Weed Science

www.cambridge.org/wsc

Research Article

Cite this article: McKenzie-Gopsill A, Nyiraneza J, Arseneault H, Lynch D, Fraser T (2025). Weed seedbank community structure's response to land-use intensity and its relationships to soil properties in Atlantic Canada. Weed Sci. **73**(e58), 1–11. doi: 10.1017/wsc.2025.10025

Received: 10 February 2025
Revised: 23 April 2025
Accepted: 9 May 2025

Associate Editor:
John M. Wallace, Penn State University

Keywords:
Nematode; potato; soil health; weed suppression; weed-suppressive soil

Corresponding author:
Andrew McKenzie-Gopsill;
Email: andrew.mckenzie-gopsill@agr.gc.ca

Weed seedbank community structure's response to land-use intensity and its relationships to soil properties in Atlantic Canada

Andrew McKenzie-Gopsill[1], Judith Nyiraneza[1], Hannah Arseneault[2], Derek Lynch[3] and Tandra Fraser[1]

[1]Research Scientist, Charlottetown Research and Development Centre, Agriculture and Agri-Food Canada, Charlottetown, PE C1A 4N6, Canada; [2]Graduate Student, Charlottetown Research and Development Centre, Agriculture and Agri-Food Canada, Charlottetown, PE C1A 4N6, Canada and [3]Department of Plant, Food and Environmental Sciences, Dalhousie University, Truro, NS B2N 5E3, Canada

Abstract

A diversity of management and environmental factors influence weed seedbank community composition, yet the conditions under which each of these factors is an important driver of the weed seedbank are poorly understood. To investigate this relationship, we used a series of univariate and multivariate analyses to test associations between soil health, nematode community composition parameters, and the composition of the weed seedbank at 59 agricultural sites in the Prince Edward Island Soil Quality Monitoring (PEI SQM) Network spanning a range of land-use intensities and using potato (*Solanum tuberosum* L.) production systems as a case study. Land-use intensity is a nonstandard term that refers to increasing agricultural activity, including tillage and use of synthetic inputs to sustain high crop yield. Sites were classified into low, medium, and high land-use intensity categories based on frequency of potato cultivation in the past 10 yr. A total of 36 different weed species were found across all sites, and while neither seedbank density nor species richness was influenced by land-use intensity, community assemblage was. Seedbank communities at low land-use intensity sites were largely associated with grass weeds and other weakly competitive species, positively correlated with soil CO_2 respiration and nematode community richness and diversity, and negatively correlated with the carbon to nitrogen ratio. In contrast, seedbank communities at medium and high land-use intensity sites were similar and composed of many highly competitive weedy species and correlated with the frequency of potato in the rotation and soil N and K, two commonly used soil fertility inputs. The absence of common agricultural weed species at low land-use intensity sites filtered by soil edaphic factors and abundance of neutral species despite past history of annual cropping suggest that these sites are not refuges for these species and may present a template for the design of weed seed–suppressive soils.

Introduction

Potato (*Solanum tuberosum* L.) production is highly tillage intensive and characterized by high levels of soil disturbance during field preparation and planting and soil erosion postharvest. These practices are associated with declines in soil organic matter and increased soil bacterial biomass in addition to decreased density of many weed seed predators, including fungi, Collembola, and earthworms (Boiteau et al. 2014; Nyiraneza et al. 2017). A shift away from potato production and increased rotation length from 2 to 4 yr can reverse many declines in soil biological activity in as a little as 4 yr (Nelson et al. 2009). In Canada, the Atlantic provinces of New Brunswick and Prince Edward Island are major potato production centers accounting for 35% of total Canadian harvested potato acreage (Agriculture and Agri-Food Canada 2023). Across this region, potatoes are typically grown on a 2-yr rotation of small grains followed by potatoes or a 3-yr rotation of small grains followed by forage followed by potatoes. Herbicide use in this rotation is highly dependent on crop, with chemical weed management used in potato (84%) or cereal (67%) and rarely on forages (Thomas et al. 1994). Tillage is used throughout this rotation, with limited implementation of conservation tillage practices across the region and soil often left bare through the winter. Despite the diversity of management practices employed across this rotation, producers have limited chemical weed management options (Ganie et al. 2023), and herbicide resistance is an increasing challenge (McKenzie-Gopsill et al. 2020). Seedbank management and improved predictability of weed species occurrence and persistence may provide producers an additional tool for improving sustainability of weed management in potato production systems.

The weed seedbank community is shaped by a combination of environmental factors and long-term management practices. The seedbank represents the seed soil reservoir, buffering against local extinction events and facilitating new and reoccurring weed infestations in annual cropping systems (Cousens and Mortimer 1995). The persistence of weed seeds varies across species due to inherent differences in seed longevity and their interaction with soil edaphic factors. Many soil factors directly influence the biological activity of soil micro- and macroorganisms, which can serve as weed seed predators, yet few studies have sought linkages between soil biological activity and weed seedbank community structure. A greater understanding of how soil biological activity influences seedbank structure and the interactions with management practices may offer a framework for manipulating the seedbank and development of weed seed–suppressive soils (Kremer and Li 2003).

The weed seedbank is considered a better indicator of the long-term impact of management than in-season weed populations (Hawes et al. 2010), yet previous efforts to link species occurrences to abiotic and biotic factors have been largely mixed. At broad geographic scales, climatic conditions, including elevation (Nowak et al. 2015) and maximum and minimum temperatures during the growing season, tend to be the primary drivers of weed seedbank community composition (Schwartz et al. 2015; Smith et al. 2018; Young et al. 2013). In comparison, many management practices that operate at the local scale, including crop rotation, frequency of herbicide use, and use of herbicide-tolerant crops (Schwartz et al. 2015), have a more limited ability to alter weed seedbank composition due to the seedbank's buffering capacity from multiple seasons' seed rain (Plue et al. 2021). However, there are several ways in which crop management may influence seedbank composition. For example, as tillage depth and frequency increases, there is a shift toward a more uniform seedbank throughout the plow layer, increasing the stochasticity of emerged weed populations (Carter and Ivany 2006). Further, organic systems, which are often reliant on tillage and cultivation for weed management, tend to have a larger and more species-diverse seedbanks compared with conventional systems, due to reduced weed control efficacy (José-María and Sans 2011). As such, this presents the challenge to predicting weed infestations in any given year in potato rotations when considering the primary management practices utilized are tillage, cultivation, and infrequent herbicide use.

Recent studies at smaller spatial scales have begun to demonstrate the importance of local variation in soil edaphic factors for shaping the seedbank community and could improve our ability to predict weed infestations in potato (Lowry et al. 2021; Smith et al. 2018). For example, soil pH, moisture, and C/N are important for explaining seedbank community structure within USDA hardiness zones on organic vegetable and grain farms in the northeastern United States (Smith et al. 2018). Similarly, soil texture and pH accounted for more of the variation in seedbanks in northeastern India than did geographic region or tillage intensity (Lowry et al. 2021). These soil edaphic factors dictate water-holding capacity and, through their interaction with local climatic conditions, tend to be the primary determinants of weed species establishment, growth, fecundity, and seedbank persistence for many species (Davis et al. 2005; Long et al. 2009; Pakeman et al. 2012; Young et al. 2013). The activity of soil micro- and macroorganisms, which can be effective seed consumers and drive microbial decay and predation of weed seeds, are also influenced by soil water-holding capacity, soil pH, and soil nutrient cycling and may arrest or hasten declines in seedbank density (Chee-Sandford et al. 2006; Davis et al. 2008). Seed persistence can increase in soils with higher pH and lower C/N (Pakeman et al. 2012) due to shifts in the microbial community from fungal dominance to bacterial dominance. This may exclude various saprotrophic fungi responsible for weed seed mortality (Wagner and Mirschunas 2008). However, increased biological activity of soil under high organic matter and low C/N can promote increased microbial activity and growth of weed-suppressive soil bacteria (Kremer and Li 2003) and drive species-specific declines in the weed seedbank (De Cauwer et al. 2011). In addition, nematode communities with degraded channel (CI) and enrichment indices (EI) have been associated with increased weed pressure and decreased weed seed predation (Wang et al. 2022). Nematode communities can be reliable indicators of soil food web structure and connectivity (Ferris 2010), and their presence and feeding behavior can influence bacterial and fungal populations (Djigal et al. 2004; Kane et al. 2022). The CI and EI measure trophic connections in the soil food web and resource availability and cycling, respectively, and can be manipulated through changes in agronomic practices (Puissant et al. 2021). Despite the linkages between land-use intensity factors that affect soil biological activity and seeds in the weed seedbank, these soil edaphic factors have not been considered in past models to predict weed seedbank community structure. Further, manipulating nitrogen availability through high carbon inputs and changes in soil microbial activity can select against nitrophilic and highly competitive weed communities such as common lambsquarters (*Chenopodium album* L.) and redroot pigweed (*Amaranthus retroflexus* L.) (Gannett et al. 2024a, 2024b). Therefore, improvements to our understanding of how soil biology relates to weed seedbank community composition can improve our ability to predict species occurrences in the seedbank and provide a template for selecting management practices that create weed seed–suppressive soil conditions.

