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Revegetation dynamics of cliff faces in abandoned limestone quarries

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Summary

1. Revegetation dynamics on vertical cliff faces in abandoned limestone quarries were examined at 18 sites in southern Ontario, Canada.
2. A wide range of biotic and abiotic variables were measured in randomly positioned plots at each site.
3. Quarry walls ranged in age from 17 to 92 years since abandonment and this known chronosequence was used to investigate successional patterns in the vegetation.
4. Site age and the density of trees adjacent to the quarry walls had the strongest influence on vegetation community composition and abundance.
5. During the first 70 years of abandonment, species richness was high and variable. Community composition was also extremely variable during this period.
6. After 70 years, species richness on quarry walls dropped suddenly and the variation in vegetation composition was reduced.
7. This period of sudden change correlates with the growth of neighbouring trees on the quarry floor that start to shade the quarry walls at about 60 years since abandonment.
8. The final form of the vegetation community on the vertical cliffs in long-abandoned quarries is similar to the naturally occurring community on cliffs of the Niagara Escarpment.
9. The results of this study suggest that natural successional processes can be used to rehabilitate the vertical cliff faces that are produced in limestone quarry operations.
10. The benefits of allowing natural processes to rehabilitate the walls of abandoned limestone quarries are: the recruitment of an uncommon, but native component of biodiversity; a reduced initial cost; and a reduced long-term maintenance cost.
11. It is recommended that abandoned limestone quarries should not be rehabilitated by backfilling of exposed quarry walls.

Key-words: Niagara Escarpment, primary plant succession, quarry walls, vegetation chronosequence.

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Introduction

Cliff faces have long been recognized by a small number of authors as habitats that support plant and animal communities with a wide variety of fugitive or endemic species (Jackson & Sheldon 1949; Davis 1951; Maser, Rodiek & Thomas 1979). Vertical rock faces provide refuge for rare and endangered species. They facilitate the migration of less competitive relict species and are, therefore, important to the evolution of these taxa (Godwin 1956; Bunce 1968; Walker 1987). Despite this, many ecologists perceive cliffs to be dangerous habitats with an unimportant and depauperate flora. As a consequence, descriptive experimental work involving cliffs is uncommon. Recent ecological studies of the Niagara Escarpment in southern Ontario, Canada, have shown that its cliffs support the most ancient undisturbed old-growth forest in all of eastern North America. The forest is comprised of uneven-aged stunted and deformed *Thuja occidentalis* L. (eastern white cedar) trees living to 1650 years of age, as well as a predictable community of shrubs, herbs, pteridophytes, bryophytes and lichens, including many rare taxa (Larson *et al.* 1989; Larson & Kelly 1991).

Adjacent to the Niagara Escarpment is the one of the highest concentrations of limestone quarries in North America (Gorrie 1993). In many of these quarries, cliff faces resembling those of natural escarpments are created that require rehabilitation following abandonment. Current rehabilitation policies in Ontario recommend backfilling of exposed quarry walls to achieve uniform 1:2 slopes. This method of rehabilitation is practical in situations where quarry walls are extremely unstable and where overburden for backfilling is readily available, but impractical and costly where this is not the case. An alternative solution is leaving the quarry walls intact and implementing rehabilitation strategies that preserve and enhance natural cliff face features. If the aim of restoration efforts is to replicate natural cliff habitats and their associated plant communities, it is necessary to understand the process and the end products of natural colonization on quarry walls. There have been many studies of primary succession in abandoned quarries, but these have focused on the floors, spoil banks and scree slopes within them (Locket 1945; Skaller 1977; Usher 1979; Bradshaw, Marrs & Roberts 1982; Davis *et al.* 1985; Ash, Gemmell & Bradshaw 1994) rather than the vertical faces.

The approaches used to study succession in abandoned quarries have been highly variable. Dixon & Hambler (1984), Hambler & Dixon (1986) and Davis, Lakhani & Brown (1993) used permanent plots on the floors of individual quarries and monitored vegetation establishment over several years in response to various treatments. Other studies (Skaller 1977; Reinking 1979; Usher 1979) examined the revegetation of different sections of quarries which had been abandoned sequentially. The use of chronosequences for analysing primary succession in quarries has not been exploited. Chronosequences have been used widely in successional studies conducted on gravel pits (Aarssen & Epp 1990; Borgegard 1990) and glacier forelands (Matthews 1976, 1978, 1979; Matthews & Whittaker 1987). Chronosequences serve as substitutes for observations of vegetation change over time at a single site. This approach is based on the assumption that spatial variation among sites of known ages will accurately reflect temporal changes (Whittaker 1989). This assumption can be tested in comparative work by ensuring that there is replication of sites.

In this study a site-replicated chronosequence was used to: (i) determine to what degree the physical, geographical and biological characteristics of each site influence the structure and composition of species assemblages colonizing quarry walls; and (ii) ascertain whether primary plant succession on quarry walls is deterministic or stochastic.

Methods

SITE SELECTION

During the spring of 1993, 187 limestone quarry walls throughout southern Ontario were visited and their suitability for inclusion into the study was assessed based on the following criteria: (i) quarries had to be dolomitic in composition in order to provide a relatively uniform geochemical substrate for comparison in the chronosequence; (ii) the slope of all quarry faces had to be $90° \pm 5°$ to comply with the definition of a cliff habitat; (iii) age and history of each quarry wall had to be obtainable; (iv) height and length of each quarry wall needed to be large enough to accommodate 10 non-overlapping 3×3-m quadrats; (v) sites had to be free of evidence indicating severe human disturbance in order to investigate accurately successional patterns; and (vi) quarry walls had to be stable enough so as not to compromise the safety of the researchers. Of the 187 quarries assessed, only 40 were classified as suitable and 18 of these were randomly selected so as to permit geographical replication within time (quarry age) and temporal replication within space. Three age categories (1900–30, 1931–56, 1957–80) and three geographical categories using latitude (42°00′00″N–43°15′00″N, 43°15′01″N–43°32′00″N, 43°32′01″N–45°00′00″N) were generated for this purpose (Fig. 1). The resulting geographical distribution of sites is represented in Fig. 2. More detailed information on each quarry site is provided in Table 1.

VEGETATION SAMPLING

Quarry wall vegetation was sampled within ten 3×3-m plots, positioned randomly on the quarry wall. The presence of vascular plants, bryophytes and lichens was recorded for each of the nine 1×1-m subplots in each plot. Species frequency was calculated for plots based on a presence/absence basis in the subplots. Vegetation sampling was also carried out on both the quarry top and floor, but these data were intended to be treated as independent variables that might influence the recolonization of the quarry wall. The herbaceous layer on the quarry tops and floors was sampled within a single 50-m transect positioned parallel to the wall at a distance of no more than 10 m from the wall. Five 1×1-m quadrats were sampled along this transect. Each 1×1-m quadrat was divided into 25 subplots, and the presence/absence of vascular plants and bryophytes was tabulated as above to calculate percentage shoot frequency. This sampling design provided a total of five plots each for the quarry floor and quarry top. The tree and shrub canopies were sampled using a single 50×2-m belt transect parallel to the wall that was placed within 10 m of the quarry wall on both the quarry floor and top and positioned so as to include a representative sample of the adjacent vegetation. The frequency, composition and height of all tree and shrub species was then recorded for this transect. All stems greater than 1 m in height encountered along the transect were classified into one of three height categories (1–2 m, 2–3 m and >3 m). These measurements provided data on

