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Invasion of trees in secondary succession on the New Jersey piedmont

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BUELL, M. F., H. F. BUELL, and J. A. SMALL (Rutgers Univ., New Brunswick, N.J.), and T. G. SICCAMA (Yale Univ., New Haven, Conn). Invasion of trees in secondary succession on the New Jersey piedmont. Bull. Torrey Bot. Club 98: 67–74. 1971.—Establishment of tree seedlings in early stages of old-field succession on soil derived from Triassic red shales of the piedmont of New Jersey is reported. The studies were made at the Hutcheson Memorial Forest preserve. On fields abandoned from cultivation at two-year intervals starting with 1958 permanent quadrats were established and sampled annually. Results showed that, as a rule, tree seedlings do not become established during the first year but begin to appear the second year, with new ones continuing to appear in successive years. Mortality of previously established individuals is also common during the early stages of succession. During early successional stages, when much bare soil is exposed, heaving due to freeze-thaw cycles in winter is one of the major influences in hindering early establishment of tree seedlings.

Old-field succession on the piedmont of New Jersey has been described as being initiated by a massive growth of *Ambrosia artemisiifolia* and a strong dominance of *Oenothera parviflora.* With these is associated a large number (90 species) of herbs —annual, biennial, and perennial—, many of which become more important later. By the fifth year *Aster* and *Solidago* species attain dominance (Bard, 1952). According to Bard's study, *Aster* and *Solidago* species are still prominent after 25 years but are accompanied by an equally abundant coverage of *Andropogon.* By this time the growth and spread of trees and shrub clones has appreciably reduced the proportion of the area occupied by old-field herbaceous species. Bard found that tree species invade young fields within a few years after abandonment and by the fifth year begin to appear above the herbs. *Juniperus virginiana, Prunus serotina, Acer rubrum,* and *Cornus florida* are typical old-field tree species of central New Jersey.

Bard's study of old-field succession, like most other such studies (Oosting, 1942; Quarterman, 1957; Drew, 1942; Bazzaz, 1968), made use of different fields whose history (time cultivation ceased, etc.) could be ascertained. Hence fields were used that had been abandoned for varying lengths of time and starting with different years. The reasonable assumption is made that succession within a local area on a uniform substratum follows a generally predictable course and that any one field, within limits, represents a stage through which all others will pass or have passed.

In 1958 we initiated a study of old-field succession in which we retired from cultivation 2 separate units (½ to 1 hectare in size) at two-year intervals and have kept records on their vegetation through annual surveys. Our objective has been to follow succession on specific areas over a period of time with a view to learning more precisely the sequence of events during the course of vegetational change. This procedure, while requiring years to accomplish, eliminates any uncertainties of substratum differences and takes into consideration minor climatic oscillations. In fact, it was directed in part toward arriving at answers to the influence of minor climatic variations, an influence which Bard believed was the cause of anomalies in the sequence she constructed. The specific objective of the research reported here is to examine the characteristics of the invasion of old fields by tree species.

The study was made in the fields associated with the William L. Hutcheson Memorial Forest, adjacent to the town of East Millstone in central New Jersey. The tract

