

Notes on Succession in Old Fields in Southeastern Ontario: the Herbs

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Crowder, A., R. Harmsen, and S. E. Blatt. 2007. Notes on succession in old fields in southeastern Ontario: the herbs. *Canadian Field-Naturalist* 121(2): 182-190.

Vegetation in abandoned hayfields was monitored during 1976-1998. An earlier successional stage followed ploughing. Changes in tree, shrub and vine populations have been reported earlier and showed expected increases in species richness and cover. Highest species richness of herbs occurred three years after ploughing. Non-woody species richness trended irregularly downward, while non-woody cover was variable, peaking in 1987. Within the herbaceous community, year-to-year changes in cover and frequency of species in the following selected groups are reported here: 18 grasses including sown and adventive species; 13 legumes including two sown species; 14 macroforbs of the *Compositae*, including a goldenrod, *Solidago canadensis*, which dominated parts of the fields; a rosette weed, *Taraxacum officinalis*; sedges, horsetails and some other minor components. Grasses and goldenrods were grazed, sometimes intensively and repeatedly, by insects; grasses were impacted by skipper larvae (*Thymelicus lineola*), and goldenrods by beetle larvae (*Trirhabda* spp.). Effects of repeated outbreaks on host plant cover are shown for two plots (100 m²) matching the scale of outbreaks.

Key Words: old field herbs, phytophagous insects, plant succession, goldenrods, grasses, legumes, Ontario.

Two abandoned hayfields in southeastern Ontario were selected as sites in which to investigate possible effects of insect herbivory on early stages of secondary succession. The location, geology, history of land use, and soils have been described earlier (Crowder and Harmsen 1998). Their nutrient status was discussed by Epp and Aarssen (1988). Estimates of increasing cover and abundance of trees, shrubs and vines (51 species) during 1976-1998 were shown to follow classic successional models, although with unusual pioneer species. After two decades the structure of the vegetation had become heterogeneous, with groves of small trees, shrub thickets, patches dominated by macroforbs and patches still dominated by grasses. Cover varied with fluctuations of weather from year to year, while soil differences influenced cover and species richness.

Most successional studies on old fields use synoptic records from fields of different ages, a method which obscures minor fluctuations and differences between fields. In this paper, year-to-year observations are used to follow temporal changes in the herbaceous community and to relate its cover and species richness to those of the woody layers. Herbaceous species found in 27 experimental plots are listed to allow comparisons with other areas; lichens and bryophytes are omitted. Differences in soil texture (Crowder and Harmsen 1998) influenced cover and richness.

Within the herbaceous community, details of temporal change in selected groups of plants and some specific interactions are reported here. Grasses were the main constituents of the hayfields, including both agricultural and adventives species. Legumes also included sown and invasive species. Invasive macroforbs,

mainly *Solidago* and *Aster* species, dominated parts of the fields; population changes of 15 species are reported. *Taraxacum officinalis*, Dandelion, was selected to represent rosette plants. Sedges, horsetails and a few other minor components are described.

During the decades when vegetation was monitored, arthropods were also sampled (McBrien et al. 1983). Two insect populations had repetitive outbreaks which caused significant decreases of plant cover, and are therefore the only arthropods reported here. Larvae of the hesperiid European Skipper (*Thymelicus lineola*) grazed on grasses, particularly on Timothy, *Phleum pratense* (Henderson 1986). Larvae of beetles of the genus *Trirhabda* Le Conte (Coleoptera, Chrysomelidae), mostly *Trirhabda virgata*, grazed primarily on leaves of *Solidago canadensis*, causing intense defoliation. The strong effect of one or more outbreaks of beetles on plant vigour was replicated experimentally (McBrien and Harmsen 1987). These defoliations can cause changes in successional pathways at the grass-macroforb stage by affecting the relative dominance of grass or goldenrods. Blatt et al. (2001) have used these data to develop a successional model including herbivore effects, showing possible outcomes for the herbs.

Methods

A hayfield abandoned in 1970 and one mown for hay until 1975 were selected at Queen's University Biology Station at Opinicon, Frontenac County, Ontario (44°03'N, 76°0'W). Nine permanent plots, each 100 m², were demarcated in 1975 in the older field, which was called S field, for *Solidago*. Eighteen similar

plots were placed in the younger field, and nine of these were ploughed once; these ploughed plots were called P and the undisturbed plots G, for grass. All plant species present in the 27 plots were listed in June and September of sampling years: 1976-1988, 1995, 1998. Cover was estimated using five randomly placed quadrats within each plot; cover values used in this paper were from September (McBrien et al. 1983; Henderson 1986). Each quadrat was 50 cm × 50 cm in area. Values were compared using Scheffe's mean separation test (Zar 1984; Blatt et al. 2003). Percentage frequency, the number of quadrats in which a species was recorded at a particular time (Mellinger 1972; Eriksson and Jakobssen 1998), was used as a measure of relative abundance (Maycock and Guzikowa 1984).

Nomenclature follows Newmaster et al. (1998); voucher specimens were lodged at the Fowler Herbarium, Queen's University. Lichens, mosses and liverworts have been omitted from this paper.

Results and Discussion

Species richness of woody species and of herbs per 100 m² plot, through 1976-1998, is shown in Figure 1. Note gaps in sampling after 1988. Herb richness trended downward with high annual variance while woody species richness increased over time (see Crowder and Harmsen 1998).

