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# SOME COMPARISONS BETWEEN VIRGIN FOREST AND ADJACENT AREAS OF SECONDARY SUCCESSION

By J. E. POTZGER AND RAY C. FRIESNER

The almost unbroken deciduous forest of Indiana of a century ago has been reduced to isolated patches, and few of the remaining timbered areas may truly be termed virgin forest. These small tracts of undisturbed forest are thus of great ecological importance. One such small area of undisturbed forest is owned by Mr. August Mauntel, six miles southwest of Holland in Dubois county. Mr. Mauntel is an old settler in Dubois county and has seen the region develop from forest primeval to a busy agricultural community. He says that the area in question has been disturbed very little by cultural influences. Minor changes, of course, have occurred as a result of some necessitated drainage in the neighborhood, but this influenced the upland where the area of study is located but very little. About fifteen years ago most of the timber still remaining on the farm was cut except the wooded area studied in the present paper. Much of the timber in the adjacent lowland had been *Liriodendron* and *Juglans nigra*, while the forest of the higher hills consisted chiefly of oak and hickory. The present wooded area is listed as classified forest with the Indiana Forestry Department. Fifteen acres on the north (Section A) have never been cut and have suffered but little from grazing (about fifteen years ago cattle could roam the forest from adjacent fields during the winter, but little damage was done); about twelve acres on the southwest (Section B) were partially lumbered fifty-five years ago, *i. e.*, the large trees were cut; the southwest corner (Section C) was entirely cleared seventy years ago and has since been permitted to develop into forest according to the natural law of succession of the region. This offered an excellent opportunity for comparative study of undisturbed forest and two stages of secondary succession. Dead and fallen trees have been and are removed annually.

## METHODS OF STUDY

The primary aim was to study the woody species both as to climax and successional features, especially as to reproduction, number of species

represented in the various areas and constancy of the climax. To this end fifty quadrats of 100 square meters each were laid out in each of the three types of wooded sections. The quadrats comprised about 10 per cent of the total area.

A strong cord was measured off in ten-meter lengths and loops tied; these were slipped over stakes driven into the ground at each corner of a quadrat; direction was held by aid of a pocket compass. One person laid out the quadrats, another called the species and made measurements of DBH. of all woody plants one inch or over in diameter, while a third person made the tabulations according to quadrats numbered in proper succession. Diameter measurements were made with a pair of tree calipers. Trees one inch or more in diameter were measured, all woody plants below one inch in diameter but a meter or more in height were counted and tabulated, and in a one-meter quadrat in each ten-meter area the seedlings of woody species were listed.

## PLANTS OF THE GROUND COVER

The floor of the forest was remarkably devoid of both herbaceous and woody species. *Rhus toxicodendron* was, without doubt, the most frequent species. Some of the more common species were: *Botrychium virginianum*, *Polystichum acrostichoides*, *Phegopteris hexagonoptera*, *Agrostis perennans*, *Brachyelytrum erectum*, *Iris cristata*, *Hieracium scabrum*, *Heuchera americana*, *Desmodium rotundifolium*, *Gillenia stipulata* and occasionally *Liparis liliifolium*.

## GENERAL ASPECT OF SECTION A—VIRGIN TIMBER

Physiographically the whole area is a low elevation of rather stony soil. The crowns of the trees in Section A form a dense canopy, giving a very subdued light on the floor of the forest. The outstanding features are the abundance of large trees widely spaced, the sparse herbaceous cover and the scattered representation of seedlings of the dominant species (Table I). In certain patches, *Rhus toxicodendron* was the most prominent member of the ground flora; in fact, at times it covered the ground completely. Humus and decaying leaves formed a deep cover layer on the soil. The three areas are all typical oak-hickory forest. Not only is the virgin timber area (Section A) of this type, but the developing Section C is, again, reverting to oak-hickory climax

through various stages of succession from open field to forest. Of the early successional stages there still remain such relics as *Rhus copallina*, *Rubus* sp., *Tecoma radicans* and *Sassafras variifolium*, as well as dense stands of Liquidambar.