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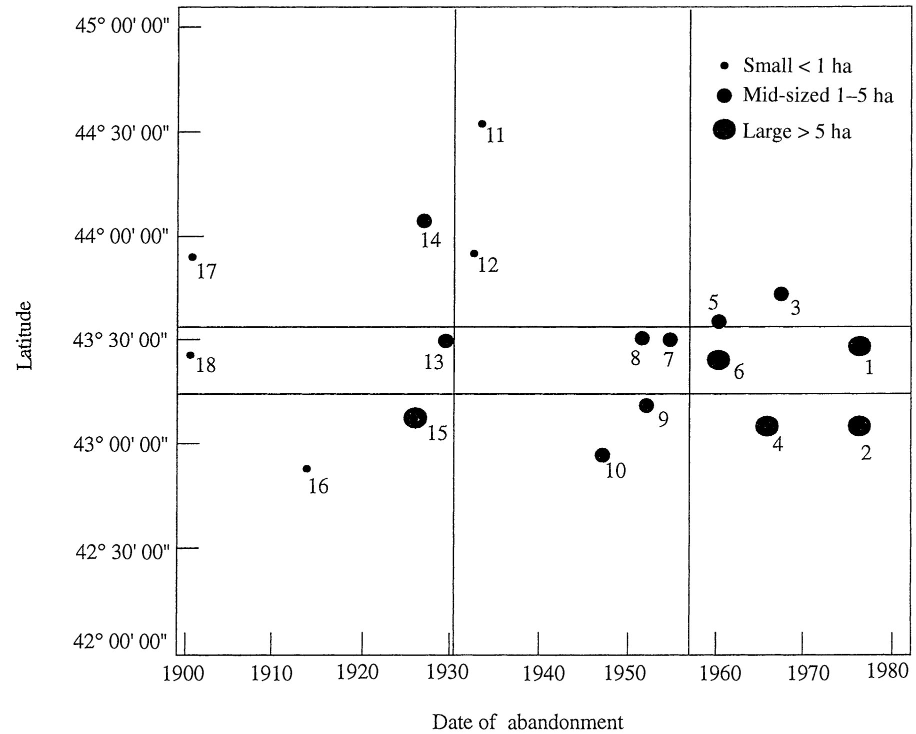


Fig. 1. Site distribution in time (date of abandonment) and space (latitude).

the extent of canopy development in the adjacent vegetation and were used as independent environmental variables in the analysis of quarry wall vegetation. Nomenclature for vascular plants followed that of Gleason & Cronquist (1963). Bryophytes followed Crum (1976), liverworts followed Shuster (1977) and lichens followed Brodo (1981). For the purposes of this study Phanerophytes and Chamaephytes were classified as trees and shrubs, while Hemicryptophytes and Cryptophytes were classified as herbs. Cryptogams were classified as bryophytes and lichens.

ENVIRONMENTAL VARIABLES

For each quarry wall the date of abandonment was determined. The precise geographical position of each site in UTM co-ordinates was obtained from Derry *et al.* & Ontario Geological Survey (1989). The size of each quarry was classified on an ordinal scale of 1–3, 1 for quarries <1 ha, 2 for quarries 1–5 ha, and 3 for quarries >5 ha. The aspect of each quarry wall plot was recorded using a compass. Substrate stability was measured qualitatively on an ordinal scale of 1–4; 1 being very stable and 4 being very unstable. Ledges were defined as horizontal protrusions from the quarry wall extending >30 cm. Ledge frequency was the percentage of subplots that had ledges. The geological formations comprising each quarry wall were also recorded.

DATA ANALYSIS

The relationship between vegetation and environment was investigated using both indirect and direct gradient analysis (*sensu* Whittaker 1956, 1967). Detrended Canonical Correspondence Analysis (DCCA) was performed on quarry wall vegetation frequency data using environmental variables collected at the plot and site levels. Detrended Correspondence Analysis (DCA) was carried out on vegetation frequency data collected from quarry walls, floors and tops only as a means of exploring general trends in vegetation both within and among sites. All analyses were performed using the program CANOCO (Ter Braak 1987).

Results

SITE CHARACTERISTICS

Dates of abandonment of the quarry sites ranged from 1901 to 1976. The greatest distance between sites was nearly 350 km (sites 16 and 14) (Fig. 2). Sites varied greatly in both depth and area. Two of the smaller older sites (17 and 18) were situated adjacent to natural escarpments and were well concealed by dense *Thuja occidentalis* forest (similar to that shown in Fig. 3a). Other sites (16, 1, 6, 15, 4, 2 and 3) were completely open and exposed with very little adjacent vegetation cover (Fig. 3b). Sites 7, 16, 1, 9 and 12 were water filled to varying degrees, and three of these (16, 1 and 9) lacked talus slopes. Sites 1 and 6 were the largest, each covering over 100 ha, while sites 11, 17 and 18 were the smallest, covering less than 1 ha. Quarry size was inversely related to site age ($r = -0{\cdot}58$ at $P < 0{\cdot}05$). Quarry walls ranged in height from 23 m at site 8 to 4 m at site 18, and had aspects of every direction. The percentage of plots

