

VEGETATION DYNAMICS IN AN EXPERIMENTALLY FRAGMENTED LANDSCAPE¹

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Abstract. In spatially heterogeneous habitats, plant community change may reflect spatially localized population-level processes that are sensitive to the size of an average habitat patch. However, local species turnover can also be determined by initial conditions and large-scale processes, in which case patch size effects may be overridden. To examine the role of patch size in directing secondary succession, we subdivided a newly abandoned agricultural field into an array of experimental patches (32, 288, and 5000 m², grouped to sample equivalent portions of the field), and have thereafter censused the resident plant and animal communities at regular intervals. Here we report results from the first 6 yr of studies on the changing vascular plant community in an experimentally fragmented landscape. The general course of change in all patches followed a trajectory typical of old-field succession, toward increasing dominance by longer lived and larger plant species. The same group of species that dominated at the start of the study continued to dominate after 6 yr, although in very different proportional abundances. Larger patches were more species rich than their smaller counterparts, and had a higher proportion of nonshared species, but the additional species were transient and low in abundance. Spatial heterogeneity in vegetation, measured as local community dissimilarity, increased in all patches but to a lesser extent in the largest patches, where censuses of nearby permanent quadrats indicated less divergence over time. At a population level, the strongest effect of patch size was that local populations of clonal species were more prone to disappear from the smallest patches. Nevertheless, summary measures of temporal community change did not reflect significant differences in localized species turnover. We conclude that patch size does not markedly affect the rate or pattern of early secondary succession, at the scales imposed in our experiment.

Key words: colonization; habitat fragmentation; old field; patch size; population persistence; secondary succession; spatial dynamics; spatial heterogeneity; species-area relations.

INTRODUCTION

The spatial context of plant succession

Succession, directional temporal change in species composition or relative abundances, is a central theme in plant community ecology (Glenn-Lewin et al. 1992, Miles and Walton 1993, McCook 1994). Studies of succession have particularly emphasized life history strategies and interspecific interactions [e.g., competition (Tilman 1987), and herbivory (Hendrix et al. 1988)] as driving forces in vegetation dynamics (Pickett et al. 1987, Usher 1987a, Glenn-Lewin 1992). Yet it has long been recognized that the rate and pattern of succession may also reflect spatial factors (Glenn-Lewin 1992, McCook 1994). Gleason's (1927, 1928) original counterpoint to Clements' holistic portrait stressed spatial heterogeneity as a generator of complexity in succession. More recently Horn (1981), among others,

has observed that variability in the patterns of secondary succession can reflect variation in the composition and spatial proximity of seed sources (Tilman 1988; for examples see Nip-van der Voort et al. 1979, Wood and del Moral 1987).

Pickett and McDonnell (1989) have argued that differential species performance due to trade-offs between traits is the core process of succession. A trade-off between colonizing ability and traits such as competitive ability (Connell and Slatyer 1977, Tilman 1988, Pickett and McDonnell 1989) can lead to successional dynamics characterized by sequential local colonizations and extinctions (Johnstone 1986). These population processes are also at the heart of classical island biogeographic theory (MacArthur and Wilson 1967). A central aim in this paper is to argue that the spatial attributes of communities emphasized in island biogeography, i.e., the area occupied by a community, its distance from source pools for colonists, and the filtering of dispersers through intermediate sites, should be explicitly incorporated into succession theory.

Experimental manipulations on islands (reviewed in Schoener 1989) have played an important role in illuminating how island or patch area and distance from source pools can influence community dynamics. Field

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experiments in marine benthic systems have shown that patch size can likewise affect succession (Sousa 1984). A growing literature identifies dispersal and colonization as key driving factors in terrestrial succession (e.g., van der Valk 1992, Whittaker and Bush 1993). However, among over a thousand studies of plant secondary succession (Rejmánek 1995), we are unaware of any experiments that specifically assess the role of habitat area for succession in isolated patches.

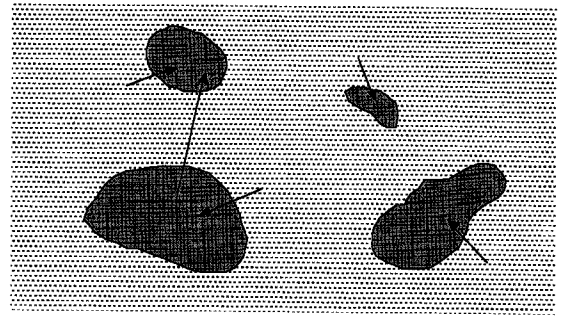
In this paper, we first lay out a schematic conceptual framework for discussing patch size effects in succession. The conceptual framework aims at generality and so is presented using simple verbal arguments, rather than formal mathematical models. We then describe the results of an experiment in which successional dynamics were monitored in an artificially fragmented landscape, and interpret the findings in light of our conceptual framework. The experiment we describe is ongoing; the data reported here are from the first 6 yr of the project. Some of the ideas sketched below may pertain more forcefully to later stages of succession than in the early stages reported here.

Patch size and the rate of succession

Patch size may directly affect abiotic conditions or resources and thereby influence secondary succession. For example, biomass accumulation can be considerably higher in larger disturbance patches in forests (Phillips and Shure 1990), and colonization by pioneer species is enhanced in larger treefall gaps by higher insolation (Denslow 1980). Here we set aside such direct effects and concentrate on the implications for succession of spatial aspects of population dynamics. We find it useful to contrast three spatial scenarios: (1) "null" patches, (2) embedded patches, and (3) isolated patches.

1) Null patches exist when patchiness (as discerned by an investigator) does not significantly influence succession. The "initial floristic composition" hypothesis of Egler (1954) states that all species occurring during a successional sequence are present from the outset (e.g., in a seed bank), or else very rapidly invade in full force following patch creation. Succession occurs primarily due to differential growth and interspecific interactions in the community defined by this initial array. The size of a given successional patch need not matter if all patches effectively sample the same source pool of propagules. A null patch model makes the strong assumptions that colonizing species richness is independent of patch size, and that populations low in number are not more vulnerable to extinctions on small patches. These assumptions are generally incompatible with views of succession that emphasize spatiotemporal dynamics (e.g., Czárán and Bartha 1992). Nonetheless, a null patch model may adequately describe secondary succession in patchwork systems with a copious initial propagule pool and little subsequent col-

a. Embedded patches



b. Isolated patches

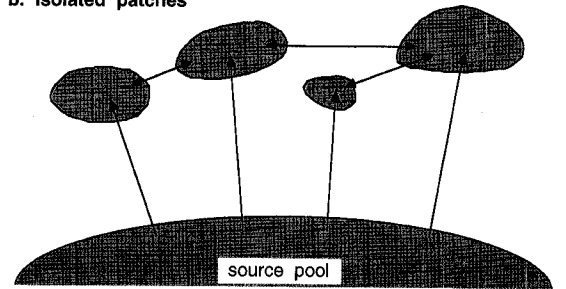


FIG. 1. Two hypothetical patch types occurring during succession. Arrows indicate the direction of species migrations. Stippled areas indicate usable habitat. Embedded patches (a) can receive migrants from a larger body of usable habitat. In isolated patches (b), the only migration routes are from distant source pools, or among patches.

onization. In such cases, the rate and pattern of succession should be independent of patch size.

