Demography of Meadow and Spotted Knapweed Populations in New York

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Abstract - *Centaurea stoebe* subsp. *micranthos* (Spotted Knapweed) and the hybrid *C. x moncktonii* (Meadow Knapweed) are perennial forbs introduced from Europe; the latter also originated from hybridization in North America of 2 other introduced knapweed species. They are invasive in grasslands and pastures in various regions of North America, including increasingly in the Northeast. We collected data from 4 life stages on 11 different demographic rates involving germination, survival, growth, and fecundity. We monitored 4 populations of Meadow Knapweed and 3 populations of Spotted Knapweed over 3 years in New York State by marking and tracking individual plants. Both knapweeds showed moderate to high rates of seed germination, very low survival of dormant seeds, and low survival of early vegetative stages with some site-specific exceptions. Survival of older vegetative and flowering plants was generally moderate to high. The main life-history differences between knapweed taxa involved more rapid maturation to and higher mortality of the flowering stage of Spotted Knapweed, a greater tendency for Spotted Knapweed to alternate between a flowering and vegetative state, and the potential for Meadow Knapweed to grow much larger in size. Spotted Knapweed matured more slowly in New York than in more western populations. Also, the flower head-infesting fly *Urophora quadrifasciata* and weevils *Larinus* spp. were present at all study sites. These data add to the knowledge of knapweed demography and can offer insights into the continued expansion and control of these invasive plants.

Introduction

Various species of *Centaurea* (knapweed; Asteraceae) were introduced from Europe and Asia beginning in the mid-1800s and infest more than 2 million ha of rangeland, pastures, and other field habitats in North America, particularly in western regions (Roché and Roché 1991, Winston et al. 2012). *Centaurea stoebe* L. subsp. *micranthos* (Gugler) Hayek (= *C. maculosa* auct. non Lam., *C. biebersteinii* DC.) (Spotted Knapweed), a short-lived perennial, was introduced from Europe in contaminated *Medicago sativa* L. (Alfalfa) and soil ballast (Sheley et al. 1998). Because a diploid ($2n = 18$) form found only in Europe is distinctly different from the tetraploid ($2n = 36$) form found in Europe and North America (Mráz et al. 2011), some authors refer to the introduced Spotted Knapweed as *C. stoebe* L. sensu lato (Winston et al. 2014). It is found in 46 US states and 6 Canadian provinces (Winston et al. 2012). Spotted Knapweed has been a major weed problem in western rangelands and pastures and is considered an increasing problem or concern in drier sites in eastern states such as Arkansas, Michigan, and New York (Akin-Fajiye and Gurevitch 2018, Carson and Landis 2014, Minteer et al. 2014, Winston et al. 2012).

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It reduces forage production for cattle and wildlife and negatively affects plant communities (Watson and Renney 1974). Numerous control measures have been used against it with varying degrees of success, including fire, hand pulling, mowing, herbicides, and biological control (Emery and Gross 2005, Sheley et al. 1998). Thirteen biological control agents have been released in North America with some more recent efforts in eastern states and provinces (Bourchier and Van Hezewijk 2013, Carson and Landis 2014, Minteer et al. 2014, Story 2002, Winston et al. 2012). Biological control agents reportedly established (Story 2002) or observed by us to be present in the Northeast include capitula (flower head)-infesting flies *Urophora affinis* Frauenfeld and *U. quadrifasciata* (Meigen) (Diptera: Tephritidae), and flower head-infesting weevils *Larinus* spp. (Coleoptera: Curculionidae). While western populations of Spotted Knapweed have been extensively studied, little work has been done on northeastern populations (Akin-Fajiye and Gurevitch 2018, 2020).

Centaurea x moncktonii C.E. Britt. (= *C. debeauxii* Gren. & Godr., *C. jacea* L. nothosubsp. *pratensis* (W.D.J. Koch) Čelak, *C. pratensis* Thuill. [illegitimate name]) (Meadow Knapweed) is a short- to long-lived perennial and fertile hybrid between *C. nigra* L. (Black Knapweed) and *C. jacea* L. (Brown Knapweed). Brown Knapweed and Black Knapweed were introduced into North America from Europe in the 1800s, and it is possible that Meadow Knapweed was also introduced (Roché and Roché 1991). They were likely introduced via ship ballast, but Brown Knapweed was also grown as a hay or forage crop (known as Bull Clover), and both Brown and Black Knapweed are grown as ornamentals (Roché and Johnson 2003, Roché and Roché 1991). Meadow Knapweed was cultivated as a winter forage in Oregon (Roché and Roché 1991). Meadow Knapweed is morphologically variable, approaching either parental species in appearance. It freely backcrosses with the parental species and has continued to increase in abundance, whereas pure parental forms do not appear to persist in some areas of hybridization (Lachmuth et al. 2019, Roché and Johnson 2003, Roché and Roché 1991). *Centaurea nigrescens* Willd. (Vochin Knapweed) may also be involved in this hybrid swarm (Keil and Ochsmann 2006, Lachmuth et al. 2019). Meadow Knapweed is found in 26 US states and 5 Canadian provinces (Keil and Ochsmann 2006, Poindexter et al. 2011, Winston et al. 2012), and is common in New York State (L.R. Milbrath and J. Biazzo, pers. observ.).

Meadow Knapweed prefers moist habitats such as meadows, irrigated pastures, riparian zones, and moist forest openings—habitats abundant in the Northeast (Roché and Johnson 2003). It is considered a weed in the Pacific Northwest and California, interfering with plant communities and forage production (Coombs et al. 2004, Roché and Johnson 2003). However, to date only 1 control study involving mowing and herbicides has been published, from Washington State (Miller and Lucero 2014). Although not originally targeted for biological control, some agents released against Spotted Knapweed and other species have established on Meadow Knapweed in the Pacific Northwest (Coombs et al. 2004), California (Woods et al. 2008), and the Northeast (*U. quadrifasciata, Larinus* spp.; (L.R. Milbrath and J. Biazzo, pers. observ.). It is unclear what impact these agents have on Meadow Knapweed populations (Woods et al. 2008). No information has been published on the demography of Meadow Knapweed, i.e., birth, growth, and death rates for a population.

