INVASION OF TREES IN SECONDARY SUCCESSION IN THE LAND-BETWEEN-THE-LAKES, TENNESSEE

JANET FAY LEE

INVASION OF TREES IN SECONDARY SUCCESSION

IN

THE LAND-BETWEEN-THE-LAKES, TENNESSEE

An Abstract

Presented to

the Graduate Council of

Austin Peay State University

In Partial fulfillment

of the Requirements for the Degree

Master of Science

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by

Janet Fay Lee

August, 1972

ABSTRACT

The invasion of trees in secondary succession was studied in ten abandoned fields in the Land-Between-The-Lakes area of the Northwestern Highland Rim in Stewart County, Tennessee. Five of these fields had been abandoned for three years with the last crop of four being corn and the fifth tobacco. The remaining five fields had been abandoned for four years with the last crop being corn.

Sampling was accomplished by the quadrat method. Ten 20.5 feet by 20.5 feet random plots were taken in each field to yield a one-tenth acre sample per field. Tree seedlings within these plots were mapped and recorded initially in June, 1971. Second and third surveys of the same plots were taken in August, 1971 and April, 1972. For each species present the following parameters were determined: density, relative density, frequency, relative frequency, dominance, relative dominance, species summer mortality rate, comparative summer mortality rate, species winter mortality rate, and comparative winter mortality rate. A summarized total value or the Importance Value Index was obtained by the addition of the relative values.

A total of seventeen species was found in three-year fields; the major species were _Ulmus_ spp., _Diospyros virginiana_, _Rhus copallina_, _Liquidambar styraciflua_, and _Prunus serotina_. Twenty species were found in the four-year fields; the major species were _Acer saccharum_, _Diospyros virginiana_, _Platanus occidentalis_, _Liquidambar styraciflua_, and _Rhus copallina_.

INVASION OF TREES IN SECONDARY SUCCESSION IN THE LAND-BETWEEN-THE-LAKES, TENNESSEE

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August, 1972

To the Graduate Council:

I am submitting herewith a Thesis written by Janet Fay Lee entitled "Invasion of Trees in Secondary Succession in the Land-Between-The-Lakes, Tennessee." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Biology.

Edward W. Chester
Major Professor

We have read this thesis and recommend its acceptance:

Floyd L. Brown
Second Committee Member

Floyd M. Ford
Third Committee Member

Accepted for the Council:

Wayne E. Stamper
Dean of the Graduate School

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CHAPTER I

INTRODUCTION

With time the natural vegetation of any abandoned agricultural area undergoes changes both in species composition and in the sociological characteristics of the species present. The rate of change and species involved are influenced by a complex of environmental factors. The progressive re-vegetation of an area disturbed by man, animals, or physical forces is termed secondary succession. According to Smith (1966), this type of succession frequently occurs on a substrate low in nutrients and organic matter, excessively wet or dry environments, very bright sunlight, wide variations of surface temperature, animal disturbances, erosion, and settling movements. Since seedlings of most species have narrow tolerance limits and unique environmental requirements, only those seedlings which can tolerate extreme environments will be able to invade and survive on newly abandoned land.

According to Rogers (1971), the Land-Between-The-Lakes Recreation Area came into being in 1965 when the Corps of Engineers closed the gates of Barkley Dam, filling the Cumberland River valley and creating Lake Barkley. In 1944 the Tennessee Valley Authority had completed Kentucky Dam on the Tennessee River creating Lake Kentucky. The 170,000-acre area between the two man-made lakes is being developed as a recreation and conservation education area by the Tennessee Valley Authority.

This recreation area is approximately forty miles long and six to eight miles wide and includes portions of Trigg and Lyon Counties, Kentucky and Stewart County, Tennessee. Before being established as a recreational site, the area was composed of several communities, a number of small farms, and a 60,000 acre wildlife refuge. Now, most of the former buildings, utility lines, and advertising signboards have been removed (Ellis, Wofford, and Chester, 1971). Detailed descriptions of the study area are given by McReynolds (1969) and Heilman (1971).

There are few areas that are left undisturbed in which secondary succession may be studied. Austin Peay State University is fortunate to have been authorized by the Tennessee Valley Authority to use certain fields of known ages and histories in the Land-Between-The-Lakes for various types of successional research. This thesis takes advantage of this area in order to study (1) the invasion and establishment of tree species in the early stages of old-field succession and (2) some of the factors that influence the rates of succession. Data from these fields should reveal phytosociological relationships and give some idea of the tolerance limits of tree seedlings from spring to summer of one year and during the following winter. Comparisons of findings will be made with previous studies in other geographical areas.

CHAPTER II

LITERATURE REVIEW

It has long been recognized that forests are not static, but that their composition and structure changes with time as a result of natural development and of disturbances such as fire, windthrow, clearing, and climatic changes. Spurr (1952) points out that this concept was implied by several early Roman writers and by nineteenth-century western European foresters such as Laurent in 1849.

According to Spurr (1952), the first detailed North American report of composition changes was prepared by Dawson in 1847 and dealt primarily with the maritime provinces. He recognized the effects of windthrow and fire in the forests found by the original European settlers and the results of later agricultural use of the land.

Oosting (1942) did an extensive ecological analysis of the plant communities of the Piedmont region of North Carolina. McQuilkin (1940) made a study in the Piedmont Plateau region dealing with pine invasion in abandoned fields, and Keever (1950) related several factors as causes of succession in old fields of the North Carolina Piedmont. Crafton and Wells (1934), also working in North Carolina, discuss the early stages of succession based upon general observations, types of soil, and on the invasion of plants into spaded squares.

Bard (1952) investigated fields in different successive stages of natural re-vegetation in order to determine the major changes in the vegetation and soil occurring on the Piedmont of New Jersey. Another study on the New Jersey Piedmont was done by Buell, Buell, Small, and Siccama (1971) and concerned the invasion of trees in secondary succession. McCormick and Buell (1957) studied the natural re-vegetation of a plowed field in the New Jersey Pine Barrens.

Certain ecological factors play a role in determining the tolerance of invading tree seedlings. Kozlowski (1949) related light and water in relation to growth and competition of Piedmont forest tree species. Bormann (1953) dealt specifically with Pinus taeda and Liquidambar styraciflua and the factors determining the role of these two species in the Piedmont of North Carolina. Minkler (1946) studied old-field reforestation in the Great Appalachian Valley as related to some ecological factors. Duncan (1935) studied the root systems of four species of woody plants which occurred frequently in the old fields in southern Indiana, and Hosner and Gramey (1970) investigated the relative growth of three forest species on soils associated with different succession stages in Virginia.

