

Secondary Succession in an Illinoian Tillplain Habitat¹

J. E. POTZGER, Butler University

ESTHER POTZGER, Canterbury College

The work presented here marks the beginning of an observation on the progress of secondary succession on an abandoned farm adjacent to a comparatively little disturbed mature stand of the sweet gum-red maple-beech type of forest. Observation was based on twenty 10-meter-square permanent quadrats. The land has not been under cultivation for about fifteen years, and forest is well established as a vigorous young *Liquidambar-Acer rubrum* associes.

Since appearance of Cowles (1) classical studies on succession in dunes habitats ecologists have been conscious of the dynamic aspect of vegetation. This characteristic is present both in primary and secondary succession. The literature does not lack papers on progress of secondary succession based on short-time observations or on inference, but it lacks reports on actual changes shown by long-period and repeated observations in the same area. Also, the authors do not know of a single paper which deals with secondary succession in the unique sweet gum-red maple-beech association. Hence, a study of the type forming the basis of this paper seems to be justified.

The area studied has an excellent location. It is bordered by a rather mature forest of the type to which succession is progressing, and being a part of Versailles State Park, cultural influences will play no part in the years to come. It would, of course, have been most desirable to have records from the very beginning of the succession tendencies, but it is fortunate at least that succession has not advanced far beyond the first wave of invaders, who apparently were able to establish themselves under least favorable soil moisture of the abandoned field. Likewise, at this stage the young trees have not produced seeds and so played no part in the seedling population.

Geography and Physiography

The area is within the limits of Versailles State Park, one mile east of Versailles, Ripley County, Indiana. The region as a whole lies within the severely leached Illinoian Tillplain. Habitat sites are varied because of the proximity to Laughery Creek and its tributaries. In spite of cutting action of the streams, there are still some extensive table lands

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with poor drainage, and these are characterized, as described previously by the senior author (3), by the sweet gum-red maple-beech type of forest association. The abandoned field under consideration is located a half mile east of the fire tower road, within the park proper. Topographically it is a flat, poorly-drained table land bordering on a better drained low upland.

Methods

The association complex of the adjacent mature forest was studied on basis of twenty 10-meter-square quadrats. These were taken with a ten-meter skip between each quadrat along two lines west of the abandoned field, at about 100 and 200 feet from the young forest. Results are shown in Table I. The twenty permanent quadrats are of the same size dimension as those taken in the mature forest. They, too, were separated by a skip of ten meters. They are arranged in three lines, representing different distances from the mature forest. Quadrats 1 to 7

TABLE I. Tabulation of woody species in twenty 10-meter-square quadrats in mature stand of *Liquidambar-Acer rubrum-Fagus* type forest, adjacent to area of secondary succession.

Species	Number of stems in seven diameter-classes in inches								Per cent F.I.
	Below 1 in.	1-2	3-5	6-8	9-15	16-20	Above 20	Total stems	
<i>Acer rubrum</i>	8	24	24	16	16	4	1	93	75
<i>Acer saccharum</i>	4	3	2		1		1	11	35
<i>Amelanchier canadensis</i>		1	1					2	5
<i>Carpinus caroliniana</i>	29	25	12	1				67	60
<i>Carya laciniosa</i>	6	3	1					10	15
<i>C. ovata</i>	27	18	8	2	2			59	80
<i>Cornus florida</i>	11	4						15	30
<i>Fagus grandifolia</i>	28	44	18	2			3	95	80
<i>Fraxinus americana</i>	19	13	5	4				41	70
<i>Liquidambar styraciflua</i>	1	3	9	5	5	4		27	65
<i>Liriodendron tulipifera</i>		1	1	1	1	1		5	20
<i>Morus rubra</i>	2							2	5
<i>Nyssa sylvatica</i>	1	1	3	2	3			10	25
<i>Ostrya virginiana</i>	16	2	2					20	20
<i>Platanus occidentalis</i>					1			1	5
<i>Prunus serotina</i>	1				1			2	10
<i>Quercus alba</i>	11	5	7	3	3		1	30	70
<i>Q. bicolor</i>				1	1			2	5
<i>Q. borealis</i> var. <i>maxima</i>	4	5	4	2	6	1		22	65
<i>Q. palustris</i>						1		1	5
<i>Sassafras albidum</i>	1		8	11	1			21	55
<i>Ulmus americana</i>	2	7	6	2	1			18	40
<i>Ulmus thomasi</i>		2						2	5
<i>Corylus americana</i>		7						7	10
<i>Lindera benzoin</i>	78							78	20
<i>Smilax glauca</i>	89							89	50
<i>Viburnum dentatum</i>	38							38	35
<i>Vitis</i> sp?		1						1	5