In response to intensifying soil erosion, the Prince Edward Island Department of Agriculture established the Prince Edward Island Soil Quality Monitoring (PEI SQM) Network in 1998 to determine and report on changes in soil health over time (Arseneault et al. 2024; Nyiraneza et al. 2017; Uwituze et al. 2022). This long-term network includes sites with a variety of tillage intensities and frequencies; crop rotations, including those with and without potato; and agronomic practices. The PEI SQM Network has and continues to provide valuable current and historical information and serves as a resource for the continued monitoring of soil health metrics across the province, yet it has lacked data on the weed seedbank. Following the most recent sampling regime of a subset of the PEI SQM Network (Arseneault et al. 2024), this yielded us the opportunity to ask whether we could provide a greater understanding of how management and soil edaphic factors shape weed seedbank community structure. Further, we sought to determine conditions under which management practices versus soil edaphic factors have a greater association with the weed seedbank. We hypothesized that the relative importance of soil biological factors would be greater at low land-use intensity sites, whereas the relative importance of management practices would be greater at medium and high land-use intensity sites for shaping the weed seedbank community. It is through an improved holistic understanding of relationships between management and soil edaphic factors and the conditions under which these factors influence seedbank community composition that we can

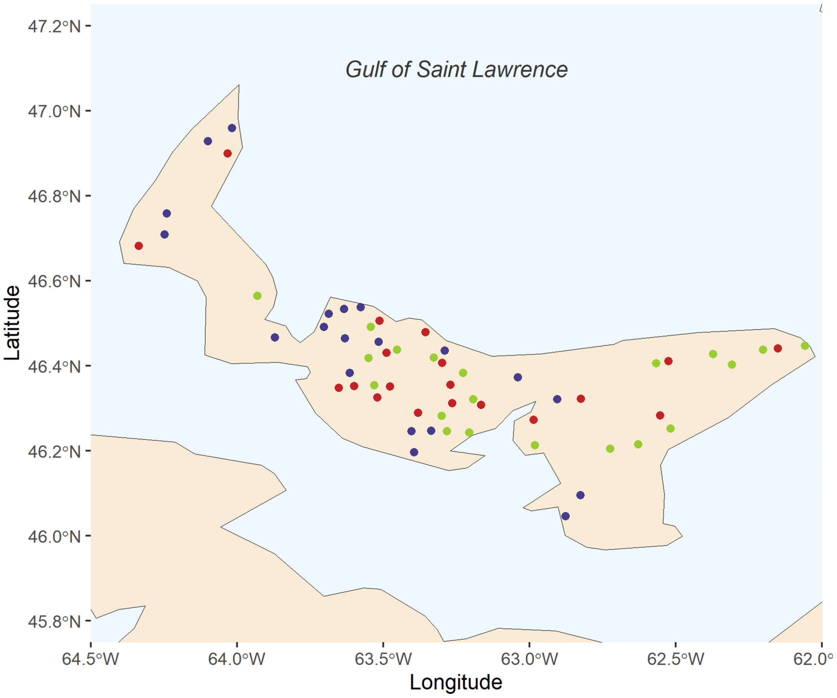

Figure 1. Map of sampling locations across Prince Edward Island, Canada, from the PEI Soil Quality Monitoring (PEI SQM) Network. Sites are colored according to land-use intensity: red, low land-use intensity; green, medium land-use intensity; blue, high land-use intensity. Locations are approximate to ensure anonymity of landowners.

improve the sustainability of weed management in potato production by laying the framework for the development of weed seed–suppressive soils.

Materials and Methods

Site Selection and Soil Chemical and Biological Analysis

Here, we provide a short description of site selection, soil collection, and soil chemical and biological analyses. For a full description, see Arseneault et al. (2024). The geography of Prince Edward Island is relatively uniform, with rolling hills and minimal changes in elevation (0 to 140 m above sea level) and soils in the Podzolic and Spodsol soil orders, which are sandy and acidic, with low nutrient content (Nyiraneza et al. 2017). Prince Edward Island has a humid continental climate that is moderated by its location in the Gulf of Saint Lawrence, with annual mean precipitation of ~1,000 mm and maximum and minimum temperatures of 19 and −8 C, respectively. To determine how weed seedbank communities were impacted by land-use intensity and soil edaphic and biological factors across this relatively uniform climate and geography, 59 sites were selected (29 sites in 2018 and 30 sites in 2019) from the PEI SQM Network (Figure 1). The PEI SQM Network was established in 1998 by the PEI Department of Agriculture to monitor changes in soil quality and health and includes 232 sample locations randomized from a 4 by 4 km provincial grid. All sites were classified into low (no potato production in the last 10 yr), medium (no potato production in the last 4 yr), and high land-use (potato production in the last 4 yr) intensity based on the frequency of potatoes in rotation in the previous 10 yr (see Supplementary Figure S1 for cropping history of the previous 20 yr). Potato production can involve more than five soil disturbance events in a single growing season. Therefore, 10 sites per land-use intensity level were randomly selected to capture a wide range of land-use intensities, a diversity of management practices, and differences in soil carbon due to soil disturbance. Due to site access limitations, only nine sites classified as high land-use intensity were sampled in 2018. Land-use intensity is a nonstandard term but is defined here as increasing agricultural intensification, including use of tillage, synthetic fertilizers and pesticides, and reduced cropping system diversity to sustain higher crop yield and production (Postma-Blaauw et al. 2012). Low land-use intensity sites were managed and unmanaged pastures, forages, grass hedgerows, or forested hedgerows. Medium land-use intensity sites were small grains, grass–legume forage mixtures, soybean [*Glycine max* (L.) Merr.], or corn (*Zea mays* L.). High land-use intensity sites were potato production or a potato rotation of small grains, followed by forage, followed by potato.

Data Collection

To investigate relationships between management practices, soil edaphic factors, metrics of soil biological activity, and weed seedbanks across land-use intensity sites, soil samples were collected at each centrally georeferenced point from the 59 sites across the PEI SQM Network. Four additional subsamples were then collected from each site—one each 20 m to the north, east, south, and west of the central point. Sampling was conducted in mid-July to early August in each year. At this stage in the season, annual weed recruitment would have progressed at each site, yet no new seed set is likely to have occurred. At each of the five sampling points, eight soil cores (0-15 cm depth, 5-cm diameter, total volume of 2,356 cm^3 per subsample) were collected and homogenized, resulting in five samples per field. Samples were divided into half fresh soil for nematode and seedbank analysis and half air-dried and sieved to <2 mm for soil chemical analysis.

Soil Analysis

For a full description of soil chemical analysis, see Arseneault et al. (2024). Briefly, soil pH was determined on air-dried soils using a 1:1 soil:water ratio. Soil nutrients were extracted using the Mehlich III protocol (Mehlich 1984) and quantified by inductively coupled plasma mass spectrometry (820 MS ICPMS; Varian Medical Systems, Palo Alto, CA, USA). Total C and N were determined by combustion using a VarioMAX CN Elementar analyzer (Elementar American, Mt Laurel, NJ, USA). Soil CO_2 respiration following rewetting was determined on 2-mm-sieved and rewet soils after a 4-d incubation period at 25 C by measuring headspace CO_2 in a gas analyzer and was used as a proxy for soil CO_2 respiration (LI-830 and LI-850, Li-Cor Biosciences, Lincoln, NE, USA; Haney and Haney 2010). NO_3/NH_4 was measured in soil extracts with 1 M KCl on a Lachat Quik Chem 8500 Flow Injection Analyzer (Hach, London, ON, Canada).