The range of species richness was 7-65 in ploughed (P) plots, 6-42 in grass-dominated (G) plots, and 6-33 in *Solidago* (S) plots. Species richness of herbs and of woody plants in a grass plot (G1) and a ploughed plot (P2) are shown in Figures 2 and 3. Because soil texture was found to be correlated with species richness, the selected plots were matched for texture; both are sandy, with relatively low richness (Crowder and Harmsen 1998). Note the difference in scale between Figures 2B and 3B. Species richness peaked in P2 three years after ploughing when several weedy species were present (cf. Armesto and Pickett 1985).

Herbaceous taxa observed in 27 plots during 1976-1998 are listed in Table 1, in alphabetical order, with English names added (Newmaster et al. 1998). The closest comparable study site is a 50-year-old field, at Erindale (Toronto area), described by Maycock and Guzikowa (1984), in which 93% of the species listed at Opinicon were found. Other old fields in Ontario have been described by Lamoureaux (1970), Reader (1990) and Reader and Buck (1991). Fewer of the Opinicon species (37%) were found in abandoned hayfields in New York State described by Mellinger (1972), and only 20% in old fields in Quebec (Dansereau and Gille 1949). The proportion of introduced species at Opinicon was 37%, which is higher than the average for the Kingston region (Beschel et al. 1970). They included both crop plants and weeds.

During 1976-1998 the cover value of woody plants for all plots combined increased significantly (Crowder and Harmsen 1998); herbaceous cover, however, did

not decrease significantly over time (Figure 1). Mean percent cover of non-woody species in 1998 was not significantly different from that in 1988, 1986, 1984, 1978, 1977 and 1976. Years with high cover were 1979, 1980, 1981, 1985, or 1987 (Figure 1). These values suggest that herbaceous cover was related to year-to-year changes in weather or herbivory rather than to a steady increase in shading. No correlations of cover values with available climatic data were found, although the years with low cover had partial droughts that caused soil cracking.

Herb cover in selected plots is shown in Figures 2A and 3A, with relatively low variance between years. Plot G1 consistently had higher values than P2. The main components of herb cover are discussed in the following section. The hayfields had been sown with *Phleum pratense* (Timothy) and *Poa pratensis* (Kentucky Blue Grass), which maintained their frequency after the cessation of mowing (see Table 2). Mellinger (1972) also reported their high frequency in old hayfields in New York. In the Opinicon fields the two species are associated randomly (Epp and Aarssen 1988).

Table 2 lists annual percentage frequency of nine grass species. The most frequent invasive grasses have been *Elymus repens*, *Poa compressa* and *Calamagrostis canadensis*. Other less common invasive grasses, not shown on Table 2, were *Bromus inermis* ssp. *pumellianus*, *Echinochloa crusgalli*, *Elymus trachycaulon* ssp. *trachycaulon*, *Muhlenbergia mexicana*, *Panicum acuminatum*, *Poa capillare*, *Poa annua*, *Setaria pumila* and *Setaria viridis*. Annual cover of all grass species in all plots varied from a mean of 35% in 1998 to a mean of 87% in 1987. Cover in the G (grass) plots exceeded 100% in some years, because layers of two or more species developed. Differences between the three sets of plots were not consistent.

Cover of grasses did not show synchronous trends within sets of plots. Changes in grass cover were not correlated with soil texture; the two plots shown in Figures 2 and 3 were matched for soil texture but the undisturbed plot G1 in Figure 2 had high grass cover and the ploughed plot in Figure 3 had not. A temporal pattern in the grass-dominated plot showed successive peaks three to five years apart followed by declines in cover values. This pattern was typical of grass-dominated plots. The disturbed ploughed plot shown in Figure 3 had two less marked peaks and declines. Herbivory was demonstrated by Henderson (1986) to reduce grass cover significantly; he counted larvae of a hesperiid European Skipper (*Thymelicus lineola*) and found that peaks of larval numbers coincided with low cover of *Elymus repens*, *Phleum pratense* and *Poa pratensis*, and low concentrations of skipper larvae with high grass cover. The grass species differed in their capacity to recover after an insect outbreak, with *Phleum pratense* being most negatively affected. Outbreak behaviour by the European Skipper has been documented by Pengelly (1961) elsewhere in Ontario.

TABLE 1. Alphabetic list of herbs recorded within 27 plots during 1975-1998 at two old fields at Opinicon, with English names. Nomenclature follows Newmaster et al. (1998).