2) Embedded patches (Fig. 1a) arise when localized disturbance occurs in a matrix of pre-existing vegetation, which then serves as the source pool for colonists (one kind of "area source" for dispersal; see Greene and Johnson 1989). The rate of succession in embedded patches should vary inversely with patch size, because dispersal generally declines with increasing distance from source areas (Andersen 1991), and the average distance from a random point within a patch to potential sources for propagules in the surrounding matrix increases with patch size. If colonization is a rate-limiting factor in succession, smaller embedded patches should experience an overall higher rate of colonization and thus undergo succession more rapidly. This "area effect" is, in fact, a disguised distance effect. Most previous work on patch size and succession has dealt with embedded patches. In intertidal communities, the rate of colonization of empty patches by sessile invertebrates varies inversely with patch size (Paine and Levin 1981), as does the rate of algal succession (Sousa 1984, Farrell 1989). Likewise, larger old fields undergo plant succession more slowly (Golley 1965, McMahon 1980), particularly in their centers (Golley et al. 1994).

3) In isolated patches (Fig. 1b), colonization from

an external source pool or among patches involves traversing unsuitable habitats. Because (by definition) isolated patches are further from source pools, succession should tend to be slower on isolated than on embedded patches. Two lines of thought suggest that the rate of succession should increase with patch size for isolated patches. First, larger patches provide larger targets for colonizing species. Colonization rarely occurs immediately across an entire patch; instead, colonists establish beachheads, then spread by local, within-patch dispersal (the nucleation model of Yarranton and Morrison 1974). Moody and Mack (1988) used models of plant invasion to show that multiple, scattered foci of invasion dramatically increase the rate of expansion of invading species. Larger isolated patches could proceed through secondary succession more rapidly than smaller ones, simply because they harbor more potential nucleation sites. If poor long-distance colonizers are good at short-distance dispersal, the rate of succession on a large patch can be enhanced by initial establishment elsewhere on the same patch (Holt 1992).

Second, early colonists in secondary succession can inhibit later arrivals (Connell and Slatyer 1977). When the probability of self-replacement increases with local abundance, initial colonists may enjoy a sustained advantage over later arrivals (Horn 1975, 1981). Priority effects should be enhanced on small, isolated patches, where new species are less likely to arrive in numbers sufficient to overcome advantages of prior occupancy; small isolated patches might become trapped at early successional stages.

Countervailing effects, due to generation length and recruitment dynamics, might lead to faster succession on very small patches, where maximal population sizes are small, and most individuals live near a patch edge. If colonization is insignificant relative to within-patch events, the pace of succession could be driven by the rate of species loss. Due to demographic stochasticity, small populations (e.g., $N < 20$) have a high probability of local extinction per generation (Richter-Dyn and Goel 1972, Leigh 1981). The absolute rate of such extinctions varies inversely with generation length (Pimm 1991). High dispersal rates (which typify early successional species) may increase extinction risks on very small patches, because much in situ seed production can be "wasted" due to dispersal beyond the patch edge (an effect quantified in the minimum patch size models of plankton ecology; see Okubo 1980).

The influence of patch size on secondary plant succession in isolated patches depends on the relative strength of these effects. The countervailing effects of patch size on succession rate are likely to matter only in very small patches, which necessarily harbor few individuals of any given species, all near a patch edge. In larger patches, we surmise that the opportunity for a given species to establish at multiple sites enhances the overall colonization rate of otherwise poor dispersers.

Experimental objectives

Secondary succession expresses the cumulative population dynamics of many different plant species, each with distinct dispersal syndromes and responses to local environments. Whether a given patch is "isolated" or "embedded" depends on attributes of the species in question, as well as the spatial relation between that patch and its surrounding landscape matrix (Halpern and Harmon 1983, Harris 1984). Successional patches in natural landscapes are therefore likely to be a blend of the three idealized patch types discussed above. However, with experimental manipulation, successional patches can in principle be created that closely correspond either to idealized embedded patches (e.g., experimentally generated gaps in natural vegetation), or to isolated patches. Our experiment was designed to produce relatively isolated patches.

Our broad objective was to determine whether the size of isolated patches influences population and community patterns and processes during the dynamic, early phases of secondary succession. The specific hypothesis we tested is that the rate of change in species and life form composition should vary with patch size. We further hypothesized that patch size should influence plant community diversity, spatial patterning, local population persistence, and species turnover during succession.

To an ever increasing extent, future studies of secondary succession (e.g., in restoration ecology) will be conducted against a background of habitat fragmentation, in arrays of patches varying in size and spatial separation (Dunn et al. 1993). This prospect lends a practical urgency to the need to examine the interplay of successional dynamics and habitat fragmentation.

METHODS

Study site and experimental design

The site is a 12-ha field in northeast Kansas, part of the University of Kansas' Nelson Environmental Study Area (Fitch and Kettle 1988). The historical natural vegetation in this region was a transitional mosaic of tallgrass prairie and oak-hickory forest (Kuchler 1974, Greller 1988). Farmed prior to 1970, the experimental field lay fallow for 9 yr and was reclaimed for agriculture in 1980. In June 1984, the field was mowed and disked (but not plowed), and subdivided into an array of experimental patches (Fig. 2). The patches have since been left undisturbed to proceed through secondary succession. The area surrounding and separating all patches is mowed once every 2 wk during the growing season. The landscape adjacent to the experimental field includes a mixture of midsuccessional and older secondary (oak-hickory) woodlands, plus open pasture dominated by cool-season grasses.

Experiments in spatial ecology necessarily involve compromises, because their components (e.g., shapes, distances, and arrangement) are interdependent. Our

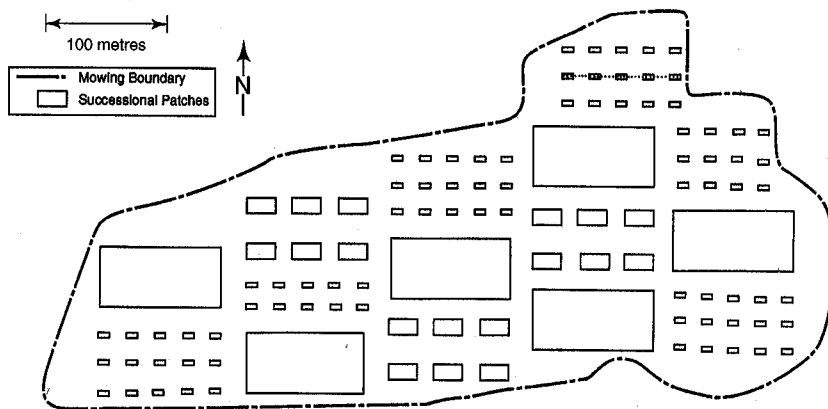


FIG. 2. Diagrammatic map of the experimental site. Rectangles represent undisturbed patches undergoing succession since summer 1984. Areas between and surrounding patches are continuously mowed to the border of the field (dashed line). Patch dimensions are 4×8 m (32 m^2), 12×24 m (288 m^2), and 50×100 m (0.5 ha). The dotted line through small patches in upper right represents site of transect sampled to compare vegetation in patches with that in the intervening mowed areas.

