Teaching Seed Bank Ecology in an Undergraduate Laboratory Exercise[1]

EMILIE E. REGNIER[2]

Abstract. The study of weed life cycles, reproductive strategies, and the soil seed bank is emphasized in the undergraduate weed science course at Ohio State University as central to an understanding of the survival of weeds in the environment. A laboratory exercise was conducted every spring and fall academic quarter from 1991 to 1993 to demonstrate the effects of long-term cropping and soil disturbance histories on weed seed banks and aboveground weed communities. Five sites with diverse histories of culture were sampled; these included a field cultivated in vegetables under continuous conventional tillage for 59 yr, a field cultivated in field corn under continuous no-tillage for 11 yr, a 24 yr-old turfgrass research farm, a 70 yr-old forest, and a section of the forest border. Students conducted a survey of the weeds growing at the sites and separated and identified seeds from soil samples over a 3-wk period in weekly 2-h laboratory periods. Students wrote reports interpreting the data based on their knowledge of the site histories, weed life cycles, and weed seed production and longevity characteristics. The data were consistent over academic quarters as well as with published research, indicating that the survey and soil sampling techniques provided a reasonably accurate representation of the weed flora and soil seed populations. Weeds found growing at the sites were primarily summer annuals at the vegetable site, and a mix of summer and winter annuals, biennials, and perennials at the remaining sites. Annual weeds dominated the seed banks of all sites with common lambsquarters, pigweed spp., and common purslane being the most commonly found seeds. The presence of most seeds in the soil could be explained by a combination of species seed production and seed longevity characteristics and species abundance in the standing community. Interpretation of the data required students to integrate and apply lecture material and provided an excellent thinking exercise. **Nomenclature:** Common lambsquarters, *Chenopodium album* L. #[3] CHEAL; common purslane, *Portulaca oleracea* L. # POROL; pigweed, *Amaranthus* spp.; corn, *Zea mays* L.**Additional index words:** Tillage systems, weed biology, weed ecology.

INTRODUCTION

Weed biology and ecology comprise about half of the lecture material for the undergraduate weed science course at Ohio State University. The long-term effects of weed management practices are emphasized, with the goal of preparing students to predict the impact of weed management practices on weed populations over time. The study of weed life cycles, their reproductive strategies, and the soil seed bank is stressed as being central to an understanding of how weeds perpetuate themselves in the environment.

In general, only a few different species comprise the majority of seeds in agricultural seed banks (45). In Ohio, six or fewer species comprised over 90% of the seed banks in continuous corn, with common lambsquarters, pigweed spp., and fall panicum (*Panicum dichotomiflorum* Michx.) being the most common species (4). Weed species diversity in the seed banks of corn fields subjected to different long-term tillage regimes increased as soil disturbance decreased due to an increase in winter annual, biennial, and perennial weed species (4). There was little correlation between the seed bank and aboveground community, which was attributed in part to differing seed production and seed longevity characteristics of specific weeds (4). Seeds of some weeds persist in the soil long after agriculture has been abandoned, contributing to the well-documented lack of relationship between the seed bank and standing vegetation in late-successional and climax communities (27, 28).

The observation and study of actual habitats is a natural instructional tool. A soil seed bank laboratory exercise, modeled after research conducted by Cardina, et al. (4),

[1]Received for publication Mar. 7, 1994 and in revised form Sept. 13, 1994.

[2]Asst. Prof., Dep. Agron., Ohio State Univ., Columbus, OH 43210. Research support provided in part by state and federal funds appropriated to The Ohio Agric. Res. and Develop. Cent., The Ohio State Univ. J. Art. No. 113-94.

[3]Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Revised 1989. Available from WSSA, 1508 West University Ave., Champaign, IL 61821-3133.

was developed and introduced in the undergraduate weed science course at Ohio State University in spring 1991. The instructional objectives of the exercise were to illustrate principles of weed ecology and biology and to expose students to the long-term effects of diverse land management practices on weed communities. In this paper, the field and laboratory procedures are described, the data are compared to published research, and the exercise evaluated with regard to the instructional objectives.

MATERIALS AND METHODS

Site histories. Five sites demonstrating a range of long-term soil and vegetation disturbance histories were selected at the Ohio State University Waterman Farm Complex, Columbus, OH. They were a conventional tillage vegetable field, a no-tillage corn field, a turfgrass research farm, an old-field successional forest, and a section of the forest border. All sites were located on a Crosby silt loam soil (fine, mixed, mesic Aeric Ochraqualfs) except the vegetable field, which was on a Celina silt loam soil (fine, mixed mesic Aquic Hapludalfs). The turfgrass, forest, and no-tillage corn sites were approximately adjacent to each other, whereas the vegetable site was 0.4 km away from the other sites. Students were given a brief history of the sites, as follows, with the exception that only the general nature and effects of herbicide use were explained.

The vegetable site was established in 1932 and had the highest degree of long-term soil disturbance among sites. Tillage generally consisted of disking in the fall following crop harvest, moldboard plowing to a depth of 20 to 25 cm in the spring followed by at least one disking prior to planting, and postemergence cultivation with occasional hand-hoeing through mid-summer. Crops planted from 1981 to 1993 included soybean (*Glycine max* L. Merr.), cucumber (*Cucumis sativus* L.), popcorn (*Zea mays* L.), squash (*Cucurbita maxima* Duch.), red clover (*Trifolium pratense* L.), potato (*Solanum tuberosum* L.), sweet corn (*Zea mays* L.), tomato (*Lycopersicon esculentum* Mill.), pumpkin (*Cucurbita pepo* L.), muskmelon (*Cucumis melo* L.), and field corn, with sweet corn being the most frequently planted crop. Crops were generally planted in early June and fertilizer was applied based on soil test recommendations. Depending on the year and crop, metolachlor [2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl)acetamide], metribuzin [4-amino-6-(1,1-dimethylethyl)-3-(methylthio)-1,2,4-triazin-5(4*H*)-one], or cyanazine {2-[[4-chloro-6-(ethylamino)-1,3,5-triazin-2-yl]amino]-2-methylpropanenitrile} were applied at label-specified rates. The most commonly used herbicide was metolachlor. No herbicides were applied to tomato or red clover crops.

The no-tillage corn field was converted from alfalfa (*Medicago sativa* L.) to no-tillage corn in 1980 and received no soil disturbance other than corn planting. All aboveground vegetation was physically removed to approximately a 20-cm height in early September when corn was harvested for silage, and some vegetation was killed or partially killed in the spring through herbicide application at corn planting. Manure was the only fertilizer used until 1990, whereafter 46 kg/ha N as 28% urea-ammonium nitrate solution was applied annually plus manure. Corn was planted mid-May in 76-cm rows. Atrazine [6-chloro-*N*-ethyl-(N′-(1-methylethyl)-1,3,5-triazine-2,4-diamine] plus cyanazine and 2,4-D [(2,4-dichlorophenoxy)acetic acid] were applied at planting at label-specified rates.