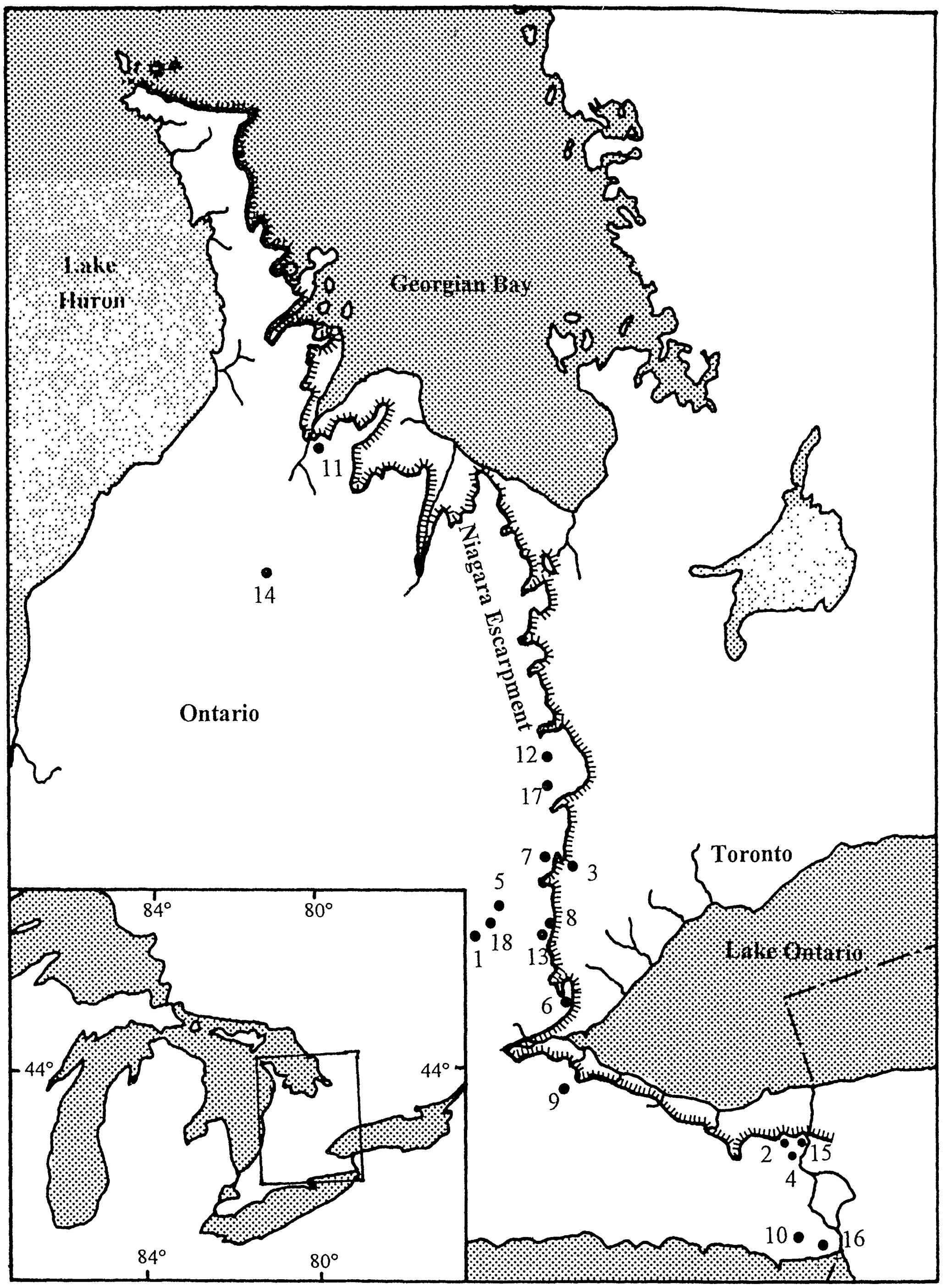


Fig. 2. Map of south-western Ontario, Canada, depicting site locations and site numbers.

facing north, east, south and west was 35, 16, 25 and 24%, respectively. The depth and location of each quarry determined which geological formation(s) were exposed. A total of 10 geological formations was encountered (Table 2). The Amabel formation and associated Guelph and Reynales formations were encountered in 60% of the study sites. Instability was related to the type of geological formation encountered at each site and the site's age. The mean instability values for quarry wall quadrats ranged from 2·8 (fairly unstable) at sites 7 and 3 to 1 (very stable) at sites 17 and 18 (Table 2). There was also an inverse linear relationship between site *age* and *instability* ($r = -0{\cdot}36$; $P < 0{\cdot}05$). Ledges occurred in 30·3% of the quarry wall plots. Sites situated on the Lockport–Rochester–Decew or Onondaga formations had relatively few ledges per face plot, 6·6% and 10%, respectively. In contrast, over 50% of the face plots taken at sites situated on either the Amherstburg or Amabel–Guelph formations contained ledges.

VEGETATION

A total of 189 vascular plants, 50 bryophyte species and 16 lichen species were recorded for plots on the

Table 1. Summary of site numbers, quarry names, locations, ages and sizes

Site no.	Quarry name	Latitude	Longitude	Abandonment date	Size*
1	Glenchristie	43°28′25″N	80°17′45″W	1976	Large
2	Queenston 3	43°09′10″N	79°04′30″W	1976	Large
3	Waters	43°41′25″N	79°58′30″W	1968	Mid
4	Queenston 2	43°09′15″N	79°04′40″W	1966	Large
5	Guelph	43°32′50″N	80°12′00″W	1961	Mid
6	Mt. Nemo	43°24′30″N	79°52′50″W	1961	Large
7	Arnold	43°31′45″N	79°58′40″W	1954	Mid
8	Milton	43°30′60″N	79°56′20″W	1952	Mid
9	Hannon	43°11′20″N	79°49′45″W	1951	Mid
10	Ridgemount	42°55′45″N	78°59′50″W	1946	Mid
11	East Rocks	44°32′58″N	80°55′35″W	1933	Small
12	Teen Ranch	43°53′55″N	80°03′45″W	1931	Small
13	Kelso	43°30′00″N	79°56′50″W	1930	Mid
14	Formosa	44°06′20″N	81°12′45″W	1928	Mid
15	Queenston 1	43°09′25″N	79°04′50″W	1926	Large
16	Bertie Bay	42°53′20″N	78°59′55″W	1916	Small
17	Safari	43°52′20″N	80°03′25″W	1901	Small
18	Thompson	43°29′25″N	80°16′10″W	1901	Small

* Small = <1 ha, Mid-sized = 1–5 ha, Large = >5 ha.

quarry top, wall and floor. Quarry wall quadrats ($n = 180$) contained 109 vascular plants, 32 bryophyte species and 16 lichen species. The number of species encountered on the quarry wall varied from 10 at site 12 to 51 at site 14. Quarry floor quadrats ($n = 87$) contained 147 vascular plants and 18 bryophyte species, while quarry top quadrats ($n = 102$) contained 160 vascular plants and 24 bryophyte species. The proportion of native to exotic vascular plant species from all sites was 60:40. Vegetation adjacent to the quarry walls was extremely variable. Sites 7, 16, 1, 9, 4, 12 and 3 had varying degrees of water present on the quarry floor which either excluded floor vegetation altogether or provided habitat for species with wetland affinities, such as *Typha latifolia*, *Carex aurea*, *C. flava*, *C. hystericina*, *C. rosea* and *Eleocharis erythropoda*. Sites that experienced higher levels of disturbance (1, 5, 6, 15, 4, 2 and 10) often had large expanses of exposed bedrock on both the quarry floor and top and contained species such as *Cornus stolonifera*, *Populus balsamifera*, *Rhamnus cathartica*, *Plantago major*, *P. lanceolata*, *Daucus carota*, *Chrysanthemum leucanthemum*, *Hieracium* spp., *Melilotus alba* and *Agrostis stolonifera*. Other smaller sites (11, 14, 8, 13, 17, 12 and 18) that were relatively undisturbed contained dense stands of forest adjacent to the quarry wall containing *Thuja occidentalis*, *Cystopteris bulbifera*, *Geranium robertianum* and numerous bryophytes.

VEGETATION-ENVIRONMENT RELATIONSHIPS ON QUARRY WALLS

Latitude

Changes in species composition and life-form richness occurred over the latitude gradient (Table 3). Higher numbers of lichen and bryophyte species were recorded on quarry walls among the northern sites, while fewer tree and shrub species were recorded from walls at southern sites. Herbaceous species richness on walls at northern and central regions dropped considerably with quarry age from 33 and 34 species at mid-aged sites to 20 and 28 species at older sites, while among southern sites, richness increased from 32 to 37 species over the same time range. In addition to these trends, tree canopy densities on the quarry floor were highly correlated with latitude. Regression of *F3+* and *F2–3* with latitude yielded an $r = 0{\cdot}59$ and $r = 0{\cdot}51$ at $P < 0{\cdot}05$, respectively.

