersal experiment was conducted in FBk, at the same location where seeds were harvested. This mark-recapture experiment was inspired by Kaproth and McGraw (2008), who studied seed dispersal by water of the invasive *Ailanthus altissima* (Miller) Swingle in West Virginia (USA). One thousand GH seeds, sampled in 2015, were haphazardly selected, rendered non-viable in a microwave oven, then marked with a pink spray paint (Rust-Oleum Consumer Brands, Concord, Ontario, Canada). Floatation tests in laboratory showed that the paint did not affect floatability, at least over a 24-hr period. The experiment took place during three consecutive sunny days (July 30 to August 2, 2016). The day before seed release (July 30), FBk was surveyed to measure, over a 1-km distance and at every 50 m, brook width (mean, 390 cm), water depth (mean, 27 cm), and surface water velocity (mean: 0.33 m s^{-1}). Seeds were released (August 1) in water at the upstream point of the section, at the center of the cross profile of the brook. A team of four observers surveyed (August 2) the brook over a distance of 1.1 km from the release point to recover marked seeds. The survey was conducted 17–23 hr after seed release, that is, after all seeds with an endosperm should have sunk according to the floatation experiments, and was performed downstream to upstream because the observers stirred up sediments by walking in the brook, which reduced water clarity. The status of the recovered seeds (sunk, afloat and free-running, and afloat but stuck to an obstacle) was noted, plus their position relative to the release point using a measuring wheel, and the time of recovery.

3 | RESULTS

3.1 | Production, weight, germination, and viability

GH total seed production per individual, estimated with the seeds of the terminal umbel that represent 45% of the total number of seeds (Perglová et al., 2006), was highly variable from 2014 to 2016 and between individuals, from a minimum of 3465 to a maximum of 22,853 (Table 1). Seed production ($F_{2,\ 57}$ = 25.84, p < .0001, adjusted R^2 = 0.457); weight ($F_{2,\ 57}$ = 25.11, p < .0001, adjusted R^2 = 0.450); and germination rates ($F_{2,\ 57}$ = 27.25, p < .0001, adjusted R^2 = 0.471)

TABLE 1 Giant hogweed (*Heracleum mantegazzianum*) reproduction and seed floatation data collected near the northern limit of its distribution range in North America (Québec, Canada) from 2014 to 2016

Location, year and wrapping sheet used	Individuals sampled (*n*)	Seeds per individual (*n*)[a]	Weight (g) of 100 seeds (mean ± SD)	Seed germination rate (%)	Seed viability rate (%)	Floatation time (*n* hours required for sinking *x*% of seeds with endosperm) in moving (M) or standing (S) water							
						10%M	50%M	90%M	100%M	10%S	50%S	90%S	100%S
Québec 2014: AG-19	20	Mean: 9511 Min.: 3465 Max.: 14,842	0.99 ± 0.24	Mean: 45.6 Min.: 12.0 Max.: 80.7	Mean: 50.2 Min.: 14.7 Max.: 78.0	2	3	6	8	8	11	13	14
Québec 2015: AG-15	20	Mean: 16,679 Min.: 12,837 Max.: 22,853	1.53 ± 0.18	Mean: 85.9 Min.: 50.7 Max.: 97.3	Nt				Nt				
Québec 2016: AG-15	20	Mean: 14,528 Min.: 7582 Max.: 20,376	1.66 ± 0.46	Mean: 76.9 Min.: 12.0 Max.: 92.7	Nt	1	1	4	5	3	5	9	16
Québec 2016: AG-19	5	Mean: 11,938 Min.: 9113 Max.: 14,075	1.39 ± 0.43	Mean: 58.5 Min.: 22.7 Max.: 74.0	Nt				Nt				
Czech Republic 2002[b]	56	Na	1.62 ± 0.28	Mean: 90.9	Nt				Nt				
Czech Republic 2002[c]	100	Mean: 20,671 Min.: 9974 Max.: 27,633	Na	Nt	Nt				Nt				

Note. To collect seeds, the terminal umbel of giant hogweed individuals was wrapped with an Agribon AG-19 (2014 and 2016) or AG-15 (2015 and 2016) white textile sheet. Data from the same species collected in the Czech Republic shown for comparison.

