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PLANT COMMUNITY DEVELOPMENT OF ISLE ROYALE'S MOOSE-SPRUCE
SAVANNAS

By

Michael C. Rotter

THESIS

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ABSTRACT

PLANT COMMUNITY DEVELOPMENT OF ISLE ROYALE'S MOOSE-SPRUCE SAVANNAS

By

Michael C. Rotter

On Isle Royale National Park, heavy moose browsing over the past 100 years has suppressed the regeneration of many tree species, gradually resulting in a shift towards more open forests and savannas. By 1996, 16% of the forests at the southwest end of Isle Royale had become savanna and another 20% were starting to break-up. The changes in understory vegetation brought about by savanna formation have received little attention, even though the future of moose and wolf populations on Isle Royale are tied to these vegetation changes. This study examined the vegetation of savannas ranging in age (date since formation) from <10 years to 80 years to examine how the ground flora changes along a successional pathway from initial forest breakup, to extensive grassland, and finally to a zootic subclimax dubbed "moose-spruce savanna." Ordination techniques were used to describe plant communities and to identify environmental variables that influence vegetation development. Non-parametric multiplicative regression was used to predict how these variables influenced individual plants and structure within the communities. Plant communities had a notable shift from forest herbs to ruderal species, especially non-native plants. This succession was influenced strongly by the underlying bedrock and hydrology altering moisture regimes and plant communities. *Picea glauca* and *Poa pratensis* competed in a dynamic inhibitory relationship. The former facilitated forest plants while the latter out-competed other plants and promoted open swards. These interactions are dramatically changing the character of Isle Royale's upland plant communities and will have important trophic consequences for the island.

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Michael C. Rotter
2014

DEDICATION

This thesis is dedicated to my Grandfather, Hubert Rotter, for providing my cousins and I land to roam and explore the ecology of northern Michigan.

&

To my father and mother, Mike and Judy Rotter, for always taking the scenic route home and all the nature hikes they took me on.

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This thesis follows the format prescribed by the journal *Botany*.

TABLE OF CONTENTS

List of Tables.....	(v)
List of Figures.....	(vii)
Introduction.....	1
Methods.....	5
Results.....	10
Discussion.....	15
Literature Cited.....	37
Appendix A.....	50

LIST OF TABLES

Table 1. Species richness.....	36
Table A-1. Species observed and 6-letter codes.....	50

LIST OF FIGURES

Figure 1. Map of the study area.....	24
Figure 2. NMS diagram of all plots.....	25
Figure 3. CCA of savanna sites pooled.....	26
Figure 4. Relative cover of functional groups of plants per age class.....	27
Figure 5. Relative cover of non-native plants per age class.....	28
Figure 6A. CCA of savanna plots for age classes.....	29
Figure 6B. CCA of savanna plots for plant species.....	30
Figure 7. NPMR response curves.....	31
Figure 8. CCA for 1930 and 1957 age-class plots.....	32
Figure 9. Photograph of spruce covered microsite.....	33
Figure 10. Photograph of a moose-spruce savanna.....	34
Figure 11. Flow chart of possible savanna vegetation development.....	35

Introduction

The impact of ungulate browsing in structuring plant communities is well known (Bergstrom 1992, Hobbs 1996, Côté et al. 2004). These impacts include changes to the physical structure and composition of these communities (Pastor and Naiman 1992, Ritchie et al. 1998, Gill and Beardall 2001). Grubb (1986) emphasized the importance of so-called “third party” effects in succession, whereby animals or other organisms shift the relative success of different plant species by creating gaps, altering light regimes, and influencing litter. Browsing systems have generally been shown to increase the biomass and cover of the ground flora (Snyder and Janke 1979, Augustine and McNaughton 1998). Such third-party effects can modify both the rate and pathways of succession. In northern forest ecosystems, for example, preferential browsing of early successional, deciduous tree species often leads to accelerated succession to coniferous, later successional species (Bryant and Chapin 1986, Johnston and Naiman 1990). Where herbivore densities are high, they can have particularly strong influences on plant communities (Ripple et al. 2001), potentially creating unique stable states (Augustine et al. 1998, Kotanen and Abraham 2013) and altering disturbance regimes (e.g. Savage and Swetnam 1990).

Isle Royale National Park, Keweenaw County MI USA, (Fig. 1) has a long history of botanical and ecological study (Cooper 1913, McLaren and Peterson 1994, Nelson et al. 2011), particularly the trophic dynamics of the island’s moose (*Alces alces* L.) and wolf (*Canis lupis* L.) populations (Mech 1966, Allen 1994). The isolated nature of the island (located 24 km from the nearest mainland) and relative simplicity of the food web (one large ungulate with one predator) makes it an ideal place for studying these trophic relationships. Moose colonized the island in the early 1900’s and, without any predators, the population grew almost exponentially to 1000-

5000 animals in the late 1920's and early 1930's (reviewed by Mech 1966). Over-browsing and starvation caused the population to plummet from 1933-1943. As the moose population started to recover in 1945, wolves became established on the island and kept the moose herd relatively low for two decades. The past 30 years, however, have seen major fluctuations in both the moose and wolf populations, largely driven by disease/pests, bad winters, and reproductive problems among the remaining wolves (Peterson et al. 1984, Peterson 1999, Vucetich and Peterson 2004). As of 2012, the moose herd had recovered to around 750 animals (Vucetich and Peterson 2013).

Moose on Isle Royale preferentially browse *Populus* spp., *Betula* spp., *Sorbus decora* (Sarg.) C. K. Schneid and *Abies balsamea* (L.) Mill. (Pastor et al. 1988, McInnes et al. 1992, Snyder and Janke 1976, Brandner et al. 1990). Some species, including the once common *Taxus canadensis* Marshall., were almost eliminated by the first wave of over-browsing in the 1920's and 1930's (Brown 1935). Many browse species have been more resilient, persisting as heavily pruned, hedge-like saplings for decades (e.g. *Abies balsamea*, McClaren 1996), but recent studies have emphasized the progressive loss and regeneration failure of *Abies balsamea* (Campbell 2002). Heavy browsing of tree saplings has created a demographic bottleneck where young trees fail to replace any losses of mature trees in the canopy (Risenhoover and Maass 1986, Pastor et al. 1988, McInnes et al. 1992). The result has been a gradual conversion of forest to open woodlands and savannas, particularly in the middle and southwestern end of the island. The earliest recognized savannas formed during the 1930's when the moose populations peaked at 1000-5000 animals (Gorkiewicz 2006). Since then, savanna coverage has steadily increased, and by 1996, 16.1% of the upland habitat on the western end of the island had been converted to savanna and another 20% was starting to break up with canopy cover in the 40-60% range

(Gorkiewicz 2006). Un-browsed *Picea glauca* (Moench) Voss. has increased; creating a unique zootic disclimax known as “spruce-moose savanna” (Johnston et al. 1993).

The magnitude of these changes will no doubt affect ground vegetation and have significant trophic implications for both moose and wolves on the island. The extent to which savanna formation is easily reversible is a critical question. Several long-term exclosure studies have demonstrated that long-term browsing has not only altered vegetation, but also litter quantity and quality. These alterations have “cascaded” downward to microbial processes and soil properties (McInnis et al. 1992, Pastor et al. 1993).

Although numerous studies have demonstrated the large-scale impacts of moose browsing on the island’s plant communities, little work has been done on savannas and the successional pathways that are initiated in the ground flora once the canopy is removed. The first objective of this study was to document how the composition of the savannas change over a roughly 80-year time period using a chronosequence approach, i.e. substituting savannas of different ages for an assumed temporal sequence. Because savannas form gradually, I selected only discrete, well-developed savannas that showed up on aerial photographs of the following years: 1930, 1957, 1978, 2005; thus, actual savanna ages fell somewhere between the 21- to 27-year periods between photographs. I was particularly interested in how long forest groundcover species persisted in savannas, and whether there were consistent trends in the colonization of other functional types (e.g. graminoids, old-field herbs and shrubs, invasive species).

A second, related objective was to determine whether any physical environmental (e.g. soil type) biotic factors (e.g. particular plant species, moose herbivory), or landscape factors (e.g. isolation, savanna size) influenced successional patterns both within and between savannas, possibly

leading to alternate pathways. Loss of canopy cover can strongly influence soil temperature and moisture regimes (reviewed by Bhattie et al. 2000). These changes are mediated mainly by vegetation, both pre- and post-canopy removal (e.g. loss of evapotranspiration from canopy trees). In general, canopy removal tends to increase soil moisture, particularly after high precipitation events, but soil moisture can become low following dry weather. These effects are influenced by soil characteristics (Bhattie et al. 2000), so I predicted that more heterogeneous plant communities might develop both within and between savannas depending soil depth, presence of a fragipan, and properties affecting water-holding capacity.

On the biotic side, I hypothesized that an increase of *Picea glauca* in these savannas might play an important role in determining community patterns, particularly in relationship to graminoid species like the abundant *Poa pratensis* L. Interactions between trees and grass species have been shown to be important in the development of savanna communities elsewhere (Scholes and Archer 1997). I hypothesized that *Picea glauca* could favor the re-development of patches of forest vegetation by providing shade and reduced grass competition for understory herbs. I predicted that older age class savannas would have a more heterogeneous assemblage driven by *Picea glauca* and *Poa pratensis*.

Methods

Study Area

The study area encompassed the western end of Isle Royale National Park (47° 54' 48''N; 89° 09'36''W), west of a line running roughly north from Long Point to Huginnin Cove (Fig. 1).

This area was chosen for several reasons: during the 1930's, this end of the island was densely forested, and there has been no major fires during the past 70 years (Hansen et al. 1973). Lastly, unlike the rocky outcrops of the eastern end of the island, glacial deposits provide for deeper soils that can support a more continuous forest canopy (Huber 1975), so it was much easier to distinguish moose-generated savannas from edaphic openings.

Sampling Design

Historical aerial photos from 1930, 1957, 1978 and 2005 were used to identify savannas, and savannas were chosen based on the year of first appearance. This chronosequence does not represent absolute times of savanna establishment, but represents the first year that open areas could be observed. Within each savanna, plots were randomly generated using ArcGIS (ESRI 2011). For each age class 10-11 savannas were chosen, and a minimum of 15 randomly located 5-m radius plots were sampled within each savanna. Plots were located within savannas in portions that were open in the original aerial photos (i.e. if two savannas had merged or expanded since the 1930 aerial photo, only the portion present in 1930 was considered for sampling). I was unable to develop a large enough pool of savannas for random selection. Instead, I prioritized savannas using the following criteria (1) size large enough to accommodate 15 plots, (2) unambiguous age, and (3) representation from all parts of the study area. Five reference stands with predominantly closed canopy were also sampled in the same manner.

Based on the Nature Conservancy vegetation classification map (1999) of Isle Royale, the references were found in the same general stand types as the savannas but had canopy closure >60%.

The chronosquence approach requires careful consideration of site differences (e.g. soil and stand history) that could potentially confound interpretation of temporal trends. Savannas from the 1930, 1957, and 1978 age classes were all located on very similar soil types. However, about 40% of the plots sampled in the 2005 age class were located over well-drained Arcadian-Nipissing complex soils. This soil type was not found under older age class savannas. In addition, the formation of 2005 savannas appeared to be driven, in part, by dieback of *Betula papyrifera* marshall, possibly the result of a regional outbreak of bronze birch borer (*Agrilus anxius* Order Coleoptera) that began in 1979 and lasted into the 1990's (Millers et al. 1989, Jones et al. 1993).

