THE QUARRY TO ALVAR INITIATIVE:

Final report to The Ontario Aggregate Resources Corporation

Mar. 29, 2006

by

Dr. D.W. Larson
Professor
Integrative Biology
University of Guelph

Dr. Uta Matthes
Research Associate
Integrative Biology
University of Guelph

Mr. Paul Richardson
Ph.D. candidate
Integrative Biology
University of Guelph

Ms. Shannon Tomlinson
M.Sc. candidate
Integrative Biology
University of Guelph

Acknowledgements:

The work described in this document was supported by a Collaborative Research and Development Grant from the Natural Sciences and Engineering Research Council of Canada, and the Ontario Aggregate Resources Corporation. The latter corporation also provided logistical support, advice, and encouragement for which we are grateful. We thank the many individual property holders who gave us permission to sample on their land. We also thank John Gandor, Leanne Hathaway, Rachel Cook, Pete Kelly, Kathleen Bolger, Meaghan Bell, Trevor Wilson, and Lori Klatt for assistance in the field. Lastly we thank Margaret Stalker for initiating the project and David Sterrett (TOARC) for seeing it through to an end.

Executive Summary

1. Numerous abandoned limestone quarries exist in Ontario below the Canadian Shield.

2. Current legislation requires that quarried sites be rehabilitated following abandonment.

3. Prior to this project, there was no basis in research for the rehabilitation of these quarry floors.

4. One previously unexplored question is whether these abandoned sites could represent an opportunity to expand the aerial extent of alvar vegetation communities in Ontario. Alvars are globally imperiled and hence answering this question could have benefits both to conservation of alvars and restoration of abandoned quarries at the same time.

5. A sequence of two research questions were posed: first, to what degree are abandoned limestone quarries similar to alvars in their ecological structure? Second, what factors limit the ability of alvar species to colonize abandoned quarry floors?

6. The first research question (Q1) was answered by a two-pronged approach. First, we selected 13 abandoned quarries and sampled the existing vegetation and environmental features of each site. An analysis was carried out that allowed us to characterize each site and to also examine the differences among sites. The quarries were located in the limestone regions of Ontario below the Canadian Shield.

7. Next we compared the quarry floor biophysical environment to the naturally occurring biophysical environment on 7 alvars. The data for the alvars was obtained in the mid-1990's as part of the master's project of Claudia Schaefer.

8. The second research question (Q2) was answered by carrying out work in 4 abandoned quarry sites. A manipulative field experiment was used. In this experiment, we seeded plots with alvar and quarry floor species (as controls), and also provided soil amendments such as silica sand addition, organic carbon addition, competition removal and nutrient addition.

9. We found for Q1 that the population of quarry floor sites was variable in terms of species composition, but less so in the physical environment. The quarry floor sites were also more variable than the population of alvar sites.

10. Despite this variability, quarry floors and alvars were strikingly similar. Seventy-seven of the 246 species of vascular plants, bryophytes, and lichens found on quarry floors have also been found on alvars, and 24 of the 200 vascular plant species, or 12%, were 'characteristic' of alvars as defined by Catling and Brownell (1995). In comparison, characteristic alvar species comprised 24% (86/345) of all vascular plant species in the literature on alvars proper (based on Catling and Brownell 1995), and 26% (47/180 species) in the study of alvars on the Bruce Peninsula by Schaefer and Larson (1997).

11. The physical environment of quarry floors and alvars was also very similar.

12. We conclude for question 1 that the quarry floors are much more similar to naturally occurring alvars that we expected. We feel that natural processes have been responsible for roughly a 50-60% conversion of quarry to alvar.

13. For Q2 we found strong evidence that seed limitation is the principal factor limiting the colonization of quarry floors by alvar species. Survivorship of both quarry and alvar species was similar, and soil amendments or other treatments had only small effects on survival. Addition of soil nitrogen reduced survival but silica sand addition increased survival.

14. There was a catastrophic drought in the early summer of 2005. In that period the rainfall was the lowest on record in 57 years. Despite the severity of the drought, survival of plants that we introduced was high. Alvar species planted by us had higher survival rates than quarry floor species.

15. In summary, we find that abandoned limestone quarry floors in Ontario are more structurally and functionally similar to alvar ecosystems than has been appreciated before. Natural processes have taken control of soil development and species recruitment, leading to ecosystems that have moved about halfway to becoming legitimate alvars. A more rapid development of quarry floors into these real alvars seems to require nothing more than seed and silica sand addition.

INTRODUCTION

Humans have massively altered the physical and biological features of the earth. Sanderson et al. (2002) have estimated that approximately 83% of terrestrial landscapes have been converted from 'wilderness' to areas fully or partly exploited by people. Earlier estimates by Vitousek (1994) suggested that 40% of global terrestrial net primary productivity has been redirected to human activities. These estimates of the extent of human encroachment on the planet suggest that a major effort must be expended to try to halt and, wherever possible, reverse the trend. Balmford et al. (2002) provide economic arguments to support such efforts.

Quarrying of rock represents one of the most ancient and important activities that supports human existence (Larson et al. 2004). Rock has been extracted from the earth for use in building construction, tool manufacturing and road building for many thousands of years. As human population size increases, the rates of extraction have increased proportionately. Unfortunately, the extraction of rock from the ground utterly destroys the present terrestrial ecosystem. Unless the quarried land is actively restored, the slow process of primary succession is the only mechanism by which another productive ecosystem can be produced.

In recent years there has been a growing appreciation of the need to establish a legal requirement for provincial quarry owners/operators to rehabilitate the land used for extraction. In Ontario alone, more than 6 000 pits and quarries require rehabilitation (TOARC 2003). The number of pits and quarries will continue to increase as the demands of a growing population increases (APAO 2003). It is now more important than ever to develop successful rehabilitation goals for quarry sites.

Efforts made to help solve the problem

A program known as the Management of Abandoned Aggregate Properties (MAAP) was established in 1997 to facilitate research into the rehabilitation of abandoned pits and quarries in Ontario. MAAP has been responsible for rehabilitating over 100 gravel pits to natural areas, productive farmland and recreational sites. Such restoration is relatively straightforward since the substrate left behind by gravel pit operations is similar to the glacial tills that underlie much of Canada south of the Precambrian shield. There has been less success with quarry sites because of a general lack of literature on hard-rock landscape restoration. Only two studies in North America have examined the ecology of abandoned limestone quarry floors (Skaller 1977; Browning 1998) and therefore more work of this type is necessary.

A solution to this problem

One of the main limitations to quarry restoration is the absence of clear restoration targets. It is suggested by Larson et al. (2004) that rehabilitating a degraded site to something it already closely resembles in nature could result in more successful rehabilitation. Alvar habitat appears to be superficially similar to abandoned limestone quarry floors. In this project I asked "can a type of naturally occurring rock outcrop ecosystem known as 'alvar' be used as a restoration target for abandoned limestone quarry floors in Ontario?"

Alvars as a restoration target

Alvars are open areas of flat limestone inconsistently covered with shallow, patchy soil and sparse vegetation consisting mainly of cryptogams, herbs and shrubs (Schaefer 1996; Belcher et al. 1992). Trees may be present but are not canopy forming, or they may be absent altogether. Periodic drought and flooding are important factors preventing woody species from encroaching on the cryptogamic and herbaceous vegetation (Catling and Brownell 1995; Schaefer and Larson 1997; Stark et al. 2003). These naturally occurring rock outcrop systems show extremely high levels of spatial heterogeneity of species cover. They are considered one of the most floristically-rich habitats in northern-temperate regions. The weathering of the limestone substrate forms a base-rich soil through its additions of calcium and magnesium (Catling and Brownell 1999). Despite this, almost all of the mineral matter in alvars is silicaceous sand (Stark et al. 2004).

Significance of alvars

Alvars contain a variety of rare, endangered and endemic plant and animal species. As many as 43 rare Ontario native plant species have been identified in the Great Lakes region (Catling and Brownell 1995). Not only do alvars support rare endemics but also drought-tolerant crop species or their relatives (Catling 1995). In the context of rapidly changing global climates, it may be useful to obtain knowledge of how such species function when exposed to naturally-occurring but extreme environments. Unfortunately, such research opportunities are slowly disappearing because alvars are threatened by a variety of impacts including off-road vehicle use, hiking, logging and grazing. Cottage and housing development and quarrying operations are two of the most serious threats affecting the small amounts of remaining alvar habitat (Catling and Brownell 1999).

Remaining alvar habitat

Alvars are found in the Baltic regions of Sweden and Estonia and in Michigan, New York and Ontario. Over 90% of alvars in the Great Lakes region are found in southern Ontario (Catling and Brownell 1995; Belcher *et al.* 1992; Schaefer and Larson 1997). Approximately 1 122 km^2 of the Great Lakes region is alvar habitat. This is roughly estimated to 252 to 287 alvars remaining in North America (Catling and Brownell 1995).

Conservation/preservation of alvar habitat

The Nature Conservancy has listed open alvars as provincially and globally endangered. Despite this, less than one quarter of alvar sites in North America are protected (Catling and Brownell 1995). Protecting the remaining alvars from human impact is one solution to the problem, but creating new alvar habitat is another possible solution. While quarrying of limestone is one of the main causes for the declining extent of alvars, the abandoned limestone pavements may turn out to be well suited to the re-establishment of alvar vegetation. Past qualitative research has surveyed the dominance of native plant species, native plant diversity and native plant communities throughout the alvars of the Great Lakes region of North America (Catling and Brownell 1995; Catling 1995; Catling and Brownell 1999). One of the few quantitative North American alvar studies examined both biological and physical characteristics of alvars in southern Ontario (Schaefer 1996). These quantitative data provide baseline characteristics of a naturally-occurring rock outcrop ecosystem. These data will facilitate a biological and physical comparison of data collected from abandoned limestone quarry floors in southern Ontario.

Abandoned limestone quarry floors

Limestone quarrying results in open, flat surfaces of calcareous bedrock that is unevenly covered with shallow patches of rock tailings. The relatively flat landscape, coarse and fine rock debris, stable and mobile rock piles, low levels of nutrients, flooding, drought, alkaline skeletal soils and severe temperature fluctuations are many of the physical features that distinguish quarry floors from other disturbed ecosystems (Ranson and Doody 1981; Usher 1979). A cyanobacterial community is often found on the top layers of moist soils that have accumulated in the natural depressions of the quarry floor. Hodgson (1981) has also reported that quarry floors in the UK support a rich assemblage of legumes and therophytes. It has also more recently been discovered that quarry floors provide refugia for rare endemics. This has led to classifying several quarry floors in the United Kingdom as Sites of Special Scientific Importance (Bradshaw 1994).

The extent of quarrying

Quarries are found world-wide, especially in well-developed countries. As many as 6 014 pits and quarries are supplying the aggregate demands of both the public and private sectors in Ontario, Canada. Close to 37 000 hectares of land have been converted to aggregate extraction sites, and the number of quarried landscapes continues to rise annually (TOARC 2003). Aggregate is used in greater quantities than any other natural resource in Ontario; every year, approximately 170 million tonnes of rock are consumed (APAO(b) 2005). The Aggregate Producers Association of Ontario (APAO) has projected that as the human population increases over the next 25 years, approximately four billion tonnes of aggregate will be consumed. Currently, the annual per capita consumption of aggregate is more than 16 tonnes (APAO(b) 2005).

Limestone: the most important aggregate for Ontario's quarrying industry

Limestone is a common rock formation found in almost every region of Ontario. It is particularly important to the aggregate industries in southeastern Ontario because of the shortage of local sand and gravel resources (Booth and Wahl 1989). Limestone is the main source of higher quality aggregate in Ontario. It is mainly used in the construction industry as concrete, but it is also used in the chemical, steel, glass and agricultural industries.

Rehabilitation of quarries

Despite the increasing consumption of limestone aggregate, rehabilitation of pits and quarries was not legally enforced in Ontario until recently (ARA 1997 http://www.cyber-north.com/arawhat.html). Unfortunately, there has been a minimal amount of quarry floor rehabilitation due to a limited amount of North American literature that focuses on the remediation of hard-rock landscapes. Several limestone quarry floors in the United Kingdom have been examined and experimentally rehabilitated (Bailey and Gunn 1992; Clemente et al. 2004; Davis et al. 1985; Dixon and Hambler 1984). Observational studies have also been carried out on limestone quarry sites in Great Britain (Borgegard 1990; Browning 1998; Davis 1981; Hodgson 1981; Humphries 1981; Jefferson(a) and (b) 1984; Khater *et al.* 2003; Park 1981; Ranson and Doody 1981). With only one observational study performed in North America, there is little known about the terrestrial ecosystem of a limestone quarry floor. A thorough understanding of the ecology of limestone quarry floors is necessary to develop effective rehabilitation techniques for hard-rock landscapes in North America.

OBJECTIVES AND RESEARCH QUESTIONS

The overall objective of this study is to determine whether alvars will make suitable reference targets for limestone quarry floor rehabilitation. The research questions have been divided among five main parts: 1) Abandoned limestone quarry floor survey; 2) Comparison of abandoned limestone quarry floors and alvars of southern Ontario; 3) Seed bank analysis of limestone quarry floors; 4) Comparison of soil seed banks of limestone quarry floors and alvars of southern Ontario; and 5) Seed addition experiments. Figure 1 shows a flow diagram of the various components of this work.

Part 1: Abandoned limestone quarry floor survey

The first objective of the abandoned limestone quarry floor survey is to determine the vegetative community and environmental gradients of limestone quarry floors in southern Ontario. The second objective is to determine the relationships between the species composition and the environmental variables. These results will provide a baseline for future work in restoration ecology. This survey will also provide quarry owners/operators with a baseline for limestone quarry floor rehabilitation.

Question 1

What are the biological and physical characteristics of abandoned limestone quarry floors in southern Ontario?

Prediction: Abandoned limestone quarry floors are expected to contain a high percent cover of bare rock and a patchy distribution of shallow soil. A heterogeneous cover of cryptogamic and vascular vegetation is expected to establish on the sporadic patches of soil. A high percent cover of lichens and bryophytes would also be expected because of the large areas of rock. It is therefore predicted that quarry floors will have a high species richness that will include many exotics because quarries are disturbed habitats. Grime (1977) states that stress-tolerant ruderals have adapted to rock outcrop systems because these habitats are lightly disturbed and unproductive.

Question 2

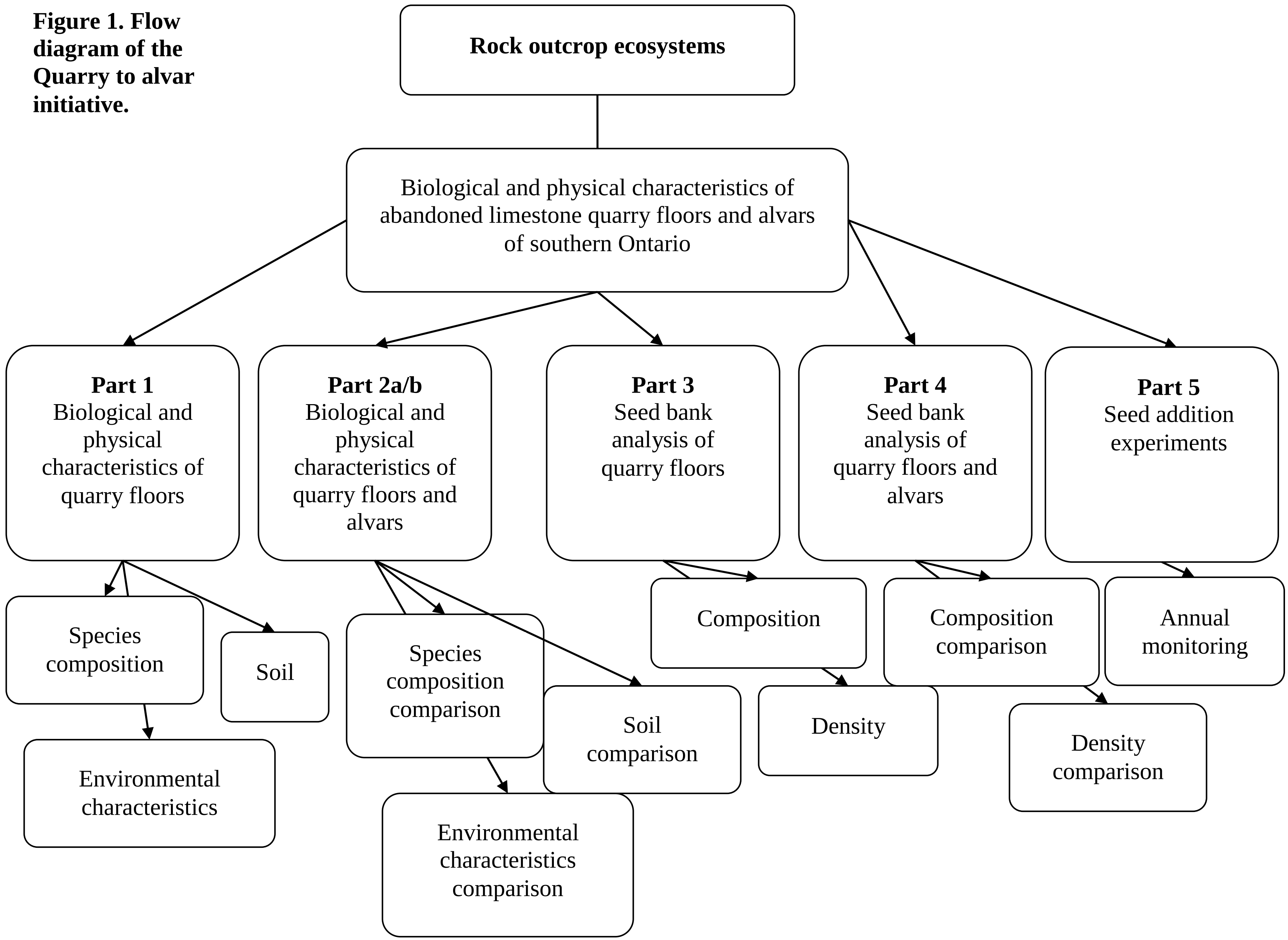
What is the relationship between the species composition and environmental variables?

Prediction: It is predicted that younger limestone quarry floors will have more exotics than older quarry floors. Browning (1998) states that a minimum of 25 years since abandonment are required before a dominant native flora can establish. It is also predicted that the soils of younger quarry floor sites will be more skeletal than the soils of older quarry floor sites. In a normal sequence of ecosystem development, soil depth, acidity levels, phosphorous, potassium, calcium, magnesium, total carbon and total nitrogen would all increase with system age (DeKovel et al. 2000 and Lee et al. 2002 *as cited by* Stark et al 2004).

Part 2: Comparison of abandoned limestone quarry floors and alvars of southern Ontario

The first objective for the comparison between the abandoned limestone quarry floor sites and the alvar sites (Schaefer 1996) is to compare the species composition of both habitats. The second objective is to determine the relationship of the species composition and the environmental

Figure 1. Flow diagram of the Quarry to alvar initiative.



variables of each habitat. The third objective is to determine which environmental characteristics are significantly controlling the species composition in both ecosystems.

Question 3
To what degree do abandoned limestone quarry floors differ ecologically from alvars?
Prediction: The environmental characteristics of limestone quarry floors and alvars should not differ significantly because both habitats are derived by massive disturbances (glacial action, wind scouring, and fire for alvars and mining for quarry floors). It is predicted that several soil characteristics of limestone quarry floors will be significantly different than those of alvar soil because the 'soils' of quarry floors are composed of rock tailings. It is also predicted that the species composition of limestone quarry floors will have a higher exotic component than the species composition of alvars because quarry floors are frequently surrounded by other anthropogenic landscape units in which exotic species thrive.

Part 3: Seed bank analysis of limestone quarry floors
The first objective of the quarry floor seed bank analysis is to determine whether a limestone quarry floor seed bank favours an exotic above-ground flora. A second objective is to determine whether there are alvar species in the quarry floor seed bank which are not present in the established quarry floor vegetation.

Question 4
How does the quarry floor seed bank richness and density compare to the above-ground species richness?
Prediction: The seed bank of quarry floors is expected to be high and composed of mainly exotic species because the above-ground vegetation is similarly composed. The density of seeds is expected to be high because the established vascular vegetation is mainly composed of stress-tolerant ruderals. The life cycle of a ruderal is very rapid and maximizes seed production (Grime 1977). Therefore, a high abundance of seeds is released from each plant adding to the seed bank.

Part 4: Comparison of soil seed banks of limestone quarry floors and alvars
The objective of the comparison between abandoned limestone quarry floor seed banks and alvar seed banks in southern Ontario is to determine the similarities and differences of the below-ground species composition of both habitats. The second objective is to compare the seed bank densities of both habitats.

Question 5
How does the seed bank species richness, density, and quality compare between quarry floor and alvar habitats?
Prediction: The seed bank species richness and density of quarry floors and alvars will be similar if we discover that the physical environment in the two habitats is acting in similar ways. The high species richness of above-ground vegetation should contribute to a high species richness in the soil seed banks of both habitats. The quarry floor seed bank will contain long-term persistent alvar species because several alvar endemics were discovered in the initial quarry floor vegetation assessment.

<u>Part 5: Seed addition experiments</u>

The objective of this part of the work is to determine if floors of abandoned limestone quarries are limited by immigration barriers alone, or whether there are other forces which critically constrain colonization success.

Question 6

When quarry floors are seeded with species that naturally occur in quarries or species that naturally occur on alvars, is the survivorship of the two groups of species the same? Will the fate of the plants be influenced by different soil amendments, by the release of competition, or by the likelihood of flooding or drought on the site?

