SECONDARY SUCCESSION ON THE PIEDMONT OF NEW JERSEY

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INTRODUCTION

Near East Millstone in Somerset County, New Jersey, there exists a fairly undisturbed forest, 40 acres in extent and containing trees some of which are at least 250 years old. The forest, known as Mettler's Woods, approximates climax; at least it is a community in which vegetational change is now exceedingly slow. By referring to the vegetational and pedologic conditions of Mettler's Woods as the presumed end-points to a succession, a comparison of fields in progression to that end-point might result in a reconstruction of the secondary successional pattern of the general area.

An investigation of fields, previously cultivated but now in successive stages of natural revegetation, was therefore undertaken in 1949 and 1950 in order to determine the major changes in the vegetation and soil occurring throughout the succession. As an adjunct to the vegetational studies, the depth and density of rooting were also analyzed. The area (40° 26′ N, 74° 36′ W to 40° 30′ N, 74° 29′ W) is located in Somerset County, New Jersey, on the Brunswick formation of the Triassic shales comprising a part of the Piedmont Plateau (Kümmel 1940). Detailed studies were made of 27 fields or stands representing nine phases of succession.

Thanks are due to Professor Murray F. Buell, for suggesting and directing this study and to Professor Jacob S. Joffe for assistance with soils problems.

METHODS AND PROCEDURES

SELECTION OF FIELDS

Since Mettler's Woods served as a reference point for the investigation, all fields investigated had to be in the same general climatic, physiographic, and pedologic area. Thus, the fields chosen are on the Piedmont Plateau within a five-mile radius of the forest, which is located near East Millstone, Somerset County. As may be seen in Fig. 1, these fields are located to the south of the Millstone and west of the Raritan Rivers in Somerset County near the towns of East Millstone, Middlebush, South Bound Brook, Griggstown, and New Brunswick.

Inasmuch as the aim of the investigation was a reconstruction of the natural successional pattern on the Piedmont, no fields showing evidence of disturbance were chosen. Owners or their agents were questioned as to the age and treatment of each

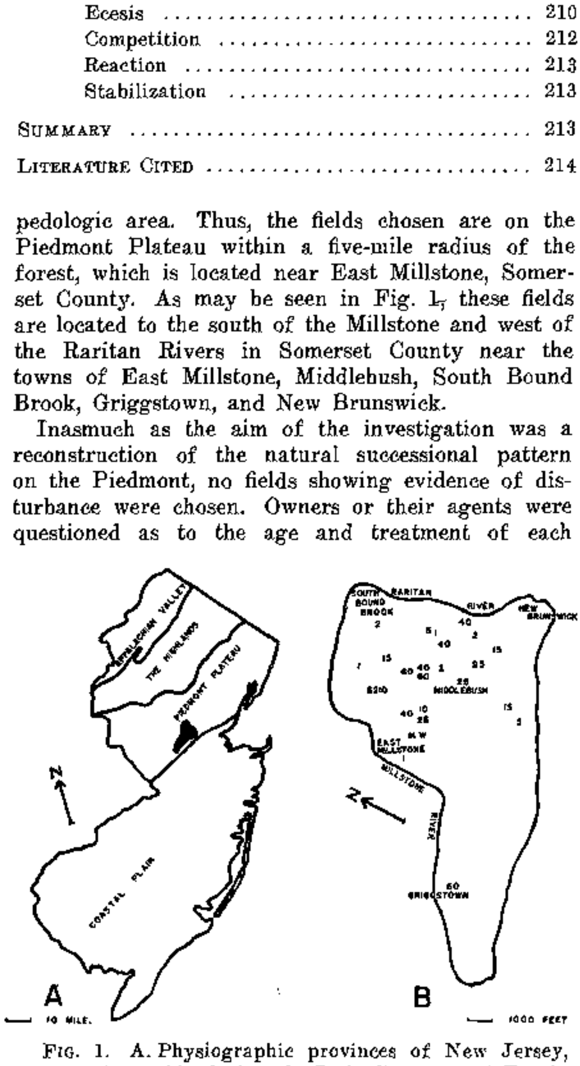

FIG. 1. A. Physiographic provinces of New Jersey, Franklin Township darkened. B. Outline map of Franklin Township, Somerset County. Investigated fields are numbered, each numeral indicating number of years since time of last cultivation. Mettler's Woods is represented by M.W.

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abandoned field. Only those fields were considered for study which, following final cultivation, were left unfertilized, unburned, unmowed, and ungrazed. If these fields were on well-drained upland sites, on a soil of the Penn series closely approximating the Penn silty clay loam of Mettler's Woods, and bearing an appreciable number of red cedars, thus indicating a fire-free history, they were selected for investigation.

In all, nine age-groups are represented in the study. (The period since abandonment is designated here as the "age" of a field.) Fields abandoned 1, 2, 5, 10, 15, 25, 40, and 60 years were investigated in addition to Mettler's Woods. Since Mettler's Woods is the sole forest of its kind extant on the local Piedmont, there could be no duplication of that age-group; however, all other age-groups were studied at least in duplicate. Four fields each of the 1- and 2-year-old age-groups and three fields each of all the other age-groups (except the 10-year) were studied. There was a paucity of 10-year-old fields, and as a result only two such fields are included.

VEGETATIONAL ANALYSES

Study of the vegetation was confined to five objectives: (1) tabulation and determination of presence of all species per field; (2) frequency, density, and basal area of individual species in arborescent strata; (3) frequency and coverage of individuals in the shrub-stratum; (4) frequency and estimated coverage of individual species in herbaceous strata; and (5) an attempted forecast of the immediate future of the field by the frequency and density of the seedlings and saplings.

The methods employed for each of the above are as follows:

(1) Specimens of the vascular species of each field were collected and deposited in the Chrysler Herbarium at Rutgers University. The nomenclature employed follows that of Gray's Manual, 8th edition (1950), with the exception of an exotic not listed therein, *Ilex serrata* Thunb. Dicotyledonous herbs devoid of flowers or fruits were identified with the aid of the foliar keys of Petersen (1949). The presence of each species in an age-group was computed as the percentage of the total number of fields in that age-group.

(2) Tree-quadrats of 10x10 meters each were employed and the diameters of all trees exceeding 1 inch d.b.h. were recorded. Frequency (number of quadrats in which a species occurs expressed as a percentage of the total number of quadrats inspected), density (number of individuals per unit area), and basal area were determined from these data.

(3) A 20-meter tape was strung diagonally across and beyond each arborescent quadrat, and the cover of shrubs and trees less than 1 inch d.b.h. was measured along this transect by the line-intercept method.

(4) In each corner of the arborescent quadrat, a ½x2 meter herb-quadrat was laid from which frequency and visually-estimated coverage could be obtained. In view of the work of Bauer (1943) and Penfound (1945), the coverage value of each herbaceous and shrubby species was used as an expression of degree of dominance.

(5) The frequency and density of seedlings were determined from those appearing in the herb-quadrats. Data for saplings were obtained from a 2x10 meter strip laid down along one edge of the arborescent quadrat.

The number and kind of quadrats varied according to the age-group. No mature trees are present on fields up to and including the 10-year old fields, therefore, no tree-quadrats were employed, all herb-quadrats being laid 20 meters apart on transect lines running approximately north and south. If shrubs appeared under the transect tape, their linear coverage was recorded. In field age-groups 1-5, 50 herb-quadrats and 50 shrub-transect tapes were laid per group. In field age-group 10, 75 of each were laid. In each of the older age-groups and Mettler's Woods, 25 tree-quadrats containing 25 shrub-transect tapes, 25 sapling strips, and 100 herb-quadrats were laid. Since these older fields were of different sizes, it was difficult to apportion the number of quadrats equally among the three or four fields per age-group. Although the number of tree-quadrats per age-group always totalled 25, no field was so small that it could not accommodate 5 tree-quadrats 10 meters apart or so large that it could accommodate more than 10. In Mettler's Woods, all 25 quadrats were laid.

SOILS ANALYSES

Certain of the physical and chemical characteristics of the soils of each field age-goup were investigated. The physical characteristics determined in the field were the degree of profile development and color. Texture was determined by mechanical analysis using the Bouyoucos hydrometer-method (Bouyoucos 1936). Moisture-holding capacity was determined by the use of Hilgard cups. Structure was determined visually upon dried samples. The amount of organic matter was determined by a modification of the Tiurin method (Tiurin 1937). The following chemical characteristics were investigated: conductivity by means of the standard Kohlrausch conductivity apparatus; pH by use of a Beckman meter and also colorimetrically; exchangeable hydrogen by a modification of the Parker (1929) and Schollenberger (1927, 1930) methods; percentage of base saturation by leaching a barium-saturated soil with dilute sulfuric acid, a method employed on occasion at the Pedology Laboratory at Rutgers University; nitrates according to the method of Eastoe & Pollard (1950); and ammonia, sulfates, and chlorides qualitatively with Nessler Reagent, barium chloride, and silver nitrate quick-tests respectively.

All samples were obtained by trench cuts wherein the exposed profile could be measured as to depth and color of horizons, earthworm activity, and degree of penetration of organic matter. Four profiles per age-group were thus sampled, every horizon being sampled each time.

ROOTS

The depth of penetration and density of the roots of the dominant species in each field age-group were studied by a modification of the root-trench method employed by Scully (1942). Since only one wall of any trench was plotted, the square trench advocated by Scully was abandoned in favor of the traditional, more easily dug rectangular trench. Each trench was 1.5 m. long, 60 cm. wide, and 15 cm. deeper than the lowest observable root. This depth varied from approximately 60 to 180 cm. The face of one of the longer walls of each trench was marked off with string and nails into 8 cm squares, a total of 1.2 m thus being delimited. According to Scully's scheme, the individual squares were plotted on graph paper, various symbols being used to designate diverse diameters and species wherever possible. One root-trench was studied in each of the younger field age-groups up to and including the ten-year old, two trenches in the fifteen to sixty-year-old groups, and four in Mettler's Woods.

RESULTS

HERBACEOUS SPECIES

A list of certain of the herbaceous species occurring on the various fields is presented in Fig. 2 together with a graphic presentation of their percentages of coverage, frequency, and presence. Of the 229 species present, only two *(Potentilla simplex, Fragaria virginiana)* were found throughout all field age-groups, while 21 were common to all but Mettler's Woods. The majority of species appeared either in a few consecutive field age-groups or sporadically in isolated age-groups with no apparent relationship between time of abandonment and invasion. Those species never occurring in quadrats but nevertheless present on the various fields have been omitted from Fig. 2. These total 62 and are as follows, the figures in parentheses indicating the field age-groups in which each species was recorded:

Agrimonia parviflora (40, 60), *Allium* sp. (MW), *Anaphalis margaritacea* (1, 5, 10), *Anemone quinque-*

