

Woody plant colonization in an experimentally fragmented landscape

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The pattern of distribution and abundance of woody plants colonizing old fields is influenced by landscape spatial features, in particular, by the distance from the old field to propagule sources and the size of the habitat patches undergoing succession. Colonization is also influenced by species life history traits, such as dispersal mode, growth form, and fecundity. As part of a long-term project studying effects of habitat fragmentation on secondary succession at the prairie-forest ecotone, we have examined the colonization patterns of early-successional woody plants in an experimentally fragmented old field, with emphasis on the three woody species [*Cornus drummondii* C. A. Mey (rough-leaved dogwood), *Ulmus rubra* Muhl. (slippery elm), and *Juniperus virginiana* L. (red cedar)], which currently dominate the woody community on the site. The shapes of the colonization curve (proportion of colonized quadrats vs time) differed between *C. drummondii* and *U. rubra*. The rate of colonization by *C. drummondii* showed a pattern of acceleration after its initial colonization, consistent with rapid in situ recruitment from clonal growth and early seed production. By contrast, colonization by *U. rubra* fits a roughly linear pattern, consistent with recruitment only from external propagule sources. For both *C. drummondii* and *U. rubra*, density is currently greater in large patches than in small patches. No patch size difference was found for *J. virginiana*. The stem density of both *C. drummondii* and *U. rubra* exponentially decreased with distance to external propagule sources. The negative exponential pattern of *U. rubra* (wind-dispersed) with distance is sharper than that of *C. drummondii* (bird-dispersed). Moreover, the amount of spatial variation in density explained by distance to source is greater on small patches. Our results highlight the importance of life history traits of colonizing species and spatial aspects of habitat during succession.

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Habitat fragmentation is a topic of growing concern among ecologists and conservation biologists (Noss and Csuti 1994, Schwartz 1997). As in island biogeography (MacArthur and Wilson 1967), two spatial features of the patches comprising fragmented habitats – the area of the patches themselves, and their distances from other propagule sources – can affect population and community dynamics. Habitat fragmentation in complex landscapes also often involves other long-term and large-scale ecological processes, such as disturbance

(Saunders et al. 1991, Esseen 1994). Following disturbance or changes in landuse, many systems experience succession (directional changes in vegetation composition or structure (Glenn-Lewin et al. 1992)). Studies of vegetation dynamics have traditionally emphasized factors such as life history strategies, competition, and herbivory as drivers in succession (Miles 1987). Spatial aspects of succession have been best documented in studies of the effect of distance from seed source on woody plant colonization into old fields (Buell et al.

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1971, Harrison and Werner 1984, McDonnell 1986, Gill and Marks 1991, Myster and Pickett 1992, Burton and Bazzaz 1995, Berkowitz et al. 1995). However, the effect of patch size per se on secondary succession has rarely been examined.

In the autumn of 1984, a long-term experiment was initiated in the forest-prairie ecotone of northeast Kansas, aimed at documenting the effects of fragmentation, especially with regard to patch size and landscape position, on the rate and pattern of secondary succession (Fig. 1). During the first 6 years of this study (1984–1990) the system was dominated by herbaceous, old-field species (e.g. perennial species in the genera *Aster* and *Solidago*), and there were only minor effects of patch size on succession (Robinson et al. 1992, Holt et al. 1995). In more recent years, we have observed an acceleration of invasion by woody species into the site. In this paper, we document how patch size is now exerting an increasingly large effect upon succession as woody plant invasion proceeds apace, and discuss some plausible biological mechanisms which could produce these spatial effects. We will also analyze the effect of distance from sources upon the magnitude of these patch size effects.

Before presenting our methods and results, we first present two general models for colonizing dynamics, distinguished by the assumptions made regarding the in situ recruitment of colonizing species. We sketch some general features of distance effects on woody plant colonization in succession and outline why one might also expect to observe patch size effects. We then present specific hypotheses regarding the dominant woody species in our system.

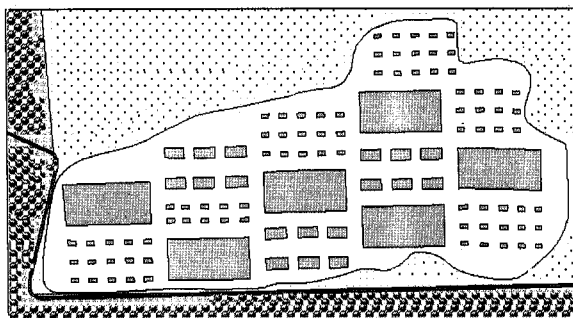


Fig. 1. Study site: Kansas Biotic Succession Facility (KBSF), part of the Univ. of Kansas Nelson Environmental Study Area. The interstitial area is mowed to a low turf. The source is a mixed-species deciduous woodland. All the species found on the KBSF site are found in reasonable abundance in these woods (as well as species that have not yet colonized). In particular, a study by Marshall (1994) showed that *C. drummondii* and *U. rubra* were present abundantly along the entire edge of the depicted forest area, and several hundred mature *J. virginiana* were scattered in the woods to the south.

Two contrasting modes of woody plant colonization

The overall pattern of woody plant colonization in an old field is determined by a combination of distant and in situ propagule sources. Consider colonization by idealized species showing one or the other (but not both) mode of colonization.

1) Dispersal solely from external sources. If a species can not produce propagules in the successional time frame in question (e.g., a long-lived tree colonizing an old field), then its pattern of colonization must reflect entirely dispersal from external propagule sources, modified by subsequent mortality. A simple model (that ignores position within a field) to describe such colonization is as follows. Assume that colonization of empty sites occurs at a constant rate per empty site, and that there is no death leading to new empty sites. The following model describes a field being "filled up" by external colonization

$$\frac{dp}{dt} = c(1 - p), \quad (1)$$

where p is the proportion of sites (e.g., quadrats) colonized, and c is a constant depending on the availability of propagules arriving from external sources. With external inputs alone, the number of colonized sites first increases roughly linearly, then gradually levels off asymptotically as empty sites become occupied (Fig. 2a).

2) Internal recruitment. By contrast, species with short maturation time, high reproductive rate, and good short-distance dispersal abilities can contribute propagules to an old field in a relatively short time after initial establishment. If the rate of input of outside propagules is small enough to be ignored compared to the rate of propagule production by colonists, following initial establishment, a logistic equation can depict colonization dynamics:

$$\frac{dp}{dt} = r p (1 - p). \quad (2)$$

Here, r is a constant that combines both fecundity and within-field dispersal abilities of the species. The rate of population growth depends on an intrinsic "growth rate" of colonization of empty sites (r), the number of previously colonized sites (p), and the number of uncolonized sites ($1 - p$). The number of colonized sites increases slowly at the beginning, because of the small number of previously colonized sites available to provide propagules. The number of occupied sites then increases quickly, because there are substantial numbers of both previously colonized sites and uncolonized sites. But eventually, the number of colonized sites levels off when most local sites have been colonized (Fig. 2b).