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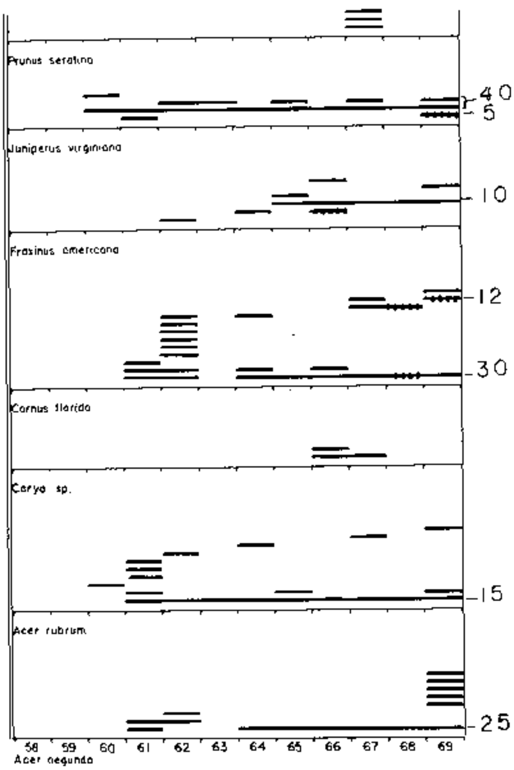
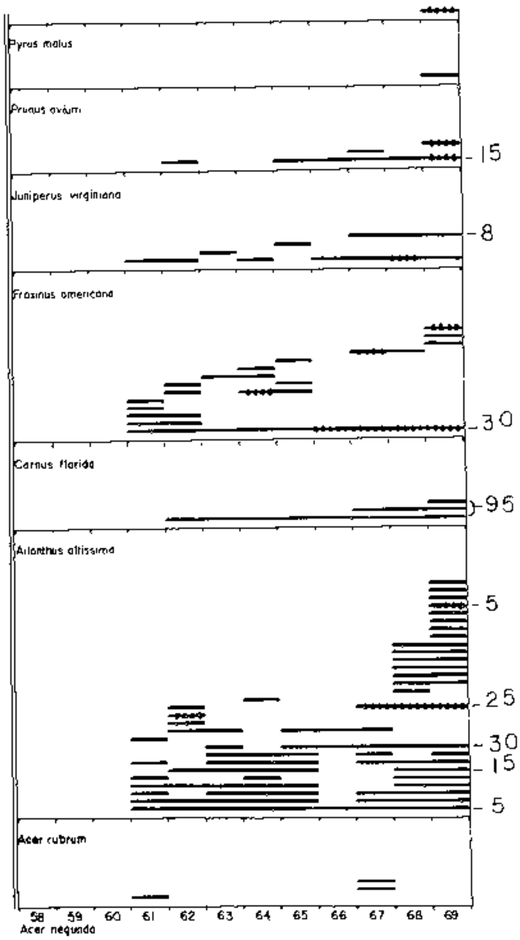
is located on flat to gently rolling terrain underlain by Triassic red shale, and has a relatively uniform soil throughout the area occupied by the fields used in this study (Ugolini, 1964). The property of which the forest and adjacent fields are a part was settled in 1701 (Buell, 1957). Hence, although we do not know the exact date when the land was first cleared for farming, cultivation has been sufficiently long and sufficiently thorough to have entirely eliminated any vegetatively reproducing fragments of trees formerly present.

Methods. We sampled the vegetation using systematically arranged quadrats. In each unit field we set up 48 one-half-by-two-meter quadrats along parallel lines in such a way as to distribute them uniformly throughout the area to be sampled. The data recorded of the tree species occurring on these plots included the number of seedlings present and an estimate of the percent of ground covered by the foliage of the trees. The latter measurement included cover contributed by seedlings occurring adjacent to the plots and overspreading them as the seedlings grew larger. Such instances appear on the figures in a distinctive symbol.

Our data are derived from ten field units (designated by a letter and a number), two of which were allowed to proceed toward natural revegetation in 1958 (D1, C3), two in 1960 (D2, D3), two in 1962 (E1, E2), two in 1964 (C6, C7), and two in 1966 (C4, C5). The conditions under which they were initiated were not uniform. In the first place, the weather conditions of these years were very different (Table 1). In the second place the imme-



FIELD D-1



FIELD C-3

diately preceding use of the fields was not the same. Fields C3 and D1 were both abandoned after the harvest of a soybean and sorghum crop of 1957. Field D2 was abandoned after a soybean-sorghum harvest of 1959, and D3 was like it but was prepared for planting in the spring of 1960 and then abandoned. Field E1 was simply left in orchard grass sod after the hay crop was harvested in 1961, and E2 was like it except that it was plowed and disced in late June 1962. Field C6 after 3 years as an