Nematode Community Analysis

Nematodes were extracted from 100 g of fresh soil using the Cobbs sieving and decanting method and stored at 4 C until identification (Caveness and Jensen 1955; Freckman et al. 1975). Total nematodes in the samples were counted live on an inverted microscope (Zeiss Primovert, Zeiss, Oberkochen, Germany) at 40× to 100× magnification. The first 100 encountered nematodes per sample were identified to family level and adjusted to reflect relative abundance in 100 g of dried soil. Nematode community analysis of this study site was previously published by Arseneault et al. (2024). Subsequently, the following indices of nematode community structure were calculated using Nematode Joint Indicator Analysis (Sieriebriennikov et al. 2014): maturity index, which includes free-living nematodes with colonizer-persister (cp) values of 1 to 5; maturity index 2-5, which includes only free-living nematodes with cp 2 to 5; Sigma maturity index, which includes all nematodes; the CI, which measures the contribution of fungi to decomposition in the soil food web; the basal index, which measures the abundance of nematodes tolerant of soil disturbance; the EI, which indicates the presence of opportunistic nematodes; and the structure index, which indicates the presence of nematodes sensitive to soil disturbance.

Seedbank Analysis

Before analysis, soil was coald stratified at 4 C for 6 mo to break dormancy. The volume of remaining fresh soil (500 to 750 cm^3) was measured and spread out on plastic trays filled with sterile sand and placed in the greenhouse. Greenhouse conditions were set to mimic the outside environment during the growing season and consisted of a 16-h photoperiod and temperature cycles of 20/15 C. Natural sunlight was supplemented with high-pressure sodium lights set to deliver 400 μmol m^{-2} s^{-1} at canopy height when natural light dropped below 1,500 μmol m^{-2} s^{-1}. Trays were watered daily and monitored for seedling emergence. Emerged seedlings were identified to species, counted, and removed to determine the total number of readily germinable seeds per sample. Seedlings that could not be immediately identified were transplanted to larger pots and maintained under the same greenhouse conditions until they contained enough anatomical features to be identified to species. All emerged seedlings in a sample that were not the crop planted that year at the site were considered weeds. When seedling emergence ceased, samples were air-dried before being stirred and rewatered to stimulate germination. The process of drying, mixing, and rewetting was repeated across ~ 8 mo until no further seedling emergence occurred (McKenzie-Gopsill et al. 2024).

Statistical Analysis

All data analysis was conducted in the R software environment (RStudio v. 4.3.2; R Core Team 2023). Before analysis, a number of measures of species abundance and diversity were determined to broadly describe the weed seedbank community. First, total weed seedling density representing the readily germinable fraction of the seedbank was calculated as the sum of all emerged seedlings in a sample and adjusted based on volume of soil. Values were then expressed as readily germinable seeds per square meter in the rhizosphere based on the area sampled by the soil auger. We then calculated a series of diversity indices to quantify community structure in each sample. Species richness was determined as the total number of unique species within a sample, Shannon diversity as $H' = -\sum p_i^2(\log p_i)$, where p_i is the proportion of species i in a sample, and Pielou's evenness as $E = H'/\ln(\text{richness})$. All data were averaged across subsamples within each site for subsequent analysis.

To account for management practices, we counted the frequency of the following crop groups over the previous 20 yr in each field using the following categories: cereal, corn, forage, grass hedgerow, pasture, potato, soybean, wooded hedgerow, and other (Supplementary Figure S1). Cereals were mostly spring barley (*Hordeum vulgare* L.) but also included spring wheat (*Triticum aestivum* L.). Forage and pastures included various legume and grass species, including but not limited to red clover (*Trifolium pratense* L.), alfalfa (*Medicago sativa* L.), and timothy (*Phleum pratense* L.), and only differed in their use; pastures were grazed, whereas forages were cut. Crops included in the other category were other root crops besides potato, including carrots [*Daucus carota* ssp. *sativus* (Hoffm.) Arcang.] and turnip (*Brassica rapa* L.), as well as canola (*Brassica napus* L.). To evaluate the effects of land-use intensity on weed seedbank community metrics, including seedbank density, species richness, Shannon diversity, and Pielou's evenness, linear mixed-effects models were constructed using the *lme* function in the R package NLME (Pinheiro et al. 2023). Two sets of linear contrast statements were then constructed to compare weed seedbank density and diversity across land-use intensity sites. First, low land-use intensity sites were compared with medium and high land-use intensity sites, and second, medium land-use intensity sites were compared with high land-use intensity sites. Model assumptions were evaluated by visual inspection of residual plots.

To investigate relationships between weed seedbank community structure, management practices, and soil edaphic factors across the PEI SQM Network, we used the approach of Smith et al. (2018) and Lowry et al. (2021). First, nonmetric multidimensional scaling (NMDS) was performed using the *metanmds* function in the R package VEGAN (Oksanen et al. 2022) with 250 runs to initially characterize weed seedbank community structure across land-use intensity. Before NMDS analysis, rare species, defined as those with fewer than five occurrences, were removed from the dataset. Remaining species abundance values were $\log(x+1)$ transformed and used to generate a Bray-Curtis dissimilarity matrix. The number of dimensions was determined by comparing NMDS runs and evaluating when decreasing the number of dimensions from six to one no longer reduced stress by greater than five units (McCune et al. 2002).

Table 1. Variation in weed seedbank community metrics across land-use intensity at sites in the Prince Edward Island Soil Quality Monitoring Network (PEI SQM): *F*-statistics and P-values from the ANOVA and contrast statements, as well as the least-squares mean ± SE of low, medium, and high land-use intensity, are shown.

	Density (seeds m^{-2})	Species richness	Shannon diversity	Pielou's evenness
Land-use intensity	$F(2, 55) = 0.61$, $P = 0.547$	$F(2, 55) = 1.91$, $P = 0.158$	$F(2, 55) = 5.14$, $P = 0.009$	$F(2, 55) = 5.00$, $P = 0.010$
Contrasts				
Low vs. medium + high	$F(1, 55) = 0.19$, $P = 0.666$	$F(1, 55) = 2.70$, $P = 0.106$	$F(1, 55) = 4.13$, $P = 0.047$	$F(1, 55) = 1.37$, $P = 0.247$
Medium vs. high	$F(1, 55) = 0.96$, $P = 0.332$	$F(1, 55) = 1.75$, $P = 0.191$	$F(1, 55) = 7.43$, $P = 0.009$	$F(1, 55) = 10.22$, $P = 0.002$
LS means				
Low	16,684 ± 2,800	3.33 ± 0.33	0.72 ± 0.08	0.59 ± 0.04
Medium	16,302 ± 2,742	4.23 ± 0.33	1.04 ± 0.08	0.74 ± 0.04
High	21,523 ± 2,994	3.68 ± 0.36	0.76 ± 0.08	0.56 ± 0.05

To determine whether weed seedbank communities differed by land-use intensity across PEI, we used permutational multivariate analysis of variance (PerMANOVA) using the *adonis2* function in the R package VEGAN (Oksanen et al. 2022) with 999 permutations. Indicator species analysis was used to determine which weed species were associated with different levels of land-use intensity with the *multipatt* function in the R package INDICSPECIES (De Cáceres et al. 2023). Indicator values (IndVal) were calculated according to Dufrêne and Legendre (1997) and represent the specificity and fidelity of a particular species to a level of land-use intensity. IndVal ranges from 0 to 1, where 1 indicates perfect association with a group. The significance of each association between land-use intensity and specific species was determined with a Monte Carlo procedure (999 permutations).

We used Pearson's correlation coefficients to investigate the strength and directionality of relationships between management, soil edaphic factors, nematode community metrics, and all measures of weed seedbank community structure, including NMDS axes, seedbank density, species richness, Shannon diversity, and Pielou's evenness. Following the advice of Smith et al. (2018) and Lowry et al. (2021), we considered values greater than 0.2 to have a strong correlation with weed seedbank community structure metrics. The relative importance of relationships was further investigated with partial least-squares regression (PLSR) using the *plsr* function in the R package PLS (Liland et al. 2023). Response variables were the two NMDS axis scores, weed seedbank density, Shannon diversity, and evenness. All management data, soil edaphic factors, and nematode community metrics, including soil pH, Mg, K, Ca, B, Cu, Zn, P, C%, N%, soil CO_2 respiration, NO_3, C/N, nematode maturity index, maturity index 2-5, sigma maturity index, CI, basal index, EI, the abundances of plant parasites, fungivores, bacterivores, predators nematodes, nematode richness, nematode Shannon diversity, and total nematode abundance, were included as predictor variables in the initial model. The number of components to retain in the final models was determined according to Carrascal et al. (2009), whereby only components that explained >5% of variance were retained. Predictor variables with variable importance values >0.8 were retained in the final models. Model predictive power was determined with *K*-fold cross validation ($K = 10$).

