

Advance regeneration and seed banking of woody plants in Ohio pine plantations: Implications for landscape change

Francisco J. Artigas and Ralph E.J. Boerner

Environmental Biology Program and Department of Botany, The Ohio State University, 1735 Neil Avenue, Columbus, OH 43210 USA

Keywords: landscape ecology, pine, succession, seeds, regeneration, Ohio, hardwood forest

Abstract

Silviculturally-managed pine plantations within southern Ohio are chronically disturbed patches of introduced vegetation distinct from the surrounding matrix of hardwood forest. To determine the successional pathways by which such pine stands might blend back into the hardwood forest matrix under different types of silvicultural management, we determined the current status of hardwood regeneration under 24 pine stands. Stands of *Pinus virginiana* (Virginiapine) had the highest density of hardwood seedlings and saplings (20,560 stems ha⁻¹) whereas *P. strobus* (white pine) stands averaged only 7090 hardwood stems ha⁻¹; *P. resinosa* (red pine) stands were intermediate. The most abundant hardwood seedling and sapling species under pine canopies were *Acer rubrum* and *Cornus florida*. DCA ordination of the seedling + sapling assemblages clustered most of the *P. resinosa* and *P. strobus* stands in the center of the ordination along with a group of species which are common in second-growth forests of the area. *P. virginiana* stands, in contrast, were scattered throughout the ordination space. Most of the woody species common in second-growth forests of the region were also common in the pine understory. Multiple regression indicated that large plantations with deeper litter, higher soil pH and lower total hardwood density had the greatest abundance of mesic-site species in the understory. This relationship did not hold for *P. resinosa* stands, however, due to more frequent and intense silvicultural intervention. The seed bank was not an important source of woody seedlings to the understory assemblage under intact pine plantations. The vegetation of 1–4 yr old clear-cut sites was dominated by wind and bird dispersed species which were generally absent from the understory of intact plantations. We conclude these chronically disturbed planted patches will revert to matrix vegetation faster if the disturbance is allowed to end in a gradual manner through stand senescence than if it is abruptly ended by clear-cutting.

Introduction

Before the settlement of Ohio by Europeans, the landscape of eastern and southern Ohio was dominated by hardwood forest (Gordon 1969). The forest matrix was broken in areas by stream and river corridors and by patches of younger vegetation where physical forces such as fire, tornados,

and ice storms had disturbed the forest (Canham and Loucks 1984; Boerner and Cho 1987; Boerner *et al.* 1988). Thus, this area of Ohio was a mosaic of forest patches of different ages since disturbance (Pickett and Thompson 1978).

The hilly southern Ohio landscape changed drastically by the early 1900s. Ridgetops had been cleared and fertile hillside soils had been heavily

eroded. The economic depression of the 1920s and 1930s and the depletion of soil fertility made many small subsistence farms uneconomical and farm abandonment became common. The state began acquiring land and initiated conservation programs to reforest the land, mainly by planting pines (ODNR 1981).

By 1940, the landscape of Hocking County, south-central Ohio, was a mixture of second growth hardwood forests, pine plantations, and areas of human development. Today 71% of Hocking State Forest is second-growth hardwood forest in which are scattered 433 ha of pine plantation patches (>9% of the county land area). Most of these pines are 24–60 yr old and are being managed for sawlog production. Over the long term, reversion of these plantation sites to hardwood forest is considered desirable (ODNR 1981). Decisions regarding such management must be made soon in order to save deteriorating sites and to take advantage of opportunities to maximize growth of hardwoods already present.

Three possible fates exist for these plantation patches. First, they may be clear-cut and replanted in pine. In this case the chronic disturbance is maintained silviculturally and the planted patch remains distinct from the matrix indefinitely. Second, plantations may be clear-cut and allowed to succeed to second-growth forest with or without management. In this case, the chronic disturbance ends abruptly and eventually the patch blends back into the matrix. Third, the pine plantations may not be harvested, but instead allowed to senesce. In such sites, succession to second-growth hardwood forest resembling the matrix will also occur. However, it will likely be by different pathways and/or rates than in clear-cut sites because open areas in senescent plantations will be smaller and will open sporadically over time (Bormann and Likens 1979).

After clear-cutting, populations of understory plants, including advance regeneration of woody plants, are reduced and the physical and chemical properties of the forest floor changed. Subsequent succession will involve colonization of plants from the seed bank and from outside the patch, as well as growth of the remaining advance regeneration. In contrast, in senescent plantations canopy gaps

will develop sporadically as single trees die and fall. We hypothesize that the advance regeneration under those gaps will be more important in determining the pathways of subsequent succession here than in clear cuts.

To help predict the pathways of future succession under these scenarios, and to evaluate the relative role of advance regeneration and seed banks within the planted/chronic disturbance patch vs immigration from the matrix, we have attempted to answer the following questions: (1) What is the status of hardwood regeneration under plantations of different pine species and ages? (2) What environmental factors are important in determining the community composition of hardwood regeneration in the pine plantations? (3) How important are the seed bank and seed dispersal from the outside in controlling the early stages of succession following stand senescence or clear cutting?

The study area

Hocking State Forest is located within the unglaciated Appalachian Plateau region of southern Ohio. The topography is hilly with steep valleys, many of which have high cliffs and ledges. Prior to European settlement, the south- and west-facing slopes were dominated by white oak forest in which *Quercus alba*, *Q. velutina*, *Carya* spp., *Acer rubrum*, *Cornus florida*, *Fraxinus americana*, and *Prunus serotina* were common (Gordon 1969). Mesic, lower slope positions often had significant amounts of *Fa& grandifolia* and *Betula lenta* as well. Presettlement ridgetops were covered by chestnut-chestnut oak forests in which *Castanea dentata*, *Q. prinus*, *Q. velutina*, *Oxydendrum arboreum*, and *Pinus virginiana* were common (Gordon 1969). Today's second-growth forests are much the same in species composition as the presettlement forests, with the exception of the reduction of *Castanea dentata* to isolated stump sprouts (Boerner and Crozier 1983). Most pine stands are located on ridgetops and south-facing slopes in patches that average 0.5–10.0 ha.

