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Change in Leafy Spurge (*Euphorbia esula*) Density and Soil Seedbank Composition 10 Years following Release of *Aphthona* spp. Biological Control Agents

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Flea beetles (*Aphthona* spp.) were released in the Little Missouri National Grasslands (LMNG) in western North Dakota in 1999 to control leafy spurge. The changes in leafy spurge density and soil seedbank composition were evaluated on two ecological sites 10 yr (2009) after *Aphthona* spp. release to monitor the effectiveness of the insects on weed control and the associated changes in plant communities. In 2009, leafy spurge stem density averaged 2 and 9 stems m^{-2} (0.19 to 0.84 ft^{-2}) in the loamy overflow and loamy sites, respectively, compared with 110 and 78 stems m^{-2}, respectively, in 1999. Leafy spurge constituted nearly 67% of the loamy overflow seedbank in 1999, compared with 2% in 2009. In the loamy seedbank, the weed represented nearly 70% in 1999, compared with approximately 15% in 2009. As leafy spurge abundance was reduced, native species richness and seed count increased 10 yr after *Aphthona* spp. release. Late seral species represented 17% of the loamy overflow seedbank in 2009, an increase from 5% in 1999. However, Kentucky bluegrass, a nontarget weedy species, increased more than 250% in the loamy overflow seedbank. Late seral species were 38% of the loamy seedbank in 2009, compared with 13% in 1999. The number of native species increased from 31 in 1999 to 39 in 2009 in the loamy overflow seedbank, but only changed from 32 to 34 species in the loamy site during the same period. The reestablishment of native species has been slow, but seedbank analysis indicates the number and type of species found before the leafy spurge infestation have increased. Planting native species in selected areas may have reduced the lag time in these species return to the seedbank and reduced invasion from other nondesirable species, such as Kentucky bluegrass.
Nomenclature: Leafy spurge flea beetle, *Aphthona* spp.; Kentucky bluegrass, *Poa pratensis* L.; leafy spurge, *Euphorbia esula* L. EPHES.

Key words: Biological control, invasive species, leafy spurge flea beetle, revegetation.

Soil seedbank analysis provides insight on the historical and future composition of aboveground vegetation in an ecosystem (Cavers 1994; Thompson and Grime 1979). Seedbank composition assessment can help determine whether restoration, such as seeding, is necessary to improve the development and quality of an ecosystem because aboveground vegetation does not always correspond to seed composition within the soil (Cardina and Sparrow 1996; Thompson and Grime 1979).

Aphthona nigriscutis and *Aphthona lacertosa* were introduced to the United States in the mid-1980s (Julien and Griffiths 1999) for biological control of leafy spurge (*Euphorbia esula* L.) (Lym 1998; Lym and Carlson 2002). Once established, *Aphthona* spp. have reduced leafy spurge cover, density, and biomass (Kirby et al. 2000). Leafy spurge was reduced nearly 70% during a 14-yr period after *Aphthona* spp. were released in north-central Montana (Lesica and Hanna 2004, 2009). Significant reductions of leafy spurge root biomass occurred within 2 to 3 yr after release in several areas of North Dakota (Kirby et al. 2000). However, the long-term effect on native species recovery following biological control of leafy spurge has generally been slow (Butler and Wacker 2010) and may be site dependent (Lesica and Hanna 2009).

A leafy spurge soil seedbank study was first conducted in the Little Missouri National Grasslands (LMNG) in

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Management Implications

The leafy spurge (*Euphorbia esula* L.) biological control agents *Aphthona nigriscutis* and *Aphthona lacertosa* were introduced to the Little Missouri National Grasslands (LMNG) in western North Dakota in 1999 to control the invasive weed. At the same time, 12 sites each on loamy overflow and loamy soils were established for evaluation of change in leafy spurge density and soil seedbank. In 2009, 10 yr after *Aphthona* spp. release, leafy spurge stem density had decreased by an average of 94% in the loamy overflow and loamy sites. At the same time leafy spurge seed decreased in the loamy overflow seedbank from 67% in 1999 to only 2% in 2009 and from 70% in 1999 to approximately 15% after 10 yr at the loamy site. As leafy spurge was successfully controlled in the LMNG, native species richness increased in the soil seedbank. Prairie Junegrass was a prevalent native species in the loamy overflow seedbank in 2009, and some late seral species that appeared by 2009 included textile onion (*Allium textile* A. Nels. & J.F. Macbr.), shy wallflower [*Erysimum inconspicuum* (S. Wats.) MacM.], locoweed [*Oxytropis campestris* (L.) DC.], and prairie groundsel [*Packera plattensis* (Nutt.) W.A. Weber & A. Löve]. However, from 2004 to 2009, there was a substantial increase in Kentucky bluegrass (*Poa pratensis* L.) in the loamy overflow seedbank. The increase in Kentucky bluegrass was most likely enabled by the reduction in leafy spurge and above-average precipitation, which provided a favorable habitat for growth and invasion. Although Kentucky bluegrass may become a problem species in the LMNG, an increasing trend in native species was observed in the soil seedbank following the reduction of leafy spurge. Desirable forb species and native grasses could be seeded within 5 yr following leafy spurge reduction to reduce opportunistic invaders, such as Kentucky bluegrass, and to provide additional seed sources for more-rapid reestablishment of the native flora.

western North Dakota in 1999 (Cline 2002). *Aphthona* spp. were released to control leafy spurge, and the change in seedbank composition over time was evaluated. Forty-three species germinated from the loamy overflow sites and 40 species from the loamy sites. The most abundant species included leafy spurge (70%), Kentucky bluegrass (*Poa pratensis* L.), prairie Junegrass [*Koeleria macrantha* (Ledeb.) J.A. Schultes], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], and green needlegrass [*Nassella viridula* (Trin.) Barkworth].