<i>Acalypha virginica</i> . Copperleaf	<i>Fragaria virginiana</i> . Wild Strawberry
<i>Achillea millefolium</i> ssp. <i>millefolium</i> . Yarrow	<i>Galinsoga quadriradiata</i> . Quickweed
<i>Agrimonia gryposepala</i> . Hooked Agrimony	<i>Galium obtusum</i> . Wild Madder
<i>Agrostis gigantea</i> . Redtop	<i>Galium trifidum</i> ssp. <i>trifidum</i> . Small Bedstraw
<i>Ambrosia artemisiifolia</i> . Common Ragweed	<i>Gentiana andrewsii</i> . Bottle Gentian
<i>Anaphalis margaritacea</i> . Pearly Everlasting	<i>Geranium bicknellii</i> . Bicknell's Crane's Bill
<i>Anemone canadensis</i> . Canada Anemone	<i>Geum aleppicum</i> . Yellow Avens
<i>Antennaria neglecta</i> . Field Pussytoes	<i>Geum canadense</i> . White Avens
<i>Antennaria parlinii</i> . Plantain-leaved Pussytoes	<i>Hieracium aurantiacum</i> . Orange Hawkweed
<i>Arctium minus</i> ssp. <i>minus</i> . Common Burdock	<i>Hieracium piloselloides</i> . King Devil
<i>Artemisia absinthium</i> . Absinth	<i>Hypericum perforatum</i> . Common St. John's Wort
<i>Asclepias syriaca</i> . Common Milkweed	<i>Juncus dudleyi</i> . Dudley's Rush
<i>Aster cordifolius</i> . Heart-leaved Aster	<i>Lactuca canadensis</i> . Wild Lettuce
<i>Aster ericoides</i> . Heath Aster	<i>Lepidium campestre</i> . Field Peppergrass
<i>Aster lanceolatus</i> . Panicked Aster (includes <i>Aster simplex</i>)	<i>Lithospermum officinale</i> . Gromwell
<i>Aster lateriflorus</i> . Calico Aster	<i>Lobelia inflata</i> . Indian Tobacco
<i>Aster umbellatus</i> . Flat-topped White Aster	<i>Lycopus americanus</i> . Cut-leaved Water Horehound
<i>Aster urophyllus</i> . Arrow-leaved Aster	<i>Lycopus uniflorus</i> . Water Horehound
<i>Barbarea vulgaris</i> . Wintercress	<i>Lysimachia terrestris</i> . Yellow Loosestrife
<i>Bromus inermis</i> ssp. <i>pumpellianus</i> . Smooth Brome	<i>Medicago lupulina</i> . Black Medick
<i>Calamagrostis canadensis</i> . Canada Blue Joint	<i>Medicago sativa</i> ssp. <i>sativa</i> . Alfalfa
<i>Capsella bursa-pastoris</i> . Shepherd's Purse	<i>Medicago sativa</i> ssp. <i>falcata</i> . Medick
<i>Carex aurea</i> . Sedge	<i>Melilotus alba</i> . White Sweet Clover
<i>Carex communis</i> . Common Sedge	<i>Melilotus officinalis</i> . Yellow Sweet Clover
<i>Carex debilis</i> . Sedge	<i>Mentha arvensis</i> ssp. <i>borealis</i> . Wild Mint
<i>Carex foenea</i> . Sedge	<i>Muhlenbergia mexicana</i> . Dropseed
<i>Carex gracillima</i> . Filiform Sedge	<i>Oenothera perennis</i> . Sundrops
<i>Carex granularis</i> . Granular Sedge	<i>Onoclea sensibilis</i> . Sensitive Fern
<i>Carex laxiflora</i> . Slender Sedge	<i>Osmunda regalis</i> . Royal Fern
<i>Carex normalis</i> . Normal Sedge	<i>Oxalis stricta</i> . Yellow Wood Sorrel
<i>Carex scoparia</i> . Sedge	<i>Panicum acuminatum</i> . Woolly Panic Grass
<i>Carex vulpinoidea</i> . Fox Sedge	<i>Panicum capillare</i> . Witch Grass
<i>Cerastium fontanum</i> ssp. <i>triviale</i> . Common Mouse-ear Chickweed	<i>Panicum depauperatum</i> . Starved Panic Grass
<i>Chenopodium simplex</i> . Maple-leaved Goosefoot	<i>Phleum pratense</i> . Timothy
<i>Chrysanthemum leucanthemum</i> . Ox-eye Daisy	<i>Physalis heterophylla</i> . Clammy Ground Cherry
<i>Cichorium intybus</i> . Chicory	<i>Plantago lanceolata</i> . Narrow-leaved Plantain
<i>Cirsium arvense</i> . Canada Thistle	<i>Plantago major</i> . Common Plantain
<i>Clinopodium vulgare</i> . Wild Basil	<i>Plantago rugelii</i> . Rugel's Plantain
<i>Convolvulus arvensis</i> . Field Bindweed	<i>Poa annua</i> . Annual Blue Grass
<i>Conyza canadensis</i> . Canada Fleabane	<i>Poa compressa</i> . Canada Blue Grass
<i>Dactylis glomerata</i> . Orchard Grass	<i>Poa pratensis</i> ssp. <i>pratensis</i> . Kentucky Blue Grass
<i>Danthonia spicata</i> . Poverty Oat Grass	<i>Polygonum convolvulus</i> . Black Bindweed
<i>Daucus carota</i> . Wild Carrot	<i>Polygonum persicaria</i> . Lady's Thumb
<i>Dianthus armeria</i> . Deptford Pink	<i>Polygonum sagittatum</i> . Arrowleaved Tear-Thumb
<i>Echinochloa crusgalli</i> . Echinochloa	<i>Potentilla argentea</i> . Silvery Cinquefoil
<i>Echium vulgare</i> . Blueweed	<i>Potentilla canadensis</i> . Old Field Cinquefoil
<i>Elymus repens</i> . Couchgrass	<i>Potentilla inclinata</i> . Downy Cinquefoil
<i>Elymus trachycaulus</i> ssp. <i>trachycaulus</i> . Slender Wheat Grass	<i>Potentilla norvegica</i> . Rough Cinquefoil
<i>Epilobium hirsutum</i> . Hairy Willow Herb	<i>Potentilla recta</i> . Erect Cinquefoil
<i>Equisetum arvense</i> . Field Horsetail	<i>Prunella vulgaris</i> ssp. <i>vulgaris</i> . Selfheal
<i>Equisetum hyemale</i> . Scouring Rush	<i>Ranunculus abortivus</i> . Kidney-leaf Buttercup
<i>Erigeron annuus</i> . Daisy Fleabane	<i>Ranunculus acris</i> . Field Buttercup
<i>Erigeron philadelphicus</i> ssp. <i>philadelphicus</i> . Common Fleabane	<i>Rudbeckia hirta</i> . Black-eyed Susan
<i>Erigeron strigosus</i> . Lesser Fleabane	<i>Rumex acetosella</i> ssp. <i>acetosella</i> . Sheep Sorrel
<i>Eupatorium maculatum</i> . Joe Pye Weed	<i>Rumex crispus</i> . Curly Dock
<i>Eupatorium perfoliatum</i> . Boneset	<i>Sanicula marilandica</i> . Black Snakeroot
<i>Eupatorium rugosum</i> . White Snakeroot	<i>Setaria pumila</i> . Yellow Foxtail
<i>Euthamia graminifolia</i> . Grass-leaved Goldenrod	<i>Setaria viridis</i> . Green Foxtail
<i>Fragaria vesca</i> ssp. <i>americana</i> . Wood Strawberry	<i>Silene vulgaris</i> . Bladder Campion
	<i>Sisymbrium officinale</i> . Hedge-Mustard
	<i>Sisyrinchium angustifolium</i> . Blue-eyed Grass
	<i>Solidago caesia</i> . Blue-stemmed Goldenrod