Although there have been many studies on secondary succession in the southeastern United States, only one other study has been made on the Western Highland Rim of Tennessee. This study (McReynolds, 1969) observed early secondary succession on abandoned farmland in the Land-Between-The-Lakes. Two other comparable works have been done in nearby areas. Quarterman (1957) investigated early plant succession in the Central or Nashville Basin of Tennessee. Bazzaz (1968) worked in the Shawnee Hills of southern Illinois; fields of eight different ages ranging from one year to forty years old were investigated.

CHAPTER III

METHODS AND MATERIALS

The quadrat method was used for sampling. Within each field ten 20.5 feet by 20.5 feet plots were randomly selected to yield a one-tenth acre sample per field. Species of tree seedlings and numbers present in each plot were recorded and mapped initially in mid-June, 1971; a survey of these same species was made in late August, 1971 and disappearances noted; the final count was taken during the following year in late April, 1972.

The parameters determined for each species were density, relative density, frequency, relative frequency, dominance, which was estimated cover after Braun-Blanquet (1932), relative dominance, species summer mortality rate, comparative summer mortality rate, species winter mortality rate, and comparative winter mortality rate. A summary figure, Importance Value Index, which was derived from the addition of the three relative values, was determined also for each species.

The following formulas were used in calculations:

1. Density =

$$\frac{\text{number of a species}}{\text{one acre}}$$

2. Relative Density =

$$\frac{\text{density of a species}}{\text{total densities of all species}} \quad X \quad 100$$

3. Frequency =

$$\frac{\text{number of plots a species occurs}}{\text{total number of plots sampled}}$$

4. Relative Frequency =

$$\frac{\text{frequency of a species}}{\text{total frequencies of all species}} \times 100$$

5. Dominance (Cover) =

Coverage Classes (Braun-Blanquet, 1932):

x	less than 1% coverage
1	1%-5%
2	6%-25%
3	26%-50%
4	51%-75%
5	76%-100%

6. Relative Dominance =

$$\frac{\text{dominance of a species}}{\text{total dominance of all species}} \times 100$$

7. Species Summer Mortality Rate =

$$\frac{\text{number of a species missing in fall survey}}{\text{total initial number of a species}} \times 100$$

8. Comparative Summer Mortality Rate =

$$\frac{\text{number of a species missing fall survey}}{\text{total number found missing of all species in fall survey}} \times 100$$

9. Species Winter Mortality Rate =

$$\frac{\text{number of a species missing in spring survey}}{\text{number of a species existing after fall survey}} \times 100$$

10. Comparative Winter Mortality Rate =

$$\frac{\text{number of a species missing in spring survey}}{\text{total number missing of all species in spring survey}} \times 100$$

11. Total One-Year Mortality Rate =

$$\frac{\text{Total number of a species missing both surveys}}{\text{initial number of a species}} \times 100$$

12. Importance Value Index (IVI) =

Relative Density + Relative Frequency + Relative Dominance

CHAPTER IV

RESULTS

Five fields which had been abandoned for three years were studied. Seventeen tree species were found but only two, Prunus serotina and Ulmus spp. (including alata, americana, and rubra), were found in all five fields (Table I). A comparison of taxa densities for three-year fields is given in Table II and frequencies in Table III. Computations and Importance Values for all three-year species are shown in Table IV.

In comparison, Quarterman (1957) found only two tree species in her three-year fields with Ulmus and Celtis being the most important woody components (Table V). Bazzaz (1968) mentioned only Diospyros virginiana in his study of three-year fields in Illinois.

In this study Ulmus spp. far outranked other species in Importance Value Index in three-year fields, having three times the IVI of the second species, Diospyros virginiana (Table IV). Rhus copallina, Liquidambar styraciflua, and Prunus serotina followed. Ulmus spp. had an overwhelming density of almost ten times that of the second species, Liquidambar styraciflua (Table III).

Acer rubrum had the highest summer mortality rate followed by Ulmus spp. and Juniperus virginiana (Table I). Summer mortality rates for each three-year field is shown in Table VI, and total summer mortality rates are given in Table I. Acer rubrum also had the highest winter mortality rate followed by Ulmus spp. and

Fraxinus spp. Total winter mortality rates for each three-year species are shown in Table I and rates for each three-year field in Table VII. Total individual and comparative mortality rates are shown in Table VIII.

Five fields which had been abandoned for four years were studied. Twenty species were found with only one species, *Diospyros virginiana*, found in all five fields (Table IX). Found in four of the five fields were *Acer saccharum*, *Rhus copallina*, and *Ulmus* spp. Quarterman (1957) found four taxa with *Ulmus* and *Celtis* highest in her four to eight-year fields in the Central Basin of Tennessee (Table V). Bazzaz (1968) found *Diospyros virginiana*, *Sassafras albidum*, *Ulmus alata*, *Juniperus virginiana*, and *Rhus* spp. with the first of the five species being the dominant.

Densities and frequencies for the four-year fields are Shown in Tables X and XI. *Acer saccharum* had the highest Importance Value Index followed by *Diospyros virginiana* (Table XII). Three new important species were next in value: *Platanus occidentalis*, *Liquidambar styraciflua*, and *Rhus copallina*. *Acer saccharum* also had the highest density value, far above the next in value or *Platanus occidentalis*.

Acer rubrum obtained the highest species summer and winter mortality rates (Table IX) in the four-year fields. *Acer saccharum* had the highest comparative summer and winter mortality rates (Table IX). *Quercus* spp. experienced a very high winter mortality rate (Table IX). Summer mortality rates for each four-year field are shown in Tables XIII and XIV.