Section A naturally excels in the greater abundance of large trees, of which the oaks have by far the greatest number; *Quercus alba*, with its eighty-eight stems above 1 inch DBH., and *Quercus velutina*, with twenty-nine stems, taking the lead (Table I). Of course, the combined *Carya* group, with a total of 189 stems, outnumbers that of *Quercus* with 128 stems, but *Quercus* outclasses *Carya* by greater size of stem. *Carya* has a total of 900 diameter-inches, while *Quercus* has a total of 1356 diameter-inches in the fifty quadrats studied. This is an average of 4.8 inches for *Carya* and 10.5 inches for *Quercus*. In fact, the stems of *Carya* are conspicuous by their small size, most of them being below 12 inches. The wide spacing of the trees tells a graphic story of great mortality among the young trees which probably germinated in the shade, which may even have survived to reach a diameter of a few inches and, under the stress of increased demand on the products of photosynthesis and water, found the habitat lacking in adequate supply of light and moisture. This is in full accord with experimental evidence obtained by Stallard (5). Evidently the process of perpetuation of a climax forest is more a matter of establishing the dominant species in open places which occur when trees die or are blown down, than a continuous crowding in of young growth between the crowns of older trees. No doubt most of the younger trees tabulated in a survey will never reach maturity. To cite an example, *Carya* is represented by 174 stems below 1 inch DBH. and *Quercus* by 143, yet, only thirty-five stems of *Quercus* over 15 inches and only seventeen of *Carya* 10 inches or over are present. Mortality must certainly be high among *Fraxinus* species, with 475 stems below 1 inch and only two trees above 10 inches.

It seems quite evident that the present oak-hickory woods is typical, permitting the conclusion that the much-pictured forest of giant trees of the primeval forest was made up primarily of trees 30 to 36 inches DBH., and trees above that size were the exception rather than the rule. Random measurements of all large oaks seen in Section A disclosed them to be within the 28 to 32 inch DBH. range. This is also substantiated by Table III of Cain's (2) paper dealing with virgin forest in Spring Mill State Park. His figures in general are quite comparable with those of the present study. In twenty-five quadrats 10 by 10

meters he lists 309 stems of which but three are above 30 inches DBH.; in fifty quadrats of the present study there are 533 stems with five trees of 30 inches or over. The same features are quite evident in Dillon's woods, a piece of virgin timber in Dubois county, which was observed during a general survey.

Section A is also unique on account of the absence of the common second layer trees, *i. e.*, *Carpinus caroliniana* and *Ostrya virginiana*. In this respect, too, the Mauntel woods parallels Donaldson's woods (Cain (2), Table III). The only second layer tree which was present in any worthwhile representation was *Cornus florida*. In the frequency classes (Table II) for the three sections it was persistently present in class E. In Section A it appeared in 88 per cent of the quadrats. *Diospyros virginiana* was present in 34 per cent of the quadrats, indicating that it is able to germinate successfully in shade and compete with the dominant species in the earlier stages, but finds these environmental conditions intolerable with increasing size and age. Seeding is apparently carried on by opossums from several trees along the border of woods and field.

*Acer saccharum* and *Fagus grandifolia* have a very negligible representation and it seems that they will not form the climax forest here, since they have not established themselves in the developing area C during the past seventy years.

### SECTION B—PARTLY CUT-OVER

This section was outstanding by trees of smaller size-range and patches of dense undergrowth, otherwise resembling more the virgin timber area. In the case of *Quercus alba* the size difference is not so pronounced. Section A had twenty-seven trees of this species of 20 inches or over DBH., while Section B had twelve trees of that size. The cutting of trees admitted more light, the moisture of the soil increased by the elimination of some of the stand and this resulted in more rapid growth. The section also shows a marked *Quercus-Carya* aspect. *Cornus florida* is the only second-layer tree represented, having a frequency of 88 per cent, which is the same as in Section A (Table I). *Quercus alba* shows a more marked increase in number of trees in the size range of I to 10 inches DBH. In Section B there are ninety-two, while Section A has but fifty-five such young trees. This points again to the conclusion that reproduction in undisturbed timber is more a