Prediction: Quarry species will perform better than alvar species when exposed to similar stresses. Survivorship of all species will be increased by addition of nitrogen, removal of competition, addition of organic matter, and addition of silica sand. Portions of sites exposed to episodic drought or flooding will have lower survivorship than intermediate, more mesic sites.

METHODS

Abandoned limestone quarry floor survey:

Quarry floor sites

Thirteen abandoned limestone quarries were randomly chosen across southern Ontario, Canada. Site selection was based on four criteria: substrate, size, disturbance and permission. Limestone or dolomite quarry floors required enough space to contain 25 non-overlapping quadrats. Minimal current disturbance to the quarry floors was required. This included minimal amounts of garbage, fire pits and human traffic. Permission from the quarry owner was also necessary.

The thirteen quarry floor sites were found throughout southern Ontario, Canada in or near the following cities: Collingwood, Guelph, Rockwood, Georgetown (two sites), Limehouse, Cambridge, Puslinch, Kingston, Grimsby, Russell, Springvale and Wiarton (Figure 2). Eight of these sites were surveyed throughout the summer of 2003. The same eight sites with the addition of five more quarry floors were surveyed in the summer of 2004. Each site was surveyed a minimum of three times in order to account for the early- and late-emerging vegetation.

Quarry floor sampling design

The sampling design was based on that used in Schaefer (1996). Five transects were randomly chosen from a total of 20, each 18° apart from each other (360° divided by 20). A compass was used to determine where the selected transects would fall. The five transects were systematically placed from the centre of the quarry floor to either the base of the talus slope or to the quarry wall if the talus slope was absent. The length of each transect was measured and divided by five to determine where each quadrat would be placed. Five quadrats were spaced equidistantly along each transect. This prevented any overlapping of quadrats. Each quadrat measured 0.4 m x 1.6 m and was divided into 16, 20 cm x 20 cm cells. The quadrats were placed on the transect so that the 0.4 m side of the quadrat ran parallel to the line and the 1.6 m side of the quadrat ran orthogonal to it; the transect ran through the middle of each quadrat (Figure 3). A total of 325 quadrats were surveyed across 13 quarry floors in southern Ontario.

Quarry floor survey

Both biotic and abiotic components were surveyed at each quarry site. The biotic components included recording the presence/absence of every lichen, bryophyte and vascular plant species in each cell of each quadrat to determine the percent frequency of a species. Identification was done on site, but for difficult identifications, the species were brought back to the lab and identified by Carole Ann Lacroix at the OAC Herbarium, Biodiversity Institute of Ontario, Canada. Nomenclature for vascular species mainly followed Newmaster et al. (1998). Nomenclature for bryophytes followed Crum (1983), and lichen nomenclature followed Brodo (2001).

The physical environment of the quarry floors and the relationship between the physical environment and the species composition were analysed. The physical components included recording the percent cover of woody debris, leaf litter, bare rock, soil, bryophytes, lichens and canopy in each cell of every quadrat. Each of the environmental variables was estimated and assigned to one of five categories: 0, 1-25%, 26-50%, 51-75% and 76-100%. Soil depth was measured to the nearest centimeter in 10 randomly chosen cells in every quadrat.

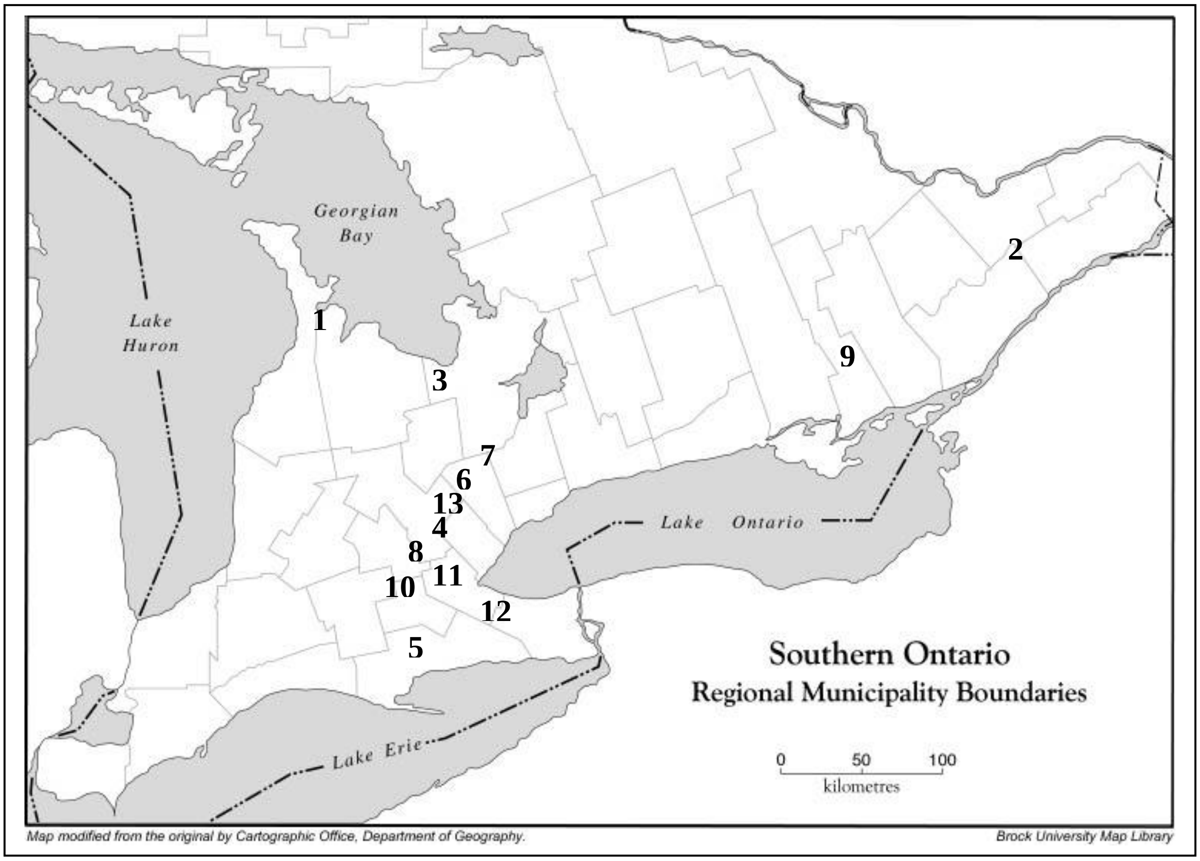


Figure 2. Map of southern Ontario, Canada indicating the 13 quarry floor sites used in this study. 1: Wiarton; 2: Russell; 3: Collingwood; 4: Rockwood; 5: Springvale; 6: Muldoon Pit; 7: Glen Williams; 8: Guelph; 9: Kingston; 10: Cambridge; 11: Fletcher Creek; 12: Grimsby; 13: Limehouse. Quarry sites are listed in order of age since abandonment.

Surface water cover and age were based on separate ranking systems. The 'water' rank was based on the number of visits where water was present in each quadrat. A rank of zero indicated that there was no water present during the first visit (and therefore there was no water present for the remaining visits); a rank of one meant that water was present only during the first visit; a rank of two meant that water was present during the first and second visits; and three indicated that water was present for all three visits. Sporadic water accumulation did not occur on any quarry floor site throughout the summer.

An age rank was also created for the quarry floors. The quarry floors ranged from 12-88 years post abandonment. A rank of one represented ages of 1-20 years since abandonment; a rank of two represented ages 21-40 years since abandonment; three represented ages of 41-60 years since

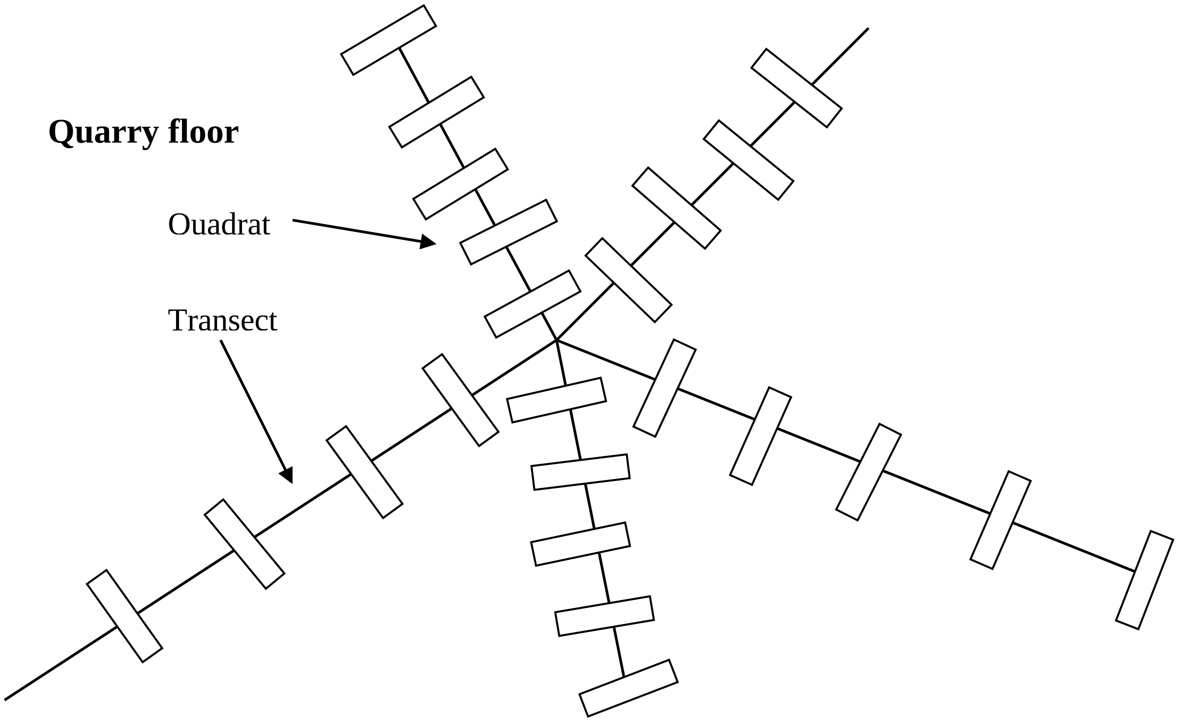


Figure 3. Sampling design showing the placement of transects and quadrats on the abandoned limestone quarry floors. The sampling design from Schaefer (1996) was used for this study.

abandonment; four represented 61-80 years since abandonment; and five represented 81-100 years since abandonment.

A digital thermistor-based DS1921G Thermochron iButton® was used in each quadrat to record the ground surface temperature at consistent intervals throughout the day for the entire duration of the summer field season in 2004. The iButtons were accurate within ±1°C. Each iButton was inserted into a balloon to protect it from water damage. One iButton was buried approximately 1 cm below the soil surface in the same cell of each quadrat to facilitate the retrieval process. If there was no soil in the entire quadrat, the iButton, in the balloon, was taped to the rock surface using opaque, grey tape. The iButtons were buried in May 2004 and removed in September 2004. The iButtons were programmed to record the ground-surface temperature every 90 minutes for the entire field season. Once the iButton was collected, it was inserted into a DS1402D Blue Dot Receptor. The information was then downloaded to a computer.

A Garmin Global Positioning System (GPS) was used to map the coordinates of all surveyed quadrats and the centres of each quarry floor.

Quarry floor soil analysis
A detailed soil analysis was performed on five random soil samples from each quarry site. A soil sample was randomly chosen from one quadrat on each transect. A minimum of 150 ml of soil was collected by combining soil cores from each cell in the quadrat. If the randomly chosen quadrat contained less than 150 ml of soil, another quadrat was randomly chosen from that transect.

A separate set of soil samples was collected to perform a bulk density analysis. Five quadrats were randomly chosen (one from each transect). Three random sub-samples of soil were collected from each of the quadrats. A 2 ml soil core was collected from each cell and placed in a coin envelope, sealed and refrigerated. A total of 6 ml was collected from each quadrat. A mean bulk density value for each quadrat was calculated from the three sub-samples. In 2003, soil was sent to Laboratory Services, University of Guelph to perform the detailed analyses. The components that were analysed included phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), ammonium (NH4-N), nitrate (NO3-N) (all mg/kg), total nitrogen (N), inorganic carbon (C), organic C, total C (all %dry), pH and particle size of percent silt, sand and clay. Bulk density (g/cm^3) and calcium carbonate (CaCO3) (%) were analyzed by the Cliff Ecology Research Group. All soil samples collected in 2004 were sent to Agri-Food Laboratories in Guelph, Ontario. The lab performed each of the tests listed above, with the addition of organic matter (%) and cation exchange (CEC).

Comparison of abandoned limestone quarry floors and alvars of southern Ontario
The alvar sites used in the comparison of quarry floors and alvars were located on the Bruce Peninsula, Ontario, Canada. There were seven sites where mature trees had average ages that ranged from 79 to 423 years old. The age ranks that were used in the quarry floor survey were also attributed to each of the alvar sites. The alvar age ranks continued from number five, which represented 81-100 years old; six represented 101-200 years old; seven represented 201-300 years old; eight represented 301-400 years old; and nine represented ages from 401-500 years old. Specific details concerning the alvar study on the Bruce Peninsula can be found in Schaefer (1996) and Schaefer and Larson (1997).

The detailed soil analyses of the quarry floors were compared to results from Schaefer (1996) and Stark et al. (2004). Stark et al. (2004) examined the soils of alvars on the Bruce Peninsula of Ontario, Canada.

Seed bank analysis of limestone quarry floors and alvars
A seed bank is an accumulation of viable seeds that are produced in the area and/or arrive from surrounding areas and germinate over an extended period of time, depending on the environmental conditions (Harper 1959; Harper 1977; Fenner 1985).

Stark et al. (2003) performed the only North American alvar seed bank analysis on the Bruce Peninsula in southern Ontario. They concluded that many of the above ground species on the alvars were represented by the seed banks; however, when seed density was converted to a per unit measurement, North American alvar densities were much lower than European alvar seed densities (Bakker *et al.* 1996; Milberg and Hansson 1994). The seed bank data collected from the alvars in southern Ontario provide an excellent opportunity to compare seed bank data from abandoned limestone quarry floors.

Seed bank sites

Soil seed bank samples were collected from the same quarry floor sites that were used in the quarry floor survey. The Grimsby site was the only quarry not included in the seed bank analysis because permission for soil removal was not granted.

Seed bank sampling design and soil collection

A 20 cm x 20 cm cell was randomly chosen from each quadrat that contained soil. The canopy cover and soil depths were measured before the soil seed bank samples were removed. All seedlings that had germinated prior to soil collection in the chosen cell were identified, counted and added to the seed densities. The soil in the 20 cm^2 subplot was collected up to a maximum depth of 5 cm or to the bedrock where the soil was too shallow. Harper (1977) concluded that the seed density is highest in the top 2.5 cm of soil and decreases rapidly with increasing soil depth. Therefore 5 cm should be deep enough to collect the majority of seeds. The volume of each soil sample was recorded and sealed in a plastic bag. Each sample was immediately refrigerated.

The soil was collected in the early spring of May 2004. Collecting the soil samples for a seed bank analysis was not done in the early spring for several reasons. Collecting soil samples after natural stratification (chilling) has resulted in a higher number of emerging seedlings than seed bank samples collected in the fall (Bakker *et al.* 1996; Roberts 1981). Thompson and Grime (1979) found that seed banks of disturbed habitats were capable of germinating immediately after removal if moved to suitable green house conditions. Also, collecting seed bank samples in the early spring helps prevent the loss of viable seeds due to predation.

Soil samples were not collected from every quadrat due to flooding or lack of soil. A total of 269 soil samples were collected. There is a general consensus in the literature that seed number estimates can be improved by collecting a large number of small samples rather than a small number of large samples (Benoit *et al.* 1989; Bigwood and Inouye 1988; Roberts 1981).

Seed bank concentration method

The concentration method and germination trials were done in two sets because of the large volume of soil samples and the lack of available greenhouse space. All soil samples were concentrated using the methods of ter Heerdt et al. (1996). Each sample was concentrated by spraying a harsh stream of water over the soil and organic matter, through a coarse sieve with holes larger than the largest expected seeds (5 mm) to remove any coarse materials such as stems, roots or rocks. Some of the soil samples contained moss cushions. Mosses can be seed traps in the field (Zamfir 2000), so each moss cushion was sprayed and sorted through carefully. The soil samples were then sprayed through a fine sieve with mesh holes smaller than the smallest expected seeds (0.5 mm) to remove finer soil materials. The concentrated samples were mixed with water. The wet concentrated seed mixture was added to trays containing a 5 cm thick layer of sterilized potting soil (Pro-Mix: Premier Horticulture Inc.) which was covered with a 1 cm thick layer of inorganic soil amendment (Profile™ Porous Ceramic). The inorganic soil amendment separated the concentrated seed mixture from the soil to facilitate the removal of seedlings without damaging their roots (Bakker et al. 1996). The layer of the concentrated samples was not thicker than 5 mm. This ensured that the seeds received adequate amounts of light and were exposed to warmer air temperatures (3-5 mm is recommended).

Seed bank germination trials

The first set of germination trials lasted from June 2004 through September 2004, and the second set of trials lasted from October 2004 through February 2005. Thompson and Grime (1979) concluded that germination after five weeks was insignificant. ter Heerdt et al. (1996) concluded that most species should germinate by the sixth week when using concentrated samples. Bakker et al. (1996) recommended that some seed banks may need as much as 18 weeks for all viable seeds to germinate. The germination trials for the first group of trays lasted approximately 14 weeks; the second group required approximately 18 weeks before seedling emergence ceased.

The concentrated seed mixture and soil amendment were periodically disturbed by breaking up the seed mix exposing more seeds to the surface to promote germination. Results show that periodically disturbing a seed mixture will increase the number of seedlings (Jefferson and Usher 1987; Roberts 1981; ter Heerdt et al. 1996). The soil samples were disturbed until nothing germinated for two weeks.

The samples were watered on a daily basis to ensure that the concentrated seed mixture contained enough water to facilitate seed germination (Humphries 1981). ter Heerdt et al. (1999) performed a water-management regime on sandy soil seed banks and determined that the most successful watering treatment was to keep the samples very wet but not water-logged. Sand is the dominant particulate in the soils of quarry floors in southern Ontario; therefore the above watering treatment was applied to the quarry floor seed bank samples. The first set of samples was watered daily because of the high temperatures and long hours of sunlight. The second set of samples was watered less often, approximately every second or third day because of the slightly cooler green house temperatures and shorter hours of sunlight. The trays were rotated to different sections of the greenhouse benches. Trays placed closer to the edges of the benches dried out more quickly than the interior trays.

As seedlings emerged, they were removed to ensure adequate germination conditions. Immediate removal is necessary when applying the concentration method because the seed density can be very high. The shadows of emerging seedlings can reduce the germination of other seeds in the seed mixture (ter Heerdt et al. 1996). The seedlings were either identified, counted and discarded or transplanted and grown until identification was possible, then counted and discarded. No transplanted seedlings died in either seed bank germination trial.

Statistical Methods:

Ordination

Gradient analysis is a collection of techniques that can broadly be defined as any method that relates species composition to hypothetical or measured environmental gradients (Leps and Smilauer 2003; Whittaker 1967). The arrangement of samples in relation to one or more gradients is known as ordination, which is a research tool that can help ecologists explain plant or animal assemblages (Whittaker 1967; ter Braak 1994). In the following multivariate analyses, the dependent (or response) variables are the frequencies of the species in the quadrats; the independent (also called explanatory or predictor) variables are the environmental variables.

Ordinations of species frequency data were performed using CANOCO 4.5 (ter Braak and Smilauer 2002). The graphical representations were plotted using CanoDraw 4 (Smilauer 2002). There are a variety of ordination techniques that can be used in multivariate analyses. Indirect gradient analysis is a technique that analyses the response variable(s) without any predictor variables. The most common indirect techniques include principal component analysis (PCA), correspondence analysis (CA), detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMDS).

Direct gradient analysis is an ordination technique that can be performed if a predictor variable dataset is available (environmental variables). The goal of direct gradient analysis is to determine the relationship between the species frequencies (response variables) and the measured environmental variables. The most prominent direct ordination techniques include redundancy analysis (RDA) and canonical correspondence analysis (CCA).

Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were the indirect and direct multivariate techniques used to analyze the data sets for this study. Leps and Smilauer (2003) suggest a simple method to determine which ordination techniques to use when performing multivariate analyses. There are two models to choose from based on the shape of the relationship between the frequency (or abundance) of each species and the axes (representing environmental gradients): a model of linear species response or a model of unimodal species response. A trial version of the analysis should be run. This will provide a log output with a list of gradient lengths (the lengths of the first four axes). If the longest length is greater than 4.0 standard deviations, a unimodal method should be used (DCA, CA, or CCA). If the longest length is less than 3.0 standard deviations, a linear model should be used (PCA or RDA). Either model can be applied if the longest length is between 3.0 and 4.0 standard deviations. One should be aware of two other important factors when deciding to use a unimodal model: the response variables require the same units and contain no missing samples (Leps and Smilauer 2003).

Ordination results are commonly displayed using ordination diagrams. An ordination diagram of a DCA contains samples (quadrats) and species, and an ordination diagram of a CCA contains samples, species and environmental variables (ter Braak 1987). The graphical outputs of the CCA use arrows to represent the direction and strength of the environmental variables.

The ordination axes are also known as eigenvectors which have a corresponding eigenvalue (λ). A higher eigenvalue represents a higher amount of explained variation. Axis one explains the most variation, and axes two, three and four explain increasingly lesser amounts of the variation (ter Braak and van Tongeren 1987). The distribution of samples along the axes demonstrates the similarities and dissimilarities among samples. Samples that are closer together have a higher number of species in common. Samples that are farther apart have fewer species in common. Sample points that are more than four units/standard deviations apart have a very low probability of sharing any species (Leps and Smilauer 2003; ter Braak and van Tongeren 1987).