Development of control tactics requires an understanding of plant demography. Matrix population models are one tool that can aid in identifying key points to disrupt in a plant's life cycle (Caswell 2001), and therefore optimize biological and traditional control programs (Emery and Gross 2005, Milbrath et al. 2018). Field data on the survival, growth, and reproduction (vital rates) of different life stages are needed to parameterize these models. Matrix population models have been developed for Spotted Knapweed in Colorado, Michigan, and southeastern New York (Akin-Fajiye and Gurevitch 2020, Emery and Gross 2005, Maines et al. 2013a), but demographic studies are generally lacking for northeastern infestations of Spotted Knapweed. No such studies exist for Meadow Knapweed. Thus, we report and compare vital rate and population density data for several northeastern populations of Spotted Knapwed and Meadow Knapweed.

Field-Site Description

We monitored 3 Spotted Knapweed and 4 Meadow Knapweed populations in New York State at sites where the infestations were not actively managed (Table 1); all study locations were at least 7 km apart. The 2 knapweed taxa are not known to co-occur in the same fields in New York except at a few, mainly roadside, locations. The Spotted Knapweed site at McEnteer (private property in south-central New York) is a waste area composed of gravel and sand near the Susquehanna River that had been excavated 30 years earlier for highway fill. Our 2 northern study locations

Table 1. Soil characteristics of populations of Spotted Knapweed and Meadow Knapweed in New York State (NRCS 2020). FLNF = Finger Lakes National Forest.

Spotted Knapweed locations

	McEnteer	Black Pond	Wehle
County	Tioga	Jefferson	Jefferson
Lat., Long.	42°5'9"N, 76°18'28"W	43°47'36"N, 76°13'32"W	43°51'35"N, 76°17'32"W
Soil series	Howard gravelly loam, 0–3% slopes	Beaches, Saprists and Aquents, ponded	Galoo-Rock outcrop complex, 0–8% slopes
Drainage	Well drained	Somewhat excessively drained	Excessively drained

Meadow Knapweed locations

	Jacobson	McLean	FLNF	Fort Plain
County	Cortland	Tompkins	Schuyler	Montgomery
Lat., Long.	42°29'53"N, 76°14'51"W	42°32'43"N, 76°16'5"W	42°31'42"N, 76°46'35"W	42°54'1"N, 74°44'45"W
Soil series	Erie silt loam, 8–15% slopes	Howard and Palmyra soils, 25–35% slopes	Erie silt loam, 3–8% slopes	Hornell silt loam, 3–8% slopes
Drainage	Somewhat poorly drained	Well drained	Somewhat poorly drained	Somewhat poorly drained

for Spotted Knapweed occur on the eastern shore of Lake Ontario: a shallow-soil alvar (limestone barrens) field at Robert G. Wehle State Park and an interior sand dune habitat at Black Pond Wildlife Management Area. Spotted Knapweed was probably at Black Pond prior to 1990 (Bonnano et al. 1998), but it is unknown when the other 2 sites were invaded.

We selected 3 Meadow Knapweed populations in west-central New York. The Jacobson site (private property) is a little-used hay field; Meadow Knapweed was first noticed at least 10 years ago (R. Jacobson, landowner, Dryden, NY, pers. comm.). This population is considered to be the most Black Knapweed-like in terms of its genetic ancestry (Lachmuth et al. 2019). McLean Meadow (Cornell Botanic Gardens) is a formerly abandoned pasture that has been mowed every few years since 1988 to reduce woody shrubs and trees and maintain it as a meadow; Meadow Knapweed became noticeably abundant in the mid-1990s. The Finger Lakes National Forest site (FLNF, USDA Forest Service) is a pasture that has been periodically mowed; Meadow Knapweed has likely been present since the 1990s (M. Deller, land manager, Rochester, VT, pers. comm.). The fourth Meadow Knapweed location (Fort Plain, private property) is located in eastern New York. It had been in hay production or grass fallow for many years and was heavily infested by 2008 (M. delPuerto, land manager, Albany, NY, pers. comm.). Unlike the well- to excessively drained soils of the Spotted Knapweed sites, the Meadow Knapweed sites are mostly poorly drained (Table 1). The widely distributed fly *U. quadrifasciata* was present at all knapweed sites. Our intent was to avoid locations with *Larinus* spp. weevils, but this was not possible. We deposited voucher specimens of Meadow Knapweed with the Liberty Hyde Bailey Hortorium (BH), Cornell University, Ithaca, NY.

Methods

Knapweed life history

Spotted Knapweed is a tap-rooted, short-lived herbaceous perennial that may live up to 8 or 9 years (Sheley et al. 1998). The plants overwinter as a rosette of leaves; the leaves are highly divided. It produces one to several flowering stems 30–100 cm tall with flower heads up to 6 mm in diameter (Watson and Renney 1974). We've observed flowering in New York from July to September and seed dispersal beginning in August. Spotted Knapweed reproduces by seeds, but also produces multiple rosettes on older root crowns or from some very short, lateral shoots (Watson and Renney 1974). Germination occurs in autumn and spring, and plants typically flower in their second year in western states. They can flower every year thereafter, although adult flowering plants may revert to a vegetative state in some years (Emery and Gross 2005). Seeds may remain dormant for at least 8 years (Davis et al. 1993).

