

PLANT COMMUNITY DEVELOPMENT IN AN ABANDONED LIMESTONE QUARRY; A DEMOGRAPHIC ASSESSMENT

Kenneth M. Klemow
Department of Biology
Wilkes College
Wilkes-Barre, Pennsylvania 18766, U.S.A.

ABSTRACT

Colonization of plants in an abandoned limestone quarry near Syracuse, New York has proceeded slowly since the site was mined 50 years ago. To understand plant community development in the quarry, populations of four dominant monocarpic species (*Erucastrum gallicum*, *Melilotus alba*, *Picris hieracioides* and *Echium vulgare*) were intensively monitored from 1976 to 1981 on two sites that differed in density and substrate character: the sparse and dense sites. Measurements of substrate properties on each site and rainfall were also made and related to population performance. Densities of all species fluctuated during each year due to episodes of seedling recruitment followed by heavy mortality that appeared to primarily result from desiccation. Densities also varied between years, apparently due to variability in rainfall. Densities of *P. hieracioides* declined during the study whereas those of *E. vulgare* increased. No overall trend was observed in the other species. Annual fluctuations in density were consistently less pronounced on the dense site, apparently due to ameliorating influences of both vegetation and substrate. Community development in the quarry appears to be temporally erratic, depending upon variability in rainfall and its influence on the individual species.

1. INTRODUCTION

Humans use large amounts of metals and minerals that are extracted from the earth. One extraction method is surface mining, in which a layer of overlying material and, subsequently the desired commodity, is removed by an open excavation. Surface mining causes localized but severe disturbance to plant and animal communities because both the vegetation and topsoil are completely removed. New vegetation must colonize a substrate that is physically and chemically stressful.

Ecological studies of surface-mined sites have typically focused on the manipulation of the substrate and vegetation for reclamation [1-4]. Natural colonization and community development has been studied less often on strip-mined sites. Because of economic and social considerations, most studies of natural revegetation have been made on areas that were mined for coal and metallic ores [5-8]. Conversely, natural revegetation in abandoned limestone quarries has received little attention until recently [9-10]. Much remains to be learned about colonization and community development in surface-mined sites,

particularly in limestone quarries. Such studies could yield new insights into cost-efficient ways of reclaiming surface-mined sites.

To fully evaluate the distribution and abundance of plants and to determine the forces that lead to vegetation change, it is necessary to examine population-level (demographic) attributes of the plant species [11]. Several demographic studies of plant species colonizing mined sites have been conducted, mostly within the past 15 years [12-16]. However, each of those studies have focused on a single species and have been of 1 or 2 year duration. To best understand community development and to pinpoint the factors that inhibit succession on mined sites, a multi-year approach incorporating concurrent demographic analyses of several species is needed.

To that end, a 5-year study was conducted in an abandoned limestone quarry near Syracuse, New York. Revegetation has proceeded slowly since the site was mined in the 1920's. The quarry substrate is rocky, calcareous, infertile and excessively drained [13, 17-18]. The purposes of this study were: (1) to investigate community development in the quarry by evaluating the demography of the component species, and (2) to pinpoint those factors that have inhibited succession by relating demography to edaphic and micrometeorological conditions.

2. THE STUDY SITE

The study was conducted in the Jamesville Limestone Quarry operated by the Allied Corporation. The quarry is located 9 km southeast of Syracuse, New York (43°00'N, 76°09'W) along a band of Devonian limestone that runs between Albany and Buffalo in upstate New York. Surface mining for carbonate rock began in the 1890's and continues today. Land holdings of the quarry consist of about 1200 ha, of which 650 ha have been disturbed by mining or dumping. This study was made in a 7.9 ha section of the quarry that was mined during the 1920's and subsequently abandoned. The mining process removed the original beech-maple-hemlock forest, the soil and 5-10 m of bedrock. The substrate that remains is composed of calcareous rocks, stone-sized fragments and fine material. The substrate also contains varying amounts of cinder from coal-burning locomotives involved in the mining process.

Natural revegetation has proceeded slowly in the 50 years following abandonment. The plant community contains a mixture of herbs, shrubs, vines and stunted trees. The dominant herbs include Melilotus alba Desr., Picris hieracioides L., Hieracium florentinum All., Erucastrum gallicum (Willd.) O.E. Schulz, Asclepias tuberosa L., Echium vulgare L., and Hypericum perforatum L. (nomenclature follows [19]). Woody plants include Rhus typhina L., Vitis riparia Michx., Lonicera tatarica L., Prunus virginiana L., Populus tremuloides Michx., and Rubus sp., among others. The plant community exhibits marked patterning in both species composition and cover due to microtopographic heterogeneity [13].

To determine how substrate conditions and the density of the surrounding vegetation affect community development, vegetation was sampled on two sites that were separated by about 40 m. These sites, named the sparse and dense sites, each measured approximately 5 x 20 m. Species composition was similar on the two sites, but the density of most species was greater on the dense site (Table 1). Likewise, in mid-June 1976, percent cover was 41% and 8% on the dense and sparse sites, respectively [20].

The substrate on both sites was rocky as fine material (<0.2 cm diameter) accounted for only about 22% of the weight of the substrate (Table 2). About

Table 1. Densities (m^{-2}) of plants on the sparse and dense sites, Jamesville Quarry, Syracuse, New York, on 26 May 1976. Symbols for life histories are: A = annual, B = biennial, P = perennial.

Technical name	Common name	Life History	Sparse site	Dense site
<u>Erucastrum gallicum</u>	french rocket	A	49.3	3.4
<u>Silene cserei</u>	catchfly	A	3.4	0.0
<u>Melilotus alba</u>	white sweet clover	B	61.9	464.6
<u>Picris hieracioides</u>	bitterweed	B	56.0	477.2
<u>Daucus carota</u>	Queen Anne's lace	B	6.3	54.3
<u>Echium vulgare</u>	viper's bugloss	B	1.3	49.7
<u>Hypericum perforatum</u>	St. Johnswort	P	20.4	690.1
<u>Hieracium florentinum</u>	hawkweed	P	14.1	65.7
<u>Asclepias tuberosa</u>	butterflyweed	P	10.5	35.4
<u>Chrysanthemum leucanthemum</u>	daisy	P	4.8	5.1
<u>Sanguisorba minor</u>	burnet	P	1.3	0.0

Table 2. Substrate properties on the sparse and dense sites; values in the first two columns are mean \pm S.D. and, in parentheses, the number of observations; results of one-way analysis of variance comparing sites are presented in column 4; N.S. = not significant at $\alpha=0.05$. Data from Klemow & Raynal [18], reprinted with permission.