The turfgrass research farm was converted from corn and soybean production to turfgrass in 1967. Turf grasses were maintained as a dense and competitive cover through frequent mowing, irrigation, fertilization, and pesticide application. A creeping bentgrass (*Agrostis palustris* Huds.) green was selected for study in spring and fall 1991 and spring 1992, and a Kentucky bluegrass (*Poa pratensis* L.)/perennial ryegrass (*Lolium perenne* L.) perimeter site was studied in spring 1993. The only soil disturbance occurred on the bentgrass green, which was aerated every other year. Fertilization of bentgrass consisted of application of 37 kg N/ha once a month from April to October and 49 kg N/ha per year in the perimeter area. On the bentgrass green, pendimethalin [*N*-(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzenamine] and bensulide {*O,O*-bis(1-methylethyl)*S*-[2-[(phenylsulfonyl)amino]ethyl]phosphorodithioate} were applied each spring and a tank-mixture of 2,4-D, mecoprop [(±)-2-(4-chloro-2-methylphenoxy)-propanoic acid] and dicamba (3,6-dichloro-2-methoxybenzoic acid) was applied postemergence during each summer at label-specified rates. The same herbicides were applied to the perimeter area, but were not applied each year. Bentgrass was mowed to 1.3 cm three times per week whereas the perimeter area was mowed to 5 cm two times per week. The two turfgrass areas were approximately 90 m apart. Because of the proximity of the two areas and similarity in weed control and aboveground weed communities, results for the two areas were combined.

Table 1. Common and scientific names and five-letter Bayer code for weeds identified in this study or listed in other tables.

Common name	Scientific name	Bayer code	Common name	Scientific name	Bayer code
Annual bluegrass	*Poa annua* L.	POAAN	Green foxtail	*Setaria viridis* (L.) Beauv.	SETVI
Annual fleabane	*Erigeron annuus* (L.) Pers.	ERIAN	Ground ivy	*Glechoma hederacea* L.	GLEHE
Annual sowthistle	*Sonchus oleraceus* L.	SONOL	Hedge bindweed	*Calystegia sepium* (L.) R. Br.	CAGSE
Barnyardgrass	*Echinochloa crus-galli* (L.) Beauv.	ECHCG	Henbit	*Lamium amplexicaule* L.	LAMAM
Bitter nightshade	*Solanum dulcamara* L.	SOLDU	Honeyvine milkweed	*Ampelamus albidus* (Nutt.) Britt.	AMPAL
Black medic	*Medicago lupulina* L.	MEDLU	Horsenettle	*Solanum carolinense* L.	SOLCA
Blackseed plantain	*Plantago rugelii* Dcne.	PLARU	Ivyleaf speedwell	*Veronica hederifolia* L.	VERHE
Broadleaf dock	*Rumex obtusifolius* L.	RUMOB	Jimsonweed	*Datura stramonium* L.	DATST
Broadleaf plantain	*Plantago major* L.	PLAMA	Johnsongrass	*Sorghum halepense* (L.) Pers.	SORHA
Buckhorn plantain	*Plantago lanceolata* L.	PLALA	Large crabgrass	*Digitaria sanguinalis* (L.) Scop.	DIGSA
Bulrush spp.[a]	*Scirpus* spp.	—	Mouseear chickweed	*Cerastium vulgatum* L.	CERVU
Bull thistle	*Cirsium vulgare* (Savi) Tenore	CIRVU	Pennsylvania bittercress	*Cardamine pensylvanica* Muhl ex. Willd.	CARPE
Canada goldenrod	*Solidago canadensis* L.	SOOCA	Pennsylvania smartweed	*Polygonum pensylvanicum* L.	POLPY
Canada thistle	*Cirsium arvense* (L.) Scop.	CIRAR	Pigweed spp.	*Amaranthus* spp.	—
Carpetweed	*Mollugo verticillata* L.	MOLVE	Pineappleweed	*Matricaria matricarioides* (Less.) C. L. Porter	MATMT
Catchweed bedstraw	*Galium aparine* L.	GALAP			
Chicory	*Cichorium intybus* L.	CICIN	Poison-ivy	*Toxicodendron radicans* (L.) Ktze.	TOXRA
Common burdock	*Arctium minus* (Hill) Bernh.	ARFMI	Prickly lettuce	*Lactuca serriola* L.	LACSE
Common chickweed	*Stellaria media* (L.) Vill.	STEME	Prostrate knotweed	*Polygonum aviculare* L.	POLAV
Common groundsel	*Senecio vulgaris* L.	SENVU	Purple deadnettle	*Lamium purpureum* L.	LAMPU
Common lambsquarters	*Chenopodium album* L.	CHEAL	Purslane speedwell	*Veronica peregrina* L.	VERPG
Common mallow	*Malva neglecta* Wallr.	MALNE	Quackgrass	*Elytrigia repens* (L.) Nevski	AGRRE
Common pokeweed	*Phytolacca americana* L.	PHTAM	Redroot pigweed	*Amaranthus retroflexus* L.	AMARE
Common purslane	*Portulaca oleracea* L.	POROL	Rough avens	*Geum virginianum* L.	—
Common ragweed	*Ambrosia artemisiifolia* L.	AMBEL	Shepherd's-purse	*Capsella bursa-pastoris* (L.) Medicus	CAPBP
Curly dock	*Rumex crispus* L.	RUMCR	Smallflower galinsoga	*Galinsoga parviflora* Cav.	GASPA
Dandelion	*Taraxacum officinale* Weber in Wiggers	TAROF	Spring whitlowgrass	*Draba verna* L.	ERPVE
Downy brome	*Bromus tectorum* L.	BROTE	Treacle mustard	*Erysimum repandum* L.	—
Eastern black nightshade	*Solanum ptycanthum* Dun.	SOLPT	Velvetleaf	*Abutilon theophrasti* Medicus	ABUTH
Fall panicum	*Panicum dichotomiflorum* Michx.	PANDI	Venice mallow	*Hibiscus trionum* L.	HIBTR
Field bindweed	*Convolvulus arvensis* L.	CONAR	Violet spp.	*Viola* spp.	—
Field pennycress	*Thlaspi arvense* L.	THLAR	White clover	*Trifolium repens* L.	TRFRE
Field violet	*Viola arvensis* Murr.	VIOAR	Wild grape spp.	*Vitis* spp.	—
Garlic mustard	*Alliaria petiolata* (Bieb.) Cavara & Grande	ALAPE	White heath aster	*Aster pilosus* Willd.	ASTPI
			Yellow foxtail	*Setaria glauca* (L.) Beauv.	SETLU
Giant foxtail	*Setaria faberi* Herrm.	SETFA	Yellow nutsedge	*Cyperus esculentus* L.	CYPES
Giant ragweed	*Ambrosia trifida* L.	AMBTR	Yellow rocket	*Barbarea vulgaris* R. Br.	BARVU
Goldenrod spp.	*Solidago* spp.	—	Yellow woodsorrel	*Oxalis stricta* L.	OXAST
Goosegrass	*Eleusine indica* (L.) Gaertn.	ELEIN			

[a]Bulrush, pigweed, goldenrod, wild grape, and violet spp. were identified only to genus due to difficulties in distinguishing species in the seed or seedling stage.