TABLE 1. (continued)

<i>Solidago canadensis</i> . Canada Goldenrod	<i>Tragopogon dubius</i> . Goatsbeard
<i>Solidago gigantea</i> . Tall Goldenrod	<i>Tragopogon pratensis</i> ssp. <i>pratensis</i> . Showy Goatsbeard
<i>Solidago juncea</i> . Early Goldenrod	<i>Trifolium aureum</i> . Yellow Clover
<i>Solidago nemoralis</i> ssp. <i>nemoralis</i> . Gray Goldenrod	<i>Trifolium campestre</i> . Smaller Hop Clover
<i>Solidago rugosa</i> . Rough-stemmed Goldenrod	<i>Trifolium hybridum</i> . Alsike Clover
<i>Sonchus asper</i> ssp. <i>asper</i> . Spiny Sow-thistle	<i>Trifolium pratense</i> . Red Clover
<i>Spiranthes romanzoffiana</i> . Hooded Ladies' Tresses	<i>Verbascum thapsus</i> . Common Mullein
<i>Stellaria borealis</i> ssp. <i>borealis</i> . Northern Stitchwort	<i>Verbena hastata</i> . Blue Vervain
<i>Stellaria graminea</i> . Stitchwort	<i>Veronica serpyllifolia</i> ssp. <i>serpyllifolia</i> . Thyme-leaved Speedwell
<i>Stellaria media</i> . Chickweed	<i>Vicia cracca</i> . Cow Vetch
<i>Taraxacum officinale</i> . Dandelion	<i>Vicia sativa</i> ssp. <i>nigra</i> . Common Vetch
<i>Teucrium canadense</i> ssp. <i>canadense</i> . Germander	<i>Vicia tetrasperma</i> . Slender Vetch
<i>Thlaspi arvense</i> . Field Pennycress	<i>Viola</i> sp. Violet

Larval outbreaks are considered to affect the successional pathway in the Opinicon fields in a model developed from our data by Blatt et al. (2001). When insect herbivory on grasses in old fields was studied by Brown et al. (1988), *Elymus repens* was the grass species most affected by Homoptera/Auchenorrhyncha; these authors considered that both texture and structure of the successional vegetation were affected by the insects.

The initial seed mix contained *Medicago sativa* ssp. *sativa* (Alfalfa) and possibly *Trifolium pratense* (Red Clover) which have persisted in the fields. *Medicago sativa* frequency was 3-5% in 1976-1980, rose to 12% in 1983 and fell again to 2% in the 1990s. *Trifolium pratense* frequency was 35% in 1976, fell to less than 8% during 1980-1995 and rose again to 22% in 1998. *Trifolium aureum*, *Trifolium campestre* and *Trifolium hybridum* were recorded occasionally.

Vetches (*Vicia sativa* ssp. *nigra*, *Vicia cracca*, and *Vicia tetrasperma*) became more frequent in later years with a maximal frequency of 69% for *Vicia cracca* in 1987. Possibly these straggling plants benefited from the cessation of mowing. Other legumes recorded were *Melilotus alba*, *Melilotus officinalis* and *Medicago lupulinus*, randomly distributed except for *Medicago lupulina*, which was most frequent in 1976-1979 in the ploughed plots.

Macroforb areas of the fields have been and are dominated by *Solidago canadensis* (Canada Goldenrod), which we observed to spread by both seeds and rhizomes. Its importance in old field succession in North America has been widely reported (e.g., Dale et al. 1966; Goldberg and Gross 1988). Percentage frequency of *Solidago canadensis* in all plots during 1976-1998 is shown as mean values in Table 2, starting with minimal values in 1976 and reaching a maximum in 1987-1988. Frequencies of *Solidago nemoralis* (Old Field Goldenrod), *Solidago caesia* (Blue-stemmed Goldenrod), and *Euthamia graminifolia* (Grass-leaved Goldenrod), also given in Table 2, were higher in the 1980s than in the 1970s or 1990s. When the three sets of plots were compared, *Solidago canadensis* and *Soli-*

dago caesia were found to be most frequent in the S plots (during 1976-1998 the mean frequency of *Solidago canadensis* in S plots was 47%, in the P plots 37% and in the G plots 26%). *Solidago nemoralis* and *Solidago juncea* were generally more frequent in sandy dry plots. This distribution may be explained by different soil moisture tolerances among the congeners (Werner and Platt 1976).