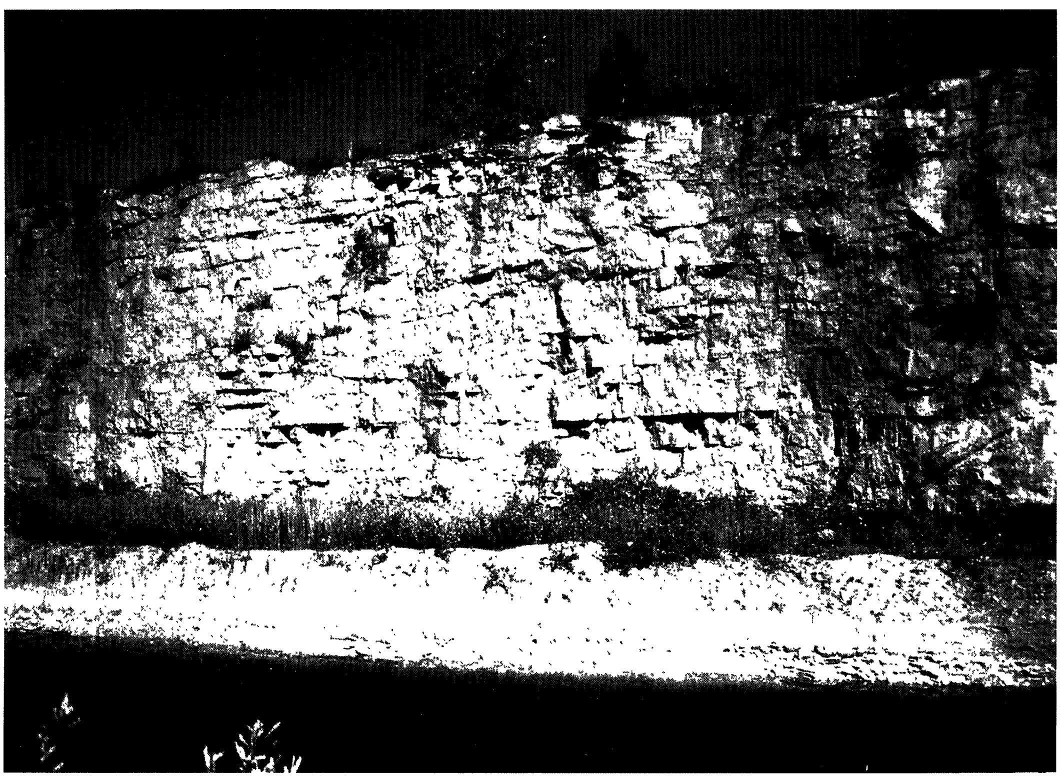
Aspect

The aspect of each quarry wall influenced species richness and composition. According to the Mann–Whitney Rank Sum test, richness values for quarry walls with southern exposures differed significantly from those with northern exposures. South-facing cliffs supported 13 species on average, while north-facing slopes supported 10 species ($P < 0{\cdot}05$). Quadrats with north-facing aspects contained 30% less herbaceous species, 10% more bryophytes, 12% more lichens and 4% more trees and shrubs.

Ledges

The presence of ledges increased species richness significantly according to the *t*-test. Quarry wall plots without ledges supported a mean of $11{\cdot}8 \pm 6{\cdot}1$ species while plots with ledges supported $13{\cdot}7 \pm 6{\cdot}6$ species ($P < 0{\cdot}05$). Almost all (94·5%) of the species found on ledges occurred with higher frequencies than their counterparts found in crevices and on the wall. Quadrats without ledges contained 10% less herbaceous

(a)



(b)

Fig. 3. (a) Photograph of the quarry wall abandoned in 1931 at site 12, now densely concealed by *Thuja occidentalis*. (b) Photograph of a younger quarry wall abandoned in 1961 at site 6, with little adjacent vegetation cover.

species and 10% more bryophyte species than quadrats with ledges.

Substrate instability

The instability of quarry walls influenced both the abundance and composition of colonizing species, but was also inversely related to age. *Thuja occidentalis* declined from being the sixth most abundant species on stable quarry walls to the tenth most abundant on unstable walls. Some lichen species such as *Lepraria lobificans*, *Verrucaria nigrescentoides*, *Cladonia cariosa*, *Caloplaca citrina*, *Caloplaca inconnexa* and *Candelariella aurella* all had relatively high abundance

Table 2. Summary of environmental variables measured, their means, standard deviations, minimum and maximum values

Environmental variable	Abbr.	Units of measure	Mean	S.D.	Min.	Max.
Quarry age	Age	years	52·2	22·5	18	95
Quarry size	Size	1 = small 2 = midsize 3 = large	2·16	0·73	1	3
Latitude	Latitude	UTM Northings	4818113	45669·1	4750200	4935600
Distance from Niagara Escarpment	DFE	Kilometers	9·64	12·5	0	45
Quarry face stability	Instability	1 = stable 2 = fairly stable 3 = fairly unstable 4 = unstable	1·83	0·77	1	4
Floor vegetation > 3 m in height	F3+	# of stems/100 m²	20·53	25·82	0	93
Floor vegetation 2–3 m in height	F2–3	# of stems/100 m²	8·67	8·72	0	26
Floor vegetation 1–2 m in height	F2–3	# of stems/100 m²	25·14	25·06	0	82
Top vegetation > 3 m in height	T3+	# of stems/100 m²	26·67	22·34	0	72
Top vegetation 2–3 m in height	T2–3	# of stems/100 m²	12·2	11	0	40
Top vegetation 1–2 m in height	T1–2	# of stems/100 m²	57·5	51	0	194
Presence of ledges	Ledges	Frequency of occurrence	0·33	0·47	0	1
Southern aspect	S	# of plots within 135°–225°	0·25	0·43	0	1
Northern aspect	N	# of plots within 226°–315°	0·35	0·48	0	1
Eastern aspect	E	# of plots within 316°–45°	0·16	0·36	0	1
Western aspect	W	# of plots within 46°–134°	0·24	0·49	0	1
Geological formations						
Amabel	AMA	Presence at a site	0·29	0·45	0	1
Onondaga	ONON	Presence at a site	0·07	0·26	0	1
Amherstburg	AMHER	Presence at a site	0·14	0·34	0	1
Lockport	LOCK	Presence at a site	0·05	0·22	0	1
Amabel-Reynales	AMA-REY	Presence at a site	0·14	0·35	0	1
Bertie-Bois Blanc	BER-BOI	Presence at a site	0·04	0·2	0	1
Amabel-Guelph	AMA-GUE	Presence at a site	0·12	0·34	0	1
Lockport-Rochester-Decew	LO-RO-DE	Presence at a site	0·13	0·47	0	1

Table 3. Number of species/life-forms found on quarry walls at 18 sites classified according to site age and latitude

Date of abandonment	1952–75			1930–51			1900–29		
Latitude	South	Central	North	South	Central	North	South	Central	North
Trees and shrubs	6	15	12	11	14	14	8	11	10
Herbs	24	33	32	32	33	34	37	20	28
Bryophytes	0	4	7	10	6	12	1	10	12
Lichens	4	1	5	3	2	6	5	4	9

Latitude for south, central and north represented in UTM northings 4700000–4782050, 4782060–4833700 and 4833710–4950000, respectively.

on stable walls, but vanished altogether on the most unstable walls. Similarly, several of the most common bryophytes (*Amblystegium varium*, *Mnium cuspidatum*, *Campylium radicale*, *Brachythecium velutinum*) and liverworts (*Jungermannia* sp., *Marchantia polymorpha*) decreased in abundance with increased instability until they were excluded. There were numerous species replacements which occurred among the bryophytes. Species such as *Bryum caespiticium*, *B. algovicium*, *Plagiothecium laetum* and *Grimmia alpicola* actually increased in abundance with an increase in substrate instability, but were absent from the most