experimental design employs patches of three sizes: small— 32 m^2 (4×8 m), medium— 288 m^2 (12×24 m), and large—0.5 ha (50×100 m). We chose these dimensions based on empirical and theoretical criteria. The smallest patches had to be large enough to permit replicated sampling within each patch, and ideally large enough to contain hundreds of ramets of the small-statured plant species common in early succession. In addition, estimates of root-mean-square dispersal distance for early colonizing species (Platt and Weiss 1977) and maximal growth rates were combined in a theoretical model of a population occupying a patch in an otherwise unsuitable matrix (Okubo 1980; R. D. Holt, *unpublished data*). Using this model, we concluded that a patch with a minimum linear dimension of 4–5 m would be above the predicted threshold for population persistence as a simple function of seed wastage. A minimum patch size of 4×8 m satisfied these criteria. A survey of experimental studies of succession (R. Holt and E. Teravainen, *unpublished data*) revealed that the size for most experimental plots was < 0.5 ha. This was, in any case, the largest patch size that could be adequately replicated, given the dimensions of the field. The medium patch size is approximately intermediate on a log scale.

We clustered small and medium-sized patches into groups of 15 and 6, respectively, such that the outer perimeter of each experimental unit spans the same total area as one large patch (0.5 ha). The minimum distance between any two patches (≈ 15 m) was intended to provide a barrier for seed dispersal of wind-dispersed herbaceous plants between patches, based on published dispersal distances (Burrows 1973, Smith and Kok 1984), as well as a barrier for small mammal movement in concurrent studies of small mammal populations (Foster and Gaines 1991, Gaines et al. 1992). All patch size units were positioned in a stratified random array, with no unit abutting another of the same

type (Fig. 2). Due to the irregular shape of the field, and the desire for increased replication of the largest patches, there were half as many (three rather than six) clusters of medium patches as of the other two types, and two of the clusters of small patches contain < 15 patches.

Field sampling

Pairs of permanent 1-m² quadrats, separated by 4 m, were delineated at regular intervals inside all patches. Small patches contain 1 pair, medium patches 2 pairs, and large patches 15 pairs. Within each small patch, one quadrat was placed a minimum of 1 m from the nearest southeast patch corner, and a second within 1 m of the southwest patch corner. This spatial pattern of sample stations is repeated for larger patches, with 30 quadrat positions in each large patch. Each spring and fall, beginning in fall 1984, we censused the quadrats, recording all species present and estimating percentage cover with a point-intercept quadrat method, modified from Goodall (1952). In 1985 and 1986, mid-summer censuses were also taken, but these added very few species to our counts, and were discontinued. During 5 of the 13 sampling periods (in the years 1984, 1986, and 1987), budget constraints restricted our censuses to only the western half (eight experimental units) of the field.

To determine whether the plant communities in our patches had become distinct from the surrounding mowed matrix, we compared quadrat samples in patches with those in adjacent mowed areas in a section of the field with the lowest rate of colonization by woody plants. In summer 1989, we censused a continuous transect of contiguous 100 1-m² quadrats through a row of five small patches, including the intervening mowed sections (as indicated in Fig. 2).

Our working assumption was that the high degree of replication and spatial interspersion of patches would

compensate for uncontrolled environmental heterogeneity. Preliminary surveys of soil chemistry and structural properties did not reveal spatial gradients in these variables. In 1984, soil core samples were taken throughout the field to examine the seed bank, but were unfortunately lost during a transfer to new facilities. Later measurements of soil water, standing nutrient pools, and rates of nitrogen mineralization indicated that patches of each size class were statistically equivalent after 5 yr of succession (Robinson et al. 1992). However, the experimental field, while under cultivation, had been terraced for erosion control. This added an element of local habitat diversity, due to microsite variation in slope and drainage throughout the field, reflected in small-scale zonation in the vegetation (Robinson et al. 1992). Moreover, we had evidence that relative densities of several small mammal species correlated with experimental patch size (Gaines et al. 1992). Given the capacity of small mammal herbivores to affect herbaceous plant communities (e.g., Edwards and Gilman 1987, Louda et al. 1990, Huntly 1991), we felt that localized small mammal disturbance could affect our results. Using field surveys and aerial photographs, in fall 1989 we classified all 416 permanent quadrats by the following categories: (1) on or off terraces; (2) on or off sloping ground, (3) whether or not waterlogged following rains; and (4) with or without evidence of small mammal disturbance (primarily burrows and runways of rodents such as *Sigmodon hispidus*, the hispid cotton rat, and *Microtus ochrogaster*, the prairie vole).

Data analysis

Species identification.—Because the 13 censuses used in our analyses were conducted by a number of different field researchers, taxonomic synonymies and ambiguities occasionally occurred in the data set. These were resolved conservatively, by lumping taxa that were not clearly distinguishable. Nomenclature follows the Great Plains Flora Association (1986).

Patch size correlations with physical variables.—Most of our results depend on information from the 416 permanent quadrats, so we examined whether quadrats in each patch size were sampling an equivalent range of heterogeneity in the physical environment. We compared the proportion of quadrats in each patch size category that were located on former terraces, on sloping ground, on waterlogged soils, or on sites with soil disturbance by small mammals, using nonparametric (*G* statistic) tests. To test for effects on species distributions, we ordinated species' cover per quadrat according to patch size, adding disturbance, waterlogging, slope, and terracing as covariables, using Canonical Correspondence Analysis (CCA, ter Braak 1992). Data for these two analyses were collected in fall 1989.

Patch differentiation from the mowed environment.—To test the assumption that the patches differed

from the mowed matrix, we compared percent cover data for the transect of 100 contiguous 1-m² quadrats. The two quadrat classes (within patch and outside patch) were compared using a metric of dissimilarity, percent remoteness, PR (Pielou 1984):

$$PR = 100 - 100[\sum \min(x_{i1}, x_{i2}) / \sum \max(x_{i1}, x_{i2})],$$

where x_{i1} = the value (in this case, relative cover) of the i^{th} species in quadrat 1 and x_{i2} = its value in quadrat 2. An important advantage of this type of metric over commonly employed dissimilarity indices, such as the Jaccard Coefficient, is that the co-occurrence of a species will force two samples into close agreement only when abundances are similar, rather than heavily weighting commonalities in simple presence or absence (Hendrickson 1979). We computed and averaged PR for three sets of quadrat pairings: all pairs of mowed quadrats, all pairs of unmowed quadrats, and all pairings between a mowed and an unmowed quadrat. Because each quadrat is represented multiple times in this analysis, statistical assumptions of independence are violated, hence testing differences is not straightforward (e.g., Inouye and Tilman 1988). We used a Monte Carlo procedure (Manly 1991) to assess significance by drawing random subsamples from each of the three quadrat pairings. One thousand sets of 100 pairings were drawn from each group to build cumulative pairwise test statistics and *P* values (Crowley 1992).