Property	Sparse site	Dense site	Signif.
Soil <1.25 cm diameter (%)*	51.1 \pm 11.8 (7)	48.7 \pm 9.96 (4)	N.S.
Soil <0.2 cm diameter (%)*	22.2 \pm 7.58 (7)	22.0 \pm 4.54 (4)	N.S.
Sand (%)	70.7 \pm 4.60 (14)	65.7 \pm 1.53 (8)	0.01
Silt (%)	18.1 \pm 3.85 (14)	24.0 \pm 1.76 (8)	0.005
Clay (%)	11.2 \pm 1.68 (14)	10.3 \pm 2.11 (8)	N.S.
Water retention (%):			
-1/3 bar	13.1 \pm 2.64 (7)	28.2 \pm 8.85 (4)	0.005
-15 bar	4.37 \pm 0.68 (7)	11.6 \pm 5.23 (4)	0.01
pH	7.64 \pm 0.04 (7)	7.56 \pm 0.05 (4)	0.025
Cation-exchange-capacity (m-equiv per 100g)	7.00 \pm 2.28 (14)	13.1 \pm 4.12 (8)	0.005
K ⁺ (m-equiv per 100g)	0.09 \pm 0.02 (14)	0.23 \pm 0.08 (8)	0.005
Mg ²⁺ (m-equiv per 100g)	0.56 \pm 0.04 (14)	0.81 \pm 0.16 (8)	0.005
Organic matter (%)	4.67 \pm 0.49 (7)	6.66 \pm 1.84 (4)	0.025

*Data for 0-10 cm stratum. Rest of Table refers to <0.2 cm soil fraction only.

half of the substrate's weight was made up of rock fragments >1.25 cm in diameter. Analyses of the fine material showed it to have a sandy-loam texture on both sites. The dense-site substrate had greater water retention, higher fertility and higher organic matter than the substrate sampled from the sparse site.

On sunny afternoons during the summer, temperatures at, and just above, the surface were 5-10°C warmer than those at a height of 100 cm [17]. During early afternoon on a typical warm, sunny day in July 1976, exposed surfaces at both sites exceeded 44°C whereas shaded surfaces were 10°C cooler. The surface on the dense site tended to be cooler on the average because more of it

was shaded. Temperatures on exposed and shaded surfaces were very similar on cloudy days. Therefore, site-related differences in surface temperature only occurred on sunny days, particularly in the summer when the vegetation was most developed.

3. METHODS

Permanent quadrats for sampling vegetation were established on both sites in late May 1976. Twenty-one quadrats, each measuring 0.5 x 0.5 m were randomly positioned on the sparse site. Five 0.5 x 0.5 m quadrats and thirteen 0.2 x 0.2 m quadrats were randomly positioned on the dense site. A larger area was sampled on the sparse site because the density of plants was lower there. Each quadrat was examined every two weeks during the growing seasons of 1976-1979. In 1980 and 1981, the quadrats were examined three times each. Quadrats were not examined during the winters because of frequent snow cover.

All plants within the quadrats were mapped on coordinate paper during the first examination in May 1976. A wooden frame measuring 0.5 x 0.5 m facilitated the mapping procedure. When the quadrats were examined at subsequent dates, the maps were brought up to date, accounting for emergence of new individuals and mortality of old ones. At each sampling, each plant was categorized into one of three life-history classes: seedlings, established-vegetative individuals (Table 3), and reproductive individuals. The number of seeds produced by reproductive plants was determined in 1980 and 1981 according to methods detailed elsewhere [21]. The methods allowed estimates to be made for each species of both the mean number of seeds produced per plant and the density of seeds (m^{-2}) on each site in each year.

The total number of plants present at each sampling date was determined for each species on each site. All plants that appeared between successive sampling dates were grouped together into separate cohorts. The proportion of the cohort that survived to each subsequent sampling date was determined and the data were plotted as survivorship curves. Survivorship curves are useful because they enable one to determine (1) the age at which most plants die, and (2) any relationships between mortality and temporally variable environmental conditions, particularly rainfall. Many cohorts were identified due to the frequency of sampling. The fates of only selected, representative cohorts will be presented, however.

For each species, the number of plants in each life-history category (seed, seedling, established or reproductive) was also determined for each sampling date on each site. The proportion of seeds that produced seedlings was estimated by dividing the number of seedlings that emerged each year by the estimated number of seeds produced prior to emergence. The proportion of

Table 3. Minimum sizes for established plants on the sparse and dense sites, Jamesville Quarry, Syracuse, New York. Plants smaller than the listed size were classified as seedlings.

Species	Size (cm)	Organ measured
<u>Erucastrium gallicum</u>	1.5	stem
<u>Melilotus alba</u>	3.0	stem
<u>Picris hieracioides</u>	2.0	rosette leaf
<u>Echium vulgare</u>	2.0	rosette leaf

seedlings that established and the proportion of established plants that reproduced were determined for each year's seedling crop. Mean proportions, based on the entire study, were also determined by pooling the data from all years.

The proportions of transition between successive life-history stages were used to determine the rate of population change through time. First, rates of population change per generation (R_0) were estimated for each species on each site by multiplying the proportion of seeds that produced seedlings by the proportion of seedlings that established, then by the proportion of established plants that reproduced and then by the number of seeds produced by mature plants. Second, the R_0 values were converted to annual rates of change (λ_{VT}) by taking the g^{th} root of R_0 where g represents the mean number of years per generation [22] of each species on each site. The mean length of time that seeds of each species remain in the soil was estimated according to the method of Klemow [21] and was taken into account when g was determined.