TABLE I

SPECIES FOUND IN THREE-YEAR FIELDS AND MORTALITY RATES

SPECIES	No. Fields Occur.	No. Found Spring, '71	No. Found Fall, '71	Percent Summer Mortality	No. Found Spring, '72	Percent Winter Mortality	Total 1-Year Mort. (%)
Acer rubrum	2	11	3	72.7	1	66.7	90.9
Acer saccharum	4	132	116	12.1	102	12.1	22.7
Cornus florida	1	2	2	0.0	2	0.0	0.0
Diospyros virginiana	4	95	94	1.1	78	17.0	17.9
Fraxinus spp.	1	18	18	0.0	9	50.0	50.0
Juglans nigra	2	25	23	8.0	23	0.0	8.0
Juniperus virginiana	2	2	1	50.0	1	0.0	50.0
Liquidambar styraciflua	2	227	219	3.5	205	6.4	9.6
Liriodendron tulipifera	1	16	16	0.0	16	0.0	0.0
Platanus occidentalis	3	29	25	13.8	19	24.0	34.5
Prunus serotina	5	76	75	1.3	72	4.0	5.3
Quercus spp.	3	5	4	20.0	4	0.0	20.0
Rhus copallina	3	105	105	0.0	104	1.0	1.0
Rhus glabra	3	3	3	0.0	2	33.3	33.3
Robinia pseudoacacia	1	3	3	0.0	3	0.0	0.0
Sassafras albidum	3	46	38	17.4	36	5.3	21.8
Ulmus spp.	5	2,122	1,009	52.5	336	65.2	78.9

TABLE II

A COMPARISON OF DENSITIES
IN THREE-YEAR FIELDS

SPECIES	IVI	FIELD NUMBERS				
		5	6	9	10	13
Acer rubrum	4.7	—	60	—	—	80
Acer saccharum	13.3	100	40	—	490	50
Cornus florida	2.3	—	—	20	—	—
Diospyros virginiana	37.9	—	560	120	130	140
Fraxinus spp.	4.5	—	—	—	—	180
Juglans nigra	5.2	190	—	80	—	—
Juniperus virginiana	6.2	—	10	—	10	—
Liquidambar styraciflua	19.0	—	190	—	2,130	—
Liriodendron tulipifera	6.1	—	110	—	—	—
Platanus occidentalis	7.6	100	—	—	30	10
Prunus serotina	18.8	30	20	580	80	10
Quercus spp.	6.8	—	10	20	10	—
Rhus copallina	22.2	—	770	70	220	—
Rhus glabra	6.7	—	30	—	20	10
Robinia pseudoacacia	2.3	30	—	—	—	—
Sassafras albidum	18.5	120	260	70	—	—
Ulmus spp.	116.5	250	440	450	630	19,450

TABLE III

A COMPARISON OF FREQUENCIES
IN THREE-YEAR FIELDS

SPECIES	IVI	FIELD NUMBERS				
		5	6	9	10	13
Acer rubrum	4.7	--	.6	--	--	.4
Acer saccharum	13.3	.7	.2	--	1.0	.4
Cornus florida	2.3	--	--	.2	--	--
Diospyros virginiana	37.9	--	.3	.4	.4	.4
Fraxinus spp.	4.5	--	--	--	--	.6
Juglans nigra	5.2	.9	--	.4	--	--
Juniperus virginiana	6.2	--	.1	--	.1	--
Liquidambar styraciflua	19.0	--	.7	--	.7	--
Liriodendron tulipifera	6.1	--	.2	--	--	--
Platanus occidentalis	7.6	.5	--	--	.2	.1
Prunus serotina	18.8	.2	.2	.9	.2	.1
Quercus spp.	6.8	--	.1	.1	.1	--
Rhus copallina	22.2	--	.2	.3	.5	--
Rhus glabra	6.7	--	.1	--	.1	.1
Robinia pseudoacacia	2.3	.2	--	--	--	--
Sassafras albidum	18.5	.4	.5	.1	--	--
Ulmus spp.	116.5	.9	.9	.4	.9	1.0

TABLE IV

SUMMARY OF VEGETATIONAL ANALYSIS (MODIFIED FROM COX, 1971)
THREE-YEAR FIELDS

SPECIES	Total Number	Den-sity	Rel. Dens.	Dom.	Rel. Dom.	Freq.	Rel. Freq.	IVI
Ulmus spp.	2,122	4,244	72.7	19	32.7	.10	11.1	116.5
Diospyros virginiana	95	190	3.3	15	25.8	.08	8.8	37.9
Rhus copallina	105	210	3.6	7	12.0	.06	6.6	22.2
Liquidambar styraciflua	227	454	7.8	4	6.8	.04	4.4	19.0
Prunus serotina	76	152	2.6	3	5.1	.10	11.1	18.8
Sassafras albidum	46	92	1.6	6	10.3	.06	6.6	18.5
Acer saccharum	132	264	4.5	x	x	.08	8.8	13.3
Platanus occidentalis	29	58	1.0	x	x	.06	6.6	7.6
Quercus spp.	5	10	.2	x	x	.06	6.6	6.8
Rhus glabra	3	6	.1	x	x	.06	6.6	6.7
Juniperus virginiana	2	4	.1	1	1.7	.04	4.4	6.2
Liriodendron tulipifera	16	32	.5	2	3.4	.02	2.2	6.1
Juglans nigra	25	50	.8	x	x	.04	4.4	5.2
Acer rubrum	11	22	.3	x	x	.04	4.4	4.7
Fraxinus spp.	18	36	.6	1	1.7	.02	2.2	4.5
Cornus florida	2	4	.1	x	x	.02	2.2	2.3
Robinia pseudoacacia	3	6	.1	x	x	.02	2.2	2.3

TABLE V

COMPARISON OF MAJOR SPECIES
OF THE CENTRAL BASIN (QUARTERMAN, 1957) AND NORTHWESTERN HIGHLAND RIM,
THREE AND FOUR-YEAR FIELDS

CENTRAL BASIN	DFD INDEX		NORTHWESTERN HIGHLAND RIM	IVI	
	3 yr.	4-8 yr.		3 yr.	4 yr.
Celtis spp.	14.7	30.0	Acer rubrum	4.7	7.3
Ulmus spp.	15.0	80.0	Acer saccharum	13.3	62.7
Rhus typhina	--	12.0	Catalpa speciosa	--	8.2
Maclura pomifera	--	12.0	Cornus florida	2.3	2.3
			Diospyros virginiana	38.0	44.3
			Fraxinus spp.	4.5	2.3
			Juglans nigra	5.2	6.9
			Juniperus virginiana	6.2	2.6
			Liquidambar styraciflua	19.0	29.3
			Liriodendron tulipifera	6.1	3.5
			Morus rubra	--	5.0
			Pinus taeda	--	11.2
			Platanus occidentalis	7.6	30.8
			Prunus americana	--	2.8
			Prunus serotina	18.8	12.3
			Quercus spp.	6.8	7.2
			Rhus copallina	22.2	22.4
			Rhus glabra	6.7	15.0
			Robinia pseudoacacia	2.3	--
			Sassafras albidum	18.5	7.2
			Ulmus spp.	116.5	17.0