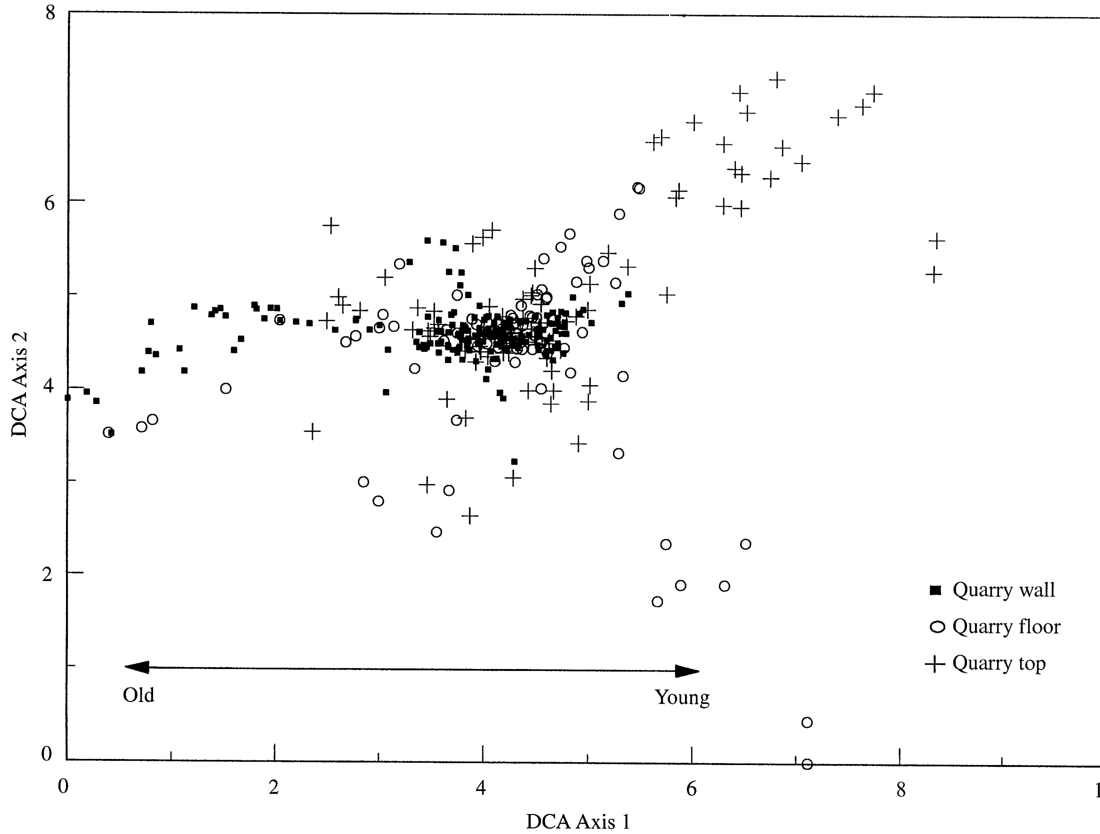


Fig. 4. DCA ordination of all quadrats from the complete data set depicting axes 1 and 2 ($\lambda_1 = 0{\cdot}737$, $\lambda_2 = 0{\cdot}277$ respectively). Arrow indicates relative quarry age.

unstable surfaces. However, the majority of common ruderal herbaceous species were not influenced by instability.

MULTIVARIATE ANALYSES

In order to provide background data on large-scale structural variance in the vegetation composition for the entire quarry, the vegetation composition of quarry walls, floor and top quadrats combined was analysed among all sites using DCA. Eigenvalues for the first four DCA axes were 0·737, 0·277, 0·208 and 0·171, respectively. In the DCA ordination of quadrats (Fig. 4), points representing quarry wall quadrats are much more concentrated than quarry floor and top quadrats, indicating that quarry walls share a similar species composition and structure. The distribution of points representing quarry wall, floor and top quadrats reveals convergence between walls and their surrounding vegetation during succession. This is demonstrated in Fig. 4 where the age axis parallels axis 1 increasing from right to left.

The concentrated and convergent distribution of points representing quarry wall quadrats justified an exclusive examination of wall data using ordination. The DCCA ordination of the quarry wall data set yielded eigenvalues of 0·634, 0·448, 0·251 and 0·145 for the first four axes, respectively. The environmental variables which explained most of the variation in species scores along the first DCCA axis were age and *F3+* with canonical correlation coefficients of 0·638 and 0·604, respectively (Table 4). The right side of the ordination diagram (Fig. 5a) depicts species associated with oldest quarry sites along the age gradient. Species that are found in this section of the diagram include *Mnium cuspidatum*, *Amblystegium varium*, *Brachythecium velutinum*, *Marchantia polymorpha*, *Jungermannia* spp., *Lepraria lobificans*, *Cladonia cariosa*, *Thuja occidentalis* and *Cystopteris bulbifera*. Along the second DCCA axis, the variables *T2–3* and latitude explained most of the variation in species scores with correlation coefficients of −0·759 and 0·482, respectively. Species found near the bottom of the DCCA biplot included mainly bryophytes and lichens present at northern sites with fairly dense tree canopies in their surroundings. In contrast, species present at the top of the ordination diagram such as *Sedum acre*, *Bidens vulgata* and *Asclepias syriaca* characterize more open sites with increased light availability. In the DCCA ordination of sites (Fig. 5b), the oldest sites (15, 16, 17 and 18) are positioned to the upper and right side of the diagram. These sites are characterized by a dense *Thuja occidentalis* canopy in the adjacent vegetation on the quarry floors. The remaining younger and mid-aged sites form a tighter cluster near the centre of the ordination.

Table 4. DCCA inter-set correlations of environmental variables for axes 1–4

Variable	Axis 1	Variable	Axis 2	Variable	Axis 3	Variable	Axis 4
AGE	**0·638**	S	**0·487**	T1–2	**0·383**	Instability	**0·209**
F3+	**0·604**	E	0·047	T3+	**0·339**	DFE	0·07
T3+	**0·336**	Age	−0·002	F2–3	**0·165**	T3+	0·054
N	**0·296**	Ledges	**−0·184**	Size	**0·159**	N	0·023
Latitude	**0·177**	Instability	**−0·201**	N	0·104	Age	−0·02
DFE	0·104	Size	**−0·226**	S	0·043	S	−0·049
Ledges	0·091	T1–2	**−0·382**	F3+	0·027	T1–2	−0·063
F2–3	−0·074	F3+	**−0·417**	E	0·022	Ledges	−0·104
E	−0·086	N	**−0·433**	T2–3	0·005	E	−0·132
T2–3	−0·093	F1–2	**−0·437**	F1–2	0·003	Size	−0·141
S	−0·21	F2–3	**−0·443**	Age	−0·001	Latitude	**−0·187**
F1–2	**−0·218**	DFE	**−0·468**	DFE	−0·003	T2–3	**−0·191**
T1–2	**−0·27**	T3+	**−0·482**	Ledges	−0·049	F3+	**−0·193**
Instability	**−0·334**	Latitude	**−0·575**	Instability	−0·109	F2–3	**−0·219**
Size	**−0·45**	T2–3	**−0·759**	Latitude	**−0·436**	F1–2	**−0·434**

Values in bold represent correlation coefficients which are significantly correlated with a particular axis at $\alpha < 0{\cdot}05$.

SPECIES RICHNESS AND ABUNDANCE OVER TIME

Species richness and trends in community composition show that, during a long period of time from initial abandonment to 70 years, richness remains high and relatively constant, but then decreases rapidly, and that community composition changes from shorter lived ruderal species to longer lived stress-tolerators. Recently abandoned quarry walls (1957–80) had a mean of 33 species, which increased to 40 species for mid-aged sites (1931–56), and finally decreased to 28 species for older sites (1900–30) (Fig. 6). The two oldest sites in the chronosequence contained 10 and 12 species, respectively. Initially, these two points were considered anomalies so several other similar aged quarries were inventoried, and found to contain 10 and 13 species, thus verifying the trend. At 16 of the 18 sites, bryophytes were the most abundant life form on the quarry wall, followed by vascular plants then lichens (Fig. 7).

INDIVIDUAL SPECIES RESPONSES TO SITE AGE

When the response of four of the most common species occurring on quarry walls was plotted against site age some interesting trends are revealed. Ruderals such as *Chrysanthemum leucanthemum* and *Daucus carota* had high initial frequency values at young to mid-aged sites, but decreased at older sites where they were often absent (Figs 8a,b). Other plants, such as *Cystopteris bulbifera* and *Thuja occidentalis*, were either absent or appeared with low frequencies at young to mid-aged sites then increased in frequency rapidly at older sites (Figs 8c,d).