Meadow Knapweed is a short- to long-lived herbaceous perennial. The related Brown Knapweed is reported to live at least 10 years (Tamm 1956). The plants overwinter as a rosette of leaves. One to several stems, 50–100 cm or more tall, are produced from a semi-woody rootstock (Roché and Johnson 2003). It is only taprooted as a seedling; as an adult plant, Meadow Knapweed produces fleshy roots. Leaves are not divided, and basal leaves can be up to 15 cm long and 3 cm wide (Roché and Johnson 2003). In New York, we have observed that plants flower from June to September, and once mature, flower annually. The flower heads are up to 20 mm wide (Miller and Lucero 2014). Seeds begin to drop from flower heads in July or later, which continues into November. Like Spotted Knapweed, Meadow Knapweed reproduces by seeds but also produces multiple rosettes from the root crown. We have observed seeds to germinate mainly in the spring.

We identified 4 life stages for monitoring vital rates of germination, survival, transitions to other life stages, and fecundity: seeds, seedlings, vegetative plants, and flowering plants. We defined seedlings as those individuals experiencing their first summer of growth. Vegetative individuals included those in at least their second summer of growth (juveniles not yet flowering) as well as some flowering plants that had reverted to a vegetative state. For purposes of population modeling, we primarily measured vital rates on an annual cycle from August to the following August (usually before seed dispersal) for 3 years (2016–2019).

Vital rate data

We established 10 groups of permanent quadrats and seed germination trays at each location to estimate vital rates. For most sites, we placed quadrat groups along 2 transects (5 per transect) in June 2016. Quadrat groups were 3–10 m apart within each transect, and the 2 transects were 10–20 m apart, depending on the size of the knapweed infestation. For the Black Pond site, we used a single transect due to the linear nature of the sand dune habitat. To prevent damage from *Odocoileus virginianus* (Zimmermann) (White-tailed Deer) at the Wehle site, we erected a 15 m x 46 m x 2.4 m (high) deer fence exclosure (Tenax C-Flex HD, Tenax Corporation, Baltimore, MD). We established new quadrats next to the original quadrats (transition year 1: 2016–2017) within each group in each of the 2 subsequent years of the study (year 2: 2017–2018, year 3: 2018–2019).

We estimated annual germination and seed survival rates using germination trays. We collected soil for the trays from each of the locations and steam pasteurized it at 82.2 °C (180 °F) for at least 30 minutes to eliminate contaminating seeds (Baker and Roistacher 1957), except for the Black Pond site where we dug sand directly from the neighboring lake beach. We annually collected mature flower heads from at least 40 plants at the same site in which the seeds were to be sown. We cleaned and counted the seeds into lots of 200 using a seed counter (Seedburo Seed Counter, Seedburo Equipment Co., Des Plaines, IL). We estimated initial seed viability by cold-wet stratifying 3 lots of 200 seeds at 4 °C for 2 months, then germinating the seeds in an incubator set at 25 °C when lights were on and 20 °C when lights were off and a photoperiod of 14:10 h (L:D). We tested remaining non-germinated seeds for viability by squeezing the seeds with a forceps. We considered hard seeds viable based on previous assessments with a 1% solution of tetrazolium chloride (98% viable; L.R. Milbrath, unpubl. data). Unfilled or dead seeds readily collapsed. We used the percentage of viable seeds as a correction factor when calculating germination and seed survival rates.

Germination trays were 18 cm in diameter and 5 cm deep, cut from the bottom of a 7.6-L (2-gallon) pot (Poly-Tainer can no. 2B, Nursery Suppliers Inc., Chambersburg, PA). We secured inside the pot a cylinder of 30 x 30 mesh (140 openings per cm^2) stainless steel wire cloth that was 10 cm high (McMaster-Carr, Robbinsville, NJ) and an additional mesh floor to prevent seeds from washing out of the pot. We dug the trays into the ground and secured them with sod staples, filled them with pasteurized soil to a depth of 5 cm, and sprinkled seeds (200 per tray) over the soil surface. A ventilated lid was attached to prevent seeds from raining into the trays from surrounding knapweed plants. The lid was 23 cm in diameter and 5 cm high, cut from the top of a 7.6-L (2-gallon) pot, and a layer of fiberglass 20 x 20 mesh (62 openings per cm^2) window screening overlayed with organza was glued to the pot rim. We hung a drape of copper 5 x 5 mesh that was 13 cm long (Nixalite of America Inc., East Moline, IL) from the lid to minimize entrance of slugs into the trays, as we had observed slugs destroying knapweed seedlings. At several sites, we secured a conical wire basket (mesh 2.5 cm high x 2 to 13 cm wide from bottom to top; Topiary Art Works and Greenhouses LLC, Clearwater, KS) over each tray to prevent damage from large vertebrates.

We deployed 10 germination trays per location in September and used a new set of trays for each year of the study. We estimated percentage germination by counting and removing newly emerged seedlings in October, November, April, May, June, and July. We harvested the trays by late July, prior to the start of the annual seed rain, and refrigerated the soil at 4 °C for 3–4 months. The soil was then spread into 24 cm x 51 cm trays covered with a clear lid, watered as needed, and held at 20–30 °C and a photoperiod of 14:10 hr (L:D) in a greenhouse for 4 weeks. We counted emerged seedlings, which were assumed to represent surviving seeds. We calculated percentage seed survival as: number of seedlings/(corrected initial number of seeds - number of previously field-counted seedlings).