Landscape level variables were derived in ArcGIS (ESRI 2011). Savannas were digitized as patches and total area and core area (area of savanna >10 m from forest edge) were calculated. Distances between neighboring savannas were measured to determine isolation. For this purpose, savannas <10 m away from each other were considered linked. Distance of savannas from Lake Superior was determined because coastal communities were a likely source population for many ruderal species. Soil and bedrock data were accessed from the NRSC Soil data mart (Soil Survey Staff, 2011) and imported into the GIS layers.

Field sampling took place June through August of 2012. Within each plot I visually estimated vegetation cover for each vascular plant species, bare ground, woody debris, rock, and litter using a modified Braun-Blanquet scale: +=<1%, 1=1-5%, 2=5-10%, 3=10-20% 4= 20-40%,

5=40-60%, 6=60-80%, 7=80-100%. Bryophytes and lichen species were lumped into their respective groups. Tree and shrub cover were recorded at two different height levels: 1.3 m and <1.3 m. Tree DBH was measured within the plots. Vascular plant taxonomy follows Voss and Reznicek (2012) and fern and fern relatives follow Cobb et al. (2005). All plant species found are listed in Appendix A.

Litter depth was measured by allowing a 22 g, 3.0cm –diameter washer to slide down a steel rod until the washer was supported by litter, and then using a ruler to measure the height above the top of the A horizon. This was repeated 5 times in each plot to obtain an average litter depth. Soil depth was measured by pushing a 6.3-mm diameter steel rod into the soil until hitting bedrock or a gravel layer. Depth was taken at 10 locations within each plot and averaged. Canopy openness (%), diffuse light, total direct beam, and total radiation were determined from hemispherical photos taken with a Nikon Coolpix 990 with a FC-E8 fisheye converter. Photos were taken at height of 1.3 m at plot center, and then processed using Gap Light Analyzer version 2 (Fraser et al. 1999).

Data analysis

I primarily used multivariate regression and ordination methods to address the main objectives. Non-metric multidimensional scaling (NMS) was used to examine differences in species composition among different savanna age classes (objective 1). Canonical Correspondence Analysis (CCA) community tested which physical and biotic variables modified the proposed temporal sequence (objective 2). This approach also helped differentiate between physical site differences and age related trends. CCA provides a community-level view of these patterns, but I also used non-parametric multiplicative regression (NPMR) to model individual species response to important environmental variables, as revealed in the CCA. Finally, separate analyses were

conducted at the plot and savanna scale to compare compositional trends both within and between savannas. Species with <10 occurrences were excluded from the ordinations to reduce the effects of rare species. All ordinations were performed using PC-ORD version 6 (McCune and Mefford 2011).

NMS is highly effective at recovering patterns from ecological community data that could contain non-normal data or data in arbitrary scales that can plague other forms of ordination (McCune and Grace 2002). Additionally, NMS produces an ordination solution that would not be influenced by unmeasured variables, allowing comparison to the CCA which constrains the ordination to the measured variables. Sorenson distance measure was used to measure similarity. NMS was run on “Auto pilot” mode under the “slow and thorough” method (40 runs with real data and 50 Monte Carlo iterations) in PC-Ord 6 (McCune and Mefford 2011).

CCA was used to analyze compositional patterns in savanna plots and sites with respect to supplied environmental variables. CCA was chosen because it is not heavily influenced by unmeasured variables, and for its performance with highly inter-correlated environmental variables (Palmer 1993). CCA analyses were conducted for (1) all plots (n= 687) and (2) across savanna sites and reference stands (n=46). In the site-level ordination, average cover for each species was input into the species matrix, and landscape metrics were added to the environmental matrix. NMS analysis revealed that older savannas were more heterogeneous in plant composition than younger savannas, so I also analyzed just the 1957 and 1930 savanna plots with CCA to explore whether any environmental variables could explain this divergent pattern. One hundred iterations of the Monte Carlo randomization tests were used to determine significance for each CCA.

Nonparametric multiplicative regression (NPMR) was used to model the performance of species under the measured environmental variables. Due to plant richness and the number of environmental variables, important variables from the ordinations, species with exemplary response, and models with a $p < 0.05$ from a 20-iteration Monte Carlo randomization test were chosen for this analysis. Models were additionally evaluated using xr^2 . Like r^2 , xr^2 can be used to evaluate model quality. However, xr^2 uses a cross validation of the residual sum of squares in relation to the total sum of squares. Using NPMR is useful as it avoids the unrealistic assumption of a simple linear or non-linear response of a species to a variable (McCune 2006). NPMR was performed in HyperNiche version 2.2 (McCune and Mefford 2009).

Finally, I graphed the relative cover and species richness of different functional groups, including non-native species, across the chronosequence. All species were grouped as either old field, forest, or edge based on published flora accounts (Voss 1996, Voss and Reznicek 2012).

Results

Vegetation composition across age classes

Plot and site-level ordinations confirmed shifts in vegetation communities between age classes (Fig. 2, Fig. 3.). At the plot scale (Fig. 2), reference plots and the 2005 age class plots had a relatively tight cluster. Plots from 1978 overlapped strongly with 2005. Moving toward the origin of axis 1, the older age class plots (1957 and 1930) diverge into a more heterogeneous assemblage. Most plots from 1957 and 1930 were shifted far to the left (i.e. maximally different than closed forest), but some plots from 1930 also overlapped with reference plots, and 1957 overlapped with 2005 plots.

Forest species (e.g. *Oxalis acetosella* L., *Coptis trifolia* (L.) Salisb., *Huperzia lucidula* (Michx.)R.Trevis) were poorly represented in all savannas; even in the 2005 age class, forest species comprised just 10% of the relative cover (Fig. 4). Forest species were slightly more abundant in older age classes but their relative cover never completely rebounded. *O. acetosella* and *H. lucidula* were examples of this trend.

Species such as *Rubus parviflorus* Nutt., *Diervella lonicera* Mill., and *Eurybia macrophylla* (L.) Cass. were overwhelmingly dominant in the youngest savannas. Relative cover of edge species dropped in older savannas, especially *E. macrophylla*, but *R. parviflorus* was well represented in even the oldest savannas.

Relative cover of old field species increased with savanna age, reaching a maximum of nearly 40% in the 1930 age class, led by *Poa pratensis* L. and *Hieracium* spp. Relative cover of *Poa* was near maximum in 1978 savannas, whereas *Hieracium* spp. and *Clinopodium vulgare* L.

peaked in 1957 and 1930, respectively. Non-native species were almost non-existent in the reference stands, but were increasingly common in older savannas. In the 1930 age class, non-native species made up 18% of the relative cover and 14% of the total species richness (Fig. 5).

Differences in the relative cover of functional groups (forest, edge, and old field species), were also reflected in changes of species richness across the chronosequence (Table 1). Overall, 202 species were recorded, with the lowest richness (86 species) in the reference areas and the highest in the 1930 age class (149 species). A secondary peak in richness was noted in the 2005 age class. In contrast, mean richness at the plot level (21-23 species) was remarkably consistent across age classes.

Environmental factors related to chronosequence trends

Light-CCA revealed several of the key variables related to compositional variation among savanna age classes. CCA of all savanna plots (Fig. 6) indicated that the amount of solar radiation was highly correlated with the first axis ($r=0.60$). Savanna age classes were also aligned somewhat sequentially along the first axis; but as expected many plots in the older savannas were shaded and had understories more indicative of closed forest. A plethora of old-field species were associated with older savannas in high light situations, especially *Poa* spp., *Phleum pratense* L., *Bromus ciliatus* L., *Hieracium* spp., *Clinopodium vulgare*, and *Taraxacum officinale* F.W. Wigg. Shrubs characteristic of these areas included *Sambucus racemosa* L., *Prunus virginiana* L., *Crataegus douglasii* Lindl., *Rubus strigosus* Michx., and *Ribes oxycanthoides* L. Interestingly, several forest herbs (e.g. *Maianthemum canadense* Desf., *Streptopus lanceolatus* (Aiton) Reveal, *Pyrolla elliptica* Nutt.) were shifted towards higher light situations. Field observations confirmed that these species were common in open savanna and not just under

isolated trees. Plots in the 2005 and 1978 savannas occupied intermediate positions along the light gradient.

NPMR models demonstrate response curves of several species to solar radiation (Fig. 7A).

Huperzia lucidulum, a clubmoss commonly found in closed forest, declines precipitously with even moderate light. *Coptis trifolia* (L.) Salisb. and *Spinulum annotinum* (L.) A. Haines are more resilient to high sunlight but eventually decline. *Linnaea borealis* L. shows a tolerance across a wide range of light conditions. Other species increased dramatically with higher solar radiation; for example, *Hieracium* spp. and *Clinopodium vulgare* both increased dramatically with increasing solar radiation ($xr^2=0.114$ and 0.090 , respectively). *Poa pratensis* ($xr^2=0.279$) also increased with increasing solar radiation, however, it declined slightly at the most intense radiation levels. The CCA results suggested that the perennial forest herb *Steptopus lanceolatus* was persistent in open savannas; NPMR models confirm that this species is tolerant across a wide range of light and moisture conditions. It should be noted that these graphs do not represent true physiological responses, because potential confounding variables (e.g. soil moisture, competition, temporal trends in colonization) were not taken into account.

Soils--Several soil/bedrock variables were correlated with axis 2 in the plot level CCA (Fig. 6), including presence of basalt/conglomerate bedrock ($r=0.47$), presence of a fragipan ($r=-0.52$), and volumetric soil moisture ($r=0.36$). Species strongly associated with higher soil moisture and fragipan included *Matteuccia struthiopteris* (L.) Todaro, *Thalictrum dasycarpum* Fisch. & Ave-Lall., *Heracleum maximum* Bartram, and *Carex intumescens* Rudge, particularly in plots from the 1930 savannas. At the other extreme, species associated with drier soils and basalt/conglomerate bedrock included plants typical of open "barrens" (e.g. *Danthonia spicata* (L.) Roem. & Schult., *Diervilla lonicera* Mill., *Anaphalis margaritacea* (L.) Benth., lower right

of Fig. 6B) as well as plants typical of dry, acidic woodland (*Pteridium aquilinum* (L.) Kuhn, *Chimaphila umbellata* (L.) W.P.C. Barton, and *Orthilia secunda* (L.) House; lower left of Fig. 6B). Again, many of the plots associated with this vegetation were from the 1930 age class.

Several representative NPMR species response curves to soil moisture are shown in Fig. 7. *Poa pratensis* ($xr^2=0.042$) declined sharply with an increase in water content. *Cornus canadensis* L. ($xr^2=0.033$) declined with increasing water content but declined only at higher water content values and only gradually (Fig. 7). As mentioned earlier, *Streptopus lanceolatus* cover did not vary much across a wide range of moisture levels ($xr^2=0.07$).

To better understand the extreme variability in species composition in older savannas, I performed CCA just on plots from 1957 and 1930 age classes. This ordination confirmed that vegetation in older savannas was segregated along both sunlight and moisture gradients. These vectors were orthogonal, indicating soil moisture was largely independent of site openness (Fig. 8).