General successional trends.—Herbaceous plant communities vary substantially through time, even in nonsuccessional vegetation (cf. Grubb 1986). A census-by-census summary for all species we encountered is beyond the scope of this paper. To simplify, we grouped plants by life history characters, so as to portray general temporal sequences. We computed average percent cover of annual grasses, annual forbs, perennial grasses, perennial forbs, and woody plants at each census, by patch size.

Species-area and rank abundance relationships.—At each census, species counts were summed over each treatment unit (one large patch or cluster of small or medium patches), and averaged by patch size. To compare species richness among patches of different sizes, we grouped patches of each size class and performed species-area regressions, testing \ln patch size vs. (1) \ln (species) per patch, and (2) \ln (species) per quadrat. To compare community-level diversity in more detail across patch sizes, we used rank-log abundance curves (May 1975) for patches of each size. Year-by-year results did not vary, and we report here the cumulative totals for 6 yr, including the identities of the 10 most abundant species in each patch size class. We also examined the relative abundances of those species that persisted for the full duration, in at least one patch of each size class. This entailed summarizing the relative percent cover of this subset of species at annual intervals, by patch size. This analysis began with the fall 1984 sample, to include the very first cohort, presum-

TABLE 1. Number of quadrats located in each microenvironmental category.

Microenvironment	Small patches	Medium patches	Large patches
Total number of pairs	164	72	180
On sloping ground	70	39	68
On or near former agricultural terraces	41	22	38
Subject to waterlogging	12	9	14
With soil disturbed by small mammals	28*	3	9

* The proportion of quadrats on soils disturbed by small mammals varied with patch size ($G_{2df} = 17.05$, $P = 0.0002$).

ably representing the initial seed and bud bank (few outside species had the opportunity to recruit, between June 1984 disking and the fall 1984 census).

Persistence of species and local populations.—Species turnover as a function of patch size was measured over the 6-yr period from 1984 to 1989. To portray changes in species composition, we grouped all species presence-absence data collected each year by patch size, comparing species losses and gains between successive years, and over the full interval. To analyze those changes, we used Sørensen's index of Community Correspondence:

$$CC = (2c/a + b),$$

where c is the number of species in common, a the number of species at time t , and b the number of species at time $t + 1$. CC is the equivalent of an inverse of species turnover, as well as a measure of temporal similarity in species composition among communities (Mueller-Dombois and Ellenberg 1974, Bornkamm, 1981). At the level of individual species, we analyzed the proportion of original local populations (a "local population" here means that species x was present in quadrat y in 1985) that persisted to the end of the current study (i.e., species x continued to be found in quadrat y in 1989). The 5-yr interval was chosen because all 416 quadrats were censused in both years.

Spatial and temporal trends in local community dissimilarity.—We tested whether spatial heterogeneity

among local (i.e., within-quadrat) communities varied with patch size, using the same metric of community dissimilarity as in our comparison of mowed and unmowed habitat (PR). All pairwise combinations of individual quadrats were compared within each cluster of small and medium patches, or each large patch, and within each large patch, giving an indication of whether habitat subdivision leads to divergence at a fine scale. To examine temporal trends in spatial heterogeneity, we applied this analysis to data from both 1985 and 1989, and compared distributions of PR for each patch size class, using nonparametric comparisons of frequency distributions. To examine how community heterogeneity varied spatially, we plotted these same data against distance between each quadrat pair. In this latter case, scatter plots contain data from only three large patches and three small patch clusters, for clarity. Medium patches were excluded because average distances between their sampling quadrats were set in a different array, and the distribution of interquadrat distances was not comparable.

RESULTS

Patch size correlation with physical environmental variables

Most variation in the categorical environmental factors examined did not differ significantly among patches of each size, the one exception being disturbance caused by small mammals, which was more prevalent in small patches (Table 1). Ordination revealed only weak correlations between species composition and environmental variables examined (Table 2). The four ordination axes had low eigenvalues, indicating either that unmeasured factors contributed more strongly to the variability observed, or that species composition itself was relatively invariable among replicates. The latter possibility gains support from direct measures of the pattern of community diversity, as reported below.

Patch differentiation from the mowed environment

Data from contiguous quadrats sampled in summer 1989 indicate that the experimental patches shared 39

TABLE 2. Correlation matrix from ordination (CCA) of percent cover of 91 species on patch size and local habitat characteristics. Censuses of species cover and assignment of habitat classifications were made in fall 1989. Axis eigenvalues are reported in parentheses.

	Species axis 1 (0.087)	Species axis 2 (0.061)	Species axis 31 (0.047)	Species axis 4 (0.041)	Patch size	Slope	Terrace	Waterlogging	Disturbance
Species axis 1	1.000								
Species axis 2	0.032	1.000							
Species axis 3	-0.027	-0.038	1.000						
Species axis 4	-0.085	-0.001	-0.122	1.000					
Patch size	-0.536	-0.016	0.116	-0.051	1.000				
Slope	-0.086	-0.024	-0.009	0.328	0.019	1.000			
Terrace	0.051	0.007	-0.028	0.015	-0.085	-0.325	1.000		
Waterlogging	0.132	0.111	0.435	-0.016	0.007	-0.213	0.231	1.000	
Disturbance	0.417	0.530	-0.106	-0.023	-0.151	-0.603	-0.057	-0.006	1.000

TABLE 3. Comparisons of community dissimilarity (PR, percent remoteness, defined in text) among all pairings ($N = 4950$) of 100 contiguous 1-m² quadrats through a group of small (32 m²) patches, and the mowed area between them. Transect location is indicated in Fig. 2.

Quadrat pairing	Mean dissimilarity (PR)*	Variance
Patch : patch	69.75 ^a	489.74
Patch : mowed	96.76 ^{ab}	12.39
Mowed : mowed	67.21 ^b	98.40

* Values with the same alphabetic superscripts are significantly different at the 99% confidence level. (Monte Carlo Scheffé F values: a = 911.53; b = 1091.60.)

out of 50 species with the mowed matrix, but relative abundances of most plant species differed greatly between the two habitat types. Two taxa (*Solidago canadensis* and *Melilotus* spp.) accounted for over half of total percent cover in the patches, whereas eight others (*Lespedeza stipulacea*, *Geranium carolinianum*, *Lepidium virginicum*, *Aster pilosus*, *Taraxacum officinale*,

Oxalis dillennii, *Lactuca canadensis*, and *Hedeoma hispidum*) represented 52% of the total plant cover in the mowed area. The latter appeared better able to grow and set seed when mown. Community dissimilarity values portray two very distinct vegetation types. Matching quadrat pairs were $\approx 30\%$ self-similar, but quadrat pairs from contrasting habitats were almost entirely unlike, with small variance (Table 3). Furthermore, PR values for the mowed quadrats have a Poisson-like distribution, while those for the experimental patches are truncated and strongly left tailed, with large variance (data not shown). Although the experimental patches presumably shared the same original species pool as the mowed interstitial area, the plant communities of the two habitat types have diverged.