The surface soils of the region have formed in place by the weathering of sandstone, shale, and

Table 1. Site characteristics of 24 pine plantations of three different species in Hocking State Forest, Ohio. Means and standard errors (in parentheses) are given; within rows, means followed by the same lower case letter were not significantly different at $p \leq 0.05$.

Parameter	<i>Pinus resinosa</i>	<i>P. strobus</i>	<i>P. virginiana</i>
Age (yr)	44.0a (3.0)	42.0a (3.0)	42.0a (2.0)
Density (stems ha ⁻¹)	1449a (30)	475c (43)	778b (74)
Pine dbh (cm)	24.2a (1.2)	34.8b (2.2)	23.7a (0.1)
Basal area (m ² ha ⁻¹)	32.8a (3.7)	41.0b (3.2)	32.0a (2.1)
Hardwood litter (%)	8.2b (1.8)	2.8a (1.6)	17.5c (2.4)
Litter depth (cm)	4.0b (0.2)	4.7a (0.3)	3.2c (0.3)
Slope angle (°)	10.4a (2.7)	8.2a (1.0)	9.3a (1.2)
Irradiance ¹	14.6a (2.7)	13.2a (2.6)	17.2a (3.5)
Stand area (ha)	2.3a (0.2)	4.0b (0.5)	4.4b (0.6)
Isolation (%)	28.2a (4.3)	42.7a (6.2)	30.0a (5.7)

¹ Percent of ambient irradiance reaching the forest floor

conglomerate. These soils range from 20–30 cm depth on ridgetops to > 1 m in lower slope positions. They are generally acid (pH 3.6–5.0) and low in both organic matter and natural fertility (Soil Conservation Service 1988). Annual precipitation averages 101 cm, with over 50% occurring during the spring and early summer months (Wolfe *et al.* 1949).

Twenty-four pine stands dominated by one of three different species were selected from aerial photographs and topographic maps: nine stands of *Pinus resinosa* Ait. (red pine), eight of *P. strobus* L. (white pine), and seven of *P. virginiana* Mill. (Virginia pine). The silvicultural history of each stand was obtained from the Ohio Division of Forestry (C. Foster, personal communication). The choice of which pines were planted on a site dependent solely on seedling availability at the state nursery. The object was to revegetate abandoned and as quickly as possible. In general, plantations were kept relatively clear of hardwood saplings through the first decade of growth and hardwood saplings may have been removed during thinning cuts thereafter. *P. resinosa* plantations were more intensively managed in this way than were the other two species (C. Foster, personal communication). We selected plantations in which field inspection and management records showed no indication of cutting or herbicide use in the past decade. The sites did not differ significantly among pine species (ANOVA, $p > 0.10$). In age, slope, forest floor irradiance, or

isolation (Table 1, methods described below). Despite our attempts to select a set of sites with minimum variation among pine species, they did differ significantly in pine density, mean pine dbh, pine basal area, stand area, litter depth and percent hardwood litter (Table 1).

Methods

Field and laboratory methods

The pine stands were sampled between September 1986 and June 1987. In each stand, 1–320 × 20 m quadrats were established depending on the size of the stand, and the dbh of all pines was measured. Two subquadrats, 5 × 5 m were established within each quadrat and used to determine the composition of the hardwood advance regeneration. In each subquadrat, the number of seedlings (stems < 50 cm height) of each species, the basal diameter and species of all saplings (height > 50 cm and basal diameter ≤ 2 cm), and dbh and species of all trees (stems > 2 cm) was recorded. Nomenclature of woody plants follows Braun (1961).

Soil samples of approximately 400 g of the A horizon were taken in each quadrat, air-dried in the laboratory for three weeks, and analyzed for pH (1:5 paste in water: Peech 1965) and texture (hydrometer method: Grigal 1973). For purposes of regression analysis, texture was entered as percent silt plus clay.

The depth of the litter layer was measured at eight randomly chosen points in each quadrat. Two 0.5 m² litter samples were taken from each quadrat and the proportion of hardwood vs pine litter determined after air-drying.

The size of each stand was calculated with a polar planimeter from aerial photographs. The percent isolation of each stand was an estimate of the percent of the perimeter of each stand that could potentially represent a barrier to seed-dispersing mammals (*e.g.*, roads, agricultural fields).

The percent of ambient irradiance which reached the forest floor was measured at six points in each stand with a Li-Cor **LI-185B** photometer equipped with an integrating sphere. This integrating sphere captured both direct and diffuse light and eliminated some of the angle effect (Marshall and Woodward **1985**). All measurements were made under clear sky conditions between **10 AM** and **3 PM**.

Statistical analysis

Detrended Correspondence Analysis (DCA) (Hill and Gauch **1980**) was used to analyze the hardwood assemblage under the pine stands. The seedling + sapling data used for this ordination were weighted by the basal diameter of each stem, with all seedlings being counted as having basal diameter of **0.2** cm.

To determine which environmental variable could best predict the hardwood understory composition, axis scores from the ordination were compared with environmental conditions and mensurational characteristics from each stand. The environmental conditions, used were: slope, aspect, irradiance, soil texture, soil pH, litter depth, percent hardwood litter, density of hardwood trees, stand area, and isolation. The mensurational characteristics were: pine species, age of pines, density, mean dbh, and basal area. Regression models for all stands together and for each pine type were constructed using multiple and forward-selection stepwise regression using a significance level of 0.05 (S.A.S. **1986**). Densities of seedlings and saplings were compared among plots and pine species by

Analysis of Variance followed by Ryan-Einot-Gabriel-Welsch Modified F-tests (S.A.S. **1986**).