The old-field successional forest had previously been in pasture and consisted of ash (*Fraxinus* spp.), beech (*Fagus* spp.), and maple (*Acer* spp.), with the most mature trees being approximately 70 yr old. The area sampled was located 30 m from the edge of the forest under a dense and uniform tree canopy with little understory.

The border site was a strip of herbaceous vegetation approximately 4 m wide located along the eastern edge of the forest immediately adjacent to a farm road, and was mowed occasionally during the summer. There was no soil disturbance nor herbicide application to the vegetation. The rear of the border was partially shaded during late afternoon.

Weed survey and soil sampling. In the first week of the exercise, students were divided into small groups to survey and record weeds growing at each site and to take soil samples for later characterization of the soil seed banks. This took place in mid-October for the fall quarter and in mid-April for the spring quarter during a 2-h laboratory period. The vegetable and no-tillage corn sites were surveyed and sampled every spring and fall of 1991 to 1993; the turfgrass farm in spring and fall of 1991, and again in spring of 1992 and 1993; the forest border in spring and fall of 1991 and 1993; and the forest interior in spring and fall of 1991 and 1992. Weed survey data from spring 1992 were not kept by the instructor and are therefore missing for that quarter. All weed species identified in the weed survey and in the soil seed bank over the study period are listed in Table 1.

To survey the aboveground flora, flags were positioned at regular intervals along opposite sides of the site, and groups selected a "corridor" between two flags, walked from one side to the other to identify weeds, and recorded their relative abundance on the return using a scale of 1 (very rare) to 5 (very common). The scale was first used in fall 1992; in previous quarters students recorded the weeds observed without rating their abundance. No attempt was made to identify and record spring ephemerals in the forest interior. Weeds identified by students that appeared unusual or inconsistent with the instructor's observations were verified by the instructor in a subsequent visit to the site, as needed.

During the weed survey, students randomly took a total of 20 soil cores each measuring 3.2 cm in diam and 7.5 cm in depth from each site, giving a total of 160 cm^2 soil surface area sampled per site. Soil cores were stored at 4 C in closed plastic bags until seed separation.

Seed extraction. During the second week of the exercise, soil cores for each site were broken up, mixed, and soil dry weight determined from two 25-g samples dried for 24 h at 65 C. Students worked in pairs to separate seeds from a small soil sample (25 to 50 g). A sample size of 40 g was found to work best for the allotted time. An approximately equal number of soil samples was processed for each site with at least two samples per site. The total amount of soil sampled per site varied with student enrollment (enrollment ranged from 27 to 45 over the study period) and averaged 130 g/quarter.

Seeds were separated from soil by dispersion and flotation with sodium hexametaphosphate, sodium bicarbonate, and magnesium sulfate according to the method of Malone (18). The procedure required only a small amount of water and chemicals and was accomplished easily in a dry laboratory in approximately 1 hr. To emphasize the accessibility of the materials, Calgon[4] and Epsom salts were used as the source for sodium hexametaphosphate and magnesium sulfate, respectively (18). The floating seeds and other organic material were decanted through a 200-ml plastic beaker on which the closed end was replaced with a 0.25 mm mesh nylon screen. Rinse bottles were used to remove seeds adhering to the walls of the containers and to wash soil particles through the sieve. The decanted material was left to dry in labelled sieves until the following week. During the remainder of the laboratory period, students were given an introduction to the identification of seeds previously found to be common in the soil as well as seeds of other common weeds.

Seed identification. In the third week of the exercise, students were quizzed on seed identification and then worked in pairs to identify seeds in their samples. Students first separated seeds from other particles with fine tweezers under a dissecting microscope and then identified and counted all seeds with the aid of Delorit's manual on seed identification (9). Seeds not listed in the manual [e.g., *Lamium* spp., spring whitlowgrass (*Draba verna* L.), *Viola* spp., and *Scirpus* spp.] were identified through comparison with seeds previously collected from the field or by using other seed identification manuals (19, 24). Seeds that could not be identified with available manuals were classified as "unknown." The instructor verified accuracy of seed identification during or after the laboratory period. The procedure required about 1.5 h for seeds extracted from a 40-g soil sample. Samples from sites with dense roots in the soil, such as at the turfgrass site, were more time-consuming to process, and students often required assistance in distinguishing seeds from non-seed material.

Laboratory report. Data for both the aboveground weed survey and the soil seed bank were pooled and averaged, then redistributed to students, along with the dry weight of the soil samples taken from the various sites. Students prepared individual reports for which they assembled the data in tabular form for each site, with weed species arranged by life cycle. Total seed number data were expressed on an area basis to a depth of 7.5 cm, assuming 2 242 150 kg soil/ha in the 15 cm plow depth (20). The composition of the seed bank was expressed as percent, by species, of the total number of seeds. Students were instructed to interpret the weed and seed bank data with respect to soil disturbance and cropping characteristics of the sites, weed life cycles, and weed seed production and longevity. A table similar to Table 2 was distributed to students as a source of information on weed seed production and seed longevity.

RESULTS AND DISCUSSION

Site effects on aboveground weed flora and seed banks. Because aboveground weeds were not numerically rated in all quarters of the study, only weed survey data representative of the quarters in which weeds were rated are shown in Table 3. To permit evaluation of the consistency of the results from quarter to quarter, the frequency of occurrence of a species in the aboveground flora, i.e., the

[4]Beecham Products, Beecham, Inc. Pittsburgh, PA 15230

Table 2. Maximum reported seed production and seed longevity in soil for weeds commonly found in this study. Weed species are arranged by life cycle.