The seedbank study was repeated in 2004, 5 yr after the 1999 *Aphthona* spp. release (Cline et al. 2008; Juricek 2006). The same procedure and methods were used as employed in the Cline (2002) study, except the flea beetles had spread throughout the entire study area. Leafy spurge stem density was reduced approximately 90% by the *Aphthona* spp. during the 5 yr. Leafy spurge seed in the soil seedbank also decreased 66% in the loamy overflow sites and 79% in the loamy sites. The most-abundant species were still leafy spurge and Kentucky bluegrass, and native plant species had not recovered following leafy spurge reduction.

The purpose of this research was to reevaluate change in the leafy spurge stand density and the soil seedbank composition 10 yr following the leafy spurge control program using *Aphthona* spp. in western North Dakota. Evaluating the seedbank is the first step in gaining insight into the potential secondary succession of long-term leafy spurge–infested rangeland following *Aphthona* spp. release.

Materials and Methods

A soil seedbank study was established in the LMNG in western North Dakota to evaluate species composition change 10 yr following leafy spurge control by *Aphthona* spp. The LMNG covers 500,000 ha (123,550 ac) in western North Dakota and consists of many gullies, ravines, and buttes (Hopkins et al. 1986). The predominant soils include well-drained loams, clay loams, and sandy loams. The soils derived from soft clayey shales and sandstones are unstable and are highly susceptible to erosion. The annual precipitation near the LMNG in Medora, ND, fluctuated widely during the past 50 yr with an average of 390 mm yr^{-1} (15.35 in yr^{-1}) (USDC-NOAA-NRCDC 1949–2010). Historically, grazing was the primary land use in the LMNG (Hopkins et al. 1986), but now, oil and gas development have increased dramatically (NDIC-OGD 2011).

There were 24 sites established in 1999 for seedbank analysis as described by Cline et al. (2008). A mixture of 3,000 *A. lacertosa* and *Aphthona czwalinae* and 3,000 *A. nigriscutis* flea beetles were released for leafy spurge control. Each site was geocoded with a global positioning system and marked on topographic maps. Sites were also marked with labeled polyvinyl chloride posts and two plastic surveyor stakes. One stake was located in the center of the site, and another stake was located at 90° to the right of the center and perpendicular to the maximum water flow of the slope.

There are numerous vegetation types in the LMNG. Clements et al. (1929) identified nine major grassland communities in the same general area where this study was conducted. The mixed grass prairie vegetation type was the most-abundant type encountered in this research. The dominant plant species included blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths], western wheatgrass [*Pascopyrum smithii* (Rydb.) Á. Löve], needle-and-thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth], green needlegrass, prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], and little bluestem (Cline 2002; Juricek 2006). Woody vegetation species among the prairie species included common cottonwood (*Populus deltoides* Marshall), silver buffaloberry [*Shepherdia argentea* (Pursh) Nutt.], western snowberry (*Symphoricarpos occidentalis* Hook.), and creeping juniper (*Juniperus horizontalis* Moench).

The seedbank study was conducted on 12 loamy overflow and 12 loamy sites, as defined by the U.S.

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Department of Agriculture Natural Resources Conservation Service (USDA-NRCS) Ecological Site Description System (USDA-NRCS 2007). Locations were originally chosen in 1999 based on leafy spurge density (uninfested, light, moderate, and heavy), soil type, and vegetation composition (Cline 2002). The light, moderate, and heavy leafy spurge infestations averaged approximately 87, 127, and 224 stems m^{-2} (8, 12, and 21 stems ft^{-2}), respectively, from the loamy overflow sites and 46, 83, and 183 stems m^{-2}, respectively, from the loamy sites.

Leafy spurge stem density was counted, and soil cores were collected for seedbank analysis in mid-August 2009 from each of the 24 original sites. The sites were 255 m^2 (2,745 ft^2) and separated into eight equal transects radiating clockwise from the center at 45° angles, with transect three always pointing north from the center point (Cline 2002). Stem density was determined by counting the number of stems in four 0.25-m^2 quadrats placed at 1-m (3.281-ft) intervals on the cardinal directions. Additionally, four soil cores at 1-m intervals were excavated from each of five transects that were chosen at random. Each soil core was removed using a standard golf-hole cutter to a depth of 5 cm (1.97 in) with a 10-cm diameter. If a sampling fell on a previously selected transect, the subsequent samples were taken on the same arc 1° to the right or left of the previous sample in 2004 or 2009, respectively. Soil samples were refrigerated at 3 C (37.4 F) before seedbank evaluation for at least 14 d to overcome dormancy, as suggested by Perez et al. (1998).

Seedbank analysis was conducted by seed germination methods outlined by Ter Heerdt et al. (1996). A mixture of steam-sterilized soil and commercial plant-growth media (Sunshine Mix No. 1®, Sun Gro Horticulture, Bellevue, WA 98008) was added to 28- by 56-cm greenhouse trays to a 2.5-cm depth and topped with a 3- to 5-cm-thick layer of sterile silica sand. Four soil cores from each transect were combined and washed with tap water through a coarse (4-mm) and fine (0.2-mm) sieve to remove debris and unwanted plant material, such as roots (which could produce shoots and bias the study) and thatch. Tap water was added to the soil samples to form a slurry, and the mixture was poured into a tray as the top layer. All trays were placed in the greenhouse and watered daily. Greenhouse temperature was maintained between 20 and 28 C, and natural light was supplemented with halide lamps at 450 $\mu E\ m^{-2}\ s^{-1}$ for a 16-h photoperiod. Once seedlings emerged, they were identified, recorded, and removed. Unknown seedlings were transplanted to allow further growth until proper identification was possible. The study was conducted for approximately 24 wk.

Coefficients of conservatism values (C-value) were assigned to plant species based on an assessment by the Northern Great Plains Floristic Quality Assessment Panel (2001). The C-value ranges from 0 to 10, with 0 for plant species that inhabit highly disturbed (early seral) areas and 10 for undisturbed, natural (late seral) areas. Early seral species had a C-value of 3 or less, and late seral species had a C-value of 4 or greater (Cline 2002).