CANOCO 4.5 (ter Braak and Smilauer 2002) uses a Monte Carlo permutation test to determine the significance of a constrained axis (Leps and Smilauer 2003). A maximum of 499 permutations are run for each test. Each environmental variable can be tested individually or jointly to determine whether the variable(s) are significantly explaining the variation of an axis. The environmental variables are listed in the permutation output in the order of most significant to least significant. A p-value of $p<0.05$ is used if testing each environmental variable individually, but if several environmental variables are jointly tested, the Bonferroni correction is applied (dividing the p-value by the number of variables).

Detrended correspondence analysis (DCA)
The goal of unconstrained ordination, also known as indirect gradient analysis, is to find axes that explain the greatest amount of variation for the community composition regardless of any measured environmental variables. Unconstrained ordination is used when there are no measured environmental variables or there is no a priori knowledge of a species-environment relationship (Leps and Smilauer 2003).

Solely using a DCA will not determine which amount of the variability is explained by the measured environmental variables. This explanation is provided when using constrained ordinations.

Canonical correspondence analysis (CCA)
In constrained ordination, the goal is to use the measured environmental variables to explain as much of the variation as possible in the species composition. Constrained ordination can be used if there are one or more environmental variables, a number of species and no a priori knowledge of a species-environment relationship (Leps and Smilauer 2003).

Constrained ordination is also known as direct gradient analysis. Canonical correspondence analysis (CCA) is a technique that is used for such analyses. A CCA uses the measured environmental variables from the data set to explain the variation found in the species composition. The axes correspond to the greatest variability in species frequencies among quadrats that can be explained by the environmental variables (Leps and Smilauer 2003).

Eigenvalues of the ordination axes always decrease between the DCA and CCA of the same data. If the CCA eigenvalues are considerably less than those in the DCA, the measured environmental variables do not explain the variation of the data set well. Therefore, the true environmental gradients that are controlling the species composition have not been measured. If the eigenvalues are high and have similar values in the DCA and the CCA, then one or more of the measured environmental variables are important in explaining the variation in the species composition. Unconstrained and constrained ordinations are complementary approaches. Both should be used when investigating the factors that control the species composition.

Analysis of variance
An analysis of variance (ANOVA) was used to determine which environmental variables were significantly different between quarry floors and alvars of southern Ontario. SAS version 9.1

(SAS Institute) was used for all Anovas. Most variables were transformed to meet the assumptions of ANOVA. Back-transformed least squares means were indicated throughout the corresponding tables. Alpha levels of α=0.05 were used for all Anovas.

Table 1 provides a list of all variables and analyses performed in the research categories which were introduced in the methods section.

Regression analysis
A regression was used to determine a relationship between the proportion of exotics and age of each quarry floor site. An alpha level of α=0.05 was used for the regression.

A regression was also used to determine whether there was a relationship between the results of the detailed soil analysis and the age of quarry floors. More than half of the soil variables were transformed to meet the assumptions. The p-value was adjusted by applying the Bonferroni correction (dividing the p-value by the number of variables) because the same soil sample was used for the analysis of each of the 18 soil parameters. This resulted in a p-value of $p<0.0028$ for tests at α=0.05. SAS version 9.1 (SAS Institute) was used for all regressions.

Analysis – PART 1: Abandoned limestone quarry floor survey
a) Species composition – quarry floors
The presence of each lichen, bryophyte and vascular plant species was recorded in each cell for all quadrats. The percent frequency of each species was then calculated for each quadrat. The average species richness was also calculated for each quadrat. Measurements of environmental variables were recorded in every cell to provide a mean value for each quadrat. Soil properties were measured at the quadrat scale.

b) Regression of non-native species proportions and age of quarry floors
A regression analysis was used to determine a relationship between the proportion of non-native quarry floor species and ages of the 13 quarry floor sites. The data were transformed to meet the assumptions. Alpha level of α=0.05 was used.

c) Regression of soil variables and age of quarry floors
Regression analyses were performed to determine a relationship between each of the 18 soil variables and age of the 13 quarry floor sites. Many of the variables were transformed to meet the assumptions. The Bonferroni corrections set the p-value at $p<0.0028$ for tests at α=0.05.

d) Detrended correspondence analysis – quarry floors
A DCA was run using 523 quadrats and 246 species from the 13 quarry floor sites. The 523 quadrats were a combination of 200 quadrats (8 sites) sampled in 2003 plus 323 quadrats sampled in 2004 (13 sites, including the eight quarry floor sites from 2003). The 246 species were a combination of lichens, bryophytes and vascular plants. There were many species which were found once in only one quadrat. Therefore, rare species were downweighed before an analysis was run to reduce outlier effects. The data collected from 2003 and 2004 were compared

Table 1. List of surveyed and/or analyzed biological, environmental and soil characteristics from both quarry floors and alvars of southern Ontario. Analyses and/or variables are listed according to categories 1 through 4.

Category	**Habitat**	**Analyses and/or variables**
1: Abandoned limestone quarry floor survey	Limestone quarry floors in southern Ontario	**Measured environmental variables:** age, presence/absence of water, percent cover of woody debris, leaf litter, bare rock, soil, bryophytes, lichens, canopy (below and above eye level), mean minimum, mean maximum and mean soil depth (cm) and ground surface temperature °C **Measured soil variables:** P (phosphorous) mg/kg, K (potassium) mg/kg, Ca (calcium) mg/kg, Mg (magnesium) mg/kg, NH4-N (ammonium) mg/kg, NO3-N (nitrate) mg/kg, CaCO3 (calcium carbonate) %, total N (total nitrogen) %, total C (total carbon) %, inorganic C %, organic C %, organic matter %, pH, bulk density g/cm^3, % sand, % silt, % clay, CEC **Percent frequency** **Biological:** lichen, bryophyte and vascular plant species **DCA** **Biological:** frequencies of lichen, bryophyte and vascular plant species **CCA** **Environmental:** (species composition of DCA) plus age, presence of water, minimum, maximum and mean soil depths, percent cover of woody debris, leaf litter, soil, bare rock, lichens, bryophytes and canopy – above and below eye level and ground surface temperature
2a: Comparison of abandoned limestone quarry floors and alvars of southern Ontario	Limestone quarry floors and alvars of southern Ontario	**Percent frequency** **Biological:** lichen, bryophyte and vascular plant species. In particular, endemic, rare, native and common species **ANOVA** **Environmental:** mean percent cover of woody debris, bare rock, bryophytes and lichens, soil depth and ground surface temperature (excluded from analysis)

Cont'd 2a: Comparison of abandoned limestone quarry floors and alvars of southern Ontario	**Cont'd** Limestone quarry floors and alvars of southern Ontario	**Soil:** P, K, Ca, Mg, NH4-N, NO3-N, total N, total C, inorganic C, organic C, organic matter, pH, bulk density and % sand, % silt, % clay **DCA** **Biological:** frequencies of lichen, bryophyte and vascular plant species grouped as growing only on quarry floors, growing only on alvars or growing in both habitats **CCA** **Environmental:** (species composition of DCA) plus habitat (covariable), age, minimum, maximum and mean soil depths and percent cover of woody debris, bare rock, bryophytes and lichens
2b: Comparison of a subset of abandoned limestone quarry floor and alvar quadrats of southern Ontario	Limestone quarry floors and alvars of southern Ontario	**DCA** **Biological:** frequencies of lichen, bryophyte and vascular plant species grouped as growing only on quarry floors, growing only on alvars or growing in both habitats **CCA** **Environmental:** (species composition of DCA) plus habitat (covariable), age, minimum, maximum and mean soil depths and percent cover of woody debris, bare rock, bryophytes and lichens **Soil:** P, K, Ca, Mg, NH4-N, NO3-N, pH and organic matter
3: Seed bank analysis of limestone quarry floors	Limestone quarry floors in southern Ontario	**Biological:** a quarry floor seed bank species list and a quarry floor vascular species list
4: Comparison of soil seed banks of limestone quarry floors and alvars of southern Ontario	Limestone quarry floors and alvars of southern Ontario	**Biological:** a quarry floor seed bank species list, an alvar seed bank species list and an established alvar vascular species list

in a DCA to determine any sampling variation due to year. The graphical output of quadrats and species from each field season illustrated an overlap of 2003 and 2004 data. This indicated that year was not a variable affecting the species distribution.

e) Canonical correspondence analysis – quarry floors

A CCA was run using the same quadrats and species used in the DCA with the addition of 15 environmental variables (Table 1). If a variable was highly correlated with another variable, shown by a variable inflation factor (VIF) of greater than 10, it was deleted from the analysis. Mean soil depth was deleted because of its high VIF. Rare species were downweighed.

Analysis – PART 2a: Comparison of abandoned limestone quarry floors and alvars of southern Ontario

a) Comparisons of the species composition and environmental variables of both habitats

Species richness and frequency values were compared between quarry floor and alvar habitats. Endemic, rare, native and common species were compared between the two habitats.

An ANOVA was performed on the quarry floor and alvar environmental variables (Table 1) to determine whether these variables were significantly different between the two habitats. All variables were transformed to meet the assumptions of ANOVA. Back-transformed least squares means were reported throughout the respective tables. Alpha level of α=0.05 were used for all ANOVAs.

b) Detrended correspondence analysis – quarry floors and alvars

A DCA was run using 696 quadrats (a combination of 523 quarry floor quadrats and 173 alvar quadrats) and 447 species (a combination of species found growing only on quarry floors, species found growing only on alvars, and species found growing on both quarry floors and alvars). The species composition included lichens, bryophytes and vascular plants. Two alvar quadrats were extreme outliers and were removed from the analysis. The rare species were downweighed. The vascular species *Eleocharis* cf. *erythropoda* was downweighed further to reduce its influence. Extreme outliers can be further downweighed in a DCA or CCA. Applying a stronger downweight value attempts to "pull" the outlier closer to the rest of the data points. If applying the strongest downweight value to an outlier does not draw it in with the rest of the distribution, then the data point(s) can be deleted from the analysis.

c) Canonical correspondence analysis – quarry floors and alvars

A CCA was run using the same quadrats and species, plus nine environmental variables (Table 1). All rare species were downweighed. *Eleocharis* cf. *erythropoda* was further downweighed to a value of 0.05. Mean soil depth was deleted from the environmental variables because of its high VIF.

A Monte Carlo permutation test was performed to determine which environmental variables were significantly controlling the species composition in both habitats. The maximum number of permutations was used to run the test. Habitat was labeled as a covariable to remove its influence. The remaining variables were jointly tested to determine the significance of axis one. If habitat was accounting for the variation of axis one, then the new CCA eigenvalues should be lower than the original CCA eigenvalues. The p-value was adjusted by applying the Bonferroni correction (dividing the p-value by the number of variables) because the variables were jointly, rather than individually, tested. This resulted in a p-value of $p<0.0071$ for tests at $\alpha=0.05$.

Analysis – PART 2b: Comparison of a subset of abandoned limestone quarry floor and alvar quadrats of southern Ontario

A subset of quarry floor and alvar quadrats was used to collect samples for detailed soil analyses. For these quadrats, eight soil variables were available in addition to the nine original environmental variables. DCA and CCA were performed on this subset of quadrats.

a) Comparisons of the soil characteristics of both habitats

An ANOVA was performed on the quarry floor and alvar soil variables (Table 1) to determine whether these variables were significantly different between the two habitats. Most variables were transformed to meet the assumptions of ANOVA. Back-transformed least squares means were reported throughout the respective tables. Alpha level of $\alpha=0.05$ were used for all ANOVAs.

b) Detrended correspondence analysis – data subset

A DCA was run using 183 of the 696 quadrats and 317 of the 447 species. An average of seven quadrats from each quarry site and five quadrats from each alvar site was used in the subset data analysis. The species were a combination of all three life form groups (lichens, bryophytes and vascular plants) found growing only on quarry floors, growing only on alvars and growing in both habitats. One of the alvar quadrats was deleted from the analysis because it was an extreme outlier. All rare species were downweighed.

c) Canonical correspondence analysis – data subset

A CCA was run using the same quadrats and species used in the DCA with the addition of 17 environmental variables (Table 1). The extreme outlier in the corresponding DCA was deleted from the CCA. Mean soil depth was removed from the analysis.

A Monte Carlo permutation test was performed on the data subset using the maximum number of permutations. Habitat was labeled as a covariable. The remaining environmental variables were jointly tested. The Bonferroni corrections set the p-value at $p<0.0036$ for tests at $\alpha=0.05$.

Analysis – PART 3: Seed bank analysis of limestone quarry floors

Seed bank species richness and abundance were determined at each site. A list of species present in the quarry floor seed bank was compared to a list of vascular species growing on the quarry floors to determine whether the seed bank represented the above-ground vegetation. The native/exotic status of each species was determined. The number of exotics in the seed bank was compared to the number of exotics growing on the quarry floors.

Analysis – PART 4: Comparison of soil seed banks of limestone quarry floors and alvars of southern Ontario

A quarry floor seed bank species richness list was compared to an alvar seed bank species richness list to determine the number seed bank species found in both soil seed banks. A list of quarry floor seed bank species was also compared to a list of species growing on alvar habitat to determine the number of quarry floor seed bank species that are found growing on alvars.

PART 5: Seed addition experiments

Four quarry sites were selected based on time since abandonment (all >25 years since last operated), lack of post-abandonment disturbance, and geographic location (sites were spread across a reasonably large area in southern Ontario, with locations in Springvale, Puslinch, Georgetown, and Duntroon). At each site 54 plots (30cm x 60 cm) were permanently installed in early June 2004. Eighteen plots were randomly placed in each of three relative elevation blocks (Low, Medium, and High) at each site; 6 treatments were randomly allocated among the plots in each block, resulting in three treatment replicates per elevation block per site (36 treatment replicate among all four sites).

The six treatments involved seeding plots with either a suite of 18 characteristic alvar species (four treatments), a suite of 5 characteristic exotic quarry species (1 treatment), or both species suites (1 treatment). The two treatments involving the quarry suite left plots untouched in all other respects, as did one of the alvar-only seed treatments. The remaining three treatments involved altering plots in the following ways: i) mixing quarry soil with introduced sterile sand and peat moss, ii) mixing quarry soil with introduced sterile sand, peat moss, and nitrogen fertilizer, or iii) removing all resident plants from plots by applying glyphosphate before planting, and weeding regularly after planting. Each plot was observed three times between planting and first frost (early October 2004), then twice more - once in the early spring 2005 and then once after a catastrophic drought that took place in May and June 2005. Regular monitoring will continue until fall 2008. Response variables were measured to estimate the colonization success of the introduced species suites: the total richness, total density (number of stems per plot), and density of each species were recorded, for all species planted. Additionally, the relative elevation of each plot was measured and used as a covariable in data analysis where appropriate.

Hypothesized constraints on alvar species establishment were tested via variance analysis and pre-planned contrasts of the treatment responses. It was expected that if immigration difficulty is a major constraint on the colonization success of alvar species, establishment patterns would be similar between untreated alvar-seeded plots, and untreated quarry-seeded plots. If excessive lime in quarry soils limits alvar species success, then establishment should be better at plots diluted with sand and organic matter than at untreated plots. If nitrogen paucity limits alvar species success, establishment should be better at plots treated with sand, organic matter, and nitrogen fertilizer than at plots treated with just sand and organic matter. If competition with resident quarry species constrains alvar species success, then plots where all potential competitors are removed should show improved establishment over untreated plots. Finally, if competition with establishing exotic quarry species constrains alvar species success, then untreated plots receiving only alvar seeds should show better establishment of alvar species than plots receiving both the alvar and quarry species suites.

RESULTS

PART 1: Abandoned limestone quarry floor survey
a) Species composition – quarry floors

A total of 246 species were found on the limestone quarry floors at all sites combined in this study. There were 200 vascular plant species, 14 bryophyte species and 32 lichen species (Appendix 1). Seventy-seven species were found growing both on quarry floors and on alvars out of a total of 246 species (vascular plants, bryophytes, lichens). Twenty-four of the 200 vascular plant species were 'characteristic' of alvars. This compares with 86/345 for literature on alvars proper (based on Catling and Brownell 1995) and 47/180 species for the study of alvars on the Bruce Peninsula by Shaefer and Larson (1997). This means that 12%, 24%, and 26% respectfully represents the percentage of the vascular plant species that are characteristic of alvars, as found in this study, and in two separate studies of alvars.

The three most abundant vascular plant species (>10% frequency) were *Panicum acuminatum* var. *acuminatum, Poa compressa*, and *Sedum acre*. The quarry floor bryophyte species richness was lower than both the vascular species richness and lichen species richness. Only two bryophyte species, *Tortella tortuosa* and *Bryum lisae* var. *cuspidatium*, had a greater frequency than three percent. Three lichen taxa had a frequency greater than five percent. These taxa were *Verrucaria* sp., *Verrucaria nigrescens* and *Cladonia symphycarpia*.

Three species, *Asclepias sullivantii*, *Bidens coronata* and *Senecio obovatus*, were considered rare to uncommon or very rare in Ontario. Their percent frequencies were 0.02%, 0.33% and 2.13%, respectively. Approximately 60% of the quarry floor vascular plant species were native to Ontario (Appendix 1).

Sampled quadrats ($0.64 m^2$) averaged a richness of 7.23 vascular plant species, 0.39 bryophyte species and 1.10 lichen species for a total mean species richness of 8.72 species/quadrat (Table 2). The maximum species richness in a quarry floor quadrat was 23 species. The Kingston quarry site contained the lowest average species richness (4.76 species/quadrat). This site did not contain any bryophytes or lichens on the quarry floor. A total of 15 vascular plant species were surveyed at the Kingston quarry site. The Muldoon Pit quarry site had the highest total and average species richness: (81 species and 11.9 species/quadrat). Springvale and Wiarton quarry sites also had high average species richness values of 6.08 species/quadrat and 10.96 species/quadrat, respectively.

The quarries ranged in age from 12 to 88 years since abandonment. Results for the thirteen environmental variables that were measured at each site are presented in Table 3. Mean percent cover for bare rock for all quarry floor sites combined was 25.68%. Soil depth ranged from an average of 1.55 cm at the Limehouse quarry site to 6.06 cm at the Georgetown quarry site. The average soil depth for all quarry floors together was 3.05 cm. Mean percent cover for bryophytes for all quarry floor sites combined was 5.37%. Several quarry floor sites, such as Wiarton, Collingwood, Kingston and Grimsby, contained no bryophyte cover. The Guelph and Limehouse quarry floor sites had 11.04% and 22.88% cover of bryophytes, respectively. The average ground surface temperature for all quarry floor sites was high at 41.36 °C. Ground surface temperature ranged from 45.48 °C at the Muldoon Pit quarry site to 38.16 °C at the Russell quarry site.

Results of the detailed soil analysis that was performed on five soil samples from each site are shown in Table 4. The main mineral matter of quarry floor soils was sand (52.86%), but despite this the soil was base rich (pH 7.69). The average phosphorus level for all quarry floor

Table 2. Average species richness for abandoned limestone quarry floor sites in southern Ontario. Species richness is measured by # of species per plot (above value).

Site names and codes	Age	Total species richness	Number of natives	Number of exotics	Average vascular species richness	Average bryophyte species richness	Average lichen species richness	Average species richness
All quarry floor sites		246	107	77 (39.5%)	7.23	0.39	1.10	8.72
Wiarton – Wiar	12	35	22	11 (33.3%)	10.12	0	0.84	10.96
Russell – Russ	19	50	22	20 (47.6%)	11.16	0.60	0.40	12.16
Collingwood – Coll	20	20	14	5 (26.3%)	5.68	0	0.72	6.4
Rockwood – Rock	23	43	24	10 (29.4%)	4.50	0.68	0.90	6.08
Springvale – Spri	26	56	22	21 (48.8%)	9.40	0.08	2.42	11.9
Muldoon Pit – Muld	27	81	37	27 (42.2%)	9.46	0.84	2.18	12.48
Georgetown – Geor	39	52	34	13 (27.7%)	6.26	0.21	0.92	7.38
Guelph – Guel	46	68	29	27 (48.2%)	6.67	0.45	0.78	7.9
Kingston – King	68	15	11	4 (26.7%)	4.76	0	0	4.76
Cambridge – Camb	69	75	31	31 (50%)	8.6	0.40	1.48	10.48
Fletchers – Flet	76	53	27	12 (30.8%)	5.04	0.40	2.10	7.54
Grimsby – Grim	79	43	30	12 (28.6%)	5.84	0	0.43	6.27
Limehouse – Lime	88	31	12	11 (47.8%)	6.48	1.44	1.08	9

Table 3. Mean values of environmental variables recorded for abandoned limestone quarry floors in southern Ontario. Means and standard errors are given for each site and for all quarry floor sites together. Minimum and maximum values for each environmental variable are in bold.