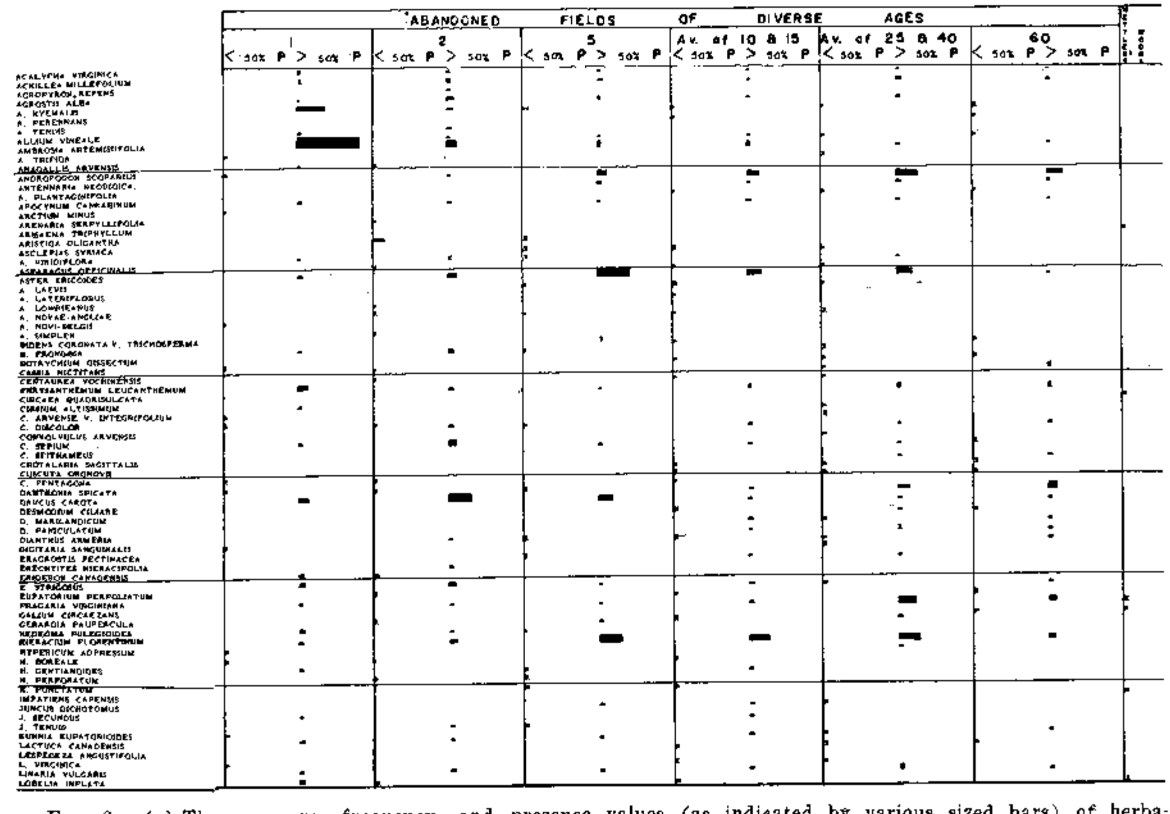

FIG. 2. (a) The coverage, frequency, and presence values (as indicated by various sized bars) of herbaceous species sampled on abandoned fields of diverse ages and in Mettler's Woods. The values for field age-groups 10 and 15 and those for 25 and 40 have been averaged. The width of each bar is an indication of the frequency, the length an indication of the coverage value of the given species, each bar being placed in one of the two columns designating presence values of more or less than 50%. For example, *Ambrosia artemisiifolia* occurred in 100% of the one-year-old fields (hence its location in the second column of field age-group one), its total frequency value for that age-group was 88% (width of bar) and its coverage value was 31.76% (length of bar). All species exhibiting estimated coverage values of 1.50% or less and frequencies of less than 20% are indicated by bars the size of that accorded *Anagallis arvensis* in the first column. An *X* indicates the occurrence of a species on the fields but not in quadrats. No presence values are indicated for Mettler's Woods since it was the sole stand of a mature forest investigated. *Andropogon scoparius* was sampled before it was mature; therefore, some *A. virginicus* probably included.

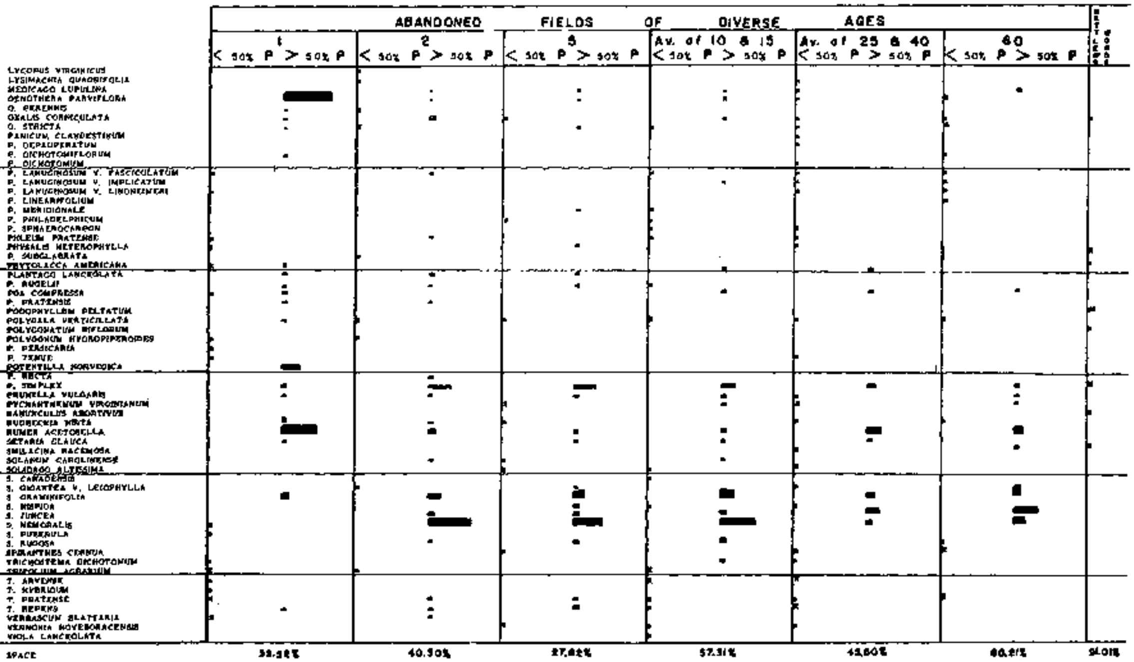

FIG. 2. (b): continuation of Fig. 2a.

folia (MW), *Anthemis arvensis* (1, 2), *Anthoxanthum odoratum* (1, 2, 5), *Asclepias tuberosa* (2), *Aster puniceus* (2), *A. schreberi* (MW), *Barbarea vulgaris* (5), *Bidens laevis* (40), *Carex laxiflora* v. *gracillima* (MW), *C. radiata* (MW), *C. setacea* (2), *Carex* sp. (15), *Cassia fasciculata* (10), *Chenopodium album* (MW), *Cichorim intybus* (2), *Cirsium pumilum* (1), *C. vulgaris* (2, 5, 10, 40), *Claytonia virginica* (MW), *Commelina virginica* (40), *Desmodium nudiflorum* (MW), *Echium vulgare* (1), *Erigeron annuus* (10), *Euphorbia vermiculata* (2), *Festuca obtusa* (MW), *Galinsoga parviflora* (2), *Galium pilosum* (MW), *Glyceria striata* (MW), *Heuchera americana* (MW), *Hieracium scabrum* (10), *Hypericum canadense* (5), *H. mutilum* (1, 2), *Juncus effusus* (1), *Lappula echinata* (2), *Leersia virginica* (MW), *Lepidium densiflorum* (1), *Lespedeza capitata* (60), *Lotus corniculatus* (25), *Luzula multiflora* (MW), *Lycopodium tristachyum* (60), *Melilotus officinalis* (2), *Monotropa uniflora* (MW), *Oenothera biennis* (25), *O. fruticosa* (40), *Osmorhiza claytoni* (MW), *Paronychia canadensis* (MW), *Poa annua* (2), *Polygala sanguinea* (5, 10, 40), *Polygonum hydropiper* (MW), *P. pensylvanicum* (2, 10), *Ranunculus recurvatus* (MW), *Saxifraga virginiensis* (MW), *Solidago uliginosa* (2), *S. uliginosa* v. *linoides* (MW), *Stachys tenuifolia* v. *platyphylla* (40), *Taraxacum officinale* (1), *Triodia flava* (40), *Verbascum thapsus* (2), *Viola affinis* (MW), and *Viola papilionacea* (MW).

Similarly, species which occurred in but one field age-group, if their estimated coverage was less than 0.10% are omitted. These in turn total 28 and are as follows:

Amphicarpa bracteata (MW), *Anemonella thalictroides* (MW), *Artemisia tridentata* (25), *Asclepias quadrifolia* (MW), *Botrychium virginianum* (MW), *Carex cephalophora* (MW), *Cerastium vulgatum* (5), *Danthonia sericea* (25), *Galium aparine* (MW), *G. triflorum* (MW), *Geranium maculatum* (MW), *Geum canadense* (MW), *Hibiscus trionum* (60), *Maianthemum canadense* (MW), *Panicum boscii* (1), *P. latifolium* (60), *Pilea pumila* (MW), *Polygonum convolvulus* (1), *Raphanus raphanistrum* (1), *Rumex crispus* (1), *Sanicula canadensis* (MW), *Symplocarpus foetidus* (MW), *Tiarella cordifolia* (MW), *Uvularia perfoliata* (MW), *U. sessilifolia* (MW), *Viola latiuscula* (60), *V. sagittata* (40), and *Viola* sp. (MW).

The remaining 139 species are listed in Fig. 2, the various bars representing the average coverage, frequency, and presence value of each species in the diverse field age-groups. The values for field age-groups 10 and 15 and those for 25 and 40 were averaged to reduce the size of the figure.

The various species ranged in coverage from considerably less than 1% to almost 32%. The coverage values in Fig. 2 must be interpreted cautiously. They are estimates which have been averaged, hence in themselves representing values ranging from much above or below the mean to slight deviations from it. Since they are not absolute values they show only trends of dominancy. These trends may appear more or less decisive depending on the variations of coverage and frequency of given species in the several fields of any field age-group. Although certain of the trends may be obliterated by resorting to a consideration of averages only, it may thus be shown that the invasion and ecesis even of the dominant species is not as consistent on the Piedmont of New Jersey as described for the Piedmont of North Carolina (Oosting 1942).

Soon after cultivation of a field is halted, a weedy flora invades the field. The one-year-old fields support a great growth of ragweed *(Ambrosia artemisiifolia)* towards the end of the summer, and it is this species which appears to be dominant in absolute coverage, but if one were to consider the growing season as a whole, evening primrose *(Oenothera parviflora)* would dominate. The latter loses all importance after the first year, and though it and other evening primroses appear spottily in older fields, the genus never regains its original dominance. *Rumex acetosella* and *Agrostis hyemalis* are consistently high in newly abandoned fields, the former maintaining its coverage as long as a quarter-century later, the latter dwindling after a decade. Of the ninety-four species found in the one-year-old fields (Table 1), twenty-six were annuals: an approximate one-fourth of the total species. This proportion would be increased somewhat if one were to consider the coverage of all the annuals in relation to the total coverage of all species sampled within the quadrats (Table 2). It is evident that almost one-third of the one-year-old fields is covered with therophytes, half of these annuals being common to the younger fields only, the others maintaining their coverage or appearing sporadically in the older fields. With the exception of *Solidago juncea* (which attained more than 2% coverage on the two-year-old fields, and therefore may be present on some newly abandoned fields), all the herbaceous perennials later assuming dominancy are present in the one-year-old fields. While a striking decrease in therophytes is noted both floristically (Table 1) and in dominance (Table 2) from the youngest to the oldest fields, there is not the preponderance of annuals often noted in newly-abandoned fields (Oosting 1942). Despite the high degree of colonization noted, almost 40% of the area of the one-year-old fields was untenanted by herbs. Although it may have supported lichens or seedlings, this area was devoid of herbaceous growth and as such was recorded as "space" in the herb layers (Fig. 2).

An additional feature to be noted is the relatively large proportion of species non-indigenous to eastern North America (Table 3). Almost 29% of the species are not native, this percentage decreasing measurably with length of abandonment.

The two-year-old fields differ from the one-year-old fields in the higher coverage and frequency of goldenrods and other perennials, and a decrease in the annual coverage (Fig. 2, Table 2). Goldenrods (especially *Solidago nemoralis)* contribute most to the aspect of the fields, but *Daucus carota* and *Potentilla simplex* are fairly important also. Unlike the above species, with coverage values exceeding 10%, the majority of the species exhibit values below 2%. Some of these, like *Anagallis arvensis* and *Verbascum blattaria* are restricted to fairly recently aban-

TABLE 1. Life-form spectra (in percent) of all species present on abandoned fields of diverse ages and in Mettler's Woods. Figures in parentheses indicate plants which are juvenile or immature specimens of species which at maturity are in the given life-form. Life-form categories follow those assigned by Ennis (1928).

Age	Total	P	MP	mP	N	Ch	H	G	Th
1......	94	0	(3.2)	(4.3)	0	0	53.2	11.7	27.6
2......	104	(1.0)	(3.8)	(5.8)	1.0	0	53.8	11.5	23.1
5......	95	(2.1)	(8.4)	(10.5)	2.1	2.1	49.5	8.4	16.9
10......	91	(2.2)	(9.9)	(8.8)	0	2.2	51.6	4.4	20.9
15......	96	(5.2)	(15.6)	(9.4)	2.1	2.1	47.9	7.3	10.4
25......	104	(3.8)	(9.5)	13.5	1.0	2.9	48.1	10.6	10.6
40......	122	(5.7)	(10.8)	13.1	2.5	1.6	42.6	9.8	13.9
60......	104	(7.7)	(13.5)	10.6	2.9	1.9	42.3	8.6	12.5
M W...	115	15.7	13.9	13.9	2.6	0.9	30.4	15.6	7.0

P — Megaphanerophytes: Tall trees over 30 m. in height.
MP — Mesophanerophytes: Trees 8-30 m. in height.
mP — Microphanerophytes: Low trees 2-8 m. in height.
N — Nanophanerophytes: Shrubs under 2 m. in height but over 25 cm. tall.
Ch — Chamaephytes: Low shrubs with buds borne less than 25 cm. above surface.
H — Hemicryptophytes: Herbs with perennating bud at surface; often covered by debris.
G — Geophytes: Herbs with perennating bud buried in soil.
Th — Therophytes: Annuals.