Three classes of λ_{VT} estimates were obtained for each species on each site. The first was based on proportions of transition of each life-history stage to the next for plants from all years pooled, and represented the mean rate of change over the course of the study. The second was based on the highest annual proportions of each transition and represented the rate of change that would be obtained under optimum conditions (based on the years observed). The third was based on the lowest annual proportions and represented the rate of change under the poorest observed conditions.

The population flux of four species (*Erucastrum gallicum*, *Melilotus alba*, *Picris hieracioides* and *Echium vulgare*) will be presented in this paper. These species are the dominant monocarpic herbs growing in the quarry and their performance gives an excellent indication as to the demographic attributes of the other species.

4. RESULTS

Four categories of information will be presented in this section for each of the four species: (1) life-history attributes; (2) changes in total densities through time; (3) survivorship of representative cohorts; and (4) estimation of the rates of density change through time. For *Melilotus alba*, *Picris hieracioides* and *Echium vulgare*, demographic data will be presented describing population performance on both the sparse and dense sites. For *Erucastrum gallicum*, demographic data of only the sparse-site population will be presented because the population on the dense site rarely exceeded 10 individuals for most of the study.

4.1. Life-History Attributes

Each of the four species exhibited a strict monocarpic life-history, meaning that individuals always died after they reproduced. There were, however, marked differences between the species in other life-history attributes such as the time of year in which most seedlings emerged and the age at which individuals reproduced.

Erucastrum gallicum displayed a typical summer annual life-history. Most seedlings emerged during April and early May and plants grew vegetatively throughout the summer. Plants flowered and set seed from late July until early

November. Very few plants survived the winter as vegetative individuals; most survived as seeds.

Seedlings of Melilotus alba also emerged in April and May. Plants grew vegetatively throughout their first summer and fall and then died back in November. Plants overwintered as a taproot with buds at the soil surface. During their second summer, new stems were produced, and bore flowers and seeds from July until late October. Because plants always died after their second year of growth, M. alba exhibited an obligate biennial life-history [18].

Most seedlings of Picris hieracioides emerged in September and October, whereas those of Echium vulgare emerged either in the late summer, fall or spring. Individuals of both species grew vegetatively and formed rosettes during their first summer. After overwintering, some individuals produced flowering shoots during their second summer. Reproduction was typically delayed for one or more years, however. Both P. hieracioides and E. vulgare exhibited a facultative biennial life-history [23].

4.2 Temporal Flux in Total Densities

Densities of all four species fluctuated markedly during each year (Fig. 1). Fluctuations in the density of the annual Erucastrum gallicum (Fig. 1(a)) was expected because the species is an annual and the population occurs in the form of seeds during the winter and as growing, photosynthesizing plants during the spring, summer and fall. Densities of the other three species fluctuated during each year as well, even though individuals had the capacity to survive the winter (Fig. 1(b-g)). The annual fluctuation in those species resulted from rather large flushes of seedling emergence each year and rapid mortality of seedlings (see below). In M. alba and P. hieracioides, peak densities each year were typically 20-100 times greater than the lowest densities (Fig. 1(b-e)). In E. vulgare, peak densities were only 2-4 times greater than the lowest (Fig. 1(f-g)). Densities of established individuals did not fluctuate nearly as much within each year as did densities of seedlings.

Densities also varied markedly between years, although the four species differed among each other in the way densities changed from year to year. Densities of E. gallicum and M. alba were both higher in 1978 than in any other year (Fig. 1(a-c)). For E. gallicum, the peak density was about 185 plants m^{-2} in April, 1978; 3-8 times higher than the peaks observed in any other year (Fig. 1(a)). For M. alba, densities in April 1978 were 220 and 1270 m^{-2} on the sparse and dense sites, respectively (Fig. 1(b-c)). Peak densities during the other years were 18-62 plants m^{-2} on the sparse site and 260-900 m^{-2} on the dense site. Densities of E. gallicum and M. alba neither consistently increased nor decreased over the 6-year duration of the study.

For P. hieracioides, peak densities were markedly higher during 1976 and 1977 than during 1979 and 1980 (Fig. 1(d-e)). Moreover, densities of established plants declined on both sites such that the density in August 1981 was 9.0% and 9.6% of that in August 1976 on the sparse and dense sites, respectively.

Whereas densities of P. hieracioides declined markedly during the study, those of E. vulgare increased on both sites (Fig. 1(f-g)). On the sparse site, populations tended to peak at higher densities each succeeding year (Fig. 1(f)). Moreover, the population of established plants increased rather steadily from 0.4 plants m^{-2} in August 1976 to about 3.0 m^{-2} in August 1981.