A third important factor was revealed in this analysis: spruce cover. This was recorded at 1.3 m height, picking up mostly lower tree boughs and saplings. Beneath spruce cover, many woodland species occur, especially those associated with more acidic conditions (*Linnaea borealis*, *Coptis trifolia*, *Cornus canadensis*, and several club mosses). These spruce “gardens” were extremely diverse at a scale of $< 1 \text{ m}^2$ (Fig. 9). The occurrence of *Taxus canadensis* in these gardens is notable because it is highly preferred by moose.

Litter depth also appeared to influence compositional patterns, although only in the site level ordination (see Fig. 3). This litter was composed mainly of dead grasses in savannas. NPMR models show a variety of responses for forest herbs (Fig. 7). For example, *Picea glauca* and

Cornus canadensis sharply declined with increasing litter depth ($xr^2 = 0.03$ and 0.06 respectively). *Streptopus lanceolatus*, another forest species, was not influenced by the change in litter depth ($xr^2 = 0.01$) but *Hieracium* spp. had an increase in cover with higher litter depth ($xr^2 = 0.226$).

Within versus among savanna trends in composition

Similar to the NMS (Fig. 2), earlier age class savannas (Reference and 2005 age classes) were relatively homogenous in composition (Fig. 4). Older age class savannas (1930 and 1957), in contrast, were far more variable. The convex hull polygons show a striking pattern of expansion across age classes (Fig. 3). One key environmental variable that explains this at the savanna level is site openness. Some of the older savannas segregate into ones that are very open ($r = 0.60$ for axis 1) whereas others are more closed in, especially by *Picea glauca*. Savanna core area was the only landscape variable that was important ($r = -0.414$ for axis 1); most of the smaller savannas were from the 2005 age class, whereas the largest savannas were from 1957 and 1930. This could explain the higher representation of edge species in the 2005 savannas.

Moose pellet counts also varied across the chronosequence. I counted pellets of all ages, because this variable was only meant to be a general indicator of moose activity. In addition, pellets are formed only in the fall, winter, and early spring on Isle Royale; in the summer their use of aquatic plants produces watery droppings. The highest pellet counts occurred in reference stands and the 2005 age class savannas. Very few pellets were found in the large, open savannas.

Discussion

Savanna composition over time

Interpretation of chronosequences can be problematic when site and time variables are confounded or when historical legacies (e.g. past disturbance history) are not considered (Johnson and Miyanishi 2008). However, chronosequence studies can be an important tool to predict long term ecological trends, particularly if applied to certain succession sequences and when a careful review of factors in the study area are considered (Walker et al. 2010).

Fortunately, Isle Royale has a long history of vegetation research, moose exclosures dating back 65 years, long-term permanent plot records, aerial and ground photographs, and eyewitness accounts that are consistent with the general successional trends derived from this chronosequence. Additionally, the CCA approach takes into account soil differences and how they modify vegetation trends independent of the savanna age.

Both Ruthven (1906) and Adams (1909) portray the pre-moose forests at the western end of Isle Royale as densely forested; in some areas the understory was described as nearly impenetrable. Based on the 1930 aerial photographs, which are of exceptional quality, the forests in the study area were still quite intact at that time, with the exception of a few openings mostly south of Feldtman Lake. Moose exclosures in the study area, one that dates back to 1948 (Krefting 1974), and comparisons with vegetation on islands in the archipelago that are inaccessible to moose, leave no doubt that moose browsing has been the primary force creating these openings (Snyder and Janke 1976, Pastor et al. 1988, McInnes et al. 1992).

The understory of the reference areas in this study were very similar to the closed forests c. 1905 described by Cooper (1913). However, the overstory composition has no doubt shifted, with less

Abies balsamea and *Betula papyrifera* but more *Picea glauca* (McInnes et al. 1992, Campell 2002). Understory composition was relatively homogeneous, which is likely a component of buffering effects from canopy shade and hydraulic lift of forest tree species (Caldwell et al. 1998). Closed canopy areas had relatively low species richness, high abundance of forest herbs, and few non-native plant species. These mixed deciduous conifer forests are the starting point of the chronosequence (Fig. 11A).

As the forests fall apart, through natural senescence or a disturbance, an increase in light starts to shift vegetation composition. These remnant forests (Fig. 11B) are the start of a mosaic of change within the savannas. The 2005 age class had an increase in richness over the reference areas; this increase was driven by the large increase of edge species, a modest influx in old field species, and the persistence of forest species. The increase in edge species in young savannas forming in the 1970's is corroborated by eyewitness accounts and photographs. However, thickets composed of saplings of preferred deciduous tree species (e.g. *Sorbus decora*) were evidently more common in the past (Alan Rebertus, personal communication). The steep decline of forest species bottoms out and stabilizes for the 1978 through the 1930 age classes (Fig. 4). Relative abundance of edge species also declined with savanna age, but the abundance of old field species increased greatly and contributed to higher species richness in older age classes. The change in functional groups includes a rapid increase in the abundance and representation of non-native plant species. Indeed, large swards of the oldest savannas are overwhelmingly dominated by the non-natives *Poa pratensis* and *Hieracium* spp.

Forest herbs were poorly represented in the dry open savannas (Fig. 11C), suggesting they were either out-competed or simply could not tolerate the open conditions. However, some forest species appeared to be remarkably persistent in savannas, even in some areas densely overgrown

with *Poa pratensis*. Persistence of many forest herbs in savannas can be explained by two mechanisms: (1) tolerance of open savanna conditions and (2) persistence and/or colonization of micro-refugia within the savanna matrix. Forest understory species that appear to be especially tolerant of open savanna conditions include *Streptopus lanceolatus*, *Linnaea borealis*, *Maianthemum canadense*, and *Clintonia borealis*. NMPR models show these species were found across a wide range of light, moisture, and litter depths (Fig. 7). The presence of *Maianthemum canadense* in open savannas was unexpected given that it has been reported to be somewhat sensitive to excessive light (Sparling 1967). One likely explanation is that these species enjoy some benefit of shade and extra moisture by growing underneath dense grass cover. Such niche partitioning has been well described for prairie communities (Knapp et al. 1993). However, competition with graminoids for limited moisture and nutrients may hinder the growth of other forb species, so the interactions likely depend on the life histories of specific species. Of note, the persistent species above also form extensive clonal networks where water and nutrient sharing may buffer plants from extinction. *Clintonia borealis*, for example, freely shares nutrients through rhizome connection throughout the entire clone (Ashmun et al. 1982). The other way forest species persist in savannas is by growing under the shade of isolated trees, especially *Picea glauca*, which moderates the environment (see Alternate Successional Pathways for the role of *Picea* and *Poa*).

The general trend of loss of forest herbs and increase in old-field species, including non-native species, has been observed in other situations with large densities of herbivores, most notably with the impacts of white-tailed deer (*Odocoileus virginianus* Zimmermann) in eastern deciduous forests (Knight et al. 2009, Relva 2010). Moose themselves have also been implicated

in the spread and establishment of non-native plants in the boreal zone (Rose and Hermanutz 2004).

Alternative Successional Sequences

The changes to the composition of the vegetation communities across upland forests on Isle Royale, as implied by this chronosequence, are dramatic. The homogenous assemblages of native plant communities are replaced by a divergent set of plant communities. However, all communities see a precipitous loss of shade-loving forest plants and a dramatic increase in old field and non-native plant species. The composition of the oldest savannas (1957 and 1930), however, implies that succession may become bi- or multidirectional. All the ordination results indicate that some open portions of older savannas achieve maximum dissimilarity to closed forest. A good example is the extensive swards that are overwhelmingly dominated by *Poa pratensis* and *Hieraceum* spp. Paradoxically, other areas appear to be undergoing a reversion towards forest understories, which is being driven by the invasion of spruce. *Picea glauca* acts both as a refuge for persistence of forest herbs and a nucleus for their re-colonization. The islands of spruce habitat, however, represent a very different environment than the original forests. First, spruce in savannas are mostly open-grown; their dense boughs extend to ground level and block light very effectively. Second, their needle litter, which creates acidic soils and limits many nutrients also affect species composition (Pastor et al. 1988, McInnes et al. 1992). The groundcover under savanna spruce was largely barren, with many herbs strongly favoring edges.

As the buffering effects of the canopy are lost, divergence in the understory plant communities is driven increasingly by the underlying geological context as well as a key interaction among

several plant species. These interactions shape the vegetation development in the savannas and may play an important role in the future of Isle Royale's forests.

Soil moisture played an important role in determining plant cover in savannas. Across savanna plots, increased soil moisture was found over areas with a fragipan creating a wet glade community (Fig. 11D). As the canopy declines, water is increasingly pooled over these hard clay layers, favoring *Matteuccia struthiopteris*, *Thalictrum dasycarpum*, *Carex intumescens*, and *Heracleum maximum*.

Savannas over a fragipan layer sharply contrast with those over conglomerate/ basalt formations. As these areas lose the buffering abilities of a forest canopy, moisture is lost through rapid drainage and high evapotranspiration rates, creating a dry open savanna community (Fig. 11C). *Pteridium aquilinum*, *Danthonia spicata*, *Chimaphila umbellata*., and other xeric plants are associated in these areas. This divergence become increasingly apparent as a savanna ages by allowing underlying geological features to have a much more prominent role in dictating vegetation communities, providing two alternate communities. This divergence demonstrates the impacts that moose activities are having on the forest's hydrological cycle.

Changes associated with underlying bedrock may also mediate the dynamic competition between two keystone species in savannas: *Picea glauca* and *Poa pratensis*. Grass species can inhibit the establishment of *Picea glauca* (Chhin and Wang 2002). *Picea glauca* can establish in heavy grass only in microsites with soil moisture retention, which is consistent with my NPMR models (Fig. 7). In contrast, when *Picea glauca* reaches the canopy it can inhibit *Poa pratensis* through shading. Similar to other savanna communities, shade provided by trees (*Picea glauca* in this

case) may be an important refuge for the persistence of some vascular plants that are inhibited by both increased levels of solar radiation and competition from increased *Poa pratensis* cover.

During savanna formation, *Picea glauca* most likely becomes established due to the removal of a heavily shaded over story and a competitive edge over the preferred browse species. However during this period *Poa pratensis* rapidly increases in cover. The establishment of *Picea glauca* is most likely controlled by a chance introduction before *Poa pratensis* can establish. *Poa pratensis* holds a distinct dispersal advantage over *Picea glauca*. The dispersal ability of *Picea glauca* is limited by proximity and direction from a seed source (Stewart et al. 1998). *Poa pratensis* is an aggressive grass species that can spread easily from both rhizomes and seeds. Seeds of *Poa* spp. have been shown to effectively disperse long distances in the hooves and fur of large ungulates (Myers et al. 2004, Couvreur et al. 2004).

The presence of *Picea glauca* in a savanna community probably has a twofold effect: creating a micro-environment around the base of the tree, and providing a refuge for preferred browse species. The shade under *Picea glauca* provides for greater cover of understory plants and suppressing the coverage of old field species, most likely through shading. Higher levels of moisture underneath these isolated trees may allow for persistence of understory herbaceous species (Scholes and Archer 1997). This was shown by a rebound of *Oxalis acetosella* in older savannas (Fig. 4).

Picea glauca may also provide an herbivory refuge for certain plant species. Associational resistance (“defense guilds” *sensu* Atsatt and O’Dowd 1976) has been shown to effectively defend plants against large generalist herbivores (Olf et al. 1999, Callaway et al. 2005). The

preferred browse species *Sorbus decora*, *Betula papyrifera* and *Taxus canadensis* are associated with spruce cover in the older age class savanna plots.