TABLE 2. Life-form spectra based on list of species present in quadrats on abandoned fields of diverse ages and in Mettler's Woods (upper figures) and spectra based on their coverage values (lower figures), the latter in percentage. The percentages of the spectra based on cover represent the percentage that each life-form contributes to the total coverage contributed by all life-forms. Figures in parentheses indicate plants which are juvenile or immature specimens of species which at maturity are in the given life-form. For explanation of symbols, see Table 1.

Age	Total	P	MP	mP	N	Ch	H	G	Th
1........	73	0	(2)	(3)	0	0	38	9	21
		0	0.31	0.28	0	0	65.59	2.12	31.69
2........	72	(1)	(4)	(1)	0	0	41	10	15
		0.01	0.23	1.21	0	0	78.11	5.42	15.01
5........	63	(1)	(4)	(2)	1	2	36	6	11
		0.06	0.97	0.45	0.15	0.19	91.97	0.77	5.43
10........	68	(2)	(8)	(7)	0	1	37	3	10
		0.67	1.20	1.54	0	1.03	86.65	1.70	7.20
15........	75	(2)	(10)	(4)	1	2	41	7	8
		0.11	6.49	6.83	0.89	0.77	80.45	2.87	1.58
25........	79	(4)	(6)	8	1	3	41	9	7
		0.86	10.21	5.51	0.65	0.81	79.49	1.13	2.33
40........	87	(5)	(10)	10	1	1	40	9	11
		0.67	20.15	9.23	0.14	1.35	63.78	3.33	1.34
60........	76	(6)	13	8	1	1	32	5	10
		2.52	58.49	9.12	0.05	0.06	27.17	1.15	1.44
M W.....	50	8	5	6	2	1	12	13	3
		55.24	30.28	0.53	12.01	0.01	0.19	1.60	0.14

TABLE 3. Number and percentage of non-indigenous species (following Gray's Manual, 8th ed.) on abandoned fields of diverse ages and in Mettler's Woods.

Age of Field	Non-Indigenes	Total Species	% Non-Indigenes
1........	27	94	28.72
2........	33	104	31.73
5........	21	95	22.11
10........	12	91	13.19
15........	17	96	17.71
25........	21	104	20.19
40........	21	122	17.21
60........	16	104	15.38
M W......	5	115	4.35

doned fields, while others, like *Achillea millefolium* and *Acalypha virginica*, exhibiting fair frequency but low cover, appear in all fields from the youngest to the oldest despite a diminution in frequency and cover. Another difference in the two-year-old fields lies in the successional nature of the dominant species: there is no rapid decline or extinction of these species following the second year of abandonment as there is in the case of the dominants of the one-year-old fields. Indeed, a two-year-old field may often be best marked by the abundance of dead Oenothera stalks. The area unoccupied by herbs remains essentially unchanged.

The five-year-old fields maintain high goldenrod coverage and in addition exhibit much *Aster ericoides.* This species attains a 2% coverage in one-year-old fields, more than doubles it in two-year-old fields, and exhibits a 15% coverage in the five-year-old fields. An ubiquitous hawkweed, *Hieracium florentinum,* also present throughout the succession, is quite noticeable at this stage. *Potentilla simplex* and *Daucus carota* are still extensive. *Andropogon scoparius,* although present throughout the succession, becomes appreciable within five years of abandonment and maintains varyingly high coverage thereafter. The percentage of therophytes has dropped to almost 17, the coverage of 11 annuals on quadrats equalling 5.43% of total coverage (Tables 1 & 2). The percentage of non-indigenes has also decreased (Table 3). Only 28% of the herb layer is space, this being the lowest recorded, and indicates the greatest herbaceous colonization. As woody colonization increases, herb coverage decreases with a concomitant increase in the space of the herb layer.

The herbaceous aspect of the ten-year-old fields is decidedly a Solidago-Andropogon one with a strong admixture of *Aster ericoides* and *Hieracium florentinum.* Of all age-groups studied, the ten-year-old fields exhibit the greatest growth of goldenrods, especially *Solidago nemoralis* and *S. graminifolia.* Towards late autumn, the broomsedges *(Andropogon scoparius* and *A. virginicus)* actually appear more conspicuous than they were at the time of sampling (late summer). *Potentilla simplex* and *Erigeron strigosus* are somewhat less important than *Aster ericoides* and *Hieracium florentinum* but still noteworthy. A second hawkweed, *H. scabrum*, appears on the drier stretches of one field. The slight increase in therophytes (Table 1) is occasioned by the invasion of a few annuals common to older fields, e.g., *Crotallaria sagittalis.* Similarly, the slight increase in coverage of annual species (Table 2) may result from the increase of *Erigeron strigosus.* Non-indigenes have decreased to about 13% of the species present (Table 3). The increase in woody species to be noted later is responsible for the increase of total space devoid of herbaceous cover, from 27.92% in five-year-old fields to 32.09% in ten-year-old fields.

Lichen coverage, heretofore negligible, is quite extensive. No data were assembled regarding the frequency and coverage values of lichens, but the species encountered in the various age-groups are listed in Table 4.

TABLE 4. Floristic analysis of lichens present on abandoned fields of diverse ages. Identifications by Dr. John W. Thomson, Jr. of the University of Wisconsin.

Species	Abandoned Fields						
	2	5	10	15	25	40	60
Cladonia sp.	*						
C. atlantica Evans f. *squamosissima* Evans						*	
C. capitata (Michaux) Spreng. f. *imbricata* (Nyl.) Evans		*					
C. chlorophaea (Floerke) Spreng.							*
f. *carpophora* (Floerke) Anders						*	
f. *pseudotrachyna* Harn.				*			
f. *pterygota* (Floerke) Vainio					*		
f. *simplex* (Hoffm.) Arn.				*		*	
C. coniocraea (Floerke) Spreng. f. *ceratodes* (Floerke) Dalla Torre & Sarnth.		*					
C. cristatella Tuck.			*				*
f. *squamosissima* Robbins							*
f. *vestita* Tuck.		*	*	*	*	*	
C. fimbriata (L.) Fr.		*			*		
C. macilenta Hoffm. f. *styracella* (Ach.) Vainio						*	
C. mateocyatha Robbins							*
C. subcariosa Nyl.		*		*			*
f. *evoluta* Vainio			*	*	*	*	
f. *squamulosa* Robbins					*		

Fields abandoned for fifteen years differ slightly in their herbaceous aspect from the ten-year-old fields because of the increase of Andropogon and the reduction of *Solidago nemoralis* and *S. graminifolia.* Despite this, the goldenrods collectively maintain a higher coverage value than the broomsedges, and appear to be dominant. Moreover, two other goldenrods increase in coverage; these are *S. juncea* and *S. rugosa. Hieracium florentinum* is more than equivalent in coverage to the Andropogons, but its flattened rosette belies its dominance in comparison to the taller, robust broomsedges. *Potentilla simplex* has a comparatively high coverage value, as does *Fragaria virginiana,* the two species which are present from the one-year-old fields to the forest itself. *Danthonia spicata* attains a fair coverage. The number of annuals is low, and their coverage is even lower (Tables 1 & 2). The non-indigenes have increased somewhat, but this is in large part the result of the entrance of woody forms at a rapid rate. Total space unoccupied by herbs equals more than 42%.

The twenty-five-year-old fields exhibit less goldenrod coverage than fifteen-year-old fields, despite an increase in *Solidago juncea. Aster ericoides* is the most conspicuous single dominant. *Hieracium florentinum* is almost as important as the aster, but of course rarely seems so. The Andropogons form only a fraction of their former (and seemingly subsequent!) coverage; this obtained on the three fields studied. An explanation of the significance of this highly perverse situation will be attempted later. *Rumex acetosella* would appear to rank beneath Aster and *Hieracium florentinum* in coverage value, but an abnormally high (23%) value for one field distorted the average, considering the 1% each exhibited in the other fields. *Fragaria virginiana, Danthonia spicata,* and *Potentilla simplex* are widespread, and *Linaria vulgaris* attains its highest frequency on these fields. The number of therophytes (Table 1) is not too different from those present on the fifteen-year-old fields, but their coverage is slightly higher (Table 2). A slight increase in non-indigenous species is noted (Table 3), still the result of invading woody species. The total space unoccupied by herbs is almost 43%.

The forty-year-old fields are characterized by Andropogons with appreciable admixtures of the goldenrods, especially *Solidago juncea. Fragaria virginiana* and *Danthonia spicata* are important subdominants. Of the species contributing less to total coverage, *Apocynum cannabinum* and *Antennaria neodioica* reach their peaks here both as to frequency and coverage. Woodland species begin to enter the succession: e.g., *Smilacina racemosa* is noted for the first time. The lichen cover is extensive and rich in species (Table 4). Although the therophyte flora appears high (Table 1), the coverage is low (Table 2). Non-indigenous species are gradually decreasing in number (Table 3), a resumption of the trend broken slightly in the fifteenth to twenty-fifth years following abandonment. Area unoccupied by herbs in the forty-year old fields averaged 48.21%.

The oldest fields of the study had been abandoned for approximately sixty years. The total cover of herbs was only about 40%. The dominant species are *Solidago juncea* and the Andropogons. *Solidago nemoralis, Rumex acetosella,* and *Danthonia spicata* are sub-dominant, but the decrease in cover is not the only factor which distinguishes these fields herbaceously from the younger sites. *Smilacina racemosa* and *Galium circaezans,* species in the oak-hickory forest, are found in the more mesic nooks of these fields. *Hieracium florentinum* and *Aster ericoides* contribute little to total coverage. *Fragaria virginiana* is still quite evident. Therophytes are low in total number and rather low in coverage (Tables 1 & 2). The non-indigenous species comprise only about 15% of the total species, a decided decrease since the beginning of the succession (Table 3).

In Mettler's Woods, as the growing season progresses, the herbaceous vegetation is gradually reduced from an earlier maximum coverage to approximately 10% of the total area of soil available for colonization, yet despite this, 57 species maintain themselves on the forest floor. While never rich in species in comparison to younger fields, the herbaceous flora is greatest towards late summer, although total coverage is greatest in mid-spring prior to leaf-unfolding of the trees with attendant closing of the forest canopy. The quadrat data were obtained in early June at a time when *Podophyllum peltatum*

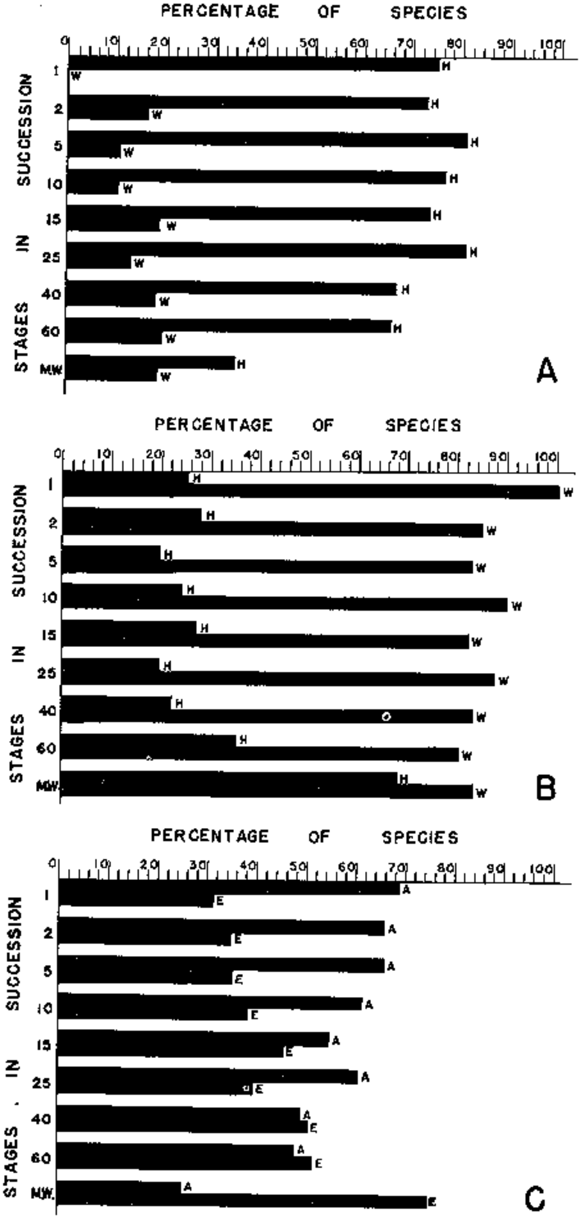

FIG. 3. Percentage of herbs, woody species and total flora disseminated by wind or animals (Ridley 1930) on abandoned fields and in Mettler's Woods.