Species	Life cycle[a]	Seeds per plant[b]	Reference	Seed longevity[c]	Reference
		no.		yr	
Annual bluegrass	SA, WA, CP	36 000	41	68*	14
Carpetweed	SA	15 000	34	85*	14
Common lambsquarters	SA	500,000	15	39	39
				1700**	14
Common purslane	SA	242 540	23	40	8
Common ragweed	SA	62 000	10	39	39
Eastern black nightshade	SA	480 000	35	39	39
Fall panicum	SA	500 000	11	10	3
Field violet	SA, WA	46 000	12	400**	14
Giant foxtail	SA	10 000	32	—[d]	
Giant ragweed	SA	1 650	33	21	39
Goosegrass	SA	135 000	15	6	39
Green foxtail	SA	12 000	40	39	39
Jimsonweed	SA	23 400	26	39	39
Large crabgrass	SA	150 000	15	50*	14
Pennsylvania smartweed	SA	19 300	45	30	39
Redroot pigweed	SA	229 180	34	40	8
Prostrate knotweed	SA	6 380	34	400**	14
Velvetleaf	SA	32 000	Cardina[e]	39	39
Yellow foxtail	SA	8 000	31	30	8
Common chickweed	WA, SA	15 000	34	30	8
				600**	14
Field pennycress	WA	20 000	2	30	39
Purple deadnettle	WA	—		600**	14
Shepherd's-purse	WA	38 500	34	35	8
Annual fleabane	B, WA, SA	100 000	36	35	14
Common burdock	B	31 600	33	—	—
Garlic mustard	B	3 300	7	—	—
Prickly lettuce	B	27 900	45	3	39
Broadleaf dock	SP	60 000	6	39	39
Broadleaf plantain	SP	36 150	33	40	8
Curly dock	SP	40 000	6	80	8
Dandelion	SP	17 860	30	68*	14
Canada thistle	CP	5 300	25	25	17
Yellow woodsorrel	CP	570	33	85*	14
Field bindweed	CP	300	42	20	38
Canada goldenrod	CP	3 070	43	50*	14
Horsenettle	CP	5 000	1	—	—
Johnsongrass	CP	28 000	21	12	21
Quackgrass	CP	400	44	10	39
Yellow nutsedge	CP	890	37	21	39

[a]SA = summer annual; WA = winter annual; B = biennial; SP = simple perennial; CP = creeping perennial.

[b]For creeping perennials, seed number is given per stem rather than per plant.

[c]Seed longevity was determined by studies in which 1) (no asterisk) seeds were buried in the soil at known dates and subsequently retrieved at regular intervals, 2) (single asterisk) seeds were recovered from soil beneath a meadow, pasture or forest and their age determined indirectly by the age of the aboveground community, or 3) (double asterisk) seed longevity was determined by carbon dating of associated soil (Odum, 1965, in Ref. 14).

[d]Dashes indicate no information was available at the time of publication.

[e]J. Cardina (unpublished).

ratio of the number of quarters a species was observed to the total number of quarters the site was surveyed, is also shown (Table 3).

Weed survey data were reasonably consistent across quarters for a given site (Table 3), particularly for species equally visible in fall and spring, such as biennials and cool-season perennials. Summer annuals, winter annuals, and warm-season perennials tended to be rated lower in abundance in the season of their emergence, when plants were small. Weeds such as common purslane and carpet-

Table 3. Aboveground species abundance representative of the study period (1991 to 1993) and frequency of occurrence of species aboveground for five sites, including a field under 59 yr of conventional tillage vegetable production, a field under 11 yr of no-tillage corn production, a 24 yr-old turfgrass farm, the border of a 70 yr-old forest, and the interior of the same forest. Species are arranged by life cycle.

		Cropping/vegetative history									
Species	Life cycle[a]	Vegetable	No-till corn	Turfgrass	Forest border	Forest interior	Vegetable	No-till corn	Turfgrass	Forest border	Forest interior
		Aboveground species abundance[b,c]					Aboveground species frequency[d]				
Annual bluegrass	SA	—	1	1	—	—	—	1/5	3/3	—	—
Annual sowthistle	SA	—	—	—	—	—	—	1/5	—	—	—
Barnyardgrass	SA	1	—	—	—	—	1/5	1/5	—	—	—
Carpetweed	SA	1	—	—	—	—	1/5	—	—	—	—
Catchweed bedstraw	SA	—	—	—	1	—	—	—	—	2/4	—
Common groundsel	SA	—	—	—	—	—	1/5	—	—	—	—
Common lambsquarters	SA	4	4	—	1	—	5/5	3/5	—	1/4	—
Common mallow	SA, B	2	—	—	—	—	4/5	1/5	—	—	—
Common purslane	SA	4	—	—	—	—	4/5	—	1/3	—	—
Eastern black nightshade	SA	1	—	—	—	—	4/5	—	—	—	—
Fall panicum	SA	1	4	—	—	—	1/5	3/5	—	—	—
Giant foxtail	SA	1	—	—	1	—	2/5	1/5	—	1/4	—
Giant ragweed	SA	—	—	—	5	—	2/5	—	—	4/4	—
Goosegrass	SA	—	—	—	1	—	—	—	—	1/4	—
Green foxtail	SA	2	1	—	—	—	2/5	2/5	—	—	—
Jimsonweed	SA	—	—	—	—	—	—	1/5	—	—	—
Large crabgrass	SA	1	—	—	—	—	2/5	—	1/3	—	—
Pennsylvania smartweed	SA	1	—	—	—	—	3/5	1/5	—	—	—
Pigweed spp.	SA	5	1	—	—	—	3/5	3/5	—	—	—
Pineappleweed	SA	—	—	—	—	—	1/5	1/5	—	—	—
Smallflower galinsoga	SA	2	—	—	—	—	4/5	—	—	—	—
Velvetleaf	SA	1	1	—	—	—	4/5	4/5	—	—	—
Venice mallow	SA	1	—	—	—	—	3/5	—	—	—	—
Violet spp.	SA, WA, CP	—	—	—	1	—	—	—	—	1/4	—
Yellow foxtail	SA	1	1	—	1	—	1/5	2/5	—	2/4	—
Common chickweed	WA, SA	—	2	1	—	—	1/5	4/5	3/3	—	—
Downy bromegrass	WA	—	—	—	—	—	1/5	1/5	—	—	—
Field pennycress	WA	—	—	—	—	—	—	2/5	—	—	—
Henbit	WA	—	—	—	—	—	—	2/5	—	—	—
Ivyleaf speedwell	WA, SA	—	—	1	—	—	—	—	1/3	—	—
Pennsylvania bittercress	WA	—	—	—	1	—	—	1/5	—	1/4	—
Purple deadnettle	WA	—	3	1	1	—	1/5	4/5	1/3	2/4	—
Purslane speedwell	WA	—	—	—	—	—	1/5	1/5	—	—	—
Shepherd's-purse	WA	—	—	—	1	—	1/5	2/5	—	1/4	—
Spring whitlowgrass	WA	—	—	—	—	—	1/5	2/5	—	—	—
Treacle mustard	WA	—	—	—	—	—	—	2/5	—	—	—
Yellow rocket	WA	—	—	—	—	—	—	1/5	—	—	—