In contrast to *Picea glauca*, *Poa pratensis* controls the vegetation community more antagonistically. Increasing cover of *Poa pratensis* leads more in litter, the mechanism by which *Poa pratensis* can inhibit the growth of other vascular plants. Rosette forming species, such as *Hieracium* spp. are able to create room around themselves and escape litter suppression (Bosy and Reader 1995). Forbs associated with *Poa pratensis* included the ruderal species *Clinopodium vulgare* and *Hieracium* spp., both of which can exploit high light levels.

An important question yet to be answered is how resistant the dense *Poa pratensis*-*Hieraceum* fields (Fig. 11E) are to further compositional changes. Does this represent a “plateau” in savanna development? *Poa* has aggressive growth habitats and produces smothering litter; whereas, in vitro studies have shown that pollen of several *Hieraceum* species are highly alleopathic (Murphy 2000). Some shrub species (e.g. *Ribes oxycanthoides*, *Sambucus racemosa*) are able to survive with *Poa pratensis*, most likely through vegetative growth and by escaping the litter through height. *Sambucus racemosa*, which moose strongly avoid, is becoming particularly common in many savannas. It is highly unlikely that any deciduous species will be able recolonize open savanna areas under the current and historical browsing pressure. In the absence of fire, the fate of many of these savannas will depend on the rate of *Picea glauca* invasion, which appears to be highly variable. Fig. 3 shows that the composition of 4-5 savannas from the 1957 and 1930 age class overlap strongly with the reference plots; these are rapidly being closed in by spruce forests (Fig. 11F). The rest, however, are being colonized more slowly and may represent an alternate stable state. Alternative stable states as the result of browsing pressure have been previously documented in forests heavily browsed by white-tailed deer (Augustine et al. 1998).

Moose, ecosystems, and the future of Isle Royale

The fluctuations in moose and wolf populations on Isle Royale have consequences for the entire island. With the moose population continuing to rebound (Vucitch and Peterson 2013), the process of savanna formation is likely to continue. As new areas of deciduous-fir forests decline (Previant et al. 2012) and moose gain access to new food resources in these areas, a growing moose herd will continue to suppress forest canopy regrowth. By 1996 this process had already affected over 36% of the upland forests on Isle Royale's southwest end (Gorkiewicz 2006). This process has changed large areas of land on the island; within these areas the vegetation communities are radically altered. Although not completely disappearing, shade tolerant forest plants are dramatically reduced in cover through this process, while *Poa pratensis* and non-native *Hieracium* spp. appear to be the big "winners." I have established several monitoring plots in the study area to see whether these communities represent a relatively stable "plateau" or whether they continue a pattern of radical change set in motion by moose.

Savanna systems depend on multiple buffering mechanisms to maintain a sparse tree/grass composition (Jeltsch et al. 2000). Continued moose browsing in addition to other disturbances, such as fire or insect outbreaks, may be necessary for the persistence of savannas on Isle Royale. The continued long-term recruitment of *Picea glauca* to the overstory, will be important to the survival of understory species. How long understory plants can persist in these refugia is not known, as is the future of *Picea glauca* in the savanna areas. If lost, there is evidence that some shade-tolerant forest species may not recover even under canopy reformation (Duffy and Meier 1992). Not all understory species are as affected by forest change; some hardy forbs such as *Clintonia borealis* persist at only slightly lower cover values. These plants may have an advantage over other understory plants in any potential spruce woodlands that form. Future

monitoring of the savannas might reveal if *Poa pratensis* can exclude any future *Picea glauca* establishments or if long term climate fluctuations or other disturbances might give *Picea glauca* the ability to establish large areas of woodlands.

The process of the collapse in the moose food base, predicted by Murie (1934), was the main cause of severe declines in the herd during the mid-1930's (Peterson et al. 1984). The tempering of the moose herd by wolves in the past half century was seen as a natural regulation of the herd. With the current decline in the wolf population (Vucitch and Peterson 2013), a large moose herd could once again build to record high levels. Savanna formation could increase as more moose chase declining food resources. Savanna communities are marked by a lack of preferred browse species and poor moose habitat, providing little food and resources for an expanding herd. These open areas provide little cover and shelter from summer heat and predators.

Although able to take advantage of an aquatic forage base in the summer, moose cannot avoid the need for utilizing savanna areas for winter browse. These open areas may provide poor cover for moose as they are more exposed to potential detection by wolves (Tolon et al. 2009). A return to the "bust and boom" moose cycle will be likely, with savanna formation being a key ecological phenomenon within this trophic chain.

Many questions remain concerning the future of the savannas on Isle Royale that only long term monitoring can reveal. This research demonstrates some of the significant trends that will influence this island wilderness as long as the moose population continues to climb. The top-down trophic consequences of moose herbivory on the plant communities are profound, and these changes, in turn, will have a bottom-up influence on the whole Isle Royale ecosystem.

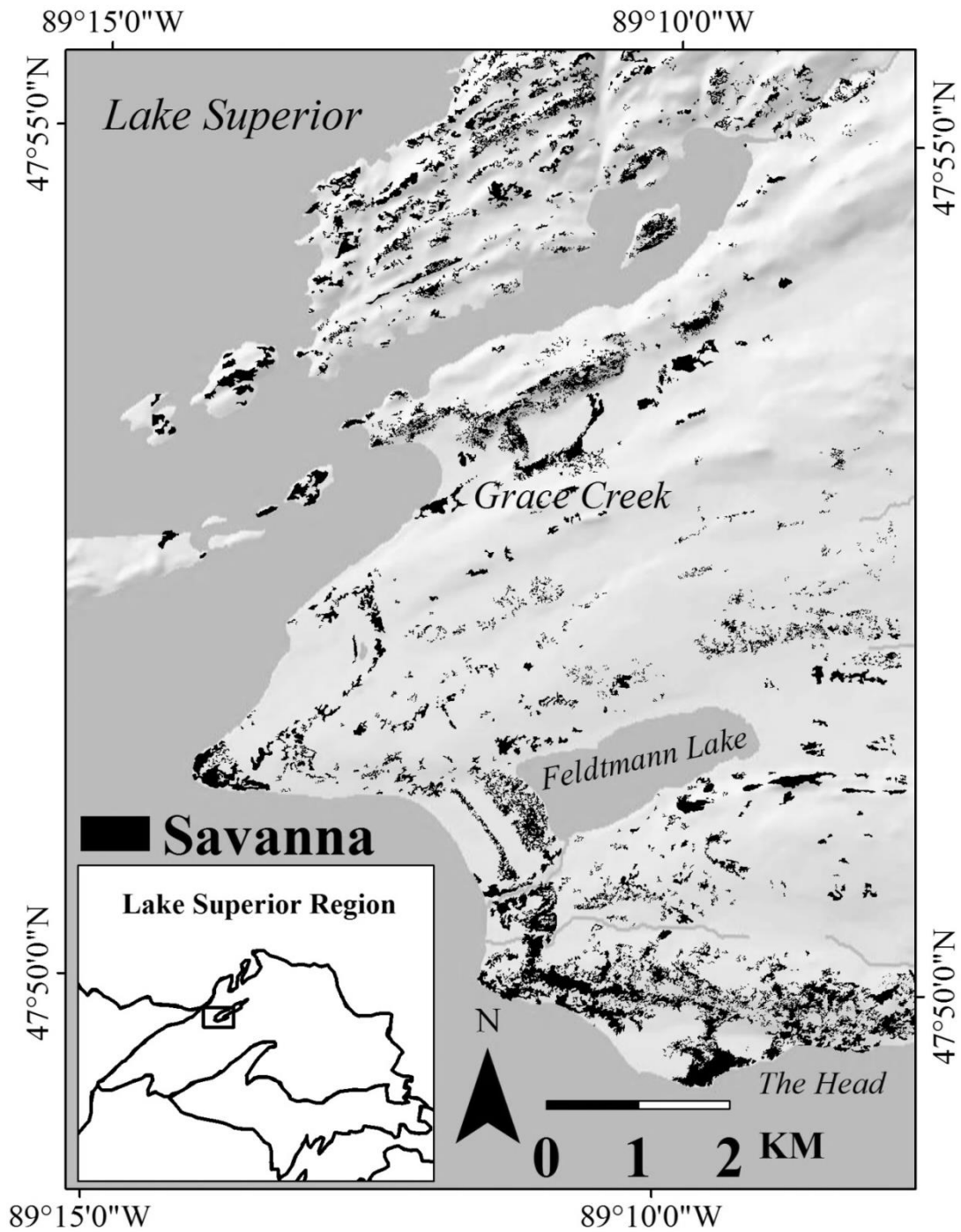


Figure 1. Map of the study area on the west end of Isle Royale. Savannas based on 2005 aerial photographs are shaded black. Inset showing location of the study area in the Lake Superior Region.

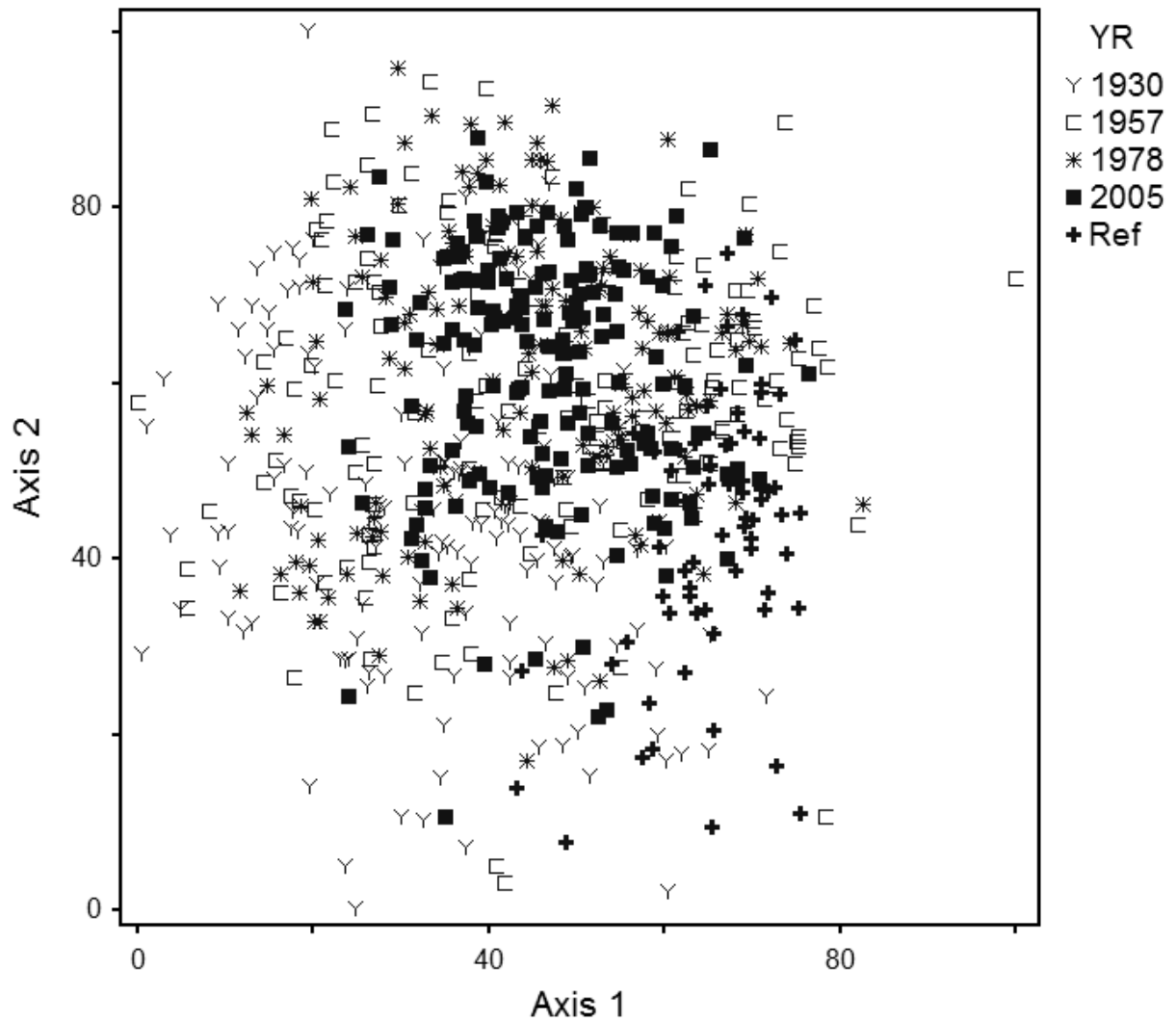


Figure 2. Non-Metric Multidimensional Scaling ordination for all sampled plots. Individual plots coded by age class. Final model was a 3 dimensional solution with a final stress of 20.1 and a final instability of <0.0001. Monte Carlo test of 50 iterations $p=0.004$.