TABLE VI

SPECIES AND COMPARATIVE SUMMER MORTALITY RATES
IN THREE-YEAR FIELDS

SPECIES	FIELD NUMBERS 5		6		9		10		13	
	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.
Acer rubrum	—	—	33	15	—	—	—	—	38	1
Acer saccharum	60	19	25	5	—	—	27	48	0	0
Cornus florida	—	—	—	—	0	0	—	—	—	—
Diospyros virginiana	—	—	0	0	0	0	0	0	1	1
Fraxinus spp.	—	—	—	—	—	—	—	—	0	0
Juglans nigra	11	6	—	—	0	0	—	—	—	—
Juniperus virginiana	—	—	100	17	—	—	0	0	—	—
Liquidambar styraciflua	—	—	0	0	—	—	4	30	—	—
Liriodendron tulipifera	—	—	0	0	—	—	—	—	—	—
Platanus occidentalis	30	9	—	—	—	—	0	0	1	1
Prunus serotina	0	0	0	0	0	0	13	4	—	—
Quercus spp.	—	—	0	0	0	0	100	4	—	—
Rhus copallina	—	—	0	0	0	0	0	0	—	—
Rhus glabra	—	—	0	0	—	—	0	0	0	0
Robinia pseudoacacia	0	0	—	—	—	—	—	—	—	—
Sassafras albidum	58	21	4	7	0	0	—	—	—	—
Ulmus spp.	60	45	18	62	16	100	6	15	56	97

TABLE VII

SPECIES AND COMPARATIVE WINTER MORTALITY RATES
IN THREE-YEAR FIELDS

SPECIES	FIELD NUMBERS 5 Sp.	5 Comp.	6 Sp.	6 Comp.	9 Sp.	9 Comp.	10 Sp.	10 Comp.	13 Sp.	13 Comp.
Acer rubrum	—	—	0	0	—	—	—	—	20	1
Acer saccharum	25	15	33	5	—	—	25	27	40	1
Cornus florida	—	—	—	—	0	0	—	—	—	—
Diospyros virginiana	—	—	13	32	17	14	31	12	23	1
Fraxinus spp.	—	—	—	—	—	—	—	—	50	2
Juglans nigra	0	0	—	—	0	0	—	—	—	—
Juniperus virginiana	—	—	0	0	—	—	0	0	—	—
Liquidambar styraciflua	—	—	26	23	—	—	4	27	—	—
Liriodendron tulipifera	—	—	0	0	—	—	—	—	—	—
Platanus occidentalis	71	39	—	—	—	—	33	3	0	0
Prunus serotina	0	0	0	0	3	14	14	3	0	0
Quercus spp.	—	—	0	0	0	0	0	0	—	—
Rhus copallina	—	—	0	0	0	0	5	3	—	—
Rhus glabra	—	—	0	0	—	—	50	3	0	0
Robinia pseudoacacia	0	0	—	—	—	—	—	—	—	—
Sassafras albidum	9	8	4	5	0	0	—	—	—	—
Ulmus spp.	50	39	22	36	26	71	12	21	79	95

TABLE VIII

SUMMARIZED SPECIES AND COMPARATIVE
SUMMER AND WINTER MORTALITY RATES IN
THREE AND FOUR-YEAR FIELDS EXPRESSED AS PERCENTAGES

SPECIES	THREE-YEAR FIELDS				FOUR-YEAR FIELDS			
	Summer		Winter		Summer		Winter	
	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.
Acer rubrum	72.7	.7	66.7	.3	16.7	1.5	60.0	4.8
Acer saccharum	12.1	1.4	12.1	1.9	13.7	71.2	7.4	34.3
Catalpa speciosa	—	—	—	—	0.0	0.0	0.0	0.0
Cornus florida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diospyros virginiana	1.1	.1	17.0	2.2	1.7	1.5	7.0	6.3
Fraxinus spp.	0.0	0.0	50.0	1.2	0.0	0.0	0.0	0.0
Juglans nigra	8.0	.2	0.0	0.0	0.0	0.0	33.3	1.6
Juniperus virginiana	50.0	.1	0.0	0.0	0.0	0.0	0.0	0.0
Liquidambar styraciflua	3.5	.1	6.4	1.9	11.3	12.1	6.3	6.3
Liriodendron tulipifera	0.0	0.0	0.0	0.0	0.0	0.0	10.0	1.6
Morus rubra	—	—	—	—	0.0	0.0	0.0	0.0
Pinus taeda	—	—	—	—	0.0	0.0	10.0	1.6
Platanus occidentalis	13.8	.3	24.0	.8	0.0	0.0	3.7	4.8
Prunus americana	—	—	—	—	0.0	0.0	0.0	0.0
Prunus serotina	1.3	.1	4.0	.4	8.3	3.0	13.6	4.8
Quercus spp.	20.0	.1	0.0	0.0	0.0	0.0	60.0	4.8
Rhus copallina	0.0	0.0	1.0	.2	0.0	0.0	26.9	10.9
Rhus glabra	0.0	0.0	33.3	.2	0.0	0.0	0.0	0.0
Robinia pseudoacacia	0.0	0.0	0.0	0.0	—	—	—	—
Sassafras albidum	17.4	.7	5.3	.3	0.0	0.0	0.0	0.0
Ulmus spp.	52.5	95.5	65.7	90.7	11.3	10.6	21.8	18.8
Total (Summer and Winter)	39.9		41.7		8.9		9.9	