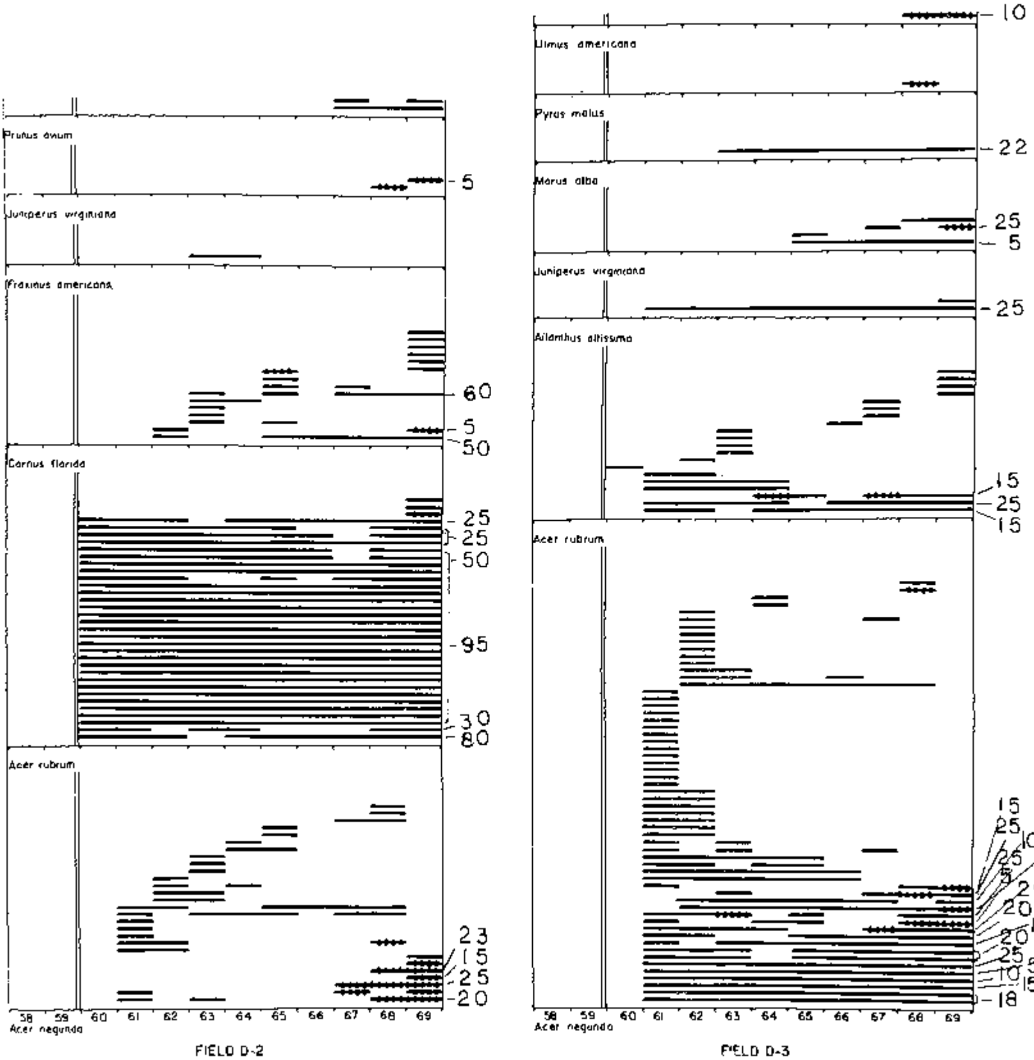


Fig. 1. Occurrence of tree seedlings in two fields abandoned for 12 years (D1 and C3) and two fields abandoned for 10 years (D2 and D3). Double vertical lines represent date field was set aside for natural revegetation. Horizontal lines at the same level—whether continuous or interrupted—indicate what are assumed to be a single individual. (See text for discussion of the validity of this assumption.) The arrangement of the lines on the graph places at the bottom the individuals present in 1969 that had started earliest, and thence upward those entering progressively later. Percentage of cover is not indicated except (extreme right) for those individuals present in 1969 having cover of 5% or more on one quadrat. Figures opposite brackets indicate that the individuals were present on one quadrat. Lines with cross bars represent cover contributed by individuals outside of the quadrat. (See text.) All individuals recorded as contributing cover are indicated on the graphs, with the exception of *Acer rubrum* in D2, where only individuals surviving into 1969 are shown; in addition, in years 1, 2, 3, 4, 5, 6, 7, 8, and 9, there were respectively the following numbers of individuals: 126, 132, 93, 137, 57, 58, 34, 17, and 10.

orchard grass hay field was abandoned following the harvest of hay in 1963. C7 had had the same history as C6 but was plowed in April of 1964. Field C5 was abandoned after harvest of a soybean crop in 1965, and C4 had been part of the same soybean crop but was plowed in April 1966. The first sampling in each unit was done the first year following the last season of agricultural use of the land, and this we refer to as the first year of succession.