Discussion

THE REVEGETATION SEQUENCE AND TIME

The abandonment of limestone quarry walls in southern Ontario, Canada, is followed by a sequence of invasions and extinctions to produce a community that is floristically diverse and highly variable in composition early in development, but more simplified and less variable in composition later on. The late stages of development are similar in composition to natural escarpments in the region (Larson *et al.* 1989). Site age by itself or together with the development of a dense tree canopy on the quarry floor (*F3+*) are the most important factors influencing species assemblages on quarry walls. Additional environmental variables, such as quarry size and substrate instability, were less important when treated as independent variables, but these two characteristics were also correlated with site age, presumably because modern quarry operations result in larger more unstable walls. Community composition and the abundances of individual taxa change over the 100-year chronosequence in a manner that is initially stochastic, but more deterministic later on. The results here show that most of the species that dominate the mature quarry walls were also present on walls as young as 25 years post-abandonment. These results do not strongly support the concept of relay floristics (*sensu* Egler 1954).

The mechanisms responsible for this transition in community structure over time were shown to be partly autogenic and partly allogenic. Changes in species abundances over time, as well as the change in canopy cover by trees growing on the quarry floors represent autogenic factors, while the increase in substrate stability over time may represent an example of an allogenic process. Traditional successional patterns have been attributed mainly to a sequence of autogenic processes (e.g. Drury & Nisbet 1973; Bazzaz 1979; Noble & Slatyer 1980; Christensen & Peet 1981; Huston & Smith 1987); however, the role of allogenic processes in explaining succession is being increasingly invoked, as in the geo-ecological approach (e.g. Matthews 1978; Matthews & Whittaker 1987; Whittaker 1989; Whittaker 1991). Obtaining a more comprehensive understanding of the processes driving succession requires an integrated approach, which examines both temporal and spatial variation (Matthews 1992). In this study, the intentional replication of sites across a two axis gradient of time and space permitted an examination of the effects of age, latitude and other variables within a context of real and often important background environmental variables.

THE REVEGETATION SEQUENCE AND OTHER ENVIRONMENTAL VARIABLES

The latitude gradient was strongly correlated with the second DCCA axis. Species such as *Asplenium trichomanes*, *Pellaea glabella*, *Cystopteris fragilis* and *Caloplaca citrina* were common on quarry walls at northern sites, but absent in the southern sites. Conversely, species such as *Acer negundo*, *Ulmus americana*, *Ambrosia artemisiifolia*, *Aster ericoides* and *Sedum acre* were exclusive to southern sites. Quarry sites in the northern region appeared to develop an adjacent forest cover on the floor and top more rapidly than sites in the south.

Langenheim (1956) demonstrated that the stability of steep slopes is important in determining species composition on earth-flows in Colorado. Species abili-