A. Percentage of herbaceous (H) and woody (W) species of each field age-group whose seeds or fruits are dispersed by the wind.

B. Percentage of herbaceous (H) and woody (W) species of each field age-group whose seeds or fruits are dispersed by birds, animals, or insects either epi- or endozoically.

C. Percentage of all the species (herbaceous and woody) of each field age-group whose seeds or fruits are disseminated by the wind (A) or by birds, animals, or insects (E).

exhibited slightly more than 3% coverage, a reduction of its previous status. The only other species at this time with more than 1% coverage is *Circaea quadrisulcata.* The majority of the species, like *Smilacina racemosa, Impatiens capensis,* and *Polygonatum biflorum* exhibit approximately 0.5% or less coverage (Fig. 2). Both the coverage and frequency values of these woodland species are much inferior to those of the younger fields. The annuals are the lowest, both in number and percentage cover, in comparison to all fields studied (Tables 1 & 2); the non-indigenes are similarly lowest in number (Table 3).

The variation in mode of dissemination of the plants occupying the diverse fields is presented graphically in Fig. 3. The herbaceous species bear fruits or seeds which are largely disseminated by wind in the early years of abandonment. Towards the climax, the population shifts and a flora dispersed mainly epizoically and endozoically occupies the fields.

WOODY SPECIES

Ninety-one woody species were found growing on the various fields. Of these 91, only two, *Prunus serotina* and *Rhus radicans* are present throughout the succession. Three more species, *Myrica pensylvanica, Rhus glabra,* and *Rubus flagellaris* occur on all the abandoned fields but not in Mettler's Woods. The other eighty-six species are variously disposed throughout the age-groups.

The coverage, frequency, and presence values of certain of the woody species occurring in the shrub layers of the various fields is shown in Fig. 4, the values for field age-groups 10 and 15 and those for 25 and 40 having been averaged. Species (39) present on the fields but not in quadrats or under line-transects, have been omitted from Fig. 4. These are here enumerated together with the field age-groups (in parentheses) in which each was recorded:

Acer ginnala (40), *A. saccharinum* (15, 60), *Amelanchier canadensis* (15, MW), *Berberis thunbergii* (MW), *B. vulgaris* (MW), *Betula nigra* (60), *Carpinus caroliniana* (MW), *Carya cordiformis* (60, MW), *C. glabra* (MW), *C. ovalis* (MW), *C. ovata* (MW), *Catalpa bignonioides* (5), *Chimaphila maculata* (MW), *Crataegus mollis* (MW), *C. pruinosa* (15), *C. intricata* v. *straminea* (5, 25, 40), *Ilex serrata* (MW), *Juglans nigra* (MW), *Lindera benzoin* (25, MW), *Liriodendron tulipifera* (MW), *Maclura pomifera* (1), *Ostrya virginiana* (MW), *Platanus occidentalis* (40), *Populus grandidentata* (40), *Quercus bicolor* (60, MW), *Q. coccinea* (15, MW), *Q. velutina* (40, MW), *Rhus copallina* (5, 25, 40, 60), *R. typhina* (2, 40), *Rosa canina* (40), *Rubus occidentalis* (MW), *R. ostryifolius* (MW), *Sambucus canadensis* (2, 10, MW), *Smilax pulverulenta* (MW), *Spiraea tomentosa* (2, 5), *Tilia americana* (MW), *Vaccinium stamineum* (MW), *Vitis cinerea* (25), *V. labrusca* (15).

The one-year-old fields have a meager, mostly unnoticed population of shrubs. Less than 2% of the

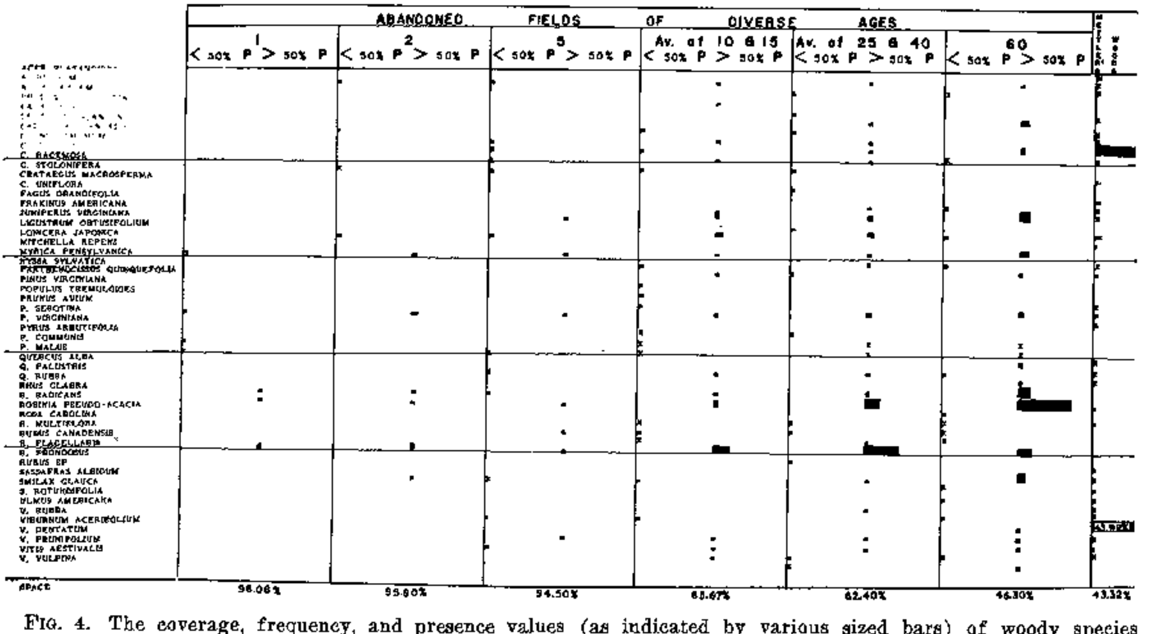

FIG. 4. The coverage, frequency, and presence values (as indicated by various sized bars) of woody species sampled in the shrub layers of abandoned fields of diverse ages and in Mettler's Woods. The values for field age-groups 10 and 15 and those for 25 and 40 have been averaged. The width of each bar is an indication of the frequency, the length an indication of the estimated coverage value of the given species, each bar being placed in one of the two columns designating the presence values of more or less than 50%. For example, *Rhus radicans* had presence and frequency values of 100% (width of bar) each and an estimated coverage value of 26.80% (length of bar) in field age-group 60. All species exhibiting estimated coverage values of 1.50% or less and frequencies of less than 20% are indicated by bars the size of that accorded *Acer rubrum* in field age-group 2. An X indicates the occurrence of a species on the fields but not in quadrats. No presence values are indicated for Mettler's Woods since it was the sole stand of a mature forest investigated.

TABLE 5. The density (D, in field age-groups 1-5, individuals per 50 sq. m.; in 10-year-old fields, individuals per 75 sq. m; and remaining field age-groups, individuals per 100 sq. m.), frequency (F), and presence (P), of arborescent seedlings encountered on abandoned fields of diverse ages and in Mettler's Woods.

Species	1	2	5	10	15	25	40	60	M W
	D F P	D F P	D F P	D F P	D F P	D F P	D F P	D F P	D F
Acer rubrum	......	1- 2-25	......	1-13 -100	1-1-100	3-2-100	......	10- 6- 66	5- 4
Carya sp.	......	......	......	......	......	......	......	......	9- 4
Cornus florida	......	......	......	......	......	......	3-3-100	14- 3- 66	168-61
Fraxinus americana	......	......	......	......	......	......	......	......	3- 3
Juniperus virginiana	......	......	5-8-100	2-2.6-100	5-4-100	10-8-100	11-8-100	39-21-100	2- 2
Prunus serotina	47-22-25	7-10-50	5-4-100	1-1.3-100	1-1-100	4-2-100	8-6-100	11- 9-100	2- 2
Pyrus communis	1- 2-25	......	......	......	......	1-1- 66	......	1- 1- 33	
Quercus alba	......	......	......	......	......	......	......	1- 1- 66	3- 3
Q. palustris	......	......	......	......	1-1-100				
Q. rubra	......	......	......	......	......	......	......	5- 5- 66	
Q. velutina	......	......	......	......	......	......	......	......	2- 2
Sassafras albidum	......	......	1-2- 33	......	......	......	23-9- 50	89-35-100	
Ulmus sp.	......	......	......	......	1-1-100				

area of the fields is covered with shrubs, seedlings or vines, about 98% of the soil surface being unoccupied by these plants. Despite low coverage values, *Rubus flagellaris, Rhus glabra,* and *R. radicans* are established here and largely remain throughout the succession (Fig. 4). If a source of seed is good, seedlings of *Prunus serotina* for example, are more numerous one year after abandonment of a field than subsequently (Table 5). It will be seen, however, that their mortality rate is quite high.

Two-year-old fields show a reduction both in shrub coverage (Fig. 4) and seedling density (Table 5) of *Prunus serotina.* Increased coverage of *Rubus flagellaris* and *Rhus radicans* is noted together with the successful invasion of an ubiquitous non-indigene, *Lonicera japonica. Myrica pensylvanica* provides greater coverage than the previous year and *Acer rubrum* first appears. The appearance of two-year-old fields is nevertheless distinguished from one-year-old fields not so much by the minor increase in shrubs but by alterations in the herbaceous flora. Total area unoccupied by shrubby growth equals about 95%.

Quite soon after abandonment, the species that especially lends character to the succession, *Juniperus virginiana,* becomes established. Several factors affect the time of ecesis, the most notable, of course, being source of seed and presence of seed-ingesting birds. The three five-year-old fields all had young red cedars, some at least two years of age. Although the four one-year- and the four two-year-old fields were all bordered by red cedar hedgerows, and there is by no means a dearth of birds feeding on red cedar in the vicinity, careful scrutiny within the fields revealed no seedlings. Investigation of a three-year-old field and a four-year-old field also proved disappointing. Nevertheless, it would appear from the presence of the two-year-old plants in the five-year-old fields, that Juniperus may enter the succession within the first five years, probably the second or third year after abandonment. *Cornus florida* also appears early but its seedlings are so scattered that they are not encountered in quadrats until later in the succession.

The change in physiognomy at the time represented by the five-year-old fields is due entirely to the woody species, now beginning to appear above the herbs (Fig. 5). The young red cedars are most striking, though often no more than half a meter tall, and contributing on the average a coverage value of much less than 1% (Fig. 4). By virtue of its spreading habit, *Myrica pensylvanica* contributes more to coverage but is approximately equal in frequency. The dogwoods *(Cornus amomum, C. florida, C. racemosa, C. stolonifera)* and the Viburnums *(V. dentatum, V. prunifolium)* occur, though not necessarily on the same field. One seedling of *Sassafras albidum* was noted, but seedlings of Juniperus and *Prunus serotina* were more numerous (Table 5). The greater growth of shrubs and the invasion of newer woody species further decreased the amount of space unoccupied by them to about 94%.

By the tenth year of abandonment (Fig. 6), the red cedars have grown another half to three-quarters of a meter, and increased to a frequency of 93%, but their coverage is only slightly higher than that obtaining for the five-year-old fields. *Rubus flagellaris* forms a dense growth in local areas, while *Myrica pensylvanica* maintains an over-all coverage of ap-

FIG. 5. Young *Juniperus virginiana* (0.5 m tall) in field abandoned 5.5 years previously. A clump of *Andropogon scoparius* is visible behind the red cedar.

proximately 1%. The dogwoods increase somewhat, and they and *Acer rubrum* appear as saplings about one meter in height. The number of seedlings of all species is low (Table 5). Space unoccupied by shrubs and immature arborescent forms equals about 93%.