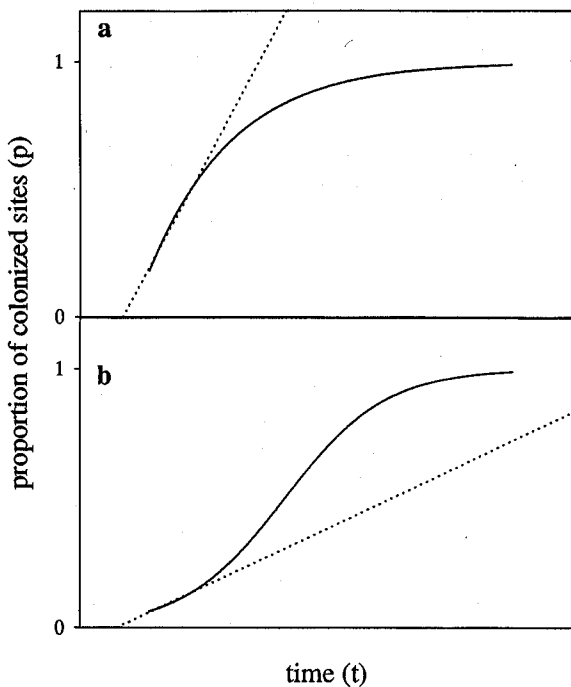


Fig. 2. Patterns of woody plant colonization in old fields. The dotted, straight lines are regression lines of proportion of colonized sites at the early stage vs time. a) Colonization is supported by external propagule sources (eq. 1 in text). This equation implies a time-course of colonization $p_T = 1 - (1 - p_0) e^{-cT}$, where T is the time elapsed since colonization began, p_0 is the initial proportion of colonized sites, and p_T is the proportion of colonized sites at time T . b) Colonization is supported by internal propagule sources (eq. 2 in text). The time-course of colonization is predicted to be.

$$p_T = \left(1 + \frac{1 - p_0}{p_0 e^{cT}} \right)^{-1}$$

Distance effects

The above conceptual models are not spatially explicit. More generally, one could let p_x be the proportion of sites at distance x from a source pool, and c_x or r_x be the colonization rate or growth rate at this distance, to depict the wave of invasion as a function of distance to the source across the field.

Early in old field succession, tree abundance typically decreases exponentially as a function of distance from nearby forest edges (Myster and Pickett 1992). The seed bank in old fields usually lacks woody species (Hughes and Fahey 1988, Gill and Marks 1991, Myster and Pickett 1992), so the distribution of woody stems at early stages of old-field succession (prior to in situ recruitment) must be primarily determined by the spatial and temporal pattern of seed dispersal from external sources. Seed rain density of woody species is expected to decrease exponentially with distance to parental trees (Hoppe 1988, Hughes and Fahey 1988,

Debussche and Isenmann 1994, Greene and Johnson 1996). The negative exponential tendency of stem density is expected to be more sharply defined for wind-dispersed species than for bird-dispersed species, because the seed distribution of a bird-dispersed species is determined by the behavior of the dispersal agent, as well as by the proximity of seed sources (McDonnell 1986, 1988).

An initial exponential pattern in the abundance of woody stems should become less distinct as succession proceeds (Myster and Pickett 1992), because of the impact of processes that are unrelated to distance to propagule sources. For instance, changes in competition, herbivory, and the attractiveness of a given area to animal dispersal agents can change the density of seedlings and adult trees (McDonnell 1986, Gill and Marks 1991, Debussche and Isenmann 1994). Moreover, for species that can reproduce rapidly, in situ recruitment (e.g. clonal growth and within-patch seed dispersal) by colonizing species should also modify the original strong signal of distance.

We hypothesized that species with bird-dispersed seeds and life histories permitting rapid in situ recruitment would show less strong distance effects in establishment.

Patch size effects

In a fragmented landscape, distance effects may overlay effects of patch size. A general conceptual framework regarding effects of patch size on the rate of secondary succession has been suggested by Holt et al. (1995). They hypothesized that in circumstances where colonization into isolated patches is important, and superior competitors are poorer dispersers, the rate of succession toward woody vegetation might be expected to increase with patch size. Holt et al. (1995) outlined a number of different mechanisms by which patch area could influence succession. For instance, a larger habitat patch could trap more colonists, as well as allow for the more efficient operation of within-patch colonization or short-distance dispersal due to clonal growth or in situ seed production.

Moreover, if species are roughly competitively equivalent, succession may proceed more slowly in small patches than in large patches due to a stronger inhibition effect of earlier colonists on later ones in small patches. Earlier colonists may inhibit invasion of later arrivals by preempting space and other resources; invasion may occur only when residents are damaged or killed (Connell and Slatyer 1977). As individual plants die, dead residents could be replaced by others either from the immediate within-patch neighborhood, or from external sources. Since a given site in a small patch is exposed to low rates of intra-patch dispersal events, compared to a similar site in a large patch, a

dead resident in a small patch is more likely to be replaced by species drawn from its immediate neighborhood, which are most likely to be early colonizing species themselves. Hence succession in small, isolated patches might get "stalled" at an early stage.

Edge effects provide another kind of "area-related" effect. In old field systems, the edge of a patch compared to the patch interior usually has harsher and more variable abiotic conditions, such as higher insolation, higher wind speed, lower soil moisture, and greater temperature fluctuations (Kapos 1989, Freidenburg 1998). An altered abiotic environment could influence processes such as germination and individual growth rates. A large patch has a proportionally smaller edge area than does a small patch. This geometrical fact may facilitate succession by providing a larger core area with moderate abiotic conditions. Finally, patches of different sizes may attract different animal dispersal agents or herbivores, due to their behavioral preferences for patches differing in area. Differences in animal behavior can affect seed dispersal as well as seed and seedling predation rates, all of which may influence the rate of vegetation succession as a function of patch size (Schweiger 1998).

Based on these ideas (see also Holt et al. 1995), we hypothesized that once woody species had begun to invade our site, after several years of such colonization woody stem density should be higher in a large patch than in a small one of the same age, given the same distance to propagule sources. We also hypothesized that this patch size effect would complement a distance effect. Moreover, we expected these spatial effects of area and distance to reflect life history differences among species, and in particular the potential for short-term local recruitment.

Species-specific predictions

We have documented in detail the colonization pattern of the three most common woody species in an experimentally fragmented old field located in the Kansas prairie/forest ecotone: *Cornus drummondii* C. A. Mey (rough-leaved dogwood), *Ulmus rubra* Muhl. (slippery elm) and *Juniperus virginiana* L. (red cedar). Because *C. drummondii* can grow clonally and matures rapidly to produce seeds, we expected its growth to be more logistic than for the other species (Fig. 2b). Given our expectation about the effects of patch size on succession, we predicted that the stem density of each species should be greater in large patches than in small patches. Given the importance of within-patch spatial dynamics as a potential mechanism leading to this pattern, we expected the area effect to be shown most strongly by *C. drummondii*. We further predicted that the stem density of early colonists should decrease exponentially with increasing distance to nearby propagule sources

for all species, but that this negative exponential pattern should deteriorate with time, as expressed in comparisons among size classes within each species. We also predicted that the negative exponential pattern in the distribution of stem densities should be sharper for the wind-dispersed species, *U. rubra*, than for the two bird-dispersed species, *C. drummondii* and *J. virginiana*.

Methods

Study site

The study was conducted at the Kansas Biotic Succession Facility (KBSF), located in northeast Kansas. KBSF is an experimentally fragmented model system for examining the long-term effect of patch size on secondary succession (Robinson et al. 1992, Holt et al. 1995) (Fig. 1). Since 1984, an array of replicates of three patch sizes (4 × 8 m, 12 × 24 m, and 50 × 100 m) has been maintained by frequent mowing of the interstitial area. The patches have undergone secondary succession without human disturbance. Permanent sample quadrats (416 before 1994 and 452 since 1994) have been used to monitor plant community composition. The overall successional trend follows the expected pattern of old-field succession in eastern and central North America (Bard 1952, Bazzaz 1968, 1996, Holt et al. 1995), with initial dominance by annual herbaceous plants, then by perennial herbaceous plants, and now by a set of early successional woody species.