	All quarry floor sites	**Wiar**	**Russ**	**Coll**	**Rock**	**Spri**	**Muld**	**Geor**	**Guel**	**Camb**	**King**	**Flet**	**Grim**	**Lime**
Age		12	19	20	21	24	29	37	44	67	68	74	77	88
Woody debris (% cover)	6.07 ±0.48	**1.22 ±0.06**	**1.22 ±0.72**	2.86 ±0.88	5.58 ±0.68	5.35 ±1.11	6.30 ±0.85	3.75 ±1.01	6.55 ±0.99	13.82 ±2.76	5.18 ±1.35	**19.68 ±3.21**	3.23 ±0.7	4.17 ±1.02
Leaf litter (% cover)	18.69 ±0.94	12.72 ±2.38	16.17 ±1.77	18.39 ±2.75	21.30 ±3.42	18.54 ±1.6	20.30 ±3.8	26.65 ±4.51	21.53 ±1.93	24.31 ±4.86	12.99 ±3.27	**0.59 ±0.28**	**36.56 ±4.65**	13.05 ±2.67
Bare rock (% cover)	25.68 ±1.49	18.18 ±4.51	3.32 ±1.45	1.49 ±0.88	**66.74 ±4.65**	20.70 ±2.7	37.25 ±5.09	21.27 ±3.3	52.05 ±5.75	34.02 ±6.82	**0.41 ±0.23**	20.20 ±3.56	20.36 ±2.25	38.88 ±5.78
Soil (% cover)	28.02 ±1.61	43.64 ±4.37	35.14 ±4.75	**76.12 ±3.95**	**4.39 ±1.12**	6.40 ±1.7	10.56 ±2.4	19.79 ±3.39	8.62 ±1.2	22.69 ±4.53	74.16 ±4.25	24.89 ±4.93	14.57 ±2.68	22.47 ±4.74
Bryophytes (% cover)	5.37 ±0.61	**0**	0.36 ±0.24	**0**	4.29 ±0.88	3.91 ±1.27	8.09 ±1.88	4.91 ±1.68	11.04 ±3.54	5.86 ±1.17	**0**	5.48 ±2.05	**0**	**22.88 ±4.14**
Lichens (% cover)	8.83 ±0.45	4.37 ±0.94	5.51 ±1.02	6.75 ±1.62	10.89 ±0.54	13.12 ±1.63	10.48 ±1.94	8.31 ±0.95	**20.73 ±2.85**	13.24 ±2.65	**0**	6.12 ±0.79	4.19 ±0.66	6.94 ±0.75
Canopy below (% cover)	38.41 ±1.23	37.41 ±4.59	**64.44 ±4.74**	20.13 ±2.14	31.43 ±4.86	46.06 ±4.01	34.25 ±4.84	44.72 ±3.07	37.09 ±4.29	29.01 ±5.8	46.38 ±4.05	41.82 ±4.66	48.96 ±3.87	**17.54 ±3.06**
Canopy above (% cover)	4.95 ±0.79	**0**	0.10 ±	**0**	0.62 ±0.43	5.43 ±3.34	9.81 ±4.27	0.65 ±0.53	5.67 ±2.11	**19.96 ±3.99**	**0**	7.87 ±4.01	8.34 ±3.14	5.88 ±2

	Quarry floor sites	Wiar	Russ	Coll	Rock	Spri	Muld	Geor	Guel	Camb	King	Flet	Grim	Lime
Mean min. soil depth (cm)	1.10 ±0.11	0.60 ±0.19	0.72 ±0.2	**2.00 ±0.18**	1.04 ±0.24	0.52 ±0.2	**0.36 ±0.13**	2.92 ±1.03	0.88 ±0.31	1.08 ±0.22	1.52 ±0.21	1.64 ±0.45	0.56 ±0.16	0.44 ±0.19
Mean max. soil depth (cm)	6.52 ±0.34	6.24 ±0.89	8.92 ±2.07	7.40 ±0.18	5.44 ±0.61	5.32 ±0.45	3.48 ±0.75	**14.96 ±2.18**	4.75 ±0.83	5.80 ±1.16	5.60 ±0.53	7.92 ±0.96	5.48 ±0.65	**3.40 ±0.7**
Mean soil depth (cm)	3.05 ±0.13	2.80 ±0.4	3.45 ±0.55	4.29 ±1.14	2.82 ±0.16	3.00 ±0.3	1.78 ±0.4	**6.06 ±0.77**	1.91 ±0.37	2.60 ±0.52	3.23 ±0.29	3.79 ±0.42	2.37 ±0.16	**1.55 ±0.35**
Surface temperature (°C)	41.36 ±0.25	41	**38.16 ±0.85**	41	41.92 ±0.68	40.56 ±0.72	**45.48 ±1.12**	42.92 ±0.85	41	42.32 ±0.9	40.56 ±1.15	42.56 ±0.9	39.88 ±0.32	41.44 ±1.28

Table 4. Mean values of soil parameters recorded in abandoned limestone quarry floors in southern Ontario. Means and standard errors are given for each site and for all quarry floor sites together. Minimum and maximum values for each soil characteristic are in bold.

Soil variable	**Southern Ontario quarry floor sites**	**Wiar**	**Russ**	**Coll**	**Rock**	**Spri**	**Muld**	**Geor**	**Guel**	**King**	**Camb**	**Flet**	**Grim**	**Lime**
P mg/kg	7.32 ±0.46	**1.97 ±0.27**	4.22 ±0.74	2.39 ±0.66	4.21 ±1.15	6.45 ±0.57	7.70 ±1.37	2.52 ±0.29	**16.54 ±2.16**	12.60 ±1.03	10.61 ±1	6.22 ±1.24	8.08 ±1.12	7.03 ±1.15
K mg/kg	112.97 ±5.7	64.28 ±6.25	129.17 ±13.99	103.92 ±6.34	**44.39 ±8.05**	156.05 ±14.11	116.88 ±13.87	78.20 ±5.53	**189.25 ±40.52**	161.68 ±14.43	115.62 ±10.48	86.44 ±12.08	121.71 ±14.44	83.92 ±13.59
Ca mg/kg	3706.63 ±138.41	2474.43 ±184.28	3142.98 ±293.82	4208.60 ±159.12	**2010.14 ±303.02**	2868.18 ±161.86	3447.95 ±239.7	3498.60 ±330.57	5363.88 ±740.73	**5628.57 ±248.02**	3443.05 ±249.38	4056.10 ±473.62	5398.51 ±332.64	2074.62 ±273.1
Mg mg/kg	558.34 ±33.56	457.48 ±43.2	331.68 ±32.41	**239.36 ±11.81**	307.02 ±52.73	310.00 ±20.68	359.84 ±38.09	557.69 ±55.96	919.75 ±154.18	315.64 ±15.75	581.84 ±98.17	**1011.38 ±165.77**	922.19 ±120.41	422.09 ±73.58
NH4-N mg/kg	11.39 ±1.63	2.72 ±0.37	3.43 ±0.84	**2.30 ±1.15**	6.04 ±2.66	5.24 ±0.55	12.09 ±3.29	9.52 ±2.79	11.01 ±5.33	3.96 ±1.04	3.95 ±0.62	**37.48 ±12.84**	26.30 ±7.37	2.35 ±0.42
NO3-N mg/kg	10.39 ±1.33	6.14 ±0.62	1.71 ±0.38	4.73 ±0.77	3.37 ±0.76	11.76 ±2.21	**0.91 ±0.16**	4.65 ±1.27	13.91 ±6.28	15.55 ±2.15	8.90 ±1.87	**24.91 ±6.98**	23.98 ±9.01	1.83 ±0.31
CaCO3 %	58.87 ±2.26	60.84 ±5.73	38.84 ±6.89	50.94 ±3.65	**98.02 ±1.06**	**11.40 ±2.31**	57.67 ±10.39	79.15 ±2.6	58.97 ±4.69	55.50 ±2.57	53.36 ±4.33	76.63 ±7.16	73.43 ±5.57	68.96 ±6.15
Total N %	0.46 ±0.04	0.21 ±0.02	0.25 ±0.08	0.15 ±0.03	**0.12 ±0.03**	0.38 ±0.03	0.32 ±0.04	0.19 ±0.03	**1.00 ±0.17**	0.40 ±0.07	0.51 ±0.07	0.92 ±0.18	0.74 ±0.13	0.29 ±0.06
Total C %	13.45 ±0.66	9.26 ±0.46	9.81 ±2.76	7.27 ±0.47	13.09 ±0.19	**5.95 ±0.86**	7.11 ±0.77	10.96 ±0.33	22.65 ±3.55	9.73 ±0.29	13.29 ±1.29	**23.63 ±2.65**	18.83 ±1.46	14.32 ±0.85
Inorganic C %	6.34 ±0.28	7.30 ±0.69	4.66 ±0.83	6.11 ±0.44	**11.27 ±0.22**	**0.51 ±0.10**	2.65 ±0.5	8.75 ±0.24	5.32 ±0.72	6.66 ±0.31	6.60 ±0.65	7.50 ±0.85	7.28 ±0.44	8.27 ±0.74
Organic C %	7.02 ±0.69	1.96 ±0.38	5.14 ±2.72	**1.16 ±0.39**	1.82 ±0.41	4.45 ±0.77	4.52 ±0.67	2.21 ±0.27	**17.33 ±4.08**	3.07 ±0.54	6.69 ±1.17	16.13 ±3.42	11.55 ±1.86	6.05 ±1.58
Organic matter %	13.10 ±1.2	3.90 ±0.4	5.26 ±1.69	**2.48 ±0.41**	6.46 ±2.76	11.37 ±2.12	9.34 ±1.11	6.54 ±0.85	**37.29 ±7.79**	5.58 ±0.67	14.16 ±2.6	23.44 ±4.85	18.58 ±3.89	8.96 ±2.07
pH	7.69 ±0.02	7.91 ±0.04	7.80 ±0.04	**8.05 ±0.06**	8.01 ±0.05	**7.26 ±0.10**	7.68 ±0.03	7.78 ±0.04	7.53 ±0.07	7.62 ±0.02	7.64 ±0.02	7.57 ±0.05	7.59 ±0.03	7.71 ±0.05

Bulk density g/cm^3	0.82 ±0.03	**1.21 ±0.04**	0.94 ±0.07	NA	1.09 ±0.1	0.80 ±0.05	0.96 ±0.03	1.13 ±0.06	0.50 ±0.07	0.84 ±0.03	0.79 ±0.09	**0.49 ±0.11**	0.51 ±0.07	0.86 ±0.14
% sand	52.86 ±1.31	38.40 ±2.05	**37.25 ±4.04**	38.20 ±2.86	**67.12 ±2.67**	44.46 ±1.98	64.75 ±2.35	58.94 ±2.83	55.30 ±6.97	48.33 ±2.19	49.85 ±5.23	55.55 ±2.83	44.62 ±6.46	60.00 ±3.56
% silt	35.58 ±1	49.80 ±1.71	**54.25 ±3.9**	47.20 ±2.21	27.89 ±2.61	39.58 ±1.74	**24.92 ±1.25**	31.76 ±2.4	34.84 ±3.57	39.33 ±1	37.52 ±4.61	33.73 ±2.83	38.20 ±2.73	31.00 ±1.93
% clay	11.31 ±0.6	11.80 ±1.28	8.50 ±.33	14.60 ±1.14	4.53 ±0.69	15.95 ±0.67	10.33 ±1.37	9.31 ±0.62	**19.76 ±4.52**	12.33 ±1.26	9.51 ±1.29	10.73 ±2.11	17.18 ±3.94	**5.04 ±0.77**
CEC	22.07 ±0.62	**17.55 ±1.22**	20.01 ±1.67	24.51 ±0.90	16.00 ±2.56	17.36 ±0.61	23.51 ±0.68	NA	24.43 ±0.82	**32.79 ±1.58**	NA	23.16 ±3.53	30.56 ±0.84	15.47 ±2.04

sites was 7.32 mg/kg. The highest amount of phosphorous, 12.60 mg/kg, was at the Kingston quarry site. The lowest amount of phosphorous, 1.97 mg/kg, was at the Wiarton quarry site. Potassium levels were highest at the Guelph quarry site (189.25 mg/kg). The lowest amount of potassium was at the Rockwood quarry site (44.39 mg/kg). The average amount of potassium for all quarry floor sites was 112.97 mg/kg. The average amount of total nitrogen across all quarry floor sites was 0.46%.

b) Detrended correspondence analysis – quarry floors

When a DCA was run using 246 species and 523 quarry quadrats, the resulting eigenvalues were moderately high for axes one and two (0.683 and 0.556). The lichen and bryophyte species were restricted to the right half of the species ordination diagram while the vascular plant species filled the entire ordination space (Figure 4). In the sample ordination diagram (Figure 5), the quadrats were clumped together by site, demonstrating a smaller variation in species composition within a quarry floor site compared to among the quarry floor sites. At several quarry floor sites there was very little variation among quadrats while at other quarry sites the variation among plots was larger. All quarry floor sites shared many of the surveyed species because all sites were within four standard deviations of each other along the ordination axes.

c) Canonical correspondence analysis – quarry floors

The eigenvalues of axes one and two of a CCA on the same data were considerably lower (0.351 and 0.282) when compared to the eigenvalues of the DCA. This suggests that there were other environmental variables not measured in this study that accounted for some of the variation of the species composition. The quadrats displayed more variation within site when compared to Figure 5, but there was still a higher variation among the sites than within (Figure 6). The quadrats from different sites were mainly separated along axis one. However, they were also separated to some degree along axis two. Age was the measured environmental variable explaining most of the variation on axis one in the CCA (Figure 6) and the direction of the age gradient was reinforced when age of the alvar sites was included (see below). Water rank, soil cover and bare rock cover were important environmental variables explaining the variation on axis two.

PART 2a: Comparison of abandoned limestone quarry floors and alvars

a) Comparisons of the species composition and abiotic factors of both habitats

The total species richness of quarry floors was 246 species. The total species richness of alvars was 283 species (Schaefer 1996). The species composition of quarry floors was composed of 200 vascular plant species, 14 bryophyte species and 32 lichen species (Appendix 1) while alvars contained 180 vascular plant species, 50 bryophyte species and 53 lichen species. There were 77 species in common between the quarry floor sites and alvar sites (Appendix 2). Five alvar endemics and 24 characteristic alvar species were growing on the quarry floor sites (of 200 vascular plant species total). Characteristic alvar species are defined as species occurring on more than 50% of surveyed alvar habitat in the Great Lakes Region (Catling and Brownell 1995). There were 23 variables that were measured both in quarry floors and alvars (Table 5 and 6). The results in Table 6 were derived from the complete data set of quarry floor and alvar quadrats. Of

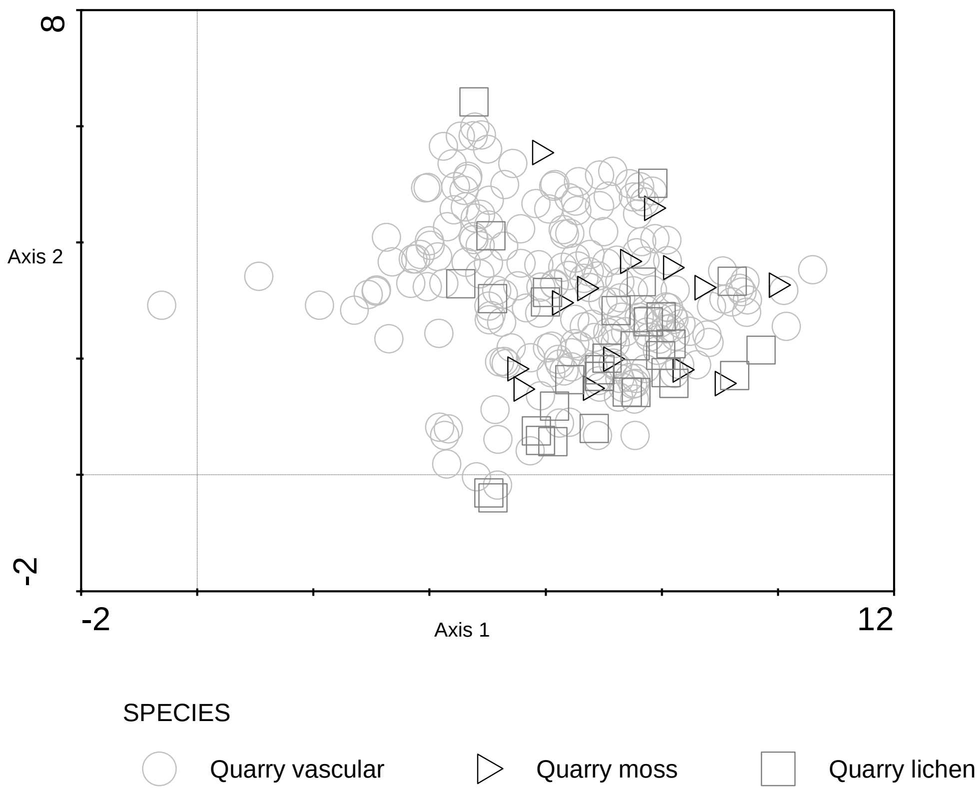


Figure 4. DCA ordination of quarry floor species. Species are separated into life forms – vascular plants, bryophytes and lichens. Eigenvalue for axis 1 = 0.683 and axis 2 = 0.556.

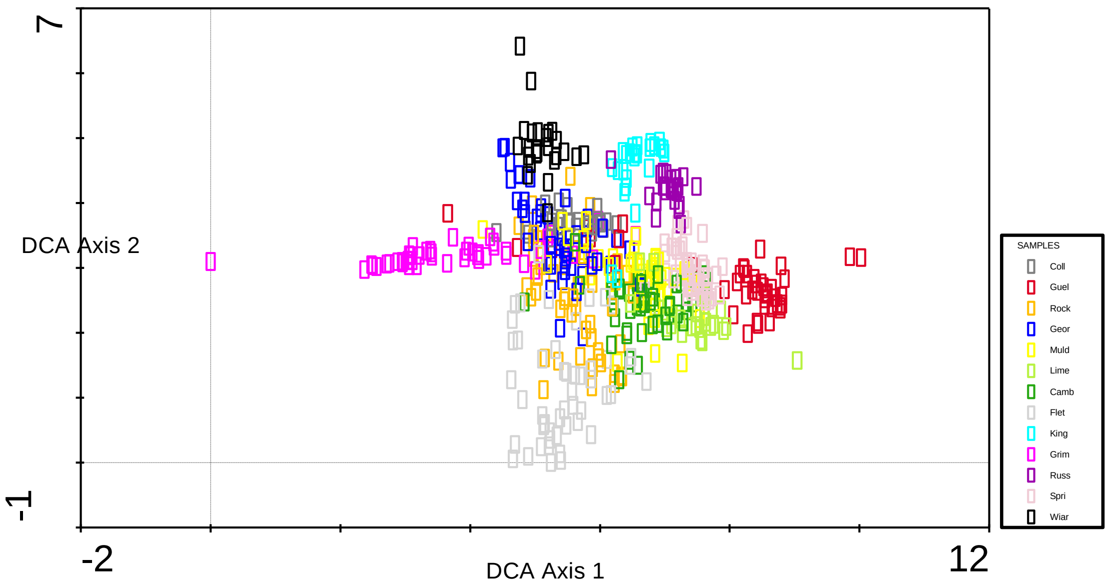


Figure 5. DCA ordination of quarry floor quadrats. The samples are grouped according to site. The eigenvalues of axis 1 = 0.683 and that of axis 2 = 0.556.

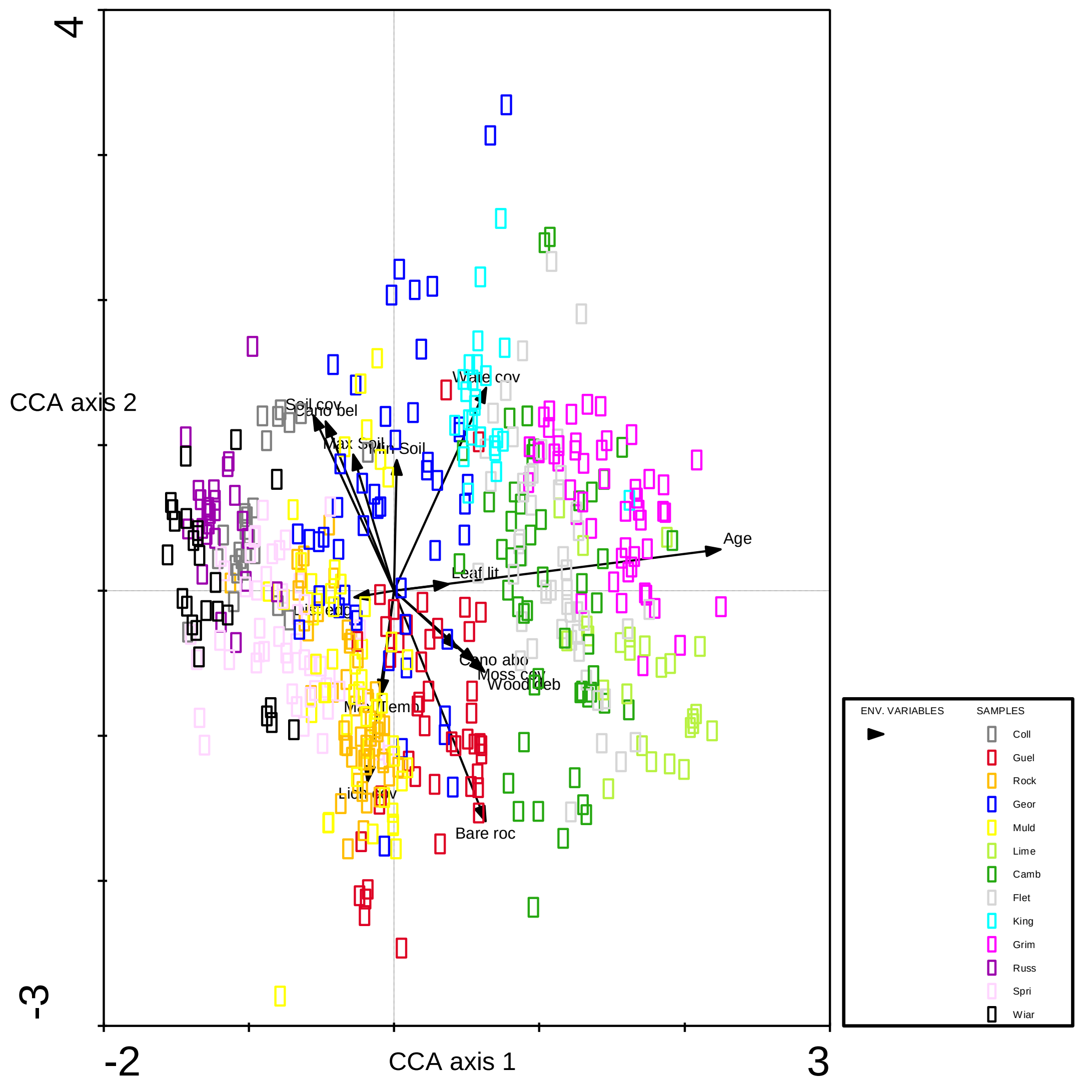


Figure 6. CCA ordination of quarry floor quadrats. The samples are grouped by site and the environmental variables are indicated by arrows. Eigenvalues are 0.351 for axis 1 and 0.282 for axis 2.

