

# Invasive Russian Knapweed (*Acroptilon repens*) Creates Large Patches Almost Entirely by Rhizomic Growth

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Russian knapweed is an outcrossing perennial invasive weed in North America that can spread by both seed and horizontal rhizomic growth leading to new shoots. The predominant mode of spread at the local scale and dispersal at the long-distance scale informs control but has not been quantitatively researched. We used amplified fragment-length polymorphisms (AFLPs) of DNA collected from 174 shoots in two discrete patches of Russian knapweed at each of three locations in Montana. Out of the 174 shoots collected, we found nine AFLP genotypes. Three out of the six patches were monotypic; the other three patches each had one rare genotype. No genotypes were shared between patches. The maximum diameter of a genet (a genetic individual) was 56.5 m. These results indicate that patch expansion at the local scale is almost entirely by rhizomes that spread and develop new shoots. At the long-distance scale, dispersal is by seed. Controlling seed development through biological control and herbicide use may be effective at stopping long-distance dispersal but may not affect expansion of existing patches.

**Nomenclature:** Russian knapweed, *Acroptilon repens* (L.) DC, *Rhaponticum repens* (L.) Hidalgo, *Centaurea repens* L.

**Key words:** AFLP, clonal, invasive plant, reproduction.

An important characteristic of a successful invasive plant species is the ability to establish in new areas and to spread locally and disperse across longer distances after initial founding events (Lockwood et al. 2005). Methods of invasion expansion can include seed from sexual or apomictic reproduction, and vegetative materials such as shoots arising from rhizomes, stolons, bulbils, tillering, and fragmentation. Examples of these reproductive methods can be found in plant invasions (e.g., *Tamarix* L. [sexual; Brotherson and Field 1987], rush skeletonweed, *Chondrilla juncea* L. [apomictic; Chaboudez 1994], *Lepidium draba* L. [rhizomes; Gleason and Cronquist 1963], mouse-ear hawkweed, *Hieracium pilosella* L. [stolons; Bishop et al. 1978], flowering rush, *Butomus umbellatus* L. [bulbils; Eckert et al. 2000], reed canarygrass, *Phalaris arundinacea* L. [tillering; Lavergne and Molofsky 2007], and alligatorweed, *Alternanthera philoxeroides* (Mart.) Griseb. [fragmentation; Jia et al. 2009]).

Overall, clonal reproduction is more prevalent in invasive than native species (Pyšek 1997), although many invasive plant species use multiple methods of reproduction to invade.

The primary mode of expansion of an invasive plant species at the local or long-distance scale is often not known. Determining how an invasive plant species reproduces and spreads can give information about its genetic structure and diversity or invasion history. For example, different knotweed species (*Fallopia* Adans.) spread by different methods; some entirely by vegetative means, and some by both sexual seed and vegetative methods, depending on whether the spread is local or long distance (Gaskin et al. 2014). Two invasive *Solidago* species in China spread locally through rhizomes and by seed over long distances (Dong et al. 2006). In addition, such information may assist in making management decisions such as timing of chemical/manual/mechanical control or guild of biological control agent to utilize (Gaskin et al. 2011; Ward et al. 2008). For instance, an ovule-feeding biological control agent may reduce seed formation without reducing parent plant survival (Ward et al. 2008); thus, in the case of invasive *Solidago*, effective control of seed could slow long-distance spread but may do nothing to limit local spread.

DOI: 10.1017/inp.2017.9

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## Management Implications

Patches of Russian knapweed are almost entirely monotypic (i.e., one plant spreading via rhizomic growth and shoot development), suggesting that rhizomic spread is responsible for within-patch growth. All patches we investigated were genetically distinct, suggesting that seed dispersal, instead of vegetative plant part dispersal, creates new patches. Controlling seed development through herbicides and biological control may be effective at stopping long-distance dispersal, but expansion of existing patches should be controlled by limiting rhizomic growth.