Study species

Cornus drummondii, *U. rubra*, and *J. virginiana* were the three most abundant tree species at the site in 1995. All three species are broadly distributed in eastern North America, ranging from the southern US north into Canada (Steyermark 1981). *Cornus drummondii* occurs in the eastern two-thirds of Kansas (Stephens 1969). Its diverse habitats include swamps, wet to dry woods, marshes, and edges of lakes and rivers (Anon. 1986). It often forms clumps of stems growing from shallow, spreading roots (Anon. 1986). The small, white, lipid-rich fruits ripen in September and October in Kansas (Stephens 1969) and are eaten mainly by birds (Willson and Whelan 1993). *Ulmus rubra* occurs in the northeast half of Kansas (Stephens 1969). Its habitats include dry uplands and rocky woods, open forested bluffs, and stream banks (Steyermark 1981). Its winged fruits (samaras) ripen in April and May in Kansas (Stephens 1969) and are dispersed by wind (Burrows 1975). *Juniperus virginiana* is common on the limestone hills of east central Kansas (Stephens 1969). Seeds mature in September in Kansas (Stephens 1969) and are eaten by birds and other animals (Holthuijzen and Sharik 1984).

Data collection

Since 1990, by which time woody species colonization had become prominent at the KBSF site, an array of 4×4 m and nested 1×1 m² permanent quadrats have been used to count woody stems. Vegetation composition, previously consisting primarily of herbaceous plants, had been sampled in the preceding 6 years in the 1×1 m quadrats (Robinson et al. 1992); the larger 4×4 m quadrats were added so as to sample more adequately invasive woody species. In each census, woody stems are grouped by species in five size classes by stem height: 0–0.25 m, 0.25–0.5 m, 0.5–1.0 m, 1.0–2.0 m, and >2.0 m. The dataset includes both the three focal species, *C. drummondii*, *U. rubra*, and *J. virginiana*, and other woody invaders, including shrub and vine species (Fig. 4 legend for list). The data reported here are mainly for the 1995 woody stem count data collected in the 164 4×4 m quadrats from small patches (4×8 m) and the 180 quadrats from large patches (50×100 m).

Data analysis

Based on 1992 aerial photographs, we created maps of the patches, the permanent sample locations inside the patches (not shown in Fig. 1), and the road indicating the boundary of the study area. The maps were created in a geographical information system (GIS) (ARC/INFO v. 7) (Fig. 1). The forest across from the KBSF south and western boundary road acts as the “mainland” source for the study area, both because of its proximity, and because prevailing winds are from the southwest. The road was thus regarded as the nearest boundary of source populations. The nearest Euclidean distance from each sampling location to the road was calculated using ARC/INFO GRID software.

The general trend of woody plant colonization was examined from the beginning of the project until 1996. Because seedlings became established in the spring, data were drawn from vegetation censuses conducted in either summer or autumn. We calculated the proportion of 1×1 m quadrats colonized by any woody species, and the proportions of quadrats colonized by each study species.

As one indication of whether a species' colonization is supported mainly by external propagule sources, or instead by internal propagule sources, we examined the shape of its colonization curve. Deviations from a linear regression of abundance against the first seven years of occupancy were examined. In order to obtain an unbiased regression slope, we jackknifed the data and carried out simple linear regression, dropping each of seven years of data systematically (Sokal and Rohlf 1995). We used the jackknifed slope and its correspond-

ing Y-intercept to project the colonization line of the first seven years. A colonization dynamic which relies entirely on external propagule sources should gradually level off with time (as in the saturation curve of Fig. 2a), so the number of colonized sites should initially fit a straight line, but with systematic deviations (residuals) below the line at later stages. By contrast, colonization dynamics with a substantial input from internal propagule sources should increase fastest at the middle stage of colonization before leveling off, so the number of colonized sites after the initial stage should deviate above the regression line (Fig. 2b).

The numbers of 4×4 m quadrats colonized by woody species and total stem counts of each woody species in 4×4 m quadrats in 1995 were also calculated.

The effects of patch size on stem density were examined using a non-parametric statistic, the Kruskal-Wallis test, because the data were not normally distributed and sample sizes in different categories were unequal. Stem densities in each size class for each species were compared between small and large patches.

The effects of distance from patches to the propagule source on stem density were examined using partitioned regression analysis, a technique that seems well suited to our system. The distributions of data points in stem density-distance scattergrams typically resemble a triangle (see Figs 8 and 9 for examples) (Thomson et al. 1996). According to Thomson et al. (1996), in a complex system the relationship between two study variables may best be reflected by data points on the outer edge or “ceiling” of the triangle (in other words, by covariation in extreme values of the two variables). The data points below the ceiling are influenced by both the study variables and other unknown or unmeasured factors. To find the relationship conveyed by data points on the “ceiling”, one can do a linear regression using all data points first, then carry out a second linear regression using only those data points with positive residuals in the previous regression. The second regression helps reveal the relationship between the extreme values of the two study variables, therefore revealing aspects of the true relationship that may otherwise be obscured. We first did simple linear regression on the \log_e transformed stem density against the distance to nearby sources. This first ordinary regression was done using all data points; the second partitioned regression was then done using those data points with positive residuals from the first regression. In practice, the partitioned regression applied to our dataset largely resulted in eliminating from the dataset quadrats with zero density. A site may be unsuitable or unoccupied for reasons unrelated to distance to sources. Including large number of unoccupied sites (due to edaphic factors) can obscure true distance effects. The second regression line was interpreted to examine the relationship between stem density and distance. The slopes from the second regressions were compared between patch sizes and

Table 1. *Cornus drummondii* distance effects: slope and R^2 values of partitioned regression of stem density as a function of distance to source habitat. $\text{Log}_e(\text{stem density} + 1)$ was the dependent variable. Distance to source was the independent variable. "1st regression" refers to the linear regression using all data points. "2nd regression" refers to the linear regression on the subset of data points that had positive residuals in the first regression. The letter next to the regression slope indicates that the null hypothesis was rejected for that test. * $0.01 \leq p < 0.05$, ** $0.001 \leq p < 0.01$, *** $p < 0.001$. a) test H_0 : slope = 0. b) test H_0 : 2nd slopes in the same size class are equal across patch sizes. c) test H_0 : all negative 2nd slope values in small patches are equal. d) test H_0 : the 2nd slope values in large patches from two large size classes, 1.0–2.0 m and > 2.0 m, are equal e) test H_0 : the 2nd slope values in large patches from two small size classes, 0–0.25 m and 0.25–0.5 m, are equal.

Size class		Small patches		Large patches	
		1st regression	2nd regression	1st regression	2nd regression
0–0.25 m	Slope	–0.00089	+0.00032 b***	+0.00562 a***	+0.00527 a***, b***, e*
	R^2	0.008	0.002	0.107	0.218
0.25–0.5 m	Slope	–0.00202 a**	–0.00192 a*, b***	+0.00304 a*	+0.00236 a**, b***, e*
	R^2	0.042	0.079	0.033	0.082
0.5–1.0 m	Slope	–0.00405 a***	–0.00356 a***, b***	+0.00052	+0.00056 b***
	R^2	0.118	0.226	0.001	0.005
1.0–2.0 m	Slope	–0.00384 a***	–0.00346 a***	–0.00005	–0.00178 a*
	R^2	0.109	0.189	0.000	0.045
> 2.0 m	Slope	–0.00308 a***	–0.00413 a***	–0.00088	–0.00404 a***
	R^2	0.138	0.339	0.004	0.151

among stem size classes within species. The legends for the tables list the statistical hypotheses we examined in both the ordinary regression and partitioned regression analyses. For instance, the symbol for test a in Table 1 denotes the existence of a significant non-zero regression coefficient relating log abundance to distance for *C. drummondii*.