The soil seedbank data were analyzed as a completely random design using the Generalized Linear Models procedure of SAS software (SAS Institute Software 2004, Version 9.1.2, SAS, Inc., Cary, NC 27513). A Fischer's Protected LSD test at $P < 0.1$ ($P < 0.05$ was considered too critical for use in this study) was calculated for mean separation to evaluate the change in species composition based on seven vegetation categories within the soil seedbank 5 and 10 yr after *Aphthona* spp. release in 1999. Soil cores were excavated in the spring and fall of 1999, but only the fall data were used for comparison. A factorial arrangement was used to compare seedling densities in seven vegetation categories between two ecological sites (loamy overflow and loamy). Seedlings were placed into one of seven categories, including (1) major invasives, (2) late-seral forbs, (3) early seral forbs, (4) late seral grasses, (5) early seral grasses, (6) hydric/mesic

Table 1. Leafy spurge stem density across original 1999 density categories and 5 and 10 yr after *Aphthona* spp. release on loamy overflow and loamy sites in the Little Missouri National Grasslands in western North Dakota.[a]

Year and leafy spurge density classification	Loamy overflow	Loamy
	stems m^{-2}	
1999		
Uninfested	0	0
Low	87	46
Moderate	127	83
High	224	183
LSD (0.05)	12	11
2004		
Uninfested	5	3
Low	1	0
Moderate	16	16
High	7	20
LSD (0.05)	10	9
2009		
Uninfested	3	9
Low	2	10
Moderate	2	4
High	1	15
LSD (0.05)	NS	NS
1999 Mean	110	78
2004 Mean	7	10
2009 Mean	2	9

[a] The 1999 and 2004 data were originally published in Cline et al. 2008 and are included here for ease of comparison.

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Table 2. Scientific name, common name, coefficient of conservatism value, and number of seedlings of plant species that emerged from soil cores excavated in mid-August, 5 and 10 yr after *Aphthona* spp. release for leafy spurge control in 1999 from 12 loamy overflow sites in southwestern North Dakota.[a]

			1999		2004		2009		
Scientific name[b]	Common name	C-value[c]	No.[d]	%[e]	No.	%	No.	%	LSD[f]
Major invasives									
Euphorbia esula L.	Leafy spurge	NV	3,358	67	1,135	17	127	2	333
Poa pratensis L.	Kentucky bluegrass	NV	1,066	21	1,226	18	3,783	64	453
Subtotal			4,424	88	2,361	35	3,910	66	440
Late seral forbs									
Allium textile A. Nelson & J.F. Macbr.	Textile onion	7	—	—	—	—	19	0.3	
Androsace occidentalis Pursh	Western rockjasmine	5	21	0.4	693	10	16	0.3	
Arabis holboelli Hornem. var. *collinsii* (Fern.) Rollins	Collins' rockcress	5	—	—	9	0.1	—	—	
Artemisia frigida Willd.	Fringed sagebrush	4	30	0.6	508	7	8	0.1	
Aster oblongifolius Nutt.	Aromatic aster	8	—	—	13	0.2	—	—	
Astragalus agrestis Douglas ex G. Don	Purple milkvetch	6	—	—	—	—	1	< 0.1	
Chenopodium simplex (Torr.) Raf.	Maple-leaved goosefoot	5	—	—	1	< 0.1	—	—	
Erysimum inconspicuum (S. Wats.) MacM.	Shy wallflower	7	—	—	—	—	1	< 0.1	
Fragaria virginiana Duchesne	Wild strawberry	4	42	0.8	—	—	—	—	
Galium boreale L.	Northern bedstraw	4	3	< 0.1	11	0.2	—	—	
Galium triflorum Michx.	Fragrant bedstraw	7	—	—	—	—	21	0.4	
Gaura coccinea var. *glabra* (Lehm.) T. & G.	Scarlet gaura	4	—	—	1	< 0.1	—	—	
Gutierrezia sarothrae (Pursh) Britt. & Rusby	Broom snakeweed	6	—	—	1	< 0.1	1	< 0.1	
Hedeoma drummondii Benth.	Drummond's falsepennyroyal	4	67	1	252	4	—	—	
Lesquerella arenosa var. *arenosa* (Richardson) Rydb.	Great Plains bladderpod	6	—	—	3	< 0.1	—	—	
Linum perenne Pursh var. *lewisii*	Prairie flax	6	—	—	5	< 0.1	37	0.6	
Lithospermum canescens (Michx.) Lehm.	Hoary puccoon	7	—	—	7	0.1	9	0.2	
Monarda fistulosa L.	Wild bergamot	5	—	—	1	< 0.1	—	—	
Oligoneuron rigidum (L.) Small	Rigid goldenrod	4	—	—	—	—	1	< 0.1	
Oxytropis spp.	Locoweed	NV	—	—	—	—	1	< 0.1	
Packera plattensis (Nutt.) W.A. Weber & A. Löve	Prairie groundsel	6	—	—	—	—	1	< 0.1	
Potentilla arguta Pursh	White cinquefoil	8	—	—	122	2	3	< 0.1	
Solidago spp.	Goldenrods	NV	2	0.1	—	—	—	—	
Subtotal			165	3	1,627	24	119	2	342
Early seral forbs									
Achillea millefolium L.	Common yarrow	3	34	0.1	104	2	136	2	
Ambrosia artemisiifolia L.	Common ragweed	0	—	—	1	< 0.1	—	—	
Artemisia ludoviciana Nutt.	White wormwood	3	25	1	30	0.4	5	< 0.1	
Brassicaceae spp.	Mustard family	NV	—	—	—	—	296	5	
Cerastium arvense L.	Field chickweed	2	—	—	4	< 0.1	4	< 0.1	

Table 2. Continued.