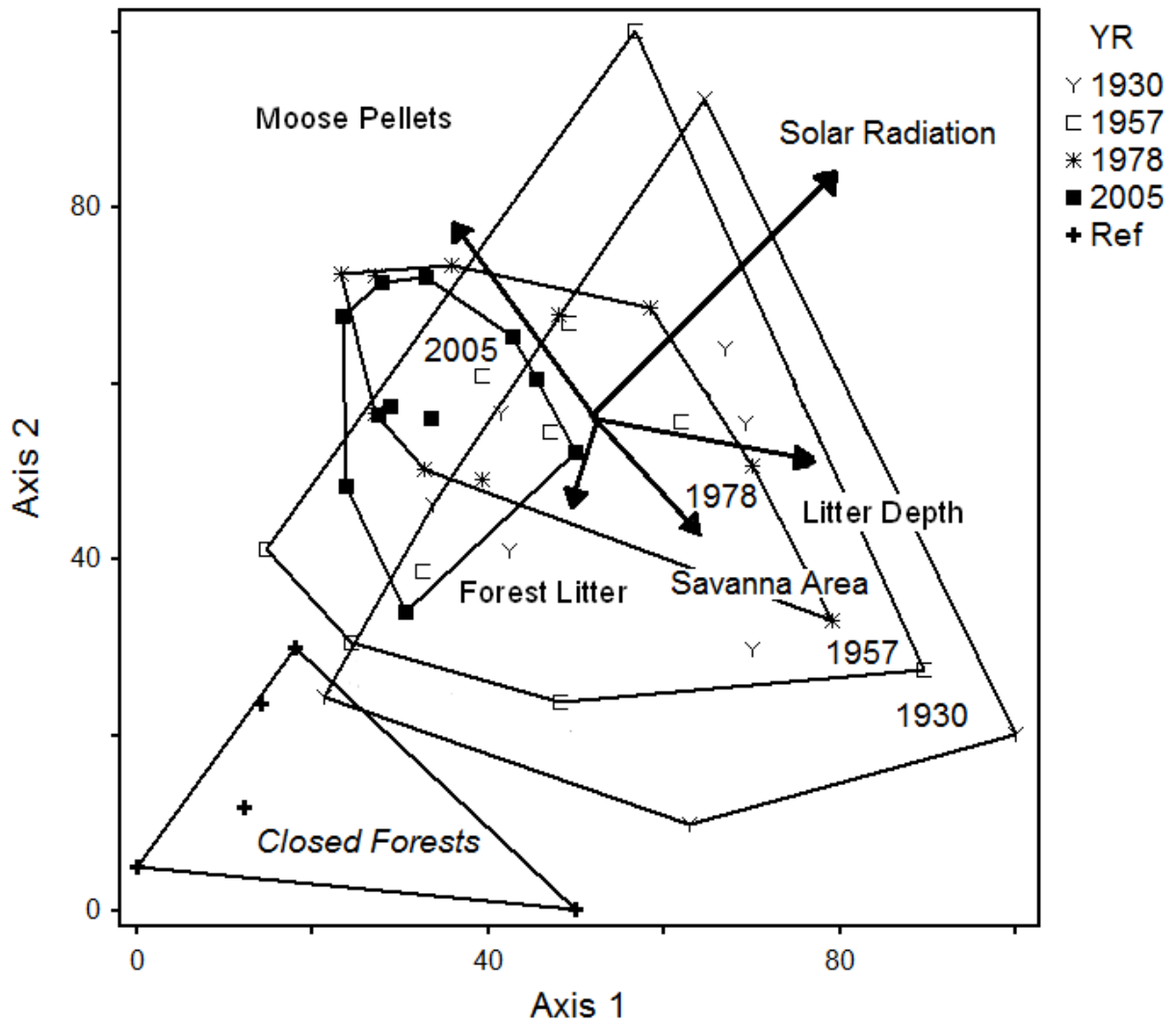


Figure 3. CCA of savannas with all data from plots within each savanna pooled. Eigenvalues for axis 1 and axis 2 were 0.295 (14.4%) and 0.208 (10.1%) respectively. For 100 iterations of Monte Carlo test $p=0.010$. Year was a categorical variable.

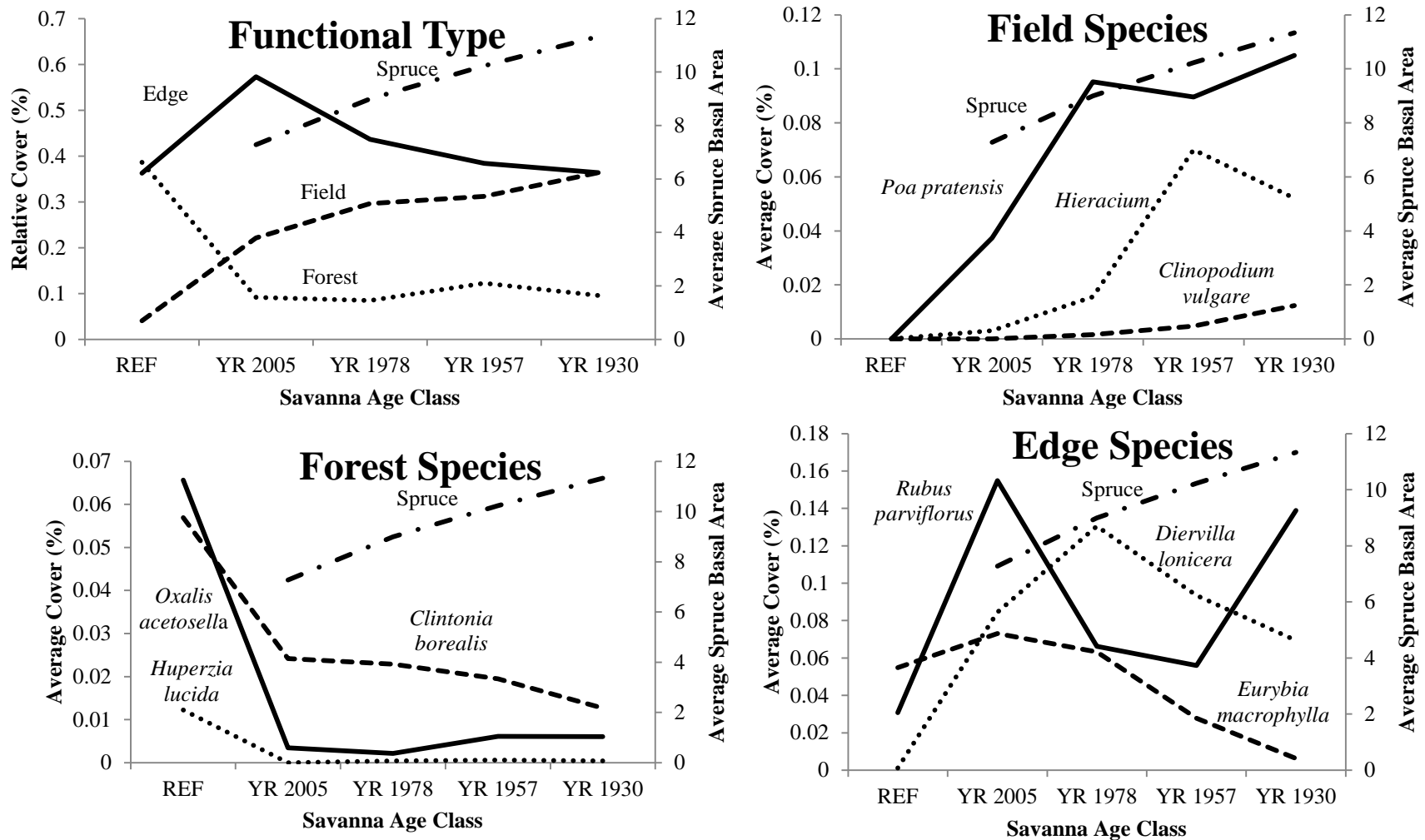


Figure 4. Relative cover of functional groups across age classes. Axis on right is the average basal area of spruce (m²/ha) for each age class

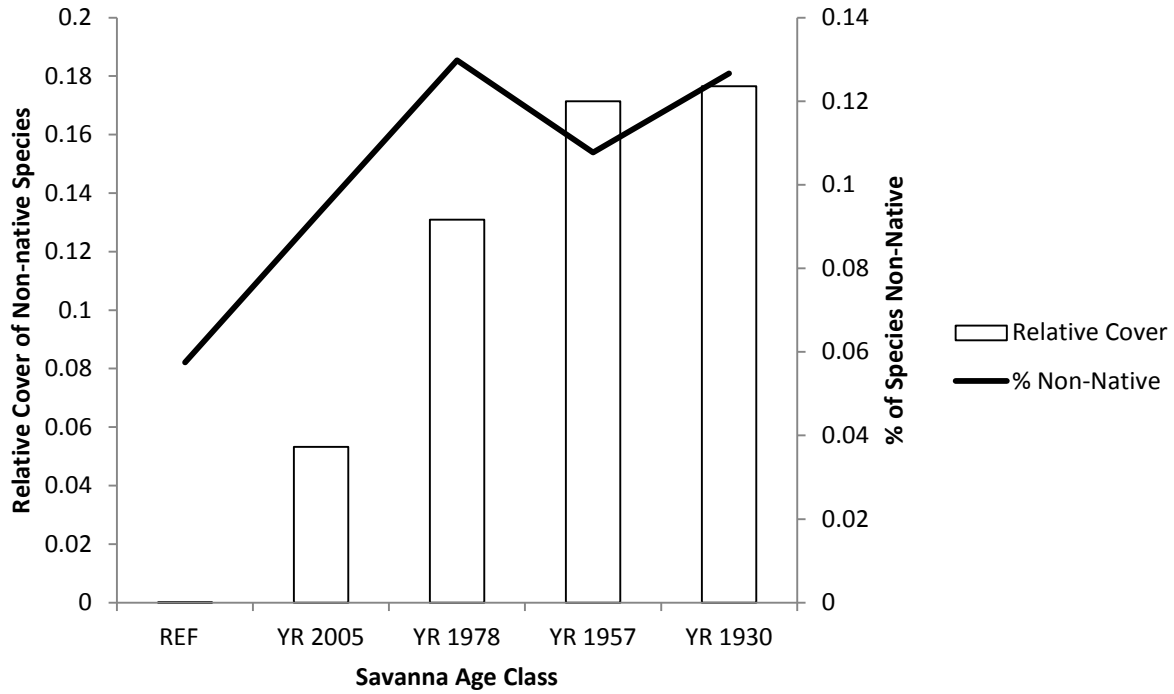


Figure 5. Relative cover of non-native plant species by age class displayed in bars. The percent of plant species richness composed of non-native species as black line by age class.