Russian knapweed [*Acroptilon repens* (L.) DC (Asteraceae)] is an invasive perennial herb from Central Asia that can both create new shoots from rhizomic growth and reproduce by seed (Morrison et al. 1995). Patches of Russian knapweed can survive for decades, and aerial parts of the plants that are removed or damaged can be rapidly replenished by the vegetative buds found on the root system (Watson 1980). Russian knapweed can produce up to 1,200 mature seeds per shoot (Ivanova 1966), and although germination is generally considered to be low (Selleck 1964), scarification and optimal temperature and light may increase germination rates to nearly 60% (Alebrahim et al. 2011; Larson and Kiemnec 2005). Seed travel by wind is apparently not an important dispersal method, as the pappus of the relatively large seed is small and deciduous (Renney 1959), but seed may often be moved by construction machinery or transportation of contaminated hay (U.S. Forest Service [USFS] 2015). Vegetative plant parts, such as root fragments 2.5 cm or more in length, are thought to be a source of new infestations (USFS 2015). The species is entomophilous and an obligate outcrosser (Harrod and Taylor 1995; Young and Clements 2003). Dense patches may have 100 to 300 shoots  $m^{-2}$  and can spread to an area of 12  $m^2$  within 2 yr (Frazier 1944; Figure 1). Russian knapweed is found primarily in the western two-thirds of the United States, where it is listed as a noxious weed in 18 states (U.S. Department of Agriculture, Natural Resources Conservation Service 2016) and subjected to a variety of management strategies, including biological control. Dense monocultures replace more valuable forage on rangeland and agricultural areas, and the species is toxic to horses (Watson 1980).

From the literature it is clear that Russian knapweed can spread locally via roots and by seed, but it is believed that seedling establishment rarely occurs within a patch (Watson 1980; JL Littlefield, unpublished data), though this statement is not supported by quantitative evidence. For this study we used molecular genotyping to determine which mode of reproduction was most prominent in six localized patches. We would expect that if both sexual and asexual reproduction occurred, isolated infestations (or patches)



Figure 1. Russian knapweed patches in Montana.

would be more likely to contain multiple genotypes, especially in larger and thus older patches.

## Materials and Methods

Fresh, undamaged leaf tissue from individual Russian knapweed shoots was collected from three locations in Montana; Birney (45.420°N, 106.439°W) (Rosebud County), Bridger (45.203°N, 108.809°W) (Carbon County), and Loma (47.959°N, 110.424°W) (Chouteau County); the three locations were separated by distances of 186 to 414 km. Two distinct patches per location were selected: one small patch less than 10 m in diameter and a larger patch greater than 10 m, representing perhaps different ages of patches. Patches were discrete, and large patches that appeared to have coalesced were not selected. Sample patches were separated by a minimum of 35 m at each location. The approximate center of each patch was determined, and the average patch diameter was measured to the nearest meter along sampling transects radiating in cardinal and intercardinal directions (N, NE, E, SE, S, SW, W, and NW). Two midsized leaves were collected from an individual stem at the center, inner, mid-, and outer portions of transects (Figure 2). The total number of plants sampled for a small patch was 25 (9 inner, 8 mid, 8 outer) and 33 plants (9 inner, 16 mid, 8 outer) for a large patch, for a total of 174 shoots. Locations were visited between July 10, 2014, and August 26, 2014. Tissue was immediately placed in silica and stored at ambient laboratory temperatures until DNA extraction.

Genomic DNA was extracted from approximately 20 mg of leaf material using a modified cetyltrimethylammonium bromide method (Hillis et al. 1996). The amplified fragment-length polymorphism (AFLP) method followed Vos et al. (1995) with modifications as in Gaskin and Kazmer (2009). All 15 selective primer combinations of *Mse*I + CAA, CAC, CAT, CTA, or CTC and *Eco*RI + AAG, ACC, or ACT were prescreened for PCR product quality