Cover values for *Solidago canadensis* ranged from 1 to 100%. Patterns were not synchronous between plots. Two examples are shown. Figure 3 shows Plot P2, with three irregular peaks of goldenrod cover, and Figure 2 shows Plot G1 with only three years of sporadic goldenrod cover. The plot with three peaks and lows (Figure 3) had a periodicity also observed in other plots, while others had one, two, or three-and-a-half episodes. Some sandy plots similar to that shown in Figure 2 failed to develop dense *Solidago* cover, and did not have a series of highs and lows.

We have found that the cover of *Solidago canadensis* was negatively and significantly correlated with larval density of three species of *Trirhabda* beetles in the field (McBrien et al. 1983; Blatt et al. 2001). *Trirhabda virgata* was most abundant. Field experiments showed that effects on biomass and cover similar to those caused by larval grazing could be produced by manual defoliation (McBrien and Harmsen 1987).

Within a field, beetle outbreaks were not synchronous between plots. Outbreaks in the two fields also occurred at different times. In the P/G field, years with several plot peaks of *Solidago* cover were 1980, 1981, and 1985, and years with most lows were 1976, 1985 and 1998. That both peaks and lows occurred in 1985 shows the small scale of the beetle outbreaks, sometimes confined to a plot 100 m². Outbreaks on a much larger scale have been reported, for example, on a scale of several hectares (Werner et al. 1980), and over two hundred insect species have been reported on *Solidago canadensis*.

Macroforbs growing to the same size as some goldenrods included the asters *Aster umbellatus* (Flat-topped White Aster) and *Aster novae-angliae* (New

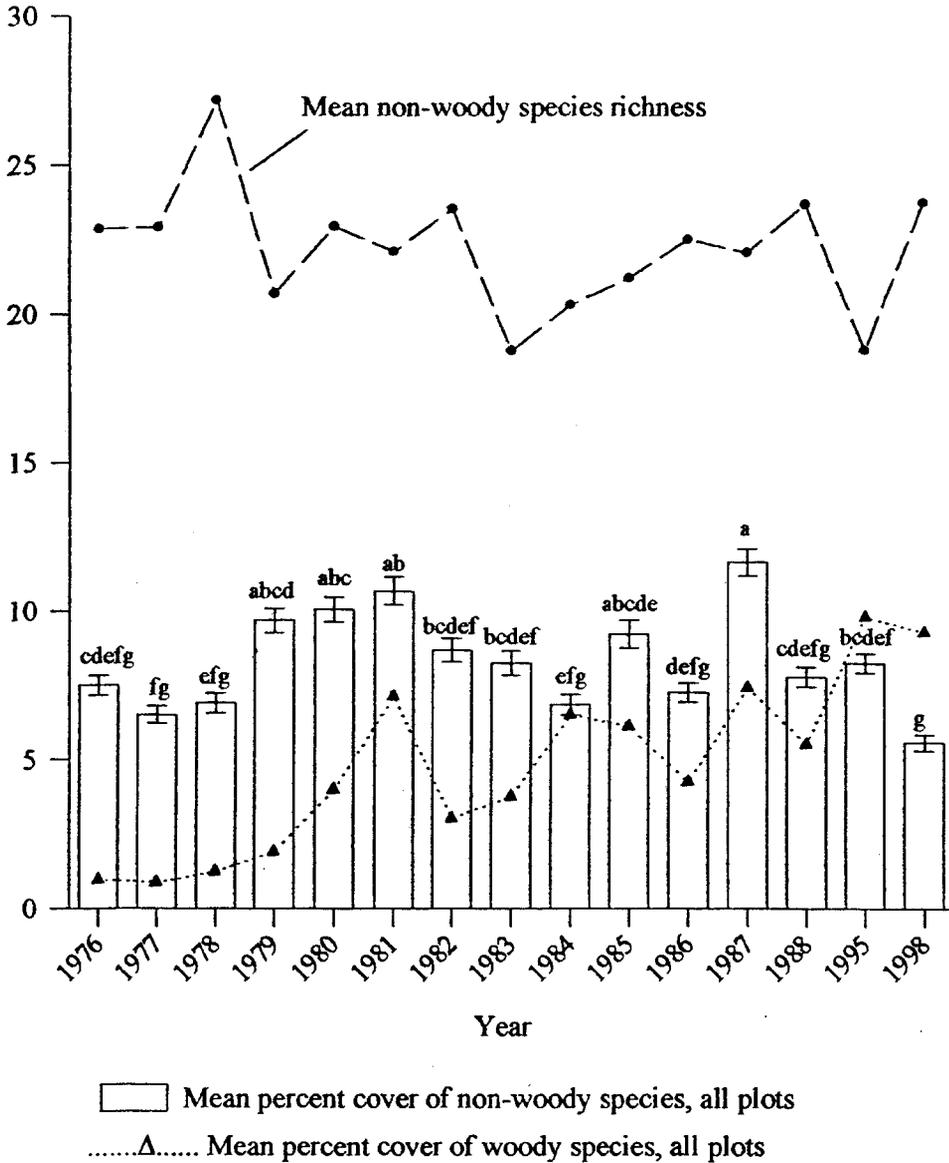


FIGURE 1. Comparison of woody and non-woody vegetation. Mean species richness of herbaceous plants in 27 plots (species number/100 m²) for the years 1976-1988, 1995 and 1998 is shown by dots. Mean percent cover of non-woody species in all plots in September is shown in the histogram; means which do not share the same letter are significantly different. Mean percent cover of woody species in all plots is indicated by a dotted line with triangles.