Scientific name[b]	Common name	C-value[c]	1999 No.[d]	1999 %[e]	2004 No.	2004 %	2009 No.	2009 %	LSD[f]
Chamaesyce glyptosperma (Engelm.) Small	Ridge-seed spurge aka ribseed sandmat	0	2	0.04	42	0.6	—	—	
Chamaesyce prostrata (Aiton) Small	Prostrate sandmat aka prostrate spurge	1	—	—	2	< 0.1	7	0.1	
Chamaesyce serpyllifolia (Pers.) Small	Thymeleaf spurge	0	—	—	—	—	193	3	
Chenopodium album L.	Common lambsquarters	NV	—	—	5	< 0.1	—	—	
Chenopodium glaucum L.	Oakleaf goosefoot	NV	—	—	7	0.1	1	< 0.1	
Chenopodium rubrum L.	Red goosefoot	2	1	0.02	—	—	—	—	
Cirsium arvense (L.) Scop.	Canada thistle	NV	1	0.02	1	< 0.01	1	< 0.1	
Convolvulus arvensis L.	Field bindweed	NV	1	0.02	—	—	—	—	
Conyza canadensis (L.) Cronq.	Horseweed	0	19	0.4	4	< 0.1	1	< 0.1	
Descurainia pinnata (Walt.) Britt.	Pinnate tansymustard	1	5	0.1	4	< 0.1	163	3	
Descurainia sophia (L.) Webb. ex Prantl	Flixweed	NV	—	—	—	—	3	< 0.1	
Draba nemorosa L.	Woodland draba	1	—	—	1,719	25	89	1	
Epilobium ciliatum Raf.	Fringed willowherb	3	—	—	1	< 0.1	—	—	
Erigeron philadelphicus L.	Philadelphia fleabane	2	3	0.1	—	—	—	—	
Erysimum asperum (Nutt.) DC.	Western wallflower	3	—	—	—	—	1	< 0.1	
Erysimum cheiranthoides L.	Wallflower mustard	NV	10	0.2	65	0.7	—	—	
Grindelia squarrosa (Pursh) Dunal	Curlycup gumweed	1	—	—	6	< 0.1	5	< 0.1	
Hedeoma hispida Pursh	Rough falsepennyroyal	2	4	0.1	—	—	—	—	
Lappula occidentalis (S. Wats.) Greene	Western stickseed	2	4	0.1	40	0.5	—	—	
Lepidium densiflorum Schrad.	Greenflower pepperweed	0	1	< 0.1	86	1	21	0.4	
Melilotus officinalis (L.) Lam.	Yellow sweetclover	NV	—	—	—	—	4	< 0.1	
Nepeta cataria L.	Catnip	NV	—	—	4	< 0.1	1	< 0.1	
Neslia paniculata (L.) Desv.	Ball mustard	NV	—	—	145	2	—	—	
Plantago elongata Pursh	Prairie plantain	3	—	—	3	< 0.1	—	—	
Plantago major L.	Broadleaf plantain	NV	4	< 0.1	—	—	—	—	
Plantago patagonica Jacq.	Woolly plantain	1	—	—	—	—	5	< 0.1	
Polygonum convolvulus L.	Wild buckwheat	NV	7	0.1	—	—	—	—	
Potentilla norvegica L.	Rough cinquefoil	0	—	—	—	—	3	< 0.1	
Ratibida columnifera (Nutt.) Woot. & Standl.	Upright prairie coneflower	3	15	0.3	41	0.6	23	0.4	
Rosa arkansana Porter	Prairie wild rose	3	1	< 0.1	—	—	—	—	
Rumex crispus L.	Curly dock	NV	—	—	1	< 0.1	—	—	
Silene noctiflora L.	Nightflowering catchfly	NV	—	—	8	0.1	1	< 0.1	
Sonchus spp.	Sowthistles	NV	13	0.3	—	—	—	—	
Symphyotrichum porteri (A. Gray) G.L. Nesom	White smooth aster	2	2	0.1	7	0.1	—	—	
Taraxacum officinale G.H. Weber ex Wiggers	Dandelion	NV	128	3	127	2	45	0.7	
Tragopogon dubius Scop.	Western salsify	NV	—	—	3	< 0.1	2	< 0.1	
Verbascum thapsus L.	Common mullein	NV	16	0.3	—	—	—	—	
Verbena bracteata Lag. & Rodr.	Prostrate vervain	0	1	< 0.1	—	—	—	—	

Table 2. Continued.

Scientific name[b]	Common name	C-value[c]	1999 No.[d]	1999 %[e]	2004 No.	2004 %	2009 No.	2009 %	LSD[f]
Subtotal			297	6	2,460	36	1,010	17	147
Late seral grasses									
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	Blue grama	7	4	< 0.1	—	—	—	—	
Calamovilfa longifolia (Hook.) Scribn.	Prairie sandreed	5	—	—	4	< 0.1	—	—	
Elymus trachycaulus (Link) Gould ex Shinners	Slender wheatgrass	6	—	—	—	—	2	< 0.1	
Hesperostipa comata (Trin. & Rupr.) Barkworth	Needle-and-thread	6	3	< 0.1	—	—	2	< 0.1	
Hesperostipa spartea (Trin.) Barkworth	Porcupinegrass	8	—	—	—	—	2	< 0.1	
Koeleria macrantha (Ledeb.) J.A. Schultes	Prairie Junegrass	7	39	0.7	—	—	758	13	
Muhlenbergia cuspidata (Torr. ex Hook) Rydb.	Plains muhly	8	1	< 0.1	—	—	—	—	
Nassella viridula (Trin.) Barkworth	Green needlegrass	5	34	0.7	112	2	24	0.4	
Poa palustris L.	Fowl bluegrass	4	—	—	44	1	—	—	
Puccinellia nuttalliana (Schult.) A.S. Hitchc.	Nuttall's alkaligrass	4	—	—	5	< 0.1	—	—	
Schizachyrium scoparium (Michx.) Nash	Little bluestem	6	1	< 0.1	12	0.2	1	< 0.1	
Sporobolus cryptandrus (Torr.) A. Gray	Sand dropseed	6	19	0.4	3	< 0.1	15	0.3	
Subtotal			101	2	180	3	804	13	251
Early seral grasses									
Agrostis scabra Willd.	Rough bentgrass	1	—	—	—	—	1	< 0.2	
Bromus inermis Leyss. ssp. *inermis*	Smooth brome	NV	—	—	96	1	—	—	
Bromus tectorum L.	Downy brome	NV	—	—	—	—	84	1	
Digitaria ischaemum (Schreb.) Schreb. ex Muhl	Smooth crabgrass	NV	13	0.3	—	—	—	—	
Distichlis spicata (L.) Greene	Saltgrass	2	—	—	—	—	2	< 0.1	
Echinochloa crus-galli (L.) Beauv.	Barnyardgrass	NV	7	0.1	—	—	—	—	
Elymus repens (L.) Gould	Quackgrass	NV	—	—	—	—	2	< 0.1	
Poa compressa L.	Canada bluegrass	NV	—	—	1	< 0.1	9	0.2	
Schedonnardus paniculatus (Nutt.) Trel.	Tumblegrass	1	21	0.4	13	0.2	—	—	
Setaria viridis (L.) Beauv.	Green foxtail	NV	1	< 0.1	—	—	—	—	
Vulpia octoflora (Walt.) Rydb.	Sixweeks fescue	0	—	—	—	—	1	< 0.1	
Subtotal			42	0.8	110	2	99	2	NS
Hydric/mesic species									
Carex spp.	Sedges	NV	12	0.2	34	0.5	5	< 0.1	
Juncus balticus Willd.	Baltic rush	5	—	—	16	0.2	—	—	
Juncus spp.	Rushes	NV	—	—	—	—	2	< 0.1	
Typha spp.	Cattails	NV	1	< 0.1	10	0.1	1	< 0.1	
Subtotal			13	0.3	60	0.8	8	0.1	5