are removed 50 feet from the forest border, quadrats 8 to 15 are removed 100 feet and quadrats 16 to 20 approximately 500 feet. Wooden stakes ($24 \times 2 \times 2$) were driven into the ground and the area was delimited by a stout cord supplied with loops at 10-meter intervals. All stems which were at least one inch in diameter were measured by DBH. with wooden calipers and grouped into five size-classes (Table II). All stems less than 1 inch DBH. were tabulated if their height was at least one meter. At the southwest corner of each large quadrat a one-meter quadrat was studied for seedling abundance of woody species (Table II). The plan is to make periodic tabulations of trees in the permanent quadrats to determine the progress and characteristics of the succession.

Results

For summarized data see Tables I to III. In the mature stand *Acer rubrum*, *Liquidambar styraciflua* and *Quercus borealis* var. *maxima* have the greatest number of stems 9 inches DBH. or over, but associated with them are many other species, important among these are species of *Quercus* and *Carya*, *Fraxinus americana* and *Fagus grandifolia* (Table I). The most abundant reproduction is evidenced by *Acer rubrum*, *Carya ovata*, *Fagus grandifolia*, *Fraxinus americana* and *Quercus alba*. These species also have the highest per cent of F. I. The association is composed of 19 species of tall trees, 4 of small trees, and 5 shrubs. An unusual feature is that eight species of tall trees have a F. I. of 55 per cent or higher.

The young forest in progress of secondary succession is marked by group segregation tendencies, where invasion and ecesis is a kind of wave-like procedure determined by age of previous invaders. This is plainly shown by difference in stem diameters and abundance of stems of these groups (table III). The first wave is represented by *Acer rubrum* and *Liquidambar styraciflua*. It should be pointed out that these first invaders are still reproducing very vigorously. Replacement of old field species, such as *Juniperus* and *Campsis radicans* is marked. The second wave is represented by *Liriodendron tulipifera*, *Nyssa sylvatica* and *Prunus serotina*. Representatives of the third wave are *Fraxinus americana*, *Robinia pseudo-acacia*, and *Ulmus americana*. Four species of *Quercus* participate in the fourth wave. If the mature forest represents the type for the ultimate forest composition of the one developing, then a fifth wave can be expected in which *Fagus*, the various *Caryas* as well as the second layer trees *Cornus florida*, *Carpinus caroliniana* and *Ostrya virginiana* will play the leading role. Also, there is still to be expected invasion and ecesis of the characteristic shrubs of the mature forest (table I). While the association is at present dominated by *Acer rubrum* and *Liquidambar*, indicated increase of competition for crown cover is foreshadowed by a number of other tall tree species (table II). At present the shrub representation is distinctly old field type, such as *Rhus glabra*, *Vitis labrusca*, and *Campsis radicans*. These will no doubt be eliminated gradually as succession by trees continues, and as light factors become modified.

TABLE II. Tabulation of woody species according to diameter of stems in inches in twenty 10-meter-square permanent quadrats in area of secondary succession, and 20 one-meter quadrats for seedling study.