[a]Assuming the terminal umbel of a giant hogweed individual represents 45% of the total number of seeds (Perglová et al., 2006).

[b]Moravcová et al. (2005), terminal umbel only.

[c]Perglová et al. (2006).

na: not available; nt: not tested.

were significantly higher in 2015 (AG-15) and 2016 (AG-15) than in 2014 (AG-19), which probably reflects (at least in part) a negative influence of the AG-19 wrapping sheet; this influence was highlighted by the difference in seed germination rates recorded in 2016 (Figure 3, AG-15 22% higher than AG-19). Seed viability tests conducted in 2014 indicated that germination tests slightly under evaluated seed viability of the AG-19 covered seeds by 5%. Mean seed production with AG-15 (14,528–16,679) was 24–42% lower than that recorded in the Czech Republic, but seed weight was very similar. However, seed germination rates in Québec were below (by 6–18%) those of the Czech Republic (Table 1).

3.2 | Floatation

Laboratory experiments showed differences between floatation times, which varied with treatment (moving or standing water) and seed weight (Table 1; Figure 4). GH seeds with endosperm sank very fast in moving water (most within 1 to 3 hr, all within 8 hr), and even in standing water, all sank within 16 hr.

3.3 | Dispersal

More than 60% (605 seeds) of the 1000 marked GH seeds released in FBk were recovered 17–23 hr later. About 81% were sunk, 4% afloat and free-running, and 15% afloat but stuck to an obstacle. More than 72% of the floating seeds were located <30 m from the release point (Figure 1b). About 61% of the seeds were recovered <40 m from the release point, 24% at 100–300 m, and only four seeds were found >300 m (the farthest: 480 m).

4 | DISCUSSION

Near its northern distribution limit in North America (Québec), GH individuals produce a lower number of seeds with a slightly lower germination rate than those introduced in Central Europe (Czech Republic). Part

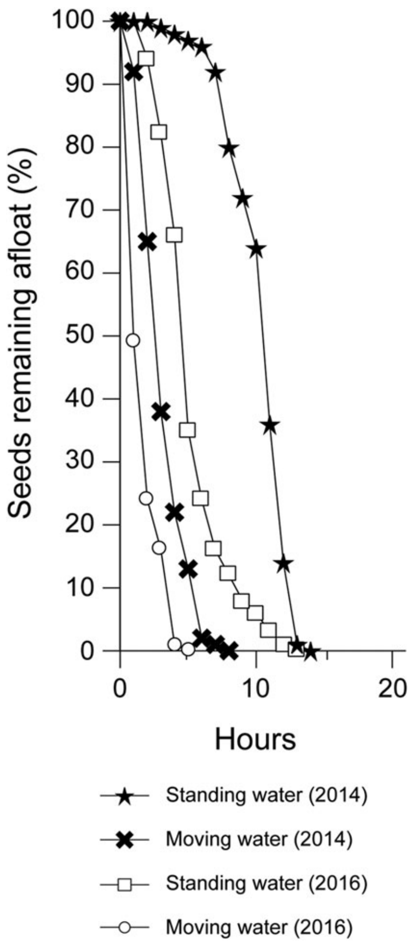

FIGURE 4 Floatation time of giant hogweed (*Heracleum mantegazzianum*) seeds with endosperm collected near Fourchette Brook (Québec, Canada), as expressed by the percentage of seeds still floating over the duration of the experiment. Different experiments are shown, which vary according to the sampling year (2014 or 2016) or treatment (moving or standing water)