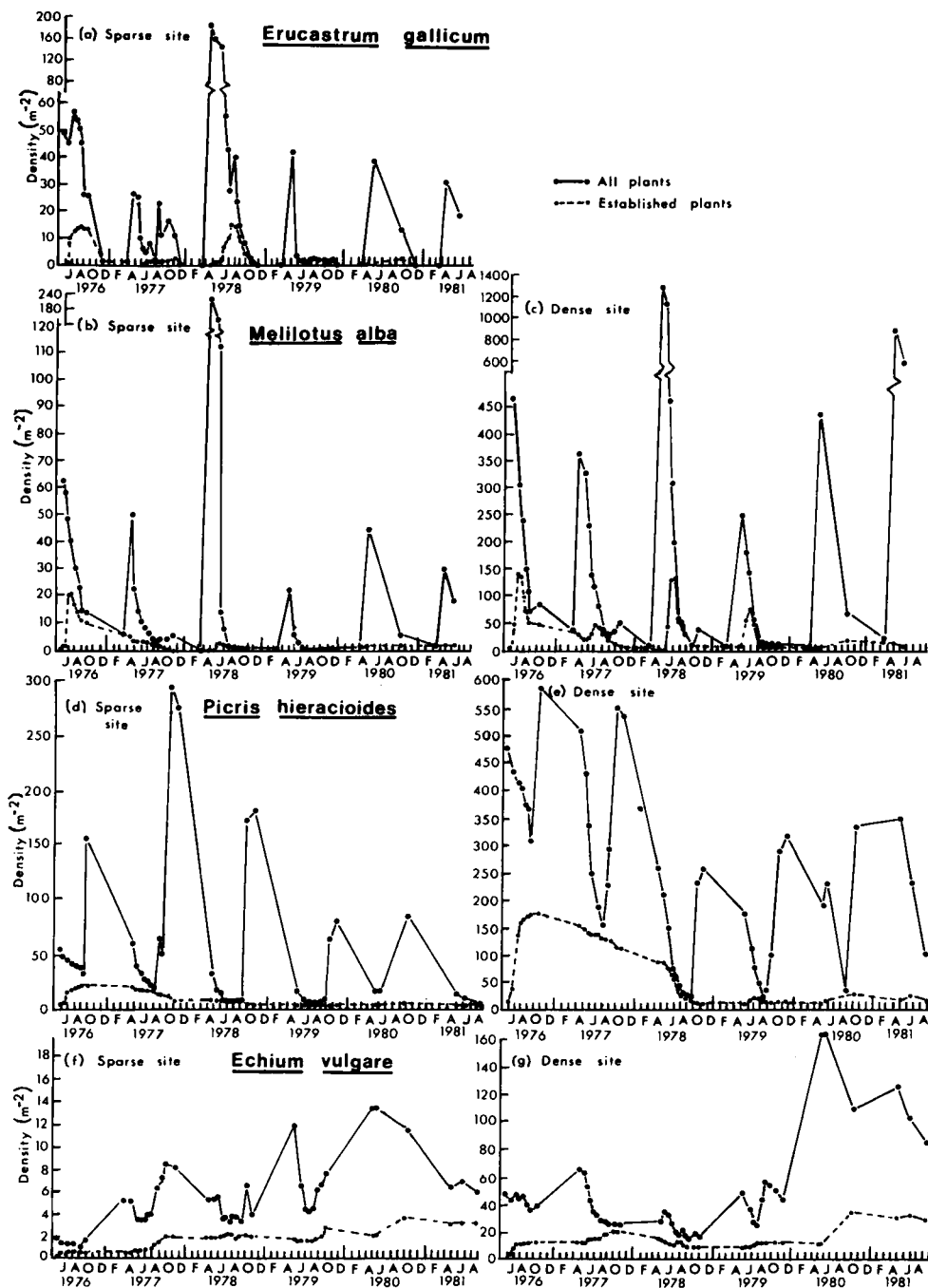


Figure 1. Total densities of four monocarpic species, Jamesville Quarry, Syracuse, New York; (d-g) from Klemow & Raynal [23], reprinted with permission.

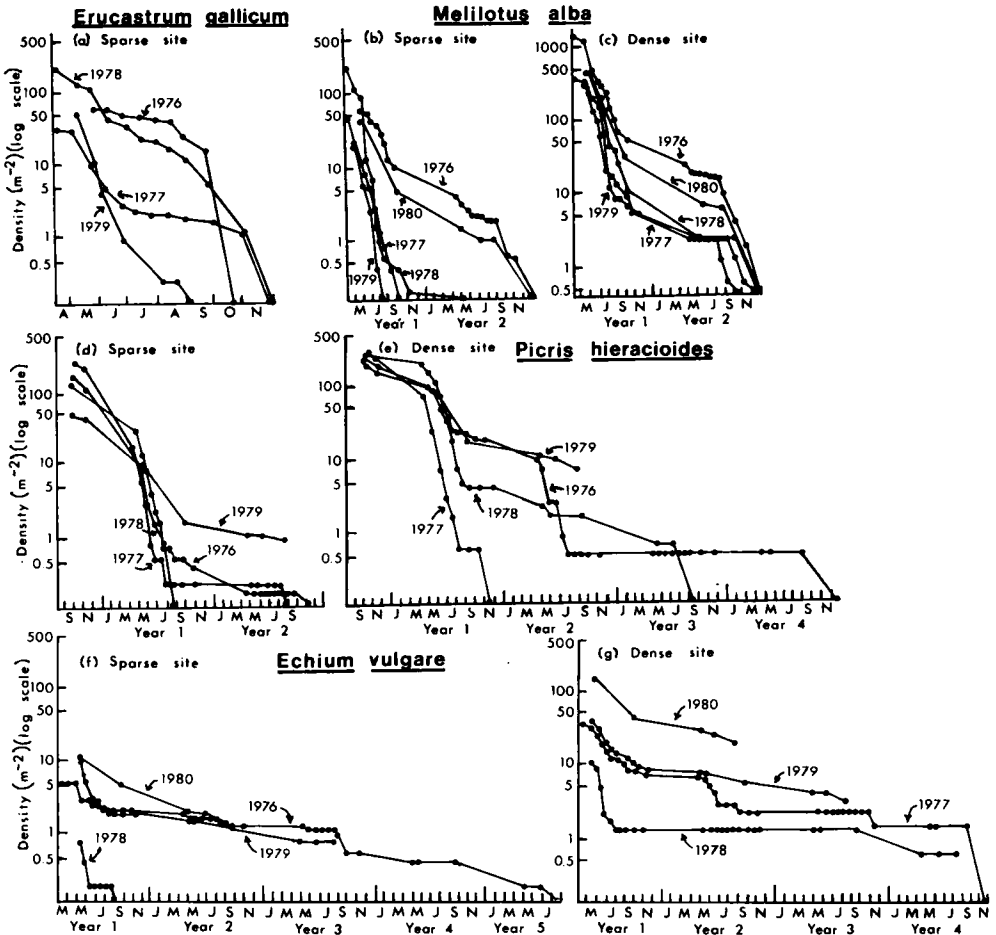


Figure 2. Survivorship curves for four monocarpic species, Jamesville Quarry, Syracuse, New York; (a) from Klemow & Raynal [24], (d-g) from Klemow & Raynal [23], reprinted with permission.

Densities on the dense site did not change much from year to year until 1980 when they increased by a factor of approximately 2 (Fig. 1(g)).