All statistical analyses were performed using MINITAB software (v. 11.13).

Results

General trends of woody plant colonization

In general, woody plants have colonized the field at a constant rate, resulting in a roughly linear relationship between proportion of quadrats colonized and time. During a span of ten years, woody plants colonized ca 80% of the 1×1 m quadrats (Fig. 3). The colonization pattern of all woody species combined was mainly determined by *C. drummondii*, the dominant woody species as measured by either frequency or abundance (Figs 3 and 4).

In 1995, *C. drummondii* was present in 389 of 452 permanent 4×4 m quadrats. It had the highest stem density among all the tree species: the average stem density over all size classes and all quadrats (including unoccupied as well as occupied quadrats) was 1.5 stems m^{-2} , and the average density over only occupied quadrats was 1.7 stems m^{-2} . *Umus rubra* was the second most common tree species, present in 233 of 452 perma-

nent 4×4 m² quadrats. Its average stem density over all size classes and all quadrats was 0.14 stems m^{-2} , and the average density over only occupied quadrats was 0.28 stems m^{-2} . *Juniperus virginiana* was the third most common tree species, present in 77 of 452 permanent 4×4 m quadrats. Its stem density was very low; the average stem density over all size classes and all quadrats was 0.013 stem m^{-2} , and the average density over only occupied quadrats was 0.081 stems m^{-2} .

The colonization of *C. drummondii* fits a logistic growth pattern, consistent with the importance of inter-

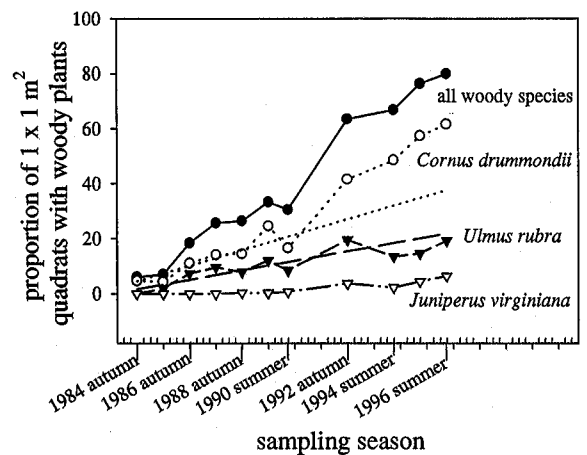
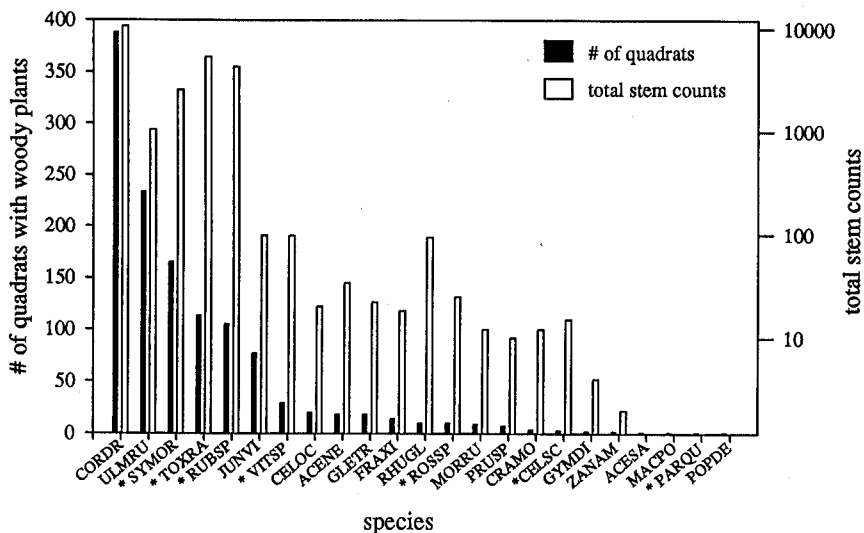


Fig. 3. Trend of woody plant colonization at KBSF. Dotted lines: regression of proportion of woody plant colonized quadrats vs time (using jackknifed slope and its corresponding Y-intercept obtained from 1984 to 1990 data), *Cornus drummondii* (upper line) and *Ulmus rubra* (lower line).

Fig. 4. Summary of frequencies and abundances of woody species found in all 452 4 × 4 m quadrats at KBSF in 1995. The following woody species were found in the quadrats (ranked by abundance, * shrub or woody vine species): *Cornus drummondii* (CORDR); *Ulmus rubra* (ULMRU); *Symphoricarpos orbiculatus* (SYMOR); *Toxicodendron radicans* (TOXRA); *Rubus* spp. (RUBSP); *Juniperus virginiana* (JUNVI); *Vitis* spp. (VITSP); *Celtis occidentalis* (CELOC); *Acer negundo* (ACENE); *Gleditsia triacanthos* (GELTR); *Fraxinus* spp. (FRAXI); *Rhus glabra* (RHUGL); *Rosa* spp. (ROSSP); *Morus rubra* (MORRU); *Prunus* spp. (PRUSP); *Crataegus mollis* (CRAMO); *Celastrus scandens* (CELSC); *Gymnocladus dioica* (GYMDI); *Zanthoxylum americanum* (ZANAM); *Acer saccharinum* (ACESA); *Maclura pomifera* (MACPO); *Parthenocissus quinquefolia* (PARQU); and *Populus deltoides* (POPDE).



nal propagule sources augmenting external seed sources (see Fig. 2b). The proportion of colonized quadrats in later years (from 1991 on) exceeded the numbers projected by extrapolating linearly from the data of earlier years (1984–1990) (Fig. 3). By contrast, colonization by *U. rubra* fits a pattern consistent with a dominant role for external seed sources (Fig. 2a). The number of colonized quadrats increased roughly linearly through all the years, with no obvious signs of saturation (Fig. 3). We did not analyze the colonization pattern of *J. virginiana*, because of its low abundance.

Patch size effects

Cornus drummondii

By 1995, patch size had affected stem densities of *C. drummondii*, particularly in small size classes. The densities of stems in the small size classes (0–0.25 m, 0.25–0.5 m, and 0.5–1.0 m) were significantly higher in large patches than in small patches ($p < 0.01$) (Fig. 5). The stems in size class 1.0–2.0 m also had higher density in larger patches, but the difference was not quite statistically significant ($p = 0.082$). No significant patch size difference was found for the stems in the largest size class, > 2.0 m.