Hardwood establishment in recent clear-cuts

Two former plantations of each pine species, **1–4** yr post clear-cut, were selected to determine the species composition of woody plants in early successional sites. These clear-cuts were within 2 km of our intact plantations, and were similar in topography, soil, age, and management to our intact plantations. The trees had been harvested by machine with the result that most of the advance regeneration, herbaceous flora and forest floor had been destroyed and the soil surface compacted. The sites were not burned prior to abandonment. In each clear-cut, seven 5 × 5 m quadrats were established randomly, at least **10 m** apart, along a transect line. The identity and density of each woody species in each quadrat was recorded. All clear-cuts were compared using the community coefficients of Sorensen and Ellenberg (Mueller-Dombois and Ellenberg **1974**).

Seed bank analysis

Three **20–30** yr old and three **50–60** yr old plantations, one of each pine species in each age class, were selected for seed bank analysis. For the mineral soil (**A** horizon) seed bank, fifty **400 g** samples were taken from each stand in June **1987**. The samples were taken systematically approximately **10 m** apart along five transects that covered the greatest topographic variability in each stand.

In the greenhouse, each sample was spread out in **25 cm** pots to an average depth to **2 cm** over sterilized sand. Seedlings were identified and removed following emergence. Selected seedlings were grown to maturity in single pots to confirm identification. Germination was monitored for three months, though most germination occurred in the first month.

To determine the litter and humus (**O** horizon) seed bank, four 1 m² forest floor samples were taken from each stand. These samples were sieved

Table 2. Mean density (stems ha⁻¹) and constancy (% of plots) of seedlings and saplings, all stands combined, in decreasing order of total density. Standard errors of the means for densities are given in parentheses.

Species	Seedlings		Saplings		Combined density
	Density	Constancy	Density	Constancy	
<i>Acer rubrum</i>	5892 (179)	92.2	1197 (118)	73.4	7089
<i>Prunus serotina</i>	1517 (326)	81.3	160 (36)	42.2	1677
<i>Sassafras albidum</i>	1446 (337)	73.4	123 (29)	35.9	1569
<i>Cornus florida</i>	603 (110)	57.8	935 (214)	70.3	1538
<i>Fagus grandifolia</i>	271 (72)	40.6	117 (33)	32.8	388
<i>Quercus alba</i>	322 (92)	29.7	49 (18)	17.2	382
<i>Quercus velutina</i>	271 (86)	34.4	65 (22)	20.3	336
<i>Quercus borealis</i>	258 (44)	54.7	52 (18)	15.6	310
<i>Fraxinus americana</i>	135 (46)	26.6	80 (24)	23.4	215
<i>Tsuga canadensis</i>	102 (41)	15.6	77 (10)	14.1	179
<i>Carya ovata</i>	151 (41)	29.7	<1 (<1)	17.2	151
<i>Liriodendron tulipifera</i>	43 (19)	9.4	62 (26)	12.5	105

through a 6 mm screen and spread in flats to an average depth of 4 cm. The samples were stirred every two weeks over the three month observation period to expose the maximum number of seeds to light. Seedling identification was based on Hitchcock and Chase (1971) and Stucky *et al.* (1981).

Results

Hardwood advance regeneration in pine plantations

Pinus strobus stands had the lowest density of seedlings and saplings combined (7090 stems ha⁻¹), compared with *P. resinosa* (14,040 stems ha⁻¹) and *P. virginiana* (20,560 stems ha⁻¹); all differences were significant at $p \leq 0.05$. *Acer rubrum* was the most abundant and frequent hardwood seedling/sapling species in the 64 plots (Table 2). Next in

abundance, with densities > 1500 stems ha⁻¹, were *Prunus serotina*, *Sassafras albidum*, and *Cornus florida*. These three species were all present in more than half of the pine plantations.

Fagus grandifolia, *Quercus alba*, *Q. velutina*, *Q. borealis*, and *Fraxinus americana* were all found at densities > 200 stems ha⁻¹, but their constancy averaged only 30%. Thus, these species tend to be abundant in sites where they occurred but were often entirely absent from a site. The least abundant and constant seedling/sapling species in the understory under intact pine canopies were *Tsuga canadensis* (a conifer), *Carya ovata*, and *Liriodendron tulipifera*.

The density of seedlings varied significantly among pine plantation types. Total seedling density was lower in stands of *P. strobus* than in stands of *P. resinosa* or *P. virginiana* (Fig. 1); this was also true for the most abundant species, *Acer rubrum*. *Prunus serotina*, *S. albidum*, *Fagus grandifolia*,

