# Time of Establishment of Red Maple (Acer rubrum) in Early Oldfield Succession

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# Time of establishment of red maple (*Acer rubrum*) in early oldfield succession

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## ABSTRACT

RANKIN, W. T. AND S. T. A. PICKETT (Department of Biological Sciences, Rutgers University, P.O. Box 1059, Piscataway, NJ 08854). Time of establishment of red maple (*Acer rubrum*) in early oldfield succession. Bull. Torrey Bot. Club 116: 182–186. 1989.—All woody stems in an old field 14 years after abandonment were cut and all individuals aged at ground level. Ninety per cent of established red maple, the structural and numerical dominant in the field, had invaded within the first 7 years since abandonment. *Fraxinus americana*, the second most important woody species, showed the reverse skew, with the majority of individuals being recent invaders. The remaining woody species, including species of *Carya*, *Quercus*, *Ulmus*, *Prunus*, and *Juniperus*, also showed delayed invasion. Young saplings were clumped in space, whereas old saplings were regularly distributed. To determine whether predation by small mammals was responsible for the cessation of establishment of red maple, partially caged seedlings were set out in a 2-yr old field, the 14-yr old field, and the adjacent old-growth forest. The highest predation intensity was found in the youngest field, a pattern the reverse of that expected if predation were responsible for the closure of the maple establishment window. That predation on seedlings had differential impact along the successional gradient represented by the different adjacent sites calls attention to the potential for impact of seedling predation in succession.

Key words: *Acer rubrum*, *Carya* sp., *Fraxinus americana*, *Juniperus virginiana*, *Nyssa sylvatica*, predation, *Prunus serotina*, *Quercus velutina*, seedling establishment, small mammal, succession, *Ulmus* sp.

An important aspect of successional dynamics is understanding the mechanisms by which invasions begin and end. The opportunity for invasion may be limited, as recognized by Gross (1980), who defined the periods during which a community is open to invasion as a successional window. In a recently abandoned agricultural field such as the site employed in this study, windows undoubtedly open as a result of perturbation. Later in succession, windows may open as a result of such population and community properties as dispersal patterns, decline in resources, and changes in community structure. Windows are probably often closed by plant–plant interactions such as competition. They may also be closed, however, by interactions with animals. For example, herbivores can substantially affect forest regeneration (Watt 1923; Ashby 1959; Jokela and Lorenz 1959; Shaw 1968) and community structure (Summerhayes 1941; Gillham 1955). The herbivores associated with seedling predation in fields and woodlands are usually mice, voles, and other small rodents (Elton 1942), as well as rabbits (Gillham 1955; Spencer 1955). Although other factors are certainly important, we shall concentrate here on herbivory as it affects plant survival at the seedling stage, because this possible mechanism for regulating invasion has been neglected in oldfield studies.

For herbivory to affect the course of succession significantly, it must affect species differentially or act differentially through time. Differential herbivory between species appears to be effective in some instances. For example, grazing by moose on Isle Royale

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apparently has favored *Picea glauca* at the expense of other canopy trees (Snyder and Janke 1976). Long-term deer exclosures in a Minnesota *Pinus resinosa* stand increased *P. strobus* and two hardwoods at the expense of *P. resinosa* (Ross *et al.* 1970). Thomas (1960) correlated juniper (*Juniperus communis*) invasion of English grasslands with the death of rabbits due to myxomytosis. Herbivores, therefore, can be a significant force in determining the direction, rate, and pattern of succession. However, differential herbivory on a single species through time, a potential mechanism for determining species invasion dynamics, has not been studied.

This study examined the temporal patterns of invasion using age class data for red maple (*Acer rubrum*) in an oldfield in the New Jersey Piedmont. Secondly, we tested the hypothesis that differential herbivory through time contributes to the invasion pattern.

**Methods and Materials.** All field experiments were performed between June and August 1981 in oldfields at the William L. Hutcheson Memorial Forest (hereafter referred to as HMF), 14 km west of New Brunswick, NJ. The environment and successional patterns have been documented by Ugolini (1964), Bard (1952), Buell *et al.* (1971) and Pickett (1982). Red maple (*Acer rubrum* L.) was selected for this study because it is important in oldfield succession in the area (Bard 1952; Buell *et al.* 1971). All experiments were analyzed using analysis of variance (ANOVA), and means were compared using the least significant difference (LSD) test (Zar 1974). The data were normalized with an arc-sine transformation.

VEGETATION MAPPING AND AGING. The purpose of this survey was to determine the age class distribution and spatial patterns of the trees invading a 14-yr field (Grid Reference E9). The species and position of every tree sapling (>2 yr) and seedling (first yr of growth) were recorded. No trees were sampled within 3 m of the path bordering the field. A section was taken from the base of each trunk, and the growth rings counted to determine the sapling's age. Nearest neighbor analysis was performed to test for clumping of the tree saplings (Clark and Evans 1954).