Ulmus rubra

Similar to *C. drummondii*, patch size affected stem densities of *U. rubra* positively (Fig. 6). For stems in the two smallest size classes (0–0.25 m and 0.25–0.5 m) stem densities were significantly higher in large patches than in small patches ($p < 0.01$). For stems in the larger size classes, 0.5–1.0 m, 1.0–2.0 m and > 2.0 m, no

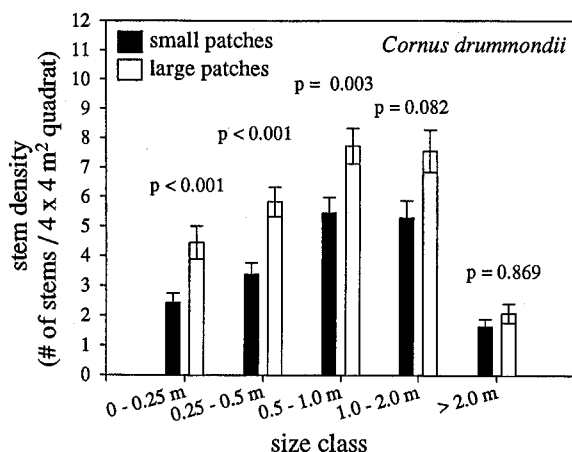


Fig. 5. Stem densities of *Cornus drummondii* (mean ± SE) by size class and patch size in 1995. P-values are from the Kruskal-Wallis test. Ho: stem densities in the same size classes are equal between small and large patch sizes.

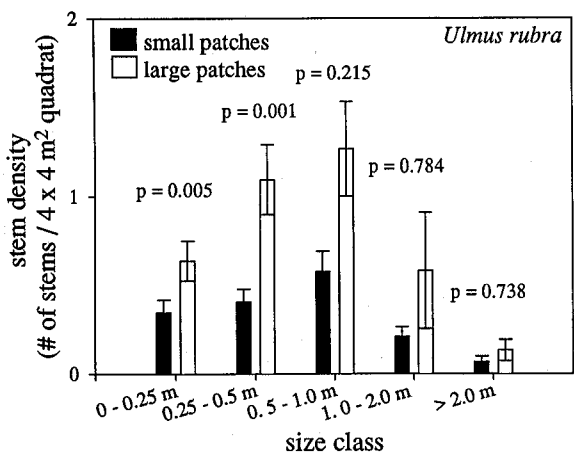


Fig. 6. Stem densities of *Ulmus rubra* (mean \pm SE) by size class and patch size in 1995. P-values and null hypothesis as in Fig. 5.

significant differences in stem densities were found between small and large patches.

Juniperus virginiana

No significant patch size differences were found for *J. virginiana* in all size classes. Indeed, if anything, stem densities seemed to be larger in small than in large patches (Fig. 7).

Some of the size-by-species classes had small stem counts, which of course might obscure real patch size effects.

Distance effects

We predicted that stem density at establishment should be negatively related with distance, but that this distance effect should deteriorate with time. It is reasonable to surmise that stems in larger size classes tend to be older and so on average colonized the field earlier than small stems (concurrent demographic studies of tagged stems

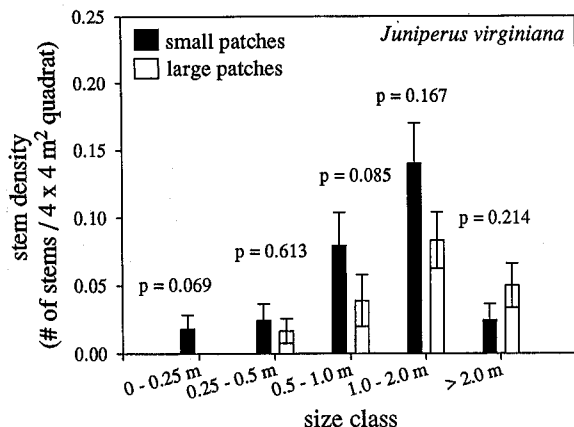


Fig. 7. Stem densities of *Juniperus virginiana* (mean \pm SE) by size class and patch size in 1995. P-values and null hypothesis as in Fig. 5.

support this hypothesis, Yao et al. unpubl.), so we interpret the order of size class, from large to small, as reflecting a temporal order of colonization, from early (large) to late (small).

Cornus drummondii

The most complex patterns are shown by *C. drummondii*. While there is considerable scatter in the data, one can still discern distance effects in this species. However, these effects vary by stem size class and patch size. Examples of the spatial pattern of abundance with distance are shown in Fig. 8. Table 1 collects the results of the regression analyses relating abundance to distance by size class and patch size (in Tables 1 and 2, the letters indicate that a null hypothesis was rejected; see Table legends for details). In the following paragraphs, we describe the somewhat complex interaction between distance and patch size for this species.

In small patches, densities in the four larger stem size classes decreased with distance (Table 1, test a, Fig. 8a), and moreover at similar rates (Table 1, test c). In large patches, stem densities in the two larger size classes also decreased with distance (Table 1, test a, Fig. 8a), and at similar rates (Table 1, test d). By contrast, the two small size classes in large patches increased in density with distance (Table 1, test a, Fig. 8b), and the size class 0–0.25 m increased more rapidly than did size class 0.25–0.5 m (Table 1, test e).

We also compared the magnitude of distance effects within a stem-size class across patch sizes. For these larger size classes (1.0–2.0 m and > 2 m) with a pattern of decreasing abundance with distance for both patch sizes, magnitude of this distance effect is similar across both patch sizes (Table 1, test b). For intermediate size classes (0.25–0.5 m and 0.5–1.0 m), stem densities decreased with distance in small patches, whereas stem densities increased with distance in large patches (Table 1, test b). Thus, there is an interaction between patch size and distance effects, depending on stem size.

In short, the negative distance effects on *C. drummondii* density is strongest in large stem size classes (which represent earlier colonization) and on small patches (which are being colonized more slowly).

Ulmus rubra

Stem densities of *U. rubra* across all size classes and for both patch sizes exponentially decreased with distance to the neighboring woodland; all but one slope from both regressions were significantly < 0 (Table 2, test a, Fig. 9). Stem densities in all size classes on small patches decreased at similar rates with distance. But stem densities in large patches decreased at different rates across size classes; the size class 0.5–1.0 m decreased the fastest (Table 2, test c). Stem densities decreased at greater rates with distance in large patches, than in small patches (Table 2, test b). The larger R^2 values in small patches than in large patches indicated that the negative exponential patterns were sharper in small patches than in large patches (Table 2).