## DBH. IN INCHES

SPECIES		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32		
<i>Quercus alba</i> .....	A	18	3	10	7	5	2	3	3	1	3	2	1				1	1		1	2	3	5	1	5	4	2		1		1	2	1	88	
	B	10	10	25	11	14	7	3	5	6	1			1	1	1		1	1	2		2	1	3	3	1					2			111	
	C	2	10	12	11	20	12	6	4	5	11	5	3	3	2								1												107
<i>Q. imbricaria</i> .....	A	1	1				1										1																	3	
	B																																	1	
	C	2	1	3	2		1	1	2				1																						13
<i>Q. borealis maxima</i> .....	A	2						1		1	1			1	1			1		1															8
	B				1		1			1	1	2											2												8
	C	2	3					1				1		1							2														10
<i>Q. velutina</i> .....	A	3	3		1			1	2	1	2			1	6	3	2	1			2												1		29
	B		2	1	1		3	5	6	6	9	6	3	6	1	1		1																	51
	C	23	12	4	5	1						1				1		1																	48
<i>Q. palustris</i> .....	A																																		—
	B																																		—
	C	1	2	2	2	2	1		2	1		1		1								1													
<i>Q. stellata</i> .....	A																																		—
	B	4	5	4	5	2	5	2	2	5		2			1	1							1												39
	C	17	5	7	3	4	5	4	4		1	1			1			1																	53
<i>Q. bicolor</i> .....	A																																		—
	B																																		—
	C	1																																	1
<i>Q. marylandica</i> .....	A																																		—
	B							1																											1
	C																																		—
<i>Robinia pseudo-acacia</i> .	A																																		—
	B																																		—
	C	3	1	1																															5
<i>Rhus copallina</i> .....	A																																		—
	B																																		—
	C	4	3																																7
<i>Sassafras variifolium</i> ....	A	3	1	1																															5
	B	6																																	6
	C	27	26	13	3																														69
<i>Ulmus americana</i> .....	A	4	4	1						1																									10
	B	2	2	1																															5
	C						2																												3
<i>U. fulva</i> .....	A				1																														1
	B	1		1																															2
	C		1	1																															2



case of occupying ground vacated by death of old trees, than continuous growth to maturity under the crowns of an established forest canopy. Evidently, trees occupy all the ground which the available water and light permit, and so limit reproduction in that area to replacement only. *Quercus velutina*, with thirty-three trees of 1 to 10 inches DBH., and *Quercus stellata*, with thirty-four such stems, also tell a story of increased reproduction as places were vacated by older trees. There is no evidence of extreme reversal to secondary succession in this partly cut-over area, since the common early successional species, such as *Rhus copallina*, Sassafras and Liquidambar, which are so prominent in Section C, are almost absent here. Fraxinus is also much reduced in number of stems (Table II).

### SECTION C—ENTIRELY CLEARED SEVENTY YEARS AGO

The outstanding features of this area are the smaller diameter of trees, dense stands, with intermittent open tracts, the presence of species of earlier successional stages and the lack of deep humus layer so evident in the other two sections. Copses were frequent, and many open patches were covered with lichens and xerophytic mosses. The latter told a graphic story of the effects of erosion after the land had been cleared. This area had about 35 per cent more species in the flora than the other areas. Developmental stage was indicated by such frequencies in woody species as: *Diospyros virginiana*, 54 per cent; *Juniperus virginiana*, 44; *Sassafras variifolium*, 36; *Liquidambar styraciflua*, 36; *Rhus copallina*, 24; and such herbaceous species as: *Potentilla canadensis*, 22; *Pycnanthemum flexuosum*, 20; *Solidago nemoralis* and *Lespedeza hirta*.

Very few trees have reached 12 inches DBH. The trees in this area are also more closely spaced, at times almost making dense stands. *Quercus palustris* is no doubt crowded out of areas A and B by other oaks which attain greater height. The whole area is very impressive by its rapidly advancing succession from open field through thicket and bramble stage to climax forest. In seventy years, oak-hickory has regained dominance, now successfully crowding out scrub species.