We estimated vital rates of seedlings using 0.25-m^2 circular quadrats (PEX, Zurn Industries LLC, Milwaukee, WI) secured with sod staples except that we used 1-m^2 circular quadrats at the McEnteer site and 1 m x 2 m or 1 m x 3 m quadrats at the Black Pond site (described below). In July 2016 (year 1), we marked up to 20 established seedlings within each quadrat with a labeled, plastic ring anchored around the base of the plant. New quadrats were established (as described below) in each of the 2 subsequent years of the study. We checked established seedling quadrats monthly to remove any newly germinated seedlings (contaminants) growing in the plastic rings. We assessed overwintering survival the following May (only years 2 and 3) and annual survival and potential transitions to other life stages the following August. Also beginning in October 2016 (Spotted Knapweed) or May 2017 (Meadow Knapweed), we marked up to 20 microquadrats with labeled metal rods within a second set of seedling quadrats. We inserted rods into groups of newly emerged seedlings (cotyledon stage). We counted the number of seedlings in October, November, May, June, and July within the area delimited by a ring 7.3 cm in diameter and centered on each rod. We established new seedling quadrats each of the 3 years of the study. We calculated new seedling survival for each quadrat (summed from all microquadrats) by dividing the final number of surviving seedlings by the maximum cumulative number of seedlings that had emerged. Following the last new seedling count in years 1 and 2, we marked up to 20 established seedlings within each quadrat and monitored them as previously described. Thus, for each year we separately monitored 2 independent seedling quadrats: 1 of new seedlings and 1 of established seedlings.

We estimated vital rates for vegetative and flowering plants by marking plants in 1 m x 1 m quadrats with PVC pipes at all plot corners, except for the Black Pond site where we used 1 m x 2 m or 1 m x 3 m quadrats due to the lower densities of Spotted Knapweed. We marked up to 20 plants of each stage (only 10 flowering plants for Meadow Knapweed due to their generally larger size) with a labeled, plastic cable tie anchored around the base of the plant in July 2016. We established new quadrats and marked new vegetative and flowering plants in the 2 successive years. We annually censused all marked plants in all quadrats in August for survival, flowering status, stem number, and number of flower heads per plant. We randomly collected 50 mature flower heads from non-experimental plants near the quadrats and counted the filled seeds per flower head to estimate the number of viable seeds produced per plant. We also collected 10 stems from a given location and dissected the flower heads for any flies (*U. quadrifasciata*) and weevils (*Larinus* spp.) to document the current infestation rate. We collected stems from only the Jacobson, McLean, and Fort Plain sites in 2017, and from all sites in 2018 and 2019, and calculated the percentage of infested flower heads.

For all vital rates, we analyzed the data with a mixed model including a repeated measures analysis using either an unstructured or autoregressive covariance structure depending on the variable (PROC MIXED, SAS version 9.4, SAS Institute, Inc., Cary, NC). We transformed proportional data using the logit transformation and log-tranformed fecundity data. We used fixed effects of species, year, and location nested within species and the random effect of quadrat nested within location nested within species. We compared means using Fisher's protected LSD test with the Bonferroni correction.

Population structure

We estimated initial population densities of the 4 life stages for each of the 7 locations in July 2016. We counted all stages except seeds in or, in some cases of seedling counts, immediately next to the 10 initial 1-m^2 (or larger) quadrats. If population densities were high, we counted vegetative and flowering plants in 0.5-m^2 quadrats. For seedling counts, we used 2 smaller quadrats (0.125 m^2) placed in opposite corners of the 1-m^2 quadrat. We sampled seeds in the seed bank by taking 15 soil cores around each of the 10 quadrats using a soil probe 7.6 cm in diameter and to a depth of 5 cm, equivalent to sampling a surface area of 0.06 m^2. We bulked the soil cores for each quadrat area and returned them to the laboratory where they were refrigerated at 4 °C for 2 weeks. We mixed the soil with a soilless potting mix (Metro-Mix 560 Sun-Coir, Sun Gro Horticulture, Agawam, MA) at a 2:1 ratio (field soil:soilless mix) to prevent crusting, spread it into 24 cm x 51 cm trays, and watered it as needed. The trays were held at 20–30 °C and a photoperiod of 14:10 hr (L:D) in a greenhouse for 2 weeks. We counted and removed emerged seedlings, then refrigerated the soil trays again for 3 months. We returned the trays to the greenhouse for another 2 weeks and counted emerged seedlings. The cumulative emergence of seedlings was used as an estimate of viable seeds per sample. For each life stage, we calculated the average density per 1 m^2 for each knapweed population.

Results

The combination of various vital rates we measured (germination, survival, transitions among life stages, fecundity) differed to varying degrees among knapweed taxa, years, and locations or populations (Table 2). Germination rates of Spotted Knapweed and Meadow Knapweed were mostly comparable among locations within a given year, although they were not necessarily similar across years for a given site (Table 3). Percentage germination was often moderate to high (41–91%) with some lower rates in the first year or at the Jacobson site (Meadow Knapweed) for all years of the study (Table 3). We observed 97–99% of Spotted Knapweed germination and 36–94% of Meadow Knapweed germination in the seed trays in autumn. Survival of non-germinated seeds after 1 year was very low across most years and locations (average = 0–10%) with 1 exception (31% at 1 Meadow Knapweed site; Table 3).

Survival of seedlings within their first year of growth (new seedlings) was mostly comparable within and among locations over time, and it varied from low to moderately high (7–74%; Table 3). The winter survival of established seedlings, i.e., entering their second year of growth as a vegetative rosette, was lower for some Meadow Knapweed populations (Jacobson and FLNF) than other sites and also was less in year 3 compared to year 2 for both Spotted Knapweed and Meadow Knapweed (Tables 4, 5). Additional mortality occurred over the subsequent summer months. As a result, the annual survival of established seedlings, which is the same as a seedling-to-vegetative rosette transition, was generally low (<33%) in all 3 years for populations of Spotted Knapweed and Meadow Knapweed with a few exceptions (Table 3). In contrast, survival of older vegetative and flowering plants from year to year was mainly moderate to high for both Spotted Knapweed and Meadow Knapweed (45–97%; Tables 3–5). The survival of flowering plants of Spotted Knapweed was less than Meadow Knapweed in all years (Tables 4, 5).