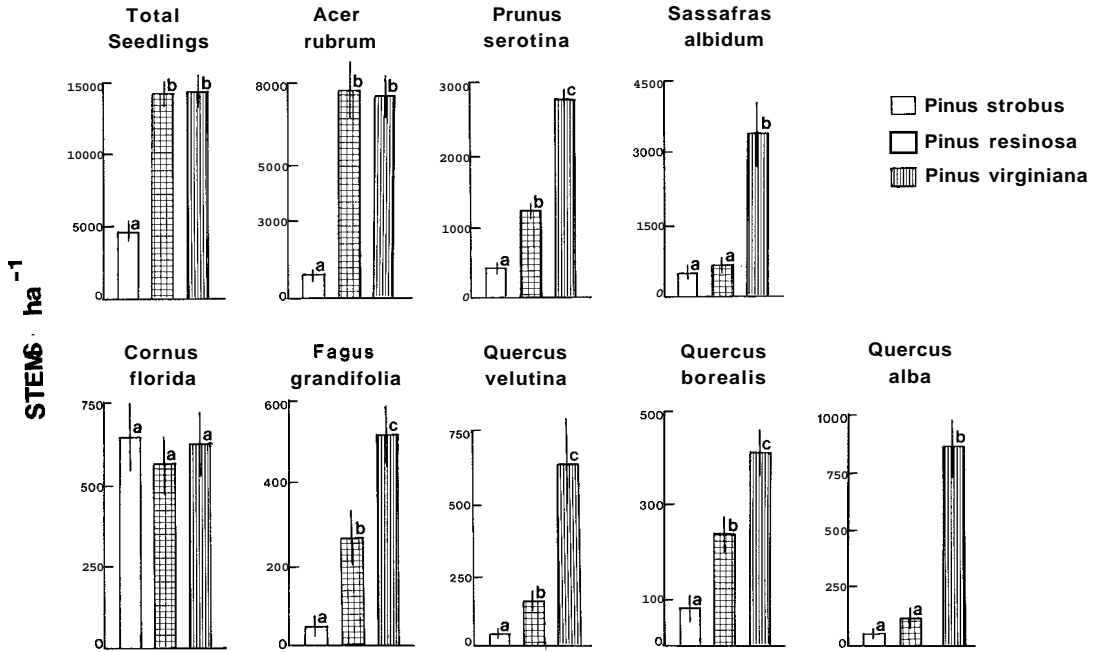


Fig. 1. Seedling densities (stems ha⁻¹) in three pine plantation types. Means plus one standard error are given and means with the same lower case letter were not significantly different at $p \leq 0.05$. Note: vertical scales differ.

Q. borealis, *Q. velutina*, and *Q. alba* seedling densities were higher in *P. virginiana* plantations than elsewhere. In contrast, *Cornus florida* seedling abundance ranged from 560 to 640 stems ha⁻¹ and did not differ among pine plantation types. Seedlings of *Carya ovata*, *Fraxinus americana*, *L. tulipifera*, and *T. canadensis* were rare in all pine types. Because of high variability within pine plantation types, we could not adequately test differences in the densities of these species among pine types.

In contrast to the seedling pattern, sapling abundances did not vary significantly among pine plantation types (Table 3). The only exception was *T. canadensis* which was significantly more abundant under *P. virginiana* than under the other two pine species.

Ordination of seedling + sapling assemblages

A cluster of species occurred in the middle of the DCA ordination space which included *Acer rubrum*, *O. arboreum*, *Q. alba*, *Q. velutina*, and

Carya ovata (Fig. 2). This central complex of species included most of the species commonly found in second-growth forests on south- or west-facing slopes in the Hocking Hills (Wolfe *et al.* 1949; Gordon 1969; Boerner and Crozier 1983).

S. albidum appeared alone at low axis 1 scores and was associated with three 54–67 yr old *P. virginiana* stands (Fig. 2). The high *S. albidum* abundance in these three stands was associated with a greater frequency of treefall gaps than was observed in the other pine sites.

The shade-tolerant and mid-tolerant species *Fagus grandifolia*, *T. canadensis*, *Betula lenta*, and *Ulmus rubra* were located in the upper axis 1/lower axis 2 region (Fig. 2). In the Hocking Hills, these species are most common in mesic sites at lower slope positions (Boerner and Crozier 1983). Located in the upper axis 1/upper axis 2 quadrant was a set of species which generally require larger disturbances for establishment: *Prunus serotina*, *P. virginiana*, and *Quercus prinus*.

Most of the *P. resinosa* and *P. strobus* stands clustered together with the central complex of species (Fig. 2); in contrast, *P. virginiana* stands were

Table 3. Density (stems ha⁻¹) and constancy (% of plots) of saplings of major hardwood species in three types of pine plantations. Standard errors of the density means are given in parentheses.

Sapling species	Plantation type					
	<i>Pinus strobus</i>		<i>Pinus resinosa</i>		<i>Pinus virginiana</i>	
	Density	Const.	Density	Const.	Density	Const.
<i>Acer rubrum</i>	1090 (253)	70.0	1024 (279)	66.7	1520 (389)	85.0
<i>Cornus florida</i>	1200 (561)	85.0	774 (231)	54.2	910 (312)	75.0
<i>Prunus serotina</i>	230 (99)	45.0	168 (41)	50.0	80 (30)	35.4
<i>Quercus borealis</i>	120 (49)	20.0	24 (18)	8.3	20 (14)	20.0
<i>Fraxinus americana</i>	110 (49)	40.0	88 (50)	20.8	40 (28)	10.0
<i>Quercus velutina</i>	110 (62)	25.0	32 (19)	8.3	60 (29)	30.0
<i>Sassafras albidum</i>	100 (37)	45.0	144 (51)	33.3	120 (62)	30.0
<i>Fagus grandifolia</i>	100 (42)	30.0	88 (60)	25.0	170 (62)	45.0
<i>Quercus alba</i>	30 (16)	15.0	8 (8)	20.8	120 (51)	10.0
<i>Liriodendron tulipifera</i>	40 (18)	15.0	128 (63)	20.8	0 (0)	0.0
<i>Carya ovata</i>	<1 (<1)	25.0	<1 (<1)	20.8	<1 (<1)	5.0
<i>Tsuga canadensis</i>	<1 (<1)	5.0	8 (8)	4.2	230 (124)	35.0

scattered throughout the ordination space. Thus, there was greater variability among *P. virginiana* stands (Coefficient of Variation in axis 1 scores = 46.8%) than *P. strobus* (CV = 12.9%) or *P. resinosa* (CV = 24.1%) stands, with all hardwood species groups being represented in at least some *P. virginiana* stands.