Despite the fluctuation within each year and between different years, densities of *M. alba*, *P. hieracioides* and *E. vulgare* were all consistently higher on the dense site (Fig. 1(b-g)).

4.3. Survivorship

Survivorship of *E. gallicum* on the sparse site varied markedly between years; more so than observed in the other three species (Fig. 2(a)). Survivorship was highest in 1976 such that 70% of the plants that emerged in the spring of that year survived until mid-August. In contrast, only 6.2% of the seedlings that emerged in spring 1977 survived to mid-August, due to very heavy mortality in May and early June. Seedlings that emerged in 1978 and 1979 suffered rather constant mortality throughout their respective summers. Plants

died very rapidly in 1979 - none of the spring recruits survived past late August and none reproduced in that year.

In Melilotus alba, seedlings that emerged in the spring exhibited comparatively low rates of survival each year (Fig. 2(b-c)). Survival was highest in 1976 and 1980 where 16% and 10% of the spring seedlings survived until autumn, respectively. Fewer than 1% of the seedlings that emerged in the intervening years survived their first growing season on the dense site and none survived on the sparse site. In all cohorts in which plants overwintered, rates of survival were higher among 2-year-old plants than among 1-year-olds.

For P. hieracioides mean rates of survival for fall recruits during their first winter was 10% and 43% on the sparse and dense sites, respectively (Fig. 2(d-e)). Mortality was typically very heavy during their first summer and, generally, fewer than 5% of the recruits survived their first year. As observed in M. alba, plants older than 1 year had higher survival than younger plants. On both sites, plants that emerged in fall 1979 had higher survival than those that emerged in 1976, 1977 or 1978. Survival of all P. hieracioides individuals present on each site at the beginning of each year was greater in 1976 than in succeeding years [23].

For seedlings of E. vulgare that emerged in the spring, rates of survival during their first summer ranged between 15% to 45% (Fig 2(f-g)). Survival rates were very high for E. vulgare plants after they attained the age of 6 months. Mortality after two years was generally due to plants completing their life cycle.

For E. gallicum, M. alba and P. hieracioides, seedling survival was highest in 1976 and second highest in 1980 (Fig. 2(a-e)). Survival was generally much poorer for plants of those three species during 1977, 1978, and 1979. Survival of E. vulgare seedlings was not consistently higher in any year (Fig. 2(f-g)).

Rates of seedling survival tended to be higher on the dense site than on the sparse site for both M. alba and P. hieracioides (Fig. 2(b-e)). For M. alba, the differential between sites in survival was most evident during 1977, 1978 and 1979. Seedling survival was higher on the dense site for P. hieracioides during their first winter and during the end of their first growing season.

4.4. Life-History Transitions and Rates of Population Flux

There was considerable variation between species, between sites, and between years in the proportion of individuals that survived to successive life-history categories and in the rates of population change through time (Table 4).

The estimate of population growth for Erucastrum gallicum using the pooled transitions was very close to 1.0, indicating that the population of that species neither increased nor decreased. As observed in Figure 1(a), however, the E. gallicum population fluctuated markedly from year to year. Therefore the proportions of survival to successive life-history stages also varied between years. When the highest annual proportions were used to estimate λ_{yr} , populations would grow by 20-fold each year under favorable conditions. Conversely, when lowest proportions were used, populations would decline by over 95% per year. Even though E. gallicum is an annual, its generation time was estimated to be 1.23 years, because some seeds remained dormant for more than one year.

The pooled λ_{yr} of the *M. alba* population on the sparse site was 0.94, indicating that i_{yr} declined slightly, whereas the population on the dense site increased by an average of 14% each year. Like *E. gallicum*, *M. alba* populations have the capacity to increase rapidly under favorable conditions, specifically by 1.7 and 5.0-fold each year on the sparse and dense sites, respectively. The populations can likewise decrease rapidly under unfavorable conditions. The percentage of seedlings that established was higher on the dense site whereas the percentage of established plants that survived to flower was higher on the sparse site.

Table 4. Proportions of plants that survive to successive life-history stages and estimates of rates of population change for 4 monocarpic species on the sparse and dense sites, Jamesville Quarry, Syracuse, New York. See text for explanation. Data for (b), (c) and (d) from [21].

(a) *Erucastrum gallicum*

Transition	Sparse site		
	Pooled	High	Low
Seedling emergence	0.180	0.311	0.074
Establishment	0.075	0.216	0.009
Flowering	0.248	0.763	0.207
Seed set	315	801	167
R_0	1.06	41.09	0.023
λ_{yr}	1.04	20.51	0.047
$g(\text{yrs})$	1.23		

(b) *Melilotus alba*

Transition	Sparse site			Dense site		
	Pooled	High	Low	Pooled	High	Low
Seedling emergence	0.252	0.252	0.252	0.253	0.667	0.113
Establishment	0.062	0.329	0.00	0.153	0.320	0.101
Flowering	0.120	0.120	0.00	0.064	0.101	0.014
Seed set	449	449	449	548	1898	346
R_0	0.84	4.20	0.00	1.36	41.00	0.055
λ_{yr}	0.94	1.70	0.00	1.14	5.03	0.28
$g(\text{yrs})$	2.7			2.3		

(c) *Picris hieracioides*

Transition	Sparse site			Dense site		
	Pooled	High	Low	Pooled	High	Low
Seedling emergence	0.320	0.758	0.227	0.437	0.828	0.330
Establishment	0.004	0.024	0.001	0.028	0.054	0.003
Flowering	0.248	0.248	0.248	0.053	0.053	0.053
Seed set	340	597	248	265	459	163
R_0	0.11	2.69	0.014	0.17	1.09	0.009
λ_{yr}	0.45	1.43	0.22	0.59	1.03	0.24
$g(\text{yrs})$	2.8			3.3		

(d) *Echium vulgare*

Transition	Sparse site			Dense site		
	Pooled	High	Low	Pooled	High	Low
Seedling emergence	0.193	0.203	0.097	0.199	0.358	0.081
Establishment	0.152	0.313	0.091	0.150	0.174	0.139
Flowering	0.360	0.600	0.000	0.343	0.429	0.250
Seed set	247	271	220	202	242	156
R_0	2.61	10.34	0.00	2.07	6.45	0.44
λ_{yr}	1.43	2.38	0.00	1.24	1.73	0.78
$g(\text{yrs})$	2.7			3.4		

As observed in Figure 1(d-e), populations of P. hieracioides declined markedly on both sites. By using the pooled transition probabilities, the rates of decline were estimated to average 55% and 41% per year on the sparse and dense sites, respectively. If conditions deteriorated further, the rate of decline would approach 80% per year. Conversely, the population appears capable of reversing its decline because the λ_{yr} values exceeded 1.0 on both sites when highest transition probabilities were used. As observed in M. alba, rates of seedling establishment were higher on the dense site whereas the proportion of established plants that flowered was higher on the sparse site.