TABLE IX

SPECIES FOUND IN FOUR-YEAR FIELDS AND MORTALITY RATES

SPECIES	No. Fields Occur	No. Found Spring, '71	No. Found Fall, '71	Percent Summer Mortality	No. Found Spring, '72	Percent Winter Mortality	Total 1-Year Mort. (%)
Acer rubrum	3	6	5	16.7	2	60.0	66.7
Acer saccharum	4	344	297	13.7	275	7.4	20.1
Catalpa speciosa	1	7	7	0.0	7	0.0	0.0
Cornus florida	1	1	1	0.0	1	0.0	0.0
Diospyros virginiana	5	58	57	1.7	53	7.0	8.6
Fraxinus spp.	1	1	1	0.0	1	0.0	0.0
Juglans nigra	3	3	3	0.0	2	33.3	33.3
Juniperus virginiana	1	3	3	0.0	3	0.0	0.0
Liquidambar styraciflua	2	71	63	11.3	59	6.3	16.9
Liriodendron tulipifera	1	10	10	0.0	9	10.0	10.0
Morus rubra	1	2	2	0.0	2	0.0	0.0
Pinus taeda	1	10	10	0.0	9	10.0	10.0
Platanus occidentalis	2	82	82	0.0	79	3.7	4.6
Prunus americana	1	5	5	0.0	5	0.0	0.0
Prunus serotina	3	24	22	8.3	19	13.6	20.4
Quercus spp.	3	5	5	0.0	2	60.0	60.0
Rhus copallina	4	26	26	0.0	19	26.9	26.9
Rhus glabra	3	25	25	0.0	25	0.0	0.0
Sassafras albidum	2	2	2	0.0	2	0.0	0.0
Ulmus spp.	4	62	55	11.3	43	21.8	30.6

TABLE X

A COMPARISON OF DENSITIES
IN FOUR-YEAR FIELDS

SPECIES	IVI	FIELD NUMBERS 0	7	8	11	12
Acer rubrum	7.3	30	10	—	—	20
Acer saccharum	62.7	140	1,420	20	1,860	—
Catàlpa speciosa	8.2	—	70	—	—	—
Cornus florida	2.3	—	—	10	—	—
Diospyros virginiana	44.3	90	160	130	70	130
Fraxinus spp.	2.3	—	—	—	—	10
Juglans nigra	6.9	—	10	10	10	—
Juniperus virginiana	2.6	—	—	30	—	—
Liquidambar styraciflua	29.3	—	550	160	—	—
Liriodendron tulipifera	3.5	—	50	—	—	—
Morus rubra	5.0	20	—	—	—	—
Pinus taeda	11.2	—	—	—	—	100
Platanus occidentalis	30.8	—	770	—	50	—
Prunus americana	2.8	—	—	—	—	50
Prunus serotina	12.3	20	140	80	—	—
Quercus spp.	7.2	—	10	10	—	30
Rhus copallina	22.4	—	50	10	180	20
Rhus glabra	15.0	30	200	20	—	—
Sassafras albidum	7.2	—	—	—	30	10
Ulmus spp.	17.0	30	130	450	10	—

TABLE XI

A COMPARISON OF FREQUENCIES
IN FOUR-YEAR FIELDS

SPECIES	IVI	FIELD NUMBERS				
		0	7	8	11	12
Acer rubrum	7.3	.2	.1	—	—	.2
Acer saccharum	62.7	.5	1.0	.1	1.0	—
Catalpa speciosa	8.2	—	.3	—	—	—
Cornus florida	2.3	—	—	.1	—	—
Diospyros virginiana	44.3	.3	.3	.3	.2	.4
Fraxinus spp.	2.3	—	—	—	—	.1
Juglans nigra	6.9	—	.1	.1	.1	—
Juniperus virginiana	2.6	—	—	.1	—	—
Liquidambar styraciflua	29.3	—	.9	.5	—	—
Liriodendron tulipifera	3.5	—	.3	—	—	—
Morus rubra	5.0	.1	—	—	—	—
Pinus taeda	11.2	—	—	—	—	.2
Platanus occidnetalis	30.8	—	.5	—	.3	—
Prunus americana	2.8	—	—	—	—	.2
Prunus serotina	12.3	.2	.7	.1	—	—
Quercus spp.	7.2	—	.1	.1	—	.2
Rhus copallina	22.2	—	.3	.1	.4	.2
Rhus glabra	15.0	.1	.1	.1	—	—
Sassafras albidum	7.2	—	—	—	.1	.1
Ulmus spp.	17.0	.2	.5	.7	.1	—

TABLE XII

SUMMARY OF VEGETATIONAL ANALYSIS (MODIFIED FROM COX, 1971), FOUR-YEAR FIELDS

SPECIES	Total Number	Density	Rel. Dens.	Dom.	Rel. Dom.	Freq.	Rel. Freq.	IVI
Acer saccharum	344	688	46.8	3	7.7	.08	8.7	62.7
Diospyros virginiana	58	116	7.8	10	25.6	.10	10.9	44.3
Platanus occidentalis	82	164	11.1	6	15.4	.04	4.3	30.8
Liquidambar styraciflua	71	142	9.6	6	15.4	.04	4.3	29.3
Rhus copallina	26	52	3.5	4	10.3	.08	8.7	22.4
Ulmus spp.	62	124	8.4	x	x	.08	8.7	17.0
Rhus glabra	25	50	3.4	2	5.1	.06	6.5	15.0
Prunus serotina	24	48	3.2	1	2.6	.06	6.5	12.3
Pinus taeda	10	20	1.3	3	7.7	.02	2.2	11.2
Catalpa speciosa	7	14	.9	2	5.1	.02	2.2	8.2
Acer rubrum	6	12	.8	x	x	.06	6.5	7.3
Quercus spp.	5	10	.7	x	x	.06	6.5	7.2
Sassafras albidum	2	4	.3	1	2.6	.04	4.3	7.2
Juglans nigra	3	6	.4	x	x	.06	6.5	6.9
Morus rubra	2	4	.3	1	2.6	.02	2.2	5.0
Liriodendron tulipifera	10	20	1.3	x	x	.02	2.2	3.5
Prunus americana	5	10	.7	x	x	.02	2.2	2.8
Juniperus virginiana	3	6	.4	x	x	.02	2.2	2.6
Cornus florida	1	2	.1	x	x	.02	2.2	2.3
Fraxinus spp.	1	2	.1	x	x	.02	2.2	2.3