England Aster). During the years of observation the percentage frequency of these two species increased (Table 2). Three smaller species, *Aster lanceolatus* (included in *Aster simplex* in Table 2), *Aster lateriflorus* and *Aster ontarionis*, have been lumped together because they were generally intermingled in straggling clumps which also increased in frequency. *Aster*

cordifolius (Heart-leaved Aster) and *Aster urophyllus* (Arrow-leaved Aster), both of which are shade-tolerant (Semple et al. 1996), had low frequency. Five of the aster species found in the Opinicon fields were recorded by Maycock and Guzikowa (1984).

When all aster species are lumped together, mean annual cover ranged from 1 to 45%. Comparing dif-

TABLE 2. Mean percentage frequency of selected herbs in all plots during 1976-1988, 1995 and 1998 (n = 162)

Year	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1995	1998
<i>Poa pratensis</i>	67	65	52	71	68	57	70	60	40	74	77	76	79	77	68
<i>Phleum pratense</i>	54	40	37	48	46	52	44	19	34	26	30	41	52	37	23
<i>Elymus repens</i>	43	22	37	37	38	25	31	25	33	35	43	49	52	30	22
<i>Poa compressa</i>	0	0	0	0	3	0	23	0	<1	<1	<1	6	23	4	3
<i>Calamagrostis canadensis</i>	0	11	2	1	0	3	1	0	1	<1	0	23	29	14	16
<i>Panicum depauperatum</i>	3	6	2	3	0	0	0	<1	<1	<1	<1	4	1	0	0
<i>Panicum lanuginosum</i>	0	4	4	1	<1	1	2	<1	<1	0	2	0	<1	0	0
<i>Dactylis glomerata</i>	1	<1	1	0	<1	0	<1	0	<1	<1	<1	1	2	0	<1
<i>Agrostis gigantea</i>	0	0	0	0	0	0	0	0	0	0	5	0	<1	0	<1
<i>Solidago canadensis</i>	33	33	40	30	43	45	43	43	38	25	37	49	49	36	39
<i>Solidago nemoralis</i>	6	0	7	6	9	9	10	8	12	9	7	7	8	3	4
<i>Solidago rugosa</i>	2	1	2	4	4	4	6	6	4	9	6	4	4	2	6
<i>Euthamia graminifolia</i>	3	3	4	5	10	12	8	6	7	9	11	12	10	8	8
<i>Solidago gigantea</i>	1	1	0	1	4	2	4	6	6	21	7	3	4	4	6
<i>Solidago caesia</i>	<1	0	<1	0	<1	<1	<1	<1	0	0	0	0	0	<1	<1
<i>Solidago juncea</i>	0	0	0	0	0	0	2	2	1	7	6	4	6	4	0
<i>Aster umbellatus</i>	2	2	7	2	6	3	7	8	9	9	12	6	11	20	26
<i>Aster novae-angliae</i>	3	1	3	2	3	6	5	3	3	6	6	9	7	7	9
<i>Aster cordifolius</i> & <i>A. urrophyllus</i>	1	8	7	8	7	8	8	4	3	4	5	5	5	3	4
<i>Aster simplex</i> , <i>A. lateriflorus</i> & <i>A. ontarionis</i>	15	19	27	20	21	19	33	27	26	25	39	38	43	33	31
<i>Aster ericoides</i>	0	1	3	0	0	0	0	0	0	0	0	2	0	0	0

ferent plots, patterns of peaks and lows like those observed in *Solidago canadensis* occurred in some plots, but with a longer periodicity ranging up to ten years. Since these fluctuations in cover were not synchronous between plots or fields, it is possible that they were due to herbivory, like the changes in *Solidago* and grasses.

Two species of horsetail, *Equisetum arvense* and *Equisetum hyemale*, were present in the P/G field throughout 1976-1998 with a combined mean percentage frequency of 68%. Both species were most frequent in sandy plots and are locally common in disturbed habitats such as sandpits (Crowder et al. 1997). Cover did not exceed 29% for the two species combined in any year, and was generally low.

Mean frequency of *Taraxacum officinale* ranged from 13% in 1981 to 37% in 1988. Dandelions were present in all three sets of plots every year, with highest frequency in the S and lowest in the G plots. The rosette growth form of *Taraxacum officinale* is similar to that of many genera in the plots, such as *Hieracium* spp. and *Antennaria parlinii*, and probably facilitates early spring growth.

Sedges, *Carex* spp., were observed in all years and in all sets of plots, but were not analysed because of difficulty in distinguishing non-flowering stages. *Carex granularis*, *Carex laxiflora* and *Carex normalis* were relatively abundant. Mean annual frequency of all species was 39% and most plants were found in plots with high moisture content (Crowder and Harmsen 1998). Mean cover was less than 2% until 1979, rose to 7% in 1987, and then declined again.