Data were usually collected in mid-July to mid-August. Nomenclature follows Fernald (1950).

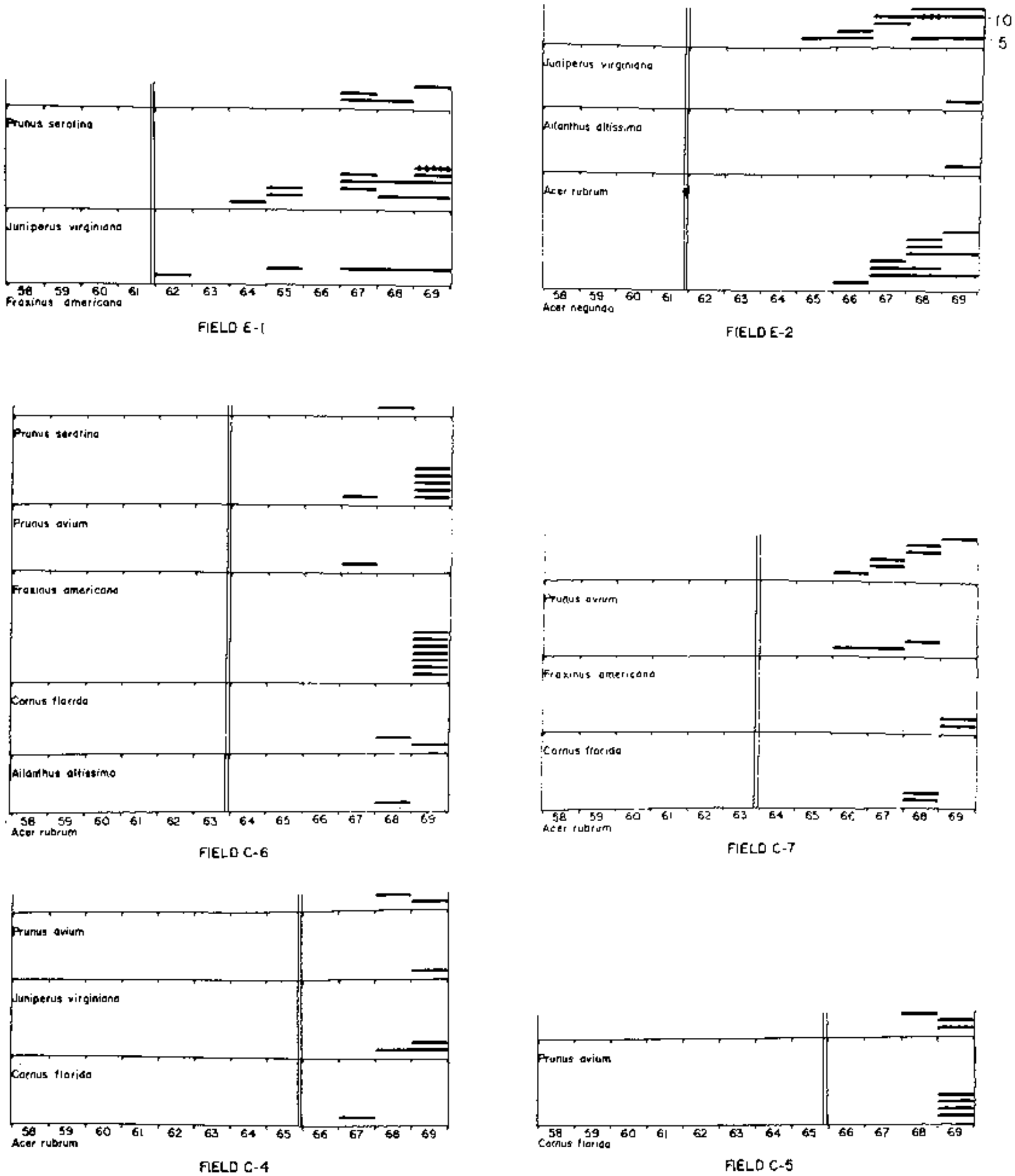


Fig. 2. Occurrence of tree seedlings in 6 fields abandoned to natural revegetation, two in 1962, two in 1964, and two in 1966. See caption of Fig. 1 for further explanation.