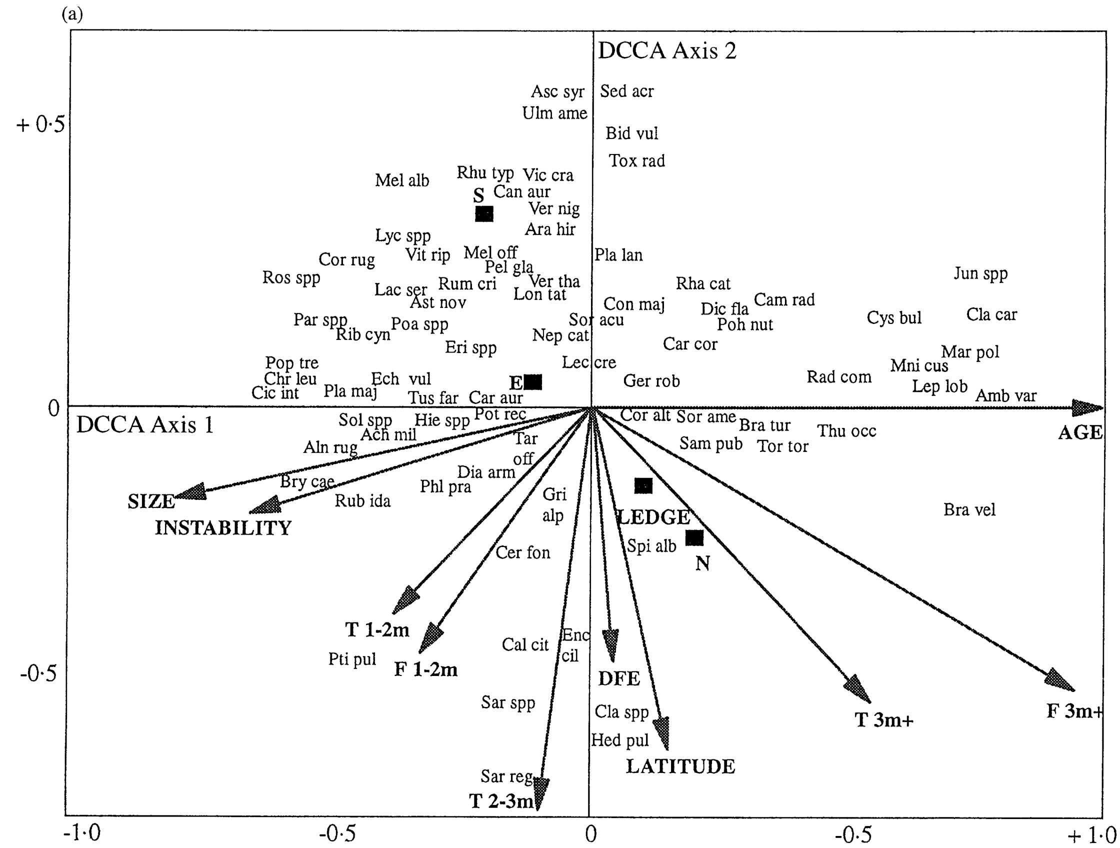


Fig. 5. (a) DCCA ordination of quarry wall species and environmental variables for axes 1 and 2. $\lambda_1 = 0{\cdot}634$ $\lambda_2 = 0{\cdot}448$. Ach mil = *Achillea millefolium*; Aln rug = *Alnus rugosa*; Amb art = *Ambrosia artemisiifolia*; Ara hir = *Arabis hirsuta*; Asc syr = *Asclepias syriaca*; Ast nov = *Aster novae-angliae*; Bid vul = *Bidens vulgata*; Bra tur = *Brachythecium turgidum*; Bra vel = *Brachythecium velutinum*; Bry cae = *Bryum caespiticium*; Cal cit = *Caloplaca citrina*; Cam rad = *Campylium radicle*; Can aur = *Candelariella aurella*; Car aur = *Carex aurea*; Car cor = *Carya cordiformis*; Cer fon = *Cerastium fontanum*; Chr leu = *Chrysanthemum leucanthemum*; Cic int = *Cichorium intybus*; Cla car = *Cladonia cariosa*; Cla spp. = *Cladonia* spp.; Con maj = *Conallaria majalis*; Cor alt = *Cornus alternifolia*; Cor rug = *Cornus rugosa*; Cys bul = *Cystopteris bulbifera*; Dia arm = *Dianthus armeria*; Dic fla = *Dicranum flagellare*; Ech vul = *Echium vulgare*; Enc cil = *Encalypta ciliata*; Eri spp. = *Erigeron* spp.; Ger rob = *Geranium robertianum*; Gri alp = *Gimmia alpicola*; Hed pul = *Hedeoma pulegoides*; Hie spp. = *Hieracium* spp.; Jun spp. = *Jungermannia* spp.; Lac ser = *Lactuca serriola*; Lec cre = *Lecanora crenulata*; Lep lob = *Lepraria lobificans*; Lon tar = *Lonicera tatarica*; Lyc spp. = *Lycopus* spp.; Mar pol = *Marchantia polymorpha*; Mel alb = *Melilotus alba*; Mel off = *Melilotus officinalis*; Mni cus = *Mnium cuspidatum*; Nep cat = *Nepeta cataria*; Par spp. = *Pathenocissus* spp.; Pel gla = *Pellaea glabella*; Phe pra = *Phleum pratense*; Pla lan = *Plantago lanceolata*; Pla maj = *Plantago major*; Poa spp. = *Poa* spp.; Poh nut = *Pohlia nutans*; Pop tre = *Populus tremuloides*; Pot rec = *Potentilla recta*; Pti pul = *Ptilidium pulcherrima*; Rad com = *Radula complanata*; Rha cat = *Rhamnus cathartica*; Rhu typ = *Rhus typhina*; Rib cyn = *Ribes cynosbati*; Ros spp. = *Rosa* spp.; Rub ida = *Rubus idaeus*; Rum cri = *Rumex crispus*; Sam pub = *Sambucus pubens*; Sar reg = *Sarcogyne regularis*; Sar spp. = *Sarcogyne* spp.; Sed acr = *Sedum acre*; Sol spp. = *Solidago* spp.; Sor acu = *Sorbus aucuparia*; Spi alb = *Spiriaea alba*; Tar off = *Taraxacum officinale*; Thu occ = *Thuja occidentalis*; Tor tor = *Tortella tortuosa*; Tox rad = *Toxicodendron radicans*; Tus far = *Tussilago farfara*; Ulm ame = *Ulmus americana*; Ver tha = *Vebascum thapsus*; Ver nig = *Verrucaria nigrescentoidea*; Vic cra = *Vicia cracca*; Vit rip = *Vitis riparia*; (b) DCCA ordination of quarry wall quadrats for axes 1 and 2. $\lambda_1 = 0{\cdot}634$ ($\lambda_2 = 0{\cdot}448$. Individual quadrats are depicted by + symbols, centroids are shown with large symbols. All site quadrats are enclosed in individual polygons with corresponding site numbers.

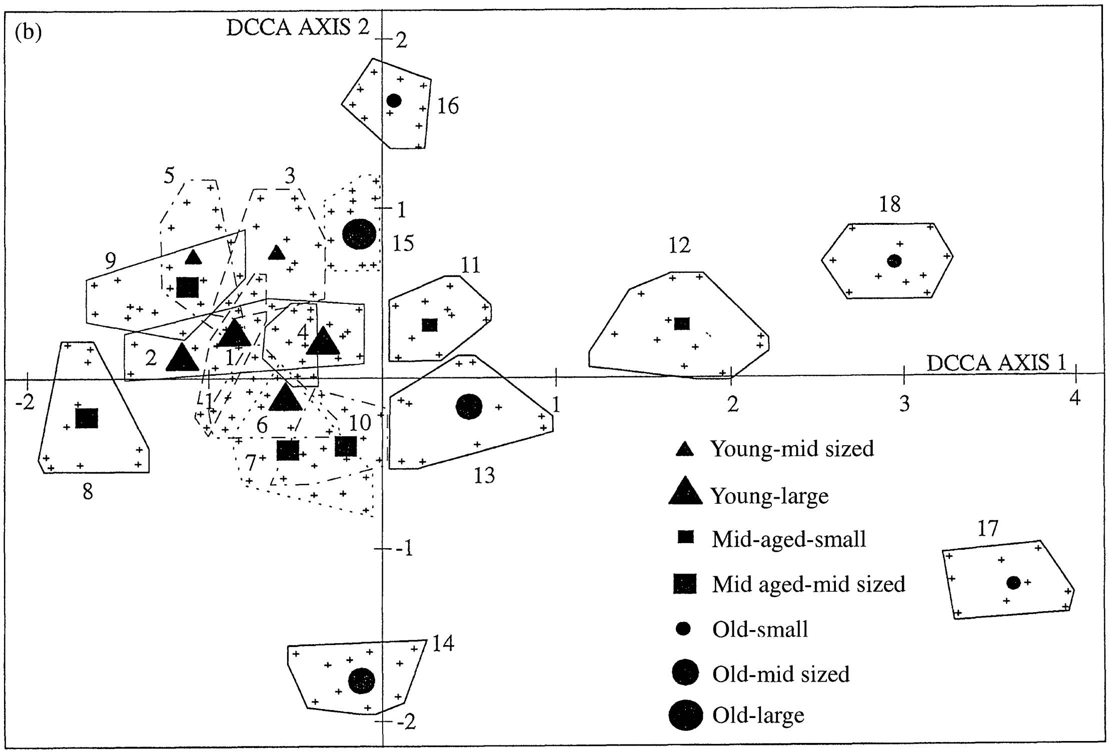


Fig. 5. *Continued.*

ties to become established on steep and unstable surfaces of varying exposures can determine which species are classified as pioneers (Greller 1974). In this study, the majority of shorter-lived annuals and perennials (ruderals *sensu* Grime 1979), such as *Chrysanthemum leucanthemum*, *Daucus carota*, *Taraxacum officinale*, *Melilotus alba*, *Poa* sp. and *Solidago* sp., are capable of reaching maturity on the most unstable quarry walls. Longer lived species (stress tolerators *sensu* Grime 1979), including the tree *Thuja occidentalis*, shrubs *Cornus stolonifera*, *Prunus virginanna*, and numerous bryophytes and lichen species, can only become established on stable walls.

Ledge frequency has been shown to be extremely important in controlling which species become established on cliff faces (Davis 1951; Bunce 1968). Ledges introduce a horizontal component to cliff faces, thus facilitating plant colonization. Bunce (1968), studying

Fig. 6. Quarry wall species richness plotted against site age for the 18 sites.

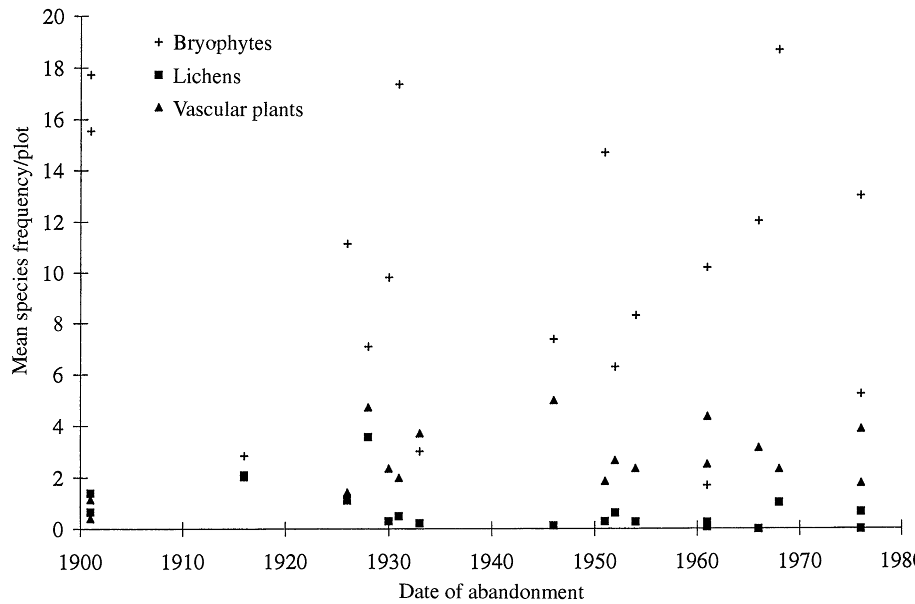


Fig. 7. Quarry wall species abundances by life-form (mean species frequency/plot) plotted against site age for 18 sites.