Table 5. Back-transformed least squares means of environmental variables from the ANOVAs comparing abandoned limestone quarry floor habitat and alvar habitat (Schaefer 1996) in southern Ontario. Results are from the complete quarry floor and alvar data set.

Environmental variable	Quarry floor habitat	Alvar habitat	Degrees of freedom	F value	p values
Woody debris (% cover)	0.04	0.02	1	1.43	p=0.2476
Bare rock (% cover)	18.25	15.09	1	0.19	p=0.6664
Bryophytes (% cover)	1.42	4.79	1	**8.05**	**p=0.0109**
Lichens (% cover)	7.02	4.49	1	2.41	p=0.1380
Soil depth (cm)	2.51	3.31	1	1.71	p=0.2071
Surface temperature (°C)	41.36	38-43			

these variables analyzed by ANOVA, only the percent cover of bryophytes was significantly different between quarry floors and alvars (Table 5). However, this result should be reviewed with caution because the data for the percent cover of bryophytes could not be transformed to completely meet the normality assumptions of ANOVA. The average ground surface temperature, soil depth and percent cover of woody debris, bare rock and lichens were not significantly different between the two habitats.

Of the 17 soil properties measured in the detailed soil analysis that were also available for alvar soils, ten were significantly different between quarry floors and alvars. Table 6 shows results obtained from the subset of quarry floor and alvar quadrats. A majority of the soil nutrient levels were higher on the alvars than on the quarry floors. The soils of quarry floor sites and alvar sites were both shallow. Average phosphorous and nitrogen levels were low on quarry floors. Total nitrogen was significantly lower on quarry floor sites than on alvar sites. Average total carbon (inorganic and organic carbon) was significantly lower on the quarry floors, but inorganic carbon was not significantly different between the two habitats. Percent sand was the dominant mineral matter of both quarry floors and alvars; however the amount of sand in the soils of each habitat was significantly different.

b) Detrended correspondence analysis – quarry floors and alvars

The DCA of both quarry floors and alvars together used a combined total of 447 species and 693 quadrats from the two habitats. The eigenvalues of axes one and two were very high (0.892 and 0.563), indicating that a lot of variation was explained by the measured variables. The quarry quadrats and alvar quadrats were clumped together in two groups that were separated on axis one, with very little overlap between quarry floor sites and alvar sites (Figure 7). Despite the separation of quarry and alvar species, approximately 17% of the total number of species was

Table 6. Least squares means from the ANOVAs comparing soil parameters between southern Ontario abandoned limestone quarry floors and southern Ontario alvars. Alvar data was taken from Schaefer (1996) and Stark *et al.* (2004). Significant p-values are in bold. An * indicates back-transformed lsmeans. All results are derived from a subset of quarry floor and alvar quadrats.

Soil characteristic	Quarry floor habitat	Alvar habitat	Degrees of freedom	F value	p-values
Mean soil depth (cm)	2.57*	3.14*	1	1.68	p= 0.2033
P (mg/kg)	6.34*	8.51*	1	2.9	p= 0.0985
K (mg/kg)	96.42*	102.95*	1	0.17	p= 0.6866
Ca (mg/kg)	3522.33*	6328*	1	17.17	**p= 0.0002**
Mg (mg/kg)	502.79*	1306.28*	1	50.4	**p= 0.0001**
NH4-N (mg/kg)	4.96*	20.10*	1	16.22	**p= 0.0004**
NO3-N (mg/kg)	4.87*	17.53*	1	10.34	**p= 0.0035**
Total N (%)	0.31*	0.73*	1	7.45	**p= 0.0124**
Total C (%)	11.51*	18.99*	1	6.51	**p= 0.0180**
Inorganic C (%)	6.32	6.42	1	0.01	p= 0.9366
Organic C (%)	4.04*	12.16*	1	9.52	**p= 0.0054**
Organic matter (%)	8.46*	21.08*	1	8.79	**p= 0.0064**
pH	7.68	7.62	1	0.41	p= 0.5258
Bulk density (g/cm3)	0.82	0.82	1	0	p= 0.9757
% sand	52.94	68.62	1	11.85	**p= 0.0027**
% silt	35.08*	21.18*	1	14.93	**p= 0.0010**
% clay	0.10*	0.09*	1	0.46	p= 0.5080

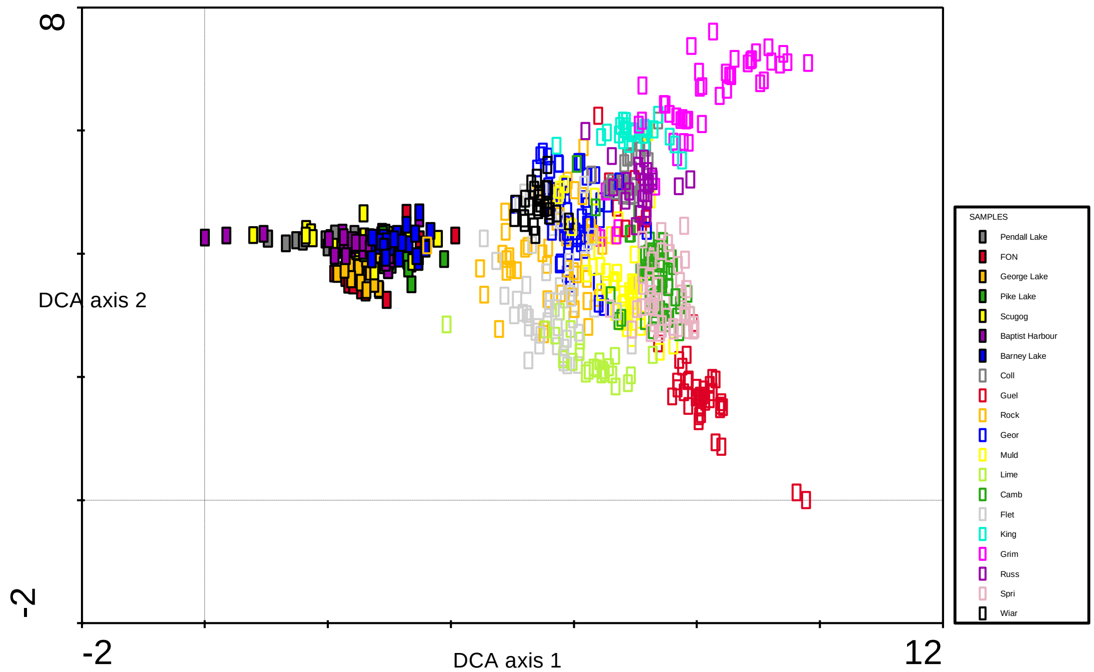


Figure 7. DCA ordination of quarry floor and alvar samples categorized by site. Eigenvalues of axis 1=0.892 and axis 2=0.563.

found growing in both habitats (Figure 8). Species composition was more variable both within and among quarry floor sites compared with alvar sites. Though there was a higher variation among the quarry floor sites, all quarry floor sites were within four standard deviations of each other. Therefore, there was a majority of species in common among the quarry floor sites. All alvar samples were closely clumped together demonstrating very little variation both within and among sites.

c) Canonical correspondence analysis – quarry floors and alvars

In the CCA of quarry floors and alvars with nine environmental variables, the eigenvalues of axes one and two were 0.73 and 0.228 which was marginally lower than those of the corresponding DCA. This indicated that most of the variation in species composition among samples was accounted for by the environmental variables measured in this study. Age rank was highly correlated with axis one. Soil depth and cover of bare rock were important variables explaining the variation on axis two (Figure 9). The samples separated into two groups, quarry floor sites

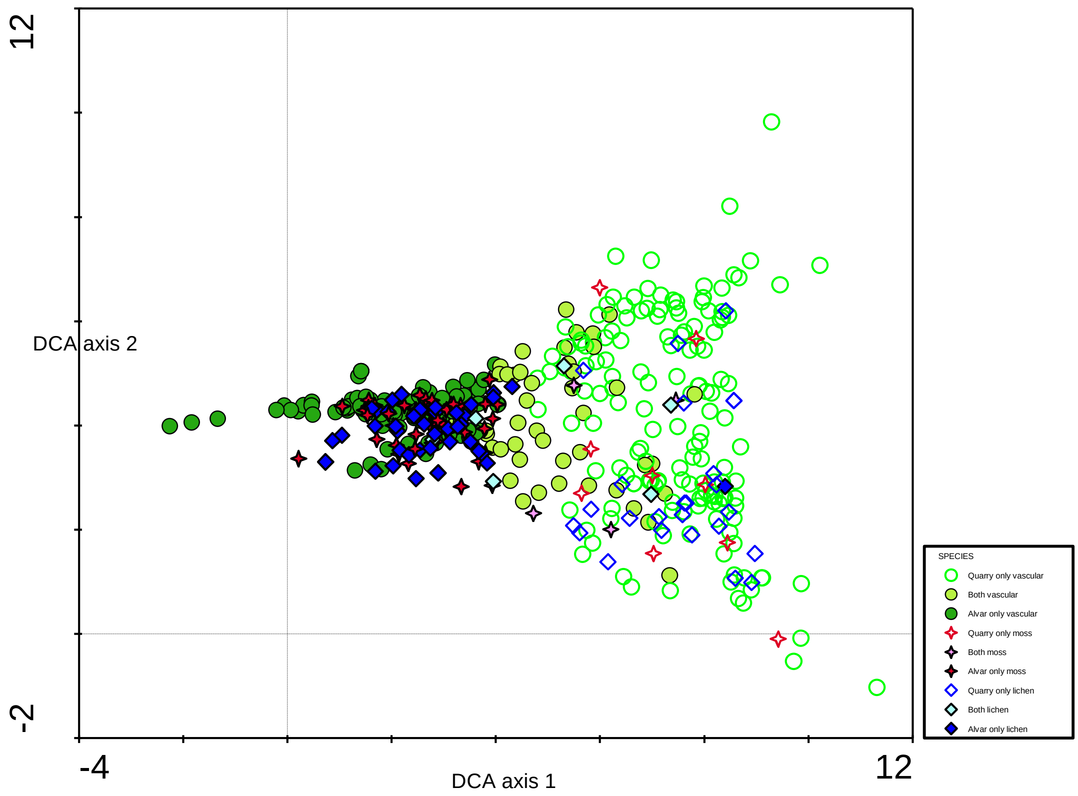


Figure 8. DCA ordination of quarry floor and alvar species. The species are separated into life forms and categorized by species growing only on the quarry floors, species growing only on the alvars, and species growing on both habitats.

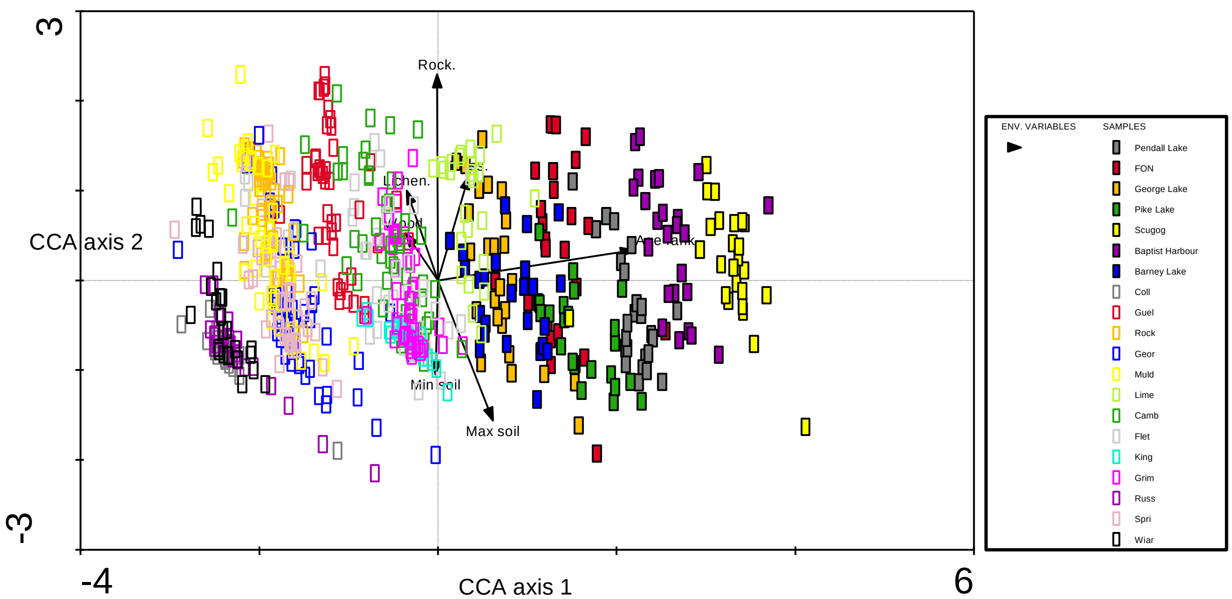


Figure 9. CCA ordination of quarry floor and alvar quadrats. The quadrats are grouped by site and the environmental variables are indicated by arrows. Eigenvalues of axis 1=0.730 and axis 2=0.228.

and alvar sites, in the ordination diagram. The CCA illustrated a higher variation in species composition within and among quarry floor sites (Figure 9) when compared to quarry floor sites in the corresponding DCA (Figure 7).

When the environmental variable “habitat” was added as a covariable to remove its influence from the analysis, the eigenvalues of the partial CCA decreased by approximately 65% (0.274 and 0.224).

A Monte Carlo permutation test determined that age, maximum soil depth, and percent cover of woody debris, bare rock, bryophytes, and lichens were all significantly controlling the species composition at quarry floor and alvar sites (p=0.002). Minimum soil depth was not a significant factor controlling the species composition in both habitats (p>0.0071).

PART 2b: Comparison of a subset of abandoned limestone quarry floor and alvar quadrats
a) Detrended correspondence analysis – data subset
A DCA was used to analyze the subset of quarry floor and alvar quadrats for which additional soil variables were available. The subset of quarry floor and alvar data displayed similar distributions of both samples and species in ordination space as with the full data set (data not shown).

b) Canonical correspondence analysis – data subset
A CCA of the data subset which included 17 environmental variables (Table 1) resulted in eigenvalues of the first and second constrained axes which were high (0.774 and 0.338). Age rank, magnesium and calcium were important environmental variables that explained a large amount of variation on axis one. Percent cover of bare rock and lichen, maximum soil depth and ammonium were important environmental variables that explained the variation on axis two, based on the length of their respective arrows (Figure 10). When the environmental variable "habitat" was defined as a covariable to remove its influence from the analysis, the eigenvalues of the CCA decreased to 0.372 and 0.302. A Monte Carlo permutation test determined that eight environmental variables, age, cover of bare rock and moss, organic matter, nitrate, ammonium, potassium and magnesium, were all significantly controlling the species composition at quarry floor and alvar sites ($p=0.002$). Percent cover of lichens and woody debris, phosphorus, pH, calcium and minimum and maximum soil depth were not significant ($p>0.0036$).

PART 3: Seed bank analysis of limestone quarry floors
A total of 16,395 seeds germinated in 252 quarry floor soil samples. There was an average of 60.95 seeds/sample (0.04/m^2). The soil samples were also measured by volume (litres) because not all samples were collected at a maximum depth of 5 cm. There was an average of 80.1 seeds/L of soil. A total of 165 species germinated in the quarry floor seed bank (Appendix 3). There were 55 species in the quarry floor seed bank which were not growing in the quarry floor vegetation. There were 85 adult quarry floor species which were not found in the quarry floor seed bank. Approximately 67% of the seed bank species (110 species) were found in both the quarry floor seed bank and established quarry floor vegetation.

The five most common species in the seed bank were *Chamaesyce vermiculata*, *Poa compressa*, *Sedum acre*, *Danthonia spicata* and *Potentilla* sp. These five species accounted for approximately 45% of the total seed bank abundance.

Approximately 44% of the species in the quarry floor seed bank were exotics. The quarry floor seed bank species list, percent abundances and native/exotic status of each species are found in Appendix 3.

PART 4: Comparison of soil seed banks of limestone quarry floors and alvars
A total of 45 species from the quarry floor seed bank were found growing on alvars in southern Ontario (Appendix 3). There were 11 species in common between the quarry floor seed bank and the alvar seed bank. These species are indicated in Appendix 3.

PART 5: Seed addition experiments
The initial establishment of alvar vegetation on quarry floor soils appears to be strongly seed-limited and weakly environment-limited. Elevation had little overall effect so its effects were pooled. The addition of seeds alone to quarry floor substrate was enough to initiate establishment

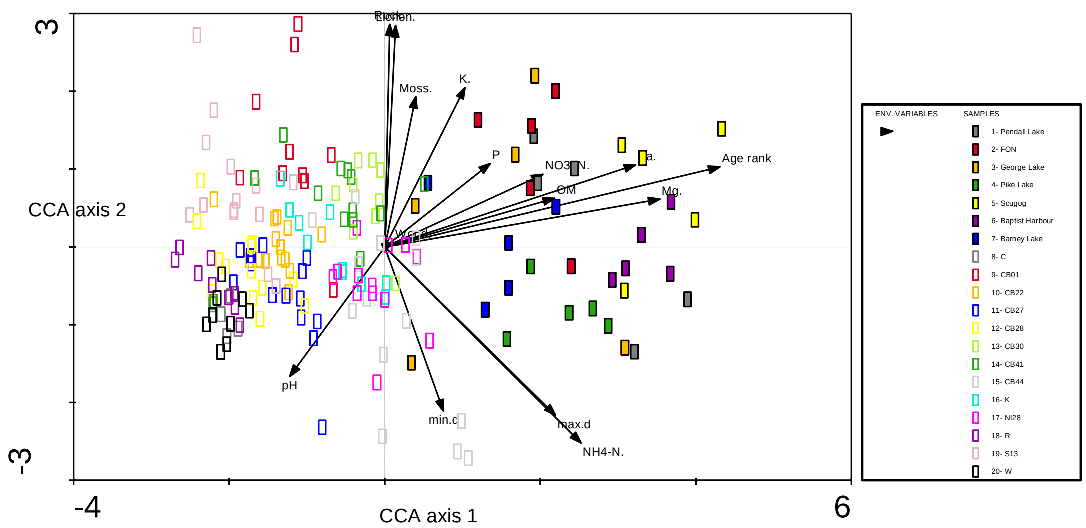


Figure 10. CCA ordination of quarry floor and alvar quadrats using the data subset. Quadrats are grouped by site and the environmental variables are indicated by arrows. Eigenvalues of axis 1=0.774 and axis 2=0.338.

of plant communities in all plots. With respect to the proportion of seeded species present and the total number of plants alive at the end of the initial growing season, plots receiving seeds of alvar origin performed only slightly worse than plots seeded with hardy weed species found to naturally colonize quarry floors (Fig. 11). Of the 18 alvar species introduced, two species never emerged from seed, and on average 7-8 species established in each seed-only plot (approximately 56-64 plants/plot in total). Both addition of sand combined with alvar seed and removal of resident vegetation resulted in plots that were richer and denser than plots receiving seeds only; nitrogen addition on the other hand led to fewer species and individuals establishing in each plot. Statistical differences among particular treatment pairs were tested for using pre-planned contrasts (data not shown); weak ($0.05 < p < 0.10$) to moderate ($0.01 < p < 0.05$) significant differences among seed-only and amended plots support that colonization is constrained by competition and sand-limitation; however, the magnitude of these differences suggest only

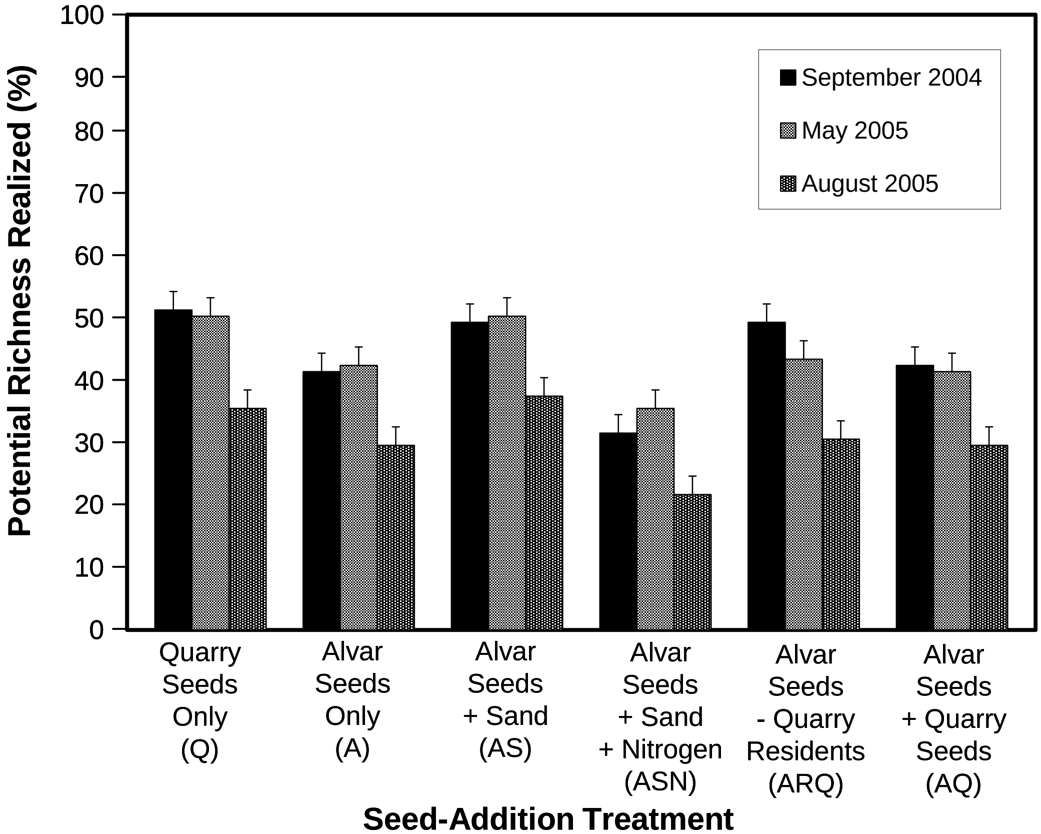


Fig. 11. Effects of seed-addition treatments on the proportion of seeded species to establish in plots in 2004 and 2005. Small plots (N=216) located on four abandoned limestone quarry floors were seeded in June 2004 with 5 weedy species typical of old quarries (treatment Q) or 18 herbaceous species typical of Ontario alvars (remaining treatments; AQ was seeded with both assemblages but only establishment of alvar species in this treatment is considered here). Alvar plots were additionally altered though substrate amendments (AS, ASN) and manipulation of potential competitors (ARQ, AQ), or left unaltered (A). Each treatment was allocated to 9 plots at each site, and percent richness realized was calculated for each plot at the end of the first growing season and in mid-spring and mid-summer of the second growing season. Columns represent least-squares means and error bars represent standard errors; see Table 7 for comparisons among treatments.

biologically weak effects (e.g. the maximum average increase in diversity due to a plot amendment was just 1.5 species). The pattern of colonization success observed in spring 2005 was almost identical to that discovered in fall 2004 (Fig. 11, Table 7). This continuity in community composition suggests that winter quarry conditions are not important environmental filters of alvar community assembly.