Populations of E. vulgare grew at annual rates that were estimated to average 43% on the sparse site and 24% on the dense site. As observed in the other three species, there was considerable year-to-year variability in annual proportions of transition to successive life-history stages. By using consistently high rates of transition, populations on the sparse and dense sites would increase by 140% and 70% each year, respectively. Under least favorable conditions, populations on the sparse site would go extinct after one generation while those on the dense site would decrease by just over 20% per year.

5. DISCUSSION

Densities of all four species fluctuated markedly within each year and between different years. Fluctuations within each year were due to large flushes of seedling recruitment followed by heavy mortality of young plants. The fact that populations fluctuated so much within each year emphasizes that it was important to repeatedly sample the site to obtain an accurate understanding of the community. A single sample would have provided an incomplete picture.

There was considerable year-to-year fluctuation in densities, survivorship and proportions of plants that survived to successive life-history stages. Fluctuations in soil moisture, caused by fluctuations in rainfall coupled with a substrate that was excessively drained, appeared to contribute most to variability in plant performance. Skaller [13] and Klemow [17] noted that the quarry substrate can dry below wilting point (-15 bars) after even 6 consecutive rainless days.

Three of the four species, Erucastrum gallicum, Melilotus alba and Picris hieracioides, appeared to be most affected by year-to-year variability in rainfall. More rain fell during the growing season of 1976 than during any other year of the study (Fig. 3). Seedling survival was highest in 1976 in both E. gallicum and M. alba. Likewise, survival of all individuals of P. hieracioides was higher in 1976 than in subsequent years. Conversely, there was considerably more juvenile mortality during 1977, 1978 and 1979; years in which there was either severe or chronic drought during the growing season. When quadrats were visited after extended rainless periods, there were many plants that had died, obviously from desiccation.

Variability in rainfall had the most effect on survivorship in E. gallicum such that all three types of survivorship patterns (Types I, II, and III [26]) were observed. Such temporal variability in survivorship has only rarely been previously observed for a single species on a single site [27]. For M. alba, mortality on the sparse site was so heavy during 1977-1979 that no plants emerging in those years survived to their second spring, and, hence, none reproduced. In addition to survivorship being highest in 1976, rates of establishment and the mean height and mean number of seeds borne by reproductive plants were all highest in that year for M. alba and P. hieracioides [21, 23]. Rainfall therefore apparently influenced a variety of demographic characteristics of the quarry plants.

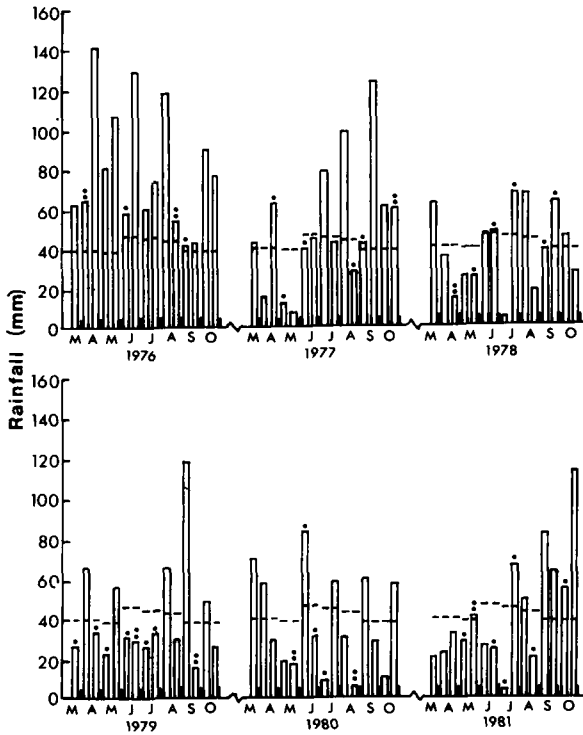


Figure 3. Rainfall in Syracuse, New York during the growing seasons of 1976 through 1981. Vertical bars indicate the cumulative rainfall in millimeters during the first 15 days and last 15 or 16 days of each month. Horizontal lines denote 30-year means for those periods. Filled circles above the bars indicate extended rainless periods; one circle, 4-7 days; two circles, 8 or more days. Data are from the National Oceanic and Atmospheric Administration, reprinted with permission from Klemow & Raynal [23].

Unlike the other three species, the demographic response of Echium vulgare did not appear to be affected by year-to-year variability in rainfall. Survival and reproduction of E. vulgare was as high during the droughts of 1977-1979, as during 1976, the year with abundant rainfall (see also [23]).

The contrasting conditions on the two sites affected the demography of all four species, particularly E. gallicum, M. alba and P. hieracioides. Rates of seedling survival and establishment were higher on the dense site for both P. hieracioides and M. alba. Higher availability of moisture and nutrients in the substrate as well as a cooler, more shaded surface on the dense site were probably responsible for the better performance of young plants there.

In contrast, once plants of those two species established, a greater proportion survived to flower on the sparse site than on the dense site. Moreover, in P. hieracioides, plants delayed reproduction longer and produced fewer seeds on the dense site. Although experimental evidence is lacking, it is likely established individuals of P. hieracioides were inhibited by comparatively high competition on the dense site after they grew to a certain large size. Other studies of facultative biennial species have demonstrated low

rates of survival, delayed reproduction and low numbers of seeds produced by plants growing in sites of high competitive stress [28-31].