We observed a wide range of seed production with substantial overlap between most populations of Spotted Knapweed and Meadow Knapweed (Table 3). For several populations, seed production was greatest in year 1 of our study. The highest estimated seed production we observed was for the FLNF and Fort Plain sites (Meadow Knapweed), averaging 1521 or more seeds per plant for most years (Table 3). Adult plants generally had 1–3 flowering stems. We counted up to 25 stems for some Spotted Knapweed plants across the 3 populations studied. Meadow Knapweed had up to 19 (McLean, Jacobson) or 100 (Fort Plain, FLNF) stems per plant. In the latter case, we counted 933 flower heads producing an estimated 38,365 seeds on a single plant.

Table 2. Analysis of variance results for vital rates of percentage germination, survival of life stages, individuals transitioning to other life stages, and fecundity among 7 populations (locations) of Spotted Knapweed and Meadow Knapweed observed over 3 years in New York State. *F* statistics (numerator and denominator degrees of freedom) and level of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Vital rate	Species	Year	Location (species)	Species*year	Year*location (species)
% germination	23.77 (1, 63.1)***	71.67 (2, 61.9)***	13.56 (5, 63)***	2.63 (2, 61.9)	5.62 (10, 88.5)***
% seed survival	1.36 (1, 92.9)	49.38 (2, 133)***	7.09 (5, 92.6)***	1.38 (2, 133)	4.8 (10, 141)***
% new seedling survival	19.95 (1, 45.8)***	1.48 (2, 54.3)	4.01 (5, 44.9)**	10.21 (2, 54.1)***	3.33 (10, 76.4)**
% winter seedling survival	12.03 (1, 65.2)***	48.16 (1, 64.2)***	14.69 (5, 62.2)***	5.10 (1, 64.4)*	1.89 (5, 61.6)
% annual seedling survival	9.51 (1, 64.3)**	28.98 (2, 60.9)***	12.34 (5, 61.7)***	6.66 (2, 61.1)**	3.51 (10, 83.1)***
% vegetative survival	1.95 (1, 51.8)	12.52 (2, 54)***	5.90 (5, 51.7)***	1.85 (2, 53.9)	4.07 (10, 76.4)***
% flowering survival	129.59 (1, 63.5)***	6.34 (2, 62)**	4.15 (5, 63.3)**	14.16 (2, 62.1)***	1.76 (10, 88.8)
% seedling to flowering	2.10 (1, 75.2)	3.20 (2, 116)*	1.30 (5, 71.7)	5.58 (2, 117)**	1.11 (10, 122)
% vegetative to flowering	2.88 (1, 57)	0.83 (2, 50.3)	1.50 (5, 57.2)	14.21 (2, 50.2)***	4.59 (10, 74.5)***
% flowering to vegetative	48.31 (1, 62.4)***	1.25 (2, 61.1)	12.90 (5, 62.2)***	11.82 (2, 61.1)***	1.62 (10, 87.8)
Fecundity	34.56 (1, 63.1)***	154.70 (2, 61.3)***	41.14 (5, 63.1)***	8.90 (2, 61.4)***	9.21 (10, 88)***

Table 3. Vital rates (untransformed mean, min–max among trays or quadrats; n = 4–10) of percentage germination, survival of life stages, individuals transitioning to other life stages, and fecundity among 7 populations of Spotted Knapweed and Meadow Knapweed observed over 3 years in New York State. FLNF = Finger Lakes National Forest. Means within each vital rate followed by the same letter are not different (Fisher's protected LSD test with Bonferroni correction, $P > 0.05$), e.g., ab or a–e (= abcde) . [Table continued on following page.]

Vital	Spotted Knapweed locations			Meadow Knapweed locations			
rate	McEnteer	Black Pond	Wehle	Jacobson	McLean	FLNF	Fort Plain
% germination							
Yr 1	14 (4–48) h	31 (2–64) efgh	72 (21–100) abcd	22 (3–62) gh	44 (2–72) d–h	9 (4–16) h	41 (8–57) d–h
Yr 2	77 (49–92) abcd	76 (19–97) abcd	91 (85–98) a	28 (3–49) efgh	85 (67–99) ab	85 (73–96) abc	70 (33–99) abcd
Yr 3	78 (55–96) abcd	71 (34–91) abcd	83 (67–598) abc	27 (6–52) fgh	56 (4–84) c–g	62 (21–93) a–e	61 (42–80) b–f
% seed survival							
Yr 1	0 (0–0) d	0 (0–0) d	0 (0–0) d	0 (0–0) d	0 (0–0) d	0 (0–0) d	0 (0–0) d
Yr 2	3 (0–19) bcd	9 (0–28) abc	3 (0–10) bcd	1 (0–1) d	31 (4–71) a	3 (0–12) bcd	10 (0–40) ab
Yr 3	1 (0–6) d	4 (0–22) bcd	3 (0–29) cd	1 (0–3) d	1 (0–4) d	5 (0–33) bcd	4 (0–23) bcd