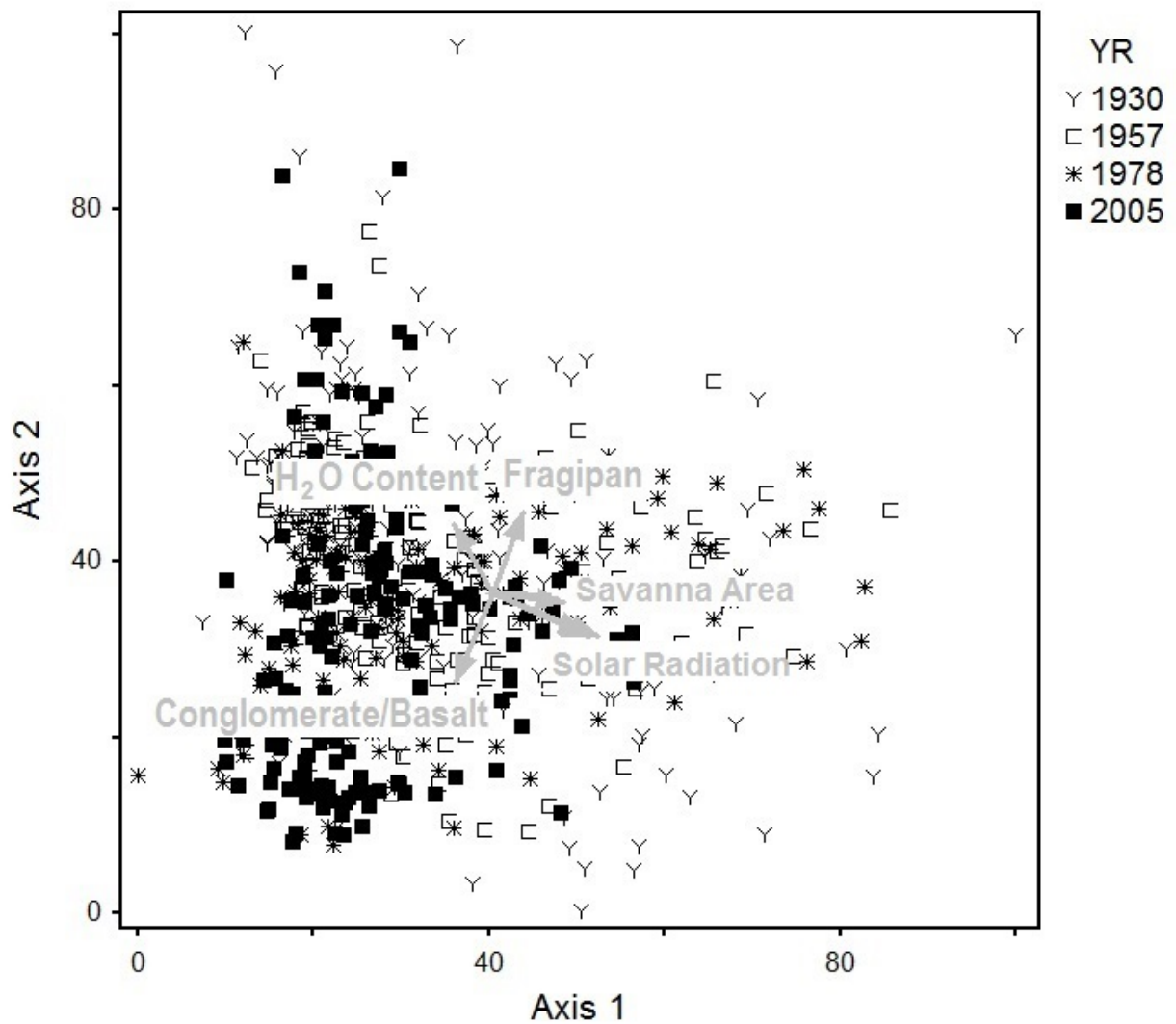


Figure 6A. CCA of savanna plots. Eigenvalues for axis 1 and axis 2 were 0.371 (4%) and 0.210 (2.3%) respectively. For 100 iterations of Monte Carlo test $p=0.010$. Individual plots labeled by age class. Variable codes in gray are Conglomerate/Basalt = On a conglomerate or basaltic bedrock, Solar radiation = total solar radiation (Mols m^2 per day), Savanna area= Savanna core area, Fragipan= Over fragipan base, and H₂O content = volumetric water content..

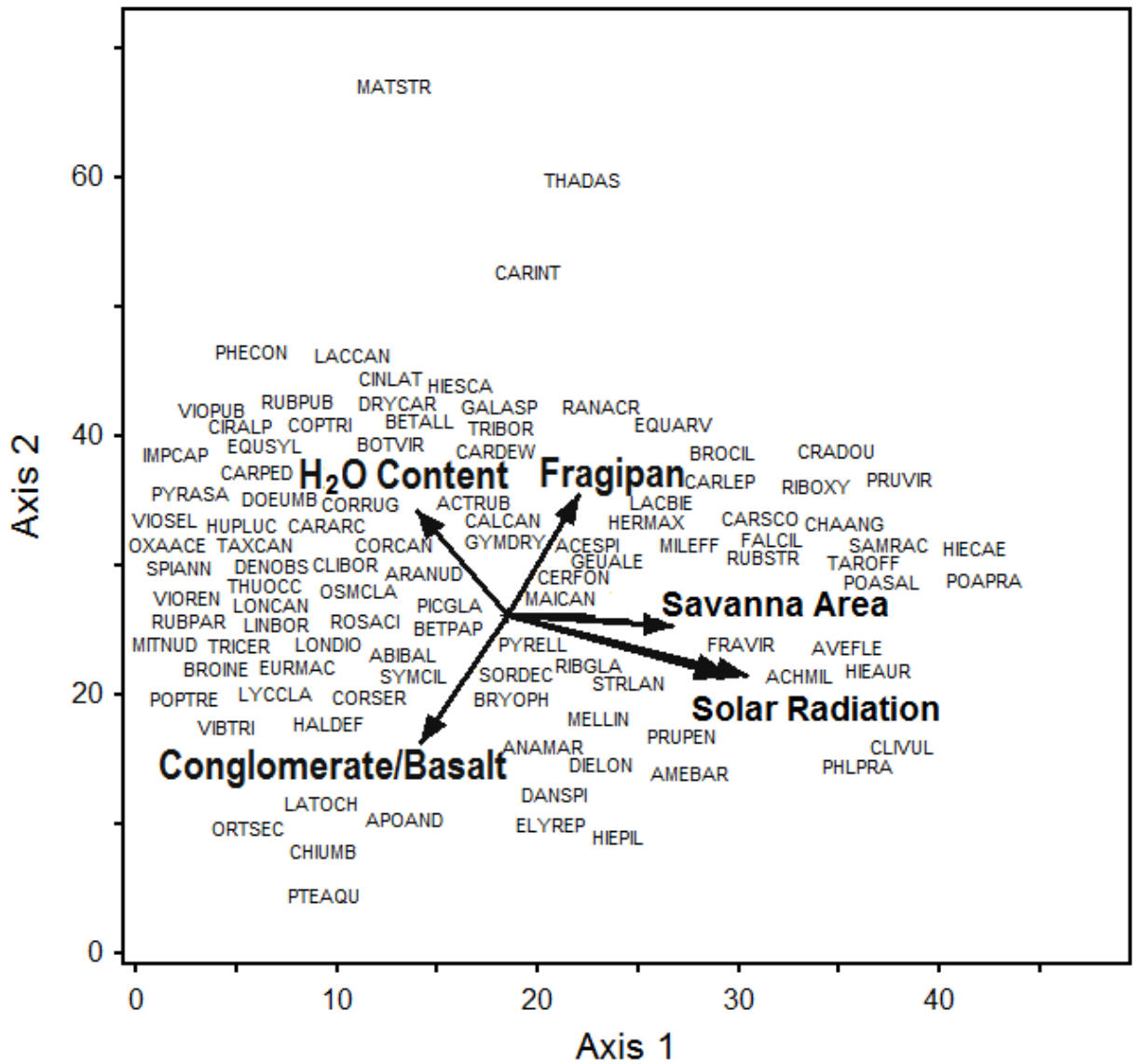


Figure 6B. CCA of savanna plots. Eigenvalues for axis 1 and axis 2 were 0.371 (4%) and 0.210 (2.3%) respectively. For 100 iterations of Monte Carlo test $p=0.010$. Species Codes are the first 3 letters of the genus and the first 3 letters of the specific epithet, see appendix A for scientific names. Scaling was min to max. Variable codes in bold are; Conglomerate/basalt = On a conglomerate or basaltic bedrock, Solar Radiation = total solar radiation (Mols m^2 per day), Savanna area= Savanna core area, Fragipan= Over fragipan base, and H₂O content = volumetric water content.