Regression of environmental and mensurational characteristics of all sites together on axis 1 scores produced a model with $r^2 = 0.55$ ($p < 0.01$). In this model axis 1 scores were positively correlated with pH, litter depth, and stand area, and negatively correlated with pine stem density. In addition, the interactions of *P. resinosa* and both litter depth and stand area were significant regression components, indicating that the relationships between litter depth, stand area and axis 1 scores which were important in predicting hardwood composition in

P. virginiana and *P. strobus* stands were not significant in *P. resinosa* stands. This was confirmed by constructing regression models for each pine species separately: for *P. virginiana* and *P. strobus* axis 1 scores were significantly correlated with stand area (+), pH (-), litter depth (+) and pine stem density (-) whereas for *P. resinosa* only the slope components for pine stem density (-) and soil pH (+) were significant.

This demonstrated that species which clustered at the upper end of axis 1 (*Fagus grandifolia*, *T. canadensis*, *B. lenta*, *U. rubra*) were most abundant in large *P. strobus* and *P. virginiana* stands with relatively low pine stem density, high soil pH, and high litter depth. In contrast, the stands in which *S. albidum* was most abundant had the lowest soil pH and litter depth.

A statistically significant regression model

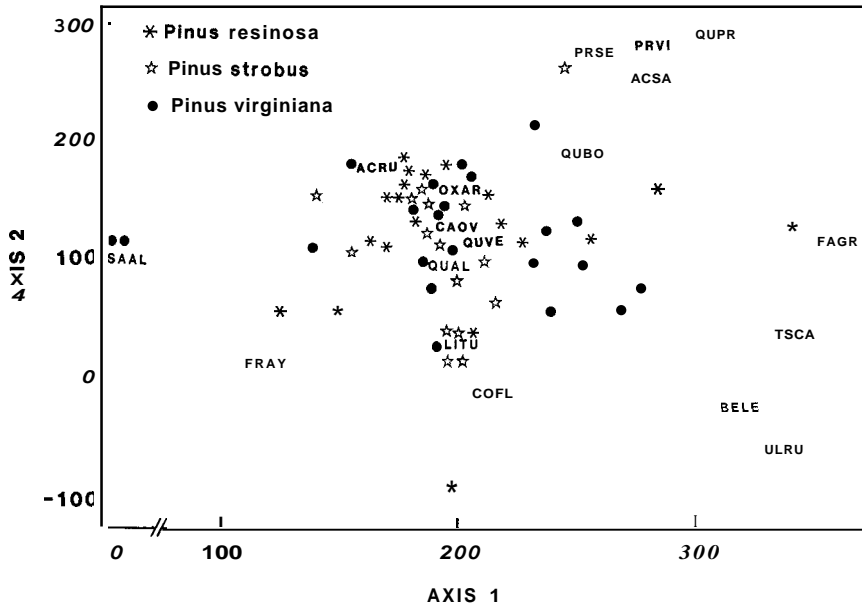


Fig. 2. DCA ordination of 64 plots in 24 pine plantations in Hocking State Forest, Ohio. Plot positions are given by symbols. Species positions are given by codes which are the first two letters of the genus and species: ACRU = *Acer rubrum*, ACSA = *Acer saccharum*, BELE = *Betula lenta*, CAO V = *Carya ovata*, COFL = *Cornus florida*, FAGR = *Fagus grandifolia*, FRAM = *Fraxinus americana*, LITU = *Liriodendron tulipifera*, OXAR = *Oxydendrum arboreum*, PRSE = *Prunus serotina*, PRVI = *Prunus virginiana*, QUAL = *Quercus alba*, QUBO = *Quercus borealis*, QUPR = *Quercus prinus*, QUVE = *Quercus velutina*, SAAL = *Sassafras albidum*, TSCA = *Tsuga canadensis*, ULRU = *Ulmus rubra*.

($p < 0.043$) could also be constructed for axis 2 scores, but as the maximum attainable r^2 was 0.089, this model lacked significant predictive value.

Woody vegetation in recent clear-cuts

Twenty-five taxa of trees and shrubs were found in the six clear-cuts (Table 4). These taxa separated into three main groups: (1) species that were abundant in the clear-cuts but not present in the understory of intact pine plantations; (2) species common in both clear-cuts and pine understories, and (3) dominants of regional second growth forests.

The most abundant species in the clear-cuts (1300–7900 stems ha^{-1}) were, in decreasing order, *Rubus* spp., *L. tulipifera*, and *S. albidum*. Based on Sorenson's Index of Similarity the average similarity in species composition among the clear-cuts was 77%, with a range of 68.4–87.0%. For comparison, the similarity among quadrats within a clear-

cut stand averaged 65%. There were no obvious trends in stand similarity related to stand age: one year old clear-cuts were as similar to four year old areas as they were to each other.

When the relative abundance of the species was incorporated by using Ellenberg's Index, the average similarity among clear-cut stands increased to 94%, indicating that species common to most sites were also present in similar densities. Ellenberg's Index for similarity among quadrats within a site averaged 72%.

Seed banks of pine plantations

A total of 34 taxa germinated from the mineral soil samples (Table 5). This seed bank was dominated by annual and perennial herbs common in agricultural old fields in southern Ohio. Only four woody species germinated from mineral soil samples, and these species were present at relatively low densities.

Table 4. Densities (stems ha⁻¹) of woody plants found in six recently clear-cut former pine plantations. Age is defined as the number of growing seasons since the winter clear-cut.