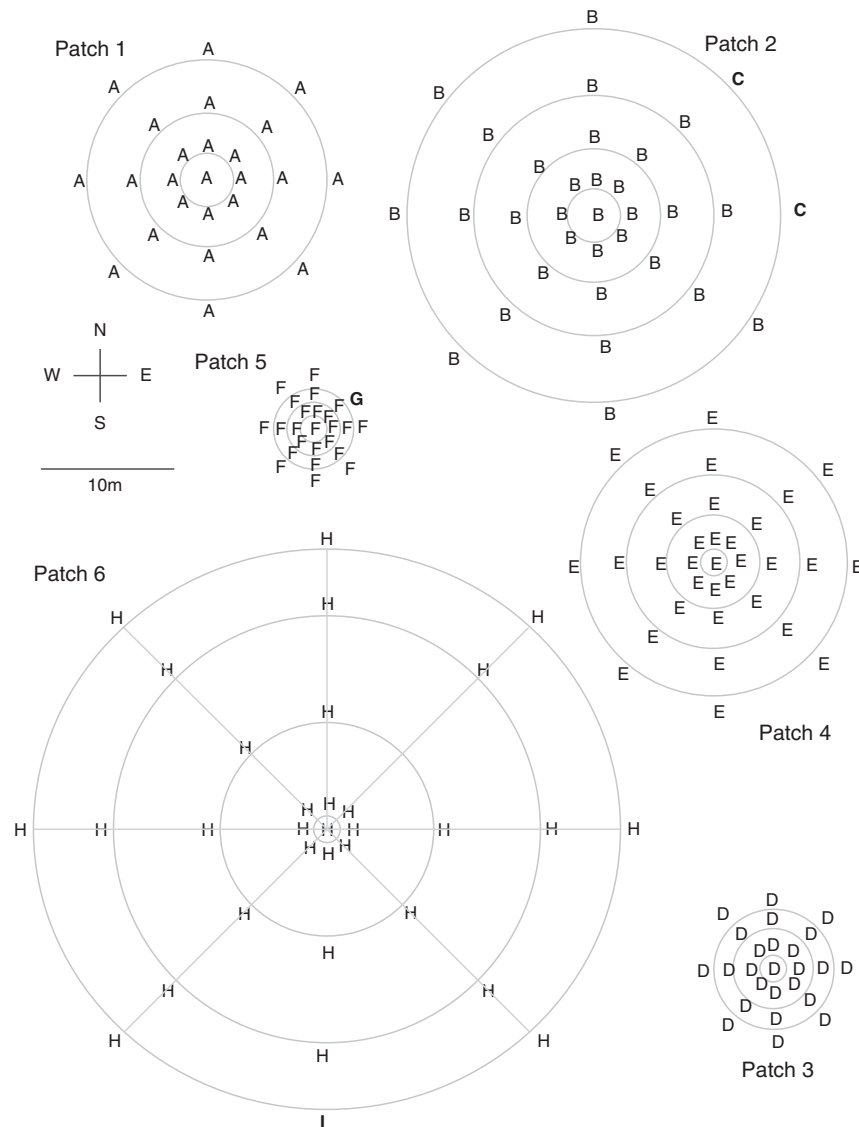


Figure 2. Approximate relative locations of 174 Russian knapweed shoots sampled from six patches in Montana. Patches 1 and 2 are from Bridger, MT; patches 3 and 4 are from Loma, MT; patches 5 and 6 are from Birney, MT. Letters A–I indicate plant genotype.

and number of variable loci using DNA from eight samples, and the most polymorphic primer pair was chosen (*MseI* + CAA/*EcoRI* + ACC). Reliable AFLP peaks (loci) were determined as in Ley and Hardy (2013). Briefly, we generated all AFLP data on an Applied Biosystems (ABI, Foster City, CA) 3130 Genetic Analyzer, including 48 repeats (28% of 174 samples). All repeats and their matching original .fas files were placed in PeakScanner Software 2 (ABI) and analyzed at a minimum peak height of 20 relative fluorescence units (rfu). The resultant .csv file from the PeakScanner sizing table was prepared with a header for tinyFLP v. 1.22 (Arthofer 2010) automatic peak scoring and selection using settings of: minimum peak height = 20,