Table 3, continued

Vital	Spotted Knapweed locations			Meadow Knapweed locations			
rate	McEnteer	Black Pond	Wehle	Jacobson	McLean	FLNF	Fort Plain
% new seedling survival							
Yr 1	54 (0–92) abc	23 (8–35) abcd	49 (24–100) ab	15 (0–39) cd	64 (53–80) ab	36 (5–76) abcd	35 (3–75) abcd
Yr 2	55 (26–68) ab	7 (0–21) d	17 (3–34) bcd	37 (8–76) abc	74 (45–89) a	44 (4–100) abc	62 (43–89) a
Yr 3	34 (0–100) abcd	38 (15–51) abcd	38 (11–75) abcd	63 (49–83) abc	59 (51–67) abc	73 (43–100) abc	61 (42–77) abc
% established seedling survival (annual)							
Yr 1	14 (0–55) b–f	25 (0–53) abcd	2 (0–10) f	2 (0–5) ef	21 (0–45) a–e	13 (0–43) b–f	7 (0–25) b–f
Yr 2	78 (37–95) a	26 (8–50) abc	39 (0–71) ab	10 (0–45) def	27 (5–55) abc	6 (0–16) cdef	26 (5–50) abc
Yr 3	32 (10–60) abc	15 (0–50) b–f	6 (0–25) cdef	1 (0–5) f	15 (0–45) b–f	2 (0–7) def	13 (0–25) b-f
% vegetative survival							
Yr 1	73 (40–100) a–e	76 (25–100) a–e	14 (0–35) e	57 (10–87) a–e	86 (56–100) ab	70 (0–100) a–e	30 (0–50) de
Yr 2	94 (83–100) a	76 (42–100) a–e	86 (60–100) abc	69 (27–93) a–e	81 (58–94) a–e	59 (0–100) a–e	69 (50–90) a–e
Yr 3	83 (65–94) abcd	47 (0–85) de	67 (40–87) a–e	61 (44–81) a–e	73 (58–79) a–e	48 (0–67) cde	44 (10–88) bcde
% vegetative to flowering							
Yr 1	81 (47–100) ab	42 (26–60) abc	41 (0–100) bc	49 (8–100) ab	60 (40–92) ab	75 (0–100) ab	36 (0–100) abc
Yr 2	78 (61–93) ab	69 (37–93) ab	74 (47–100) a	35 (19–71) ab	39 (25–53) ab	11 (0–50) c	30 (0–50) bc
Yr 3	59 (45–72) ab	20 (0–42) bc	76 (0–100) ab	63 (20–100) ab	61 (37–81) ab	36 (0–100) abc	54 (0–100) ab
Fecundity							
Yr 1	162 (71–276) e–i	330 (102–714) defg	475 (112–962) cde	181 (116–336) efi	131 (75–268) e-j	6369 (135–21,902) a	2275 (662–6901) ab
Yr 2	42 (28–58) jkl	214 (106–289) d–h	95 (57–136) f–k	98 (38–202) g-l	58 (35–96) ikl	2063 (89–5738) bc	1521 (4498–4501) abc
Yr 3	32 (20–41) k	397 (128–1920) defg	179 (92–269) fghi	92 (15–290) hjkl	87 (40–129) f–k	2171 (81–6156) bc	844 (132–1803) cd

We seldom observed established seedlings transitioning to a flowering state, i.e., in their second season of growth (<6%; Tables 4, 5). We saw this for both Meadow Knapweed (FLNF, Fort Plain) and Spotted Knapweed (McEnteer, Wehle) but usually in only 1 out of the 3 years for a given site. We observed a moderate

Table 4. Vital rates (untransformed mean, min–max among quadrats; *n* = 14–30) of percentage survival of life stages and individuals transitioning to other life stages among 7 populations of Spotted Knapweed and Meadow Knapweed averaged over years in New York State. FLNF = Finger Lakes National Forest. Means within each row followed by the same letter are not different (Fisher's protected LSD test with Bonferroni correction, *P* > 0.05).

Vital	Spotted Knapweed locations			Meadow Knapweed locations			
rate	McEnteer	Black Pond	Wehle	Jacobson	McLean	FLNF	Fort Plain
% established seedling survival (winter)							
	60 (15–95) a	38 (0–80) bc	51 (0–85) ab	11 (0–70) c	41 (5–80) ab	8 (0–30) c	42 (0–100) ab
% flowering survival							
	47 (0–86) c	66 (0–100) c	61 (0–100) c	88 (44–100) ab	91 (73–100) b	97 (75–100) a	93 (73–100) ab
% seedling to flowering							
	2 (0–17) a	0 (0–0) a	5 (0–80) a	0 (0–0) a	0 (0–0) a	3 (0–100) a	1 (0–25) a
% flowering to vegetative							
	43 (0–100) a	33 (0–100) ab	10 (0–75) cd	8 (0–29) cd	11 (0–38) bc	1 (0–11) d	2 (0–12) d

Table 5. Vital rates (untransformed mean, min–max among quadrats; *n* = 23–40) of percentage survival of life stages and individuals transitioning to other life stages of Spotted Knapweed and Meadow Knapweed observed over 3 years and averaged among populations in New York State. Means within each vital rate followed by the same letter are not different (Fisher's protected LSD test with Bonferroni correction, *P* > 0.05).

Vital rate	Spotted Knapweed	Meadow Knapweed
% established seedling survival (winter)		
Year 2	68 (17–95) a	34 (0–100) b
Year 3	26 (0–75) bc	18 (0–60) c
% flowering survival		
Year 1	35 (0–100) d	96 (80–100) a
Year 2	78 (48–100) c	91 (53–100) ab
Year 3	60 (3–89) d	89 (44–100) b
% seedling to flowering		
Year 1	0 (0–0) b	0 (0–0) b
Year 2	5 (0–80) a	0 (0–0) b
Year 3	1 (0–17) ab	3 (0–100) ab
% flowering to vegetative		
Year 1	40 (0–100) a	2 (0–20) c
Year 2	19 (0–81) ab	10 (0–38) b
Year 3	28 (0–100) a	5 (0–29) c

to high proportion (30–81%) of marked vegetative individuals annually transitioning to the flowering stage for most populations and years of the study (Table 3), including plants in their 3rd season of growth (the youngest members of this class of plants). Specifically, 39–57% of Spotted Knapweed plants flowered in their 3rd year whereas 0–7% of Meadow Knapweed plants did so (data not shown). At the Jacobson site, we never observed plants originally marked as seedlings maturing to a flowering state due to extremely high mortality of pre-flowering stages. At other sites, a few (Spotted Knapweed at all sites, Meadow Knapweed at Fort Plain and FLNF) to many (Meadow Knapweed at McLean) individuals originally marked as established seedlings in 2016 had not yet flowered by their 4th season of growth in 2019. The reversion rate of flowering plants to a vegetative state was generally higher for Spotted Knapweed than Meadow Knapweed and varied from 1% to 43% (Tables 4, 5). An adult flowering plant that became vegetative one year usually would flower again the following year.