Results. Several features of these old fields are evident in the data from this study. First, with very few exceptions, tree seedlings were not found the first year and, where they were, they showed, at the second sampling, the damaging effect of frost-heaving during their first winter. The principal exception to the general absence of tree species the first year was in D2 where a large number of *Acer rubrum* seedlings appeared in the first year (Fig. 1). One *Fraxinus* seedling appeared the first year in E1, from which a hay crop had been cut the preceding year, and one seedling of *Ailanthus*, appearing the first year in D3,

Fig. 3. Base of *Acer rubrum* from D2 as it appeared in 1970. Crook at base of stem, at ground level, was produced as result of frost-heaving the first winter.

must have started after the field was plowed in the spring of that year (Fig. 1). However, neither seedling survived into the second year. Of the many *Acer rubrum* in D2 that started in year 1, the survivors in 1969 about 2 meters tall, all, as far as we have checked, have a crook at the base of the stem (Fig. 3). We observed the development of these crooks over the course of the years. In the spring of 1959 the year-old seedlings had been completely thrown out of the ground by the frost-heaving of the preceding winter. Intense frost-heaving appears to be characteristic of the winter following the first year of succession before any appreciable amount of litter is accumulated on the ground. As the seedlings in field D2 lay on the damp ground in the spring of 1959 when growth started, the root curved downward into the soil and the stem tip curved upward, leaving the prostrate stem portion to become the crook at the base of the sapling. It is evident (see Fig. 1 explanation) that many seedlings were unable to make this adjustment and did not survive. Frost-heave curvature occurred but infrequently on D3 in the abundant *Acer negundo* which started in year 2.

One further detail about the environment of the frost-heaved red maple seedlings in field D2 needs to be mentioned. Their first winter, that of 1960–61, was unusual in two respects. There was an exceptionally long and continuous snow cover and, related to this, a record small number of freeze-thaw cycles.[1] During the course of the winter—December 1 to March 20—there were only four times that soil at both 2.5 and 5.1 cm depths went below 32°F followed by thawing. This was sufficient to completely uproot the seedlings. However, snow cover greater than 2.5 cm depth lasted from December 11 to January 2 and from January 19 to February 18 (or a total of 54 days). These two periods were separated by 17 days of continuously below freezing

Table 1. Summer rainfall data for central New Jersey. Data from N.J. Agricultural Experiment Station, New Brunswick. (From U.S. Weather Bureau Climatological Data, N.J.) Precipitation is in millimeters.

	May	June	July	Aug.	Total May–July
1958	104	76	149	83	329
1959	32	91	186	150	309
1960	108	30	282	100	420
1961	88	79	142	160	309
1962	52	100	67	104	219
1963	47	31	92	40	170
1964	34	60	187	21	281
1965	31	23	61	76	115
1966	151	15	31	74	197
1967	*93	83	181	228	357
1968	233	114	22	*184	369
1969	71	77	210	98	368

* Somerville data

[1] Snow cover and bare-ground soil temperatures at N.J. Agricultural Experiment Station, New Brunswick. Records of temperatures at 2.5, 5.1, 9.8, and 19.6 cm depths on soil bare of vegetation begin with November 1960.—U.S. Weather Bureau Climatological Data for N.J.

weather. Such conditions were apparently sufficient to protect the seedlings in their uprooted or partially uprooted condition. (The survival of these seedlings was probably aided by the unusually favorable moisture conditions prevailing in 1960 and 1961.) A more usual winter occurred in 1961–62, there being 23 times during the period November 28 to March 14 when the soil temperature at 2.5 and 5.1 cm reached below 32°F and then warmed up to above the freezing temperature. Also more characteristic was the snow cover—greater than 2.5 cm only from December 23 to January 2, February 2, February 9 to 23, and March 6 to 7 (a total of 29 days). The winter of 1962–3 had 22 freeze-thaw cycles and 1963–4 had 26; 1964–5 was extreme, with 49 freeze-thaw cycles, beginning November 21 and extending through April 5, 28 of which were after March 1.