Results and Discussion

Weed Seedbank Community Differed by Land-Use Intensity

A total of 36 different weed species were found in seedbank samples from the PEI SQM Network. Overall, the 10 most abundant species were red fescue (*Festuca rubra* L.; 25%), low cudweed (*Gnaphalium uliginosum* L.; 10%), wormseed mustard (*Erysimum cheiranthoides* L.; 9%), broadleaf plantain (*Plantago major* L.; 7%), mouse-ear chickweed [*Cerastium fontanum* Baumg. ssp. *vulgare* (Hartm.) Greuter & Burdet; 6%], field parsley (*Aphanes arvensis* L.; 5%), lesser stitchwort (*Stellaria graminea* L.; 5%), common evening primrose (*Oenothera biennis* L.; 2%), yellow woodsorrel (*Oxalis stricta* L.; 2%), and annual bluegrass (*Poa annua* L.; 2%) (Supplementary Table S1). There was wide variation in total weed seedbank density, which ranged from 1,019 to 79,112 readily germinable seeds m^{-2}, but mean seedbank density did not differ across land-use intensity ($F(2, 55) = 0.61$, $P = 0.547$; Table 1). Mean seedbank density was 16,684, 16,302, and 21,523 seeds m^{-2} for low, medium, and high land-use intensity sites, respectively (Table 1; Figure 2). Species richness also did not differ by land-use intensity ($F(2, 55) = 1.91$, $P = 0.158$) and ranged from 1 to 8 across all samples with a mean of 3.74 (Table 1). Diversity as measured by the Shannon diversity index and Pielou's evenness was highly variable and ranged from 0 to 1.57 and 0 to 1 across all sites, respectively. Despite this variability, both Shannon diversity ($F(2, 55) = 5.14$, $P = 0.009$) and Pielou's evenness ($F(2, 55) = 5.00$, $P = 0.010$) differed across land-use intensity. Contrast statements showed that Shannon diversity was lowest at low land-use intensity sites ($F(1, 55) = 4.13$, $P = 0.047$) and highest at medium land-use intensity sites ($F(1, 55) = 7.43$, $P = 0.009$; Table 1). Similarly, Pielou's evenness was highest at the medium land-use intensity sites ($F(1, 55) = 10.22$, $P = 0.002$; Table 1).

Thirty-two species were found in the low land-use intensity samples, with the most common species being *F. rubra* (27%), followed by *E. cheiranthoides* (15%) and *P. major* (8%; Figure 2). *Festuca rubra* was also the most common species in medium (24%), and high land-use intensity samples (25%; Figure 2) and was found in all but eight samples overall. A total of 30 species were found in the medium land-use intensity samples, with *G. uliginosum* (11%) and *E. cheiranthoides* (8%) being the second and third most common (Figure 2). A total of 31 species were found in the high land-use intensity samples, with *G. uliginosum* also being the second most common species (14%), followed by *C. fontanum* ssp. *vulgare* (11%; Figure 2). Many common annual species found in medium and high land-use intensity sites, including *A. retroflexus*, horseweed [*Erigeron canadensis* L.; syn.: *Conyza canadensis* (L.) Cronquist], *C. album*, wild buckwheat [*Fallopia convolvulus* (L.) Á. Löve; syn.: *Polygonum convolvulus* L. var. *convolvulus*], scentless chamomile [*Matricaria inodora* L.; syn.: *Tripleurospermum perforatum* (Mérat) M. Lainz], green foxtail [*Setaria viridis* (L.) P. Beauv.], wild mustard (*Sinapis arvensis* L.), and corn speedwell (*Veronica arvensis* L.), were either absent or represented <1% of the seedbank at low land-use intensity sites. A greater number of grass seeds representing 39% of the total seedbank was found at the low land-use intensity sites (Figure 2) compared with medium (26%; Figure 2) or high (26%;

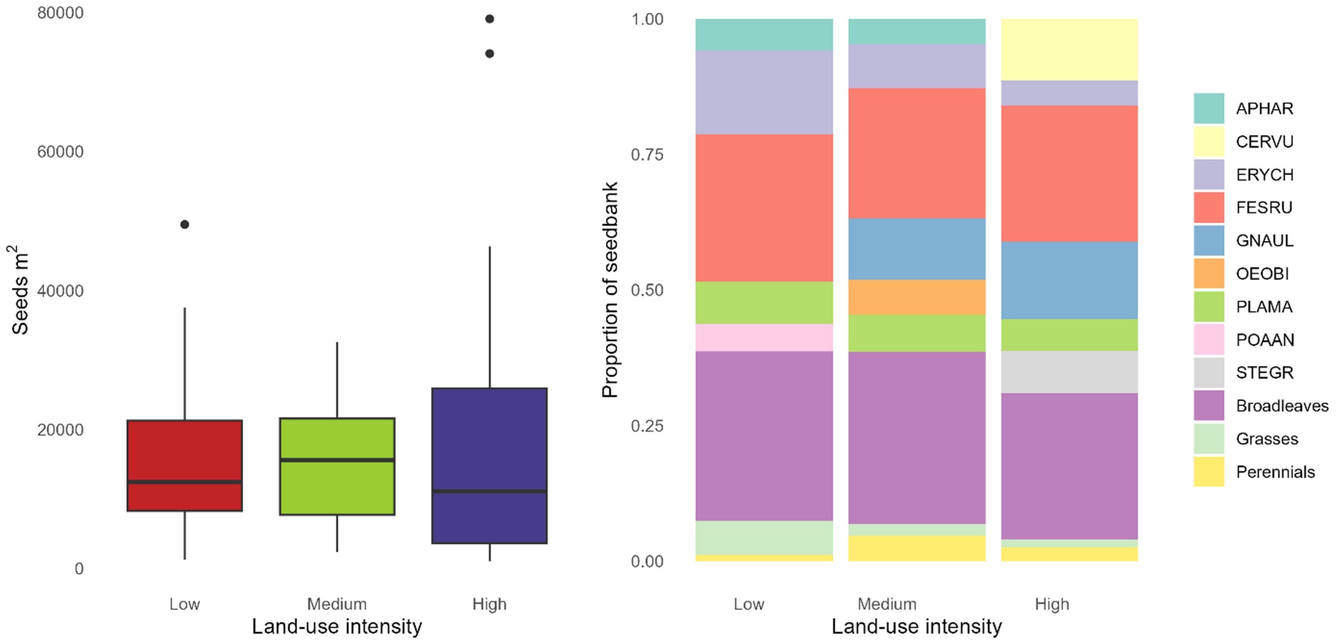

Figure 2. Total readily germinable seedbank density (seeds m^{-2}) (left) and species' proportion of the seedbank (right) at low, medium, and high land-use intensity sites. Species with <10% occurrence were grouped into annual broadleaves, annual grasses, or perennials according to their life histories. See legend for species' color descriptions. Species are listed by EPPO code.