Successional change and patch size

Overall changes in the relative abundance of life history categories proceeded in a markedly similar manner in patches of all three sizes (Fig. 3). The dominant species after 6 yr were perennial forbs of a few

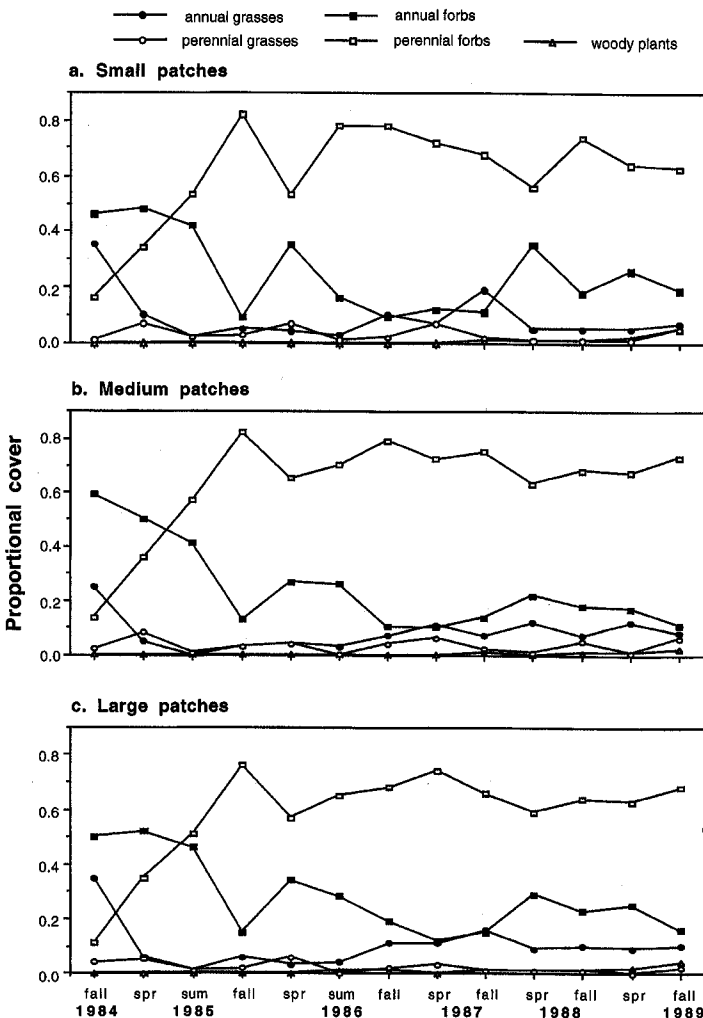


FIG. 3. Yearly seasonal changes in relative percent cover of the principal life history plant groups in (a) 82 small (32 m²), (b) 24 medium (288 m²), and (c) 6 large (0.5 ha) patches.

TABLE 4. Mean species counts (± 1 SD) for experimental units of 15 small, 6 medium, or 1 large patch. Data are from arrays of permanent quadrats within units of 10–15 small (32 m²) plots, 6 medium (288 m²) plots, and single large (0.5 ha) plots. Values in parentheses indicate the number of units censused per season. Differences in averages among plot sizes, tested with one-way factorial ANOVAs, were not significant during any season.

Season	Patch size									Field-wide total
	Small			Medium			Large			
	<i>N</i>	\bar{X}	SD	<i>N</i>	\bar{X}	SD	<i>N</i>	\bar{X}	SD	
Fall 1984	(3)	43.0	1.00	(2)	49.5	3.54	(3)	51.7	8.33	88
Spring 1985	(6)	31.7	2.58	(3)	31.7	3.77	(6)	35.2	5.12	80
Summer 1985	(6)	33.2	1.17	(3)	33.0	5.29	(6)	37.3	6.74	93
Fall 1985	(6)	35.7	10.19	(3)	34.7	12.58	(6)	37.00	10.49	91
Spring 1986	(6)	39.5	3.51	(3)	37.7	6.43	(6)	40.2	4.83	80
Summer 1986	(3)	45.0	4.36	(2)	40.5	4.95	(3)	43.7	5.51	85
Fall 1986	(3)	39.3	5.51	(2)	35.0	1.41	(3)	43.0	6.25	82

genera, replacing the annual community that first emerged after cultivation was halted. As noted for other abandoned fields in central North America, asters (*Aster* spp.) dominated for 2–3 yr, followed by goldenrods (*Solidago* spp.) (e.g., Pickett 1982, Bazzaz 1990). Perennial grasses, although very abundant in nearby prairies in the Nelson Environmental Study Area, have made a consistently minor contribution. Nine woody

plant species had colonized at least one sampling quadrat by fall 1989, but woody plants contributed little to vegetative cover after 6 yr of succession. Invasion by woody plant species has accelerated in recent years (Holt et al. 1995).

Diversity and patch size

Field-wide species richness fluctuated over the course of the study, with an average of ≈ 90 total vascular plant species observed per census period (Table 4). During all sampling periods, plant species richness per experimental unit (viz., 1 large, 6 medium, or 15 small patches) was similar. This was somewhat unexpected, since the amount of habitat area ranged from 320 to 5000 square metres. Note, however, that the actual area sampled per experimental unit was roughly equivalent. Plotting mean species per patch (averaged over all censuses) against patch size yields a regression comparable to species-area curves for island archipelagos, ($\ln \text{Species} = 1.56 + 0.23(\ln \text{Patch size})$, $R^2 = 0.74$). However, mean species counts per unit area (i.e., per 1-m² quadrat) were virtually identical among the three patch sizes [$\ln \text{Species} = 2.06 - 0.001(\ln \text{Patch size})$, $R^2 \approx 0$]. The shapes of cumulative rank-abundance curves are quite similar among the three patch types (Fig. 4). All three curves are approximate log-normal species-abundance distributions, typical of speciose communities (Preston 1962, May 1975). Furthermore, the order of the higher-ranking species is quite similar among all three patch sizes (Table 5). Finally, those species that persisted from the first to last census accounted for the great majority of cover (>80%) at every census, again regardless of patch size (Fig. 5).