	Site age					
	1	1	3	3	4	4
Group 1: Species abundant in clear-cuts but not present in the understory of intact plantations						
<i>Rubus</i> spp.	2229	3600	5943	7486	7886	3760
<i>Rhus copallina</i>	4057	1543	343	743	571	800
<i>Aralia spinosa</i>	457	57	114	2000	1657	2880
<i>Populus tremuloides</i>	229	343	914	743	685	520
<i>Rhus glabra</i>	1429	171	114	—	57	760
<i>Rhus typhina</i>	743	229	286	—	57	720
Group 2: Species common in clear-cuts and in the pine understory						
<i>Acer rubrum</i>	4171	1371	1543	1714	1086	640
<i>Sassafras albidum</i>	2171	2571	2971	2514	1943	3280
<i>Cornus florida</i>	914	571	1086	1486	2114	1160
<i>Prunus serotina</i>	971	914	1024	1314	1257	600
Group 3: Species common in regional second growth forests						
<i>Liriodendron tulipifera</i>	3943	6686	1371	1257	1657	3000
<i>Fagus grandifolia</i>	57	400	57	171	—	—
<i>Quercus velutina</i>	229	—	343	—	1086	—
<i>Quercus borealis</i>	400	114	286	686	400	40
<i>Fraxinus americana</i>	—	171	—	171	—	—
<i>Oxydendrum arboreum</i>	—	—	229	114	514	120
<i>Robinia pseudoacacia</i>	—	—	514	—	57	—
<i>Carya ovata</i>	—	—	171	—	57	120
<i>Lindera benzoin</i>	743	971	114	—	57	80
<i>Ulmus rubra</i>	—	171	114	457	—	40
<i>Asimina triloba</i>	—	—	—	—	57	40
<i>Corylus americana</i>	—	—	—	—	—	160
<i>Rosa multiflora</i>	—	—	—	—	—	40
<i>Acer saccharum</i>	—	—	—	—	—	40

The litter and humus seed bank was more diverse, with 52 germinable taxa (Table 5). The woody species present in these samples were the same three as in the mineral soil, plus *Platanus occidentalis*, *Acer rubrum*, *Ostrya virginiana*, *Aralia spinosa*, *Vitis* sp., and *Rubus* spp. However, the density of germinable seeds was lower than in the mineral soil.

Sixty percent of the species present in the mineral soil were also present in the litter/humus. The most abundant woody taxa in the litter were *L. tulipifera* and *Rubus* spp., species which were also abundant in the clear-cuts but not in the pine understory.

Discussion

The establishment and maintenance of a pine plantation in a region dominated by hardwood forest represents the insertion of a planted patch with chronic disturbance into the otherwise continuous hardwood forest matrix (Forman and Godron 1986). The turnover rate of such patches is usually fixed and will depend on the time required to reach pine maturity. Thus, the species dynamics associated with developing and older pine plantations depend largely on the silvicultural practices of the forester. If no maintenance takes place the patch will be invaded by species from the matrix. Succes-

Table 5. Mean density of germinable seeds per m² of mineral soil down to 10 cm and per m² of forest floor, all pine stands combined. Standard errors of the means are given in parentheses.

Species	Mineral soil	Forest floor
Herbaceous plants		
<i>Amaranthus albus</i>	10.7 (11.7)	0.3 (0.2)
<i>Amaranthus retroflexus</i>	—	0.6 (0.4)
<i>Ambrosia artemisiifolia</i>	63.7 (69.8)	—
<i>Antennaria parlinii</i>	—	0.2 (0.1)
<i>Asclepias</i> sp.	—	<0.1 (0.1)
<i>Aster</i> sp.	—	1.0 (0.5)
<i>Bidens bipinnata</i>	95.5 (66.8)	—
<i>Cardamine hirsuta</i>	—	3.6 (3.3)
<i>Cassia nititans</i>	32.0 (15.7)	—
<i>Cerastium</i> sp.	—	0.3 (0.0)
<i>Chenopodium album</i>	244.2 (253.7)	—
<i>Chrysanthemum leucanthemum</i>	223.7 (244.1)	22.6 (7.7)
<i>Cirsium arvensis</i>	—	1.1 (0.4)
<i>Cyperus schweinitzii</i>	—	<0.1 (0.1)
<i>Daucus carota</i>	10.7 (9.7)	<0.1 (0.1)
<i>Dichondria repens</i>	2059.5 (2183.1)	9.0 (6.7)
<i>Digitaria ischaemum</i>	626.3 (453.0)	4.7 (4.8)
<i>Erictites hieracifolia</i>	—	9.6 (2.9)
<i>Eupatorium coelesterium</i>	286.7 (314.0)	—
<i>Euphorbia</i> sp.	—	<0.1 (0.1)
<i>Fragaria virginiana</i>	127.3 (139.9)	0.8 (0.5)
<i>Hieracium longipilum</i>	—	<0.1 (0.1)
<i>Houstonia longifolia</i>	—	<0.1 (0.1)
<i>Juncus tenuis</i>	—	5.3 (3.0)
<i>Lobelia nuttallii</i>	—	1.2 (1.0)
<i>Mollugo verticillata</i>	10.7 (11.7)	—
<i>Oxalis stricta</i>	562.7 (408.6)	2.0 (1.2)
<i>Panicum capillare</i>	371.8 (275.5)	—
<i>Panicum lanuginosum</i>	1040.5 (39.6)	1.6 (1.0)
<i>Parietaria pennsylvanica</i>	223.3 (134.4)	—
<i>Phytolaca americana</i>	106.2 (116.3)	95.1 (99.7)
<i>Pilea pumila</i>	287.7 (300.2)	1.3 (0.1)
<i>Plantago lanceolata</i>	477.7 (340.7)	<0.1 (0.1)
<i>Polygonum lapathifolium</i>	—	<0.1 (0.1)
<i>Portulaca oleraceae</i>	191.8 (182.6)	<0.1 (0.1)
<i>Rumex acetosella</i>	32.7 (23.5)	—
<i>Schizachyrium scoparium</i>	—	<0.1 (0.1)
<i>Senecio</i> sp.	—	0.3 (0.2)
<i>Taraxacum officinale</i>	—	0.3 (0.1)
<i>Trifolium repens</i>	21.2 (23.2)	—
<i>Verbascum thapsus</i>	10.7 (9.7)	—
<i>Waldsteinia tragarioides</i>	97.2 (55.7)	—
Unidentified Herb		
Seedlings	277.5 (116.2)	12.7 (3.9)
Woody plants:		
<i>Acer rubrum</i>	—	<0.1 (0.1)
<i>Aralia spinosa</i>	—	0.4 (0.1)
<i>Liriodendron tulipifera</i>	42.5 (46.6)	1.6 (0.9)
<i>Ostrya virginiana</i>	—	<0.1 (0.1)
<i>Parthenocissus quinquefolia</i>	48.7 (29.8)	—
<i>Platanus occidentalis</i>	—	<0.1 (0.1)
<i>Rhus radicans</i>	116.8 (75.2)	0.8 (0.7)
<i>Rubus</i> sp.	—	0.4 (4.9)
<i>Sassafras albidum</i>	38.7 (29.7)	1.9 (1.8)
<i>Vitis</i> sp.	—	<0.1 (0.1)