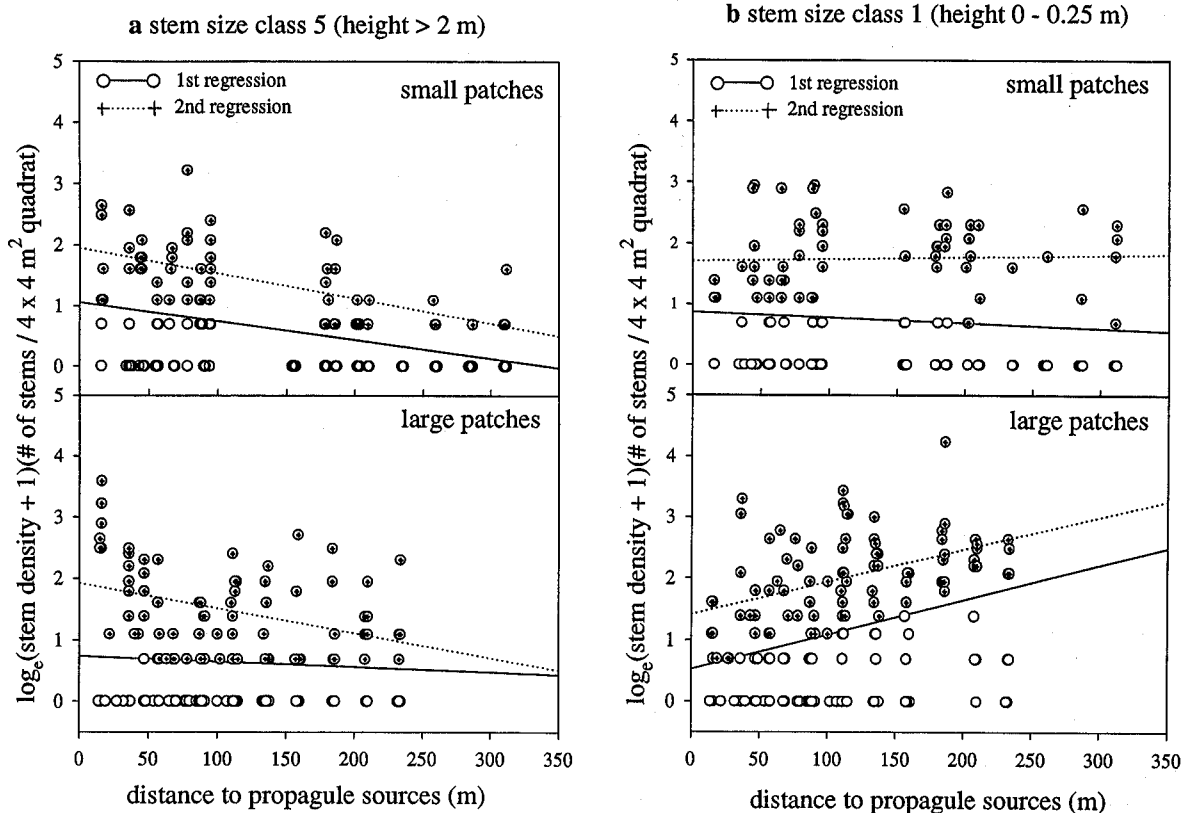


Fig. 8. Examples of the distribution of *Cornus drummondii* as a function of distance to propagule sources. "1st regression" refers to the linear regression using all data points. "2nd regression" refers to the linear regression on the subset of data points that had positive residuals in the first regression (following procedures of Thomson et al. 1996). There is a significant distance effect, but much scatter. a) stem size class 5 (height > 2 m), b) stem size class 1 (height 0–0.25 m).

Juniperus virginiana

No distance effect was detected for *J. virginiana* in any size classes or patch sizes (see Fig. 10).

In summary, the negative exponential patterns were more sharply defined for stems of *U. rubra* than for those of *C. drummondii*, as indicated by larger R^2 values and the absence of any positive effects of distance on abundance for any stem size class in the former species (Tables 1 and 2). Finally, for both species the strength (and in some instances even the sign) of distance effects seemed to depend to some degree both on patch size and on the particular stem size class considered. This suggests an interaction between patch size effects and distance effects.

Discussion

General trends of woody plant colonization

The overall rate of woody plant colonization in our system has been very fast, compared to the rates that can be gleaned from published studies of other old field successions (Table 3). The systems that we found in the

literature that could be reasonably compared to our own included fields on the Piedmont Plateau of New Jersey (Bard 1952) and in the Shawnee Hills of southern Illinois (Bazzaz 1968), sandplains at Cedar Creek Natural History Area, Minneapolis, Minnesota (Inouye et al. 1987, Tilman 1988), old fields in the Piedmont of North Carolina (Oosting 1942), and old fields at Hutcheson Memorial Forest, New Brunswick, New Jersey (Pickett 1982). However, it should be noted that the rapid colonization by woody plants in our field is largely due to a single species, *C. drummondii*. Colonization by *U. rubra* and *J. virginiana* in our field has occurred at rates similar to those reported in other old field studies (Table 3).

Eastern Kansas is located on the western edge of the eastern deciduous forest biome. Among the sites just mentioned, one might a priori expect our site to be the most inhospitable for woody plant establishment; when the study was initiated we expected a low rate of woody plant colonization. Why has the most common woody species in our field, *C. drummondii*, colonized the field at a faster speed than do the dominant species in other old field studies? This is most likely due to aspects of its natural history. Following initial establishment, *C.*

Table 2. *Ulmus rubra* distance effects: slope and R² values of partitioned regression of stem density as a function of distance to the source habitat (see Table 1 legend for definition). * 0.01 ≤ p < 0.05, ** 0.001 ≤ p < 0.01, *** p < 0.001. a) test H₀: slope = 0. b) test H₀: 2nd slopes in the same size class are equal across patch sizes. c) test H₀: 2nd slopes in the same patch size are equal across size classes.

Size classes		Small patches		Large patches	
		1st regression	2nd regression	1st regression	2nd regression
0–0.25 m	Slope	–0.0019 a***	–0.0040 a***	–0.0030 a***	–0.0042 a***, c***
	R ²	0.175	0.740	0.119	0.360
0.25–0.5 m	Slope	–0.0022 a***	–0.0041 a***, b***	–0.0046 a***	–0.0071 a***, b***, c***
	R ²	0.220	0.761	0.180	0.564
0.5–1.0 m	Slope	–0.0027 a***	0.0044 a***, b***	–0.0061 a***	–0.0093 a***, b***, c***
	R ²	0.227	0.671	0.268	0.687
1.0–2.0 m	Slope	–0.0009 a**	–0.0037 a***, b**	–0.0029 a***	–0.0068 a***, b**, c***
	R ²	0.072	0.714	0.140	0.603
> 2.0 m	Slope	–0.0002	–0.0035 a***, b**	–0.0011 a**	–0.0062 a***, b**, c***
	R ²	0.013	0.730	0.059	0.690

drummondii can quickly exhibit a substantial intra-patch contribution to colonization, resulting from its clonal production of new stems and production of large numbers of fruits at young ages and small sizes. We hesitate to draw firm conclusions about the reasons for observed differences between the patterns of woody plant colonization in our field and in other studies, however, because unknown differences in nutrient levels, distances to nearby propagule sources, and rates of propagule production in sources could also lead to differences in the rate of woody plant colonization.

After initial colonization, further establishment by *C. drummondii* may be supported mainly by internal propagule sources. *Cornus drummondii* is a clonal species, with a strong ability to produce vegetative sprouts. Moreover, *C. drummondii* starts to produce fruits even when it is as short as 1.5 m in height in our field (Yao unpubl.). Under good growing conditions, it only takes 4–6 years for a plant to grow to a height of 1.5 m. An adult plant (> 2.0 m in height) can produce over 1000 fruits per year (Yao unpubl. data). Thus, once a sapling of this species becomes established in a patch, it can send out vegetative sprouts and produce seeds to colonize much of the rest of the patch in a short time period. Our data do not permit us to distinguish between stems produced by vegetative growth versus seed germination, but we expect both reproductive modes to contribute to the observed logistic growth pattern. One factor that we are not able to quantify with our quadrat data is the contribution of seed dispersal among patches. In general this should further obscure the initial signal of distance on establishment. Our lab group is currently using a DNA fingerprinting technique (AFLP) to identify clonal individuals and establish genetic relatedness (Patrick unpubl.). We intend to use this information in the future to distinguish the

relative contribution of clonal growth and local vs long-distance seed production to the observed spatial patterns in this species.

stem size class 3 (height 0.5 - 1.0 m)