Persistence of species and local populations

Yearly and cumulative rates of change in species composition were similar among patch size treatments, measured as proportions of species lost, gained, and persisting, and Community Correspondence (Table 6a). Cumulative species counts, grouped by patch size, were

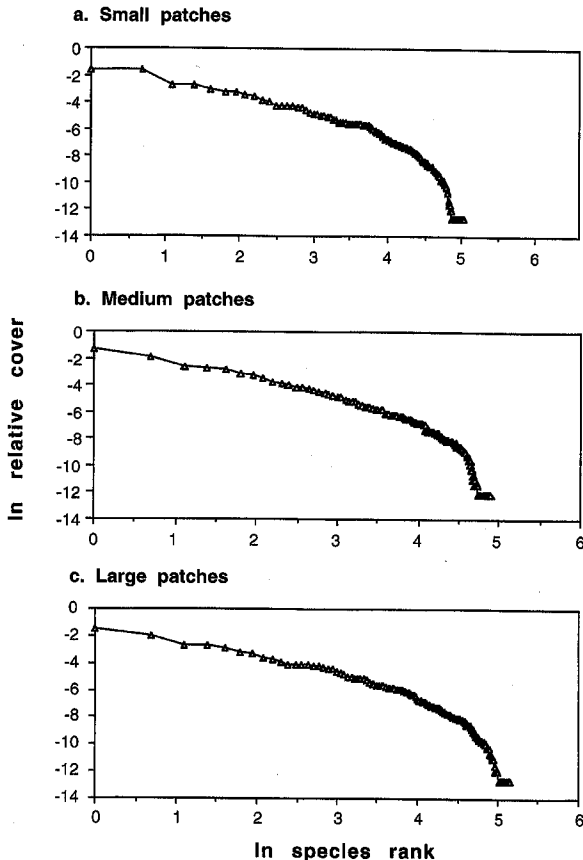


FIG. 4. Cumulative rank-abundance curves for 13 combined censuses of permanent quadrats in (a) 82 small (32 m²), (b) 24 medium (288 m²), and (c) 6 large (0.5 ha) patches.

TABLE 5. Mean relative percent cover of the first 10 ranked species in each of the three cumulative rank-abundance curves of Fig. 4.

Species	Patch size		
	Small	Medium	Large
<i>Aster pilosus</i>	20.3	27.4	22.4
<i>Solidago canadensis</i>	20.0	14.2	13.9
<i>Erigeron strigosus</i>	6.5	6.1	6.9
<i>Juncus</i> spp.*	6.1	5.7	6.8
<i>Melilotus</i> spp.†	4.8	4.0	5.3
<i>Ambrosia artemisiifolia</i>	3.6	7.1	3.9
<i>Aster simplex</i>	3.0	4.4	3.8
<i>Setaria faberi</i>	3.7	2.4	2.8
<i>Bromus japonicus</i>	1.9	3.2	2.4
<i>Galium aparine</i>	2.7	1.2	1.9
Remainder	27.1	23.5	29.9
Mean rank‡	2.3	1.8	1.9

* Primarily *J. tenuis*.

† *M. alba*, *M. officinalis*, and possible hybrids thereof.

‡ From Friedman rank means test. Differences are not significant: $\chi^2_{2df} = 1.27$, $P > 0.40$.

highest for the largest patches, which contained the highest proportion of the full species pool (Table 6b). Since this result is to a degree confounded by variation in sampling effort, noted above, a more direct comparison is between proportions of species counts in each census that are unique to a given patch size. That comparison reveals that large patches held a significantly larger proportion of nonshared species. Species unique to any patch size were generally uncommon, occupying on average 1.6 quadrats, and relatively ephemeral, with a mean duration of 1.7 yr.

On average, across all species, the proportion of original (1985) local populations lasting until 1989 did not vary with patch size. However, a highly significant difference associated with species life history traits emerged. Clonal species, those capable of vegetative

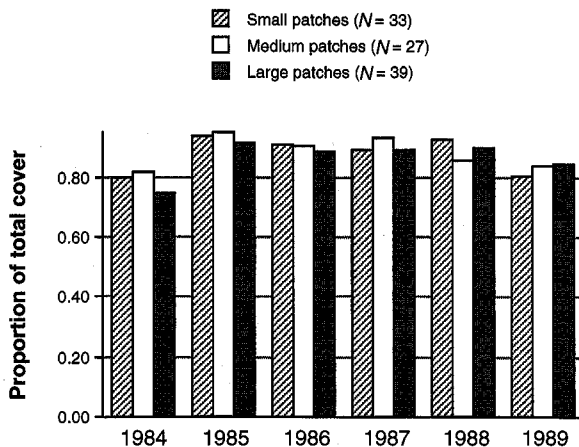


FIG. 5. Proportion of total plant cover contributed by species that persisted from the initial census (fall 1984) through the concluding census (1989) reported. Data are from permanent combined quadrats, grouped by patch size. N = count of contributing species.

TABLE 6. Year-to-year and cumulative changes in species composition, expressed as counts of species gained, lost, and persisting. Data are from permanent quadrat censuses (2–3 per year) combined by year and patch size. CC (Sørensen's Community Correspondence index) is described in the *Methods*. Transient species in cumulative counts are those observed only during the interval between the first and last census. Nonshared species are those found exclusively in patches of one size class.

a) Annual counts							
Year	Patch size	Total species	Species persisting	Species gained	Species lost	CC	
1984	Small	60		60			
	Medium	63		63			
	Large	77		77			
	All	88		88			
1985	Small	91	51	40	9	0.68	
	Medium	73	43	30	20	0.63	
	Large	103	62	41	15	0.69	
	All	120	72	48	16	0.69	
1986	Small	94	73	21	18	0.79	
	Medium	82	57	25	16	0.74	
	Large	95	80	15	23	0.81	
	All	112	95	17	25	0.82	
1987	Small	81	68	13	26	0.78	
	Medium	73	57	16	25	0.74	
	Large	92	72	20	23	0.77	
	All	102	85	17	27	0.79	
1988	Small	65	56	9	25	0.77	
	Medium	60	48	12	25	0.72	
	Large	90	67	23	25	0.74	
	All	105	79	26	23	0.76	
1989	Small	86	54	32	11	0.72	
	Medium	64	48	16	12	0.77	
	Large	81	59	22	31	0.69	
	All	108	77	31	28	0.72	
b) Cumulative counts							
Patch size	Total species observed 1984–1989	Species persisting	Species gained	Original species lost	Transient species	Non-shared species	CC
Small	146	39	47	21 (35%)*	39	10†	0.53
Medium	130	28	36	35 (56%)*	31	7	0.44
Large	164	41	40	36 (47%)*	47	23	0.52
All	190	54	54	34 (39%)*	48		0.55

* Proportion of cumulative species lost did not differ significantly among patch size treatments ($G_{2df} = 5.31$, $P = 0.07$).

† Proportion of nonshared species varied significantly with patch size treatment ($G_{2df} = 7.13$, $P < 0.03$).

reproduction via spreading stems (underground rootstocks), were less persistent within quadrats in the smallest patches (Table 7).