TABLE XIII

SPECIES AND COMPARATIVE SUMMER MORTALITY RATES
IN FOUR-YEAR FIELDS

SPECIES	FIELD NUMBERS									
	0		7		8		11		12	
	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.
Acer rubrum	0	0	100	3	—	—	—	—	0	0
Acer saccharum	29	66	17	77	0	0	10	100	—	—
Catalpa speciosa	—	—	0	0	—	—	—	—	—	—
Cornus florida	—	—	—	—	0	0	—	—	—	—
Diospyros virginiana	0	0	6	3	0	0	0	0	0	0
Fraxinus spp.	—	—	—	—	—	—	—	—	0	0
Juglans nigra	—	—	0	0	0	0	0	0	—	—
Juniperus virginiana	—	—	—	—	0	0	—	—	—	—
Liquidambar styraciflua	—	—	2	3	44	70	—	—	—	—
Liriodendron tulipifera	—	—	0	0	—	—	—	—	—	—
Morus rubra	0	0	—	—	—	—	—	—	—	—
Pinus taeda	—	—	—	—	—	—	—	—	0	0
Platanus occidentalis	—	—	0	0	—	—	0	0	—	—
Prunus americana	—	—	—	—	—	—	—	—	0	0
Prunus serotina	50	17	7	3	0	0	—	—	—	—
Quercus spp.	—	—	0	0	0	0	—	—	0	0
Rhus copallina	—	—	0	0	0	0	0	0	0	0
Rhus glabra	0	0	0	0	0	0	—	—	—	—
Sassafras albidum	—	—	—	—	—	—	0	0	0	0
Ulmus spp.	33	17	23	10	7	30	0	0	—	—

TABLE XIV

SPECIES AND COMPARATIVE WINTER MORTALITY RATES
IN FOUR-YEAR FIELDS

SPECIES	FIELD NUMBERS									
	0		7		8		11		12	
	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.	Sp.	Comp.
Acer rubrum	100	75	0	0	—	—	—	—	0	0
Acer saccharum	0	0	11	57	50	7	5	80	—	—
Catalpa speciosa	—	—	0	0	—	—	—	—	—	—
Cornus florida	—	—	—	—	0	0	—	—	—	—
Diospyros virginiana	0	0	7	4	0	0	0	0	23	43
Fraxinus spp.	—	—	—	—	—	—	—	—	0	0
Juglans nigra	—	—	0	0	100	7	0	0	—	—
Juniperus virginiana	—	—	—	—	0	0	—	—	—	—
Liquidambar styraciflua	—	—	6	13	11	7	—	—	—	—
Liriodendron tulipifera	—	—	20	4	—	—	—	—	—	—
Morus rubra	0	0	—	—	—	—	—	—	—	—
Pinus taeda	—	—	—	—	—	—	—	—	10	14
Platanus occidentalis	—	—	4	13	—	—	0	0	—	—
Prunus americana	—	—	—	—	—	—	—	—	0	0
Prunus serotina	0	0	15	9	13	7	—	—	—	—
Quercus spp.	—	—	0	0	0	0	—	—	100	43
Rhus copallina	—	—	0	0	0	0	6	10	0	0
Rhus glabra	0	0	0	0	0	0	—	—	—	—
Sassafras albidum	—	—	—	—	—	—	0	0	0	0
Ulmus spp.	50	25	0	0	24	71	100	10	—	—

CHAPTER V

DISCUSSION

Tree invasion during old-field succession has been given some attention in various regions where succession has been studied and attempts to generalize specific stages and patterns have been made. By examining the data from different areas, one can see that there does not appear to be a uniform pattern for tree invasion of old fields throughout the deciduous forest region.

Bard (1952) found that tree species invade young fields within a few years after abandonment and by the fifth year begin to appear above the herbs. According to him *Juniperus virginiana*, *Prunus serotina*, *Acer rubrum*, and *Cornus florida* are typical old-field tree species of central New Jersey. Bard further states that the invasion of *Juniperus virginiana* depends upon a seed source and the presence of seed-ingesting birds. This species usually appeared within the first five years. Bard also noted the abundance of *Prunus serotina* but stated that its mortality rate was quite high. An excellent discussion on the many aspects of succession is found within Bard's study.

Bazzaz (1968) found that from the second year on, succession in the Shawnee Hills of Illinois related to the *Aster*-*Solidago*-*Andropogon* and *Sassafras*-*Diospyros* type investigated in Missouri by Drew in 1942. The abundance of shrubby sprouts of these last two woody species was attributed to their ability to sprout from pieces of roots that had been cut and scattered by ploughing and discing. Bazzaz found that Juniperus virginiana, Rhus copallina, and Rhus glabra were disseminated by birds; all appeared during the fourth year and persisted through the forty-year fields.

Oosting (1942) stated that Pinus taeda and Pinus echinata began within five years following abandonment in North Carolina and a closed stand could be formed within ten to fifteen years. McQuilkin (1940) supports this idea and states that Crafton and Wells (1934) agree as well in their studies in North Carolina.

Duncan (1935) found that old fields of Indiana are slowly invaded by species such as Rhus copallina and Sassafras officinale. Minkler (1946) mentions only Sassafras in both intermediate and late stages of old-field succession in the Great Appalachian Valley.

Buell et al. (1971) state that some authors have gone so far as to set up models of succession; they point out that Egler (1954), who has done considerable field research in northwestern Connecticut, proposed a model for old-field succession which he termed "initial floristic succession." However, as indicated by most of the mentioned studies, tree invasion during old-field succession in the deciduous forest region does not follow a prescribed pattern but is dependent upon several ecological factors. These factors may range from existing climatic conditions to the coincidence of a good seed year.

Keever (1950) states that no species can become established and hold its place in a community unless the seedlings can survive and grow to maturity. For instance, she found that conditions of soil moisture in abandoned fields change with the increase of organic matter and the protection from evaporation by living plants and litter. In most cultivated fields the harvest of a crop removes much of the aerial portion of the plants; consequently there is a minimum of organic matter in fields when they are abandoned. Organic matter may influence the texture, water holding capacity, pH, and mineral content of the soil, and might contain some chemical substances that would be beneficial or harmful to plants growing in the soil containing it.

The idea that one plant may produce some chemical compounds which are inhibitory or toxic to other plants was advanced, according to Keever (1950), by Pickering and Bedford as early as 1914. Davis (1928) centered his work upon the toxic principles of Juglans nigra upon different species. Gant and Clebsch (1972) isolated six phytotoxic compounds from canopy washings, litter, roots, and soil cores taken within Sassafras stands; test species were significantly inhibited.