Infestations of the flower heads by seed-destroying insects (flies and/or weevils) were generally low to moderate over the 3 years of the study (Table 6). We did not quantify per capita seed loss due to insect feeding. However, we documented a large decrease in seed production at 1 Spotted Knapweed site (McEnteer) between year 1 (162 seeds per plant) and year 2 (42 seeds per plant) due in part to an observed outbreak of the weevil at the site in 2018 (overall proportion of infestation = 64%). Otherwise, the fly was much more commonly recovered than the weevil at the Spotted Knapweed sites. Meadow Knapweed sites were variable, in that the weevil was common (Jacobson), occasional (Fort Plain, McLean), or rare (FLNF). The fly was present at all Meadow Knapweed locations.

Densities of viable seeds in the seed bank recovered in summer 2016, which included a severe drought, were high for Meadow Knapweed, especially at Fort Plain, relative to Spotted Knapweed (Table 7). The densities of other life stages varied among populations. Notably, vegetative plants were scarce at the Fort Plain and FLNF sites (Table 7).

Table 6. Percentage of flower heads per stem (mean ± SD, n = 10) infested with seed-destroying insects among 7 populations of Spotted Knapweed and Meadow Knapweed observed over 3 years in New York State. FLNF = Finger Lakes National Forest.

Species/ location	Year 1	Year 2	Year 3
Spotted Knapweed			
McEnteer	-	63.8 ± 27.7	22.5 ± 27.9
Black Pond	-	27.0 ± 23.7	18.7 ± 19.9
Wehle	-	21.9 ± 30.0	36.2 ± 26.1
Meadow Knapweed			
Jacobson	26.2 ± 34.8	47.6 ± 33.4	36.1 ± 21.9
McLean	10.3 ± 9.8	2.5 ± 7.9	8.3 ± 21.2
FLNF	-	6.2 ± 8.4	0.0 ± 0.0
Fort Plain	7.9 ± 15.9	1.0 ± 2.1	4.5 ± 9.2

Discussion

Our survey is the first demographic study of the hybrid Meadow Knapweed. In addition, we have documented new information on the demography of western and northern New York populations of Spotted Knapweed. Our results suggest that, while many vital rates for the 2 taxa are similar, including across populations and over years, some notable differences in growth, survival and life-stage transitions also occur between knapweed taxa and among populations.

Our observed germination rates for Spotted Knapweed (>70% at most sites and years; Table 3) were high compared to an estimated 25% for Colorado populations (Maines et al. 2013a). We expected and observed an autumn flush of seedlings and a smaller spring flush for Spotted Knapweed at all our populations in both the field and in the germination trays (Watson and Renney 1974). The autumn flush we observed for Meadow Knapweed in the germination trays differs from the primary spring seedling flush we typically observed in the field. However, in areas where the vegetation canopy was not dense, we observed some germination in autumn as well. Spotted Knapweed seeds from a single plant are known to include non-dormant seeds, dormant seeds that respond to exposure to red light, and non-responsive dormant seeds (Nolan and Upadhyaya 1988). Spotted Knapweed seeds also have increased germination following dry storage at room temperature (Nolan and Upadhyaya 1988, Watson and Renney 1974). It is presently unknown if Meadow Knapweed seeds have similar dormancy traits. However, our germination trays likely provided good light exposure for seeds that had been held at room temperature for cleaning and processing. Thus, autumn germination of Meadow Knapweed was likely promoted. Under more natural conditions of seed dispersal, a dense canopy of plants would inhibit much of the seed from germinating in autumn (Nolan and Upadhyaya 1988). This may have occurred to some degree at the FLNF and Fort Plain sites, where autumn germination was as low as 36–41% in the trays in some years.

Survival of dormant seeds was very low across most years and sites. In contrast, Akin-Fajiye and Gurevitch (2020) reported a 21% survival rate for slightly buried Spotted Knapweed seeds, and Davis et al. (1993) reported that buried Spotted Knapweed seeds had a 56–78% viability rate after 1 year. When corrected for previous germination, seed survival in the latter case was 90–95% (Davis et al. 1993). Thus, burial appears to promote both low germination and high survival, at least in

Table 7. Population densities (number per m^2, mean ± SD, n = 10) of different life stages for 7 populations of Spotted Knapweed and Meadow Knapweed in New York State in 2016. FLNF = Finger Lakes National Forest.

Knapweed	Location	Viable seeds	Seedlings	Vegetative	Flowering
Spotted	McEnteer	62.1 ± 35.6	182.0 ± 89.1	58.2 ± 14.4	37.7 ± 7.9
Spotted	Black Pond	184.8 ± 209.1	11.4 ± 6.2	24.6 ± 17.5	14.2 ± 11.0
Spotted	Wehle	148.1 ± 90.7	27.7 ± 15.8	26.3 ± 12.0	30.1 ± 12.4
Meadow	Jacobson	1032.2 ± 583.7	58.4 ± 31.5	14.0 ± 10.9	63.2 ± 24.5
Meadow	McLean	947.7 ± 819.8	324.0 ± 193.9	27.2 ± 11.5	58.4 ± 16.7
Meadow	FLNF	2413.1 ± 1540.0	59.6 ± 113.3	2.0 ± 3.0	17.3 ± 20.6
Meadow	Fort Plain	5826.6 ± 2797.1	68.0 ± 73.8	3.7 ± 4.1	18.5 ± 12.5

the short term, as opposed to seeds lying on the soil surface as in our study. Spotted Knapweed seeds may remain dormant for at least 8 years (Davis et al. 1993), but seed bank dynamics are unknown for Meadow Knapweed.