The position of *Quercus stellata* and *Q. imbricaria* in this Quercus-Carya climax is worthy of note. From Table III it will be seen that *Q. imbricaria* is practically absent in all but the area earliest in succession (Section C) and that *Q. stellata* is relatively abundant in the

TABLE II

## FREQUENCY OF SPECIES IN FIFTY QUADRATS IN EACH AREA

SPECIES	AREA A	AREA B	AREA C
<i>Carya ovata</i> .....	100 per cent	86 per cent	68 per cent
<i>C. glabra</i> .....	76	96	34
<i>Quercus alba</i> .....	84	90	70
<i>Cornus florida</i> .....	88	88	94
<i>Fraxinus lanceolata</i> .....	83	54	62
<i>Quercus velutina</i> .....	54	80	76
<i>Q. borealis maxima</i> .....	68	52	40
<i>Prunus serotina</i> .....	60	74	24
<i>Fraxinus americana</i> .....	48	54	28
<i>Carya alba</i> .....	32	56	8
<i>Sassafras variifolium</i> .....	34	42	36
<i>Diospyros virginiana</i> .....	34	24	54
<i>Quercus stellata</i> .....	0	28	48
<i>Juniperus virginiana</i> .....	4	12	44
<i>Liquidambar styraciflua</i> .....	2	0	36
<i>Quercus imbricaria</i> .....	12	12	40
<i>Q. palustris</i> .....	0	0	30
<i>Acer rubrum</i> .....	20	4	30
<i>Nyssa sylvatica</i> .....	26	8	18
<i>Ulmus americana</i> .....	22	16	14
<i>Rhus copallina</i> .....	0	2	24
<i>Cercis canadensis</i> .....	20	14	4
<i>Acer saccharum</i> .....	16	6	6
<i>Morus rubra</i> .....	14	10	0
<i>Ulmus fulva</i> .....	8	10	4
<i>Fraxinus pennsylvanica</i> .....	8	0	12
<i>Carya cordiformis</i> .....	6	0	0
<i>Platanus occidentalis</i> .....	4	0	2
<i>Carya laciniata</i> .....	2	0	0
<i>Betula nigra</i> .....	2	0	0
<i>Juglans nigra</i> .....	0	4	2
<i>Quercus marylandica</i> .....	0	2	0
<i>Robinia pseudo-acacia</i> .....	0	2	2
<i>Liriodendron tulipifera</i> .....	0	0	16
<i>Prunus americana</i> .....	0	0	8
<i>Corylus americana</i> .....	0	0	8
<i>Crataegus</i> sp? .....	0	0	6
<i>Fagus grandifolia</i> .....	0	0	4
<i>Acer negundo</i> .....	0	0	2
<i>Carpinus caroliniana</i> .....	0	0	2
<i>Quercus bicolor</i> .....	0	0	2
Total species .....	27	26	36

<sup>1</sup>Area A contained virgin timber; Area B was partly cut 55 years ago; Area C entirely cleared 70 years ago

two stages of succession, but absent in the climax area, which is predominantly *Q. alba* and *Q. velutina* (in so far as *Quercus* is concerned). It is also worthy of note that *Q. borealis maxima* does not form an important constituent of this *Quercus-Carya* area in either successional or climax stages.

TABLE III  
SHOWING NUMBER OF STEMS OF QUERCUS-SPECIES ONE INCH OR OVER DBH.

SPECIES	SECTION C	SECTION B	SECTION A
<i>Quercus alba</i> .....	107 stems	111 stems	88 stems
<i>Q. bicolor</i> .....	1	0	0
<i>Q. borealis maxima</i> .....	10	8	8
<i>Q. imbricaria</i> .....	13	1	3
<i>Q. marylandica</i> .....	0	1	0
<i>Q. palustris</i> .....	16	0	0
<i>Q. stellata</i> .....	53	39	0
<i>Q. velutina</i> .....	48	51	29
Total .....	248	211	128

TABLE IV  
SHOWING NUMBER OF STEMS OF CARYA-SPECIES ONE INCH OR OVER DBH.

SPECIES	SECTION C	SECTION B	SECTION A
<i>Carya alba</i> .....	1 stems	15 stems	14 stems
<i>C. glabra</i> .....	20	75	68
<i>C. laciniosa</i> .....	0	0	1
<i>C. ovata</i> .....	20	29	105
<i>C. cordiformis</i> .....	0	0	1
Total .....	41	119	189

From Tables IV and VI it is seen that all of the *Carya*-species show greater numbers of stems in the final stage of succession (Section A) than in the earlier successional stage (Section C). *Carya ovata* and *C. glabra* are the chief *Carya*-components, and *Quercus alba* and *Q. velutina* the chief *Quercus*-components of this *Quercus-Carya* climax.