Kozlowski (1949) studied the effects of light intensity and soil moisture on photosynthesis, transpiration, and growth of pine and hardwood seedlings of the Piedmont forest with great weight attached to light and soil moisture. Bormann (1953) has shown that pine seedlings are more tolerant to the high-temperature, low-moisture, extremes of old-field sites than hardwood seedlings. Minkler (1946) demonstrated that hardwood seedlings may not grow well on old-field sites. He also found that not only passage of time, but site differences and proximity of seed source governed the old-field vegetative succession.

Specific studies of certain species include that by Bormann (1953) and his study of factors determining the role of loblolly pine and sweetgum in early old-field succession on the Piedmont of North Carolina. A study by Hosner and Graney (1970) evaluated the relative effects of soils associated with old-field succession upon the growth of *Pinus virginiana*, *Pinus taeda*, and *Liriodendron tulipifera*.

Another ecological factor in succession is animal disturbance. McCormick and Buell (1957) report heavy deer browsing on some species and the evident presence of rabbits in the fields of the New Jersey Pine Barrens. Buell et al. (1971) attribute the disappearance of some seedlings to insect damage and rabbit or deer browse on the New Jersey Piedmont. Minkler (1946) reported heavy rodent damage to sweetgum, black walnut, white ash, black locust, yellow poplar, and northern red oak in the Great Appalachian Valley.

This study in the Land-Between-The-Lakes found quite an abundance of deer browse. There were numerous deer "beds" and deer paths throughout many of the fields with decapitated seedlings always near-by. Extensive damage to a few older *Diospyros virginiana* was discovered in one particular field. The fall survey had recorded the trees as being from four feet to eight feet tall; during early spring the workings of wood borers had cut the trees to less than a foot high.

Keever (1950) states that the peculiarities of the life cycles of species, especially the time of year at which the seeds mature and germinate and the relation of the time of seed germination to the time at which secondary succession is initiated, often gives one species a decided advantage over another in becoming the invading dominant. Weaver and Clements (1938) emphasize the importance of adaptations which faciliate seed dispersal as a major cause in determining which species will first become established. Coile (1940) contends that factors such as seed dispersal and rooting characteristics of the particular species under shade and open conditions were of greater significance than soil changes in the establishment and replacement of the various successional stages.

Coile (1940) stresses that the difference in the time woody plants invade abandoned fields is related to availability of a good seed source, distance to seed source, and coincidence of a good seed year with climatic conditions favorable to germination and seedlings establishment. He had found that the smaller a field and the greater its proximity to a woodlot, the sooner woodland species enter. Where fields are quite removed from local woodlots, invasion may perhaps be traced to the activity of crows and other birds. Squirrels and other nut-caching rodents do not often venture into open fields, but their activity around the outskirts of forests may provide peripheral invasion. Bazzaz (1968) mentions that the proximity of a field to mature stands of oak-hickory is important not only because of increased availability of seed but also because squirrels are mainly forest and forest-edge dwellers. Bazzaz (1968) uses the example of Potzger and Potzger (1950), who concluded that the invasion of oaks and hickories into abandoned fields in Indiana was delayed because the *Liquidambar styraciflua*-*Acer rubrum* stage was not attractive to squirrels.

McQuilkin (1940) found that the availability of a seed source is the most important factor in the establishment of pine in the Piedmont of North Carolina. He found that the number of pine seedlings per acre decreased with increased distance from the source.

This study in the Land-Between-The-Lakes found *Ulmus* spp. to be the most important species in the three-year fields. *Ulmus* spp. had the highest density, dominance, frequency, and IVI value; one must remember, however, that both summer and winter mortality rates of this species was second only to that of *Acer rubrum* whose total number was small and mortality high in the three-year fields. *Ulmus* spp. was sixth in IVI value in the four-year fields but still relatively high; it occurred in four of the five fields. The mortality rates were high in both summer and winter. The highest mortality rate in the four-year fields was again *Acer rubrum*. The wind-borne seeds of these two species have a definite advantage since a good seed source was available, but as shown by the mortality rates, the seedlings are often not able to withstand the environmental conditions of the old fields. As long as *Ulmus* spp. continues to have the abundant seed source nearby, this species will probably continue to invade in vast numbers and remain a dominant in the fields.

The second most dominant species in both age fields was *Diospyros virginiana*. This species occurred in four of the three-year fields and in all of the four-year fields. Its mortality rates in both summer and winter were low. Most of the deaths were observed to be as a result of outside damage by deer and wood borers. The high IVI values and the low mortality rates indicate that Diospyros virginiana will become more predominant in the fields in the years ahead. This species has the advantage of being able to sprout from roots of previous plants. As indicated by the high dominance, these seedlings were as old as the fields, many appearing during the first year as noted by McReynolds (1969).

Acer saccharum was the highest in IVI value in the four-year fields being found in four of the fields. The abundance of this winged-seeded species can be attributed to a good seed source. A poor seed source accounts for its low seventh place in the three-year fields and still being in four fields. The IVI value was still high, however. The mortality rates were not that high which indicate a continuing dominance of Acer saccharum in the fields. Evidence of both deer browse and the effects of direct sunlight are proposed as the main causes of deaths.

Liquidambar styraciflua had the fourth highest IVI value in both age fields. This species depended largely upon seed source; it occurred in only two fields of each age, but its density and dominance were very high. McReynolds (1969) noted earlier the appearance of this species in her two-year fields which are the four-year fields in this study. The mortality rates in the three-year fields were noteworthy, and the rates in the four-year fields were much higher. As long as there is a good source, this species will remain in the succession of these fields.

Rhus copallina was third highest in the three-year fields and fifth highest in the four-year fields with the IVI values being almost the same in both age fields. This species occurred in three of the three-year fields and four of the four-year fields. The mortality rate in the three-year fields was negligible. In the four-year fields the summer mortality was zero while the winter rate was high. As long as a seed source is available, and there is a presence of seed-ingesting birds, *Rhus copallina* will continue to invade these fields.

Rhus glabra was far less important than *Rhus copallina* in the three-year fields but was found in the same number of fields. The IVI values were closer in the three-year fields with *Rhus glabra* occurring in one less field. *Rhus glabra* suffered a high winter mortality rate in the three-year field but lost no seedlings in the four-year fields.