sion and ultimate disappearance of the patch will follow.

The pine stands selected for this study were relatively similar in age, slope position, forest floor irradiance, and degree of isolation from the hardwood matrix. Other factors did, however, vary among pine species, thus creating microenvironmental differences under the three different pine canopy types. In general, stands of *P. resinosa* were the densest while *P. strobus* stands had the largest trees and lowest stem density. Stands of *P. virginiana* had the highest structural complexity, both within and among stands, and also had the least total litter and highest hardwood fraction. These differences were also reflected in hardwood species composition and density among pine types. For example, *P. virginiana* stands had the highest structural diversity and the highest density of seedlings, especially of bird-dispersed species. This is consistent with other studies which have demonstrated positive correlations between structural complexity and the input of seeds by birds (e.g., McDonnell 1988).

The most abundant hardwood seedling/sapling species under any of the pine plantations was *Acer rubrum*. This species seems well-suited to colonizing pine understories as it is wind dispersed, does not require much light to germinate, and can germinate through a moist litter cover (Schopmeyer 1975).

Prunus serotina, *Sassafras albidum*, and *Cornus florida* were all present as seedlings or saplings in over half of the pine sites. All are bird-dispersed, are common to forest edges or gaps in southern Ohio and have seeds which are more resistant to decay in moist pine litter than are the seeds of the species which generally dominate second growth forests of the region (e.g., *Fagus grandifolia*, *Quercus* spp.) (Solbrig 1975). This suggests that dispersal, seed predation, and the ability to resist decay in moist, deep pine litter may be important in determining the success of these species in the pine understory.

Though seedling densities varied by a factor of 3 among pine species, sapling abundances differed little. This suggests that post-germination mortality is higher under *P. virginiana* stands than under

either *P. strobus* or *P. resinosa*. Alternatively, with equal seed dispersion, seedling survival could now be higher in *P. virginiana* stands than under other pine species, due perhaps to recent changes in canopy structure.

The DCA ordination revealed a gradient of understory composition which correlated well with a suite of environmental factors. At one extreme of this gradient were small pine stands with low pH, little litter, and high stem density in which the understory was dominated by species common in relatively xeric second growth forests, such as *Acer rubrum*, *Oxydendrum arboreum*, *Quercus velutina*, *Q. alba*, and *Carya ovata*. At the other extreme were larger pine stands with higher pH and leaf litter cover and lower stem density whose understories had much higher densities of mesic forest species such as *Fagus grandifolia*, *Tsuga canadensis*, *Betula lenta*, and *Ulmus rubra*.

The failure of these relationships to hold as well for *P. resinosa* stands as for *P. strobus* or *P. virginiana* may be related to the more frequent and intense silvicultural intervention (C. Foster, personal communication) or to a greater amount of edge per unit area in *P. resinosa* stands. This latter assertion is consistent with map and field observations which suggest that *P. resinosa* stands tend to be narrower, smaller, and more complex in outline than the other two pine types.

The woody plant assemblage that develops after a clear-cut is dominated by wind and bird dispersed species which are generally absent from the pine understory. The post-clear-cut vegetation was independent of the pine species present earlier and any advance regeneration which might have been present. The species which are most abundant during this early successional period are also not significant components of the second-growth forest of the region, and may even delay subsequent establishment of hardwoods by shading or site pre-emption.

The seed bank was not an important source of woody seedlings to the understory of intact pine plantations. Most of the seed bank species were herbs which may play an important role in the first years after clear-cutting but which do not generally persist.

The main goal of this study is to predict the pathways and rates of succession in the older pine plantations as a function of pine species, site characteristics, and ultimate management. Landscape theory suggests that planted and chronic disturbance patches can disappear or blend into the matrix because of immigration of matrix species and extinction of the species introduced by the chronic disturbance (Forman and Godron 1986). If a pine plantation is replanted with pines the planted patch and chronic disturbance persist and even though matrix species colonize the patch repeatedly they are suppressed by silvicultural operations.

If the pine plantations are left to senesce with no management, disturbances such as ice storms with subsequent tree fall (Boerner *et al.* 1988) create gaps in the canopy into which other species may grow. The most probable species for filling these gaps are those already present in the advance regeneration. Though establishment from the seed bank and dispersal of seeds from the matrix, especially by birds, may be important in filling these gaps, those individuals will be germinating *de novo* and will have to compete with already established seedlings and saplings. Under these circumstances, the advance regeneration of species common to the matrix will probably dominate as the pine plantations degenerate.