We observed rodent activity (burrows and trails) and significant destruction of seedlings and young vegetative plants by snails and slugs at the Meadow Knapweed sites. Slug and snail populations are likely enhanced by the typically moist pasture conditions preferred by Meadow Knapweed, and plants at locations like Jacobson and FLNF seemed to be particularly vulnerable. Edwards and Crawley (1999) also documented significant rodent herbivory of seeds, and possibly seedlings, of the related Black Knapweed in an English grassland. The high mortality that we observed in Meadow Knapweed appears to result in few individuals of a given cohort becoming a flowering plant. Nevertheless such plants have the potential to grow very large at some locations (FLNF, Fort Plain). Sources of significant seedling mortality for Spotted Knapweed were less clear but included desiccation, likely enhanced by Spotted Knapweed growing in well- to excessively drained soils. Other researchers have similarly reported low survival of seedlings transitioning to a vegetative rosette stage for Spotted Knapweed (Maines et al. 2013a). In addition, we observed high mortality of all stages of plants that were buried due to erosion of sand dunes from heavy rains in 2019 at Black Pond. Previously reported emergence rates of 7–97% for Spotted Knapweed, i.e., a combination of germination and seedling survival, appear comparable to our populations (Akin-Fajiye and Gurevitch 2020, Maines et al. 2013b, Schirman 1981, Vermeire and Rinella 2009). Beyond the seedling stage, we observed higher survival for older vegetative plants, similar to reports from other studies (Maines et al. 2013b).

We never observed flowering of fall-germinated seedlings of Spotted Knapweed or spring-germinated seedlings of Meadow Knapweed in their first summer of growth, although this sometimes occurs in western populations of Spotted Knapweed (Maines et al. 2013a, Watson and Renney 1974). We also rarely saw flowering in the second summer of growth (% seedling-to-flowering transition; Tables 4, 5) for either knapweed taxon, although this is typical for Spotted Knapweed in western regions of North America (Schirman 1981, Watson and Renney 1974). Rather, for the northeastern populations we studied, at least 3 (Spotted Knapweed) or more (Meadow Knapweed) years of growth are required to mature to a reproductive state. Akin-Fajiye and Gurevitch (2020) also reported no flowering until the third growing season for a semi-natural population of Spotted Knapweed on Long Island, NY. Spotted Knapweed thus matures more quickly than Meadow Knapweed in the Northeast.

Flowering Spotted Knapweed plants tended to revert to a non-flowering state more often, and had a higher mortality rate, than Meadow Knapweed plants. Higher mortality is related to a shorter life span; Watson and Renney (1974) noted that Spotted Knapweed plants lived an average of 3–5 years in western areas of Canada, although they can live up to 9 years (Sheley et al. 1998). We do not know the average life span of Spotted Knapweed in the Northeast. Environmental stresses undoubtedly influence survival. For example, we observed high mortality of adult Spotted Knapweed following a severe drought in 2016 but not in other, wetter years

(Table 5). It is currently unknown how long Meadow Knapweed plants live or how quickly they increase in size (stem number). The maximum number of stems we observed for individual plants of Spotted Knapweed (25) was similar to stem numbers reported from western regions (Watson and Renney 1974) and for 2 of the Meadow Knapweed populations we studied. However, Meadow Knapweed has the potential to grow much larger in size than Spotted Knapweed, based on stem numbers of up to 100. Seed production by Spotted Knapweed in our study was similar to western and midwestern populations, which varies from 10 to 1100 seeds per plant depending on plant density and seasonal precipitation (Emery and Gross 2005, Watson and Renney 1974). Under irrigation, Spotted Knapweed can produce over 25,000 seeds (Watson and Renney 1974), which is as many as produced by Meadow Knapweed plants we studied, except for the largest one that produced over 38,000 seeds.

Flower head-infesting flies (*U. quadrifasciata*) and weevils (*Larinus* spp.) were present at all our study sites to varying degrees, but we do not yet know what effect these biological control agents are having on northeastern knapweed populations. *Urophora quadrifasciata* is not considered an effective biological control by itself, whereas *Larinus*, in particular *L. minutus* Gyllenhal, is credited with controlling *C. diffusa* Lam. (Diffuse Knapweed) in British Columbia, Montana, Oregon and Washington (Winston et al. 2012). Combinations of several agents, but not necessarily individual species, are helping control Spotted Knapweed in the West (Winston et al. 2014). The outbreak of *Larinus* spp. we observed at McEnteer may have helped reduce seed set and subsequent seedling recruitment of the Spotted Knapweed there in 2018. However, we did not observe large numbers of weevils in 2019 (Table 6) despite continued low seed production that year. Thus, it is not clear how effective *Larinus* spp. might be at controlling Spotted Knapweed in the Northeast. No studies have quantified seed reduction by flower head-infesting insects in Meadow Knapweed, and it is unclear how effective they would be given the much larger flower heads of Meadow Knapweed compared to Spotted Knapweed (Woods et al. 2008). For example, we counted a maximum of 48 seeds in uninfested flower heads of Spotted Knapweed versus 95 seeds for Meadow Knapweed (data not shown).

The survey data we have presented here add to the natural history of these emerging invasive species of the northeastern United States. Incorporation of these data into demographic population models will help us develop control recommendations for land managers and growers dealing with Spotted Knapweed and Meadow Knapweed.

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