In May and June 2005 all plots were exposed to the second-worst drought of the past 57 years. The effects of this perturbation on the vegetation included markedly decreased richness and total density (Fig. 11 & 12, Tables 7 & 8). The pattern of change in colonization success resulted in increased similarity among treatments; few of the treatment differences found to be statistically significant before the drought remained so after the August 2005 census. Following the drought, variation in community density within treatments increased as different plots within the same treatments exhibited different responses to the perturbation. Total density in herbaceous communities is an aggregate property correlated with net primary productivity, and as such is a useful estimator of ecosystem function (Hooper et al. 2005). In an effort to explain the diversity of drought responses with respect to this function, we characterized the temporal stability (S) of total density for each plot (S = temporal mean/temporal standard deviation; Tilman 1999), and analyzed variance in S as a function of site location, plot treatment, and realized species richness of the seeded communities as observed at the end of the experimental period (Figure 13). Alvar seeded plots were more stable than quarry seeded plots. Nitrogen addition significantly lowered the stability of the communities. Specific contrasts did show that alvar seed addition alone, or in combination with several of the treatments had significant effects on survivorship (Table 9). When log-transformed richness was regressed against log-transformed stability, a linearly positive correlation was revealed (Fig. 14). The form of the relationship is consistent with diversity/stability functions discovered in a variety of systems including grasslands, annual plant communities, and microbial microcosms (e.g. Tilman 1996; Valone & Hoffman 2004). The pattern and statistical significance of the relationship were maintained when both the sand and sand-nitrogen treatments were removed from the analysis.

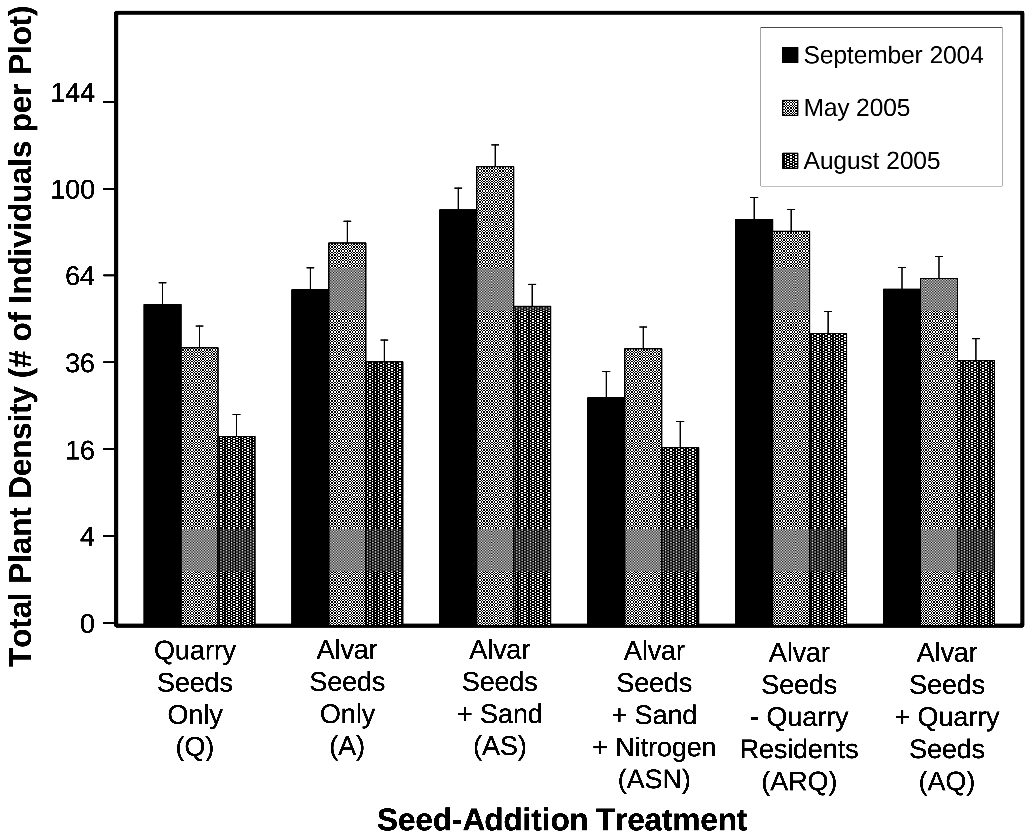


Fig. 12. Effects of seed-addition treatments on the total density of seeded plants to establish in plots in 2004 and 2005. Small plots (N=216) located on four abandoned limestone quarry floors were seeded in June 2004 with 5 weedy species typical of old quarries (treatment Q) or 18 herbaceous species typical of Ontario alvars (remaining treatments; AQ was seeded with both assemblages but only establishment of alvar species in this treatment is considered here). Alvar plots were additionally altered though substrate amendments (AS, ASN) and manipulation of potential competitors (ARQ, AQ), or left unaltered (A). Each treatment was allocated to 9 plots at each site, and the total number of seeded individuals present was calculated for each plot at the end of the first growing season and in mid-spring and mid-summer of the second growing season. Columns represent least-squared means and error bars represent standard errors; note that values are plotted on a square-root scale. See Table 8 for comparisons among treatments,

Table 7. Potential Richness Realized (%) Contrasted Between Treatment Groups Sampled Repeatedly Over Time

Contrast	*DF*	*Mean Square*	*F Value*	*Pr > F*	*Result*	*Time*Contrast (Pr > F)*
Q vs. A	1	3871.3	7.48	0.0068	Q > A	0.5028
Q vs. AS	1	0.4	0.00	0.9788	Q = AS	0.6197
Q vs. ASN	1	3987.5	7.71	0.0060	Q > ASN	0.4362
Q vs. ARQ	1	1389.2	2.69	0.1029	Q = ARQ	0.5331
Q vs. AQ	1	3327.4	6.43	0.0120	Q > AQ	0.6110
A vs. AS	1	3796.4	7.34	0.0074	AS > A	0.9808
A vs. ASN	1	3448.4	6.67	0.0106	A > ASN	0.1279
A vs. ARQ	1	622.4	1.20	0.2741	A = ARQ	0.8220
A vs. AQ	1	20.6	0.04	0.8421	A = AQ	0.7885
AS vs. ASN	1	14116.9	27.29	<0.0001	AS > ASN	0.6981
AQ vs ARQ	1	1416.7	0.81	0.3706	AQ = ARQ	0.3142

Treatment legend: Q = Quarry seeds only; A = Alvar seeds only; AS = Alvar seeds (+) sand; ASN = Alvar seeds (+) sand (+) nitrogen; ARQ = Alvar seeds (-) quarry residents; AQ = Alvar seeds (+) quarry seeds. Contrasts made between treatment pairs account for the richness of seeded species in plots as measured in September 2004, May 2005 and August 2005; a significant ($P<0.05$) “Time*Contrast” term would indicate that the relationship between two contrasted treatments changed over time.

Table 8. Total Density of Seeded Plants in Plots Contrasted Between Treatment Groups Sampled Repeatedly Over Time

Contrast	*DF*	*Mean Square*	*F Value*	*Pr > F*	*Result*	*Time*Contrast (Pr > F)*
Q vs. A	1	118.2	5.33	0.0220	A > Q	0.0097
Q vs. AS	1	516.0	23.28	<0.0001	AS > Q	0.0156
Q vs. ASN	1	210.9	9.51	0.0023	Q > ASN	0.4604
Q vs. ARQ	1	291.0	13.13	0.0004	ARQ > Q	0.5756
Q vs. AQ	1	80.9	3.65	0.0577	AQ > Q	0.0870
A vs. AS	1	140.3	6.33	0.0127	AS > A	0.6834
A vs. ASN	1	778.8	35.13	<0.0001	A > ASN	0.7275
A vs. ARQ	1	38.3	1.73	0.1903	A = ARQ	0.1311
A vs. AQ	1	3.5	0.16	0.6901	A = AQ	0.3747
AS vs. ASN	1	778.8	35.13	<0.0001	AS > ASN	0.2581
AQ vs ARQ	1	65.1	2.94	0.0882	AQ = ARQ	0.3624

Treatment legend: Q = Quarry seeds only; A = Alvar seeds only; AS = Alvar seeds (+) sand; ASN = Alvar seeds (+) sand (+) nitrogen; ARQ = Alvar seeds without quarry residents; AQ = Alvar seeds (+) quarry seeds. Contrasts made between treatment pairs account for the density of seeded species in plots as measured in September 2004, May 2005 and August 2005; significant ($p<0.05$) “Time*Contrast” terms indicate that the relationship between contrasted treatments varied with sampling date. Potential effects of significant “Treatment*Site” interactions on contrasts have been ignored.

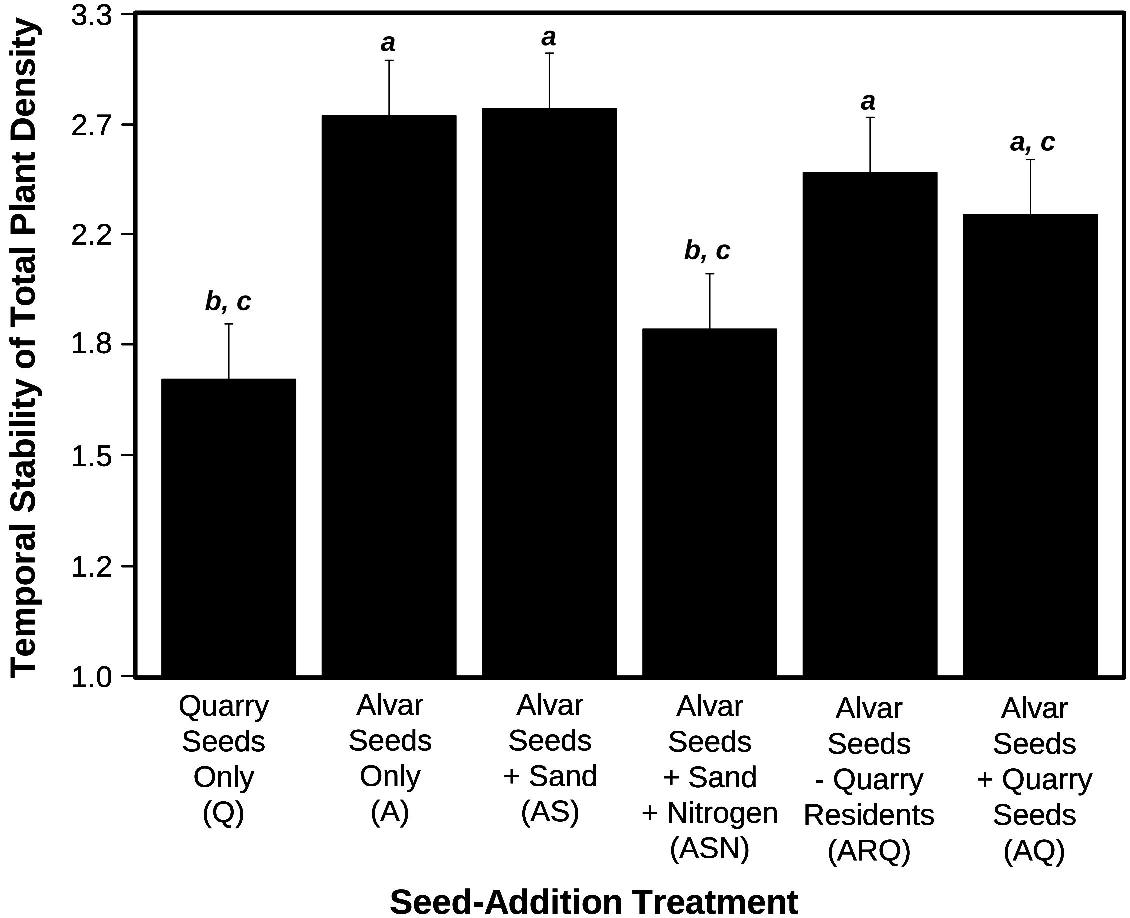


Fig. 13. Effects of seed-addition treatment on the temporal stability of total plant density in plots for the 2004-2005 period. Temporal stability was calculated for each plot as the temporal mean plot density divided by the temporal standard deviation of density, where plant density was sampled in each plot in September 2004, May 2005 and August 2005. Treatments marked with the same letter are not significantly different form each other ($P>0.05$, statistical contrasts among treatment pairs; see table 9).

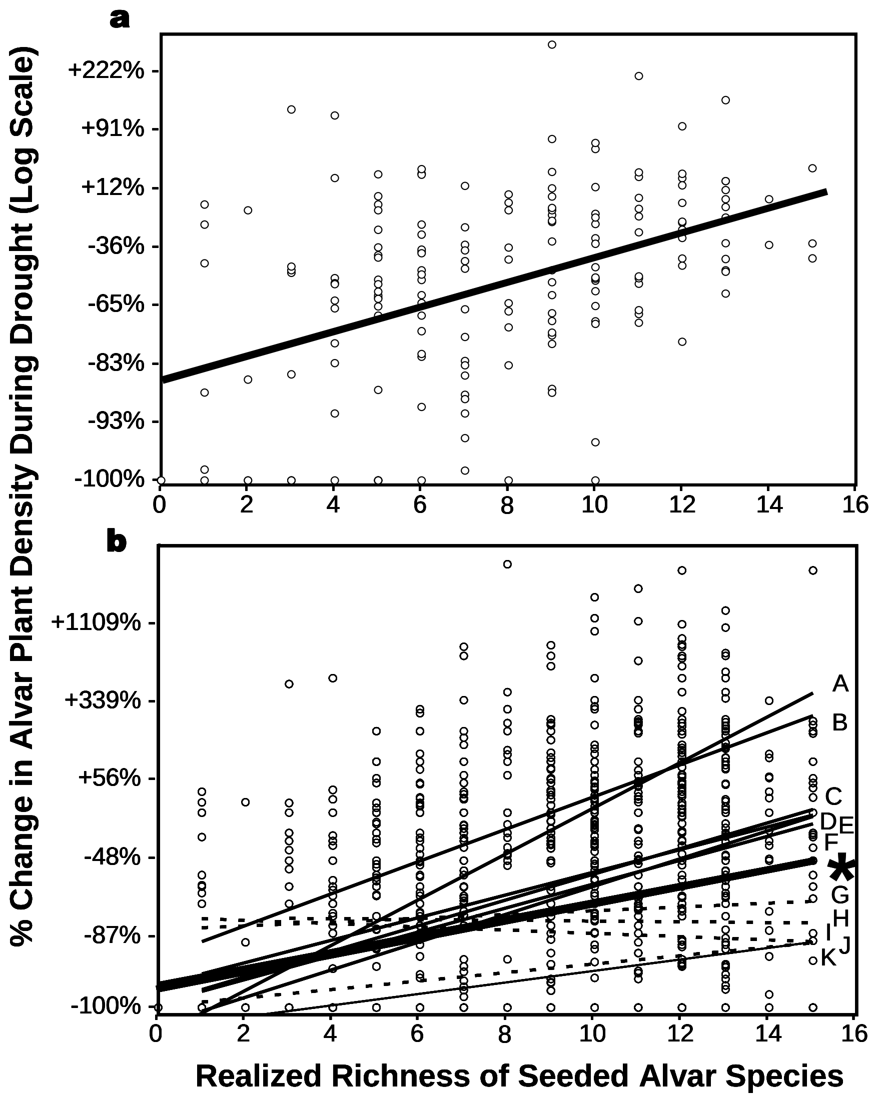


Figure 14. Effects of species richness on drought resistance in populations and communities of alvar plant species restored to abandoned limestone quarry floors. Four quarry sites experienced a natural drought throughout May and June 2005; drought resistance was calculated for each population and community as the natural logarithm of the percent change in plant density between early May and mid-August 2005. **a**, Samples correspond to communities, or the collection of all seeded alvar species present in each restoration plot (N=176) . Community drought resistance is positively and linearly related to the richness of alvar species to establish in plots during the 2004 growing season ($r=0.44$; $p<0.0001$). **b,** Samples correspond to individual species populations within plot communities (N=1369). The regression line labelled with an asterisk represents the positive relationship between community richness and drought resistance for all populations taken as a group ($r=0.26$; $p<0.0001$). Regression lines labelled “A” through “K” represent richness-resistance relationships for populations of 11 individual species common to restoration plots; solid lines represent statistically significant relationships ($p<0.01$) while dashed lines represent non-significant relationships ($p>0.13$).

Table 9. ANOVA and Contrasts for Temporal Stability of Total Plant Density as a Function of Seed-Addition Treatment

EFFECT	DF	Mean Square	F Value	Pr > F
Treatment	5	1.4667	2.37	0.0860
Site	3	4.880	7.89	0.0022
Treatment*Site	15	0.6189	1.17	0.3002
Error	191	0.5300		
Contrasts Made:				
A vs Q	1	4.0777	7.69	0.0061 (A > Q)
AS vs Q	1	4.3024	8.12	0.0049 (AS > Q)
ASN vs Q	1	0.7538	1.42	0.2345 (ASN = Q)
ARQ vs Q	1	2.5051	4.73	0.0309 (ARQ > Q)
AQ vs Q	1	1.5868	2.99	0.0852 (AQ = Q)
A vs AS	1	0.0030	0.01	0.9400 (A = AS)
A vs ARQ	1	0.1906	0.36	0.5494 (A = ARQ)
A vs AQ	1	0.5770	1.09	0.2981 (A = AQ)
A vs ASN	1	2.6309	4.96	0.0271 (A > ASN)
AS vs ASN	1	2.8105	5.30	0.0224 (AS > ASN)
AQ vs ARQ	1	0.1043	0.20	0.6578 (AQ = ARQ)

Temporal stability was calculated for each plot as the temporal mean value of total plant density divided by the temporal standard deviation of density; plots were sampled in September 2004, May 2005 and August 2005. Treatment codes are explained in Fig. 13.

Discussion

This research offers considerable opportunities to those interested in the rehabilitation or restoration of abandoned quarries in Ontario. Browning (1998) had conducted a preliminary assessment of the ecological characteristics of a small number of abandoned pits and quarries and concluded that they all had considerable value as sites that could be restored to marsh, fen, swamp, alvar and prairie ecosystems. Our current research has shown that this early assessment was correct. The floors of abandoned quarries have physical and chemical characteristics that are remarkably similar to naturally occurring alvars of the Bruce Peninsula. The major differences are the predominance of silica sand in naturally occurring alvars, the higher nitrogen and carbon concentrations in alvars, and the lower levels of calcium in quarries. On the basis of the physical and chemical properties of the skeletal soils of the quarries, we conclude that quarry floors and alvars are very similar. We do not dismiss the statistical differences in many of the variables shown in Table 6, but from the perspective of most of the plants that would be growing in these soils, the statistical differences present are largely irrelevant to their success. Even the additional of supplemental silica sand (which was the one of the treatments in Part 5) had only a modest effect on the survival of introduced plants.

The biological characteristics of the quarry floors are also much more similar to naturally occurring alvars than we suspected. Even though the species composition of quarry floors and alvars varies tremendously with age, location, and with microhabitat, quarry floors are remarkably alvar-like. Twelve percent of the vascular species on quarry floors are 'characteristic' of alvars (as defined by Catling and Brownell 1995) and this value compares with approximately 25% for naturally occurring alvars. This suggests that at least for 'characteristic species' the quarry floors sampled here are approximately half-way to becoming real alvars. The DCA ordination diagrams show another feature of the developing vegetation on quarries as it compares with alvar vegetation: the variance in species composition in the quarries is large along axis 2 compared with the alvars, and it diminishes with time. Since this contraction in variance was not seen in the CCA ordinations, it means that the environmental factor that is correlated with this variance truncation was not measured.