Species which increased in both frequency and cover during 1976-1998 included *Asclepias syriaca* (Milkweed) and *Ranunculus acris* (Field Buttercup). Species which declined in both frequency and cover included *Rumex acetosella* ssp. *acetosella* (Sheep's Sorrel), *Ambrosia artemisiifolia* (Ragweed), *Oxalis stricta* (Yellow Wood Sorrel), and *Prunella vulgaris* ssp. *lanceolata* (Self-Heal). *Rumex acetosella* and *Ambrosia artemisiifolia*, which are weedy species, were mostly in the ploughed plots, whereas *Prunella vulgaris* was initially concentrated in grass plots. A minor component with low cover value but high frequency (40-50%) was *Potentilla recta* (Erect Cinquefoil).

When grass cover was lowered by grazing of *Thymelicus lineola*, feeding preferentially on *Phleum pratense*, cover of *Solidago* and *Aster* spp. in both fields increased rapidly; they then maintained their dominance at levels equal to that of *Poa pratensis*, preventing the recovery of *Phleum pratense* (Henderson 1986; Blatt et al. 2001; Blatt et al. 2003). In addition to interactions between grasses and goldenrods, other layers were affected. For example, when the cover of *Solidago canadensis* was decreased by the feeding of beetle larvae a chamaephyte, *Fragaria virginiana* (Wild Strawberry), showed significantly increased cover (McBrien et al. 1983). This finding

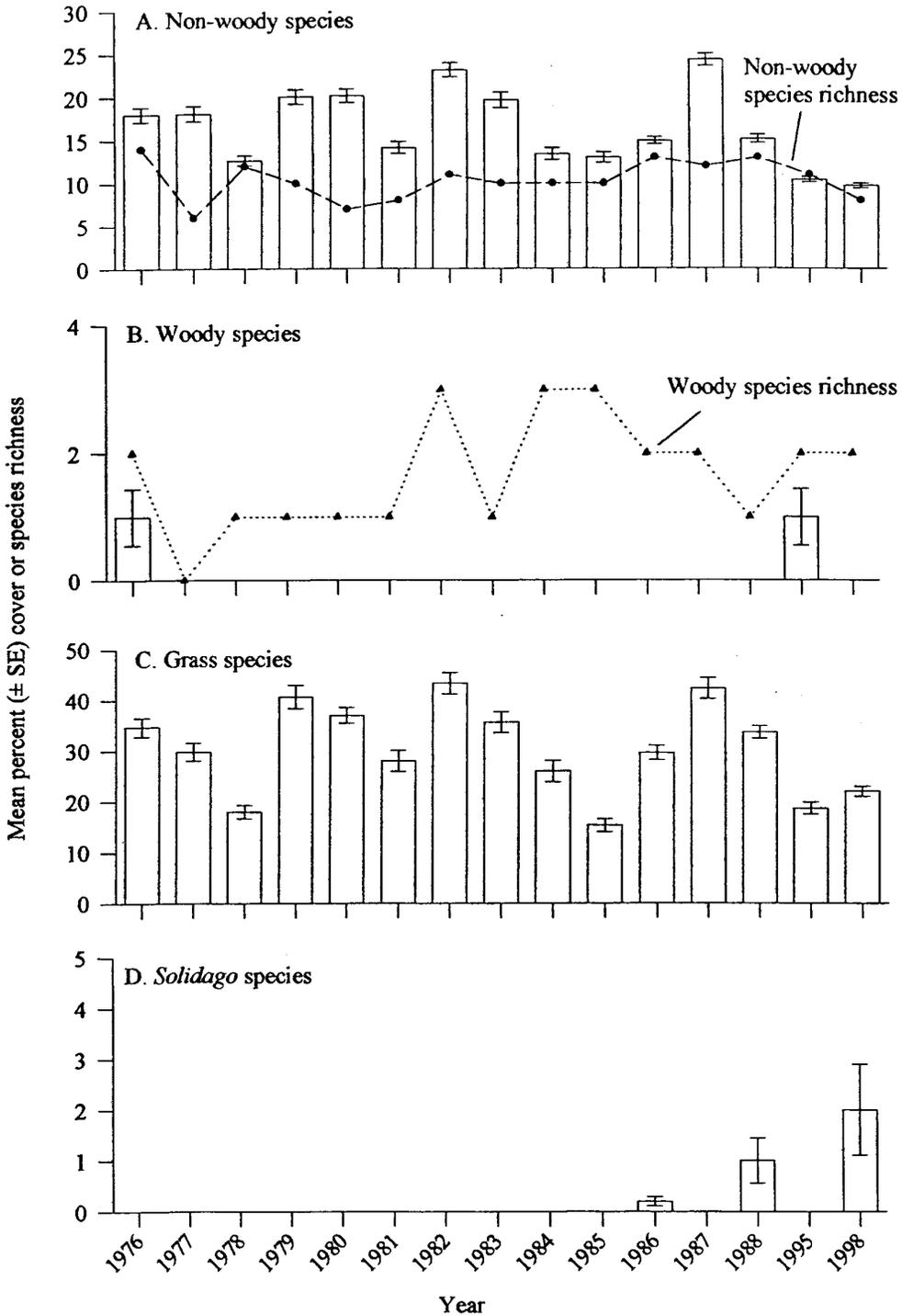


FIGURE 2. Conditions in grass plot G1 during 1976-1988, 1995 and 1998. 2A shows mean percent cover of non-woody species, and non-woody species richness (species number/100 m²). 2B shows cover and species richness of woody plants. 2C shows mean cover of all grass species. 2D shows *Solidago* species cover, which was only present in 1986, 1988 and 1998.