Annual fleabane	B, WA, SA	—	—	1	—	—	1/5	2/5	1/3	—	—
Bull thistle	B	—	—	1	—	—	1/5	—	1/3	1/4	—
Common burdock	B	—	—	1	4	—	—	—	1/3	4/4	—
Garlic mustard	B	—	—	—	4	4	—	—	—	4/4	2/3
Prickly lettuce	B	—	—	1	—	—	1/5	1/5	1/3	—	—
Black medic	SP, B, SA	—	—	1	—	—	—	—	1/3	—	—
Blackseed plantain	SP	—	—	—	—	—	—	—	—	1/4	—
Broadleaf dock	SP	—	2	—	—	—	—	3/5	—	2/4	—
Broadleaf plantain	SP	—	—	1	2	—	—	—	1/3	3/4	—
Chicory	SP	—	—	—	1	—	—	1/5	—	1/4	—
Common pokeweed	SP	—	—	—	—	—	—	1/5	—	—	—
Curly dock	SP	—	1	—	—	—	—	3/5	—	1/4	—
Dandelion	SP	2	4	3	1	—	4/5	4/5	2/3	3/4	—
Mouse-ear chickweed	SP	—	—	—	—	—	1/5	1/5	—	—	—
Rough avens	SP	—	—	—	1	—	—	—	—	1/4	—
Bitter nightshade	CP	—	—	—	—	—	—	—	—	—	1/3
Canada thistle	CP	2	2	—	1	—	5/5	5/5	—	2/4	—
Field bindweed	CP	2	2	—	—	—	4/5	4/5	—	—	—
Goldenrod	CP	—	—	—	3	—	—	—	—	3/4	—
Ground ivy	CP	—	—	—	2	—	—	—	—	3/4	—
Hedge bindweed	CP	—	3	—	—	—	—	4/5	—	—	—
Honeyvine milkweed	CP	—	1	—	1	—	—	1/5	—	1/4	—
Horsenettle	CP	—	2	—	—	—	—	2/5	—	—	—
Johnsongrass	CP	1	2	—	—	—	1/5	4/5	—	—	—
Poison-ivy	CP	—	—	—	—	2	—	—	—	—	3/3
Quackgrass	CP	—	3	1	1	—	—	5/5	1/3	2/4	—
White clover	CP	—	—	3	—	—	1/5	—	2/3	—	—
White heath aster	CP	—	—	—	2	—	—	—	—	3/4	—
Yellow nutsedge	CP	—	—	—	1	—	—	2/5	1/3	1/4	—
Wild grape spp.	WP	—	—	—	1	—	—	—	—	1/4	—

[a]SA = summer annual; WA = winter annual; B = biennial; SP = simple perennial; CP = creeping perennial; WP = woody perennial.

[b]Data were taken in fall 1993 for the vegetable, no-till corn, and forest border sites; in spring 1993 for the turfgrass site; and in fall 1992 for the forest interior.

[c]Species abundance was rated 1 to 5; 1 = very rare, 5 = very common. A dash indicates that the species was not found at the site for the specified time of evaluation.

[d]Values represent the ratio of the number of times a species was found to the total number of times the site was evaluated over the study period. A dash indicates that the species was not found at any of the times the site was evaluated. See text for details on times when sites were evaluated.

weed (*Mollugo verticillata* L.), which emerge late in the spring and senesce early in the fall, were likely underestimated in both seasons. On the whole, the survey technique resulted in a thorough representation of the aboveground weed community, particularly after rating forms were introduced. Visits to the sites by the instructor after students had conducted the surveys confirmed that students identified the vast majority of weeds correctly, and overlooked virtually no species. There were no apparent changes in the composition of the aboveground community over the 2-yr study period (data not shown). The vegetable site was dominated by summer annuals and a few creeping perennial species, as a result of intensive tillage practices, whereas the remaining sites showed a more even distribution of species among all life cycles (Table 3). Winter annuals and creeping perennials were particularly abundant at the no-tillage corn site, whereas biennials dominated the forest border (Table 3). The types of life cycles observed in the aboveground flora at the various sites were generally consistent with the frequency and timing of soil and vegetation disturbance.

Seed bank composition by species, averaged over the quarters of study, and frequency of occurrence of a species in the seed bank are shown in Table 4. Identification of seeds was more difficult for students than the identification of plants and inspection of students' assessments of species identity by the instructor during the first quarters of the exercise revealed several errors, particularly in distinguishing common lambsquarters and pigweed spp., and common purslane and common chickweed [*Stellaria media* (L.) Vill.]. A thorough introduction to the identification of these and other commonly found species followed by a quiz, as well as interaction with the instructor during the seed identification process, was essential to ensure accurate seed identification by students and greatly reduced the number of misidentified seeds.

Considering the small total amount of soil analyzed for seeds, only seeds of the most predominant species were expected to be detected with consistency (13). As expected, dominant species were found consistently each quarter, whereas minor species were found sporadically over quarters (Table 4). Percent seed bank composition by species was least variable over quarters for the vegetable site (Table 4), where intensive tillage probably resulted in a relatively uniform distribution of weeds over time. Greater variability from quarter to quarter occurred at sites with no soil disturbance (Table 4), where weed spatial distribution in the field was probably less uniform. Variation in seed bank data from quarter to quarter was not associated with season and there were no obvious changes in species composition over the study period for any of the sites (data not shown).

The results were in agreement with others showing that only a few species contribute the bulk of total seeds in agricultural seed banks (4, 45). Pigweed spp., common purslane, and common lambsquarters were common to all sites and together comprised 95% of the soil seed bank at the conventional tillage vegetable site, averaged over quarters, and approximately 50% or more of the soil seed banks at the other sites (Table 4). Common lambsquarters was the predominant species, comprising 20 to 40% of the seed bank, across sites. Common lambsquarters, pigweed spp., and common purslane were common in the standing community at the vegetable site, but were less common or absent from the aboveground floras at the other sites (Table 3). Their presence in the forest seed bank was singular in that the seeds were potentially 70 yr-old remnants of a seed bank formed when the site was cultivated (14). The predominance of common lambsquarters, pigweed spp., and common purslane in the soil compared to other summer annual species can be explained by their high seed production capacity and longevity (Table 2), ensuring the formation of a persistent seed bank whenever conditions are suitable for the plants' growth and reproduction. The relative abundance of these species in agricultural seed banks has been reported by others (13, 22, 29, 45).

Seeds of common chickweed and carpetweed were common to the soil seed banks of all sites except the forest interior (Table 4). Common chickweed was most prevalent at the no-tillage corn site, where it accounted for 21% of the seed bank, averaged over quarters. Its presence in the seed bank was consistent with the frequency of its occurrence in the standing flora (Table 3). Common chickweed has been found consistently in arable seed banks of cool temperate regions (29) and was a minor component of no-tillage continuous corn and sod seed banks in Ohio (4). Carpetweed also was found in sod and continuous corn seed banks in Ohio, but with less consistency than common chickweed.

Although soil seed banks at all sites were dominated by summer annuals, species of winter annual, biennial, and perennial life cycles comprised an increasing percentage of the total seed bank as soil disturbance decreased. Winter annuals, biennials, and perennials comprised an average of only 2% of the seed bank at the vegetable site, compared to 12% of the seed bank at the turfgrass site, and about 30%

Table 4. Species composition and frequency of occurrence of species in the soil seed bank of a field under 59 yr of conventional tillage vegetable production, a field under 11 yr of no-tillage corn production, a 24 yr-old turfgrass farm, the border of a 70 yr-old forest, and the interior of the same forest. Species are arranged by life cycle.