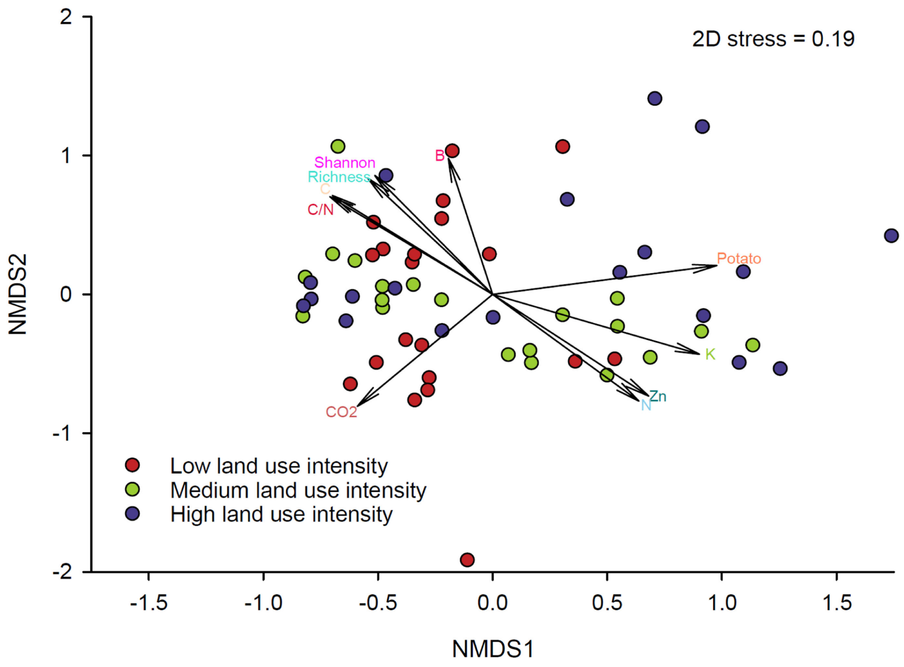

Figure 3. Biplot of nonmetric multidimensional scaling (NMDS1 and NMDS2) scores for sites, NMDS two-dimensional stress (0.19), $R^2 = 0.73$, *F*(1, 1709) = 4,645.61, $P \leq 0.0001$. Environmental vectors for management, soil edaphic factors, crop type in sampling year, and nematode community metrics with a significant ($P \leq 0.0001$) correlation to NMDS scores are shown. Note: Richness, and Shannon refer to the nematode community. See the legend for a description of the color codes.

Figure 2) land-use intensity sites. In contrast, low land-use intensity sites had fewer readily germinable seeds of perennial species (1%; Figure 2) compared with medium (5%; Figure 2) or high land-use (3%; Figure 2) sites.

The NMDS ordination resulted in a two-dimensional solution that provided a good fit (stress = 0.19, $R^2 = 0.73$, *F*(1, 1709) = 4,645.61, $P \leq 0.0001$) to the distance matrix (Figure 3). Low land-use intensity samples formed two groups with either positive or negative NMDS2 scores, whereas medium and high land-use intensity formed one group along the entire NMDS1 axis (Figure 3). PerMANOVA indicated weed seedbank communities differed by land-use intensity (*F*(2, 56) = 2.19, P = 0.003) and indicator species analysis identified several species associated with each community (Supplementary Table S2). Grass species, including redtop (*Agrostis gigantea* Roth; IndVal = 0.51, P = 0.036), smooth crabgrass [*Digitaria ischaemum* (Schreb.)

Table 2. Pearson's correlation between nonmetric multidimensional scaling (NMDS) scores and field management, weed seedbank community metrics, nematode community metrics, and soil edaphic factors.[a]

	NMDS1		NMDS2	
Variable	r	R^2	r	R^2
Management				
Frequency of potato	0.42	0.17	0.19	0.04
Frequency of pasture	−0.17	0.03	−0.16	0.03
Frequency of cereal	0.28	0.08	0.02	0.00
Frequency of corn	0.02	0.00	0.02	0.00
Frequency of soybean	0.06	0.00	0.06	0.00
Frequency of wooded hedgerow	−0.16	0.03	−0.10	0.01
Frequency of grass hedgerow	0.01	0.00	−0.05	0.00
Frequency of other crop	0.04	0.00	0.02	0.00
Frequency of forage	−0.01	0.00	0.07	0.01
Weed community				
Density	−0.22	0.05	−0.21	0.04
Species richness	−0.47	**0.22**	−0.14	0.02
Shannon	0.08	0.01	0.32	0.10
Evenness	−0.47	**0.22**	−0.1	0.00
Nematode community				
Maturity index	0.12	0.01	−0.13	0.02
Maturity index 2-5	0.05	0.00	−0.09	0.01
Sigma maturity index	0.02	0.00	−0.09	0.01
Channel index	0.25	0.07	−0.14	0.02
Basal index	0.01	0.00	0.06	0.00
Enrichment index	−0.05	0.00	0.08	0.01
Structure index	0.01	0.00	−0.09	0.01
Plant parasites	−0.05	0.00	−0.15	0.02
Fungivores	0.09	0.01	0.05	0.00
Bacterivores	−0.04	0.00	0.10	0.01
Predators	−0.05	0.00	0.02	0.00
Richness	−0.24	0.06	0.28	0.08
Shannon	−0.29	0.09	0.55	**0.30**
Total	−0.23	0.05	0.30	0.09
Edaphic				
pH	0.26	0.07	0.13	0.02
Mg	0.02	0.00	−0.10	0.01
K	0.40	0.16	−0.16	0.03
Ca	0.26	0.07	0.01	0.00
B	−0.06	0	0.37	0.14
Cu	0.23	0.05	−0.05	0.00
Zn	0.41	0.17	−0.49	**0.24**
P	−0.07	0.00	0.24	0.06
C%	−0.58	**0.33**	0.55	**0.30**
N%	0.45	**0.2**	−0.61	**0.37**
C/N	−0.59	**0.35**	0.55	**0.31**
CO_2	−0.28	0.08	−0.29	0.09
NO_3	−0.08	0.01	0.30	0.09

[a] Bold values indicate strong ($R^2 > 0.2$) Pearson's correlation.

Schreb. ex Muhl.; IndVal = 0.48, P = 0.022], and yellow foxtail [*Setaria pumila* (Poir.) Roem. & Schult. IndVal = 0.42, P = 0.039], were indicative of low land-use intensity sites (Supplementary Table S2) and were rarely found in medium and high land-use intensity samples (Supplementary Table S2). *Poa annua* (IndVal = 0.59, P = 0.016) was associated with low or medium sites and was found at only one high land-use intensity site (Supplementary Table S2). Other species indicative of medium land-use intensity sites included annual fleabane [*Erigeron annuus* (L.) Pers.; IndVal = 0.51, P = 0.005] and creeping buttercup (*Ranunculus repens* L.; IndVal = 0.53, P = 0.015), which both represented on average 2% of seedbank samples at these sites (Supplementary Table S2). *Chenopodium album* (IndVal = 0.53, P = 0.017), which was absent from low land-use intensity sites, was indicative of both medium and high land-use intensity sites, whereas *M. inodora* (IndVal = 0.46, P = 0.006) was the only species associated with high land-use intensity sites (Supplementary Table S2). These findings demonstrate that weed seedbank communities across land-use intensity sites in the PEI SQM Network are distinct, with several key species being indicative of low, medium, and high land-use intensity.

Relationship between Weed Seedbank Community Structure, Weed Species, and Soil Edaphic Factors

There was little correlation between soil edaphic factors and either the first or second NMDS axis across sites (Table 2). Of soil edaphic factors, only C% (r = −0.58, R^2 = 0.33), N% (r = 0.45, R^2 = 0.20), and the C/N (r = −0.59, R^2 = 0.35) were correlated to the first NMDS axis and Zn (r = −0.49, R^2 = 0.24), C% (r = 0.55, R^2 = 0.3), N% (r = −0.61, R^2 = 0.37), and the C/N (r = 0.55, R^2 = 0.31) with the second NMDS axis (Table 2). Weed seedbank richness and evenness were correlated to the first NMDS axis, whereas the Shannon diversity of the nematode community was correlated to the second NMDS axis. No other weed or nematode community metric or any management factor was strongly correlated to either NMDS axis (Table 2).

As simple correlations can mask complex interactions, PLSR models were used to investigate how variations in soil edaphic factors explained the variation in weed seedbank community metrics. This analysis yielded explanatory models for NMDS1 (75.75%) and NMDS2 (57.90%) with four and two components, respectively. Variables with the strongest loading on the first component of the NMDS1 PLSR model, which accounted for 48.17% of variation, included the C/N (−0.38), C% (−0.38), N% (0.34), Zn (0.34), and the Shannon diversity of the nematode community (−0.32), with a lesser influence of total nematode community abundance (−0.27) and richness (−0.26) and soil K (0.23). Similarly, N% (−0.41), C% (0.39), C/N (0.41), Zn (−0.32), and the Shannon diversity of the nematode community (0.34) had the strongest loading on the first component of the NMDS2 PLSR model followed by the total abundance (0.21) and richness (0.27) of the nematode community.