Platanus occidentalis had the third highest IVI value in the four-year fields but occurred in only two fields; its density and dominance were high. The IVI value in the three-year fields was relatively high; this species occurred in three of the five fields. Since these fields were bottomland fields, seed sources were abundant. The mortality rate in the three-year fields was high while in the four-year fields there were no seedlings lost in the summer, but a few seedlings were lost in the winter.

Prunus serotina occurred in all the three-year fields and obtained the fifth highest IVI. This species was found in three of the four-year fields and was eighth in IVI value. The mortality rate of the three-year fields was low while the rate in the four-year fields was rather high. _Prunus serotina_ as evidenced by its present frequency and good seed source will continue its invasion of these fields. McReynolds (1969) observed this species in her one-year fields which are the three-year fields of this study.

Pinus taeda and _Catalpa speciosa_ are the only two species found that were not native to this area. Only one four-year field had _Pinus taeda_, and another four-year field had _Catalpa speciosa_ yet the IVI values of both were quite high. These were the only two fields that were observed to have a good seed source of these two species. _Catalpa speciosa_ had a mortality rate of zero. _Pinus taeda_ suffered no losses until winter when the rate became relatively high. This species was recorded in a two-year field by McReynolds (1969).

Sassafras albidum was found in three of the three-year fields and in two of the four-year fields. Its IVI value was high in the three-year fields but not as high in the four-year fields. The summer mortality rate in the three-year fields was high compared to the winter mortality rate. No seedlings were lost in the four-year fields. Care was taken when sampling to avoid the "edge effects' of this species. _Sassafras albidum_ occurs frequently in pure stands which gradually spread. Recently, this has been attributed to phytotoxins (Gant and Clebsch, 1972). This mechanism, along with its ability to sprout from the roots of previous plants, gives this species an advantage over other invading species. _Sassafras albidum_ was noted by McReynolds (1969) in her two-year fields.

Juglans nigra occurred in two of the three-year fields and in three of the four-year fields. The IVI values of both age fields were low, however. The summer mortality of the three-year fields was low with no losses in the winter. No disappearances were noted in the summer in the four-year fields, this species lost one third of its species that winter. McReynolds (1969) recorded this species in her one-year fields.

Liriodendron tulipifera was found in only one field each of three-year fields and four-year fields. The IVI values were low, but the densities where the species did occur were high. A nearby seed source was noted.

Juniperus virginiana was found in two of the three-year fields and in one of the four-year fields. The number of species was small as evidenced by the low IVI values in both age fields.

In the three-year fields, *Fraxinus* spp., *Cornus florida*, and *Robinia pseudoacacia* were found in only one field each. These species obtained the lowest IVI values. The seed source of the winged *Fraxinus* spp. and of *Robinia pseudoacacia* was observed adjoining the field but not for *Cornus florida* which was probably deposited by birds. *Cornus florida* and *Robinia pseudoacacia* had mortality rates of zero. *Fraxinus* spp. had no losses during the summer but lost half the seedlings that winter.

Morus rubra and *Prunus americana* were found only in one of the four-year fields. Since no adjacent seed source was available, these two species were probably introduced by birds.

In the four-year fields *Cornus florida* and *Fraxinus* spp. were also the lowest in IVI values occurring each in only one field. Both species had a mortality rate of zero.

Using the same study areas as this study, McReynolds (1969) found Diospyros virginiana, Juglans nigra, and Prunus serotina in one-year fields. In two-year fields, Diospyros virginiana, Liquidambar styraciflua, Pinus taeda, Rhus copallina, Sassafras albidum, and Ulmus alata were found. Her one-year and two-year fields were respectively the three-year and four-year fields used later in this study. All species previously recorded were found also in this study. The McReynolds study found Diospyros virginiana to have the highest Importance Value Index of woody species in the one-year fields. This study found Ulmus spp. to have the highest IVI in the same fields. Ulmus alata was the highest in the two-year fields in her study, and next was Diospyros virginiana. This study found Acer saccharum as the highest, and Diospyros virginiana next in value in the same fields later. These two studies on the same study area indicate a consistant importance of the presence of Diospyros virginiana and Ulmus spp. In Illinois, Bazzaz (1968) found this true with Diospyros virginiana. As mentioned before, Quarterman (1957) found Ulmus and Celtis as the more important species in the early succession stages of old fields.

CHAPTER VI

SUMMARY

The invasion of trees in secondary succession was studied in ten abandoned fields in the Land-Between-The-Lakes area of the Northwestern Highland Rim in Stewart County, Tennessee. Five of these fields had been abandoned for three years with the last crop in four being corn and the fifth tobacco. The remaining five fields had been abandoned for four years with the last crop being corn.

Sampling was done by the quadrat method. Ten 20.5 feet by 20.5 feet random plots were taken in each field to yield a one-tenth acre sample per field. Tree seedlings within these plots were mapped and recorded initially in June, 1971. A second and third survey of the same plots was made in August, 1971 and April, 1972. For each species the following parameters were determined: density, relative density, frequency, relative frequency, dominance, relative dominance, species summer mortality rate, comparative summer mortality rate, species winter mortality rate, and comparative winter mortality rate. A summarized total value or the Importance Value Index was obtained by the addition of the relative values.

In the three-year fields the major species, according to their Importance Value Index, were: *Ulmus* spp., *Diospyros virginiana*, *Rhus copallina*, *Liquidambar styraciflua*, and *Prunus serotina*. In the four-year fields *Acer saccharum*,

Diospyros virginiana, Platanus occidentalis, Liquidambar styraciflua, and Rhus copallina were the most important species.

In the three-year fields, Acer rubrum had the highest summer mortality rate followed by Ulmus spp. and Juniperus virginiana. Acer rubrum also had the highest winter mortality rate followed by Ulmus spp. and Fraxinus spp. There were three species which had a total mortality rate of zero; they were Cornus florida, Liriodendron tulipifera, and Robinia pseudoacacia.

In the four-year fields, Acer rubrum had the highest summer mortality rate followed by Acer saccharum, Liquidambar styraciflua, and Ulmus spp. Seven species had a total mortality rate of zero: Catalpa speciosa, Cornus florida, Juniperus virginiana, Morus rubra, Prunus americana, Rhus glabra, and Sassafras albidum.

The total summer and winter mortality rates were close in value with the winter rates slightly more in both three and four-year fields.

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