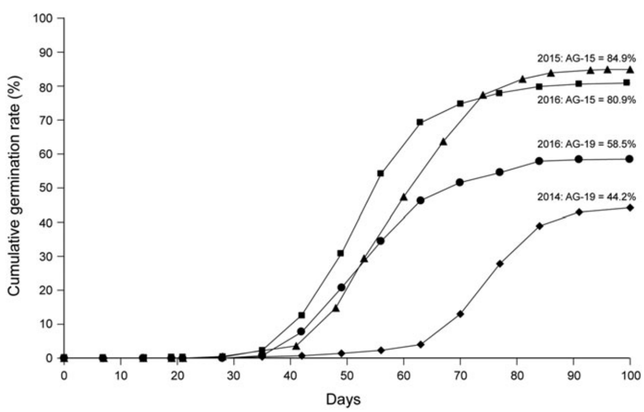

FIGURE 3 Evolution of the giant hogweed (*Heracleum mantegazzianum*) seed germination rate (all seeds considered, not the mean value per individual: percentage of seeds having germinated) over the duration of the experiment for seeds collected near Fourchette Brook (Québec, Canada) in 2014 (umbel wrapping sheet: Agribon AG-19, 3000 seeds tested from 20 individuals); 2015 (AG-15, 3000 seeds, 20 individuals); and 2016 (AG-15, 3000 seeds, 20 individuals; AG-19, 750 seeds, 5 individuals)

of the difference could be explained by the fact that we did not mimic, as per Moravcová et al. (2005), the conditions the seeds are normally exposed during germination in spring, that is, from about 2 °C at night to 13 °C in daylight (Government of Canada, 2017). A single individual may nevertheless produce a mean number of 14,000 to 16,000 seeds (up to 23,000), of which at least 75–85% are viable; this represents a considerable number of diaspores, largely enough to trigger an invasion. On the other hand, almost all seeds with endosperm that fall in water probably sink within 5 hr, and along a small brook, most are spread over short distances (<40 m) in summer. However, approximately, a quarter of the seeds will nevertheless travel 100–300 m, that is, over one order of magnitude farther than the dispersal distance reached by the vast majority of seeds carried by wind (<10 m; Pergl et al., 2011).

Some GH seeds could have travelled farther than 300 m during the dispersal experiment conducted in FBk. Considering a seed with endosperm may remain afloat 5 hr in moving water, and a surface water velocity of 0.33 m s^{-1} (measured at FBk), a certain number of seeds could have reached a maximum distance of 6 km after their release. Although theoretically, possible −39% of the marked seeds were never recovered over the 1.1 km survey— this scenario is unlikely; all recovered seeds were found <480 m from the release point, and the abundance of obstacles (vegetation, stones, tree branches, etc.) over the course of the brook would likely stop the travel well before the reaching of kilometre-long distances. Unrecovered seeds were probably simply not detected by the observers, hidden by vegetation, or masked by stirred sediments.

The establishment success of GH along FBk can certainly be explained by the abundance of high-quality habitat for the species (disturbed river banks lacking competitive shrubs, access to nutrients from agricultural inputs), and the presence of running water facilitating the spread of seeds. However, a GH individual can only reproduce once it has reached 3 to 5 years of age. Only a small fraction of the thousands of seeds produced along the river bank is likely to fall in the water in August and September, because plants generally do not overhang the water. An even smaller fraction is eventually deposited on an appropriate germination site after a few hours in water. If the seeds were spread by water only during late-summer and early-fall seasons, the invasion would probably progress at a very slow pace, maybe about 300–500 m per GH generation, as indicated by the seed dispersal test. This scenario is inconsistent with the invasion pattern observed at FBk, which was invaded by tens of thousands of individuals over an 18-km distance in less than 10 years. Winter dispersal of seeds by wind on the snow cover is unlikely because all seeds are locally (FBk) released by the end of October, well before the first snowfall (authors personal observations).

We propose an alternative scenario for the rapid spread of GH along FBk. We suggest that late fall, and especially spring floods when water flow of FBk is about 9 times that of the summer (Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques du Québec, 2017b), is the most efficient dispersal vectors for GH seeds. This is the case for a large number of riparian plant species with dormant seeds (Boedeltje, Bakker, Ten Brinke, Van Groenendael, & Soesbergen, 2004; Soomers et al., 2011; Catford & Jansson, 2014; Čuda, Rumlerová, Brůna, Skálová, & Pyšek, 2017). Floods can potentially carry thousands of seeds deposited near the parent plants, and spread them much farther than during the summer because of the velocity of flood waters. The buoyancy of GH seeds (a few hours) is very low compared to that of seeds produced by plants characteristic of riparian habitats or wet meadows (from a few days to several weeks; van den Broek et al., 2005; Carthey, Fryirs, Ralph, Bu, & Leishman, 2016), but seeds with short buoyancy time are nevertheless effectively dispersed during flood events (Truscott, Soulsby, Palmer, Newell, & Hulme, 2006). Moreover, seeds can also be deposited by floods on a more elevated position on the river bank (Kaproth & McGraw, 2008), in places safer for the survival of seedlings because they are less likely to be inundated by late spring floods; GH plants were frequently observed along FBk on the floodplain, often >10 m from the brook. We consequently hypothesize that flood dispersed seeds were responsible for the establishment of the major GH concentrations found a few kilometers from the most invaded stretch of FBk, that is, between 10.75 and 12 km, at 13.75 km and at 15.25 km, not to mention the individuals found at 20, 23, and 26 km (Figure 1a).