Species	Below 1 in.					Total seedlings					Quadrats where found	
	1	2	3	4	5	Total stems	% F.I.	Total seedlings	% F.I.	1-2-3-5-6-9-10-11-12-13-14- 16-17-18-19-20		
<i>Acer rubrum</i>	223	199	79	9		510	100	65				
<i>Acer saccharum</i>	1					1	5					
<i>Carpinus caroliniana</i>	1					1	5					
<i>Catalpa</i> sp. ?	1					1	5					
<i>Cornus florida</i>	2	1				3	5					
<i>Elaeagnis grandifolia</i>	1					1	5	1	5		11	
<i>Fraxinus americana</i>	17					17	55	2	6		6	
<i>Juniperus virginiana</i>	3		1			4	15	1	19			
<i>Liquidambar styraciflua</i>	158	175	168	55	16	1	573	100	8	1-5-6-10		
<i>Liriodendron tulipifera</i>	55	9	5	2		70	75	5	5	1-4-5-9-13		
<i>Nyssa sylvatica</i>	17	2				21	35					
<i>Populus occidentalis</i>	4	1				5	15					
<i>Populus grandidentata</i>	26	2				28	30	3				
<i>Prunus serotina</i>	4	2			1	7	20					
<i>Quercus alba</i>	2					2	10					
<i>Q. bicolor</i>	3					3	10					
<i>Q. borealis</i> var. <i>maxima</i>	1					1	5	4	6			
<i>Q. palustris</i>	8					8	5					
<i>Robinia pseudo-acacia</i>	7	1				8	10					
<i>Sassafrass albidum</i>	5	1				6	25	1	7			
<i>Ulmus americana</i>	5	1				6	20	13	13	3-4-6-8-11		
<i>Campsis radicans</i>	545	1				Shrubs	546	50	36	2-3-4-7-8-9-10-14-15		
<i>Parthenocissus quinquefolia</i>												
<i>Rhus glabra</i>	11	1					12	10	1	5		
<i>Rhus radicans</i>									14	6-7-11		
<i>Rosa</i> sp. ?	2								2	5		
<i>Rubus</i> sp. ?									58	1-2-6-9-10-11-12-13-14		
<i>Salix</i> sp. ?												
<i>Smilax glauca</i>									1	1		
<i>Viburnum dentatum</i> var. <i>deamii</i>	21								21	5		
<i>Yitis labrusca</i>	79								45	2	10	

TABLE III. Number of stems per 10-meter-square quadrat with reference to distance from the parent forest. a. quadrats 1 to 8, about 50 feet distant; b. quadrats 9 to 15, about 100 feet distant; c. quadrats 16 to 20, about 300 feet distant. Stems grouped into three size-classes.

Species	Below 1 inch	1-2 inches	3-5 inches	Total stems
<i>Acer rubrum</i>	a 11.4	24.7	1.0	37
	b 13.0	11.3	24.1
	c 7.4	2.6	.2	10.2
<i>Liquidambar styraciflua</i>	a 10.1	22.0	4.2	36.4
	b 8.1	17.0	1.4	26.5
	c 2.4	9.6	5.6	17.6
<i>Liriodendron tulipifera</i>	a 4.5	2.0	.25	6.7
	b 1.25	.37	.1	1.75
	c	1.0	1.0
<i>Nyssa sylvatica</i>	a 1.5	.37	2.0
	b .77
	c22
<i>Prunus serotina</i>	a .11
	b .2525
	c2	.2
<i>Fraxinus americana</i>	a .87	.12	1.0
	b 1.1	1.1
	c
<i>Ulmus americana</i>	a .55
	b .1	.12
	c
<i>Quercus alba</i>	a .2525
	b
	c
<i>Q. bicolor</i>	a .2525
	b .1212
	c
<i>Q. borealis</i> var. <i>maxima</i>	a
	b .1212
	c
<i>Quercus</i> sp. ?	a
	b 1.0	1.0
	c

Distance from the parent forest influences both abundance of stems of migrants (table III) as well as the progress of succession. The set of quadrats (c) which are removed 300 feet from the germule-producing forest have few of the species which constitute the second and third waves of invaders. Also, in the area removed 300 feet from the border of the parent forest 9 species of trees playing a part in the association complex in the mature forest are present while in the lines closer to the forest 14 species are present.