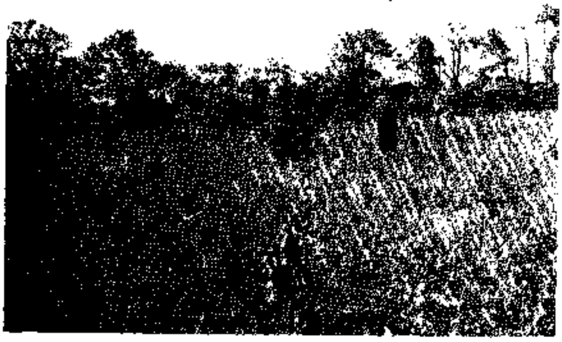

FIG. 6. Field abandoned about 10 years previously. Juniperus, 1 m tall, and other young trees of *Acer rubrum* and *Cornus florida* are evident. Andropogon is common in this field.

The fifteen-year-old fields assume an open-park aspect, for the taller red cedars are about 2.5 meters high, and the numerous young saplings of *Pyrus malus, Acer rubrum,* and *Ulmus rubra,* although not quite as tall, emphasize the increasing number of woody species (Fig. 7). Juniperus totals about 1% coverage and is the dominant tree, but the shrubs cover more ground. *Rubus flagellaris,* for example, attains a coverage value exceeding 14%, and *Rhus radicans,* which has been increasing steadily since abandonment exhibits about 4% coverage. A great growth of *Lonicera japonica* on one field distorted the average coverage of that species. Seedlings are still few in number (Table 5). The density of saplings is greatest for Juniperus (Table 6). On two of the three fifteen-year-old fields, a number of scrub pines *(Pinus virginiana)* appear to be successful. Although usually confined to succession on sandier soils, they occasionally occur on the Triassic shales. The extent of woody growth is such that the amount of soil surface not covered by shrubs or saplings equals about 74%.

TABLE 6. The density (D, number of individuals per 500 sq. m.), frequency (F), and presence (P) of saplings and shrubs encountered on abandoned fields of diverse ages and in Mettler's Woods.

Species	15	25	40	60	M W
	D F P	D F P	D F P	D F P	D F
Acer rubrum	1- 4- 33	2- 8- 66	2- 8- 50	10-16- 66	8-20
A. saccharinum	1- 4- 33				
Amelanchier canadensis	1- 4- 33				
Cornus florida	....	1- 4- 33	....	2- 8- 66	125-92
C. racemosa	1- 4- 33	5- 4- 33	....	2- 4- 23	
C. stolonifera	....	8 4- 33			
Fagus grandifolia	....	....	....	....	3-12
Fraxinus americana	....	....	....	....	22-32
Juniperus virginiana	17-48-100	19-64-100	59-64-100	90-96-100	
Pinus virginiana	4-12- 33				
Populus grandidentata	....	....	1- 4- 25		
Prunus serotina	....	3-12- 66	4-16- 75	3-12- 33	1- 4
Pyrus arbutifolia	2- 4- 33				
P. malus	....	....	1- 4- 25		
Quercus palustris	....	1- 4- 33	2- 8- 50		
Q. rubra	....	....	....	19-32- 66	
Rhus glabra	9-16- 66	13-20- 66	13-16- 50	70-68-100	
Rosa carolina	....	....	....	1- 4- 33	
Sassafras albidum	....	....	14-20- 50	70-60-100	
Ulmus rubra	1- 4- 33	7-20- 66	....	1- 4- 33	2- 4
Viburnum dentatum	....	....	....	1- 4- 33	
V. prunifolium	....	....	....	7- 4- 33	

Fields abandoned for twenty-five years exhibit red cedars of more than 1 inch d.b.h., and numerous other species. The cover of smaller plants of Juniperus in the shrub layer is still low, but *Prunus serotina* and *Sassafras albidum* have begun to increase. *Rhus radicans* maintains its inexorable trend of increase as *Rubus flagellaris* reaches its peak. Space unoccupied by shrubs and immature trees has dropped to 64%. The number of seedlings of Juniperus is somewhat in excess of the younger fields but it is still not appreciable (Table 5). Seedlings of *Prunus serotina* and *Acer rubrum* have also increased. An increase in the density of saplings is observed in the case of most species, especially Juniperus and *Rhus glabra. Cornus stolonifera* and *Ulmus rubra* are also well represented by saplings (Table 6). More than 79% of the total woody basal area is contributed by Juniperus, although this only totals 1.22 square feet on the basis of 2,500 square meters. *Quercus palustris* contributes 6.55% and *Ulmus rubra* and *Acer rubrum* contribute approximately 5% each to the total woody basal area (Table 7).

As is expected, the forty-year-old fields have a richer and more extensive shrub cover in addition to a more varied supply of taller trees (Fig. 8). Space unoccupied by shrubby growth is about 61%. Juniperus is still the most important arborescent species, but cover of its smaller trees has increased to only 2%. *Sassafras albidum,* among the arborescent species, is next in contribution to cover in the shrub layer. Of the vines and lower shrubs,

FIG. 7. Field abandoned about 15 years previously. Trees of Juniperus are 2-2.5 m tall, those of *Pyrus communis* somewhat taller, and bushes of *Viburnum prunifolium* are evident.

TABLE 7. The basal area (B.A.) in square feet, density (D, per 2500 sq. m.), and frequency (F) of trees over 1 inch d.b.h. encountered on abandoned fields of diverse ages and in Mettler's Woods.

Species	25	40	60	M. W.
	B.A. % B.A. D F	B.A. % B.A. D F	B.A. % B.A. D F	B.A. % B.A. D F
Acer ginnala		0.006- 0.20- 1- 4		
A. rubrum	0.081- 5.27- 6-12	0.051- 1.59- 5- 8	0.715- 5.37- 24-28	0.320- 0.50- 2- 8
A. saccharum				0.013- 0.02- 1- 4
Betula nigra			0.067- 0.50- 1- 4	
Carya ovalis				6.850- 9.80- 3- 12
Cornus florida	0.012- 0.80- 1- 4	0.126- 3.90- 9-16	0.928- 6.97- 30-48	13.900-19.00-331-100
Fagus grandifolia				4.370- 6.80- 10- 12
Fraxinus americana		0.031- 0.95- 2- 4	0.096- 0.72- 1- 4	0.005- 0.01- 1- 4
Juniperus virginiana	1.220-79.52-59-84	2.349-72.40-62-80	8.352-62.70-232-96	
Nyssa sylvatica			0.056- 0.42- 1- 4	
Ostrya virginiana				0.005- 0.01- 1- 4
Prunus serotina		0.062- 1.91- 3- 8	1.129- 8.48- 31-52	
Pyrus communis	0.039- 2.56- 4-16		0.083- 0.62- 3- 8	
P. malus			0.026- 0.20- 3- 4	
Quercus alba				30.540-43.80- 18- 52
Q. palustris	0.101- 6.55- 1- 4	0.153- 4.72- 1- 4		
Q. rubra			0.400- 2.98- 5-12	7.900-11.30- 4- 16
Q. velutina				6.200- 8.90- 4- 16
Sassafras albidum		0.465-14.33-20-12	1.471-11.04- 52-60	
Ulmus rubra	0.082- 5.30- 6-12			0.005- 0.01- 1- 4

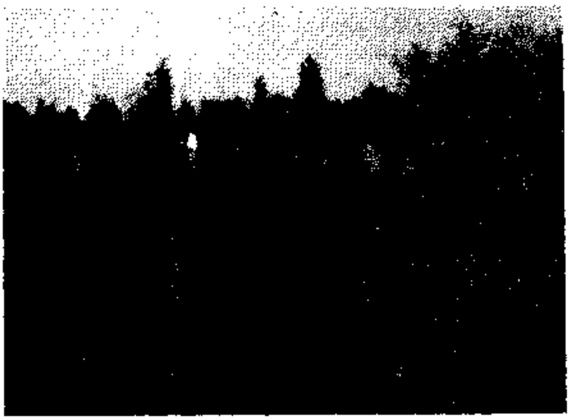

FIG. 8. Field abandoned about 40 years. Note the gradual closing of the Juniperus stand and the trees of *Prunus serotina* and *Sassafras albidum*.

Rubus flagellaris, although decreasing, still has a coverage of about 17%. *Rhus radicans* is very widespread, covering as it does 8% of the total sampled area. Of seedlings, Sassafras are the most common. Those of Juniperus are more abundant than in the preceding age-field (Table 5). There are more than four times the number of saplings of Juniperus on the 2,500 square meters sampled than any other species (Table 6). Saplings of Sassafras and shrubs of *Rhus glabra* are quite common, while saplings of *Prunus serotina* are more evident than previously. Juniperus contributes 72.4% of the total basal area of wood. The total basal area of Sassafras equals 0.46 square feet, or 14.33% of the total woody basal area (Table 7). The basal area of *Quercus palustris* has increased from that of the twenty-five-year level, but the percentage has decreased. An exotic maple, *Acer ginnala*, has invaded one of the forty-year-old fields from a neighboring landscaped estate, and it contributes 0.20% to the total woody basal area. This field also supports a specimen of *Ligustrum obtusifolium* which came from the same source.

The oldest (60-yr.) abandoned fields resemble young groves. Forty-six percent of the area is unoccupied by shrubby growth, thus approximately half the fields support some type of vine, shrub, or immature tree. Coverage figures cannot adequately convey a picture of the almost impenetrable thickets formed by this extensive growth. Growth of red cedar is at its peak in this age-group: trees of 10 inches d.b.h. and more than 5 m. tall are not uncommon (Fig. 9). Despite this, young trees cover only about 4% of the shrub layer (Fig. 4). *Sassafras albidum* contributes 3% and *Prunus serotina* contributes less than 3% to the total coverage of species in the shrub layer. But it is the vines and creeping shrubs running rampant over the fields which impart an aspect totally different from the other fields. The species which slowly and steadily increases its minute coverage from the time of initial abandonment until its dominance in the sixty-year-old fields is, of course, *Rhus radicans* which has now attained a coverage of almost 30%, largely as festoons on the red cedar trees. *Rubus flagellaris*, *Rhus glabra*, *Myrica pensylvanica*, and *Celastrus scandens*, collectively covering almost 21% of the area, also produce an effect of untrammeled growth. While never very high in coverage value, the truly mesic species characteristic of woodlands gradually supercede the long-established species and remain even when the mature forest develops. These species are *Cornus florida*, *Prunus serotina*, *Quercus alba*, *Q. rubra*, *Viburnum acerifolium*, *V. dentatum*, and *V. prunifolium*, all but the second exhibiting

FIG. 9. Field abandoned 60 years previously as seen from an adjacent field. Mature trees of Juniperus form a fairly closed stand.

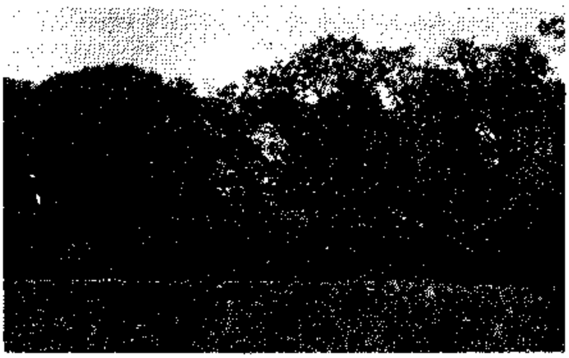

FIG. 10. Mettler's Woods as seen from an adjacent field. Note the marked stratification produced by the shorter trees, especially *Cornus florida.* Some of the tallest oaks and hickories are 24 m in height.

coverage values approximating 0.50% at this time.

The sixty-year-old fields have an abundance of seedlings, Sassafras being most numerous. Juniperus seedlings are abundant, too, but the presence of those of *Cornus florida, Quercus alba,* and *Q. rubra* has more significance despite their lesser numbers (Table 5), because these are the species important in the mature forest. Saplings of Juniperus and Sassafras contribute much to the high sapling-count, the highest noted in all the field age-groups studied. The density of the saplings of *Quercus rubra* and *Acer rubrum* is significant in that the former is higher than that displayed in Mettler's Woods, and the latter is approximately equivalent to the value in the mature forest (Table 6).

Regarding the mature trees, red cedar contributes 62.70% of the total basal area, or approximately eight square feet (Table 7). Sassafras, *Prunus serotina, Cornus florida,* and *Acer rubrum* are next in importance. *Quercus rubra* contributes almost 3%. The stage is thus set for the gradual transition towards the oak-hickory forest.