Local community divergence

A comparison of pairs of 1-m² quadrats over each 0.5-ha cluster revealed considerable variation in dissimilarity (PR) among the local plant communities (Fig. 6). Average dissimilarity was higher within single

TABLE 7. Proportion of local populations persisting from 1985 to 1989 in permanent quadrats, according to patch size. Persistence is defined as the continuing occurrence of one or more individuals of a species rooted within a quadrat.

Patch size	Total 1985 populations		Proportion extant in 1989	
	Clonal plants	Nonclonal plants	Clonal plants	Nonclonal plants
Small	667	1375	0.46*	0.38
Medium	323	578	0.63	0.43
Large	669	1529	0.58	0.37

* Persistence varied significantly with patch size for clonal plants ($G_{2df} = 30.65, P < 0.0001$).

large patches in 1985 than among clusters of either small (Kolmogorov-Smirnov [K-S] chi-square = 39.8, $P < 0.001$) or medium-sized patches (K-S chi-square = 100.2, $P < 0.0001$). However, this difference had disappeared by 1989; by then, the average experimental unit of each patch type had essentially converged on the same distribution (K-S chi-square = 0.097, $P = 0.44$, and K-S chi-square = 0.056, $P = 0.45$, for comparisons of single large patches with clusters of small and medium patches, respectively). Community simi-

larity ($100 - PR$) decreased with distance in both large and small patch size groups in 1985 (regression slopes as follows: groups of small patches = $-0.112 \pm 0.058, R^2 = 0.012$; large patches = $-0.220 \pm 0.057, R^2 = 0.041$) (Fig. 7). Data for 1989 indicate that a relationship between inter-quadrat distance and similarity held for only large patches (regression slopes: groups of small patches = $-0.038 \pm 0.045, R^2 = 0.002$; large patches = $-0.128 \pm 0.038, R^2 = 0.031$).

DISCUSSION

The current state of any plant community represents a sum of processes, including initial conditions, wide-ranging events, and spatially localized dynamics (Rejmánek 1984, Fowler 1990, Gibson and Brown 1992). The conceptual models presented in the *Introduction* suggest that the size and spatial context of habitat patches undergoing succession may have an impact on how succession occurs, provided that colonization from external source pools, coupled with local extinction and internal spatial fluxes, is important.

Habitat patchiness, succession, and species diversity

The rate of succession, measured as temporal change in the biomass of major life history groups and rates

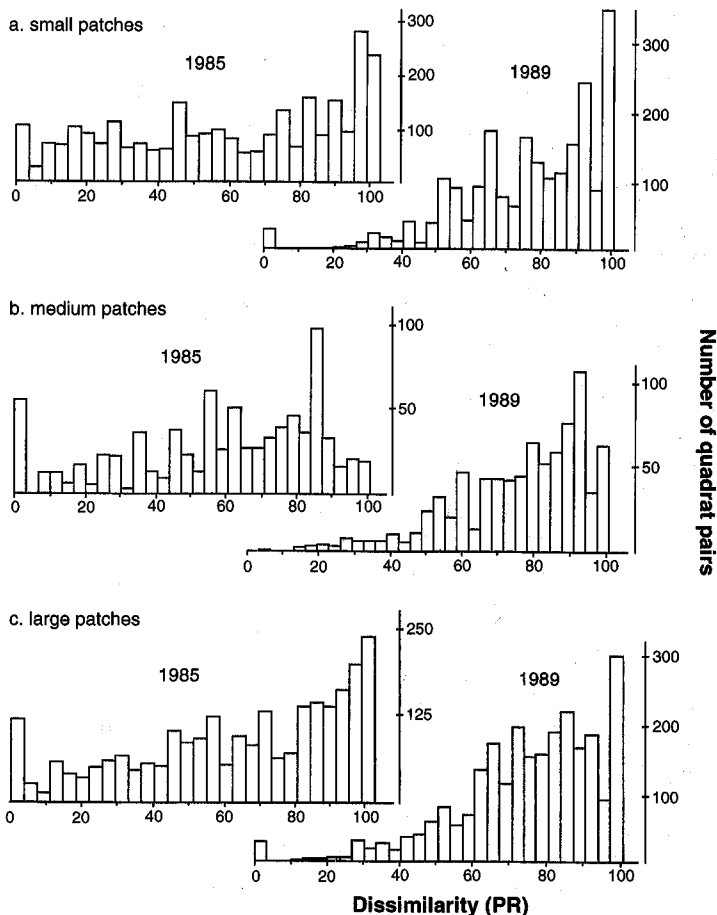


FIG. 6. Distributions of local community dissimilarity (percent remoteness, PR) in fall 1985 and fall 1989. Data represent all quadrat pairings within each of (a) the six clusters of 10–15 small (32 m²) plots, (b) the three clusters of six medium (288 m²) plots, and (c) the six large (0.5 ha) plots.

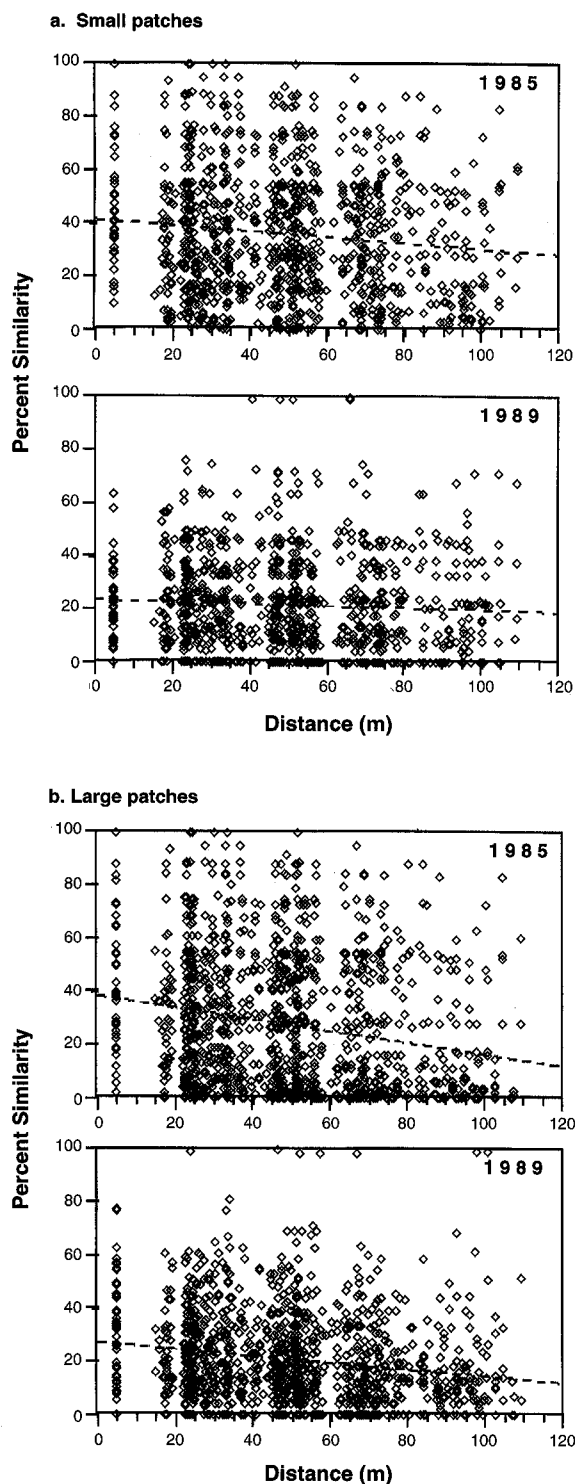


FIG. 7. Relationship between local community similarity ($100 - PR$) and distance between quadrats, from the data reported in Fig. 6. Slope values are reported in the *Results*.