Table 2. Continued.

Scientific name[b]	Common name	C-value[c]	1999 No.[d]	1999 %[e]	2004 No.	2004 %	2009 No.	2009 %	LSD[f]
Unknowns									
Lamiaceae spp.	Mint family	NV	—	—	—	—	12	0.2	
Unknown spp. 1		NV	—	—	—	—	1	< 0.1	
Unknown spp. 2		NV	—	—	—	—	3	< 0.1	
Subtotal			0	0	0	0	16	0.3	NS
Total			5,042	100	6,798	100	5,966	100	650

[a] The 1999 and 2004 data were originally published in Cline et al. 2008 and are included here for ease of comparison.

[b] Scientific nomenclature follows the Weed Science Society of America Database of Common/Scientific Names 2010 (http://wssa.net/Weeds/ID/WeedNames/namesearch.php), except as amended according to the United States Department of Agriculture (USDA)/Natural Resources Conservation Service (NRCS) PLANTS Database (2006) (http://plants.usda.gov/index.html).

[c] Coefficient of conservatism value (C-value) was assigned to plant species based on an assessment by the Northern Great Plains Floristic Quality Assessment Panel (2001). A coefficient value of NV (no value) is indicative of an introduced or unidentified species, values of 0 to 3 are indicative of species that flourish in highly disturbed habitats, and values of 4 to 10 are assigned to species from less-disturbed, natural areas.

[d] Total number of seedlings that emerged per 0.5 m^2 from soil samples collected to a depth of 5 cm.

[e] Percentage of total seedlings that emerged across all soil cores.

[f] A Fischer's Protected LSD test at $P < 0.1$ was calculated to evaluate the change in seedling number across years.

Table 3. Scientific name, common name, coefficient of conservatism value, and number of seedlings of plant species that emerged from soil cores excavated in mid-August, 5 and 10 yr after *Aphthona* spp. release for leafy spurge control in 1999 from 12 loamy sites in southwestern North Dakota.[a]

			1999		2004		2009		
Scientific name[b]	Common name	C-value[c]	No.[d]	%[e]	No.	%	No.	%	LSD[f]
Major invasives									
Euphorbia esula L.	Leafy spurge	NV	1,429	70	299	11	146	15	207
Poa pratensis L.	Kentucky bluegrass	NV	160	8	182	7	99	10	NS
Subtotal			1,589	78	481	17	245	25	303
Late seral forbs									
Allium textile A. Nelson & J.F. Macbr	Textile onion	7	—	—	1	< 0.1	1	0.1	
Androsace occidentalis Pursh	Western rockjasmine	5	12	0.5	46	2	14	1	
Arabis holboelli Hornem. var. *collinsii* (Fern) Rollins	Collins' rockcress	5	—	—	51	2	—	—	
Artemisia campestris L. subsp. *caudata* (Michx.) Hall & Clements	Field sagewort	5	3	0.1	3	0.1	1	0.1	
Artemisia dracunculus L.	Tarragon	4	—	—	3	0.1	—	—	
Artemisia frigida Willd.	Fringed sagebrush	4	42	2	265	10	21	2	
Aster oblongifolius Nutt.	Aromatic aster	8	—	—	5	0.2	—	—	
Campanula rotundifolia L.	Harebell	7	—	—	47	2	53	5	
Erysimum inconspicuum (S. Wats.) MacM.	Shy wallflower	7	—	—	—	—	1	0.1	
Fragaria virginiana Duchesne	Wild strawberry	4	3	0.1	—	—	—	—	
Galium boreale L.	Northern bedstraw	4	2	0.1	—	—	—	—	
Gutierrezia sarothrae (Pursh) Britt. & Rusby	Broom snakeweed	6	—	—	1	< 0.1	1	0.1	
Hedeoma drummondii Benth.	Drummond's falsepennyroyal	4	21	1	252	9	—	—	
Lesquerella arenosa var. *arenosa* (Richardson) Rydb.	Great Plains bladderpod	6	—	—	22	1	2	0.2	
Linum perenne Pursh var. *lewisii*	Prairie flax	6	—	—	15	1	7	0.7	
Lithospermum canescens (Michx.) Lehm.	Hoary puccoon	7	—	—	2	0.1	103	11	
Oligoneuron rigidum (L.) Small	Rigid goldenrod	4	—	—	—	—	1	0.1	
Orthocarpus luteus Nutt.	Yellow owl's-clover	6	—	—	—	—	1	0.1	
Packera plattensis (Nutt.) W.A. Weber & A. Löve	Prairie groundsel	6	—	—	—	—	2	0.2	
Solidago spp.	Goldenrods	NV	6	0.3	—	—	—	—	
Subtotal			89	4	730	26	209	21	163
Early seral forbs									
Achillea millefolium L.	Common yarrow	3	2	0.1	2	0.1	3	0.3	
Artemisia ludoviciana Nutt.	White sagewood	3	2	0.1	—	—	—	—	
Euphorbia glyptosperma Engelm. *Chamaesyce glyptosperma* (Engelm.) Small	Ridge-seeded spurge aka ribseed sandmat	0	3	0.1	5	0.2	—	—	
Chamaesyce serpyllifolia (Pers.) Small	Thymeleaf spurge	0	—	—	—	—	1	0.1	
Chenopodium album L.	Common lambsquarters	NV	—	—	1	< 0.1	12	1	
Cirsium arvense (L.) Scop.	Canada thistle	NV	—	—	—	—	2	0.2	
Conyza canadensis (L.) Cronq.	Horseweed	0	23	1	10	0.4	16	2	
Descurainia pinnata (Walt.) Britt.	Pinnate tansymustard	1	1	< 0.1	2	0.1	—	—	