In contrast, after clear-cutting much of the advance regeneration disappears with the pines. The initial successional phases are dominated by seed bank species and bird-dispersed species not common to the forest matrix. Some woody species of the forest matrix are present in the first years after clear-cut, but at low densities. Though long-term studies of succession in senescent pine plantations are lacking, we feel this study strongly suggests that if pine patches are left to senesce they will blend into the matrix relatively quickly and that this succession will be dominated by advance regeneration and early immigration. Clear-cut pine patches, in contrast, will remain distinct from the matrix for a longer period of time and the patterns of succession will be controlled by the seed bank, continued dispersal from outside the stands, and a large stochastic component. Thus, in this situation, the rate and pathways by which a chronic disturbance patch

blends back into the matrix may be determined by whether the disturbance comes to an abrupt, destructive end, as in clear-cutting, or is allowed to decrease in intensity in a gradual manner. Long-term studies of paired senescing and clear-cut plantations are necessary, however, to fully test this model of landscape change.

Acknowledgments

We thank Do-Soon Cho, Shari Koslowsky, and Hugh Crowell for help during the field season, Charles Foster of the Ohio Division of Forestry for supplying site information, Ron Stuckey and Tom Lammers for aid in seedling identification, and Bill Mitsch, Terry Logan, Dan Jacques, Amy Scherzer, Do-Soon Cho, Kathy Harris, and two anonymous reviewers for their constructive comments on an earlier draft of the manuscript. This work was supported by the Environmental Biology Graduate Program at O.S.U. and was submitted in partial fulfillment of the requirements for the M.S. degree.

Literature cited

- Boerner, R.E.J. and Crozier, C.R. 1983. Analysis of forest structure and succession in the Hocking Hills. Technical Report #940088, Division of Natural Areas & Preserves, Ohio Department of Natural Resources, Columbus, Ohio.
- Boerner, R.E.J. and Cho, D.S. 1987. Structure and composition of Goll Woods, an old-growth forest remnant in northwestern Ohio. *Bull. Torrey Bot. Club* 114: 173–179.
- Boerner, R.E.J., Runge, S.D., Cho, D.S. and Kooser, J.G. 1988. Localized ice storm damage in an Appalachian Plateau watershed. *Am. Midl. Natur.* 119: 199–208.
- Bormann, F.H. and Likens, G.E. 1979. *Pattern and process in a forested ecosystem*. Springer Verlag, Inc. NY.
- Braun, E.L. 1961. *The woody plants of Ohio*. Hafner Press, MacMillan Publishing Company, NY.
- Canham, C.D. and Loucks, O.L. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology* 65: 803–809.
- Forman, R.T.T. and Godron, M. 1986. *Landscape ecology*. John Wiley & Sons, Inc., NY.
- Gordon, R.B. 1969. The natural vegetation of Ohio in pioneer days. *Ohio Biol. Surv. Bull.* 111(2): 1–113.
- Grigal, D.F. 1973. Note on the hydrometer method of particle size analysis. Minnesota Forestry Research Note 245, University of Minnesota, St. Paul, MN.
- Hill, M.D. and Gauch, H.G. 1980. Detrended correspondence analysis: An improved ordination technique. *Vegetatio* 42: 47–59.
- Hitchcock, A.S. and Chase, A. 1971. *Manual of the grasses of the United States*, second edition. Dover Publications, NY.
- Marshall, B. and Woodward, F.I. (eds.). 1985. *Instrumentation for environmental physiology*. Society for Experimental Biology, Seminar Series Number 22. Cambridge University Press, NY.
- McDonnell, M.J. 1988. Landscape, birds, and plants: Dispersal patterns and vegetation change. *In* *Biogeography of the Island Region of Western Lake Erie: A Laboratory for Ecology and Evolution*. pp. 214–220. Edited by J.F. Downhower. Ohio State University Press, Columbus. In Press.
- Mueller-Dombois, D. and Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. John Wiley & Sons, Inc., NY.
- Ohio Division of Natural Resources (ODNR). 1981. *Masterplan for Hocking State Forest*. Technical Report, Division of Forestry, Ohio Department of Natural Resources, Columbus, OH.
- Peech, H.F. 1965. Hydrogen-ion activity. *In* *Methods of Soil Analysis*. pp. 914–920. Edited by C.A. Black. American Society of Agronomy Publication 9, Madison, WI.
- Pickett, S.T.A. and Thompson, J.N. 1978. Patch dynamics and the design of nature preserves. *Biol. Cons.* 13: 27–37.
- Shopmeyer, C.S. 1974. *Seeds of Woody Plants of the United States*. U.S.D.A. Agricultural Handbook 450. National Technical Information Service, Springfield, VA.
- Soil Conservation Service (SCS). 1988. *Soil Survey Manual for Hocking County, Ohio*. U.S.D.A. Soil Conservation Service, Logan, OH. In press.
- Solbrig, O.T. 1975. Plant population biology: An overview. *Syst. Bot.* 1: 202–206.
- Statistical Analysis System (SAS). 1986. *User's guide: Statistics, version 5*. S.A.S. Institute, Cary, NC.
- Stucky, J.M., Monaco, T.J. and Worsham, A.D. 1981. Identifying seedlings and mature weeds common in the southeastern United States. North Carolina Agricultural Research Service and Extension Service, North Carolina State University, Raleigh, NC.
- Wolfe, J.N., Wareham, R.T. and Scofield, H.T. 1949. Microclimate and macroclimate of Neotoma, a small valley in central Ohio. *Ohio Biol. Surv. Bull.* 41: 1–267.