HERBIVORY ON TRANSPLANTED SEEDLINGS. This experiment was designed to determine if differential herbivory exists along a successional gradient and if herbivory is density-dependent. Seeds from local populations of *Acer rubrum* were collected in May 1981. Seedlings were planted in plastic flats at four densities: 1 (7 × 7 cm), 6, 11 and 16 (28 × 28 cm flat) per flat, hereafter abbreviated as D = 1, D = 6, D = 11 and D = 16. Seedlings were grown in the glasshouse until the primary leaves had expanded, approximately 3.5 wk following germination. The flats were then transplanted into 3 communities at HMF: (a) a 2-yr field (Grid Reference E8) dominated by ragweed (*Ambrosia artemisiifolia*), (b) a portion of the 14-yr field described previously, dominated by *A. rubrum* saplings, and (c) an old-growth portion of HMF, the canopy of which was mixed oaks (*Quercus* spp., Buell 1957). The flats were placed in two 8-m × 8-m plots in each site. Each plot was subdivided into 16 4-$m^2$ quadrats and the flats were placed into the same corner of each quadrat in a 4 × 4 Latin square design. The flats were sunk flush into the turf, firmly packed into the soil, and the displaced soil was removed from the study area. Data were recorded as the percentage of each seedling consumed, and categorized as 0, 25, 50, 75 or 100%, depending upon the number of leaves missing from the seedling. Data were recorded weekly until mid-August, when the herbivory trends were well established.

**Results.** VEGETATION MAPPING AND AGING. A total of 1140 tree saplings and seedlings were mapped, of which 903 were *Acer rubrum* and 122 were *Fraxinus americana.* Six additional genera (Table 1) comprised 15 individuals. The nearest neighbor analysis (Clark and Evans 1954) showed the saplings of all species to be highly clumped ($R = 0.317$, $N = 254$, $P < 0.001$, where R is the ratio of observed to expected mean distances; $R = 1$ indicates a randomly distributed population). Much of the clumping is due to the clustering of 2–4-yr-old *Fraxinus americana* saplings around the stems of the older maple saplings. When analyzed separately, ash saplings between 2 and 4 yr

Table 1. Age class distribution of the six uncommon woody species in the mapped community.

| | Age (in yr) | | | | | | |
|---|---|---|---|---|---|---|---|
| Species | 1 | 2 | 3 | 4 | 5 | 6 | Total |
| *Quercus velutina* | | | 1 | | 1 | | 2 |
| *Ulmus* (*rubra*?) | | 1 | 3 | | | | 4 |
| *Prunus serotina* | | | | 1 | | | 1 |
| *Nyssa sylvatica* | | | | | | 1 | 1 |
| *Juniperus virginiana* | | 3 | 2 | | | | 5 |
| *Carya* (*ovalis*?) | | 1 | 1 | | | | 2 |

old were significantly clumped (R = 0.676, N = 108, $P < 0.001$). When saplings of all species 5 or more yr old were analyzed, however, the saplings were regularly spaced (R = 1.15, N = 139, $P < 0.01$).

The age class distribution for the red maples was skewed towards the oldest age classes (Fig. 1). Except for the first-year seedlings, the most numerous individuals were the 14-yr-old maples. The 12–14-yr age classes contained 50% of the maple saplings. Only one maple was found in the 2- and 3-yr age classes combined. *Fraxinus* had an age class distribution skewed towards the younger age classes. Most of the saplings of other woody species fell into the 2- or 3-yr categories, indicating that successful establishment did not occur during the several years immediately following abandonment of the field.

HERBIVORY ON TRANSPLANTED SEEDLINGS. The five herbivory levels originally planned for classifying the data were inappropriate because the seedlings either lived or died. The few seedlings that died from desiccation were omitted from this analysis. The statistical analysis thus compared the number of seedlings suffering predation in each community. The greatest predation occurred in the 2-yr ragweed field (Table 2), where approximately 40% of the seedlings in each flat suffered predation. This was significantly higher ($P < 0.05$) than the predation in the sapling and forest communities. Desiccated seedlings were not counted as prey, but due to both herbivory and environmental conditions, almost all of the seedlings in the ragweed field died. Mortality was not density-dependent: six of the 8 D = 1 seedlings survived, but only 4 of the 280 seedlings in the other densities combined survived (ANOVA across densities, $P < 0.20$).

**Discussion.** Ninety per cent of the maples in the community became established in the 7 years immediately following abandonment (Fig. 1). The metaphor of the

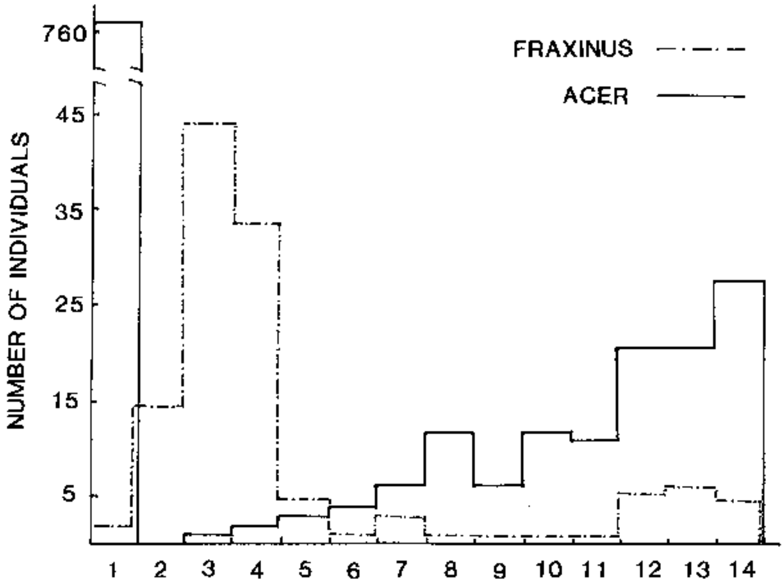

Fig. 1. Age class distribution for *Acer rubrum* and *Fraxinus americana*.