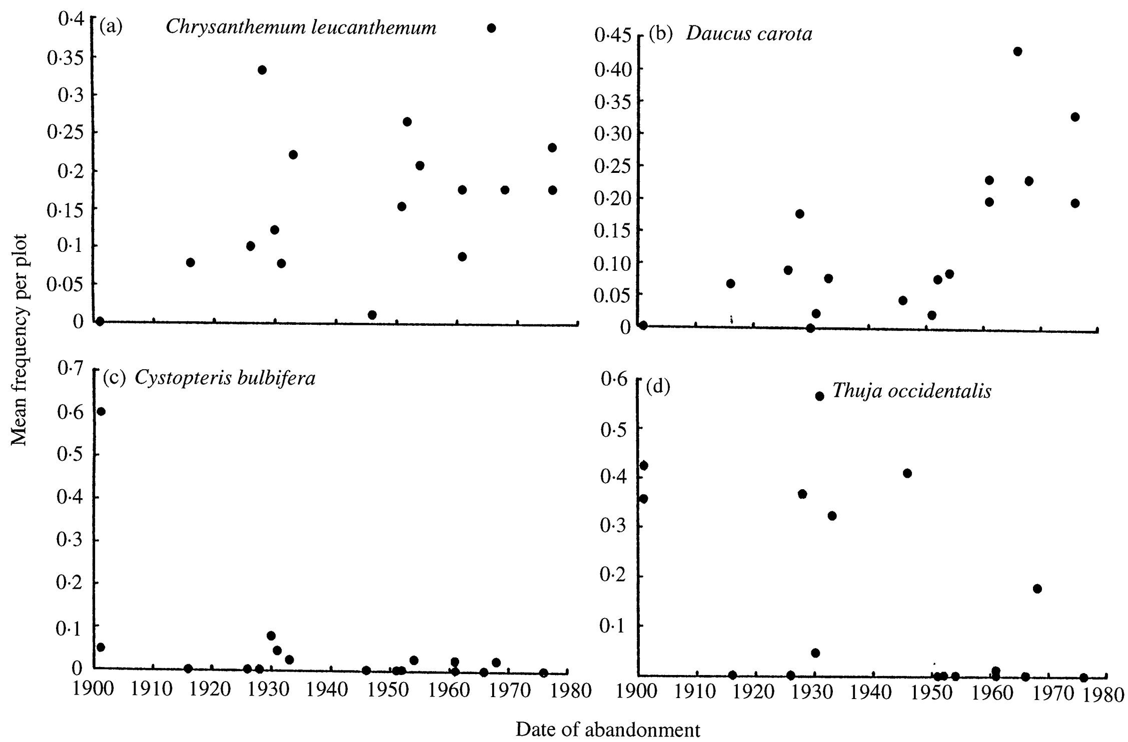


Fig. 8. Abundance (mean species frequency/plot) of four species on the quarry wall plotted against site age for 18 sites. (a) *Chrsanthemum leucanthemum*, (b) *Daucus carota*, (c) *Cystopteris bulbifera*, (d) *Thuja occidentalis*.

vegetation on mountain cliffs in Snowdonia, Wales, concluded that succession on cliff faces was accelerated by ledges, since they aided in the accumulation of organic and mineral debris. Compared to crevices, fissures, rock face and lips, ledges on cliffs contain a greater abundance of species. Bunce (1968) noted that ledges colonized by *Dryopteris filix-mas* effectively excluded colonization by other species. In this study, the abundance of all taxa found on ledges was higher than on the face and in crevices. Species compositions also differed between quadrats with and without ledges.

The effect of aspect on cliff vegetation has never been investigated quantitatively. Rishbeth (1948) made qualitative observations of vegetation on the walls of Cambridge University and found species composition to differ markedly between moister west-facing walls and drier east-facing walls. Davis (1951) examined limestone cliff vegetation around the Mediterranean and identified several distinct plant communities, with particular affinities for either north- or south-facing cliffs. Aspect is directly related to temperature, moisture and light availability. In this study, species with affinities for warmer, drier, well illuminated habitats (*Melilotus officinalis*, *Rumex crispus*, *Candelariella aurella*, *Verrucaria nigrescentoides*) were found only in quadrats with southern exposures, while species with affinities for mesic, cooler, shaded habitats (*Geranium robertianum*, *Bryum algovicum*, *Platydictya subtile*) were found only in quadrats with northern exposures.

DYNAMIC ASPECTS OF THE REVEGETATION SEQUENCE

The successional pattern presented here corresponds with Bradshaw's description of colonization on derelict or degraded lands (Bradshaw 1983; Table 1), and also agrees with the predictions of Grime's (1979) C-S-R model of succession for sites with conditions of low productivity. During early to mid stages of succession on quarry walls (20–55 years), species compositions are highly variable both within and between sites. The vegetation is dominated by weedy ruderals (*sensu* Grime 1979) capable of very long-distance dispersal. Species composition and abundance among younger quarries are highly variable. During the intermediate to later stages, species richness first increases slightly then decreases as convergence occurs. The resulting community is more predictable in composition and abundance, but still shows abundant unoccupied space in agreement with the final stage predicted by Bradshaw (1983). Growth rates are also exceptionally slow for the *Thuja occidentalis* that occur on the cliffs: radial increments with average values as low as 0·37 mm/year have been reported by Matthes-Sears & Larson (1995) for trees sampled at site 5, and these values are similar to those that have been obtained for the forested cliff faces of the Niagara Escarpment (Kelly, Cook & Larson 1992). Trees which have become established on the quarry floor and top begin to shade and shelter the quarry wall. The development of a dense tree canopy facilitates (*sensu* Connell & Slatyer 1977) the establishment of longer lived stress-tolerators (*sensu* Grime 1979), such as *Thuja occidentalis*, *Cystopteris bulbifera*, *Lepraria lobificans*, *Cladonia cariosa*, *Marchantia polymorpha*, *Mnium cuspidatum*, *Tortella tortuosa*, *Geranium robertianum* and *Amblystegium varium*. Although the processes outlined by Bradshaw were not investigated here, the results were similar. After ≈65 years of stochastic processes influencing plant colonization, the more deterministic processes of increasing tree heights and densities on the quarry floor facilitate the establishment of a distinct flora. The absence of suitable quarry sites older than 100 years in southern Ontario precludes the possibility of examining longer term successional sequences, but since the same species assemblages are found consistently on the cliff faces of natural limestone escarpments in the region it is quite possible that plant communities of the oldest quarry walls already represent the development of an endpoint or 'climax' community (*sensu* Clements 1916). Given time and the appropriate conditions, a flora similar in structure and composition to that of the ancient forests of the Niagara Escarpment may become established on abandoned limestone quarry walls.

There are three implications of these results for the management and restoration of vertical rock faces in abandoned limestone quarries. First, unlike the vegetation communities that result from rehabilitation strategies involving backfilling, the community that results from natural recolonization is sufficiently similar to natural escarpments to suggest that quarry walls will support stable assemblages of native species, that will not require future maintenance. Secondly, as long as the 100-year time-frame for recolonization is considered acceptable, no monetary expenses are incurred during the rehabilitation process. In contrast, the cost of backfilling exposed quarry walls and landscaping slopes can be substantial. Thirdly, it may be possible to accelerate succession on quarry walls by direct planting, or by the creation of suitable tree canopies on quarry floors and tops. These plantings will shade the wall and facilitate the recruitment of stress tolerators found later in the natural successional sequence.

It is recommended that the rehabilitation practice of backfilling exposed cliff faces in abandoned limestone quarries be reconsidered in favour of the more effective and less expensive alternative suggested by the above results.

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