Soil Biological Activity and Management Practices Both Act to Shape the Seedbank Community

As expected, weed seedbank communities at low land-use intensity sites that were characterized by zero soil disturbance in the previous 5 yr included a high proportion of grass species, such as *P. annua*, *A. gigantea*, *F. rubra*, and *D. ischaemum*. These seedbank communities differed from adjacent agricultural land at medium and high land-use intensity, which included species such as *C. album*, *A. retroflexus*, *M. inodora*, and *F. convolvulus*, which are known to be highly problematic in potato production (McKenzie-Gopsill et al. 2020; Van Wychen 2022). As reported in past studies, soil edaphic factors were important for weed seedbank community composition at local scales in this study, supporting a role for niche-based community assembly rules (Booth and Swanton 2002; Lowry et al. 2021; Smith et al. 2018). Yet while the importance of soil physical properties that affect water-holding capacity for seedbank community composition has been well established (Davis et al. 2005; Long et al. 2009; Pakeman et al. 2012), we show here that soil biological factors, including the species richness and diversity of the nematode community as well as the soil C/N and soil CO_2 respiration, are strong correlates of the weed seedbank and should be considered when attempting to predict weed seedbank community structure. However, as the frequency of potato production at a site increased, the correlation between soil biological factors and weed seedbank community structure decreased in favor of a stronger correlation between the seedbank community and increased soil N and K, two macronutrients often applied at high rates in potato fields. These results support our hypothesis that soil biological factors are important for influencing seedbank structure at low land-use intensity sites, whereas management practices became more important as frequency of potato production increased at medium and high land-use intensity sites.

Grass species were common indicator species of low land-use intensity soils, and their abundances are reflective of the management of these sites as field margins, pastures, grasslands, and hedgerows. The absence of recent soil disturbance at all of these sites in addition to frequent mowing in managed grasslands is known to shift the aboveground weed community toward grass species, which are tolerant of mowing, and perennial species, which depend on vegetative reproduction and a concentration of weed seeds near the soil surface (Scherner et al. 2016; Swanton et al. 2000; Teasdale et al. 2004). These sites were often associated with greater soil CO_2 respiration, yet not with other soil edaphic factors. In contrast, sites with a low proportion of grass seeds were negatively associated with *E. cheiranthoides* and a greater correlation with measures of soil nutrient cycling, including the C/N and nematode richness and diversity. This suggests that these two groups of species form distinct weed seedbank communities correlated to different measures of soil functioning, supporting its filtering role. De Cauwer et al. (2011) similarly found that presence of *P. annua* in the seedbank of an annual crop rotation was associated with decreased soil fertility and low C/N. In the PEI SQM Network, this low C/N may be the result of minimal soil disturbance combined with continuous carbon inputs through management, including mowing of grasslands near agricultural fields and litter accumulation in grass and wooded hedgerows and field margins (Ziter and MacDougall 2013). Repeated mowing, however, can promote soil compaction and shift the plant community in favor of species with deep taproots, such as brassicas, over grasses with more fibrous root systems (Schrama et al. 2013). Indeed, Mayor and Dessaint (1998) observed a similar transition in the weed seedbank from an *P. annua*-dominant community toward shepherd's purse [*Capsella bursa-pastoris* (L.) Medik.], a brassica species closely related to *E. cheiranthoides*, following repeated mowing over 6 yr, and they attributed this to the continuous emergence pattern of *C. bursa-pastoris* compared with *P. annua*, as well as mowing releasing *C. bursa-pastoris* from competition with other weeds. As we failed to detect a strong correlation between management practices and seedbank communities at low land-use intensity sites, this suggest that measures of soil biological functioning play a filtering role on weed seedbank communities when soil disturbance associated with frequent potato production is minimized, which supports our hypothesis.

Weed Seed–Suppressive Soils

While many of the low land-use intensity sites had a history of annual and perennial crop cultivation and therefore an opportunity for problematic weedy species to establish, the absence of species such as *C. album*, *A. retroflexus*, *E. canadensis*, *S. viridis*, *F. convolvulus*, and *S. arvensis* in the seedbank suggests their persistence was dramatically reduced under these environmental and management conditions. This is in contrast to reports by other authors, who have noted the presence of problematic and herbicide-resistant weeds preserved in field margins and hedgerows for decades, with these spaces serving as biological refuges and sources of reintroduction (Boutin et al. 2002; Page et al. 2019). All of these species are ruderal and highly responsive to fertility, have continuous emergence patterns, and are strongly associated with agricultural intensity and inputs, with numerous reports of herbicide resistance worldwide (Heap 2024; Hulme 2023). In addition to many grass species, low land-use intensity sites had a large proportion of low-growing species that are typically not thought to cause yield losses in agricultural systems, including *A. arvensis*, red sand-spurry [*Spergularia rubra* (L.) J. Presl. & C. Presl.], *G. uliginosum*, and creeping thyme [*Thymus praecox* Opiz ssp. *arcticus* (Durand) Jalas]. These species are shade tolerant, relatively low growing, and emerge later in the season (Okusanya and Ungar 1984; Roberts and Neilson 1982), and therefore are unlikely to interfere with crop development. Several authors have recently suggested that weed communities composed of similarly low-growing species with minimal fertility requirements are less detrimental to crop yield and may represent neutral weed communities (Adeux et al. 2019; Esposito et al. 2023a, 2023b). Communities of these low-growing species in conjunction with various grasses may be an example of niche complementarity between weed species at low land-use intensity sites and support other neutral biota in agroecosystems (Franke et al. 2009). Despite many of these species being similarly present at medium and high land-use intensity sites, the weaker role of management filters at low land-use intensity sites as compared with soil biological filters may then select for reduced species diversity in favor of improved trait complementarity and resource capture between a limited species pool at the community level, as predicated by the resource pool diversity hypothesis (Smith et al. 2010). These species may also promote other neutral biota that similarly have little effect on crop production due to varied soil resource requirements. The diversified management filters at medium and high land-use intensity sites, including frequent soil disturbance, herbicide application, and crop rotations, increase the diversity of filters enabling the preservation of species diversity in the seedbank (Adeux et al. 2023; McKenzie-Gopsill et al. 2024). Yet as potato production frequency increases in the rotation and sites move from medium to high land-use intensity, aggressive annual weed species such as *C. album* are favored over neutral weed communities.

At medium and high land-use intensity sites, there was a stronger association between potato frequency in the rotation than soil edaphic factors and the seedbank community, supporting our hypothesis. This included increased frequency of potato production, an indicator of soil disturbance and high land-use intensity, as well as increased soil N and K, two macronutrients often applied in excess in potato production. These sites were also associated with decreased soil enzyme activity and poorly structured and degraded nematode communities, suggesting lower overall biological functioning as the system became more reliant on external inputs (Arseneault et al. 2024; Uwituze et al. 2022). Weed seeds and their seed coats can be a significant carbon food source supporting bacterial and fungal populations, as well as serving as unique microhabitats within the soil profile that provide sites for colonization and protection from predation by bacterivore and fungivore protists and nematodes (Chee-Sandford et al. 2006). Previous studies have shown that greater soil biological activity can enhance soil enzyme activity and the numbers of growth-suppressive bacterial isolates that negatively affect specific weed seedling development (Kremer and Li 2003). Changes in the soil bacterial and fungal community composition can have species-specific effects, promoting or negating weed seed mortality and decay (Davis et al. 2008). Small-seed and persistent species, including *C. album* and *A. retroflexus*, invest more in physical defense mechanisms in their seed coats than chemical defense, and they are therefore more susceptible to microbial decay (Davis et al. 2008). Seedbank persistence of *C. album* and other small-seed species has been negatively correlated to total phospholipid fatty acid content in soil (De Cauwer et al. 2011; Ullrich et al. 2011), which is a common bioindicator of total microbial biomass, supporting the assertion that decreased soil biological activity may increase the persistence and therefore long-term abundance of species such as *C. album* in the seedbank. Further, the presence and abundance of select bacterivore and fungivore nematodes such as those in the Rhabditidae, Cephalobidae, and Aphenlenchoididae families can directly influence bacterial and fungal biomass and activity through their interactions with C and N cycling (Castillo et al. 2017; Kane et al. 2022). Indeed, Arseneault et al. (2024) observed that these nematode families were largely associated with low land-use intensity sites across the PEI SQM Network. The feeding activity of these nematode families could stimulate saprophytic bacteria and/or fungi known to impact weed seeds in a tropic cascade, contributing to declines in seedbank persistence of particular species. Alternatively, the lack of these species may be due to the accumulated or interactive effect of management practices acting as filters not considered in our analysis. Various crop rotations such as planting of spring and winter cereals, which were together considered as cereals here, would select for weed species with alternating emergence and life-history traits (Hald 1999). Further, the inclusion of herbicide-tolerant crops and perennial green manure or pastures (Menalled et al. 2001; Schwartz et al. 2015) at medium land-use intensity sites may have had similar predictive power of the weed seedbank community as soil biological metrics. In addition, the correlative nature of this study limits the ability to directly test these hypotheses, and future studies under controlled conditions are warranted to fully elucidate the filtering role of soil biological activity on the weed seedbank. The absence of these species at sites where soil biological filters are stronger correlates of seedbank structure than potato frequency despite a history of annual crop production, however, provides support for improved soil biological activity creating conditions of weed-suppressive soils.