of species turnover, did not significantly vary with the level of habitat patchiness. It seems fair to conclude that habitat fragmentation, at the scale imposed in this experiment, did not have a marked effect on the overall rate or pattern of early secondary succession. Spatially neutral explanations for succession, variation among plant species in life-history traits coupled with interspecific interactions, thus appeared to be of overriding importance. The successional trends reported here correspond well with those usually seen during early secondary succession in old fields in the eastern and central United States (Bard 1952, Myster and Pickett 1988, Southwood et al. 1988, Bazzaz 1990). In particular, we observed an initial brief period of dominance by weedy annuals, as is typical in recently abandoned old fields (Bornkamm 1985, Brown and Southwood 1987), followed by sequential dominance by a variety of herbaceous perennials (Pickett 1982, Inouye et al. 1987, Hendrix et al. 1988, Schmidt 1988), with a small but growing pool of woody plants. This commonly observed trajectory was not markedly affected by habitat patchiness.

Most measures of species diversity were likewise not markedly affected by the degree of local habitat subdivision. Species richness did increase with patch size, as expected among groups of variably sized islands (Preston 1962, MacArthur and Wilson 1967) or nested sampling quadrats (Gleason 1920). The mean number of species per unit area, however, did not vary among patches of different sizes. The contrast between these two types of species-area curve is generally not discussed in biogeographic analyses (Holt 1992, 1993), but it is pertinent to analyses of local community structure, and to understanding how diversity is partitioned at fine spatial scales (Kelly et al. 1989, Kohn and Walsh 1994). Nevertheless, in our study both coarse measures of diversity, such as the relative abundances of different life history forms, and finer measures, such as the number of species per square metre, generally failed to discriminate among the successional plant communities that developed on different-sized patches. Three exceptions stand out.

Patch size effects on vegetation dynamics and patterning

First, the component of species richness consisting of the total number of nonshared species, unique to a given patch size, was highest in the least subdivided system (the six largest patches). The 23 species unique to the large patches include a wide (and miscellaneous) range of life forms (seven grasses, 15 forbs, and one tree; nine annuals; 14 nonnatives). None contributed substantially to cover and all were infrequent, suggesting a stochastic, essentially nonrepeatable component of community assembly in our system.

Second, clonal species were more prone to local extinction in smaller patches. This result can be interpreted in the context of our introductory discussion on

internal patch dynamics and succession. A fraction of the potential growth of a clonal plant in an isolated patch may be wasted, if it grows outwards, but wastage is reduced on larger patches, which have less relative perimeter. Larger patches can also contain larger and better dispersed populations, capable of rapid recolonization into local vacant sites (as in a small embedded patch). It follows that clonally regenerating plants may be both more easily lost and less easily replaced on smaller patches. However, populations of early appearing clonal plants (primarily *Aster pilosus*, *A. simplex*, and *Juncus* sp.) that were lost from small patches were also highly diminished in relative cover on larger ones; although they held on longer, those populations on larger patches did not substantially inhibit succession. The predominant species among patches of all sizes after 6 yr of succession was Canada goldenrod, *Solidago canadensis*. Virtually all (>98%) of its original populations persisted and increased in patches of all sizes. One explanation for this general result lies in observations that Canada goldenrod retains inter-ramet connections for longer periods of time than many of its competitors (Bazzaz 1990).

Regardless of the mechanisms involved, such differences noted at the level of individual species were not evident in community-level measures, such as species diversity or functional group abundance. Usher (1987b) has argued that measuring plant community richness in habitat islands is inadequate for estimating the effects of habitat fragmentation on plant populations. Our results, as well as data for the animal communities in this study (Robinson et al. 1992), support that contention, and demonstrate that whole-community measures may fail to detect severe consequences for particular populations and species (see also Margules et al. 1994).

Third, we noted a difference in the fine spatial scaling of community similarity. Nearby points in space diverged in community composition during succession, but the rate of such fine-scale divergence was slower in the largest patches. As with the enhanced persistence of clonal populations on larger patches that we observed, this finding suggests that habitat subdivision breaks up the local spatial dynamics that reinforce local community similarity. Again, however, this effect of patch size on spatial patterning at this fine scale did not seem to affect the overall pattern of secondary succession.

Conclusions and future directions

With the above exceptions, patches in our fragmented system more closely resembled a "null" patch model (e.g., Egler 1954) than an isolated patch model. Abandoned agricultural fields typically contain a large seed bank that is often rich in early successional herbs. In our case, it is not unlikely that the initial seed bank was the predominant source pool for the majority of the species observed (e.g., Marks and Mohler 1985).

Many species, including the predominant species of all censuses were present from the start. The very rapidity of early secondary succession (compared to a classic primary succession) indicates that long-distance dispersal is not typically required for initial colonization, ruling out one potentially significant mechanism by which patch size would influence the rate of early succession.

In the future, as our experimental patches advance toward woodland vegetation, long-distance recruitment of wind- and bird-dispersed trees and shrubs should play a much stronger role in succession, and patch size could become increasingly important as a modulator of successional trajectories (Holt et al. 1995). In addition, other diverse processes could begin magnifying patch size effects as succession proceeds. For instance, the increasing biomass within successional patches may sharpen abiotic differences between them and the surrounding interstitial areas, differences that should be more pronounced on larger patches, given their lower perimeter-to-area ratios. Also, later successional plants may have more stringent germination requirements that are only satisfied after intermediate species have invaded and become established (e.g., Werner and Harbeck 1982, Harrison and Werner 1984), and patch size effects on one species could cascade through other, partially dependent species (Holt 1993).

Successional pathways are manifestly diverse and variable, yet broadly repetitive. This intriguing paradox has led to a wealth of inquiry, while fueling one of ecology's classic debates. In our experimental setting, the same sequence of early secondary succession was essentially repeated at all patch sizes, despite variation in the responses of individual populations. From this we conclude that, at the spatial scales imposed by our experiment, spatial dynamics plays a minor role in determining the course of early secondary succession.

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Figure 2 was prepared from aerial photographs by Kansas Remote Sensing, Inc.

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