maximum peak width = 2, minimum size = 50, maximum size = 500, size tolerance range = 0.5, minimum peak–peak distance = 1, peak height difference = 0, minimum frequency = 0.3, and maximum frequency = 99.7. The tinyFLP output file was prepared for SPAGeDi v. 1.4 (Hardy and Vekemans 2002) to test for reproducibility of peaks, using broad sense heritability ( $H^2$ ) and its significance, calculated as  $F_{st}$  of Weir and Cockerham (1984). Peaks (loci) with an  $H^2$  value of  $>0$  and  $P < 0.05$  were considered repeatable for this study (significant  $H^2$  was always  $>0.50$ ). Final allele calls for heritable loci were made with GeneMapper (ABI) at  $>50$  rfu, bin width of 1 bp.

Table 1. Pairwise Dice similarities of the nine Russian knapweed amplified fragment-length polymorphism (AFLP) genotypes from three locations, with two patches per location.

Genotype	Location 1	Location 1	Location 1	Location 2	Location 2	Location 3	Location 3	Location 3	Location 3
	Patch 1	Patch 2	Patch 2	Patch 3	Patch 4	Patch 5	Patch 5	Patch 6	Patch 6
A	1.00								
B	0.52	1.00							
C	0.55	0.52	1.00						
D	0.51	0.44	0.40	1.00					
E	0.49	0.42	0.38	0.44	1.00				
F	0.51	0.31	0.51	0.47	0.30	1.00			
G	0.43	0.36	0.42	0.49	0.41	0.59	1.00		
H	0.48	0.36	0.47	0.43	0.46	0.68	0.75	1.00	
I	0.28	0.19	0.32	0.17	0.31	0.29	0.22	0.30	1.00

Genetic similarity (Dice:  $2ab/(2a+b+c)$  where  $a$  = number of bands present in both samples,  $b$  and  $c$  = number of bands present in only one or the other sample, respectively) between genotypes was calculated using the DIS/SIMILARITY module of NTSYS-pc v. 2.1 software (Rohlf 1992). A one-way ANOVA of the Dice similarities of distinct genotypes within and between patches and locations was calculated online (Vasavada 2016).

## Results and Discussion

Patches were discrete, relatively circular in shape, and ranged from 5.4 to 9.0 m in diameter for small patches and 10.8 to 53.4 m for large patches. Plant density did not significantly differ ( $P=0.759$ ) between large and small patches (34.0 plants  $m^{-2} \pm 2.8$  SE) but did differ among locations ( $P=0.000$ ) ranging from 24.0 plants  $m^{-2} \pm 2.8$  SE (Loma) to 49.6 plants  $m^{-2} \pm 4.4$  SE (Bridger).

AFLP results originally provided us with 135 loci for *MseI* + *CAA/EcoRI* + *ACC*. The combination of PeakScanner/tinyFLP/ SPAGeDi software determined that there were 54 heritable (repeatable) loci for analysis. Using these 54 loci, we found nine genotypes in 174 sampled shoots (AFLP data provided in Supplementary File). Three out of six patches were monotypic (Figure 2); the other three patches had one rare genotype. To determine whether a rare genotype was due to AFLP error, we reran the AFLP process starting with a new restriction/ligation. In each case, the repeated genotype was identical to the original genotype. No genotypes were shared between patches, and 94% to 100% of shoots in a patch belonged to a single genet (a genetic individual). In mixed genotype patches, the rare genotype was always at the edge of the patch (Figure 2).

The maximum diameter of a genet was 56.5 m; NE-SW on patch 6. Dice genetic pairwise similarity between nonidentical

ramets (individual shoots) in all collections varied from 0.17 to 0.75, and there were no pairs of plants with Dice similarities between 0.80 and 0.99 (Table 1). Within a patch, Dice similarities between nonidentical genotypes were 0.52 (genotype B vs. C), 0.59 (F vs. G), and 0.30 (H vs. I) for an average of 0.47, while the average Dice similarity of distinct genotypes from different patches in a location was 0.49, and of distinct genotypes from different locations was 0.40. This indicates that distinct genotypes from the same patches or locations are on average more genetically similar than distinct genotypes from different locations, though these differences were not significant in a one-way ANOVA ( $P=0.1342$ ).