Species	Life cycle[a]	Cropping/vegetative history									
		Vegetable	No-till corn	Turfgrass	Forest border	Forest interior	Vegetable	No-till corn	Turfgrass	Forest border	Forest interior
		Seed bank composition (%)[b]					Frequency in seed bank[c]				
Annual bluegrass	SA	—	—	12 (24)	—	—	—	—	1/4	—	—
Barnyardgrass	SA	—	T	—	—	—	—	1/6	—	—	—
Carpetweed	SA	2 (2)	2 (2)	3 (4)	T	—	4/6	4/6	2/4	1/4	—
Common lambsquarters	SA	40 (8)	26 (19)	20 (24)	40 (21)	40 (43)	6/6	6/6	3/4	4/4	4/4
Common purslane	SA	33 (11)	11 (11)	25 (19)	6 (5)	7 (14)	6/6	5/6	4/4	3/3	1/4
Common ragweed	SA	—	—	—	T	—	—	—	—	1/4	—
Eastern black nightshade	SA	T	T	—	—	—	3/6	2/6	—	—	—
Fall panicum	SA	—	2 (2)	—	—	—	—	4/6	—	—	—
Giant ragweed	SA	—	—	—	1 (3)	—	—	—	—	1/4	—
Goosegrass	SA	—	—	—	3 (6)	—	—	—	—	1/4	—
Green foxtail	SA	—	1 (3)	—	—	—	1/6	1/6	—	—	—
Jimsonweed	SA	—	T	—	—	—	—	1/6	—	—	—
Large crabgrass	SA	—	T	—	1 (2)	—	—	1/6	—	1/4	—
Pennsylvania smartweed	SA	—	1 (2)	—	—	—	—	2/6	—	—	—
Pigweed spp.	SA	22 (4)	21 (14)	4 (8)	10 (11)	4 (5)	6/6	6/6	1/4	3/4	2/4
Prostrate knotweed	SA	—	—	2 (5)	1 (3)	—	—	—	1/4	1/4	—
Venice mallow	SA	T	—	—	—	—	1/6	—	—	—	—
Violet spp.	SA, WA, CP	—	—	8 (16)	—	T	—	—	1/4	—	1/4
Yellow foxtail	SA	—	—	—	2 (4)	—	—	—	—	1/4	—
Common chickweed	WA, SA	2 (5)	21 (18)	2 (4)	T	—	2/6	6/6	1/4	1/4	—
Field pennycress	WA	—	2 (4)	T	3 (2)	—	—	1/6	1/4	3/4	—
Purple deadnettle	WA	—	4 (5)	1 (3)	10 (10)	—	—	4/6	1/4	3/4	—
Shepherd's-purse	WA	—	2 (5)	—	—	—	—	1/6	—	—	—
Spring whitlowgrass	WA	—	T	—	—	—	—	1/6	—	—	—
Common burdock	B	—	—	—	16 (6)	—	—	—	—	4/4	—
Broadleaf dock	SP	—	T	—	1 (3)	—	—	2/6	—	1/4	—
Broadleaf plantain	SP	—	—	7 (13)	1 (3)	—	—	—	1/4	2/4	—
Buckhorn plantain	SP	—	T	—	T	—	—	1/6	—	—	—
Dandelion	SP	—	1 (2)	—	—	—	—	3/6	—	—	—
Mousear chickweed	SP	—	T	—	—	—	—	1/6	—	—	—
Bulrush spp.	CP	—	—	—	1 (2)	—	—	—	—	1/4	—
Yellow woodsorrel	CP	—	1 (2)	2 (4)	T	—	—	2/6	1/4	1/4	—
Quackgrass	CP	—	T	—	—	—	—	1/6	—	—	—
Wild grape spp.	WP	—	—	—	—	3 (7)	—	—	—	—	1/4
Unknown		T	3 (2)	15 (17)	2 (2)	46 (47)					

[a]SA = summer annual; WA = winter annual; B = biennial; SP = simple perennial; CP = creeping perennial; WP = woody perennial.

[b]Data are percent of total seed number to a depth of 7.5 cm and represent means of data taken from 1991 to 1993, with standard deviations in parentheses. T (trace) indicates species present at less than 1%. A dash indicates that the species was not found in the seed bank.

[c]Values represent the ratio of the number of times a species was found in the seed bank to the total number of times the site was evaluated over the study period. See text for details on times of evaluation.

Table 5. Number of weed species identified in the aboveground community and in the seed bank, arranged by life cycle, and total seed number (7.5 cm depth) in the soil at five sites with different long-term management histories. The sites were a field under 59 yr of conventional tillage vegetable production, a field under 11 yr of no-tillage corn production, a 24 yr-old turfgrass research farm, the border of a 70 yr-old forest, and the interior of the same forest.[a]

Site	Life cycle	Species: Above-ground	Species: Seed bank	Total seeds
		no.	no.	no./m^2
Vegetable	SA[b]	9.6 (5.1)	4.7 (1.2)	—
	WA	1.4 (2.6)	0.3 (0.5)	—
	B	0.6 (1.3)	0	—
	SP	1.0 (0.7)	0	—
	CP	2.0 (0.7)	0	—
	Total	14.6 (6.4)	5.0 (1.5)	141 450 (69 170)
No-tillage corn	SA	5.4 (4.0)	5.8 (2.2)	—
	WA	4.8 (4.8)	2.2 (1.2)	—
	B	0.4 (0.5)	0	—
	SP	2.6 (1.7)	1.2 (0.8)	—
	CP	5.6 (1.9)	0.3 (0.5)	—
	Total	18.6 (7.7)	9.5 (2.0)	87 100 (45 740)
Turfgrass	SA	2.0 (1.0)	3.3 (0.5)	—
	WA	1.7 (1.2)	0.8 (1.0)	—
	B	1.3 (2.3)	0	—
	SP	1.0 (1.0)	0.3 (0.5)	—
	CP	1.3 (0.6)	0.3 (0.5)	—
	Total	7.3 (4.9)	4.5 (1.3)	26 840 (6 870)
Forest border	SA	3.0 (2.0)	4.3 (1.5)	—
	WA	1.8 (0.9)	1.8 (0.5)	—
	B	2.8 (1.0)	1.0 (0)	—
	SP	3.0 (2.2)	0.8 (0.5)	—
	CP, WP	4.0 (2.9)	0.5 (0.6)	—
	Total	14.5 (7.4)	8.0 (2.2)	44 050 (12 150)
Forest interior[c]	Total	—		32 130 (13 980)

[a]Values represent means of data taken from 1991 to 1993, with standard deviations in parentheses. The vegetable and no-tillage corn sites were sampled six times and the remaining sites four times. See text for details on times of sampling.

[b]SA = summer annual; WA = winter annual; B = biennial; SP = simple perennial; CP = creeping perennial; WP = woody perennial.

[c]Species were not separated by life cycle due to difficulty in identifying non-weed species.

of the seed bank at the no-tillage corn and forest border sites (Table 4). The seed bank of the forest interior could not be characterized completely as to life cycles present due to the high number of non-weed seeds which were not identified (Table 4).