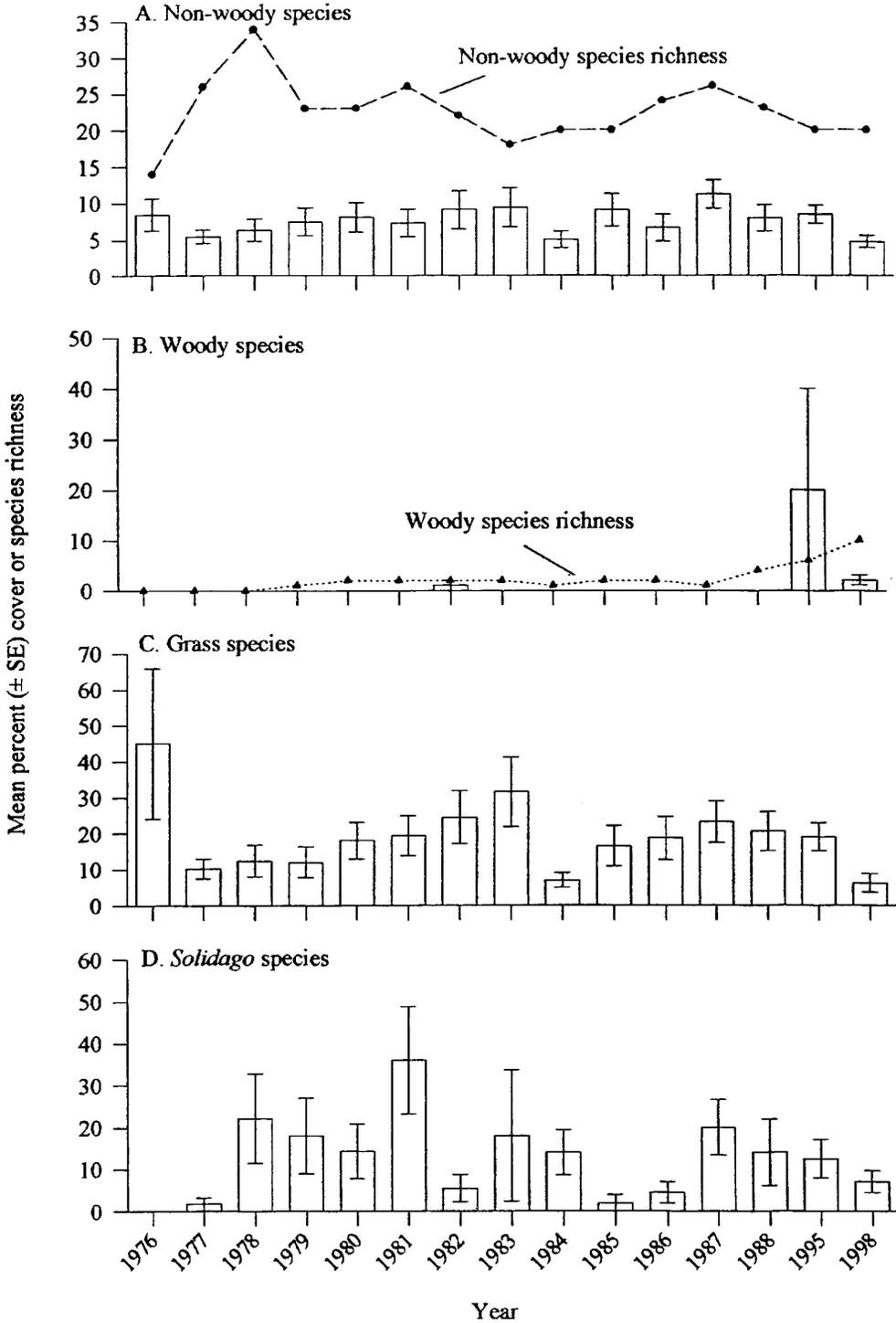


FIGURE 3. Conditions in ploughed plot P2 during 1976-1988, 1995 and 1998. 3A shows non-woody species richness (species/100 m²) and mean annual percent cover. 3B shows woody species richness and cover. 3C shows cover of all grass species with peaks and lows. 3D shows cover of *Solidago* species with peaks and lows.

has been confirmed elsewhere by Carson and Pickett (1990) who attributed it to decreased shading by the macroforb.

Shade-tolerant herbs in the plots included *Sanicula marilandica* (Black Snakeroot), *Teucrium canadense* ssp. *canadense* (Germander), *Lactuca canadensis* (Wild Lettuce), *Solidago caesia* and *Aster cordifolius*. The increase in woody plants documented by Crowder and Harmsen (1998) could have been expected to create conditions favouring increases of such shade-tolerant species. They did not, however, increase in frequency or cover over time. Presumably shaded microniches under plants such as goldenrods were present in early years and were later replaced by similar conditions under shrubs or trees.

Acknowledgments

Partial funding was received from the Ontario Ministry of Natural Resources; we particularly thank R. Wagner, S. Strobl and P. Neave. Preliminary analysis of field results was done by C. Vardy, and we thank her and the many others who helped with field surveys. Our thanks are due to J. Pringle and P. Catling who identified some of the composites and sedges. We are grateful for the continued support of Queen's University Biology Station.

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Received 16 October 2006

Accepted 28 April 2008