GH is not, of course, the only invasive plant species spread by flood events: other examples are purple jewelweed (*Impatiens glandulifera* Royle), flowering ash (*Fraxinus ornus* L.), red ash (*F. pennsylvanica* Marshall), seep monkeyflower (*Erythranthe guttata* (Fischer ex de Candolle) G.L. Nesom, and tree-of-heaven (*Ailanthus altissima* (Miller) Swingle). In all cases, floods contribute to the long-distance dispersal of diaspores (up to 8 km), and thus to the acceleration of the invasion process (Čuda et al., 2017; Kaproth & McGraw, 2008; Kowarik & Saümel, 2008; Schmiedel & Tackenberg, 2013; Thébaud & Debussche, 1991; Truscott et al., 2006).

If our hypothesis is valid, the spread of GH near its actual northern distribution limit would be less influenced in the near future by a rise of the temperatures than by a change in the magnitude or timing of flood events. An analysis of the trends (1934–2004) of the variability of spring floods for rivers located in Québec has showed that in the regions where GH reaches its northeastern range limit, floods occurred earlier and had a larger magnitude over time (Mazouz, Assani, Quessy, & Légaré, 2012). On the other hand, projections for the future (about 2050), taking into account climate warming and an associated reduction of snow precipitations, predict an advance of spring discharge by 22–34 days, and a decrease of spring flows by as much as 40% for tributaries of the St. Lawrence River (Boyer, Chaumont, Chartier, & Roy, 2010). Some of these changes could favour the establishment of GH, because river banks would be inundated for shorter periods, but others (reduction of the magnitude of floods) could also slow the spread of the species. Whatever the future of floods, such events should be taken into account by environmental managers monitoring and controlling the spread of GH. Managers often restrict the search of GH individuals to the river bank, although the flood plain as a whole should also be monitored for early detection, especially in spring, just after the emergence of seedlings and when GH individuals are easy to detect because of their rapid growth.

Models constructed to predict the dispersal of GH suggest that seeds spread over long distances may only represent a very small fraction (0.1–7.5%) of the total seed pool (Nehrbass et al., 2007; Pergl et al., 2011). Pergl et al. (2011) added that the "reduction in the seed set even at small amounts is likely to significantly affect the invasion dynamics. (…) results of our study suggest that the more important effects of [efforts to reduce the seed set] may be in decreasing the number of seeds that are available for dispersal to a large distance from mother plants rather than in simply reducing the total seed set" (p. 735). GH control campaigns conducted along FBk since 2014 have essentially focused on eliminating mature individuals (with umbels), as a first step to stop the spread of the species (Brochu, 2015). If this effort also prevents long distance dispersal of seeds from FBk to the Etchemin River system, which terminates its course at Lévis, a town of 140,000 inhabitants, the invested time and money will have been well worth it.

ACKNOWLEDGEMENTS

This research was financially supported by the Natural Sciences and Engineering Research Council of Canada (194613-2013), the Fonds de recherche du Québec Nature et Technologies (2015-PR-181294), and the Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec (PV-3.2-2014-002). The authors thank Noémie Blanchette-Forget, Catherine Dubois, Félix Gagnon, Michaël Leblanc, and Benjamin Lelong for field assistance; Jean Dubé for help with statistical analyses; Pieriane Farm (Guillaume Couture) for access to the study site and field assistance; and two anonymous reviewers for comments on an earlier draft.

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How to cite this article: Trottier N, Groeneveld E, Lavoie C. Giant hogweed at its northern distribution limit in North America: Experiments for a better understanding of its dispersal dynamics along rivers. *River Res Applic*. 2017;33:1098–1106. https://doi.org/10.1002/rra.3149