Here we show that in addition to management practices, soil biological activity as measured by soil CO_2 respiration, soil C/N, and nematode community richness and diversity are correlated to weed seedbank community structure. Together with past studies documenting declines in soil organic matter (Nyiraneza et al. 2017), soil nutrient cycling (Uwituze et al. 2022), and degraded soil structure and food web connectivity (Arseneault et al. 2024) associated with potato production, our results suggest that as potato frequency in a rotation increases, the relative role of soil biological filters for influencing the seedbank community declines. The absence of aggressive weed species and abundance of neutral weeds at sites where soil biological activity was highly correlated to the seedbank community despite a history of annual crop cultivation suggest these soil environments create conditions for selecting for less aggressive weed seedbank communities. Producers could create these soil conditions by selecting management practices such as increased rotation length, reduced soil disturbance throughout the rotation, and inclusion of perennial crops that will decrease persistence of select weedy species by creating weed seed–suppressive soils. By tracking nematode community richness and diversity as well as soil C/N and soil CO_2 respiration, potato producers could predict when weedy species are depleted in the seedbank. Further, weed seed suppresive soils could be used to reduce pressure from herbicide-resistant weeds and other species difficult to control in high soil disturbance production systems such as potato, where herbicide options are limited to improve the sustainability of weed management.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/wsc.2025.10025

Acknowledgments. We are grateful to the PEI Department of Agriculture for access to their Soil Quality Monitoring Program, and in particular to Kyra Stiles and Danny Walker for their assistance in site selection and contacting landowners. We would also like to thank Peter Webb, Lindsay Clairmont, and Danielle Murnaghan for their technical support, and participating landowners for allowing us to collect soil samples on their properties.

Funding statement. Financial support for this work was supplied by Agriculture and Agri-Food Canada (J-001757).

Competing interests. The authors have no relevant financial or non-financial interests to disclose.

References

Adeux G, Rodriguez A, Penato C, Antichi D, Carlesi S, Sbrana M, Bàrberi P, Cordeau S (2023) Long-term cover cropping in tillage-based systems filters weed community phenology: a seedbank analysis. Field Crop Res 291:108769

Adeux G, Vieren E, Carlesi S, Bàrberi P, Munier-Jolain N, Cordeau S (2019) Mitigating crop yield losses through weed diversity. Nat Sustain 2:1018–1026

Agriculture and Agri-Food Canada (2023) Potato Market Information Review 2022–2023. https://agriculture.canada.ca/en/sector/horticulture/reports/potato-market-information-review-2022-2023#a-1-3. Accessed: May 8, 2024

Arseneault H, Lynch DH, Nyiraneza J, Stiles K, Mills A, Fraser T (2024) Soil nematode communities differ across long-term land-use intensities in relation to soil physical, chemical and biological properties. Can J Soil Sci 104:482–495

Boiteau G, Goyer C, Rees HW, Zebarth BJ (2014) Differentiation of potato ecosystems on the basis of relationships among physical, chemical and biological soil parameters. Can J Soil Sci 94:463–476

Booth BD, Swanton CJ (2002) Assembly theory applied to weed communities. Weed Sci 50:2–13

Boutin C, Jobin B, Bélanger L, Choinière L (2002) Plant diversity in three types of hedgerows adjacent to cropfields. Biodivers Conserv 11:1–25

Carrascal LM, Galván I, Gordo O (2009) Partial least squares regression as an alternative to current regression methods used in ecology. Oikos 118: 681–690

Carter MR, Ivany JA (2006) Weed seed bank composition under three long-term tillage regimes on a fine sandy loam in Atlantic Canada. Soil Till Res 90:29–38

Castillo JD, Vivanco JM, Manter DK (2017) Bacterial microbiome and nematode occurrence in different potato agricultural soils. Microb Ecol 74:888–900

Caveness FE, Jensen HJ (1955) Modification of the centrifugal-flotation technique for the isolation and concentration of nematodes and their eggs from soil and plant tissue. P Helm Soc Wash 22:87–89

Chee-Sanford JC, Williams MM, Davis AS, Sims GK (2006) Do microorganisms influence seed-bank dynamics? Weed Sci 54:575–587

Cousens R, Mortimer M (1995) Dynamics of Weed Populations. New York: Cambridge University Press. 348 p

Davis AS, Cardina J, Forcella F, Johnson GA, Kegode G, Lindquist JL, Luschei EC, Renner KA, Sprague CL, Williams MM (2005) Environmental factors affecting seed persistence of annual weeds across the US corn belt. Weed Sci 53:860–868

Davis AS, Schutte BJ, Iannuzzi J, Renner KA (2008) Chemical and physical defense of weed seeds in relation to soil seedbank persistence. Weed Sci 56:676–684

De Cáceres M, Jansen F, Dell N (2023) indicspecies: Relationship between Species and Groups of Sites. R package version 1.7.14. https://cran.r-project.org/web/packages/indicspecies/index.html

De Cauwer B, D'Hose T, Cougnon M, Leroy B, Bulcke R, Reheul D (2011) Impact of the quality of organic amendments on size and composition of the weed seed bank. Weed Res 51:250–260

Djigal D, Brauman A, Diop TA, Chotte JL, Villenave C (2004) Influence of bacterial-feeding nematodes (Cephalobidae) on soil microbial communities during maize growth. Soil Biol Biochem 36:323–331

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Mongr 67:345–366

Esposito M, Cirillo V, De Vita P, Cozzolino E, Maggio A (2023a) Soil nutrition management may preserve non-detrimental weed communities in rainfed winter wheat (*T. aestivum*). Agric Ecosyst Environ 355:108596

Esposito M, Westbrook AS, Maggio A, Cirillo V, DiTommaso A (2023b) Neutral weed communities: the intersection between crop productivity, biodiversity, and weed ecosystem services. Weed Sci 71:301–311

Ferris H (2010) Form and function: metabolic footprints of nematodes in the soil food web. Eur J Soil Biol 46:97–104

Franke AC, Lotz LA, Van Der Burg WJ, Van Overbeek L (2009) The role of arable weed seeds for agroecosystem functioning. Weed Res 49:131–141

Freckman DW, Mankau R, Ferris H (1975) Nematode community structure in desert soils: nematode recovery. J Nematol 7:343

Ganie ZA, Soltani N, McKenzie-Gopsill AG, Felix J, Hutchinson PJ, Dille JA, Sikkema PH (2023) Potential potato yield loss from weed interference in the United States and Canada. Weed Technol 37:21–24

Gannett M, DiTommaso A, Son Y, Sparks JP, Reid MC, Kao-Kniffin J (2024a) Manipulating soil resource availability to alter microbial communities for weed management in agroecosystems. Soil Biol Biochem 17:109492

Gannett MA, Butler-Jones AL, DiTommaso A, Sparks JP, Kao-Kniffin J (2024b) Soil C: N impacts on soil biological health and consequences on weed control in soybean and corn systems. Weed Sci 72:402–421

Hald AB (1999) The impact of changing the season in which cereals are sown on the diversity of the weed flora in rotational fields in Denmark. J Appl Ecol 36:24–32

Haney RL, Haney EB (2010) Simple and rapid laboratory method for rewetting dry soil for incubations. Commun Soil Sci Plant 41:1493–1501

Hawes C, Squire GR, Hallett PD, Watson CA, Young M (2010) Arable plant communities as indicators of farming practice. Agric Ecosyst Environ 138:17–26