Unlike populations of the other three species, those of Erucastrum gallicum were much less developed on the dense site than on the sparse site. Poor population development of that annual species under conditions of high plant density may not be unexpected because annuals are typically restricted from habitats in which there is a dense cover of plants that inhibits seedling emergence and establishment [32]. However, the low density of E. gallicum on the dense site may not have been entirely due to competition, because the other monocarpic plants (M. alba, P. hieracioides and E. vulgare) exhibited rather high rates of seedling emergence and establishment there. Moreover, densities of E. gallicum did increase sharply on the dense site in 1981 [20], suggesting that the species did not colonize the site until that year.

The demography of E. vulgare was hardly affected by contrasting conditions on the two sites. Rates of seedling survival, establishment, flowering and the number of seeds produced per plant were all similar on the two sites. The only difference was that plants on the dense site had a slightly longer reproductive delay.

The results of this study indicate that there was variability among the four species in their role in the development of the plant community in the quarry. Populations of M. alba and P. hieracioides were apparently well established on both sites and E. gallicum was established on the sparse site at the beginning of the study. Densities of E. gallicum and M. alba fluctuated markedly from year to year but did not show a tendency to either decrease or increase. The fluctuation in densities appeared to result from rainfall that varied annually. Densities of P. hieracioides were also affected by rainfall because they declined rather sharply during the drought-prone years of 1977-1979.

For those three species, the estimation of population growth rates using the consistently highest observed rates of transition indicated that the populations have ability to grow rapidly when conditions are optimum. Thus, the density trends observed in this study would have very likely differed had the amount and distribution of rainfall differed. Moreover, densities should rise to levels exceeding those observed in this study, should a series of years of abundant, frequent rainfall occur. The abundance of unoccupied area, particularly on the sparse site, would allow densities to greatly increase. Eventually, however, population growth would cease because reproduction would be inhibited by the high density of plants.

Conversely, should conditions deteriorate and drought become even more severe, populations of all three species would be subject to extinction in the quarry. Each species has, however, life-history attributes that would delay or prevent extinction under all but the most severe conditions. In both M. alba and E. gallicum, not all seeds germinate each year and many of the ungerminated seeds remain dormant in the substrate for more than one year [21, 24]. Populations can therefore persist even when all plants that emerge in a given year die before reproducing. A bank of dormant seeds undoubtedly enabled the population of E. gallicum to persist through complete pre-reproductive mortality in 1979. Likewise, the population of M. alba persisted on the sparse site during 1978, 1979 and 1980 even though no plants reproduced in the quadrats in those years. In contrast, P. hieracioides persisted by individuals delaying reproduction, thereby creating a bank or "reserve" [30] of rosettes. Many other species, including both plants and animals, delay reproduction as a means of preventing extinction when populations are faced with periodically stressful

conditions [33-35]. Populations of all three species would probably not persist beyond four consecutive years of severe drought because few seeds or rosettes would remain alive that long. It is unlikely, however, that the quarry would be subject to more than four consecutive years of drought due to the nature of rainfall patterns in central New York State.

Populations of E. vulgare were not very well established on either site at the beginning of study, unlike those of the other three species. Instead, E. vulgare was apparently still colonizing the quarry when the study was conducted, because densities increased, even during several consecutive years of drought. Such an increase also suggests that E. vulgare is more tolerant of the xeric, infertile conditions of the quarry than the other three species. Densities of E. vulgare will probably continue to increase until the site becomes very crowded and competition inhibits growth and development.

Typically, when a plant community located in a humid, temperate area is severely disturbed by natural causes or by human actions, the site is eventually restored by an orderly progression of plant species that colonize and fill the site. In many instances, the sequence is initiated by short-lived, herbaceous plants that colonize the site. These plants are then replaced by longer-lived, perennial herbs and, ultimately by woody plants [36-38]. In the Jamesville Quarry, the severity of the disturbance has prevented such a typical successional sequence. The site contains a mixture of short-lived herbs, long-lived herbs, shrubs and trees. Among the herbaceous plants are species such as Melilotus alba and Picris hieracioides that are found on other severely disturbed sites in the northeastern United States and adjacent Canada [19]. These species are generally not being replaced by perennials and woody species, but are persisting because colonization by longer-lived plants has been slow and the site remains rather uncrowded. Although densities of P. hieracioides declined during the study, the decline was not due to the species being replaced by successional change. Instead, the species is marginally adapted to the quarry and densities declined due to inadequate rainfall. Further, E. vulgare, which increased during the study, was not a later successional species but merely an apparently more tolerant species that was late at colonizing the site.

There is considerable diversity among surface-mined sites in terms of the extent and nature of the disturbance and in terms of the proximity, dispersability and physiology of the potential colonists [4, 10]. One must therefore be careful when attempting to extrapolate the results of this study to other surface-mined sites. However, as observed in this study, it is possible (if not likely) that communities on other surface-mined sites will contain a mixture of herbs and woody plants and that succession will have been inhibited by unfavorable edaphic and micrometeorological conditions. It is also likely that: (1) the community will probably consist of species that range from being poorly adapted to those very well adapted; (2) some species that are physiologically able to grow on the site will be absent because their propagules have yet to reach the site; (3) numbers will fluctuate within a year due to episodes of seedling recruitment and mortality; and (4) numbers will fluctuate from year to year due to variability in weather patterns, particularly rainfall.

ACKNOWLEDGEMENTS

D.J. Raynal provided advice throughout this project, and this research benefitted from discussions with M. Schaedle, J. Ferrel, J. Roman, G. Bonkougou, T. Guobis and F. Raleigh. Technical assistance was provided by S. Klemow, D. Bovalino, and B. DeGeorge. SUNY College of Environmental Science and Forestry provided facilities and funding. The Allied Corporation allowed access to the study site. Wilkes College kindly provided additional funding.