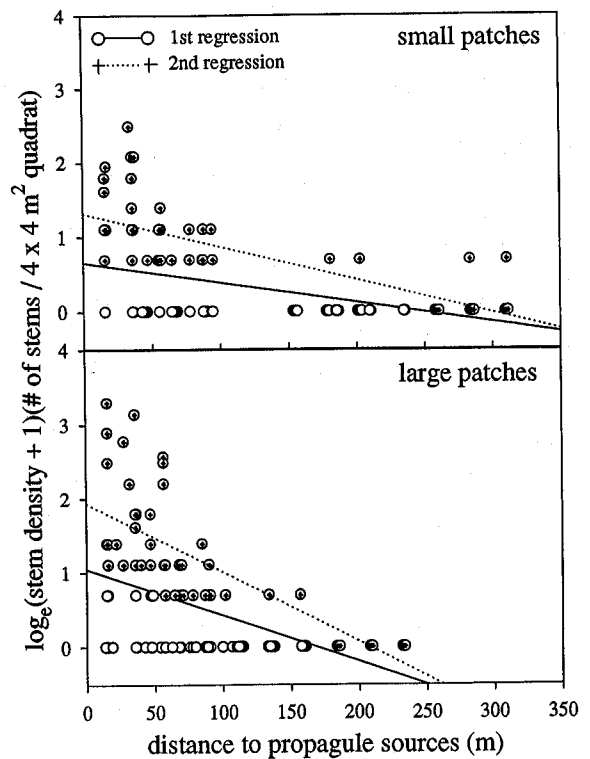


Fig. 9. An example of the distribution of *Ulmus rubra* (height 0.5–1.0 m) as a function of distance to propagule sources. "1st regression" refers to the linear regression using all data points. "2nd regression" refers to the linear regression on the subset of data points that had positive residuals in the first regression. There is a strong distance effect (compared with Fig. 8).

stem size class 3 (height 0.5 - 1.0 m)

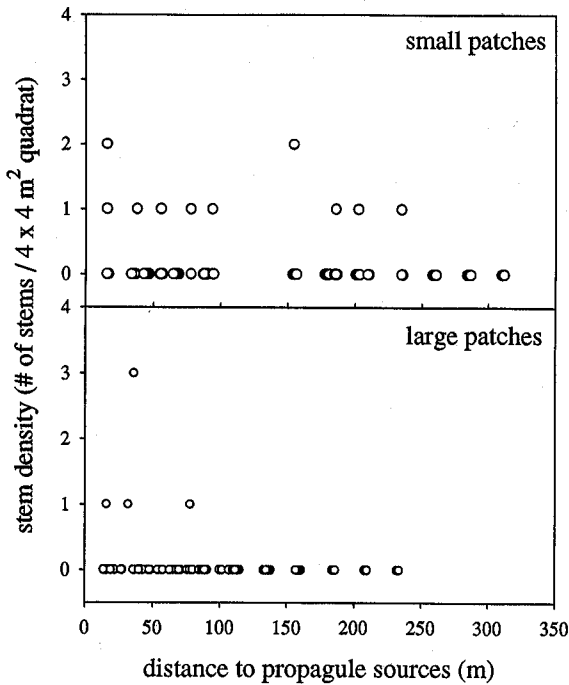


Fig. 10. An example of the distribution of *Juniperus virginiana* (height 0.5–1.0 m) as a function of distance to propagule sources.

By contrast, colonization by *U. rubra* during this same time period has likely been driven entirely by external sources. *Ulmus rubra* starts to produce fruits at heights exceeding 4–5 m in the nearby forest (Fitch pers. comm.).

In 1995, < 20 stems were taller than 4 m, and no stem at all was taller than 5 m in our sample (unpubl.). No fruit production by this species has been observed as yet in our field (Yao and Fitch unpubl.). The long time required for individuals to reach reproductive maturity, and the small number of stems in the field, strongly suggest that the colonization dynamic of this species at our site to date depends entirely on outside seed sources.

Many herbaceous plants and shrubs have life history characteristics similar to *C. drummondii*, whereas most tree species have life histories similar to *U. rubra*. One would thus expect to find logistic patterns of colonization during succession among colonizing herbaceous plants and shrubs, and gradual asymptotic patterns of occupancy among colonizing trees. The exact shape of the colonization curve, of course, should vary by both species and site.

Patch size effects

Two general classes of effects may account for the higher stem density of early successional woody species in larger patches: 1) abiotic effects of patch size, and 2) influence of patch size on dispersal dynamics.

Abiotic effects

As succession proceeds, conditions for woody plant establishment, such as appropriate levels of light intensity, soil moisture, and nutrients, may become more favorable at an earlier stage in large patches than in small ones, due to differing interior/edge ratios. We predict

Table 3. Comparison of woody plant colonization rate between Kansas fragmentation study and other studies of old field succession: Density (# of stems m⁻²), Freq. (frequency, # of occupied samples/# of all samples, %) and Cover (average ground cover, %). Blank spaces imply a species was not recorded, or data was unavailable. *KS, our system. NJ1, Piedmont Plateau of New Jersey (Bard 1952). IL, Shawnee Hill, southern Illinois (Bazzaz 1968). MN, Cedar Creek Natural History Area, Minneapolis, Minnesota (Inouye et al. 1987, Tilman 1988). NC, Piedmont of North Carolina (Oosting 1942). NJ2, Hutcheson Memorial Forest, New Brunswick, New Jersey (Pickett 1982). + include shrubs as well as trees. ++ most common species: KS, *Cornus drummondii*. NJ1, *Juniperus virginiana*. IL, *Diospyros virginiana*. NC, *Pinus* spp. NJ2, *Rhus glabra*.

Study*	Field age (yr)	All woody plants			Most common species++		
		Density	Freq.	Cover	Density	Freq.	Cover
KS	11	3.35+	97		1.5	86	19
NJ1	10	0.05		7	0.03	93	
IL	10	0.5			0.15	95	3.89
MN	10	0	0	0			
NC	11				0.27	100	
NJ2	10						<5

Study*	Field age (yr)	<i>Ulmus</i> spp.			<i>Juniperus virginiana</i>		
		Density	Freq.	Cover	Density	Freq.	Cover
KS	11	0.14	52	1.05	0.01	17	0.6
NJ1	10				0.03	93	
IL	10	0.08	90	1.5	0.01	10	0.25
MN	10						
NC	11						
NJ2	10						2–3

that as woody plant colonization continues in our system, conditions within the patches may increasingly inhibit growth of seedlings and vegetative sprouts of early successional herbaceous and woody species, favoring late successional woody species (e.g., species of *Quercus* from adjacent woodland) earlier in large than in small patches. That is to say, we predict that colonization of late successional woody species (not yet present on the site) should be observed earlier in large patches than in small patches, continuing the patch size effect on succession reported here.

Dispersal effects

There are several potential effects of patch size on dispersal. For instance, dispersal by birds may be biased toward large patches due to behavioral selection favoring use of large patches. For species that grow clonally and/or mature rapidly, larger patches also provide more possibilities for vegetative sprouts and short-distance dispersal of propagules following colonization at single nuclei. For instance, in our 4 × 4 m sampling quadrats, quadrats in large patches (50 × 100 m) adjoin the remainder of the patch from 2 to 4 sides (depending on location within the patch), but quadrats in small patches (4 × 8 m) have only one side touching the remainder of the patch (the other sides abut the closely-mown interstitial habitat). Thus, a quadrat in a large patch has more chances to receive vegetative sprouts or seeds dispersed over short distances from the rest of the patch, than does an equal-sized quadrat in a small patch. This enhanced colonization could result in a higher stem density in large patches than in small patches (see Holt 1992 for a theoretical exploration of this idea). This enhanced local colonization effect may apply to *C. drummondii*, which is clonal and matures rapidly. But this is unlikely to explain patch size effects in *U. rubra*, which is non-clonal and matures slowly.