Heap I (2024) The International Herbicide-Resistant Weed Database. www.weedscience.org. Accessed: May 9, 2024

Hulme PE (2023) Weed resistance to different herbicide modes of action is driven by agricultural intensification. Field Crop Res 292:108819

José-María L, Sans FX (2011) Weed seedbanks in arable fields: effects of management practices and surrounding landscape. Weed Res 51:631–640

Kane JL, Kotcon JB, Freedman ZB, Morrissey EM (2022) Fungivorous nematodes drive microbial diversity and carbon cycling in soil. Ecology 104: e3844

Kremer RJ, Li J (2003) Developing weed-suppressive soils through improved soil quality management. Soil Till Res 72:193–202

Liland KH, Mevik BH, Wehrens R, Hiemstra P (2023) pls: Partial Least Squares and Principal Component Regression. R package version 2.8–3. https://cran.r-project.org/web/packages/pls/index.html

Long RL, Steadman KJ, Panetta FD, Adkins SW (2009) Soil type does not affect seed ageing when soil water potential and temperature are controlled. Plant Soil 320:131–140

Lowry CJ, Brainard DC, Kumar V, Smith RG, Singh M, Kumar P, Kumar A, Kumar V, Joon RK, Jat RK, Poonia S (2021) Weed germinable seedbanks of rice-wheat systems in the Eastern Indo-Gangetic Plains: do tillage and edaphic factors explain community variation? Weed Res 61:475–485

Mayor JP, Dessaint F (1998) Influence of weed management strategies on soil seedbank diversity. Weed Res 38:95–105

McCune B, Grace JB, Urban DL (2002) Analysis of Ecological Communities. Gleneden Beach, OR: MjM Software Design. 304 p

McKenzie-Gopsill A, Graham G, Laforest M, Ibarra S, Hann S, Wagg C (2020) Occurrence and management of PSII-inhibitor-resistant *Chenopodium album* L. in Atlantic Canadian potato production. Agronomy 10:1369

McKenzie-Gopsill A, Nyiraneza J, Fillmore S (2024) Effects of cultural practices on weed community and seedbank dynamics in a potato rotation. Field Crop Res 310:109357

Mehlich A (1984) Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Commun Soil Sci Plant Anal 15:1409–1416

Menalled FD, Gross KL, Hammond M (2001) Weed aboveground and seedbank community responses to agricultural management systems. Ecol Appl 11:1586–1601

Nelson KL, Lynch DH, Boiteau G (2009) Assessment of changes in soil health throughout organic potato rotation sequences. Agric Ecosyst Environ 131:220–228

Nowak A, Nowak S, Nobis M, Nobis A (2015) Crop type and altitude are the main drivers of species composition of arable weed vegetation in Tajikistan. Weed Res 55:525–536

Nyiraneza J, Thompson B, Geng X, He J, Jiang Y, Fillmore S, Stiles K (2017) Changes in soil organic matter over 18 yr in Prince Edward Island, Canada. Can J Soil Sci 97:745–756

Oksanen J, Simpson GL, Blanchet G, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bolker B, Borcard D, *et al.* (2022) vegan: Community Ecology Package. R package version 2.6-4. https://cran.r-project.org/web/packages/vegan/index.html

Okusanya OT, Ungar IA (1984) The growth and mineral composition of three species of *Spergularia* as affected by salinity and nutrients at high salinity. Am J Bot 71:439–447

Page ER, Meloche S, McMurray B, Laforest M (2019) Refuge facilitates the preservation and accumulation of herbicide resistance traits in *Conyza canadensis*. Can J Plant Sci 99:852–861

Pakeman RJ, Small JL, Torvell L (2012) Edaphic factors influence the longevity of seeds in the soil. Plant Ecol 213:57–65

Pinheiro J, Bates D, DebRoy S, Sarkar D, EISPACK, Heisterkamp S, Van Willigen B, Ranke J (2023) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-164. https://cran.r-project.org/web/packages/nlme/index.html

Plue J, Van Calster H, Auestad I, Basto S, Bekker RM, Bruun HH, Chevalier R, Decocq G, Grandin U, Hermy M, Jacquemyn H (2021) Buffering effects of soil seed banks on plant community composition in response to land use and climate. Glob Ecol Biogeogr 30:128–139

Postma-Blaauw MB, De Goede RG, Bloem J, Faber JH, Brussaard L (2012) Agricultural intensification and de-intensification differentially affect taxonomic diversity of predatory mites, earthworms, enchytraeids, nematodes and bacteria. Appl Soil Ecol 57:39–49

Puissant J, Villenave C, Chauvin C, Plassard C, Blanchart E, Trap J (2021) Quantification of the global impact of agricultural practices on soil nematodes: a meta-analysis. Soil Biol Biochem 161:108383

R Core Team (2023) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org

Roberts HA, Neilson JE (1982) Seasonal changes in the temperature requirements for germination of buried seeds of *Aphanes arvensis* L. New Phytol 92:159–166

Scherner A, Melander B, Kudsk P (2016) Vertical distribution and composition of weed seeds within the plough layer after eleven years of contrasting crop rotation and tillage schemes. Soil Till Res 161:135–142

Schrama MJ, Cordlandwehr V, Visser EJ, Elzenga TM, de Vries Y, Bakker JP (2013) Grassland cutting regimes affect soil properties, and consequently vegetation composition and belowground plant traits. Plant Soil 366: 401–413

Schwartz LM, Gibson DJ, Gage KL, Matthews JL, Jordan DL, Owen MD, Shaw DR, Weller SC, Wilson RG, Young BG (2015) Seedbank and field emergence of weeds in glyphosate-resistant cropping systems in the United States. Weed Sci 63:425–439

Sieriebriennikov B, Ferris H, de Goede RGM (2014) NINJA: an automated calculation system for nematode-based biological monitoring. Eur J Soil Biol 61:90–93

Smith RG, Birthisel SK, Bosworth SC, Brown B, Davis TM, Gallandt ER, Hazelrigg A, Venturini E, Warren ND (2018) Environmental correlates with germinable weed seedbanks on organic farms across northern New England. Weed Sci 66:78–93

Smith RG, Mortensen DA, Ryan MR (2010) A new hypothesis for the functional role of diversity in mediating resource pools and weed–crop competition in agroecosystems. Weed Res 50:37–48

Swanton CJ, Shrestha A, Knezevic SZ, Roy RC, Ball-Coelho BR (2000) Influence of tillage type on vertical weed seedbank distribution in a sandy soil. Can J Plant Sci 80:455–457

Teasdale JR, Mangum RW, Radhakrishnan J, Cavigelli MA (2004) Weed seedbank dynamics in three organic farming crop rotations. Agron J 96:1429–1435

Thomas AG, Doohan DJ, McCully KV (1994) Weed survey of spring cereals in New Brunswick. Phytoprotection 75:113–124

Ullrich SD, Buyer JS, Cavigelli MA, Seidel R, Teasdale JR (2011) Weed seed persistence and microbial abundance in long-term organic and conventional cropping systems. Weed Sci 59:202–209

Uwituze Y, Nyiraneza J, Fraser TD, Dessureault-Rompré J, Ziadi N, Lafond J (2022) Carbon, nitrogen, phosphorus, and extracellular soil enzyme responses to different land use. Front Soil Sci 2:814554

Van Wychen L (2022) 2022 Survey of the Most Common and Troublesome Weeds in Broadleaf Crops, Fruits & Vegetables in the United States and Canada. Weed Science Society of America National Weed Survey Dataset. https://wssa.net/wp-content/uploads/2022-Weed-Survey-Broadleaf-crops.xlsx. Accessed: May 9, 2024

Wagner M, Mitschunas N (2008) Fungal effects on seed bank persistence and potential applications in weed biocontrol: a review. Basic Appl Ecol 9:191–203

Wang KH, Waisen P, Leslie AW, Paudel R, Meyer SL, Hooks CR (2022) Relationships between soil tillage systems, nematode communities and weed seed predation. Horticulturae 8:425

Young BG, Gibson DJ, Gage KL, Matthews JL, Jordan DL, Owen MD, Shaw DR, Weller SC, Wilson RG (2013) Agricultural weeds in glyphosate-resistant cropping systems in the United States. Weed Sci 61:85–97

Ziter C, MacDougall AS (2013) Nutrients and defoliation increase soil carbon inputs in grassland. Ecology 94:106–116