It is unfortunate that there was no stage transitional between the sixty-year-old fields and the mature forest. We may refer to Mettler's Woods as an example of the nearest approximation of a local climax forest (Fig. 10). The forest itself is imposing in the height and size of its dominant trees. Certain problems regarding its status may be noted from an examination of the data but these will be left for subsequent discussion. Shrubs and transgressives (young trees) occupy slightly more area than they do in the sixty-year-old fields, about 43% of the area being devoid of them. The dominant shrub is *Viburnum acerifolium* (almost 44%); the dominant transgressive is *Cornus florida* (cover, about 23%), the former also exhibiting slightly higher frequency than the latter. *Lonicera japonica* is next in importance but very low in coverage (about 2%), and another vine, *Rhus radicans,* has decreased to but a fraction of its former coverage (much less than 1%). The saplings of common trees, like *Prunus serotina, Fraxinus americana,* and *Acer rubrum* contribute very little to total coverage, but some, like *Cornus florida* (density, 125) and *Fraxinus americana* (density, 22), appear rather dense. Saplings of the dominant trees, *Quercus alba, Q. ruba,* and the species of *Carya* were observed in the forest but never found in the quadrats (Table 6). There are some seedlings of *Quercus alba* (but none in quadrats) and *Q. velutina,* but the predominant seedlings are those of *Cornus florida* (density, 168, Table 5). Seedlings of species of *Carya* were noted on the forest floor, but none appeared in the 100 square meters sampled.

The dominants are clearly indicated when considering their basal area (Table 7). *Quercus alba* contributes almost 44% to the total woody basal area. *Cornus florida* is sub-dominant with a value of 19%. *Quercus rubra* and *Q. velutina* each contributes at least 9%. *Carya ovalis* and *Fagus grandifolia,* although their basal area is low, exhibit higher percentages of frequency than any other sub-dominant.

There is little variation in the mode of dissemination of the woody forms throughout the succession (Fig. 3); regardless of the time since abandonment, approximately 84% of the woody species bear fruits or seeds dispersed by birds and animals. However, if the flora is taken as a whole, the overwhelming number of herbs in the younger fields shifts the general trend to an approximation of the herbaceous trend; *i.e.* a general decrease in wind-disseminated species and an attendant increase in faunal-disseminated species.

SOILS

The fields under investigation are located on the Brunswick formation (Kümmel 1940) of the Triassic shales which grade into soil materials of the Penn series, mostly Penn silty clay loam (U.S.D.A. Soil Survey of the Trenton Area 1926). The outstanding characteristic of this soil is the reddish color imparted to it by the slowly-weathering ferrous aluminum shales which are for the most part the result of sedimentation in quiet Triassic waters. Lack of disturbance during sedimentation produced heavy (but occasionally sandy) shale beds rather homogeneous as to particle size and mineral composition, this homogeneity to-day being reflected in the fairly uniform textural classes noted in the various horizons of the soil. These soils belong to the group of clay rocks made up of clay and clay-like minerals in association with iron and aluminum sesquioxides and other minerals in smaller quantities.

Although existing in the broad climatic belt conducive to a type of podzolization which would normally produce a brown podzolic soil, the soil must be classified as an endodynamomorphic body now largely resisting further weathering of its mineralogical fractions. The latter, having undergone considerable weathering prior to and during the Trias, bear few constituents capable of further chemical weathering. As Joffe (1937) states, "The fact that Fe, Al, and other constituents show very small differentials in the profile of the Penn silt loam . . . indicates no movement of them in the profile. And yet the B horizon is in its physical appearance typical of an illuviation horizon: it has a compact constitution. This simply means that the more highly dispersed particles are a resultant of physical disintegration with no change in composition." The small particle size, the masking presence of the red color, and the paucity of other minerals produce a nondescript, rather shallow soil material largely lacking in horizon-differentiation. This material may in time be endowed with the characteristics of a brown podzol, but must to-day be classified as an immature soil.

The typical profile is rarely more than half a meter in depth, and often less, for shale is frequently encountered within 60 cm of the surface. A layer of humus, often no more than 2 cm thick, is found in the forest and the older fields. In Mettler's Woods, this layer approximates the type designated as medium mull by Heiberg & Chandler (1941). A gradation in color, accentuated upon drying, may be noted from one horizon to the next. The Ap is often a cocoa-brown, the B a pale, rusty brown, and the C a rusty brown. Structure varies from crumbly to nutty, with a reduction in the size of the crumb-aggregates noted towards the C. A mild type of granulation is observed where the parent material contains lenses of sandstone embedded with the shale. Earthworms were noted in most of the soils especially in the B horizon.

The soil of Mettler's Woods will be discussed with reference to the properties analyzed, and then a brief review of the results of analyses of the younger fields will be presented. It is perhaps best to state at the outset that, with minor exceptions, differences between the age-groups may more often be ascribed to textural differences than to varying times of abandonment.

The soil in Mettler's Woods is more readily differentiated into horizons than that of cultivated fields, but even here the reddish color prevents facile visual identification. Textural differences of the horizon are more readily noted by insertion of a sharp trowel. A certain amount of clay settles in the B horizon during weathering, thus insuring a fairly light-textured A horizon. The A_1 is rendered even lighter by the autumnal accumulation and subsequent incorporation of organic matter. The relatively high content of organic matter in the A_1 (3.18%) is largely responsible for the high moisture-holding capacity (62.09%) for that horizon, the highest noted. The electrolytes, especially in the A_1, are high; even the nitrates, ammonia, sulfates, and chlorides appear appreciable at times. The average total exchange capacity (18.79 m.e.) is lower than that obtaining in the sixty-year-old fields (23.73 m.e.), but it represents a wider range.

The soil profiles of the younger fields are for the most part shallower than in the mature forest. Minor textural differences are to be found between the soils of the younger fields, these differences being reflected in the variations in the moisture-holding capacity and exchange capacity of the several horizons. No marked increase in the percentage of organic matter is noted with an increase in time of abandonment. Where differences in amount of organic matter do occur, they may be attributed to the degree of aeration which may vary according to the clay content. Little change is to be observed in the pH of these younger fields: the relatively high pH (6.0−6.6) of the one-year-old fields may be ascribed to the residual effects of the lime and fertilizer applied during the previous growing season, and the slightly low pH (5.4−6.0) of the soil in the five-year-old fields may be attributed to the unusual abundance of granitic pebbles, remnants of pre-Wisconsin glaciation. No discernible trends may be noted in the content of electrolytes as a whole (*viz.* conductivity) or sulfates in particular but fluctuations in nitrates, ammonia, and chlorides do occur. It would appear that fluctuations in exchangeable hydrogen probably result from differences in soil texture up to the forty-year level, after which minor increases occur owing to a greater annual accumulation of litter.

ROOTS

The density and depth of penetration of the roots of plants dispersed throughout the various abandoned fields are presented in Table 8. Each datum represents the density of the roots of various sized classes in an area 0.18 square meters (an area 1.2 m wide and 15 cm deep).

The depth of penetration of the roots as a whole appears to vary with the age of abandonment, from 60 cm in the younger fields to 1.8 m in Mettler's Woods. Fragments of shale, if not consolidated beds, are often encountered within 60 cm of the surface. The number of roots penetrating the shale increases with the age of abandonment, *e.g.* the roots of *Quercus alba* descend through almost a meter and a half of shale in Mettler's Woods. On the whole, the penetration of the shale is accompanied by a simultaneous decrease in the density of the smallest roots and an increase of the larger ones.

The greatest density of roots is observed in the

TABLE 8. The depth of penetration and density (per 0.18 sq. m.) of roots of plants encountered on abandoned fields of diverse ages and in Mettler's Woods.

Depth in cm.	Diameter in mm.	1*	2*	5*	10*	15*	25*	40*	60*	M W
0-15	< -1	990	568	868	923	867.5	1223.0	1000.5	828.0	290.5
	2-9	13	2	....	3	8.5	19.5	10.0	20.5	54.5
	10 or >	....	....	....	....	......	0.5	....	2.5	3.5
15-30	< -1	368	85	192	99	400.5	495.0	405.0	297.0	155.5
	2-9	....	....	3	....	1.5	4.0	6.5	9.5	29.3
	10 or >	....	....	....	....	......	....	....	1.5	3.3
30-45	< -1	57	43	133	63	160.0†	267.0†	186.5	133.5	115.5
	2-9	1	....	....	....	0.5	2.0	....	3.0	15.5
	10 or >	....	....	....	....	......	....	....	......	5.5
45-60	< -1	20†	7†	19†	18†	110.0†	71.5†	68.0	47.5†	86.3†
	2-9	....	....	....	....	......	1.5	....	0.5	9.7
	10 or >									
60-75	< -1	....	4†	2†	1†	14.0†	8.5†	9.5†	34.0†	85.0†
	2-9	....	....	....	....	......	0.5	....	0.5	6.6
	10 or >									
75-90	< -1	....	....	....	....	1.0†	2.0†	7.0†	9.0†	92.0†
	2-9	....	....	....	....	......	....	....	0.5	8.0
	10 or >									
90-105	<-1	....	....	....	....	......	....	0.5†	0.5†	29.3†
	2-9	....	....	....	....	......	....	....	......	4.3
	10 or >									
105-120	< -1	....	....	....	....	......	....	....	......	21.3†
	2-9	....	....	....	....	......	....	....	......	1.0
	10 or >									
120-135	< -1	....	....	....	....	......	....	....	......	2.0†
	2-9									
	10 or >									
135-150	< -1	....	....	....	....	......	....	....	......	3.6†‡
	2-9	....	....	....	....	......	....	....	......	2.3
	10 or >									
150-165	< -1									
	2-9									
	10 or >									
165-180	< -1	....	....	....	....	......	....	....	......	1.6†
	2-9	....	....	....	....	......	....	....	......	0.6
	10 or >									

*Years since time of last cultivation.
†Shale encountered.
‡Lens of hard clay encountered locally.

upper 15 cm of the soil, the vast majority of these being small roots less than 1 mm. in diameter. A decrease in the density of the smallest roots is noted towards the oldest fields, but the variations in the younger fields are insignificant if one considers that only one root-trench was studied in each. Furthermore, in age-groups five to sixty, each trench was dug about a meter away from one of the dominant specimens of *Juniperus virginiana*. If tufts of *Andropogon* happened to be in the vicinity, the density of the roots would be measurably increased. Owing to the high percentage of *Hieracium florentinum*, the greatest density of roots appears in the twenty-five-year-old age-group. There ensues a gradual, if interrupted, increase in the density of the larger roots after the second year of abandonment; the one-year old fields exhibit a somewhat greater number of these roots owing to the extensive coverage of *Rumex acetosella*. Very large roots, however, are not noted until twenty-five years after abandonment.

From 15-30 cm below the surface, the total density of roots is less than one-third of the number observed in the first fifteen centimeters. Here, too, the greatest density was encountered in the fields abandoned for twenty-five years. The decrease in the density from the first to the second 15-cm layer is of lesser magnitude in Mettler's Woods than elsewhere.

The total density of roots drops even further in the layer 30-45 cm below the surface. The twenty-five-year old fields maintain their superiority in density. Mettler's Woods, still exhibiting a lower density of small roots than that obtaining in the younger fields, maintains its superiority in numbers of larger roots.

As the roots penetrate successively deeper layers, their total density decreases, but a relative increase in density is noted with increases in age of abandonment in the case of roots of all sizes. Below 90 cm, the density of roots in Mettler's Woods rapidly declines.

DISCUSSION

TRENDS—VEGETATION

The successional trends displayed on the Piedmont of New Jersey are somewhat comparable to those observed on the southern half of the Piedmont (Crafton & Wells 1934; Billings 1938; Coile 1940; Oosting 1942) or in southern New England (Lutz 1928). Floristic composition varies from site to site, but the maintenance of certain dominants throughout the general area affords good comparison.

Fields abandoned one year are frequently dominated by ragweed *(Ambrosia artemisiifolia)* in New Jersey as well as in North Carolina (Keever 1950). Keever's results show that ragweed dominance is a product of the type of cultivation and the previous crop. In North Carolina, it may also be a dominant the second year after abandonment (Oosting 1942). Where evening primrose *(Oenothera parviflora)* is so common in one-year-old fields of New Jersey, horseweed *(Leptilon canadense)* is the dominant in North Carolina (Oosting 1942; Keever 1950); but in both regions these rapidly lose importance and are replaced by species of *Aster*, *Solidago*, and *Andropogon*.

A comparison of the degree of dominancy of these herbaceous species in the two sections of the Piedmont is impossible because the methods of field study are not comparable. The dominants of older fields are all present in newly-abandoned fields in New Jersey, while in North Carolina, their entrance may be delayed at least a year (Keever 1950). This does not in anyway hasten the succession in New Jersey; it is rather a reflection of a different climate and a resultant of the larger number of species encountered (94 in New Jersey; 35 in North Carolina as reported by Oosting 1942).