When a plant species expands to a new location, its propagule pressure may be low, presenting a high risk of local extinction (Radosevich et al. 2007). However, many invasive plant species have the ability to spread locally via clonal propagation (Pyšek 1997; Silvertown 2008), such as *Fallopia japonica* (Houtt.) Dcne. (Hollingsworth and Bailey 2000) and *Lepidium draba* L. (Gaskin 2006). This can be a useful trait for spread in outcrossing species when pollen is a limiting factor after a founding event. For longer-distance dispersal, plants may rely on biotic or abiotic movement of seed or clonal propagules, but for many taxa the prominent mode of spread is yet undetermined (Dong et al. 2006; Eckert 2002).

Genetic analysis to determine mode of spread relies on two items. First, that there are sufficiently variable DNA markers that can distinguish between nonclonal individuals. Most DNA sequence markers for plants do not show variation between closely related nonclonal individuals, but commonly used markers such as AFLPs (used in this study), simple sequence repeats (or microsatellites), and single-nucleotide polymorphisms should typically distinguish these individuals, provided that enough loci are sampled. Second, this type of analysis is not possible to perform on a self-compatible species (approximately 40% of angiosperms are

self-compatible [Igc et al. 2008]), since plant material derived from seed would be genetically identical to plant material derived from clonal reproduction in most cases, unless the plants were highly heterozygous and the DNA markers were sufficiently numerous to ensure sampling some heterozygous loci.

The three rare genotypes found (genotypes C, G, and I; Figure 2) were sufficiently different from the common genotype in each patch (0.30 to 0.59 Dice similarity) to strongly suggest that they were from outcrossed seed migration rather than a somatic mutation or AFLP error, especially as we reran the AFLP analysis on the rare genotype plants and found no AFLP error. Since none of our patches shared genotypes, we expect that long-distance dispersal in our samples was not from movement of vegetative material but from outcrossed seed, though there are reports that root fragments as small as a 2.5 cm in length can establish a new plant (USFS 2015) and could possibly be moved via animal or human disturbance. This research was performed on a limited number of patches, all in Montana, and it is possible that reproductive mode may vary in different regions or ecosystems, as it does in some other plant species (e.g., due to altitude [Weppeler and Stöcklin 2005] or genetics [Dorken and Eckert 2001]).

In the United States three biological control agents for Russian knapweed are currently approved for redistribution, including a gall wasp (*Aulacidea acroptilonica* Tyurebaev, a gall midge (*Jaapiella ivannikovi* Fedotova), and a nematode [*Subanguina picridis* (Kirjanova) Brzeski]. Both the midge and the nematode can reduce overall seed production and aboveground growth, while the wasp can, under controlled conditions, stress plants and reduce competitive ability (Djamankulova et al. 2008; Watson 1986; Winston et al. 2014). The reduction of seed by the midge and nematode may eventually limit long-distance dispersal by seed, but since the predominant mode of local (patch-scale) reproduction is by shoots arising from rhizomes, it is not known whether these agents alone can effectively limit patch expansion, as Russian knapweed patches can tolerate even severe control methods such as burning or low-frequency mowing (USFS 2015).

### Acknowledgments

We thank the Bureau of Land Management, Northern Cheyenne Nation, and the Red Flame Ranch for the use of their land as study locations; J. Birdsall, A. deMeij, and A. Quigley for fieldwork; K. Mann and J. Lassey for laboratory assistance; and two anonymous reviewers and the associate editor for their valuable comments and critiques. This research was funded through the Bureau of Land Management; the Montana Noxious Weed Trust Fund; the USDA, Animal and Plant

Health Inspection Service, W-3185 Regional Project; and the Montana State University Agricultural Experiment Station.

### Supplementary material

To view supplementary material for this article, please visit <https://doi.org/10.1017/inp.2017.9>

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Received November 15, 2016, and approved February 9, 2017.

Associate Editor for this paper: Marie Jasieniuk, University of California, Davis.