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Table 3. Continued

Scientific name[b]	Common name	C-value[c]	1999 No.[d]	1999 %[e]	2004 No.	2004 %	2009 No.	2009 %	LSD[f]
Descurainia sophia (L.) Webb. ex Prantl	Flixweed	NV	—	—	—	—	11	1	
Draba nemorosa L.	Woodland draba	1	—	—	822	29	216	22	
Epilobium ciliatum Raf.	Fringed willowherb	3	—	—	8	0.3	1	0.1	
Erigeron philadelphicus L.	Philadelphia fleabane	2	2	0.1	11	0.4	—	—	
Erysimum asperum (Nutt.) DC.	Wallflower mustard	3	3	0.1	—	—	5	0.5	
Erysimum cheiranthoides L.	Wormseed wallflower	NV	1	< 0.1	133	5	—	—	
Euphorbia maculata L.	Prostrate spurge	1	—	—	2	0.1	—	—	
Grindelia squarrosa (Pursh) Dunal	Curlycup gumweed	1	—	—	4	0.1	—	—	
Hedeoma hispida Pursh	Rough falsepennyroyal	2	—	—	—	—	3	0.3	
Lactuca serriola L.	Prickly lettuce	NV	2	0.1	—	—	—	—	
Lappula occidentalis (S. Wats.) Greene	Western stickseed	2	3	0.1	8	0.3	—	—	
Lepidium densiflorum Schrad.	Greenflower pepperweed	0	1	< 0.1	3	0.1	2	0.2	
Medicago lupulina L.	Black medic	NV	—	—	—	—	2	0.2	
Medicago sativa L.	Alfalfa	NV	—	—	—	—	1	0.1	
Melilotus officinalis (L.) Lam.	Yellow sweetclover	NV	—	—	—	—	4	0.4	
Neslia paniculata (L.) Desv.	Ball mustard	NV	—	—	140	5	—	—	
Oenothera biennis L.	Common evening-primrose	0	—	—	8	0.3	—	—	
Plantago elongata Pursh	Prairie plantain	3	—	—	9	0.3	—	—	
Plantago major L.	Broadleaf plantain	NV	4	0.2	—	—	—	—	
Plantago patagonica Jacq.	Woolly plantain	1	—	—	—	—	1	0.1	
Potentilla norvegica L.	Rough cinquefoil	0	—	—	—	—	1	0.1	
Ratibida columnifera (Nutt.) Woot. & Standl.	Upright prairie coneflower	3	6	0.2	22	1	5	0.5	
Silene noctiflora L.	Nightflowering catchfly	NV	—	—	1	< 0.1	—	—	
Sisymbrium altissimum L.	Tumble mustard	NV	6	0.3	—	—	—	—	
Sonchus spp.	Sowthistles	NV	2	0.1	—	—	—	—	
Symphyotrichum ericoides (L.) Nesom	Heath aster	2	2	0.1	3	0.1	1	0.1	
Taraxacum officinale G.H. Weber ex Wiggers	Dandelion	NV	43	2	119	4	43	4	
Tragopogon dubius Scop.	Western salsify	NV	—	—	1	< 0.1	3	0.3	
Verbascum thapsus L.	Common mullein	NV	74	4	—	—	—	—	
Subtotal			180	9	1,314	47	333	33	271
Late seral grasses									
Agropyron spicatum (Pursh) Scribn. & Sm.	Beardless wheatgrass	9	—	—	3	0.1	—	—	
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	Blue grama	7	3	0.1	—	—	—	—	
Calamovilfa longifolia (Hook.) Scribn.	Prairie sandreed	5	32	2	117	4	8	0.8	
Hesperostipa comata (Trin. & Rupr.) Barkworth	Needle-and-thread	6	4	0.2	—	—	1	0.1	
Hesperostipa spartea (Trin.) Barkworth	Porcupinegrass	8	—	—	3	0.1	3	0.3	