Secondly, many seedlings get started and last only one season. The causes for such losses are probably numerous, among them drought, insect damage, rabbit- or deer-browse, and frost-heaving in winter in the earlier years. An instance of heavy seedling mortality occurred among the *Acer rubrum* in D2. (See caption for Fig. 1.)

A third feature is the appearance of seedlings one year, their absence the next, and then reappearance the following. Here the cause of such behavior may be explained in at least three ways. The seedling may die and a new one appear two years later in the same quadrat. It is also possible that the observers may have simply failed to see a seedling recorded the preceding year in a particular plot, but this probably did not happen very often because we made it a point to search each of the quadrats for seedlings, and each year the seedlings should be appreciably larger and more conspicuous than the preceding year. A third reason for such discontinuities is the result of browsing animals, particularly rabbits, which often feed on such seedlings. We have noticed this especially since we have gone back to plots that seemed questionable after the data were compiled and found severe animal browse. In fact, the leafy part and terminal portion of the seedling may be gone, and if the damage occurs late enough in the season the seedling may have reserve for a come-back the next spring. In recording data from the plots, a small, leafless, eaten-back seedling is most easily overlooked.

Admittedly, since we recorded only the *presence* of species on quadrats and did not tag individuals, we cannot be sure that our assumption that we are dealing with the same individual (Fig. 1) is correct, just because the same species occurs on a quadrat in successive years (or skipping a year). Nevertheless, we believe that the assumption is justified as a generality, particularly as we found increasing percentages of cover over the years. (Perhaps in order here is an explanation of the fact that Fig. 1 indicates cover contributed by individuals located both inside and out of the quadrats. This situation arises from the unfortunate fact that sometimes one or more stakes marking the ends of quadrats were broken off or chewed up by animals; an error of as little as 1 cm in replacing the stake could result in the subtraction or addition of individuals to a plot.)

A fourth feature is that in three fields (D2, D3, and C3) there are large numbers of *Acer* (*A. rubrum* or *A. negundo*). While they entered in mass in D2 the first year, they have continued to enter D2, as well as D3 and C3, up to the present (Fig. 1). All three fields, as one would expect, are close to a very good seed source. Field D3 is particularly well situated with respect to prolific *Acer negundo*, accounting for the large numbers of that species in the field. For species with wind-borne fruits a nearby source is especially important in terms of seeding-in of a field.

A fifth feature is demonstrated by those trees whose seeds are carried by birds. *Cornus florida*, *Prunus avium* and *Juniperus virginiana* seldom appear before the third year, and it is not uncommon that their seedlings are continuing to appear through the 10th and 12th years. Of these three species, *Cornus* and *Prunus* are abundant in the adjacent forest, and *Juniperus* is common in nearby hedgerows and abandoned farmland.

Discussion. On the piedmont of New Jersey it would appear that tree seedlings are not characteristically present at the initiation of succession. For the most part they enter after the first year and nearly all, if not all, are able to continue to become established in the vegetation at least through 12 years.