Discussion

Secondary succession is no doubt most involved in areas where the final forest association is most complex (climax or sub-climax). The

larger the number of species participating in the crown cover, the more gradual the development in succession will be. In such an association complex there are evidently species exhibiting wide ranges of potentiality to fit into all facets of a habitat, especially also with reference to edaphic factors. In the present case *Fagus* demands better soil moisture conditions than *Liquidambar* and *Acer rubrum*. These latter two species are perhaps better adapted to cope with extremes in old field habitats. The delayed invasion by *Carya* and *Quercus* species may be due to absence of the proper animal relationships, for squirrels would hardly find great attractions to the area now occupied by the young sweet gum-red maple forest. One wonders how the seeds of sweet gum (*Liquidambar*) are carried so far, for lack of any carrying appendages it must be the lightness of the seed which adapts it to wind transportation.

In a simple association, like the one in northern forests, the senior author (4) has pointed out that secondary succession is almost non-existent, species of the climax, or sub-climax, occupy the vacated habitats almost from the beginning. That early invaders of the climax species must have the potentiality to endure environmental conditions much more severe than those of the climax forest as such was plainly shown by Gates (2) for *Acer saccharum*. This certainly must also be true for the first invaders of the area under study in Versailles Park.

Since succession is to a large extent a habitat control, it is of necessity a complex phenomenon where the elusive microclimate enters in as important factor. It functions as a selective system, which in the area under study permitted successful invasion and ecesis for some species within a period of fifteen years and prevented others, which theoretically should be there, from establishing themselves definitely in the association. The various stages in a succession require many years to reach completion. For a section in Indiana Potzger and Friesner (6) found that after 75 years of progress the final stage had not yet been reached.

The progress of succession in the fallow field at Versailles Park suggests the thought that differences in crown cover in mature forests on similar habitats may frequently be due to differences in migration, and not a habitat selection, when the area was being occupied. It is quite evident that when a crown cover closes it becomes a barrier even to tolerant species. Only death of a dominant tree will create an opening in the crown cover which might be occupied. In a developing even aged stand this may not occur for a century or more. If the oaks and beech are prevented for another 10 to 15 years from invading the area removed 300 feet from the mature forest it appears likely that sweet gum, red maple and tulip poplar will have formed a closed crown cover under which invasion may be impossible. Here would then develop a different forest cover type than in the area which is a few hundred feet closer to the source of seed dissemination, even though habitat conditions otherwise would be alike.

Summary and Conclusions

1. The paper presents a preliminary report on a permanent quadrat study of secondary succession in an Illinoian Tillplain habitat in Versailles State Park, Ripley County, Indiana.

2. The permanent quadrats are twenty 10-meter-square sampling units.

3. On basis of twenty 10-meter-square quadrats an analysis was made of an adjacent mature forest of the Illinoian Tillplain type. In this forest 19 species of tall trees participate in the crown cover. The most important dominants are *Acer rubrum*, *Liquidambar styraciflua*, and *Quercus borealis* var. *maxima*.

4. Secondary succession on the abandoned field has been in progress for about 15 years. Tree species with great abundance and largest stem diameters are *Acer rubrum* and *Liquidambar styraciflua*.

5. Succession seems to operate as waves of invasion in which always several species are involved. In order of their appearance they are *Acer rubrum* and *Liquidambar*; *Liriodendron tulipifera*, *Nyssa sylvatica* and *Prunus serotina*; *Fraxinus americana*, *Robinia pseudoacacia* and *Ulmus americana*; four species of *Quercus*. The fifth wave is not yet defined, but it should involve *Fagus* and *Carya* species as well as the second layer trees and several shrubs.

6. While at present the young forest is controlled by *Acer rubrum* and *Liquidambar* there is convincing evidence that many species will eventually participate in the crown control at the close of succession. There is further evidence that the association complex will be like or similar to that existing now in the adjacent mature forest.

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