REFERENCES

1. Hutnick, R.J., and Davis, G., (eds.), "Ecology and Reclamation of Devastated Land", Gordon and Breach, New York (1973).
2. Ferrel, J., 1974, "Vegetation Rehabilitation for a Limestone Quarry", M.S. thesis, SUNY Coll. Envir. Sci. & Forestry, Syracuse, NY (1974).
3. Down, C.G., and Stocks, J., "Environmental Impact of Mining", Wiley, New York (1977).
4. Schaller, F.W., and Sutton, P.W., (eds.), "Reclamation of Drastically Disturbed Lands", Amer. Soc. Agron., Madison, Wisc. (1978).
5. Schramm, J.R., "Plant colonization studies of black wastes from anthracite mining in Pennsylvania", Am. Philos. Soc. Trans., 56 (1) (1966).
6. Alvarez, W., Ludwig, J.A., and Harper, K.T., "Factors influencing plant colonization of mine dumps at Park City, Utah", Amer. Midl. Nat., 92, 1-11 (1974).
7. Palaniappan, V.M., "Ecology of tin tailings areas: plant communities and their succession", J. Appl. Ecol., 11, 131-150 (1974).
8. Cornwell, S.M., "Anthracite mining spoils in Pennsylvania. I. Spoil classification and plant cover studies", J. Appl. Ecol., 8, 401-409 (1977).
9. Skaller, M.P., "The ecology of natural plant colonization in a limestone quarry", In: Limestone Quarries: Responses to Land Use Pressures", Perry, E.J., and Richards, N.A., (coords.), pp. 40-71 (1977).
10. Davies, B.N.K., (ed.), "Ecology of Quarries, The Importance of Natural Vegetation", Inst. Terrest. Ecol., Cambridge (1982).
11. Harper, J.L., "Population Biology of Plants", Academic Press, New York (1977).
12. Antonovics, J., "Population dynamics of the grass Anthoxanthum odoratum on a zinc mine", J. Ecol., 60, 351-366 (1972).
13. Skaller, P.M.G., "Plant Colonization and Soil Development in the Jamesville Limestone Quarry", Ph.D. thesis, SUNY Coll. Envir. Sci. & Forestry, Syracuse, NY (1977).
14. Raynal, D.J., "Population ecology of Hieracium florentinum (Compositae) in a central New York limestone quarry", J. Appl. Ecol., 16, 287-298 (1979).
15. Guobis, T.J., "Immigration and Establishment of Centaurea maculosa Lam. in a Central New York Limestone Quarry", M.S. thesis, SUNY Coll. Envir. Sci. & Forestry, Syracuse, NY. (1980).
16. Raleigh, F.S., "Population Ecology of the Monocarpic Perennial Plant Picris hieracioides L. on Contrasting Sites", M.S. thesis, SUNY Coll. Envir. Sci. & Forestry, Syracuse, NY (1981).
17. Klemow, K.M., "Plant Population Patterning and Community Development in a Limestone Quarry", M.S. thesis, SUNY Coll. Envir. Sci. & Forestry, Syracuse, NY (1978).
18. Klemow, K.M. and Raynal, D.J., "Population ecology of Melilotus alba in a limestone quarry", J. Ecol., 69, 33-44 (1981).

19. Gleason, H.A. and Cronquist, A., "Manual of Vascular Plants of North-eastern United States and Adjacent Canada", Van Nostrand, New York (1963).
20. Klemow, K.M., unpublished data.
21. Klemow, K.M., "Demography and Seed Biology of Monocarpic Herbs Colonizing an Abandoned Limestone Quarry", Ph.D. thesis, SUNY Coll. Envir. Sci. & Forestry, Syracuse, NY (1982).
23. Klemow, K.M. and Raynal, D.J., "Demography of two facultative biennial plant species in an unproductive habitat", J. Ecol., 72, (in press) (1984).
24. Klemow, K.M. and Raynal, D.J., "Population biology of an annual plant in a temporally variable habitat", J. Ecol., 71, 691-703 (1983).
26. Deevey, E.S., "Life tables for natural populations of animals", Quart. Rev. Biol., 22, 283-314 (1947).
27. Mack, R.N. and Pyke, D.A., "The demography of Bromus tectorum: variation in time and space", J. Ecol., 71, 69-83 (1983).
28. Holt, B.R., "Effect of arrival time on recruitment, mortality, and reproduction in successional plant populations", Ecology, 53, 668-673. (1972).
29. Werner, P.A., "Predictions of fate from rosette size in teasel (Dipsacus fullonum L.)", Oecologia, 20, 197-201 (1975).
30. Baskin, J.M. and Baskin, C.C., "Studies on the autecology and population biology of the weedy monocarpic perennial, Pastinaca sativa", J. Ecol., 67, 601-610 (1979).
31. Gross, K.L., "Predictions of fate from rosette size in four "biennial" plant species: Verbascum thapsus, Oenothera biennis, Daucus carota, and Tragopogon dubius", Oecologia, 48, 209-213 (1981).
32. Grime, J.P., "Plant Strategies and Vegetation Processes", John Wiley and Sons, New York (1979).
33. Stearns, S.C., "Life-history tactics: a review of the ideas", Quart. Rev. Biol., 51, 3-47 (1976).
34. Meijden, E. van der and Waals-Kooi, R.E. van der, "The population ecology of Senecio jacobaea in a sand dune system. I. Reproductive strategy and the biennial habit", J. Ecol., 67, 131-153 (1979).
35. Klinkhamer, P.G.L. and de Jong, T.J., "Is it profitable for biennials to live longer than two years?", Ecol. Model., 20, 223-232 (1983).
36. Keever, C., "Causes of succession on old fields of the Piedmont, North Carolina", Ecol. Monogr., 20, 231-250 (1950).
37. Bazzaz, F.A., "Succession on abandoned fields in the Shawnee Hills, Southern Illinois", Ecology, 49, 924-936 (1968).
38. Mellinger, M.V. and McNaughton, S.J., "Structure and function of successional vascular plant communities in central New York", Ecol. Monogr., 45, 161-182 (1975).