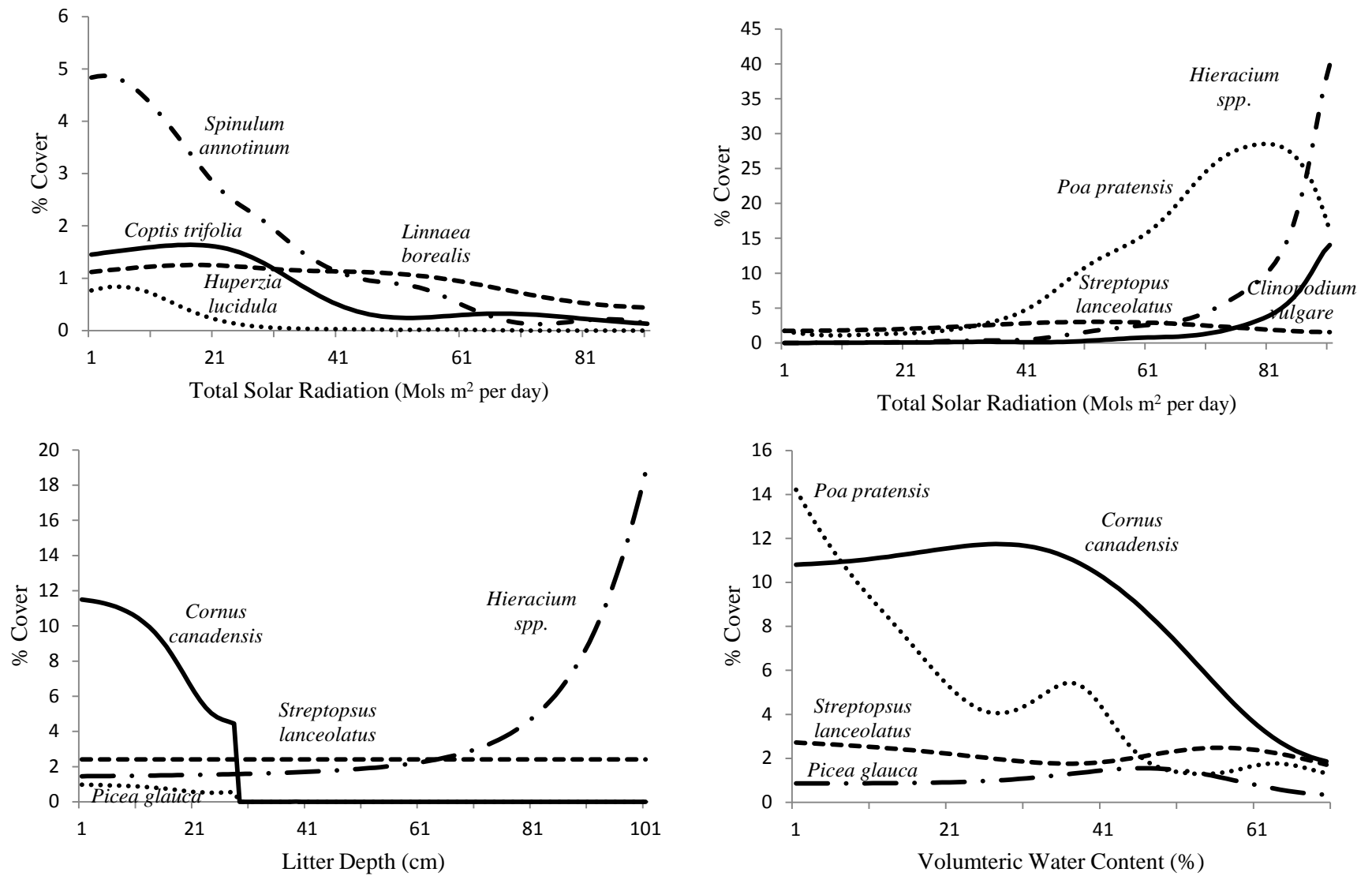


Figure 7. Response curves of selected species to important environmental variables. From local mean Gaussian models in Hyperniche. (all models $p \leq 0.05$).

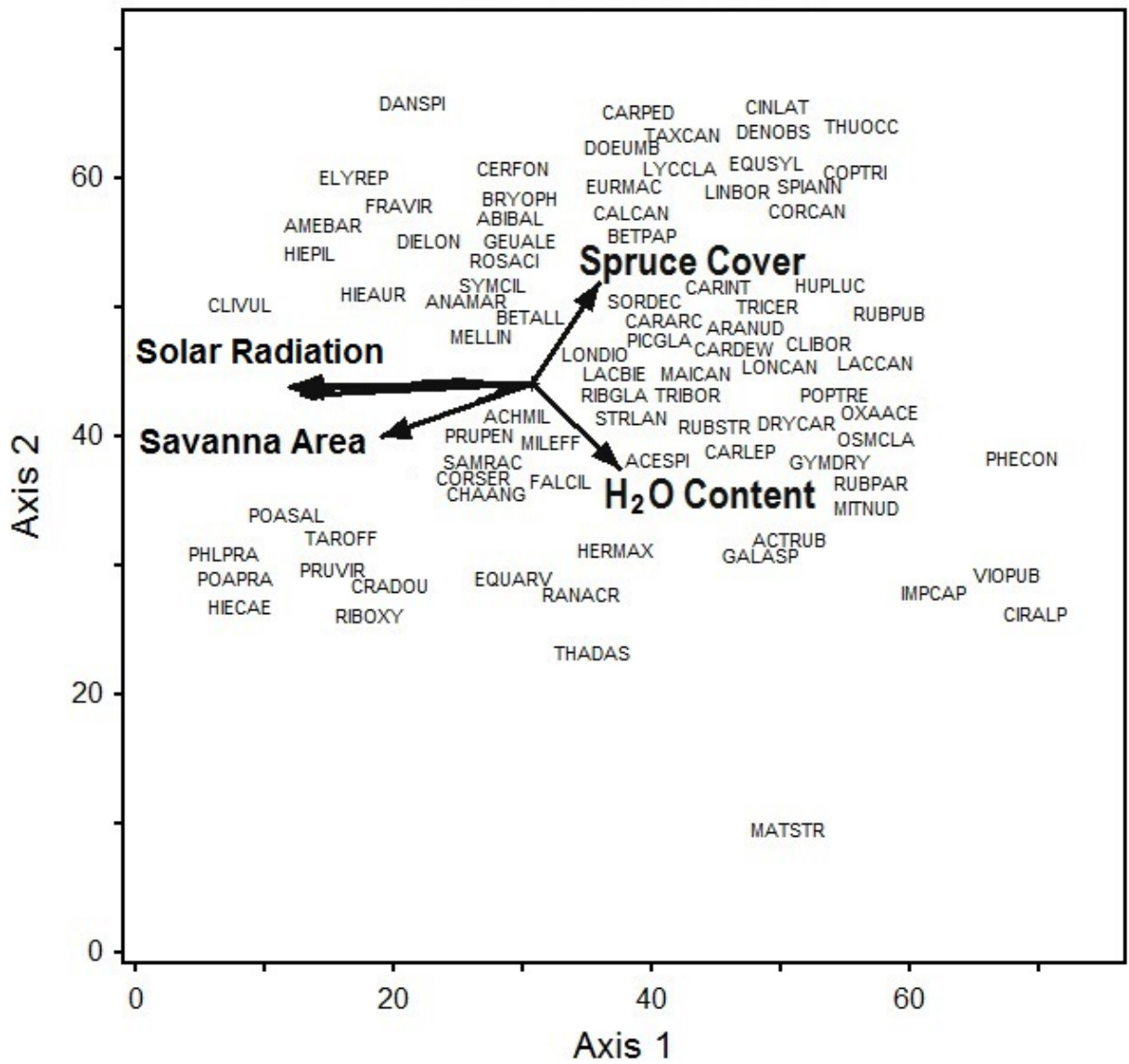


Figure 8. CCA for all savanna plots in the 1930 and 1957 savanna age class groups. Eigenvalues for axis 1 and axis 2 were 0.382 (4.4%) and 0.291 (3.4%) respectively. For 100 iterations of Monte Carlo test $p=0.010$. Variable codes in bold are Solar Radiation = total solar radiation (Mols m^2 per day), Savanna area= Savanna core area, and Spruce cover = *P. glauca* cover at breast height. Species Codes are the first 3 letters of the genus and the first 3 letter of the specific epithet, see appendix A for scientific names.



Figure 9. Forest plants underneath a mature *Picea glauca* in an open savanna. *Taxus canadensis* pictured in the middle with *Cornus canadensis* and *Gymnocarpium dryopteris* in the foreground and *Rubus parviflorus* in the background.



Figure 10. View of an open savanna community near Feltdmann Lake dominated by *Hieracium caespitosum* and *Poa pratensis*, with scattered *Picea glauca* and *Sambucus racemosa*.

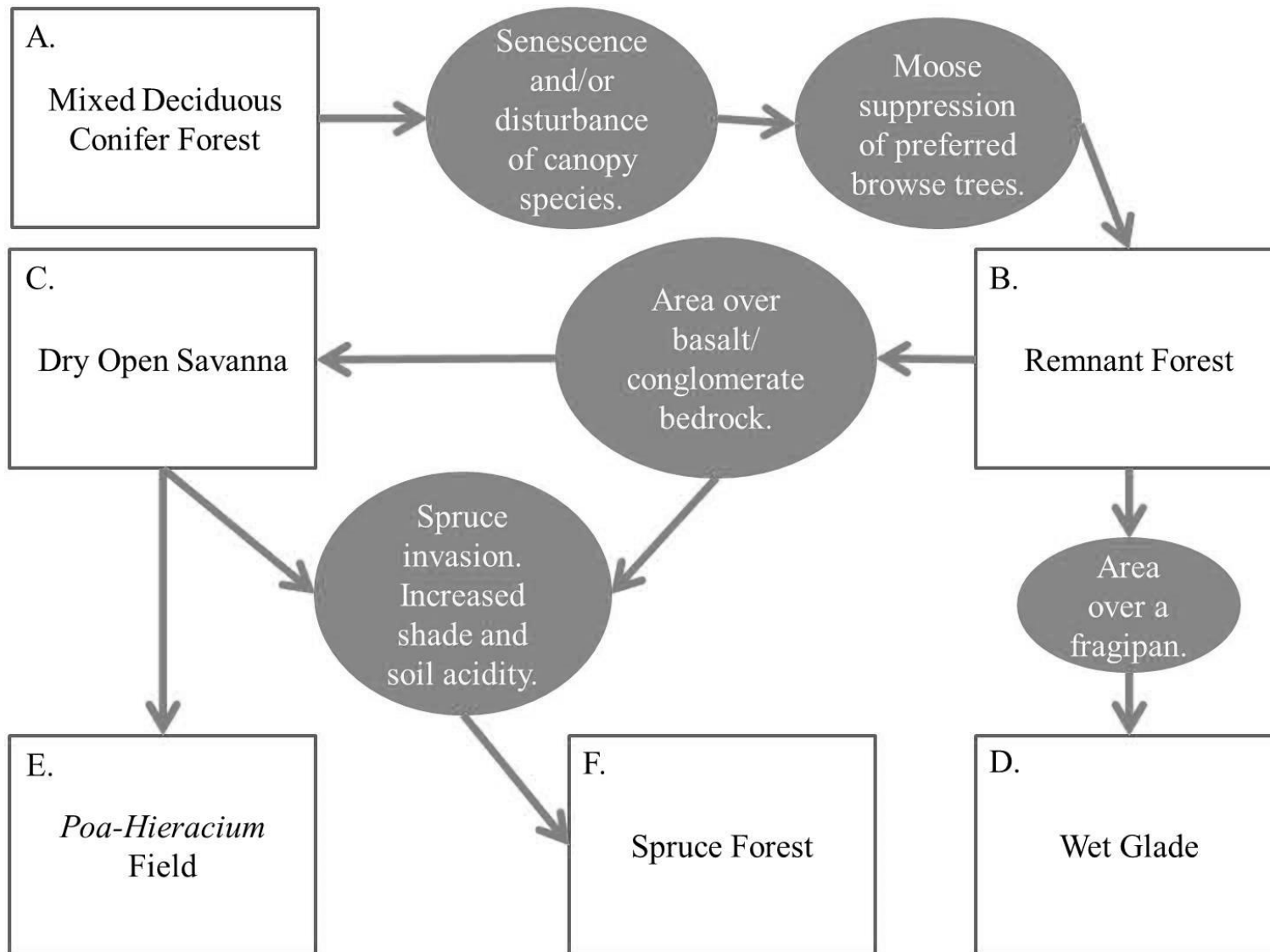


Figure 11. Flow chart of possible savanna vegetation development. Squares represent forest states and circles represent biotic and abiotic processes. A-F reference discussion in the text.

Table 1. Total richness of all age classes with estimated 1st order Jackknife. Average richness of plots for each age class with standard error.

Age Class	Richness	Jackknife	Average richness per plot
Ref	86	101.78	21.49±0.47
2005	138	164.83	23.33 ±0.30
1978	121	152.85	23.72 ± 0.37
1957	129	159.77	22.03±0.40
1930	149	179.8	22.23±0.47
All age classes	202	261.89	22.70±0.86

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APPENDIX A

Table A. Species name and 6 letter codes for all species observed, nomenclature follows Voss and Reznicek 2012.