successional window aptly describes this restricted age distribution (Gross 1980). The time of invasion can greatly affect success of herbaceous plants in succession (Holt 1972). Twenty-nine saplings in the community at the time of the study became established in the first year following abandonment of the field. On the other hand, only 1 sapling had successfully invaded the community in the 2 years prior to the study (Fig. 1), despite a presumably heavy influx of new propagules. In 1981, we counted 761 seedlings in 75 $m^2$ sampled. Since red maple consistently produces a large crop of seeds (Hutnik and Yawney 1961), we suspect this seedling total is typical of the yearly influx of seedlings into the field.

Apparent synchronous and early invasion of woody species in old fields is a common observation in the literature (Oosting 1942; Keever 1983; Werner and Harbeck 1982). However, detailed age determination and population censusing of the sort presented here are unknown to us in the literature. Previously, such synchrony and timing of invasion have been inferred from size class distribution or vegetation surveys of different sites of various ages. Preliminary work elsewhere at HMF also suggests early establishment of *Acer rubrum* (Pickett 1982; Buell *et al.* 1971). In old-growth forests, documentation of essentially even-aged cohorts of trees is also common, although the temporal resolution is coarse (Oliver 1981). In a New Hampshire forest, red maple exhibits periodic recruitment that coincides with hurricane disturbances (Henry and Swan 1974).

In contrast to *Acer rubrum*, *Fraxinus* exhibits an age distribution strongly skewed towards younger individuals. The rarity of first-year seedlings may be explained by poor seed set, since mast variation has been observed in *Fraxinus* at HMF (E. W. Stiles personal communication). The 2- to 4-yr-old *Fraxinus* saplings, the most common cohorts observed in this field, were stunted (<20 cm tall) compared to *Acer* sapling and *Fraxinus* under full sun (Goldsmith and Boudreau 1979). Because *Fraxinus* seedlings, which are initially quite tolerant of shading, rapidly become intolerant as they mature, they suffer high mortality in the first several growing seasons (Wright 1959; Fowells 1965). It may be that intermediate-aged ash saplings have a low probability of persisting in this field, and that successful ash recruitment is largely represented by the large, old individuals (Fig. 1). Thus there is the possibility that the pattern for *Fraxinus* represents an invasion window as well, but this cannot be concluded without measurements of turnover precluded by the destructive census used to determine age distributions.

Table 2. Mean seedling mortalities due to predation in three communities. The means are derived from the percentage of the total seedlings in each flat suffering mortality. The means followed by an 'x' are not significantly different ($P < 0.05$, LSD, $N = 96$ for unprotected seedlings, 24 for protected seedlings).

| Community (age) | Per cent mortality |
|---|---|
| Ragweed (2 yr) | 37.0 |
| Sapling (14 yr) | $2.1^x$ |
| Forest (old-growth) | $0.6^x$ |

The remaining tree taxa (*Carya*, *Quercus*, *Prunus*, *Ulmus* and *Juniperus*), although present in low numbers, unquestionably show patterns of recent invasion in this 14-yr old field (Table 1). No individuals of these taxa date from the first 8 years of succession. This is the commoner pattern of tree invasion into oldfields on the New Jersey Piedmont (Bard 1952; Pickett 1982). In addition, this pattern is the most frequently reported elsewhere. For example, in Michigan, Werner and Harbeck (1982) report a low-level of woody plant invasion for the first five years of abandonment of an old field.

The difference between the pattern of delayed invasion usually encountered, and the pattern of early invasion shown here for *Acer rubrum* and suggested for *Fraxinus americana* may be due to a variety of factors. Seed sources of both these wind-dispersed early establishing species are within 20 m of the site. The distance wind-dispersed species would have to cross in Werner and Harbeck's (1982) study was >400 m. That the majority of invaders in Werner and Harbeck's (1982) field were animal dispersed may indicate the impact of distance. An additional factor that may have encouraged early invasion in our field is the relative mesism of the site; it is within 100 m of an intermittent stream near the base of a gentle slope, and the soils are silt loams.

There are many issues that we were unable to address in this preliminary study. However, the documentation of a very early successional window for the invasion of *Acer rubrum*, and the demonstration of differential mortality in different aged fields are important observations of successional dynamics. Such observations both motivate comparison among species, fields having contrasting abandonment histories and resource levels, and suggest the need to discriminate among physical and biotic causes of mortality through succession.

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