Table 3. Continued

Scientific name[b]	Common name	C-value[c]	1999 No.[d]	1999 %[e]	2004 No.	2004 %	2009 No.	2009 %	LSD[f]
Koeleria macrantha (Ledeb.) J.A. Schultes	Prairie Junegrass	7	85	4	—	—	138	14	
Muhlenbergia cuspidata (Torr. ex Hook) Rydb.	Plains muhly	8	1	< 0.1	—	—	—	—	
Muhlenbergia richardsonis (Trin.) Rydb.	Mat muhly	10	—	—	4	0.1	—	—	
Nassella viridula (Trin.) Barkworth	Green needlegrass	5	9	0.4	2	0.1	3	0.3	
Poa palustris L.	Fowl bluegrass	4	—	—	41	1	—	—	
Puccinellia nuttalliana (Schult.) A.S. Hitchc.	Nuttall's alkaligrass	4	—	—	10	0.4	—	—	
Schizachyrium scoparium (Michx.) Nash	Little bluestem	6	19	0.9	31	1	7	0.7	
Sporobolus compositus (Poir.) Merr.	Composite dropseed	4	—	—	—	—	1	0.1	
Sporobolus cryptandrus (Torr.) A. Gray	Sand dropseed	6	15	0.7	2	0.1	2	0.2	
Subtotal			168	8	213	8	163	17	NS
Early seral grasses									
Bromus inermis Leyss. ssp. *inermis*	Smooth brome	NV	—	—	2	0.1	—	—	
Bromus japonicus Thunb. ex Murr.	Japanese brome	NV	2	0.1	—	—	—	—	
Echinochloa crus-galli (L.) Beauv.	Barnyardgrass	NV	1	< 0.1	—	—	—	—	
Elymus repens (L.) Gould	Quackgrass	NV	—	—	—	—	3	0.3	
Poa compressa L.	Canada bluegrass	NV	—	—	—	—	1	0.1	
Schedonnardus paniculatus (Nutt.) Trel.	Tumblegrass	1	3	0.1	3	0.1	—	—	
Subtotal			6	0.3	5	0.2	4	0.4	NS
Hydric/mesic species									
Carex spp.	Sedges	NV	19	0.9	14	0.5	2	0.2	
Juncus balticus Willd.	Baltic rush	5	—	—	1	< 0.1	—	—	
Juncus spp.	Rushes	NV	—	—	—	—	2	0.2	
Typha spp.	Cattails	NV	1	< 0.1	28	1	6	0.6	
Subtotal			20	1	43	2	10	1	NS
Unknowns									
Lamiaceae spp.	Mint family	NV	—	—	—	—	8	0.8	
Unknown spp. 1		NV	—	—	—	—	1	0.1	
Unknown spp. 2		NV	—	—	—	—	1	0.1	
Unknown spp. 3		NV	—	—	—	—	2	0.2	

Table 3. Continued

Scientific name[b]	Common name	C-value[c]	1999 No.[d]	1999 %[e]	2004 No.	2004 %	2009 No.	2009 %	LSD[f]
Unknown spp. 4		NV	—	—	—	—	1	0.1	
Subtotal			0	0	0	0	13	1	NS
Total			2,052	100	2,788	100	977	100	423

[a] The 1999 and 2004 data were originally published in Cline et al. 2008 and are included here for ease of comparison.

[b] Scientific nomenclature follows the Weed Science Society of America Database of Common/Scientific Names 2010 (http://wssa.net/Weeds/ID/WeedNames/namesearch.php), except as amended according to the United States Department of Agriculture (USDA)/Natural Resources Conservation Service (NRCS) PLANTS Database (2006) (http://plants.usda.gov/index.html).

[c] Coefficient of conservatism value (C-value) was assigned to plant species based on an assessment by the Northern Great Plains Floristic Quality Assessment Panel (2001). A coefficient value of NV (no value) is indicative of an introduced or unidentified species, values of 0 to 3 are indicative of species that flourish in highly disturbed habitats, and values of 4 to 10 are assigned to species from less-disturbed, natural areas.

[d] Total number of seedlings that emerged per 0.5 m^2 from soil samples collected to a depth of 5 cm.

[e] Percentage of total seedlings that emerged across all soil cores.

[f] A Fischer's Protected LSD test at $P < 0.1$ was calculated to evaluate the change in seedling number across years.

species, and (7) unknown species. There were 12 replicates and five subsamples for each ecological site that were analyzed separately.

Results and Discussion

Leafy spurge stem density decreased 98 and 89% from the loamy overflow and loamy sites, respectively, in the LMNG 10 yr after *Aphthona* spp. release in 1999 (Table 1). In 2009, leafy spurge stem density averaged 2 and 9 stems m^{-2} in the loamy overflow and loamy sites, respectively, compared with 110 and 78 stems m^{-2}, respectively, in 1999, and 7 and 10 stems m^{-2}, respectively, in 2004. By 2009, stem density was similar within the four original leafy spurge categories (uninfested, low, moderate, and high). These results are similar to other studies that have reported *Aphthona* spp. substantially reduced leafy spurge infestations throughout the northern Great Plains (Butler et al. 2006; Kirby et al. 2000; Lesica and Hanna 2004; Lym and Nelson 2002; Mico and Shay 2002).

Leafy spurge seed was reduced more than 96% from 3,358 seedlings 0.5 m^{-2} in 1999 to 127 seedlings in 2009 in the loamy overflow seedbank as the aboveground stem density decreased (Table 2). Leafy spurge constituted nearly 67% of the loamy overflow seedbank in 1999, compared with 17% in 2004 and 2% in 2009. For the loamy sites, leafy spurge was reduced approximately 90% from 1,429 seedlings 0.5 m^{-2} in 1999 to 146 seedlings 0.5 m^{-2} in 2009 (Table 3). Leafy spurge represented nearly 70% of the loamy seedbank in 1999, compared with approximately 11% in 2004 and 15% in 2009.

The total number of seeds (including leafy spurge) in the loamy overflow seedbank increased from 1999 to 2009 (Table 2) but decreased in the loamy seedbank (Table 3). From the loamy overflow sites, 5,966 seedlings 0.5 m^{-2} emerged in 2009, compared with 5,042 and 6,798 seedlings 0.5 m^{-2} in 1999 and 2004, respectively. A total of 977 seedlings 0.5 m^{-2} emerged from the loamy sites in 2009 compared with 2,052 and 2,788 seedlings 0.5 m^{-2} in 1999 and 2004, respectively.

Species richness in the LMNG increased 33 and 35% in the loamy overflow and loamy seedbank, respectively, 10 yr after *Aphthona* spp. release for leafy spurge control (Tables 2 and 3). A total of 57 species emerged from the loamy overflow seedbank in 2009, compared with 43 species in 1999 and 54 species in 2004. From the loamy sites, 54 species emerged in 2009, compared with 40 species in 1999 and 51 species in 2004. The increasing trend in species richness came from an increase in late seral forbs at both ecological sites from 1999 to 2004, which went from an average of 6 to 13 species.