The total number of species in the soil seed bank was highest at the no-tillage corn and forest border sites, and lowest at the vegetable and turfgrass sites (Table 5). High species numbers in the no-tillage corn and forest border seed banks were due to greater numbers of winter annuals, biennials, and perennials compared to the vegetable site (Table 5). Similarly, in the aboveground flora, winter annuals, biennials, and perennials accounted for about 73% of the total number of species observed in the aboveground community at the no-tillage corn and turfgrass sites, and 80% at the forest border site, averaged over quarters, compared to only 34% at the vegetable site (Table 5). However, total number of species in the aboveground flora was similar at the vegetable, no-tillage corn, and forest border sites, ranging from approximately 15 to 19 species, and was lowest at the turfgrass site, where an average of only seven species was observed (Table 5).

These results are in partial agreement with those of Cardina, et al. (4), who reported increased species diversity in the soil seed bank with decreased soil disturbance when comparing the effects of 25-yr continuous conventional, minimum, and no-tillage corn production on the seed bank. They also noted that the greatest overall species diversity occurred in a permanent sod growing adjacent to the corn plots and attributed greater diversity in undisturbed soils to the increased availability of niches for colonization by winter annuals, biennials, and perennials. Few species were observed at the turfgrass site in the aboveground flora and in the seed bank (Table 5), although the distribution of weeds by life cycle was similar to the no-tillage corn and forest border sites. Low species diversity at the turfgrass site probably was due to long-term intensive management of the turfgrass and diligent weed control practices, which resulted in low total weed populations.

There was less association between species found in the seed bank and those observed in the aboveground flora at the no-tillage corn, turfgrass, and forest border sites compared to the vegetable site (Tables 3 and 4), which likely was due to lower seed production by perennial weeds, as a group, compared to annual weeds (Table 2). The patch-like growth habit of creeping perennials, coupled with the limited number of soil cores also may have contributed to lack of detection of their seeds in the soil. Other researchers (4, 16) also reported few or no seeds of creeping perennials at sites where they were present in the vegetation.

Total seed numbers in the soil seed banks at the various sites (Table 5) did not reflect viable seed number since no attempt was made to distinguish between live and dead seeds. The majority of seeds appeared to be dead, as reported by others (13, 16). Total seed number at the vegetable site (141 450 seeds/m^2) was higher than that reported for vegetable crops (250 to 46 819 seeds/m^2) in a review by Cavers and Benoit (5), whereas seed number at the no-tillage corn site (87 100 seeds/m^2) was similar to the

77 800 seeds/m^2 reported by Cardina, et al. (4) for continuous corn no-tillage sites in Ohio. Total seed number at the turfgrass site (26 840 seeds/m^2) was within the range reported by Rice (28) for grasslands (287 to 31 344 seeds/m^2), but seed number for the forest interior (32 130 seeds/m^2) was higher than the range reported by Pickett and McDonnell (27) for similarly aged deciduous forests of North America (121 to 3400 seeds/m^2). The vegetable site had the greatest number of seeds of all the sites, which was consistent with the high proportion of prolific summer annual species in the standing vegetation at this site compared to the other sites. Lower seed numbers at the forest border and forest interior sites were consistent with previous research showing a decrease in seed bank size as succession progresses (27).

The presence of most species in the seed bank could be explained by their seed production capacity, seed longevity characteristics, and/or relative abundance in the aboveground flora. The uniformity of species distribution in the standing flora also would have been helpful in explaining the seed bank data (13); however, this was not evaluated as part of the class exercise.

Assessment of laboratory exercise. Students were asked to rank all laboratory exercises for their instructional value on a scale of 1 (excellent) to 5 (poor) in fall 1992 and spring 1993. The seed bank exercise received an average rating of 3.1 ± 1.3 and 2.4 ± 1.2 in those quarters, respectively, indicating that students perceived this exercise to be average to slightly above average in instructional value. The seed bank exercise generally was the only exercise which required a written report, and in spring 1991, during which a report for another laboratory exercise also was required, both exercises were ranked below other exercises that did not require reports. Students' written comments showed that those who viewed the exercise negatively objected primarily to the time and difficulty involved in writing the report. Some students felt that there was too much to cover in the report and wanted to focus on fewer sites so as to treat them in greater depth. Other students wanted more credit for the report, more diversity in the seeds found in the soil, or more in-class discussion of background information for the report as well as in-class discussion of the results.

Some of the positive written comments made by students regarding the seed bank exercise were that it allowed the study of interesting habitats, made them realize how many seeds were in the soil, was relevant to lecture and other laboratory material, helped them draw generalizations about weed types in different environments, made them think about weed life cycles versus weed management, and was a good thinking exercise. Others enjoyed the "hands-on" procedures involved in the weed survey, seed separation, and seed identification, and the experience of working in groups.

From the author's perspective, this laboratory was one of the most valuable exercises ever conducted, in that it provided a meaningful framework for teaching weed and seed identification while also demonstrating important lecture material on weed biology and ecology. Despite the limited amount of soil from which seeds were extracted and the lack of professional weed identification skills among students, the data were generally consistent over quarters and with previous research, thus illustrating well the principles taught in lecture. Students had an opportunity to examine weeds in their natural habitat and learned a simple seed separation procedure that exposed them to the condition and numbers of seeds in the soil. The ubiquity of weeds in the seed banks of environments ranging from those highly managed by man to old-field successional forest promoted an awareness of the importance of weeds in the ecology of agricultural, urban, and natural environments. The laboratory report required students to integrate and apply lecture material and proved to be a good exercise on interpretive, concise writing. There were outstanding reports every quarter and it was gratifying to see that most students grasped the relationship between disturbance, weed life cycles, and weed seed production and seed longevity in determining the nature of weed communities and the soil seed bank.

ACKNOWLEDGMENTS

The assistance of Dan Scott in preparing the data and tables is gratefully appreciated. Dan Scott, Kirk Reese, and Ted Webster provided invaluable assistance in conducting this exercise.

LITERATURE CITED

1. Bassett, I. J. and D. B. Munro. 1986. The biology of Canadian weeds. 78. *Solanum carolinense* L. and *Solanum rostratum* Dunal. Can. J. Plant Sci. 66:977–991.
2. Best, K. F. and G. I. McIntyre. 1975. The biology of Canadian weeds. 9. *Thlaspi arvense* L. Can. J. Plant Sci. 55:279–292.
3. Burnside, O. C., C. R. Fenster, L. L. Evetts, and R. F. Mumm. 1981. Germination of exhumed weed seed in Nebraska. Weed Sci. 29:577–586.
4. Cardina, J., E. Regnier, and K. Harrison. 1991. Long-term tillage effects on seed banks in three Ohio soils. Weed Sci. 39:186–194.
5. Cavers, P. B. and D. L. Benoit. 1989. Seed banks in arable land. p. 309–328

in M. A. Leck, V. T. Parker, and R. L. Simpson, eds. Ecology of Soil Seed Banks. Academic Press, New York. 462 p.