Tree invasion during old-field succession has been given some attention in various regions where succession has been studied, and there has been at least one attempt to generalize. When one examines the data from different areas it does not appear that there is a uniform pattern for tree invasion of old fields throughout the deciduous forest region, and hence little basis for generalization. Bard found one instance where there were large numbers of *Prunus serotina* seedlings in a one-year old field, but otherwise trees did not appear in appreciable numbers until after 5 years. Crafton and Wells (1934), working in North Carolina, said that, "A few years later [after the invaders, tall weeds, have been established] the old field vegetation changes again and the third phase is initiated. This time broom-sedge (*Andropogon* spp.) invades—reaches its extreme expression—then passes out with the ecesis of pines (*Pinus taeda, P. echinata,* and *P. virginiana*)." Oosting (1942), basing his statements on data from a series of fields in the Duke Forest area, wrote: "Often within three or four years of adandonment seedling pines may be found between the clumps of broom sedge." McQuilkin (1940), on the other hand, found in North Carolina that pines may sometimes enter the succession the first year or during any succeeding year. Drew (1942), studying old fields, in Missouri, found a considerable growth of sassafras and persimmon and an occasional oak or hickory coming as sprouts the first year, but the 18 other species of trees that entered by seeds were evident 6–7 years later. Bazzaz (1968) said: "Shrubby sprouts of *Sassafras* and *Diospyros*, the most abundant woody species in local succession, were found in all fields, including 1-year fields." Other trees appear in his data for 4-year fields, namely *Juniperus virginiana* and *Ulmus alata*. Quarterman (1957) studied 12 first-year fields and found three genera of woody species most important as seedlings. These were *Ulmus, Celtis,* and *Platanus*—all wind-disseminated—, with *Juniperus virginiana, Prunus serotina,* and *Acer negundo* also present. Davis and Cantlon (1969) made no mention of tree seedlings invading early old-field vegetation in Michigan. Finally, Egler (1954), who has done considerable field research in northwestern Connecticut, found tree seedlings so consistently present at the start of succession that he proposed a model for old-field succession which he called "initial floristic succession," suggesting that all phases of succession are there from the start and that succession is essentially the coming to maturity and dominance of various kinds of plants.

Data from several of these authors do not fit the "initial floristic" generalization. Our fields which have been carefully scrutinized from the start do not lend support to Egler's model either. Tree species do come in early but are not commonly present at the start of succession.

Even limiting consideration to the New Jersey piedmont, generalization as to time of appearance of tree species to be expected in old-field succession must be in rather broad terms. While we can for the most part agree with Bard (1952) that *Juniperus virginiana* is the species that especially lends character to the succession, no *Juniperus* has yet been noted in our fields C6 and C7, even in 1970, their 7th year.

Turning to other species, we find even less indication of pattern. Bard found that *Prunus serotina* appeared in fields of all ages that she studied, and, beginning with the fifth year, on all fields. We found it in quadrats only on one 5-year, one 6-year, and one 10-year field (also off-quadrat in another, C3), and it has apparently not become established on any of them. (Also an off-quadrat inventory of C3 in late 1969 included 13 individuals of *Quercus palustris*, 18 of *Q. rubra*, and 7 of *Q. velutina*. Bard found the first of these in all fields 5 or more years old, but the other two were never noted before year 40.) We may also contrast our findings with Bard's (1951, 1952) records as to other species: *Cornus florida* (appearing early as scattered seedlings, but not encountered in sample plots on fields younger than 40 years), *Prunus avium* (recorded by her only once—in year 15), *Fraxinus americana* encountered in 25- and 40-year fields), and *Acer negundo* (never recorded in her study). The common presence of these in our plots is indicative of the nearby seed source, Hutcheson Memorial Forest, an obvious significant feature in tree invasion of old fields, as noted by Beckwith (1954).

One sidelight on the uniqueness of the

old field environment at the latitude of New Jersey is the effect of frost-heaving. It is one of the features noticeable in the New Jersey old-field succession that may make for differences between succession here and elsewhere. Frost-heaving of the soil is usually intense in the earliest stages of old-field succession. Farther north continuous snow cover reduces this effect, and in the south such intensive freeze-thaw cycles do not occur. We normally have freeze-thaw cycles continuing throughout most of the winter, and these have a pronounced effect on the soil of open fields, since snow seldom lies long on the ground to serve as a moderating influence. As has been shown, tree form is affected. Undoubtedly seedling establishment is also affected, since during the winter or a dry spring following, many frost-heaved plants would succumb, with resulting heavy seedling mortality. These freeze-thaw cycles—whose effects on seedlings have been so vividly described by Schramm (1958)—, associated with long periods of exposure of the ground, are normal for central New Jersey and may be significant in seedling survival in early stages of succession. The red maples on D2 established in the summer of 1960 may well have survived the next winter because of its unusual conditions of long, protective snow cover and less extreme frost-heaving.

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