The greater variety of species on the northern Piedmont would also account for local variations in some fields from the general aster-goldenrod-broomsedge dominancy, as in the case of the occasional dominance of *Daucus carota, Potentilla simplex, Hieracium florentinum,* or *Fragaria virginiana* (Fig. 2). These deviations rarely occur over a long period, but are soon replaced by one or another of the dominant triumvirate. Occasionally, a species is present but with very low coverage in a field where one would expect it to be dominant, considering the general trend. Specifically, the rarity of Andropogon in the three widely-separated fields abandoned for twenty-five years is not symptomatic of a great reduction from the fifteen-year level, attended later by a great increase to the forty-year level. It may rather be an indicator of a poor seed-year, or a series of poor seed-years for Androgogon when these three isolated fields were newly abandoned, or some factor preventing seedling-survival. As Piemeisel (1951) states, "Destruction of a future dominant, a selective destruction, need not involve any great quantity of vegetable matter if it is at a critical time in the series."

The essential difference in the dominant herbs of the two investigated areas of the Piedmont is not in degree but in time of dominancy. Aster remains one of the dominants for a longer period, and the two dominant species of Solidago are of greater importance in New Jersey than farther south, especially in the older fields. Goldenrod dominancy in older fields has also been reported in New England (Lutz 1928).

As for the herbaceous flora as a whole, annuals are far less important here than elsewhere. In North Carolina, Oosting (1942) discovered that 57% of the species on fields abandoned one year were therophytes. In New Jersey, this number is only 28%, and even a consideration of the total coverage value of these plants reveals that less than 32% of the average one-year old field is occupied by annuals.

Despite the greater number of species, the fewer annuals, and the floristic differences in dominants, succession on the Piedmont moves with the same velocity in New Jersey as in North Carolina. The indicator species of the sub-climax, whether red cedar in the North or pines in the South, invade young fields within a few years after abandonment, and by the fifth year, appear above the herbs. Seedlings of the climax species, especially of bird-disseminated species, are established almost immediately after abandonment. Many of these succumb in competition for light and soil-status to the more vigorous herbs, but a certain number prevail and eventually attain maturity. Cherries and dogwoods are most successful, and by the sixtieth year, oaks and a few hickories are apparent in the understory. Although no field abandoned for longer than 60 years was investigated in New Jersey, Lutz (1928) reports a stand of 60-year-old red cedars in New England which had begun to deteriorate. It would appear that approximately 100 years is required for the first oaks and hickories to attain dominancy on the Piedmont of New Jersey, an equivalent period being reported by Billings (1938) in North Carolina.

With the approach to the status of the climax community, the floristic differences between areas become more pronounced. New Jersey represents an area transitional to the hemlock-hardwood forests to the North in New York and New England (Lutz 1928) and the southern oak-hickory forests with their occasional components of pine (Oosting 1942). Hemlock is not found in Mettler's Woods, but is located in cool ravines and north slopes of central New Jersey. Fewer sugar maples and beeches are found in the forests on the Piedmont of New Jersey than are common to the North; on the other hand, there is a richer proportion of oaks and hickories more reminiscent of the South.

But beyond arborescent species, differences are most noted in the ground vegetation. A few of the species may be found in forests from North Carolina to New England, but more are limited to either the South or the North. Cain (1950) states that a high proportion of geophytes in a flora is associated with a brief growing season such as might occur in a desert or that fraction of the growing season prior to post-vernal closing of the canopy in a forest. The higher percentage of geophytes (16%, Table 1) in Mettler's Woods than in oak-hickory forests of North Carolina (Oosting 1942) suggests a generally low level of light in the former. Is it possible that this is related to a general increase in the opening of the forest canopy as one proceeds from New England to the southern Piedmont, and that this variation may largely be responsible for floristic and ecological variations in the herbaceous populations?

The presence in the mature oak-hickory forest of fewer non-indigenous species than in the successional stages (Table 3) would argue for an interpretation of the oak-hickory forest, as represented by Mettler's Woods, as a closed community. It is impossible for the alien species to compete successfully with the long-established native vegetation.

TRENDS—SOILS

A summation of the analyses of certain physical and chemical properties of the soils investigated in the present study does indicate a lack of decisive correlation between any property and the age of abandonment. Where differences occur, they are more readily attributed to minor differences in the percentages of silt and clay present than to other factors. If a single abandoned field were examined over a period of 60 years, a slight amelioration in the surface might be observed in the moisture-holding capacity, exchange capacity, percentage of base saturation, and electrolytic content, all reflections of a gradual accumulation of organic matter.

Billings (1938) noted a striking change in the first 2 inches of the soil on the southern Piedmont. This improvement of the soil was due to the effects of the vegetation during the period of the succession: the copious deposit of pine needles which accumulated annually appeared to be a primary factor in the alteration of the soil. While this layer of the first two inches of soil was not sampled independently in the present study, it was included in a surface sample of approximately 15 cm; thus, any variation in the top few centimeters would be minimized in a consideration of the entire Ap horizon. The results thus represent an average of the Ap horizon. Since the seedlings of woody species present in the succession on the northern Piedmont are all equipped with long tap roots—unlike the shortleaf pines studied by Billings on the southern Piedmont—there is little value to be obtained in shallow sampling. Billings found no changes occurring in the soil beneath the surface 2 inches. Below this 2-inch layer, the differences between fields of varying ages apparently are related to differences in soil texture, an equivalent condition obtaining in New Jersey.

Another southern Piedmont study (Coile 1940) is similar in scope to Billings', but directed instead at loblolly pine succession. Coile concluded: "Physical characteristics of soil measured as volume-weight, water-holding capacity, and air-space change but little during succession and are not related in a causal manner to succession." Neither are changes in the chemical properties of the soil responsible for the entrance of the pines or the oaks. Instead, Coile attributes to time and chance the establishment of the woody forms. His interpretation of the relationships between squirrels and the size and location of the abandoned field will be reviewed later.

It would appear that red cedar succession on Penn soils is similar to loblolly succession on the Piedmont in North Carolina (Coile 1940) in that any minor changes of the soil accruing with abandonment other than accumulation of surface litter and its attendant phenomena (Billings 1938), are to be regarded more as the result than the cause of any particular succession.

TRENDS—ROOTS

The greater density of the smallest roots in the uppermost horizons of the soil and the increased density of the larger roots towards the lower horizons noted in the present study have often been observed (Billings 1938; Scully 1942).

The general depth of penetration of the roots increases with the age of abandonment of a field, a reflection of the increased percentage of woody species in the flora. Variations in the total density of roots are more dependent on the nature of the species present than the comparative texture of these soils, since lateral roots tend to be short in fine-textured soils (Anderson & Cheyney 1934). There is, however, a pronounced decrease in the density of the smallest roots of the uppermost horizon of Mettler's Woods. This decrease is due to the fewer numbers of herbaceous species in the forest.

Differences in the rooting habits of the dominant arborescent species are not such as to account for the successional pattern. Red cedar and oak seedlings both exhibit tap roots, and their growth requirements as far as soils are concerned appear to be similar. A study of root development on three soil types carried out in the Duke forest on a number of arborescent species including white oak and red cedar indicated an inverse relationship between available soil moisture and root growth of their seedlings (Duncan 1941). Both white oak and red cedar seedlings exhibited the best root growth on soils possessing a high air capacity, low porosity, and a small amount of available moisture.

It is very possible that the rooting habits of the dominant herbaceous species are responsible for their successional pattern insofar as competition for soil moisture may be of prime importance during droughts. Experimentation with these plants under different conditions of light and on varied soil textures would no doubt uncover relationships relative to the succession.

ASPECTS OF SUCCESSION

In 1916, Clements listed six stages in succession: nudation, migration, ecesis, competition, stabilization, and reaction. Nudation involves the removal of the soil, a condition important in a consideration of primary succession. However, nudation of a field may be interpreted as including only the removal of vegetation: this is the aspect of nudation involved in secondary succession. Migration of plants is effected by various means, thereby providing for invasion of plants upon an area. Ecesis entails establishment, and competition involves ". . . a struggle between individuals for growing space, both above and below ground, and for light, water, and nutrients" (Toumey & Korstian 1937, p. 156).

Each stage is, of course, completely interrelated with the others. However, if each is considered individually in an interpretation of secondary succession on the Piedmont of New Jersey, certain ecological features of this succession may be noted.

NUDATION

In secondary succession, nudation is never complete, and the extent of nudation determines the pattern of the succession. Even where the soil is plowed in preparation for planting and then abruptly abandoned prior to seeding, there does not exist a situation of true nudation. Embeded in the soil are countless seeds from previous growing seasons, and a large percentage of them is capable of germination. The pattern of a secondary succession has been reviewed in this report. Successions may vary with the degree of nudation (Dansereau 1946), but this study has been concerned only with those situations where land has been cultivated and then left idle as cultivation ceased.

MIGRATION

Migration *per se* has little meaning without a consideration of ecesis and competition, but for the moment, these latter will be omitted. The time of migration may precede by several years the actual initiation of the succession. It would be interesting to determine what percentage of the plants inhabiting a one-year-old field resulted from germination of viable seeds lodged in the soil for several preceding years. Chepil (1946) reported viability in seeds of the following species (present in the succession in New Jersey) deposited in the soil for five years: *Chenopodium album, Lepidium densiflorum, Medicago lupulina,* and *Taraxacum officinale.* However, the probability of seeds germinating very many years after deposition is unlikely. Oosting & Humphreys (1940) collected soil from successive stages in North Carolina and observed that germination tests ". . . show a succession of species, as do the plants above ground, and, in general, they are indicative of the same succession."

Where actual invasion occurs, assuming ample source of seed in each case, it would appear that the youngest fields are inhabited by herbaceous species whose fruits and seeds are largely dispersed by the wind, an inwards progression from hedgerows being noted. Not a small percentage of these wind-disseminated forms (Ridley 1930) are also transported epizoically in mud adhering to the fur and feathers of campestral birds and animals.

Dissemination of the woody species is largely effected endozoically as the succession proceeds towards the climax (Fig. 3). The smaller a field and the greater its proximity to a woodlot, the sooner will woodland species enter the succession (Coile 1940). Squirrels and other nut-caching rodents do not often venture into open fields, but minor sorties around the outskirts of forests may provide for peripheral invasion. Where fields are quite removed from local woodlots, invasion may perhaps be traced to the activity of crows and other birds, the same birds which effect dissemination of red cedar. That germination of seeds is often enhanced after ingestion by certain birds and mammals has been experimentally demonstrated by Krefting & Roe (1949).

It is evident that there is no set time in the succession that the arborescent forms first appear. Invasion and subsequent ecesis of red cedars and species dominant in later stages of the succession, like cherry, dogwood, or red maple, occur quite soon after abandonment, and if oaks and hickories are delayed until a grove is established, it may be ascribed to the reluctance of squirrels and chipmunks to traverse open fields.

ECESIS

Whatever the mode of entrance may be, the ability of a plant to become established depends on its inherent limits of tolerance and the degree to which these limits are exceeded by neighboring species, i.e. competition. It is common to consider annuals as more aggressive colonizers than are perennials during the early stages of abandonment. The life-cycle of annuals is abbreviated, hence a rapid foliation and flowering provide for a larger plant than that of a juvenile perennial often elaborating a rhizome of one sort or another. The second year of abandonment witnesses a closing of the underground network of the rhizomes and roots of the perennials to the exclusion of the annuals. Another example of the difficulty of establishment is the following. As the succession continues, bare patches of soil appear between the clumps of Andropogon. These patches are underlain immediately below the surface by the widely ramifying fibrous roots of the grass. As a result, the soil between the clumps is unoccupied except for shallow-rooting rosettes like hawkweeds (*Hieracium* spp.) or closely investing lichens. The inability of seedlings to penetate a lichen mat, or, once germinated, to withstand injury by the hygroscopically sensitive, heaving mat has been reported by Allen (1929).

The factors affecting the establishment of seedlings on mineral soil have received considerable attention. Much of this attention has centered about the so-called limiting factor for growth of climax species. Toumey (1926), in a report of his famous trenching experiments, indicated that soil moisture was often the factor limiting the growth of seedlings. Aaltonen (1926) observed that the poorer the site, the greater the light requirement; and recently, Shirley (1945), reviewing the subject, stressed the importance of assessing the interrelationship between light and other factors, but concluded that light is probably the most important factor affecting growth after the light intensity has been reduced to 20% of full sunlight.

If a discussion on the ecesis of seedlings is confined to red cedar and oak, several questions arise immediately:

1) Why does red cedar become established earlier than oak?
2) Does red cedar contribute to the ecesis of oak?
3) Why does red cedar fail to establish itself under oak?