There was a greater tendency for increased species richness and seedling emergence in the loamy overflow sites, compared with the loamy sites, 10 years after

Aphthona spp. release (Tables 2 and 3). The increase in richness was likely due to more-favorable growing conditions in the overflow sites than was present at the loamy sites. Loamy overflow soils are characterized by greater moisture availability from surface runoff and subsurface water movement, greater organic matter content, and higher fertility than loamy site soils (Hanna et al. 1982; Malo and Worcester 1975; Wolf 1987). Cline (2002) also reported twice as many seedlings emerged from the loamy overflow seedbank than the loamy seedbank because of a more-favorable habitat for growth and seed production.

Kentucky bluegrass seedling density increased more than 250% in the loamy overflow seedbank, 10 yr after *Aphthona* spp. release, from 1,066 seedlings 0.5 m^{-2} in 1999 to 1,226 and 3,783 seedlings 0.5 m^{-2} in 2004 and 2009, respectively (Table 2). The rapid increase of Kentucky bluegrass in the soil seedbank was most likely due to reduced competition from leafy spurge, which provided the grass with an opportunity to invade. Precipitation and heavy grazing may also have contributed to the invasion or provided the grass with a favorable habitat for growth and seed production. Kentucky bluegrass tends to favor a wet environment (Stubbendieck et al. 2003), and precipitation was greater from April to June in 2009 (150 mm) than it was in 2004 (50 mm), the year of soil collection (NDAWN 2011, averaged between Beach and Dickinson, ND). In contrast, Kentucky bluegrass seedling emergence from the loamy seedbank was similar across study years and averaged less than 150 seedlings 0.5 m^{-2} (Table 3).

Late seral forbs constituted approximately 3% of the loamy overflow seedbank in 1999 and 2009, with a short-term peak to 25% in 2004 (Table 2). Even though the total number of late seral forb seed was similar 10 yr after *Aphthona* spp. release, there was a trend for increased species richness. Six late seral forb species appeared in the loamy overflow seedbank in 1999 compared with 14 and 13 species in 2004 and 2009, respectively.

In contrast, late seral forb species increased in the loamy seedbank during the 10-yr study from 5% in 1999 to 21% in 2009 (Table 3). Harebell (*Campanula rotundifolia* L.) and hoary puccoon [*Lithospermum canescens* (Michx.) Lehm.] were absent in 1999 but constituted 5 and 11% of the total seedbank, respectively, by 2009.

Early seral forb seedling emergence increased in both the loamy overflow and loamy seedbank during the 10-yr period of the study (Tables 2 and 3). Late-seral forbs averaged over both sites constituted less than 10% of the seedbank in 1999 but increased to 18 and 37% in the loamy overflow and loamy sites, respectively, by 2009. The largest increase of any early seral forb in the loamy overflow site was from a Brassicaceae species, which was absent in 1999 but was 5% of the total seedbank in 2009. This plant could not be positively identified but was likely a early seral invasive forb. Woodland draba (*Draba nemorosa* L.) was absent at the start of the study, but constituted 22% of the loamy seedbank by 2009.

Late seral grass-seedling emergence increased in both the loamy overflow and loamy sites 10 yr after *Aphthona* spp. release (Tables 2 and 3). The largest increase in late seral grass was from prairie Junegrass, which averaged less than 3% of the seedbank in 1999 but was 13.5% in 2009. Species richness remained the same, and only green needlegrass, little bluestem, and sand dropseed were present at all three evaluations.

Early seral grasses represented 6% or less of the total seedbank regardless of ecological site during the 10-yr study (Tables 2 and 3). Species from the unknown and hydric/mesic categories were difficult to identify and represented a small percentage of the seedbank for both ecological sites (Tables 2 and 3).

Leafy spurge was successfully controlled in the LMNG, 10 yr after *Aphthona* spp. release, whereas native species seed increased in the soil seedbank. However, from 2004 to 2009, there was a substantial increase in Kentucky bluegrass in the loamy overflow seedbank and a decreasing trend in native species richness. The increase in Kentucky bluegrass was most likely enabled by the reduction in leafy spurge and above-average precipitation, which provided a favorable habitat for growth and invasion. Nonnative grasses also became dominant when biological control agents were used to control diffuse knapweed (*Centaurea diffusa* Lam.) in Colorado (Bush et al. 2007).

The transition of one major invasive species (leafy spurge) to another (Kentucky bluegrass) in the LMNG is not ideal but may have some positive attributes (Lesica and Hanna 2009; Stephens et al. 2009). First of all, leafy spurge is listed as a noxious weed in North Dakota, whereas Kentucky bluegrass is an invasive species that is often considered naturalized throughout North America (USDA-NRCS 2004). Kentucky bluegrass provides habitat and forage for wildlife, is included in seed mixes for road ditch revegetation, and prevents soil erosion because of a dense, vigorous root system (USDA-NRCS 2002). Ranchers may benefit from the transition because leafy spurge is not palatable to livestock, and the forage value of Kentucky bluegrass is good in the spring. However, decreased plant richness in grassland communities has been linked to lower production and forage yield (Naeem et al. 1994; Tilman et al. 1996), reduced stability following a disturbance (McNaughton 1977; Tilman and Downing 1994), and increased invasion from exotic species (Tilman 1997; Tracy and Sanderson 2004).

The *Aphthona* spp. biological control agents reduced leafy spurge successfully in the LMNG, and the weed should remain suppressed as long as the insects are present. However, change in the plant community has been slow, depending on changes in the relative recruitment rates of the various species. Land managers may face a decision whether to reseed with native species or wait until the plants return naturally. Reseeding native species in such a large area as these study sites likely would not be cost effective. However, reseeding in selected areas may allow the natives to establish and repopulate the seedbank more quickly than observed here. If this type of seeding had been done approximately 5 yr after *Aphthona* spp. release, when leafy spurge began to decline, the rapid invasion by Kentucky bluegrass may have been avoided.

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