In a general way one might draw the inference that climax forest, reduced to open meadow, will complete the various successional stages in comparatively short time. Shantz (4) found that short grass plains reestablish themselves in twenty to fifty years, and Aikman (1) reports that prairie development requires about thirty or more years to reach

the climax from cultivated field condition on Muscatine Island, Iowa. A fair picture of the climax life forms and even of the component species was reached in seventy years in this Indiana area. There are still relics of all the stages in succession, but oak-hickory-ash are showing their dominance by frequency and density. From Table V it will be noted that the total stems of *Quercus* and *Carya* over 1 inch DBH. show opposite relationships as the degree of succession advances. The number of *Carya* stems is over four times as great in the climax stage as in the earliest successional stage, while the number of *Quercus* stems is almost twice as many in the earliest stage of succession as it is in the climax stage. From this it would appear that *Carya*-species find a more difficult environment when in competition with so many individuals as are present in earlier stages of succession than they do when in competition with the smaller number of better spaced individuals of the climax, while *Quercus*-species show the opposite condition.

The same relationship is shown between younger specimens of *Carya* and *Quercus* (Table V) in the earliest successional stages and climax. Seedlings of *Fraxinus* apparently find the habitat more congenial in the climax stage than in the stages of succession. Table V shows over five times as many *Fraxinus* seedlings in the climax as in the earliest successional stage. From these considerations it would appear that *Carya* and *Fraxinus* are both less fitted to the xerophytic conditions of earlier successional stages than some of the *Quercus*-species. This is also indicated by the apparent high mortality among these species in the young-tree stage when they are in root competition with the mature trees of the climax forest.

The successional stages are characterized by the decreasing total number of species as the climax forest is approached. Lutz (3) found the same feature in the virgin forest at Heart's Content in Pennsylvania, and makes the following conjecture: "This poverty of species may be interpreted as an expression of the ecologically advanced character of the community. As a community advances toward the climax, it tends, more and more, to be composed of a relatively small number of specialized species" (p. 11). This interpretation stands approved by the observational evidence of the present work. Sections A and B are about equal, with twenty-seven and twenty-six species of trees respectively, while Section C, with thirty-six species, has about 33 per cent more than the other stages. This is due to representation of species of successional stages. There is no indication of a beech-maple succession.

This may be due to the physiographic influences of the region, *i. e.*, too rigorous a habitat for them. If beech-maple were the climax here, these species should have come in while Section C was developing.

TABLE V

DENSITY OF CARYA, QUERCUS AND FRAXINUS — BOTH LARGER AND SMALLER SIZE CLASSES, DERIVED FROM FIFTY QUADRATS TEN BY TEN METERS IN EACH SECTION

SIZE RANGE	GENERA	SECTION		
		A	B	C
One inch or over DBH. . . . .	Carya . . . . .	189	119	41
	Quercus . . . . .	128	211	248
	Fraxinus . . . . .	83	27	32
Below one inch DBH. 1 meter or over in height. . . . .	Carya . . . . .	174	305	83
	Quercus . . . . .	143	198	240
	Fraxinus . . . . .	475	150	91

TABLE VII

STEMS OF WOODY SPECIES IN 5,000 SQUARE METERS OF QUADRAT AREA IN EACH SECTION

SIZE RANGE	SECTION			TOTAL
	A	B	C	
Under 1 inch DBH., 1 meter or higher . . . . .	1207	1059	937	3203
Plants 1-10 inches DBH. . . . .	473	429	682	1584
Plants 11-18 inches DBH. . . . .	71	47	37	155
Plants 19-32 inches DBH. . . . .	34	17	4	55
Total stems over 1 inch . . . . .	578	493	723	1794
Total stems . . . . .	1785	1552	1660	4997

Table VI lists number of stems of each woody species under 1 inch DBH. but over 1 meter high. This is summarized and compared with larger stems in Table VII. The final stage of succession shows the largest number of stems under 1 inch and the earliest successional stage shows the smallest number. Stems over 1 inch are largest in number in the earliest stage of succession and smaller in number in the climax area. This is probably due to the fact that the more mesophytic and generally less rigorous habitat of the final stage of succession permits a larger number of seedlings and saplings to get a start than is the case in the earlier successional stage. As growth continues, however, larger percentages of young trees are killed in the struggle for light and water in the final successional stages than in the earlier.