6. Cavers, P. and J. Harper. 1964. Biological flora of the British Isles: *Rumex obtusifolius* and *Rumex crispus*. J. Ecol. 52:737–766.
7. Cavers, P. B., M. I. Heagy, and R. F. Kokron. 1979. The biology of Canadian weeds. 35. *Alliaria petiolata* (M. Bieb.) Cavara and Grande. Can. J. Plant. Sci. 59:217–229.
8. Darlington, H. and G. Steinbauer. 1961. The 80 year period of Dr. Beal's seed viability experiment. Am. J. Bot. 38:379–381.
9. Delorit, R. J. 1970. An Illustrated Taxonomy Manual of Weed Seeds. Agronomy Publications, River Falls, WI. 175 p.
10. Dickerson, C. T., Jr. and R. D. Sweet. 1971. Common ragweed ecotypes. Weed Sci. 19:64–66.
11. Doersch, R. 1987. Fall panicum—a native American. Crops Soils Mag. 39(7):10–11.
12. Doohan, D. J. and T. J. Monaco. 1992. The biology of Canadian weeds. 99. *Viola arvensis* Murr. Can. J. Plant Sci. 72:187–201.
13. Forcella, F., R. G. Wilson, K. A. Renner, J. Dekker, R. G. Harvey, D. A. Alm, D. D. Buhler, and J. Cardina. 1992. Weed seedbanks of the U.S. Corn Belt: magnitude, variation, emergence, and application. Weed Sci. 40:636–644.
14. Harrington, J. F. 1972. Seed storage and longevity. p. 145–245 *in* T. T. Kozlowski, ed. Seed Biology, Vol. 3. Academic Press, New York. 422 p.
15. Holm, L. G., D. L. Plucknett, J. V. Pancho, and J. P. Herberger. 1977. The World's Worst Weeds—Distribution and Biology. The University Press of Hawaii, Honolulu. 609 p.
16. Jensen, H. A. 1969. Content of buried seed in arable soil in Denmark and its relation to the weed population. Dan. Bot. Ark. 27:1–55.
17. Madsen, S. B. 1962. Germination of buried and dry stored seeds. III. 1934–1960. Proc. Int. Seed Test. Assn. 27:920–928.
18. Malone, C. R. 1967. A rapid method for enumeration of viable seed in soil. Weed Sci. 15:381–382.
19. Martin, A. C. and W. D. Barkley. 1961. Seed Identification Manual. Univ. of California Press, Berkeley, Los Angeles and London. 221 p.
20. Martin, J. W. and W. H. Leonard. 1967. p. 988 *in* Principles of Field Crop Production, 2nd Ed. MacMillan Co., New York. 1044 p.
21. McWhorter, C. G. 1989. History, biology, and control of Johnsongrass. Rev. Weed Sci. 4:85–121.
22. Menges, R. M. 1987. Weed seed population dynamics during six years of weed management systems in crop rotations on irrigated soil. Weed Sci. 35:328–332.
23. Miyanishi, K. and P. B. Cavers. 1980. The biology of Canadian weeds. 40. *Portulaca oleracea* L. Can. J. Plant Sci. 60:953–963.
24. Montgomery, F. H. 1977. Seeds and Fruits of Plants of Eastern Canada and Northeastern United States. Univ. of Toronto Press, Toronto and Buffalo. 232 p.
25. Moore, R. J. 1975. The biology of Canadian weeds. 13. *Cirsium arvense* (L.) Scop. Can. J. Plant Sci. 55:1033–1048.
26. Muenscher, W. C. 1955. p. 4 *in* Weeds. MacMillan Co, New York. 340 p.
27. Pickett, S. T. A. and M. J. McDonnell. 1989. Seed bank dynamics in temperate deciduous forest. p. 123–147 *in* M. A. Leck, V. T. Parker, and R. L. Simpson, eds. Ecology of Soil Seed Banks. Academic Press, New York. 462 p.
28. Rice, K. J. 1989. Impacts of seed banks on grassland community structure and population dynamics. p. 211–230 *in* M. A. Leck, V. T. Parker, and R. L. Simpson, eds. Ecology of Soil Seed Banks. Academic Press, New York. 462 p.
29. Roberts, H. A. 1981. Seed banks in soil. Adv. Appl. Biol. 6:1–55.
30. Roberts, H. F. 1936. Seed production in the dandelion. Sci. Agric. 17:235–242.
31. Santelmann, P. W., J. A. Meade, and R. A. Peters. 1963. Growth and development of yellow foxtail and giant foxtail. Weeds 11:139–142.
32. Schreiber, M. M. 1965. Effect of date of planting and stage of cutting on seed production of giant foxtail. Weeds 13:60–62.
33. Stevens, O. A. 1932. The number and weight of seeds produced by weeds. Am. J. Bot. 19:784–794.
34. Stevens, O. A. 1957. Weights of seeds and numbers per plant. Weeds 5:46–55.
35. Stoller, E. W. and R. A. Myers. 1989. Effects of shading and soybean (*Glycine max* L.) interference on *Solanum ptycanthum* (Dun.) (eastern black nightshade) growth and development. Weed Res. 29:307–316.
36. Stratton, D. A. 1991. Life history variation within populations of an asexual plant, *Erigeron annuus* (Asteraceae). Am. J. Bot. 78:723–728.
37. Thullen, R. J. and P. E. Keeley. 1979. Seed production and germination in *Cyperus esculentus* and *Cyperus rotundus*. Weed Sci. 27:502–505.
38. Timmons, F. 1949. Duration of viability of bindweed seed under field conditions and experimental results in the control of bindweed seedlings. Agron. J. 41:130–133.
39. Toole, E. H. and E. Brown. 1946. Final results of the Duvel buried seed experiment. J. Agric. Res. 72:201–210.
40. Vanden Born, W. H. 1971. Green foxtail: seed dormancy, germination and growth. Can. J. Plant Sci. 51:53–59.
41. Warwick, S. I. 1979. The biology of Canadian weeds. 37. *Poa annua* L. Can. J. Plant Sci. 59:1053–1066.
42. Weaver, S. E. and W. R. Riley. 1982. The biology of Canadian weeds. 53. *Convolvulus arvensis* L. Can. J. Plant Sci. 62:461–472.
43. Werner, P. A., I. K. Bradbury, and R. S. Gross. 1980. The biology of Canadian weeds. 45. *Solidago canadensis* L. Can. J. Plant Sci. 60:1393–1409.
44. Werner, P. A. and Rioux, R. 1977. The biology of Canadian weeds. 24. *Agropyron repens* (L.) Beauv. Can. J. Plant Sci. 57:905–919.
45. Wilson, R. G. 1988. Biology of weed seeds in the soil. p. 25–39 *in* M. A. Altieri and M. Liebman, eds. Weed Management in Agroecosystems: Ecological Approaches. CRC Press, Boca Raton, FL. 354 p.