The density of *J. virginiana* tends to be higher in small patches than in large patches, a pattern opposite that of *C. drummondii* and *U. rubra*. This may be because *J. virginiana* prefers relatively open sites for colonization. We have observed that *J. virginiana* is a pioneer species typically associated with patches of eroded, bare ground, which were scattered across the site in the early years of the study (Holt unpubl.). This species apparently does not establish well in the more competitive situation of denser vegetation cover that occurs later in succession in deep soils, or with less erosion. This is consistent with the observations that *J. virginiana* overall prefers xeric and generally open habitats (Ormsbee et al. 1976, Marks 1983, Holthuijzen and Sharik 1984). Since small patches are at an earlier successional stage than large patches, with a large proportion of their area along edges exposed to regular mowing, there may be more disturbed sites for *J. virginiana* to become established in small than in large patches. The absence of a distance effect in this species may reflect the overriding importance of patches of bare

ground for its establishment. Distance effects in establishment of others species such as *C. drummondii* and *U. rubra* would tend to reduce the availability of suitable sites near the source area, obscuring any distance effects. (However, at spatial scales much larger than those in our study, we would expect to observe distance effects.) We expect little further colonization by this species as succession proceeds, so the distribution of mature junipers will eventually reflect the spatially sporadic sites available for establishment at an early stage of succession.

In our system, succession towards woody vegetation has proceeded faster in larger isolated patches, than in smaller isolated patches. However, in other systems similar effects of patch size may not be as noticeable. In any given system, there is likely to be a threshold value in patch size, above which further increases in size will not substantially affect successional dynamics. The mechanisms proposed above predicting patch size effects are all scale-dependent. If all patches being compared were considerably greater in area than individual plant size, modal dispersal distances, or clonal growth distances, one might not observe marked patch size effects on plant community dynamics. For convenience of communication, we refer to a "threshold" patch size, above which further increases in patch area do not markedly influence plant dynamics (though we recognize that this "threshold" is just one point on a continuum of diminishing response). This threshold value should vary among ecosystems. For example, the threshold value above which area is inconsequential for habitat patches in a grassland ecosystem may be much smaller than for patches in a forest ecosystem. The two biomes differ greatly in dominant plant stature, as well as in the likely magnitude of abiotic differences between patches and the surrounding matrix. The threshold value may also depend upon the mechanisms driving the observed patch size effect. For instance, if a lower edge/interior ratio in larger patches leads to a faster rate of succession via effects on abiotic conditions, then the increment in succession rate with patch size should continually decrease as habitat size increases, and become negligibly small at low edge/interior ratios.

Distance effects

Stem densities of *C. drummondii* in the two largest size classes in large patches, and in the four largest size classes in small patches, decreased exponentially with distance to nearby propagule sources (albeit with considerable scatter). A similar pattern was displayed by *U. rubra*, in all size classes and on both patch sizes. Moreover, stems of both *C. drummondii* and *U. rubra* had a sharper exponential pattern in small than in large patches. This suggests that the earlier the stage of woody plant colonization (e.g., on small patches at present in our system), the sharper or clearer the negative exponential

pattern of establishment with distance from external sources may be.

As colonization and succession proceed, the negative exponential pattern of establishment with distance should become less distinct, because other factors become more important and gradually override the initial importance of distance from external sources. In our systems, this appears to be the case for the abundance pattern of *C. drummondii* in smaller size classes in large patches. The low density of small stems near the source presumably reflects inhibition in recent establishment by previously established plants, now in the tall stem classes. For instance, the closed overstory canopy formed by tall stems could shade sufficiently to prevent survival of vegetative sprouts or seedlings (using hemispherical photograph data of leaf area index, Yao and Rich unpubl.). The openness of overstory canopy increases with distance, a pattern inverse to the density of previously established, tall stems. There may be much greater opportunity at present of establishing small stems at a greater distance from the source, leading to the positive distance effect in establishment of small stems shown in Fig. 8a.

The negative exponential distance pattern is sharper in *U. rubra* than in *C. drummondii*. As hypothesized in the Introduction and explained in more detail above, this may reflect differences in dispersal modes, basic growth habits, and the potential for between-patch colonization by *C. drummondii*.

The bird dispersed *C. drummondii* and the wind-dispersed *U. rubra* started to colonize the field at about the same time in our system (Fig. 3). This differs from the pattern usually observed in studies of old field succession. More typically, wind-dispersed woody plants tend to colonize first, and later, bird-dispersed woody plants appear, due to the importance of perch sites provided by early colonizing wind-dispersed trees (Bazzaz 1996). This suggests that in fields close to propagule sources (in our case, adjacent forest), dispersal mode may not strongly influence the relative timing of colonization of different woody plant species. Differences in dispersal mode should be expected to become more important in studies focused on patches undergoing succession that are much further away from source populations than the patches in our system.

Conclusions

We found that spatial patterns of woody plant colonization in old fields are affected by the interplay of two factors: 1) the life history characteristics of the colonizing species, and 2) the spatial attributes of the habitat undergoing succession, in particular the size of the habitat patch and its distance to source populations. These results are generalizable to many other systems that are undergoing succession.

Life history characteristics of the colonizing species determine the temporal pattern of colonization. Species able to reproduce shortly after establishment, e.g. herbaceous plants and shrubs, follow a logistic colonization pattern with a phase of accelerated establishment; species with long maturation time, e.g. trees, should instead show an initially linear trend which asymptotes without obvious acceleration. Life history characteristics may also cause or reinforce patch size effects. Clonal growth habits or rapid maturation permitting strong short-distance dispersal could result in higher abundance in larger patches. Life history characteristics can also override the effects of distance to nearby propagule sources on the abundance and distribution of colonizing species. Wind-dispersed, non-clonal species should have a sharper negative exponential distribution of stem density with distance than bird-dispersed, clonal species, at least initially.

In our system, succession in recent years has proceeded at faster rates in larger isolated patches, and the effects of patch size have become stronger with time. All the patches entered old field succession at the same time in autumn, 1984. No significant patch size differences in vegetation dynamics were found during the first six years of succession, when the site was dominated by herbaceous species (Holt et al. 1995), but in the next five years, stem densities of early successional tree species became significantly higher in large patches than in small patches. However, as noted above, we would be cautious about extrapolating these results to a much wider range of patch sizes. The quantitative expression of this scaling effect of patch size on succession may vary with ecosystem characteristics and the mechanisms underlying the patch size effect. It is possible even in our system that patch size effects on succession may become obscure at a later successional stage.

As in other studies, in our system woody plant colonization has proceeded faster in sites that are closer to source populations. Moreover, these distance effects appear to become less important as succession proceeds. In contrast to the usual observation that wind-dispersed woody plant species colonize before bird-dispersed species in old fields remote from source populations, colonization of woody plants with different dispersal modes may occur at more or less the same time in fields that are very close to source populations. This appears to be true at our site.

Our study demonstrates that spatial characteristics of habitats such as area and distance have strong effects on succession, and that these effects depend upon life history characteristics of the colonizing organisms. Such spatial influences are expected in all successional systems, and could explain much of the variability observed among different studies in the same biome (Horn 1981). A consideration of relationships between habitat characteristics (patch size and proximity to source) and life history traits is essential for conservation and for enhancing the success of restoration efforts.

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