TABLE VI

DENSITY OF WOODY SPECIES BELOW ONE INCH DBH., ONE METER OR OVER IN HEIGHT, DERIVED FROM FIFTY QUADRATS TEN BY TEN METERS IN EACH SECTION

SPECIES	SECTION A	SECTION B	SECTION C
<i>Acer negundo</i>	0	0	2
<i>A. saccharum</i>	6	1	2
<i>A. rubrum</i>	12	2	18
<i>Asimina triloba</i>	5	0	0
<i>Carpinus caroliniana</i>	0	0	4
<i>Carya alba</i>	12	54	3
<i>C. cordiformis</i>	4	0	0
<i>C. glabra</i>	35	119	23
<i>C. ovata</i>	123	132	57
<i>Cercis canadensis</i>	28	21	2
<i>Cornus florida</i>	145	110	155
<i>Corylus americana</i>	7	0	9
<i>Crataegus</i> sp.	0	0	4
<i>Diospyros virginiana</i>	30	20	41
<i>Fagus grandifolia</i>	0	0	2
<i>Fraxinus americana</i>	57	76	5
<i>F. lanceolata</i>	415	74	72
<i>F. pennsylvanica</i>	3	0	14
<i>Juniperus virginiana</i>	2	6	49
<i>Juglans nigra</i>	0	1	1
<i>Liquidambar styraciflua</i>	1	0	35
<i>Liriodendron tulipifera</i>	0	0	2
<i>Morus rubra</i>	16	2	0
<i>Nyssa sylvatica</i>	26	6	9
<i>Prunus americana</i>	0	0	45
<i>P. serotina</i>	96	177	18
<i>Quercus alba</i>	59	59	19
<i>Q. borealis maxima</i>	55	32	21
<i>Q. imbricaria</i>	4	5	45
<i>Q. palustris</i>	0	0	8
<i>Q. stellata</i>	0	38	59
<i>Q. velutina</i>	25	64	88
<i>Rhus copallina</i>	0	1	37
<i>Robina pseudo-acacia</i>	0	2	1
<i>Sassafras variifolium</i>	29	44	70
<i>Ulmus americana</i>	6	8	7
<i>U. fulva</i>	4	5	4
<i>Viburnum acerifolium</i>	1	0	0
<i>V. prunifolium</i>	0	0	4
<i>V. pubescens</i>	1	0	0
Total	1207	1059	937

## SUMMARY AND CONCLUSIONS

1. The Mauntel woods in Dubois county, Indiana, is a typical oak-hickory association.

2. Both areas of secondary succession are reverting to the oak-hickory climax.

3. The earliest successional stage is outstanding in its greater number of species and presence of relics from earlier successional stages.

4. There appears to be little difference between reproduction in virgin forest and adjacent areas of secondary succession.

5. Indications are that very large trees were the unusual rather than the common occurrence in the forest primeval. Oak seems to have been most common between 24-32 inches DBH. in mature stands.

6. Reproduction in virgin timber apparently is a matter of occupying vacated territory rather than a continuous growth of young trees under the crowns of a mature stand.

7. *Quercus stellata* and *Q. imbricaria* are characteristic of earlier successional stages, but are essentially absent from the final stage.

8. *Carya*-species are few in number of stems in earlier successional stages, but form a prominent part in the forest of the final stage.

9. The chief components of the oak-hickory climax here studied are *Q. alba*, *Q. velutina*, *C. glabra* and *C. ovata*.

10. Mortality appears to be high in the case of *Fraxinus*.

11. *Cornus florida* is the only second-layer tree of any consequence.

12. There are no indications that beech-maple association will succeed the oak-hickory association in the area studied.

Our sincere thanks are here expressed to Mr. Mauntel for scientific foresight in preserving the area here under study and for his kindness in permitting our work to be done on it.

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