Species Name	Code	Species Name	Code
<i>Abies balsamea</i>	ABIBAL	<i>Athyrium filix-femina</i>	ATHFIL
<i>Acer saccharum</i>	ACESAC	<i>Avenella flexuosa</i>	AVEFLE
<i>Acer spicatum</i>	ACESPI	<i>Betula alleghaniensis</i>	BETALL
<i>Achillea millefolium</i>	ACHMIL	<i>Betula papyrifera</i>	BETPAP
<i>Actaea rubra</i>	ACTRUB	<i>Botrychium minganense</i>	BOTMIN
<i>Agrimonia striata</i>	AGRSTR	<i>Botrychium multifidum</i>	BOTMUL
<i>Agrostis scabra</i>	AGRSCA	<i>Botrychium simplex</i>	BOTSIM
<i>Allium schoenoprasum</i>	ALLSCH	<i>Botrychium virginianum</i>	BOTVIR
<i>Alnus incana</i>	ALNINC	<i>Bromus ciliates</i>	BROCIL
<i>Amelanchier arborea</i>	AMEARB	<i>Bromus inermis</i>	BROINE
<i>Amelanchier bartramiana</i>	AMEBAR	<i>Bryophyte</i>	BRYOPH
<i>Anaphalis margaritacea</i>	ANAMAR	<i>Calamagrostis canadensis</i>	CALCAN
<i>Anemone canadensis</i>	ANECAN	<i>Carex arctata</i>	CARARC
<i>Anemone cylindrica</i>	ANECYL	<i>Carex brunnescens</i>	CARBRU
<i>Antennaria howellii</i>	ANTHOW	<i>Carex crinite</i>	CARCRI
<i>Apocynum androsaemifolium</i>	APOAND	<i>Carex deweyana</i>	CARDEW
<i>Aquilegia canadensis</i>	AQUCAN	<i>Carex disperma</i>	CARDIS
<i>Aralia nudicaulis</i>	ARANUD	<i>Carex gracillima</i>	CARGRA
<i>Arctostaphylos uva-ursi</i>	ARCUVA	<i>Carex houghtoniana</i>	CARHOU

Appendix A. Continued

Species Name	Code	Species Name	Code
<i>Carex hystericina</i>	CARHYS	<i>Cornus rugosa</i>	CORRUG
<i>Carex intumescens</i>	CARINT	<i>Cornus sericea</i>	CORSER
<i>Carex leptonevia</i>	CARLEP	<i>Corylus cornuta</i>	CORCOR
<i>Carex pedunculata</i>	CARPED	<i>Crataegus douglasii</i>	CRADOU
<i>Carex pensylvanica</i>	CARPEN	<i>Cynoglossum boreale</i>	CYNBOR
<i>Carex scoparia</i>	CARSCO	<i>Danthonia spicata</i>	DANSPI
<i>Carex stricta</i>	CARSTR	<i>Dendriycopodium dendroideum</i>	DENDEN
<i>Cerastium fontanum</i>	CERFON	<i>Dendrolycopodium obscurum</i>	DENOBS
<i>Chamerion angustifolium</i>	CHAANG	<i>Dianthus plumarius</i>	DIAPLU
<i>Chenopodium album</i>	CHEALB	<i>Diervilla lonicera</i>	DIELON
<i>Chimaphila umbellata</i>	CHIUMB	<i>Diphasiastrum complanatum</i>	DIPCOM
<i>Cinna latifolia</i>	CINLAT	<i>Doellingeria umbellata</i>	DOEUMB
<i>Circea alpina</i>	CIRALP	<i>Dryopteris carthusiana</i>	DRYCAR
<i>Cirsium arvense</i>	CIRARV	<i>Elymus repens</i>	ELYREP
<i>Cirsium vulgare</i>	CIRVUL	<i>Elymus wiegandii</i>	ELYWIE
<i>Clematis virginiana</i>	CLEVIR	<i>Epilobium ciliatum</i>	EPICIL
<i>Clinopodium vulgare</i>	CLIVUL	<i>Equisetum arvense</i>	EQUARV
<i>Clintonia borealis</i>	CLIBOR	<i>Equisetum hyemale</i>	EQUHYE
<i>Coeloglossum viride</i>	COEVIR	<i>Equisetum palustre</i>	EQUPAL
<i>Comandra umbellata</i>	COMUMB	<i>Equisetum sylvaticum</i>	EQUSYL
<i>Coptis trifolia</i>	COPTRI	<i>Erigeron strigosus</i>	ERISTR
<i>Corallorhiza maculata</i>	CORMAC	<i>Eurybia macrophylla</i>	EURMAC
<i>Corallorhiza striata</i>	CORSTR	<i>Euthamia graminifolia</i>	EUTGRA
<i>Cornus canadensis</i>	CORCAN		

Appendix A. Continued

Species Name	Code	Species Name	Code
<i>Fallopia cilinodis</i>	FALCIL	<i>Lactuca biennis</i>	LACBIE
<i>Fragaria vesca</i>	FRAVES	<i>Lactuca canadensis</i>	LACCAN
<i>Fragaria virginiana</i>	FRAVIR	<i>Lathyrus japonicus</i>	LATJAP
<i>Fraxinus nigra</i>	FRANIG	<i>Lathyrus ochroleucus</i>	LATOCH
<i>Galeopsis tetrahit</i>	GALTET	<i>Linnaea borealis</i>	LINBOR
<i>Galium asprellum</i>	GALASP	<i>Lonicera canadensis</i>	LONCAN
<i>Galium boreale</i>	GALBOR	<i>Lonicera dioica</i>	LONDIO
<i>Geranium bicknellii</i>	GERBIC	<i>Lycopodium clavatum</i>	LYCCLA
<i>Geum aleppicum</i>	GEUALE	<i>Maianthemum canadense</i>	MAICAN
<i>Goodyera oblongifolia</i>	GOOBL	<i>Maianthemum racemosum</i>	MAIRAC
<i>Gymnocarpium dryopteris</i>	GYMDRY	<i>Matteuccia struthiopteris</i>	MATSTR
<i>Halenia deflexa</i>	HALDEF	<i>Melampyrum lineare</i>	MELLIN
<i>Hepatica americana</i>	HEPAME	<i>Mentha arvensis</i>	MENARV
<i>Heracleum maximum</i>	HERMAX	<i>Milium effusum</i>	MILEFF
<i>Hieracium aurantiacum</i>	HIEAUR	<i>Mitella nuda</i>	MITNUD
<i>Hieracium caespitosum</i>	HIECAE	<i>Moneses uniflora</i>	MOEUNI
<i>Hieracium kalmii</i>	HIEKAL	<i>Monotropa uniflora</i>	MONUNI
<i>Hieracium pilosella</i>	HIEPIL	<i>Oenothera biennis</i>	OENBIE
<i>Hieracium scabrum</i>	HIESCA	<i>Orthilia secunda</i>	ORTSEC
<i>Hieracium umbellatum</i>	HIEUMB	<i>Oryzopsis asperifolia</i>	ORYASP
<i>Huperzia lucidula</i>	HUPLUC	<i>Osmunda claytoniana</i>	OSMCLA
<i>Impatiens capensis</i>	IMPCAP	<i>Osmunda regalis</i>	OSMREG
<i>Iris versicolor</i>	IRIVER	<i>Oxalis acetosella</i>	OXAACE
<i>Juniperus communis</i>	JUNCOM	<i>Phegopteris connectilis</i>	PHECON

Appendix A. Continued

Species Name	Code	Species Name	Code
<i>Phleum pratense</i>	PHLPRA	<i>Rhamnus alnifolia</i>	RHAALN
<i>Picea glauca</i>	PICGLA	<i>Rhododendron groenlandicum</i>	RHOGRO
<i>Picea mariana</i>	PICMAR	<i>Ribes glandulosum</i>	RIBGLA
<i>Pinus strobus</i>	PINSTRO	<i>Ribes lacustre</i>	RIBLAC
<i>Platanthera huronensis</i>	PLAHUR	<i>Ribes oxyacanthoides</i>	RIBOXY
<i>Platanthera orbiculata</i>	PLAORB	<i>Rosa acicularis</i>	ROSACI
<i>Poa compressa</i>	POACOM	<i>Rubus parviflorus</i>	RUBPAR
<i>Poa palustris</i>	POAPAL	<i>Rubus pubescens</i>	RUBPUB
<i>Poa pratensis</i>	POAPRA	<i>Rubus strigosus</i>	RUBSTR
<i>Poa saltuensis</i>	POASAL	<i>Rumex acetosella</i>	RUMACE
<i>Polygonum douglasii</i>	POLDOU	<i>Salix bebbiana</i>	SALBEB
<i>Polypodium virginianum</i>	POLVIR	<i>Salix discolor</i>	SALDIS
<i>Populus balsamifera</i>	POPBAL	<i>Sambucus racemosa</i>	SAMRAC
<i>Populus tremuloides</i>	POPTRE	<i>Schoenoplectus pungens</i>	SCHPUN
<i>Prenanthes alba</i>	PREALB	<i>Scirpus cyperinus</i>	SCICYP
<i>Prunus pensylvanica</i>	PRUPEN	<i>Scutellaria galericulata</i>	SCUGAL
<i>Prunus virginiana</i>	PRUVIR	<i>Silene noctiflora</i>	SILNOC
<i>Pteridium aquilinum</i>	PTEAQU	<i>Solidago altissima</i>	SOLALT
<i>Pyrola asarifolia</i>	PYRASA	<i>Sorbus decora</i>	SORDEC
<i>Pyrola chlorantha</i>	PYRCHL	<i>Spinulum annotinum</i>	SPIANN
<i>Pyrola elliptica</i>	PYRELL	<i>Stellaria graminea</i>	STEGRA
<i>Pyrola minor</i>	PYRMIN	<i>Streptopus lanceolatus</i>	STRLAN
<i>Ranunculus acris</i>	RANACR	<i>Symphyotrichum ciliolatum</i>	SYMCIL
<i>Ranunculus recurvatus</i>	RANREC	<i>Symphyotrichum puniceum</i>	SYMPUN

Appendix A. Continued

Species Name	Code
<i>Symplocarpus foetidus</i>	SYMFOE
<i>Taraxacum officinale</i>	TAROFF
<i>Taxus canadensis</i>	TAXCAN
<i>Thalictrum dasycarpum</i>	THADAS
<i>Thuja occidentalis</i>	THUOCC
<i>Tragopogon pratensis</i>	TRAPRA
<i>Trientalis borealis</i>	TRIBOR
<i>Trifolium aureum</i>	TRIAUR
<i>Trifolium pratense</i>	TRIPRA
<i>Trillium cernuum</i>	TRICER
<i>Urtica dioica</i>	URTDIO
<i>Vaccinium angustifolium</i>	VACANG
<i>Vaccinium myrtilloides</i>	VACMYR
<i>Veronica officinalis</i>	VEROFF
<i>Viburnum trilobum</i>	VIBTRI
<i>Vicia americana</i>	VICAME
<i>Viola blanda</i>	VIOBLA
<i>Viola pubescens</i>	VIOPUB
<i>Viola renifolia</i>	VIOREN
<i>Viola selkirkii</i>	VIOSEL
<i>Viola sororia</i>	VIOSOR