Exotic species are much more common on quarry floors than on alvars, but in the last portion of the project we found that once alvar species were seeded into quarry floors, their survival was actually better than that of the exotic weed species that already occupied the site. What this means is that quarries hold large numbers of exotic weed species principally because there is a substantial seed rain from neighbouring disturbed habitats. This was confirmed by the seed bank analysis included here. The artificial seeding experiment also showed that the ability of the quarry floor vegetation to persist in the face of a catastrophic drought is greater when the component species have an alvar origin. This result augers well for the widespread sowing of alvar seeds on abandoned quarry properties across the province.

Our findings are biologically significant from a theoretical point of view as well because it is consistent with the hypothesis that diversity begets functional stability in harsh and unproductive environments, which implies that restoration practices that generate greater diversity will be more successful in limiting reversion of restored systems back to degraded states. Many new questions are raised by this finding, however: What is the nature of the interactions that promote stability in harsh environments? Is functional stability actually influenced by species diversity itself, or by the particular set of environmental filters that produce diversity patterns in stressed but heterogeneous environments? In terms of restoring quarry floors to alvars, we have seen that overcoming immigration barriers is enough to initiate alvar community development, but the richness and density of such communities is highly variable under conditions of fixed seed input. Successful colonization tends to be weakly limited by soil sand content and the presence of quarry resident species, but not by nitrogen paucity. Additional monitoring and experimentation with quarry-floor alvar communities is required to better understand mechanisms and determinants of long-term restoration success and ecological stability in unproductive and degraded environments.

Recommendations for quarry operators

On the basis of the work done in this project, we suggest the following best practices for the restoration and management of abandoned limestone quarries in Ontario.

1. Quarry floors can be made into reconstituted alvars principally by the input of alvar seeds. While the whole array of alvar species was not tested in this work, we predict that the broader the array of alvar species used in plantings, the greater the chance that the quarries can be used to extend the range of alvar endemics.
2. Seed of alvar plants should be collected and/or grown by experienced people. The possibility should be considered of collaborating with the Royal Botanical Gardens.
3. Success of planted species should be monitored at each site, and the range of 'best performers' should be expanded at each site.
4. The existing vegetation should not in any way be removed or interfered with. Operators need not worry about the plants already growing on the quarry floor. Even the weedy plants have had a rock outcrop origin and hence may contribute to the stability of the site.
5. An emphasis should be placed on making as diverse a planting as possible.
6. All seeding should take place in spring.
7. Sites used to grow alvar species should also be used as seed sources for additional plantings.
8. Success of the restoration should not be judged by percent vegetation cover, since open rock is itself a feature of alvars.
9. Soil amendments are largely unnecessary. A mixture of sand and compost will add nutrients and carbon. Amended soil depth in vegetated areas should not exceed 2 cm.
10. The existing soil should not be tampered with.
11. Do not fertilize - especially with nitrogen.
12. Spatial heterogeneity should be manufactured at small and large scales, using rocky debris.
13. Human traffic should be discouraged to reduce mortality due to trampling.
14. Quarries should be purchased and set aside. An abandoned quarry is a youthful alvar.
14. Operators should apply for ANSI status for abandoned sites. Plants, herptiles, and birds may all benefit from the spatial heterogeneity at the sites.
15. Signage should be posted to indicate that abandoned quarry sites are nature preserves.
16. No money should be spent on turning quarries into golf courses, theme parks, agricultural fields, or forests. They are fine as alvars.
17. Records of the restoration work should be kept and successes or failures communicated to other property owners. This will form the basis of adaptive management in the future.
18. Quarry operators should advertise restoration activites.

References

[APAO] Aggregate Producers Association of Ontario. c2003-2005. Importance of Aggregate: About Aggregates #5 [Internet]. Mississauga, Ontario: APAO; [cited 2003 March]. Available from: http://www.apao.com/Downloads/publicationsPFDs/Importance%20of%20Aggregates.pdf.

Bailey D, Gunn J. 1992. Landform replication research in two English limestone quarries. In: Achieving Land Use Potential Through Reclamation, 9th Annual National ASSMR Meeting.

Bakker JP, Bakker ES, Rosen E, Verweij GL, Bekker RM. 1996. Soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* shrubland. Journal of Vegetative Science 7:165-176.

Balmford A, Bruner A, Cooper P, Costanza R, Farber S, Green RE, Jenkins M, Jefferiss P, Jessamy V, Madden J, Munro K, Myers N, Naeem S, Paavola J, Rayment M, Rosendo S, Roughgarden J, Trumper K, Turner RK. 2002. Economic reasons for conserving wild nature. Science 297:950-953.

Belcher JW, Keddy PA, Catling PM. 1992. Alvar vegetation in Canada: a multi-variate description at two scales. Canadian Journal of Botany 70:1279-1291.

Bengtsson K, Prentice HC, Rosen E, Moberg R, Sjogren E. 1988. The dry alvar grasslands of Oland: ecological amplitudes of plant species in relation to vegetation composition. Acta Phytogeographica Suecica 76:21-46.

Benoit DL, Kenkel NC, Cavers PB. 1989. Factors influencing the precision of soil seed bank estimates. Canadian Journal of Botany 67:2833-2840.

Bigwood DW, Inouye DW. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. Ecology 69:497-507.

Booth DM, Wahl. 1989. Limestone industries of Ontario. Volume 1 – Geology, properties and economics. Ontario, Canada: Ministry of Natural Resources. 158p.

Borgegard S-O. 1990. Vegetation development in abandoned gravel pits: effects of surrounding vegetation, substrate and regionality. Journal of Vegetation Science 1:675-682.

Bradshaw AD. 1987. The reclamation of derelict land and the ecology of ecosystems. In: Jordan WR, Gilpin ME, Aber JD. Restoration Ecology: A synthetic approach to ecological research. Cambridge: Cambridge University Press. 53-74 p.

Bradshaw A. 1994. Industrial wasteland. Naturopa 76:21-22.

Brady NC. 1974. The nature and properties of soils. 8th edition. New York: Macmillan Publishing Co. Inc. 639p.

Brodo IM, Sharnoff SD, Sharnoff S. 2001. Lichens of North America. New Haven and London: Yale University Press. 795p.

Browning MHR. 1998. Abandoned pits and quarry sites: living experiments. Ontario Ministry of Natural Resources.

Catling PM. 1995. The extent of confinement of vascular plants to alvars in Southern Ontario. The Canadian Field-Naturalist 109:172-181.

Catling PM, Brownell VR. 1995. A review of the alvars of the Great Lakes region: distribution, floristic composition, biogeography and protection. The Canadian Field-Naturalist 109:143-171.

Catling PM, Brownell VR. 1999. Alvars of the Great Lakes Region. In: Anderson, R.C., James, S.F. and Baskin, J.M, editors. Savannas, Barrens, and Rock Outcrop Plant Communities of North America. United States of America: Cambridge University Press. 375-391p.

Clemente AS, Werner C, Maguas C, Cabral MS, Martins-Loucao MA, Correia O. 2004. Restoration of a limestone quarry: effect of soil amendments on the establishment of native Mediterranean *Sclerophyllous* shrubs. Restoration Ecology 12:20-28.

Crum H. 1983. Mosses of the Great Lakes Forest. Ann Arbor, Michigan: University of Michigan Press. 404p.

Davis BNK. 1981. Regional variation in quarries. In: Ecology of Quarries. Institute of Terrestrial Ecology, Cambridge, England: 12-19p.

Davis BNK, Lakhani KH, Brown MC, Park DG. 1985. Early seral communities in a limestone quarry: an experimental study of treatment effects on cover and richness of vegetation. Journal of Applied Ecology 22:473-490.

Dixon JM, Hambler DJ. 1984. An experimental approach to the reclamation of a limestone quarry floor: the first three years. Environmental Conservation 11:19-28.

De Kovel CGF, Van Mierlo AJEM, Wilms YJO, Berendse F. 2000. Carbon and nitrogen in soil and vegetation at sites differing in successional age. Plant Ecology 149:43-50.

Due North Resources. c1997. What is the aggregate resources act? [Internet]. Sturgeon Falls (ON): Ministry of Natural Resources; [cited January 2006]. Available from: http://www.cyber-north.com/arawhat.html

Fenner M. 1985. Seed Ecology. New York: Chapman and Hall. 151p.

Grime JP. 1977. Evidence for the existence for three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111(982):1169-1194.

Harper JL. 1959. The biology of weeds. Oxford: Blackwell Scientific Publications. Factors controlling plant numbers; 119-132p.

Harper J. 1977. The seed bank. In: *Population Biology of Plants*. Academic Press: London: 83-110p.

Hodgson JG. 1981. The botanical interest and value of quarries. In: Ecology of Quarries. Institute of Terrestrial Ecology, Cambridge, England: 3-11p.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, and others. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3-35 (2005).

Humphries RN. 1981. The establishment of vegetation on quarry materials: Physical and chemical constraints. In: Ecology of Quarries. Institute of Terrestrial Ecology, Cambridge, England, UK: 55-61p.

Jefferson RG(a). 1984. Quarries and wildlife conservation in the Yorkshire Wolds, England. Biological Conservation 29:363-380.

Jefferson RG(b). 1984. The vascular flora of disused chalk pits and quarries in the Yorkshire Wolds. Naturalist 109:19-22.

Jefferson RG, Usher MB. 1987. The seed bank in soils of disused chalk quarries in the Yorkshire Wolds, England: implications for conservation management. Biological Conservation 42:287-302.

Jongman RHG, ter Braak CJF, van Tongeren OFR. 1987. Data analysis in community and landscape ecology. Netherlands: Centre for Agricultural Publishing and Documentation. 299p.

Khater C, Martin A, Maillet J. 2003. Spontaneous vegetation dynamics and restoration prospects for limestone quarries in Lebanon. Applied Vegetation Science 6:199-204.

Krahulec F, Rosen E, van der Maarel E. 1986. Preliminary classification and ecology of dry grassland communities on Olands Stora Alvar (Sweden). Nordic Journal of Botany 6(6):797-809.

Larson DW, Matthes U, Kelly PE, Lundholm J, Gerrath J. 2004. The urban cliff revolution. New findings on the origins and evolution of human habitats. Ontario, Canada: Fitzhenry and Whiteside. 198p.

Leps J, Smilauer P. 2003. Multivariate analysis of ecological data using CANOCO. United Kingdom: Cambridge University Press. 269p.

Milberg P, Hansson ML. 1994. Soil seed bank and species turnover in a limestone grassland. Journal of Vegetative Science 5:35-42.

Newmaster SG, Lehela A, Uhlig PWC, Oldham MJ. 1998. Ontario plant list. Ontario, Canada: Queen's Printer for Ontario.

Park DG. 1981. Seedling demography in quarry habitats. In: Ecology of Quarries. Institute of Terrestrial Ecology, Cambridge, England: 32-40p.

Ranson CE, Doody JP. 1981. Quarries and nature conservation – objectives and management. In: Ecology of Quarries. Institute of Terrestrial Ecology, Cambridge, England: 20-26p.

Roberts HA. 1981. Seed banks in soils. In: Advances in Applied Biology 6:1-56.

Sanderson EW, Jaieth M, Levy MA, Redford KH, Wanncbo AV, Woolmer G. 2002. The human footprint and the last of the wild. BioScience 52(10):891-904.

Schaefer CA. 1996. Plant community structure and environmental conditions of alvars of the Bruce Peninsula, Ontario, Canada. Master's thesis, University of Guelph, Ontario. 156p.

Schaefer CA, Larson DW. 1997. Vegetation, environment characteristics and ideas on the maintenance of alvars on the Bruce Peninsula, Canada. Journal of Vegetative Science 8:797-810.

Skaller MP. 1977. The Ecology of Natural Plant Colonization in a Limestone Quarry. In: Perry EJ, Richards NA. Limestone Quarries: Responses to Land Use Pressures. Department of Landscape Architecture and Regional Planning. University of Pennsylvania: 40-71p.

Stark KE, Lundholm JT, Larson DW. 2003. Relationships between seed banks and spatial heterogeneity of North American alvar vegetation. Journal of Vegetative Science **14**:205-212.

Stark KE, Lundholm JT, Larson DW. 2004. Arrested development of soil on alvars of Ontario, Canada: Implications for conservation and restoration. Natural Areas Journal 24(2):95-100.

ter Braak CJF. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69:69-77.

ter Braak CJF. 1994. Canonical community ordination. Part I: Basic theory and linear methods. Ecoscience 1(2):127-140.

ter Braak CJF, Smilauer P. 2002. CANOCO reference manual and CanoDraw for Windows user's guide (version 4.5). United States of America: Biometrics, Wageningen and Ceske Budejovice. 499p.

ter Heerdt GNJ, Schutter A, Bakker JP. 1999. The effect of water supply on seed-bank analysis using the seedling-emergence method. Functional Ecology 13:428-430.

ter Heerdt GNJ, Verweij GL, Bekker RM, Bakker JP. 1996. An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. Functional Ecology 10:144-151.
Thompson K, Grime JP. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67:893-921.
Tilman, D. Biodiversity: population versus ecosystem stability. *Ecology* 77:350-363 (1996).
[TOARC] The Ontario Aggregate Resources Corporation. 2003. Mineral Aggregates in Ontario.
Usher M. 1979. Natural communities of plants and animals in disused quarries. Journal of Environmental Management 8:223-236.
Valone, T.J., and Hoffman, C.D. A mechanistic examination of diversity-stability relationships in annual plant communities. *Oikos* 103:519-527 (2003).
van der Maarel E. 1988. Floristic diversity and guild structure in the grasslands of Oland's Stora Alvar. Acta Phytogeographica Suecica 76:53-65.
Vitousek PM. 1994. Beyond global warming: ecology and global change. Ecology 75(7):1861-1876.
Whittaker RH. 1967. Gradient analysis of vegetation. Biological Reviews 42:207-264.
Zamfir M. 2000. Effects of bryophytes and lichens on seedling emergence of alvar plants: vidence from greenhouse experiments. Oikos 88:603-611.

Appendix 1. Abandoned limestone quarry floor species list of vascular plants, bryophytes and lichens. Species codes are used in multivariate analyses. Average percent frequency is provided for each species. Native/exotic status is provided for the vascular plant species.

	Quarry floor vascular plants	Code	Origin	% Frequency
1	*Acalypha virginica var. rhomboidea*	Acalviva	Native	2.06
2	*Acer rubrum*	Acerrubr	Native	0.01
3	*Acer saccharum ssp. saccharum*	Acersacc	Native	0.26
4	*Acer sp.*	Acersp.		0.05
5	*Achillea millefolium ssp. millefolium*	Achimille	Exotic	0.76
6	*Acinos arvensis*	Acinarve	Exotic	1.3
7	*Agalinis tenuifolia var. tenuifolia*	Agalteva	Native	0.1
8	*Agrostis cf. gigantea*	Agrocfgi	Exotic	0.12
9	*Agrostis gigantea*	Agrogiga	Exotic	1.04
10	*Agrostis sp.*	Agrosp.		0.18
11	*Agrostis stolonifera*	Agrostol	Native	2.13
12	*Ambrosia artemisiifolia*	Ambrarte	Native	4.9
13	*Anemone quinquefolia var. quinquefolia*	Anemquin	Native	0.22
14	*Anemone virginiana var. virginiana*	Anemviva	Native	0.06
15	*Apocynum cannabinum var. hypericifolium*	Apoccava	Native	0.26
16	*Arenaria serpyllifolia*	Arenserp	Exotic	3.6
17	*Asclepias cf. syriaca*	Asclcfsy	Native	0.53
18	*Asclepias sullivantii*	Asclsull	Native	0.02
19	*Asclepias syriaca*	Asclsyri	Native	0.02
20	*Aster cf. puniceus var. puniceus*	Astecfpu	Native	0.16
21	*Aster cordifolius*	Astecord	Native	0.01
22	*Aster ericoides ssp. ericoides*	Asteerva	Native	0.08
23	*Aster lanceolatus ssp. lanceolatus*	Astelanv	Native	0.94
24	*Aster lateriflorus*	Astelate	Native	0.1
25	*Aster novae-angliae*	Astenova	Native	0.18
26	*Aster pilosus var. pilosus*	Astepilo	Native	2.87
27	*Aster puniceus var. puniceus*	Astepuni	Native	0.19
28	*Aster sp.*	Astesp.		0.56
29	*Barbarea vulgaris*	Barbvulg	Exotic	0.01
30	*Berberis vulgaris*	Berbvulg	Exotic	0.04
31	*Betula papyrifera*	Betupapy	Native	1.31
32	*Bidens coronata*	Bidecoro	Native	0.33
33	*Bidens frondosa*	Bidefron	Native	0.37
34	*Bromus hordeacus ssp. hordeaceus*	Bromhord	Exotic	0.31
35	*Bromus inermis ssp. inermis*	Brominer	Exotic	0.29
36	*Carex aurea*	Careaure	Native	1.31
37	*Carex eburnea*	Careebur	Native	0.1
38	*Carex flacca*	Careflac	Exotic	2.75
39	*Carex flava*	Careflav	Native	3.76
40	*Carex granularis*	Caregran	Native	0.45

41	*Carex hystercina*	Carehyst	Native	0.31
42	*Carex laxiflora*	Carelaxi	Native	1.52
43	*Carex pseudo-cyperus*	Carepseu	Native	0.02
44	*Carex sp.*	Caresp.		2.14
45	*Carex viridula ssp. viridula*	Careviri	Native	0.23
46	*Carex vulpinoidea*	Carevulp	Native	0.02
47	*Centaurea maculosa*	Centmacu	Exotic	0.81
48	*Cerastium fontanum*	Cerafont	Exotic	0.29
49	*cf. Symphoricarpos occidentalis*	cfSyocci	Exotic	0.01
50	*cf. Vibernum sp.*	cfVisp.		0.05
51	*Chaenorrhinum minus*	Chaeminu	Exotic	0.07
52	*Chamaesyce maculata*	Chammacu	Exotic	0.69
53	*Chamaesyce vermiculata*	Chamverm	Native	7.72
54	*Chrysanthemum leucanthemum*	Chryleuc	Exotic	4.86
55	*Cichorium intybus*	Cichinty	Exotic	0.45
56	*Cirsium sp.*	Cirssp.		0.02
57	*Cirsium vulgare*	Cirsvulg	Exotic	0.05
58	*Conyza canadensis*	Conycana	Native	0.04
59	*Cornus foemina ssp. racemosa*	Cornfova	Native	0.06
60	*Cornus sp.*	Cornsp.		0.04
61	*Cornus stolonifera*	Cornstol	Native	1.34
62	*Crataegus mollis*	Cratmoll	Native	0.05
63	*Dactylis glomerata*	Dactglom	Exotic	0.5
64	*Danthonia spicata*	Dantspic	Native	6.41
65	*Daucus carota*	Dauccaro	Exotic	7.48
66	*Echium vulgare*	Echivulg	Exotic	0.19
67	*Eleocharis cf. erythropoda*	Eleocfer	Native	0.16
68	*Eleocharis erythropoda*	Eleoeryt	Native	0.55
69	*Epilobium parviflorum*	Epilparv	Exotic	0.36
70	*Equisetum sp.*	Equisp.		0.82
71	*Equisetum variegatum ssp. variegatum*	Equivari	Native	2.56
72	*Erigeron annuus*	Erigannu	Native	0.76
73	*Erigeron sp.*	Erigsp.		0.23
74	*Erigeron strigosus*	Erigstri	Native	2.27
75	*Eupatorium perfoliatum*	Eupaperf	Native	0.11
76	*Euphorbia cyparissias*	Euphcypa	Exotic	0.16
77	*Euthamia graminifolia*	Euthgram	Native	2.47
78	*Fragaria sp.*	Fragsp.		1.09
79	*Fragaria vesca ssp. americana*	Fragvesc	Native	1.95
80	*Fragaria virginiana*	Fragvirg	Native	0.71
81	*Fraxinus americana*	Fraxamer	Native	0.07
82	*Fraxinus pennsylvanica*	Fraxpenn	Native	0.29
83	*Galium mollugo*	Galimoll	Exotic	1.7
84	*Geranium robertianum*	Gerarobe	Exotic	1.11
85	*Hesperis matronalis*	Hespmatr	Exotic	0.01