Although no experimental evidence is available, certain conjectural statements may be proffered regarding these questions. The invasion of red cedar prior to that of oak has been demonstrated. Although a few seedlings of oaks appear early in the succession, the only oak exhibiting ecesis within five years after abandonment is pin oak (Fig. 4), a member of the late stage of the succession, occasionally present in the wetter parts of Mettler's Woods. (The presence of pin oak in the young fields of the vicinity does not necessarily suggest that these fields exhibit poor drainage. While Gray's Manual states that *Quercus palustris* is a species inhabiting swampy woods and bottoms at low altitudes (p. 546), in central New Jersey it occupies a much wider range of habitat. For example, in addition to its occurrence in young, abandoned fields on upland sites, it is often found on the dry bluffs above the Raritan River.)

Within fifteen years after abandonment, the more consistently mesic oaks appear, and by the sixtieth year, a few are often members of the understory. The reason that red cedar becomes established earlier in the succession than the oaks is obviously because of its greater ease of invasion. Since a number of oaks do become established fairly early in the succession, putative deficiencies or excesses of certain environmental factors may not be responsible for lack of establishment. More probably, it is the source and mode of transfer of seed discussed above which limits the number of oaks appearing in younger fields. Although saplings of oaks are found in all fields abandoned for more than five years (Fig. 4), the seedlings were so scattered that there were never more than five noted in 100 sq m of any one field age-group (Table 5). The above discussion of chronology has therefore been based on field experience coupled with data of the sapling population.

Does red cedar contribute to the ecesis of oak? According to the concept of succession at first outlined by Clements, one stage in succession actually paves the way for the succeeding stage by altering the environment in such a way as to make it unfavorable for itself but favorable for the newer stage. An example of this has been nicely demonstrated on the southern Piedmont in the case of shortleaf (Billings 1938) and loblolly pine (Coile 1940). In both cases, the annual accumulation of pine needles produces a thick, hygroscopic mat of litter rather impenetrable to the short roots of pine seedlings. Oak seedlings, equipped with taproots sometimes twice the length of the shoot, easily descend through the mat and are able to tap the mineral soil below. The pine seedlings suffer extinction presumably through desiccation (Billings 1938) or starvation (Kozlowski 1949).

Such a situation does not obtain on the northern Piedmont. The accumulation of litter never exceeds a fine, crumbly mat about two centimeters thick, since red cedar and dogwood leaves, for example, are fairly rich in calcium (Coile 1933; Chandler 1939; Bard 1946) and are readily digested by the earthworms present throughout the succession. Although a slight increase in the moisture-holding capacity of the Ap horizon is noted after a few years of abandonment, this level is sustained with little change until after the oaks are established, when a second, mild increase occurs. No other edaphic factor varies appreciably throughout the sere, and therefore, one is again tempted to consider the maturing red cedar stand merely as a lure to woodland rodents. It is probable that any stand of trees, whether red cedar, sassafras, dogwood, or pin oak, would provide enough shelter for such animals, and thus acorns would be brought into the field.

A second supposition, advanced by Shirley (1945) is that pioneer woody species such as red cedar rarely cast shade dense enough to preclude invasion of other species, but their shade and root competition may markedly reduce the growth of all but the most tolerant species. Lutz (1928) considers that ". . . the shade of red cedar . . . is so slight that it has little if any detrimental influence on the growth of the young hardwoods; in fact it may be beneficial to them during juvenile growth since it lowers soil temperature and evaporation." The ability of oak seedlings to maintain growth at very low light intensities has been demonstrated experimentally by Gia (1927) and more recently by Kozlowski (1949).

Thus it would appear that red cedars or any pioneer trees may aid in the establishment of oak by (1) forming a grove providing shelter for rodents and their introduction of acorns; (2) providing shade which restricts competition from exacting heliophiles ("sunlovers"); and (3) providing a reduction in soil temperature and evaporation.

Why does red cedar fail to establish itself under oak? Since red cedar is known to grow in a variety of habitats ranging from stream banks to exposed bluffs (Oosting 1942), it apparently exhibits a very wide tolerance to extremes in the supply of soil moisture. As has been stated previously, the moisture-holding capacity of the surface soil may perhaps increase after the oaks are mature, and thus if there is no drought, there is obviously no dearth of water. Even if intense competition for water should occur from actively growing oak trees, there is neither a morphological or ecological deterrent to the growth of red cedar, since the seedlings exhibit fine tap roots and the tree is known to be unusually resistant to drought (Stiles & Melchers 1935; Albertson & Weaver 1945). It would seem that red cedar probably fails to establish itself under oak because of the intense shade cast by the latter. Experimentation such as that performed on pine and oak by Kozlowski (1949), designed to determine the photosynthetic rate and output of a species under varying amounts of soil moisture, is essential for an elucidation of the reasons red cedar fails to establish itself under oak.

COMPETITION

Competition is an all-inclusive term embracing features of migration, ecesis, reaction, and stabilization, and often employed when the specific factors responsible for a given situation are unknown or poorly understood. Competition may be inter- or intraspecific, but ecological techniques and knowledge are such that the effects of interspecific competition on succession have just begun to be investigated (Keever 1950; Piemeisel 1951).

As Keever (1950) has demonstrated, the forces of competition may be elucidated if the life-cycles and tolerances of the organisms investigated are clearly understood. None of the three species she studied in North Carolina, *Leptilon canadense, Aster pilosus,* and *Andropogon virginicus,* is present as a dominant on the Piedmont of New Jersey, but the latter two have ecological equivalents here: *Aster ericoides* and *Andropogon scoparius.* If it may be assumed that their life-cycles and tolerances are similar to those of their counterparts, the differences between their interrelationships in New Jersey and North Carolina may be briefly outlined.

At the time of abandonment at the close of the growing season, seeds of all subsequent herbaceous dominants are already present or brought into the field by the various agents of dissemination. Evening primrose—like horseweeds in North Carolina—germinates at the end of the growing season, winters as a rosette, and produces a tall, vigorous floral shoot the following summer. It may produce another rosette the following winter. Ragweed, a summer annual, is most abundant towards the end of the growing season. Since horseweed is not present, aster cannot be stunted by decay products of its roots and tops. What, then, delays aster for a few years on the northern Piedmont? Aster, germinating in the spring, matures in the late summer and autumn. Keever has demonstrated that *Aster pilosus* makes its best growth with abundant light and water. It is therefore possible that the taller evening primroses and ragweed shade the young northern asters and inhibit their maximum growth. Shading or inhibition continues for a few years until aster becomes the dominant species in approximately the fifth year rather than the second as in North Carolina. Exactly why it is delayed for such a long period is unknown. It nevertheless does maintain high coverage for twenty years, but is eventually repressed by the more drought-resistant broomsedge (Keever 1950), for there is generally an inverse relationship between the coverage values of the two species; in other words, when the coverage of one is high, the coverage of the other is low.

Again unlike the situation in North Carolina, Andropogon does not assume dominancy the third year of abandonment but around the fifteenth. Although it is able to compete successfully with less drought-resistant species, it requires full light (Keever 1950). Its long delay may probably be ascribed to effects of the very successful goldenrod, *Solidago nemoralis*. Why the latter should rapidly lose dominance after the tenth year is unknown, but that broomsedge quickly fills the breach is doubtless significant.

The relationships between the dominant herbaceous species and the invading woody forms is at present only dimly comprehended, and it is to investigations similar in scope to that of Keever's which one must look for aid in explaining the progression of plants during succession.

REACTION

In succession on the Piedmont of New Jersey, there is no dramatic reaction imposed on the environment by the plants such as was exhibited in the annual deposition of pine litter in North Carolina (Billings 1938). A mild replacement of the calcium content of the soil is annually effected by deposition of leaves of red cedar and flowering dogwood. Such local enrichment is neither excessive nor important in providing a better site for oak germination, since the pH of the surface soil does not alter much during the succession as a whole.

Bonner (1950) and Keever (1950) have demonstrated the effects of toxicity of decaying parts of various species such as Encelia and Leptilon. It would appear that living plants may also exude substances inimicable to other species, but this phenomenon requires further substantiation. As yet, succession in New Jersey cannot be explained in terms of pure reaction.

STABILIZATION

Stabilization of the climax community requires its self-perpetuation through adequate maintenance of reproduction. Mettler's Woods, the nearest approach to climax, may exhibit shortcomings in this respect: the number of oak seedlings is very low. While hickory seedlings are more common than oak, they are far surpassed in numbers by dogwood seedlings. Similarly, there are more saplings of dogwood than oak. Oak sprouts are, of course, observed, as are a few seedlings on the margin of the forest (cf. Oosting & Kramer 1946), but the prolonged maintenance of this woodlot as an oak-hickory forest is questioned because of its unique position in the general area.

There are few large or small forests in Somerset County and these are often maintained as game preserves. Mettler's Woods represents such an area in a wide radius of ever-increasing suburbanization. The population-pressures of squirrels, chipmunks, and other small animals feeding on acorns and hickory nuts are probably intensified by the restrictions on hunting. As long as huge populations of rodents and crows and other birds, annually deprived of more feeding ground, converge on Mettler's Wood's, the number of nuts escaping destruction will be small. When the low supply of food will begin to make inroads on the animal population and the ratio between the demand and food is gradually diminished, then an improvement in the status of Mettler's Woods may be expected. But disregarding the problem presented by the animal population for the moment, a less pessimistic view of the forest may be obtained if one stops to realize the reproductive requirements of an oak forest. While the number of seedlings per 100 sq m seems very low, it may represent an amount sufficient to replenish the forest. Many of the larger oak trees are over two hundred years old, and it is not improbable that they may survive another century. Replacement of these slowly expiring monarchs requires but a few seedlings. Admittedly, the larger the number of seedlings, the more assured is the forest of its future dominants, but for the occasional tree toppling during a wind-storm or dying from some other cause, there is an adequate number of sprouts, saplings, or seedlings any one of which may take its place. It is for this reason that the consideration of Mettler's Woods as representing a climax community may be warranted.

SUMMARY

The successional pattern on upland sites on the Triassic shales of the Piedmont Plateau in New Jersey has been studied, and the following are its salient features:

1. *Vegetation*

a) Fields abandoned for one year contain the subsequent herbaceous dominants in insignificant

amounts, but the immediate dominants are usually *Ambrosia artemisiifolia* and *Oenothera parviflora.*

b) By the second year of abandonment, *Solidago nemoralis* assumes dominance and remains important for approximately fifteen years, when *S. juncea* supercedes it and becomes the dominant herb of 60-year-old fields.

c) *Aster ericoides* increases to dominancy by the fifth year and may maintain high coverage for approximately twenty more years.

d) *Andropogon scoparius* (with some *A. virginicus)* assumes dominancy by the fifteenth year and remains important for more than forty-five years.

e) *Juniperus virginiana* invades young fields within the first few years and becomes the dominant arborescent species for over sixty years.

f) Most of the arborescent species of the oak-hickory forest enter the succession before the red cedar is mature. Oaks and hickories are well established and are in the understory by the sixtieth year of abandonment.

g) The two dominant shrubs of the succession are *Rubus flagellaris* and *Rhus radicans*, the former demonstrating maximum coverage in fields abandoned for approximately twenty-five years, the latter at approximately sixty years, the oldest abandoned field studied.

h) As succession progresses, the number of annuals and non-indigenous species decreases and the number of those species whose fruits are disseminated epizoically or endozoically is increased.

2. *Soils*

There appears to be a lack of decisive correlation between any of the investigated physical and chemical properties of the soil and the age of abandonment of the fields. Discrepancies appeared to be due to the slight but important textural differences between the soils. It may be demonstrated that the organic matter content, moisture-holding capacity, total exchange capacity, conductivity, and nitrate content may increase slightly towards the oak-hickory forest, but this cannot be demonstrated in fields of varying textural qualities. This situation could only be ascertained if a single field were investigated periodically over a protracted period of time.

3. *Roots*

Depth of penetration of the roots increases with the age of abandonment. The greatest density of roots is noted in the upper 15 cm. of the soil in every stage. The smallest roots are encountered in the upper horizons, the larger ones in the lower horizons. There is no evidence in the comparative root systems of the earlier and later arborescent dominants to indicate their differential competitive ability.

4. *Causation*

Causation of succession is to be sought in a study of the life-cycles and tolerances of the various species including those members of the animal population instrumental in seed dispersal. An elucidation of the reactions of all the species—both plants and animals—to variations in light and its effect may aid in deciphering the successional pattern whether in connection with interspecific competition, survival of seedlings of diverse species, or the activities of certain rodents while introducing the dominant arborescent species of the climax forest into younger fields.

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