86	*Hieracium cf. caespitosum ssp. caespitosum*	Hiercfca	Exotic	1.47
87	*Hieracium cf. piloselloides*	Hiercfpi	Exotic	0.82
88	*Hieracium pilosella*	Hierpila	Exotic	1.92
89	*Hieracium piloselloides*	Hierpils	Exotic	2.81
90	*Hieracium sp.*	Hiersp.		6.68
91	*Hypericum perforatum*	Hypeperf	Exotic	0.96
92	*Juncus articulatus*	Juncarti	Native	6.56
93	*Juncus cf. nodosus*	Junccfno	Native	1.37
94	*Juncus cf. tenuis*	Junccfte	Native	
95	*Juncus cf. torreyi*	Junccfto	Native	0.45
96	*Juncus dudleyi*	Juncdudl	Native	0.33
97	*Juncus nodosus*	Juncnodo	Native	0.29
98	*Juncus torreyi*	Junctorr	Native	1.98
99	*Juniperus communis*	Junicomm	Native	0.01
100	*Lactuca serriola*	Lactserr	Exotic	0.29
101	*Larix larcina*	Larilarc	Native	0.02
102	*Lepidium virginicum*	Lepivirg	Native	0.26
103	*Linaria vulgaris*	Linavulg	Exotic	0.04
104	*Lonicera cf. canadensis*	Lonicfca	Native	0.02
105	*Lonicera sp.*	Lonisp.		0.06
106	*Lonicera tatarica*	Lonitata	Exotic	0.12
107	*Lotus corniculatus*	Lotucorn	Exotic	5.51
108	*Lycopus americanus*	Lycoamer	Native	1.64
109	*Lythrum salcaria*	Lythsali	Exotic	1.98
110	*Medicago lupulina*	Medilupu	Exotic	1.14
111	*Melilotus alba*	Melialba	Exotic	3.79
112	*Melilotus officinalis*	Melioffi	Exotic	0.53
113	*Muhlenbergia glomerata*	Muhlglom	Native	0.26
114	*Oenothera biennis*	Oenobien	Native	0.02
115	*Ostrya virginiana*	Ostrvirg	Native	0.01
116	*Oxalis sp.*	Oxalsp.		0.11
117	*Panicum acuminatum var. acuminatum*	Paniacva	Native	18.36
118	*Panicum capillare*	Panicapi	Native	0.02
119	*Panicum philadelphicum*	Paniphil	Native	1.4
120	*Panicum sp.*	Panisp.		0.16
121	*Parthenocissus quinquefolia*	Partquin	Native	0.04
122	*Phalaris arundinaceae*	Phalarun	Native	0.96
123	*Phleum pratense*	Phleprat	Exotic	0.92
124	*Phragmites australis*	Phraaust	Native	0.26
125	*Physocarpus opulifolius*	Physopul	Native	0.06
126	*Pinus banksiana*	Pinubank	Native	0.02
127	*Plantago lanceolata*	Planlanc	Exotic	5.44
128	*Plantago major*	Planmajo	Exotic	0.79
129	*Plantago sp.*	Plansp.		0.14
130	*Poa compressa*	Poacomp	Native	17.07

131	*Populus balsamifera ssp. balsamifera*	Popubals	Native	0.65
132	*Populus nigra*	Popunigr	Exotic	0.01
133	*Potentilla argentea*	Potearge	Exotic	0.47
134	*Potentilla recta*	Poterect	Exotic	5.47
135	*Potentilla sp.*	Potesp.		0.04
136	*Prunella vulgaris ssp. vulgaris*	Prunvulg	Exotic	0.99
137	*Prunus pensylvanica*	Prunpens	Native	0.24
138	*Prunus sp.*	Prunsp.		0.07
139	*Prunus virginiana ssp. virginiana*	Prunvirg	Native	0.08
140	*Ranunuculus acris*	Ranuacri	Exotic	0.1
141	*Rhamnus alnifolia*	Rhamalni	Native	0.05
142	*Rhamnus frangula*	Rhamfran	Exotic	1.58
143	*Rhamnus sp.*	Rhamsp.		0.2
144	*Rhus radicans ssp. negundo*	Rhusradi	Native	0.30
145	*Rhus typhina*	Rhustyph	Native	0.17
146	*Rhynchospora capillacea*	Rhyncapi	Native	2.23
147	*Rosa multiflora*	Rosamult	Exotic	0.01
148	*Rubus occidentalis*	Rubuocci	Native	0.49
149	*Rumex crispus*	Rumecris	Exotic	0.11
150	*Salix cf. candida*	Salicfca	Native	0.05
151	*Salix cf. fragilis*	Salicffr	Exotic	0.04
152	*Salix cf. purpurea*	Salicfpu	Exotic	0.18
153	*Salix cf. viminalis*	Salicfvi	Exotic	0.06
154	*Salix eriocephala*	Salierio	Native	0.12
155	*Salix exigua*	Saliexig	Native	0.01
156	*Salix fragilis*	Salifrag	Exotic	0.01
157	*Salix petiolaris*	Salipeti	Native	0.14
158	*Salix purpurea*	Salipurp	Exotic	0.04
159	*Salix sp.*	Salisp.		0.08
160	*Sanguisorba minor*	Sangmino	Exotic	2.03
161	*Scirpus atrovirens*	Sciratro	Native	0.78
162	*Scirpus validus*	Scirvali	Native	0.01
163	*Sedum acre*	Seduacre	Exotic	10.84
164	*Senecio obovatus*	Seneobov	Native	2.13
165	*Setaria pumila*	Setapumi	Exotic	0.01
166	*Setaria viridis*	Setaviri	Exotic	0.38
167	*Silene vulgaris*	Silevulg	Exotic	0.11
168	*Sisyrinchium montanum*	Sisymont	Native	0.51
169	*Solidago altissima var. altissima*	Solialva	Native	0.24
170	*Solidago canadensis var. canadensis*	Solicava	Native	0.88
171	*Solidago cf. altissima var. altissima*	Solicfal	Native	0.02
172	*Solidago cf. canadensis*	Solicfca	Native	1.14
173	*Solidago cf. hispida var. hispida*	Solicfhi	Native	0.01
174	*Solidago cf. nemoralis ssp. nemoralis*	Solicfne	Native	0.38
175	*Solidago gigantea*	Soligiga	Native	0.44

176	*Solidago juncea*	Solijunc	Native	1.1
177	*Solidago nemoralis ssp. nemoralis*	Solinemo	Native	1.47
178	*Solidago ptarmicoides*	Soliptar	Native	0.79
179	*Solidago rugosa ssp. rugosa*	Solirugo	Native	0.42
180	*Solidago sp.*	Solisp.		0.43
181	*Sporobolus neglectus*	Spornegl	Native	1.58
182	*Sporobolus vaginiflorus*	Sporvagi	Native	0.22
183	*Tanacetum vulgare*	Tanavulg	Exotic	0.12
184	*Taraxicum officinale*	Taraoffi	Exotic	1.1
185	*Thuja occidentalis*	Thujocci	Native	5.76
186	*Trichostema brachiatum*	Tricbrac	Native	1.85
187	*Trifolium campestre*	Trifcamp	Exotic	0.16
188	*Trifolium cf. campestre*	Trifcfca	Exotic	0.19
189	*Trifolium hybridium ssp. elegans*	Trifhybr	Exotic	0.04
190	*Trifolium pratense*	Trifprat	Exotic	0.53
191	*Trifolium sp.*	Trifsp.		1.16
192	*Tussilago farfara*	Tussfarf	Exotic	0.17
193	*Typha angustifolia*	Typhangu	Native	0.3
194	*Verbascum thapsus*	Verbthap	Exotic	0.13
195	*Veronica officinalis*	Verooffi	Exotic	0.06
196	*Veronica sp.*	Verosp.		0.04
197	*Viburnum lentago*	Vibulent	Native	0.01
198	*Vicia cracca*	Vicicrac	Exotic	0.14
199	*Viola sp.*	Violsp.		0.18
200	*Vitis riparia*	Vitiripa	Native	0.04

	Quarry floor bryophytes	**Code**	**% Frequency**
1	*Bryum caespitosum*	Bryucaes	1.55
2	*Bryum cf. argenteum*	Bryucfar	1.03
3	*Bryum lisae var. cuspidatium*	Bryulisa	3.38
4	*Ceratodon purpureus*	Cerapurp	0.02
5	*Drepanocladus cf. aduneus*	Drepcfad	0.65
6	*Fissidens adianthoides*	Fissadia	1.68
7	*Grimmia alpicola*	Grimalpi	1.52
8	*Mnium cuspidatum*	Mniucusp	0.33
9	*Myurella julacea*	Myurjula	0.1
10	*Tortella cf. fragilis*	Tortcffr	0.02
11	*Tortella tortuosa*	Torttort	6.92
12	*Tortula ruralis*	Tortrura	0.19
13	*unknown acrocarp*	unknacro	0.19
14	*unknown pleurocarp*	unknpleu	0.13

	Quarry floor lichens	Code	% Frequency
1	*Acarospora glaucocarpa*	Acarglau	0.01
2	*Bacidia sp.*	Bacisp	0.18
3	*Caloplaca arenaria*	Caloaren	0.65
4	*Caloplaca feracissima*	Calofera	2.34
5	*Candelariella aurella*	Candaure	2.09
6	*Candelariella heidelbergensis*	Candheid	2.03
7	*cf. Bacidia sp.*	cfBacisp	0.18
8	*cf. Caloplaca velana*	cfCavela	0.43
9	*cf. Psorotichia schaereri*	cfPsscha	1.96
10	*cf. Candelariella heidelbergensis*	cfCaheid	0.9
11	*Cladonia coniocraea*	Cladconi	0.07
12	*Cladonia rei*	Cladrei	1.61
13	*Cladonia symphycarpia*	Cladsymp	5.17
14	*Dermatocarpon lachneum*	Dermlach	0.38
15	*Lecanora cf. muralis*	Lecacfmu	0.02
16	*Lecanora dispersa*	Lecadisp	0.08
17	*Lecanora muralis*	Lecamura	0.07
18	*Lecidella stigmatea*	Lecistig	0.19
19	*Lepraria sp.*	Leprsp	0.12
20	*Nephroma resupinatum*	Nephresu	0.6
21	*Phaeophyscia cf. orbicularis*	Phaecfor	0.06
22	*Physciella chloantha*	Physstel	0.1
23	*Physcia stellaris*	Physchlo	0.08
24	*Protoblastenia rupestris*	Protrupe	0.67
25	*Psora decipiens*	Psordeci	0.63
26	*Rinodina bischoffii*	Rinobisc	0.32
27	*Sarcogyne regularis*	Sarcregu	2.53
28	*Sterile brown crust*	sterilec	1.46
29	*Verrucaria nigrescens*	Vernigr	7.68
30	*Verrucaria sp.*	Verrsp	19.54
31	*Xanthoparmelia cf. centrifuga*	Xantcfce	0.01
32	*Xanthoparmelia cumberlandia*	Xantcumb	0.1

Appendix 2. Average species frequencies of vascular plants, bryophytes and lichens found growing on both abandoned limestone quarry floors and alvars in southern Ontario. Bold species are those that are characteristic of alvar habitat (found in > 50% of alvars surveyed by Catling 1995).
*** 50-70% confinement level (percentage of a species' range that is in an alvar)**
**** 71-85% confinement level**
***** 86-100% confinement level**

Vascular plants on both quarry floors and alvars	**Quarry % frequency**	**Alvar % frequency**
Achillea millefolium	0.76	0.12
Agalinis tenuifolia var. tenuifolia	0.1	
Agrostis gigantea	1.04	0.33
Agrostis stolonifera	2.13	0.06
Ambrosia artemisiifolia	4.9	
Anemone virginiana var. virginiana	0.06	
Arenaria serpyllifolia	3.6	0.03
Asclepias syriaca	0.02	
Aster cordifolius	0.01	
Aster lanceolatus	0.94	
Aster lateriflorus	0.1	
*Aster pilosus var. pilosus**	2.87	
Betula papyrifera	1.31	0.12
Carex aurea	1.31	0.45
Carex eburnea	0.1	19.82
Carex flava	3.76	0.95
Carex granularis	0.45	0.89
Carex hystericina	0.31	
Carex viridula ssp. viridula	0.23	
Carex vulpinoidea	0.02	
Cornus foemina ssp. racemosa	0.06	
Cornus stolonifera	1.34	0.06
Danthonia spicata	6.41	11.07
Daucus carota	7.48	0.03
Eleocharis erythropoda	0.55	
Equisetum variegatum	2.56	0.18
Erigeron strigosus	2.27	
Euthamia graminifolia	2.47	
Fragaria vesca	1.95	0.03
Fragaria virginiana	0.71	0.63
Fraxinus americana	0.07	
Fraxinus pennsylvanica	0.29	
Hieracium sp.	6.68	0.51
Hypericum perforatum	0.96	1.10
Juncus cf. nodosus	1.37	0.27

Juncus dudleyi	0.33	1.22
Juncus torreyi	1.98	
Juniperus communis	0.01	1.40
Larix larcina	0.02	0.03
Lycopus americanus	1.64	0.74
Muhlenbergia glomerata*	0.26	0.92
Panicum capillare	0.02	
Panicum philadelphicum**	1.4	0.24
Physocarpus opulifolius	0.06	0.24
Pinus banksiana	0.02	0.12
Poa compressa	17.07	3.78
Potentilla recta	5.47	
Prunella vulgaris ssp. vulgaris	0.99	
Prunus virginiana	0.08	3.93
Rhamnus alnifolia	0.05	0.12
Rhus typhina	0.17	
Rhynochospora capillacea	2.23	0.33
Salix exigua	0.01	0.03
Scirpus atrovirens	0.78	
Sedum acre	10.84	
Sisyrinchium montanum	0.51	0.48
Solidago canadensis	0.88	0.03
Solidago gigantea	0.44	
Solidago juncea	1.1	0.09
Solidago nemoralis	1.47	0.83
Solidago ptarmicoides***	0.79	15.80
Sporobolus vaginiflorus	0.22	1.67
Thuja occidentalis	5.76	
Trichostema brachiatum***	1.85	2.92
Trifolium sp.	1.16	0.03
Vitis riparia	0.04	
Bryophytes on both quarry floors and alvars	**Quarry % frequency**	**Alvar % frequency**
Bryum lisae var. cuspidatium	3.38	0.03
Fissidens adianthoides	1.68	0.77
Myurella julacea	0.1	0.95
Tortella ruralis	0.19	0.06
Tortella tortuosa	6.92	7.23
Lichens on both quarry floors and alvars	**Quarry % frequency**	**Alvar % frequency**
Acarospora glaucocarpa	0.01	2.64
Protoblastenia rupestris	0.67	11.99
Psora decipiens	0.63	5.82

Sarcogyne regularis	2.53	0.29
Sterile brown crust	1.46	0.18
Verrucaria sp.	19.54	0.07

Appendix 3. Abandoned limestone quarry floor seed bank species list. The percent abundances of species that compose the seed bank and the native/exotic status of each species are provided. Species in bold were found in the quarry floor seed bank and in the established quarry floor vegetation (110 species).
Species with an * were found in the quarry floor seed bank and growing on alvar habitat in southern Ontario (45 species). ~ indicates species in common between the quarry floor seed bank and alvar seed bank.

Quarry seed bank species	**Percent abundance of species in the seed bank**	**Status**
Acer saccharaum	0.01	Native
***Acer* sp.**	0.01	
Achillea millefolium*	0.13	Exotic
Acinos arvensis	0.15	Exotic
Agalinis tenuifolia* var. *tenuifolia*	0.02	Native
Ambrosia artemisiifolia*	0.39	Native
Anemone quinquefolia	0.01	Native
Apocynum cannabinum* var. *hypericifolium	0.06	Native
***Arenaria serpyllifolia*~**	1.2	Exotic
Asclepias cf. *syriaca*	0.11	Native
Aster cf. *lanceolatus* ssp. *lanceolatus*	0.02	Native
Aster cf. *vimineus*	0.07	Native
Aster lanceolatus* ssp. *lanceolatus*	0.05	Native
Aster novae-angliae	0.01	Native
Aster pilosus* var. *pilosus*	0.09	Native
***Aster* sp.**	0.32	
***Betula papyrifera*~**	0.69	Native
Carex cf. *aurea*	0.04	Native
Carex* cf. *garberi*	0.1	Native
Carex cf. *laxiflora*	1.46	Native
Carex cf. *pensylvanica*	0.02	Native
Carex cf. *retrorsa*	0.02	Native
Carex cf. *vulpinoides*	0.08	Native
Carex flacca	0.33	Exotic
Carex flava*	0.18	Native
Carex granularis*	0.1	Native
***Carex* sp.~**	0.01	
Centaurea maculosa	0.02	Exotic
Cerastium fontanum	0.15	Exotic
cf. *Aster pilosus* var. *pilosus*	0.02	Native
cf. *Aster* sp.	0.01	Native
cf. *Bromus kalmii*	0.26	Native
cf. *Chrysosplenium americanum*	0.33	Native

cf. *Phleum pratense*	0.13	Native
cf. *Poa compressa*	0.02	Native
cf. *Portulaca oleraceae*	0.34	Exotic
cf. *Sanicula* sp.	0.02	
cf. *Silene vulgaris*	0.01	Exotic
cf. *Sporobolus cryptandrus*	0.02	Native
cf. *Tussilago farfara*	0.01	Exotic
cf. *Urtica dioica*	0.01	Exotic
Chaenorrhinum minus	0.02	Exotic
Chamaesyce maculata	0.14	Exotic
Chamaesyce vermiculata	16.07	Native
Chenopodium album	0.01	Exotic
Chenopodium glaucum	0.01	Exotic
Chrysanthemum leucanthemum	1.59	Exotic
Cirsium vulgare	0.02	Exotic
Cornus stolonifera*	0.01	Native
Dactylis glomerata	0.02	Exotic
Danthonia spicata*~	6.11	Native
Daucus carota*	0.77	Exotic
Dianthus armeria	0.03	Exotic
Draba cf. *verna*	0.71	Exotic
Draba verna	0.06	Exotic
Echium vulgare	0.01	Exotic
Eleocharis* cf. *erythropoda	0.49	Native
Epilobium parviflorum	1.26	Exotic
***Equisetum* sp.**	0.02	
Eragrostis pectinacea	0.07	Native
Erigeron annuus	0.05	Native
*Erigeron philadelphicus**	0.01	Native
***Erigeron* sp.**	0.1	
Erigeron strigosus*	0.21	Native
Eupatorium perfoliatum*	0.06	Native
Euphorbia cyparissias	0.01	Exotic
Euthamia graminifolia*	0.83	Native
***Fragaria* sp.**	0.01	
Fragaria vesca*	0.29	Native
Fragaria virginiana*	0.01	Native
Galium mollugo	0.08	Exotic
Geranium robertianum	0.33	Exotic
Hieracium* cf. *piloselloides	0.02	Exotic
Hieracium gronovii	0.01	Exotic
Hieracium pilosella	1.07	Exotic
Hieracium piloselloides	0.19	Exotic
Hieracium pratense	0.09	Exotic
Hieracium* sp.	0.57	

Hypericum perforatum*~	3.1	Exotic
Juncus articulatus	0.02	Native
Juncus bufonis	0.02	Native
Juncus cf. *dudleyi*	0.01	Native
Juncus* cf. *nodosus*	0.34	Native
Juncus dudleyi*~	0.06	Native
Juncus sp.	0.01	
Juniperus communis*	0.01	Native
Lactuca serriola~	0.03	Exotic
***Lonicera* sp.**	0.01	
Lotus corniculatus	1.12	Exotic
Lycopus americanus*	0.35	Native
Lycopus uniflorus	0.04	Native
Lythrum salicaria	0.04	Exotic
Medicago lupulina	0.4	Exotic
Melilotus alba	0.94	Exotic
Melilotus officinalis	0.01	Exotic
Muhlenbergia glomerata*	0.01	Native
Nepeta cataria	0.02	Exotic
Oenothera parviflora	0.05	Native
Oxalis europaea	0.01	Exotic
Oxalis stricta	0.28	Exotic
Panicum acuminatum~	2.46	Native
Panicum philadelphicum*	2.64	Native
***Panicum* sp.**	0.01	
Phalaris arundinaceae	0.04	Native
Phleum pratense	4.58	Native
Plantago lanceolata	0.34	Exotic
Plantago major	0.13	Exotic
Poa cf. *compressa*	0.66	Native
Poa compressa*	9.98	Native
Poa pretense*	0.04	Native
Populus balsamifera	0.01	Native
Portulaca orilacea	2.32	Exotic
Potentilla argentea	0.15	Exotic
*Potentilla norvegica**	1.15	Native
Potentilla recta*	3.2	Exotic
***Potentilla* sp.**	5.28	
Prunella vulgaris*	0.01	Exotic
Prunus pensylvanica	0.01	Native
Prunus virginiana*	0.24	Native
Rhamnus alnifolia*	0.01	Native
Rhamnus cf. *frangula*	0.02	Exotic
Rhamnus frangula	0.06	Exotic
Rhus radicans	0.01	Native

Rhynchospora capillacea*	4.58	Native
Rorippa islandica var. *islandica*	0.01	Native
Rubus cf. *occidentalis*	0.04	Native
Rubus occidentalis	0.31	Native
Rubus sp.	0.01	
Rumex cf. *obtusifolius*	0.01	Exotic
Rumex crispus	0.01	Exotic
Salix* cf. *purpurea	0.01	Exotic
Sambucus sp.	0.01	
Sanguisorba minor	0.88	Exotic
Sedum acre*	8.19	Exotic
Sedum cf. *purpureum*	0.01	Exotic
Senecio obovatus	0.61	Native
Setaria viridis	0.05	Exotic
Silene vulgaris	0.1	Exotic
Sisyrinchium montanum*	0.02	Native
Solanum nigrum	0.02	Exotic
Solidago altissima	0.01	Native
Solidago canadensis*	0.29	Native
Solidago* cf. *altissima	0.29	Native
Solidago* cf. *canadensis	0.4	Native
Solidago* cf. *nemoralis	0.2	Native
Solidago cf. *ohioensis*	0.01	Native
Solidago gigantean*	0.12	Native
Solidago juncea*	0.08	Native
Solidago nemoralis*	0.11	Native
Solidago ptarmicoides*~	0.01	Native
***Solidago* sp.**	0.04	
Sonchus arvensis	0.01	Exotic
Sporobolus cryptandrus	0.03	Native
Sporobolus neglectus~	0.65	Native
Sporobolus vaginiflorus*	0.12	Native
Stellaria media	1.24	Exotic
Taraxacum officinale	0.24	Exotic
Thuja occidentalis*	0.13	Native
Triadenum fraseri	0.02	Native
Trifolium cf. *procumbens*	0.04	Exotic
Trifolium dubium	0.01	Exotic
Trifolium pratense	0.02	Exotic
Trifolium* sp.	0.06	
Typha angustifolia	0.03	Native
Verbascum thapsis~	2.37	Exotic
Vicia cracca	0.01	Exotic